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REVISION OF THE GENUS *ADACTYLIDIUM* CROSS (ACARI: HETEROSTIGMATA: ACAROPHENACIDAE), MITES ASSOCIATED WITH THRIPS (THYSANOPTERA)

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Abstract.—The genus *Adactylidium* is revised; four nominal species (*A. beeri* Cross, *A. nicolae* Krczal, *A. costarricensis* Goldarazena, Jordana, and Zhang, and *A. moundi* Goldarazena, Jordana, and Zhang) and ten new species (***A. brasiliensis*** **Goldarazena and Ochoa**, ***A. crespii*** **Goldarazena and OConnor**, ***A. ficorum*** **Goldarazena and Ochoa**, ***A. flechtmanni*** **Goldarazena and Ochoa**, ***A. irregularis*** **Goldarazena and Ochoa**, ***A. lindquisti*** **Jordana and Goldarazena**, ***A. mooniensis*** **Goldarazena and Jordana**, ***A. morazae*** **Goldarazena and Ochoa**, ***A. rumanicus*** **Jordana and Goldarazena**, and ***A. smileyi*** **Goldarazena and Ochoa**) are described and illustrated. The species are associated with numerous species of thrips from the Palearctic, Nearctic, Neotropical, and Australian regions. Phylogenetic analysis resulted in a single cladogram resolved at the species level. A list of thrips hosts and a key to female *Adactylidium* are provided. These mites have potential importance in the biological control of thrips pests in agricultural systems.

Resumen.— En este trabajo se hace una revisión del género *Adactylidium,* se describen cuatro especies nominales, (*A. beeri* Cross, *A. nicolae* Krczal, *A. moundi* Goldarazena, Jordana and Zhang y *A. costarricensis* Goldarazena, Jordana and Zhang) y diez nuevas especies (***A. brasiliensis*** **Goldarazena y Ochoa**, ***A. crespii*** **Goldarazena y OConnor**, ***A. ficorum*** **Goldarazena y Ochoa**, ***A. flechtmanni*** **Goldarazena y Ochoa**, ***A. irregularis*** **Goldarazena y Ochoa**, ***A. lindquisti*** **Jordana y Goldarazena**, ***A. mooniensis*** **Goldarazena y Jordana**, ***A. morazae*** **Goldarazena y Ochoa**, ***A. rumanicus*** **Jordana y Goldarazena**, y ***A. smileyi*** **Goldarazena y Ochoa**). Estas especies de ácaros están asociadas con varias especies de thrips de las regiones Paleártica, Neártica, Neotropical y Australiana. El análisis filogenético da sólo un cladograma tras la aplicación de una prueba de máxima parsimonia para las especies de *Adactylidium.* Se incluye una lista de los tisanópteros hospedadores y una clave dicotómica para la identificación de hembras adultas de las especies de *Adactylidium.* Estos ácaros tienen una importancia potencial en el control biológico de thrips que son plaga en sistemas agrícolas.

Key Words: Heterostigmata, parasitoid, ectoparasite, biological control

Mites of the family Acarophenacidae (Acari: Heterostigmata) are egg parasitoids on various species of insects (Cross 1965, Kaliszewski et al. 1995, Goldarazena et al. 1997, 1999). Trägårdh (1905) and Newstead and Duvall (1918) described the first two species of acarophenacid mites. Magowski (1994) described the fossil genus *Protophenax* from three specimens attached to a coccid (Homoptera), while species in the extant genera *Aethiophenax, Paracarophenax,* and some *Acarophenax* have been associated with several beetle families (Coleoptera) (Redikortsev 1947, Rack 1959, Cross and Krantz 1964, Cross 1965, Mahunka 1975). *Adactylidium* species have been associated with several genera of thrips (Thysanoptera) (Cross 1965, Goldarazena et al. 1997), while host associations of *Paradactylidium* and *Aegiptophenax* species are unknown (Mahunka 1975, Rady 1992, Goldarazena et al. 1999).

The genus *Adactylidium* was proposed by Cross (1965) for the species *A. beeri* collected from unidentified thrips from Michigan, U.S.A., *A. nicolae* (Krczal 1959) collected from tree lichens in France, and two undetermined species collected on different host thrips from Colombia, and from Florida and New York, U.S.A. Later, several specimens collected from *Gynaikothrips ficorum* (Marchal) in Brazil were identified as *A. beeri* by Cross (Flechtmann and Pereira 1967). Goldarazena et al. (1997) described two more species, *A. costarricensis,* collected from several species of tubuliferan thrips in the rain forest of Costa Rica, and *A. moundi,* collected from sporophagous thrips in northern Spain.

We have examined material from the Cross collection deposited in the Division of Plant Industry, Florida Department of Agriculture; the University of São Paulo, Brazil; the Ohio State University; the National Museum of Natural History, Smithsonian Institution; and additional specimens collected by the authors. Among this material we recognized ten new species. Comparison of these new species with the holotypes of *A. costarricensis, A. moundi,* and paratypes of *A. beeri, A. nicolae,* allows us to propose a new diagnosis of the genus *Adactylidium.* In this paper, we redescribe the previously known species and describe the new species. We provide information on host associations and geographic distribution of the species as well as the results of a phylogenetic analysis of their relationships, and a key to the species is provided.

MATERIALS AND METHODS

We obtained most mite specimens from research collections in the United States and Brazil. The senior author collected the specimens from Australia and Spain. Thrips were collected in AGA medium and examined under a Wild dissecting microscope. Mites were removed from the thrips body with a pin and mounted directly in Hoyer's medium. Slide-mounted mite specimens were examined using differential interference contrast and phase contrast optics, (Olympus® BX 50 and Leica® DMR microscopes). The drawings were made with a camera lucida. SEM pictures were made using a Zeiss® scanning electron microscope after coating with 16 nm of gold. Collection data for the host thrips were managed using the Zootron database (Ariño 1987, 1989).

Institutions providing specimens for examination are as follows: Division of Plant Industry, Florida Department of Agriculture, Gainesville (FSCA), The Acarology Laboratory, Museum of Biological Diversity, The Ohio State University, Columbus (OSAL), Museum of Zoology, University of Michigan, Ann Arbor (UMMZ), Seção de Insectos, Museu de Zoologia, Universidade de São Paulo, Brazil (ESALQ), National Museum of Natural History, Smithsonian Institution, Washington (USNM) (mite collection located in Beltsville, Maryland), Museo de Zoología, Departamento de Zoología y Ecología, Universidad de Navarra, (MZUNAV), Zoologisches Institut und Zoologisches Museum, University of Hamburg (ZIZM). Type and voucher specimens of some of the mite species will be deposited in the above mentioned institutions and also in: The Natural History Museum, London (BMNH), Project ALAS-Instituto Nacional de Biodiversidad-OTS, La Selva, Costa Rica (INBIO), Division of Entomology, CSIRO, Canberra, Australia (CSIRO).

The terminology used follows that of Lindquist (1986). All measurements are given in micrometers (μm). Where specimen locality information was unambiguous, latitude and longitude for collection sites was taken from the GEOnet Names Server (GNS), maintained by the U.S. National Imagery and Mapping Agency. When a locality was not listed in the GNS database, or when the locality could not be determined unambiguously from among multiple GNS listings, latitude and longitude are not reported. In order to avoid unwieldly long author lists, authorships of the new species are attributed to the individuals most responsible for the descriptions of the specimens.

Adactylidium Cross

Adactylidium Cross 1965: 142.
Type-species: *Adactylidium beeri* Cross 1965, by original designation.

Diagnosis.—*Female:* gnathosomal apodeme long, triramous but medial branch weak, thicker and broadly rounded posteriorly; palpal tibiotarsal solenidion reduced to tiny peg-like structure; palps completely reduced, rounded and fused with gnathosoma; vertical setae v_1 and v_2 absent; claw on leg I absent; tarsus I setae *u′* and *u″* absent; tarsus III with setae *tc′* absent. *Male:* gnathosomal apodemes absent, tarsus I with setae *u′–u″* present, pretarsus I absent, without claws on pretarsi II–IV.

Leg setation in *Adactylidium* consists maximally of the following setae; reductions from this complement are indicated in the individual species descriptions: leg I, femur (*d, l′, v″*), genu (*l′, l″, v′, v″*), tibia (*d, l′, l″, v′, v″, k*), tarsus (*pv′, pv″, pl′, pl″, s, tc′, tc″, ft′, ft″*); leg II, femur (*d, l′, v″*), genu (*l′, l″, v′*), tibia (*d, l′, v′, v″*), tarsus (*pv′, pv″, tc′, tc″, u′, u″*); leg III, femur (*d, v′*), genu (*l′, v′*), tibia (*d, l′, v′, v″*), tarsus (*pv′, pv″, u′, u″*); leg IV, femur (*v′*), genu (*v′*), tibia (*d, l′, v′, v″*), tarsus (*pv′, tc″, u′, u″*).

Females of *Adactylidium* and *Paradactylidium* are similar in lacking claws on pretarsi II–IV, the absence of setae *p′–p″* on tarsus I, the absence of idiosomal setae *ps,* and reduced palpal tibiotarsal solenidion. Females of *Paradactylidium* exhibit a unique form of the gnathosomal apodeme which is looped posteriorly. In *Paradactylidium,* the reduced palps are more elongate, and the palpal tibiotarsal solenidion is less reduced than in *Adactylidium. Paradactylidium* species retain propodosomal setae v_1, setae *u′* and *u″* on tarsus I, and seta *tc′* on tarsus III. Females of *Adactylidium, Paradactylidium, Acarophenax, Aethiophenax, Paracarophenax,* and *Aegiptophenax* are similar in having a hypognathous gnathosoma with reduced and fused palps, while *Protophenax* presents a prognathous gnathosoma and retains very small, inconspicuous palps.

Remarks.—In most species of *Adactylidium,* there is a ventroapical indentation on tarsus I, possibly a remnant of the base of the absent pretarsus. Goldarazena et al. (1997) illustrated the presence of setae *3b, 4a, 4b,* and *ps* on the ventral view of *A. costarricensis* and *A. moundi.* However, examination and comparison of the new material with specimens of all the extant genera of the family Acarophenacidae revealed that these setae are actually *3c, 4b, 4c,* and *ag* respectively.

KEY TO THE SPECIES OF *ADACTYLIDIUM* (NON-PHYSOGASTRIC FEMALES)

1. Gnathosomal apodeme with medial projections (Fig. 11) 2
– Gnathosomal apodeme without medial projections (Fig. 85) 7
2. Tibiotarsus I with *tc′* and *tc″* distinctly shorter than *ft′* and *ft″* (Fig. 12) 3

– Tibiotarsus I with *tc'*, *tc''*, *ft'*, and *ft''* all similar in length (Fig. 135) 6

3. Base of seta c_1 anteromedial to c_2; aggenital plate striated (Fig. 9) 4

– base of seta c_1 on the same transverse line as c_2; aggenital plate smooth, not striated 4

4. Gnathosomal apodeme with a distal notch; tergite C longer than wide; setae h_1 as long as h_2 (Figs. 7–15) . . . . *A. costarricensis* Goldarazena, Jordana, and Zhang

– Gnathosomal apodeme smooth distally; tergite C wider than long; setae h_1 three times longer than h_2 (Figs. 99–107) . . . . *A. mooniensis* Goldarazena and Jordana

5. Setae sc_1 as long as sc_2; apodemes III not united with poststernal apodeme (Figs. 129–134) . . . . *A. smileyi* Goldarazena and Ochoa

– Setae sc_1 three times longer than sc_2; apodemes III united with poststernal apodeme (Figs. 43–49) . . . . *A. crespii* Goldarazena and OConnor

6. Pseudanal plate without spines (Figs. 90–98) . . . . *A. lindquisti* Jordana and Goldarazena

– Pseudanal plate with three small distal spines (Figs. 120–128) . . . . *A. rumanicus* Jordana and Goldarazena

7. Dorsal setae *c, d, e* and *f* barbed; tibiotarsus I lacking setae *pv'* and *pv''*; genu IV without setae (Figs. 35–42) . . . . *A. brasiliensis* Goldarazena and Ochoa

– Dorsal setae *c, d, e* and *f* smooth or slightly serrated; tibiotarsus I usually with setae *pv'* and *pv''* present (Fig. 139; absent in *A. moundi*, Fig. 21); genu IV with one seta 8

8. Seta *f* three times longer than seta *e*; metapodosoma with anteromedial ventral lobe; poststernal apodeme entire; tarsus III with solenidion ω (Figs. 25–34) . . . . *A. nicolae* Krczal

– Setae *e* and *f* similar in length, metapodosoma without anteromedial ventral lobe; poststernal apodeme divided, reduced or absent; tarsus III without solenidion ω 9

9. Coxal seta *1b* present (Fig. 75); poststernal apodeme reduced to a small ellipsoidal nodule distally 10

– Coxal seta *1b* absent; poststernal apodeme fragmented, reduced or absent 11

10. Gnathosomal apodeme with a pair of indentations distally; seta *4b* present; solenidion on tibiotarsus I capitate (Figs. 113–119) . . . . *A. morazae* Goldarazena and Ochoa

– Gnathosomal apodeme without indentations; seta *4b* absent; solenidion on tibiotarsus I rod-like (Figs. 73–81) . . . . *A. flechtmanni* Goldarazena and Ochoa

11. Genu II with two setae; prosternal apodeme without a knob distally; poststernal apodeme not fragmented 12

– Genu II with three setae; prosternal apodeme with a knob distally (Fig. 2); poststernal apodeme fragmented 13

12. Setae sc_1 longer than sc_2; apodemes V reduced; poststernal apodeme reduced (Figs. 56–62) . . . . *A. ficorum* Goldarazena and Ochoa

– Setae sc_1 as long as sc_2; apodemes V present, well sclerotized; poststernal apodeme absent (Figs. 82–89) . . . . *A. irregularis* Goldarazena and Ochoa

13. Gnathosomal apodeme smooth distally; tibiotarsus I with 15 setae, genu III with one setae Figs. 1–6) . . . . *A. beeri* Cross

– Gnathosomal apodeme lobed, tibiotarsus I with 13 setae (*pv'*, *pv''* absent); genu III with two setae (Figs. 16–24) . . . . *A. moundi* Goldarazena, Jordana, and Zhang

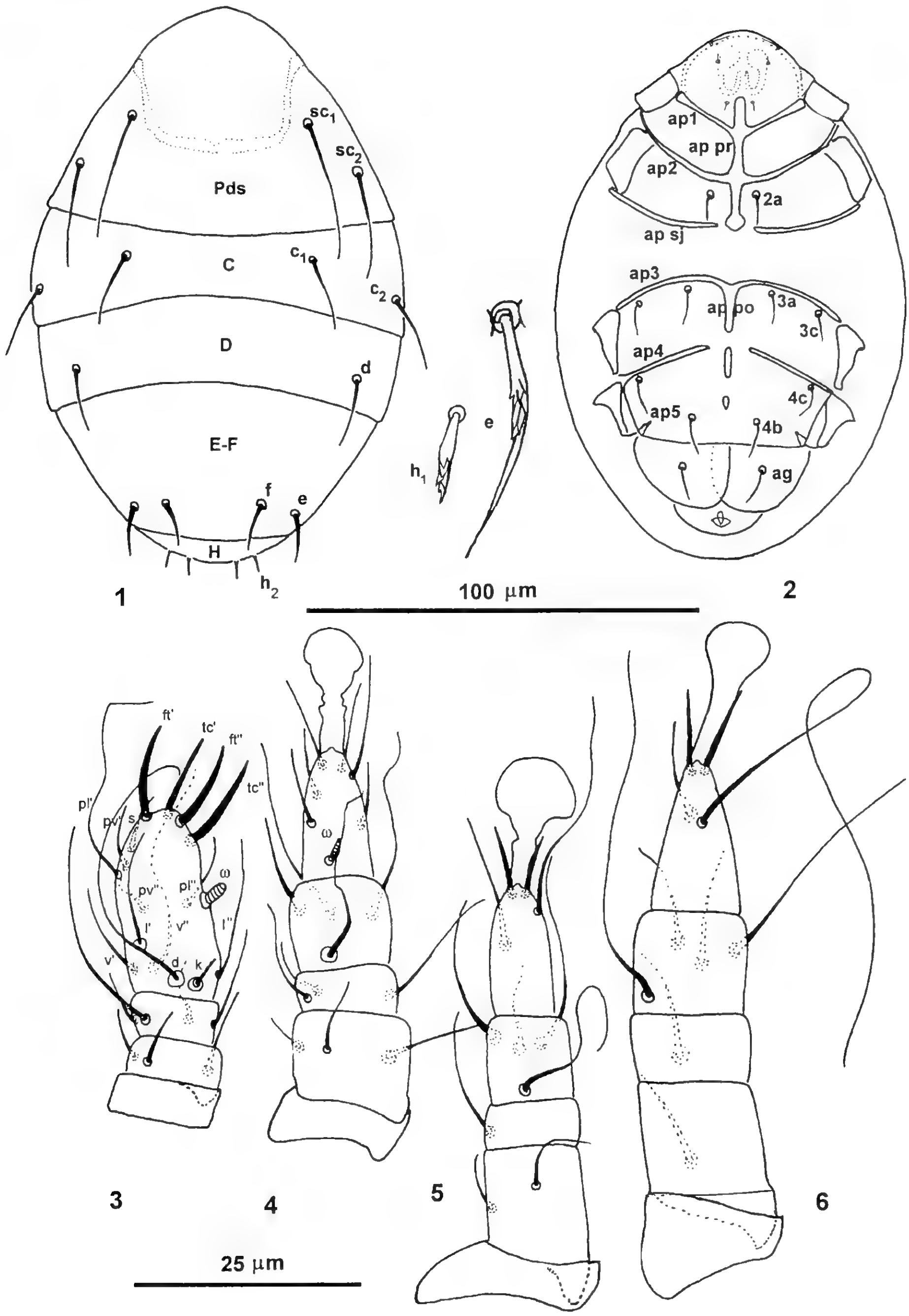
Adactylidium beeri Cross
(Figs. 1–6, 135)

Adactylidium beeri Cross 1965: 145.

Diagnosis.—The female of *A. beeri* can be distinguished by a combination of setal characters: presence of setae *4b*, absence of setae *1b*, and presence of only one seta on genu III.

Description.—*Female:* Idiosoma (Figs. 1–2) oval, length of paratype and range of “metatype” and three additional specimens 135 (120–140), width 88 (77–88). Gnathosoma with dorsal and ventral subcapitular setae, and palpal tibiotarsal setae short and setiform. Cheliceral stylets thick and curved. Pharynx long, dense, with thin muscular walls. Gnathosomal apodeme conspicuous basally (Fig. 1). Stigma located inside podocephalic opening, main tracheal trunks with unsclerotized atria and undivided postatrial structures.

Dorsum (Fig. 1). Finely punctate; prodorsal shield subtriangular. Prodorsal setae sc_1 26 (20–26) and sc_2 22 (17–22) slender and simple. Base of sc_1 anteromedial of sc_2. Tergite C with setae c_1 23 (16–23) and setae c_2 21 (15–21) simple, slender and subequal in length; base of c_1 slightly anteromedial of c_2. Tergite C and D similar in length. Tergite D with setae *d* 22 (17–22) slender, apparently smooth to slightly serrate. Ter-



Figs. 1–6. *Adactylidium beeri,* female 1, Dorsal. 2, Ventral. 3–6, Legs I–IV.

gite E–F with setae e 21 (16–22) and setae f 21 (17–22) slender, serrate in the middle region (Fig. 1) and subequal in length. Tergite H with two pairs of subequal setae, short, stout and serrate; setae h_1 7 (7–11), setae h_2 7 (7–10).

Venter (Fig. 2). Apodemes I well developed, united with prosternal apodemes;

prosternal apodeme uninterrupted and thick; apodemes II well developed, united with prosternal apodeme. Prosternal apodeme not united with sejugal apodeme; sejugal apodeme divided in two equal curved sections. Apodemes III longer than apodemes IV, conspicuous and curved, united with poststernal apodeme. Apodemes IV not united with poststernal apodeme. Poststernal apodeme weak, fragmented into two to three sections. Apodemes V reduced. Setae *1b* absent; *2a* 8 (8–14); coxal fields III with two setae, *3a* 13 (11–13) and *3c* 10 (10–14), and coxal fields IV with two setae *4b* 8 (8–11) and *4c* 10 (10–15). One pair of *ag* setae present 9 (9–11), aggenital plate smooth.

Legs (Figs. 3–6, 135). Leg I 31 (32–35), leg II 52 (51–54) , leg III 52 (52–55), and leg IV 55 (53–56). Number of setae and solenidia on femur, genu, tibia, and tarsus, respectively: leg I: 3–4–6+9 (ω) (Fig. 3); leg II: 3–3–4–6 (ω); leg III: 2–1 (*l′* absent)–4–4; leg IV: 1–1–4–4. Solenidion ω of tibiotarsus I slightly shorter and wider than solenidion ω of tarsus II, both stout and rod like. Tibiotarsus I with a ventral, subapical indentation and with setae *ft′*, *ft″*, *tc′*, and *tc″* stout, cylindrical, and subequal in length, remaining setae simple and filiform.

Male: Unknown.

Material examined.—One paratype ♀ (#4 of Cross 1965) collected from thorax of unidentified host thrips. # M-58-5, USA: Michigan, Cheboygan Co., University of Michigan Biological Station, 45°33′N, 84°40′W, 2 August 1958, R. E. Beer, PVA-L-P: VIII-58 (USNM); 1 ♀, labeled "metatype" in Cross' hand with same collection data (FSCA); 5 ♀ collected from the abdomen of *Leptothrips distalis* (Hood) (originally identified as *Haplothrips* sp.) on *Larrea divaricata* Cav. flowers, USA: California, Inyo Co., Mazourka Canyon Road, 7 mi. E. of Independence, 36°48′10″N, 118°11′57″W, 16 Sept. 1969, T. Kono and M. S. Wasbauer, No. 69J16-3 (FSCA).

Remarks.—Dr. J. S. Ashe, University of Kansas, looked repeatedly for the holotype and 3 paratypes stated by Cross to be deposited in the Snow Entomological Museum at the University of Kansas and for the voucher specimen of the original host thrips, # M-58-5 from Michigan, but neither the mites nor host specimen could be located. Identification of one specimen as a "metatype" by Cross follows traditional usage of the term as a topotypical specimen compared with the holotype by the original author (Nichols and Schuh 1989). The California specimens have the dorsum finely punctate, a characteristic not obvious on the paratype collected in Michigan. Examination of one of the thrips collected from California (originally labeled as *Haplothrips* sp.) by Mr. S. Nakahara, SEL-USDA, Maryland, U.S.A., revealed that it was actually *Leptothrips distalis* (Thysanoptera: Phlaeothripidae).

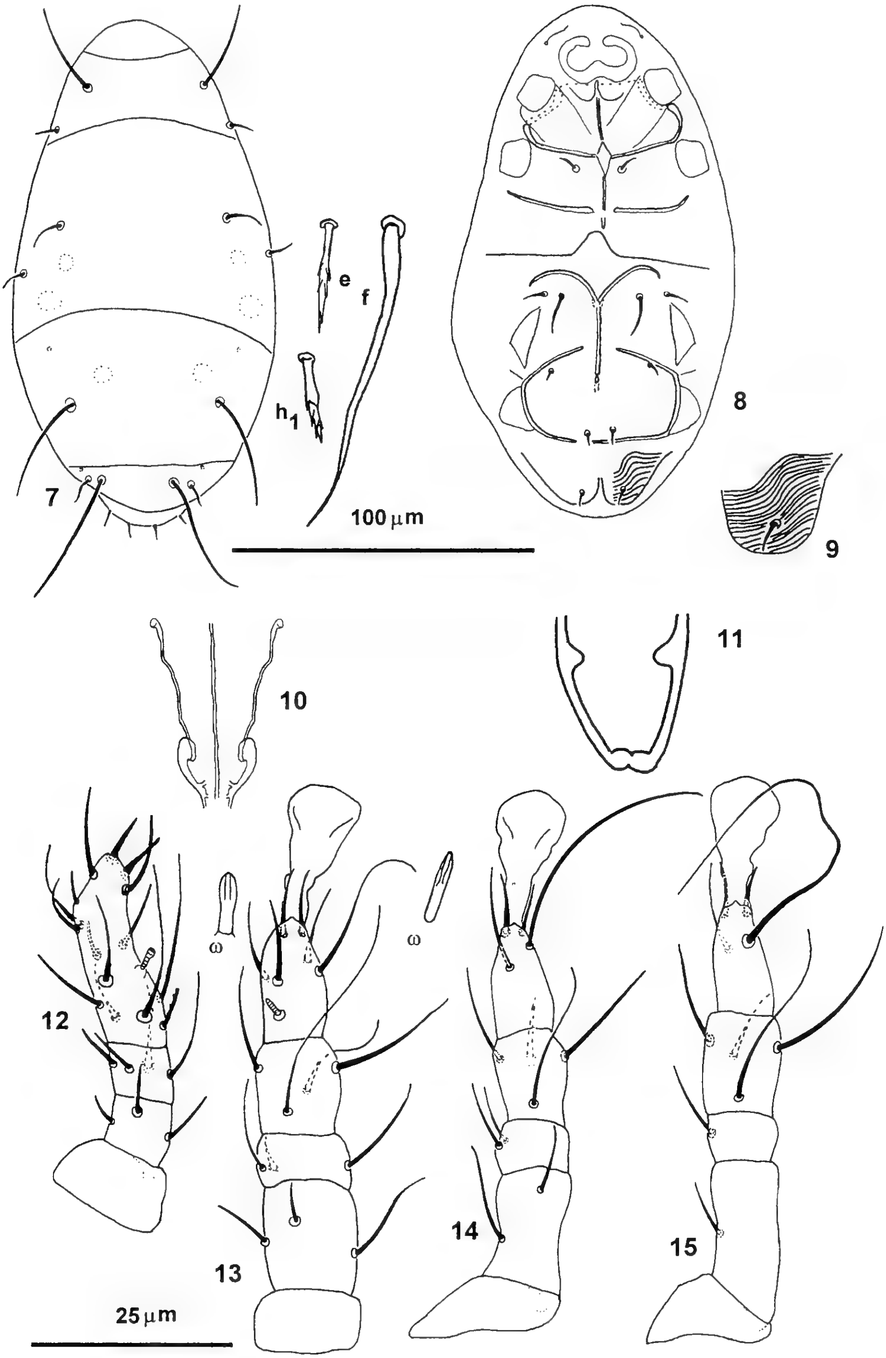
Adactylidium costarricensis Goldarazena, Jordana, and Zhang
(Figs. 7–15)

Adactylidium costarricensis Goldarazena, Jordana, and Zhang 1997: 267.

Diagnosis.—The female of *A. costarricensis* is distinguished by having tergite C longer than wide and striations on the aggenital plate.

Description.—*Female:* Idiosoma (Figs. 7–8) elongate, ovoid, length 155–164, width 79–84. Gnathosoma with two pairs of setae, one dorsal and one ventral, proximal pair inconspicuous. Cheliceral stylets curved. Pharynx very long, dense, with thin muscular walls. Gnathosomal apodeme with medial projections (Fig. 11). Stigma located inside the podocephalic opening, main tracheal trunks with long unsclerotized atria and divided broad postatrial structures (Fig. 10).

Dorsum. (Fig. 7). Prodorsal shield subquadrate. Prodorsal setae sc_1 (45–48) and sc_2 (8–11) slender and simple. Base of sc_1 anteromedial of sc_2. Setae c_1 (15–18) longer than c_2 (9–11) simple (in some specimens c_1 is three times c_2), base of setae c_1 an-



Figs. 7–15. *Adactylidium costarricensis,* female 7, Dorsal. 8, Ventral. 9, Striation on aggenital plate. 10, Tracheal trunks. 11, Gnathosomal apodeme. 12–15, Legs I–IV.

teromedial to c_2. Tergite D wider than long, with setae *d* (36–40). Tergite E–F with setae *f* (50–58) three times longer than setae *e* (8–11), setae *e* serrate. Tergite H with two pairs of subequal, short, serrate setae h_1 (7–9), h_2 (6–7). Body with reticulate sculpturing pattern formed by contiguous depressions.

Venter (Fig. 8). Apodemes I absent; prosternal apodeme uninterrupted and extending to sejugal apodeme. Apodemes II conspicuous and curved, united with prosternal apodeme. Sejugal apodeme reduced to a lateral fragment on either side not united with prosternal apodeme. Apodemes III well developed and united to poststernal apodeme; apodemes IV well sclerotized, not united with poststernal apodeme. Poststernal apodeme uninterrupted distally. Apodemes V well developed. Setae *1b* absent; *2a* (19–21); coxal fields III with two pairs *3a* (19–20) and *3c* (14–16), and coxal fields IV with two pairs *4c* (9–10) and *4c* (7). One pair of *ag* setae present (6).

Legs (Figs. 12–15). Leg I (46–49), leg II (70–74), leg III (75–79), and leg IV (68–72). Number of setae and solenidia on femur, genu, tibia, and tarsus, respectively: leg I: 3–4–6+9 (ω); leg II: 3–3–4–6 (ω); leg III: 2–2–4–4; leg IV: 1–1–4–4. Solenidion ω of tibiotarsus I capitate (Figs. 12), slightly shorter than solenidion ω of tarsus II. Solenidion on tarsus II rod-like (Figs. 13). Tibiotarsus I with a ventral subapical indentation; with setae *tc′*, *tc″*, *ft′*, and *ft″* stout and cylindrical, (*ft*) two times longer than (*tc*).

Male: Unknown.

Material examined.—Holotype and 8 paratype ♀ collected on sporophagous thrips (holotype ex *Zactinothrips* sp.; four paratypes ex *Elaphrothrips laevicollis* (Bagnall); one paratype ex *Actinothrips* sp.; one paratype ex *Pristothrips albipunctatus* Hood and other paratype ex *Psalidothrips* sp.), COSTA RICA: Heredia, La Selva Biological Station, near Puerto Viejo, 10°26′N, 84°01′W, 25–29 November 1992, L. A. Mound (MZUNAV, INBIO, USNM).

Remarks.—The female of *A. costarricensis* resembles that of *A. nicolae* but can be distinguished by lacking setae *1b* on coxal fields I, and by the absence of solenidion ω on tarsus III. In *A. nicolae* setae *1b* is present, and solenidion ω is present on tarsus III.

Adactylidium moundi Goldarazena, Jordana, and Zhang
(Figs. 16–24)

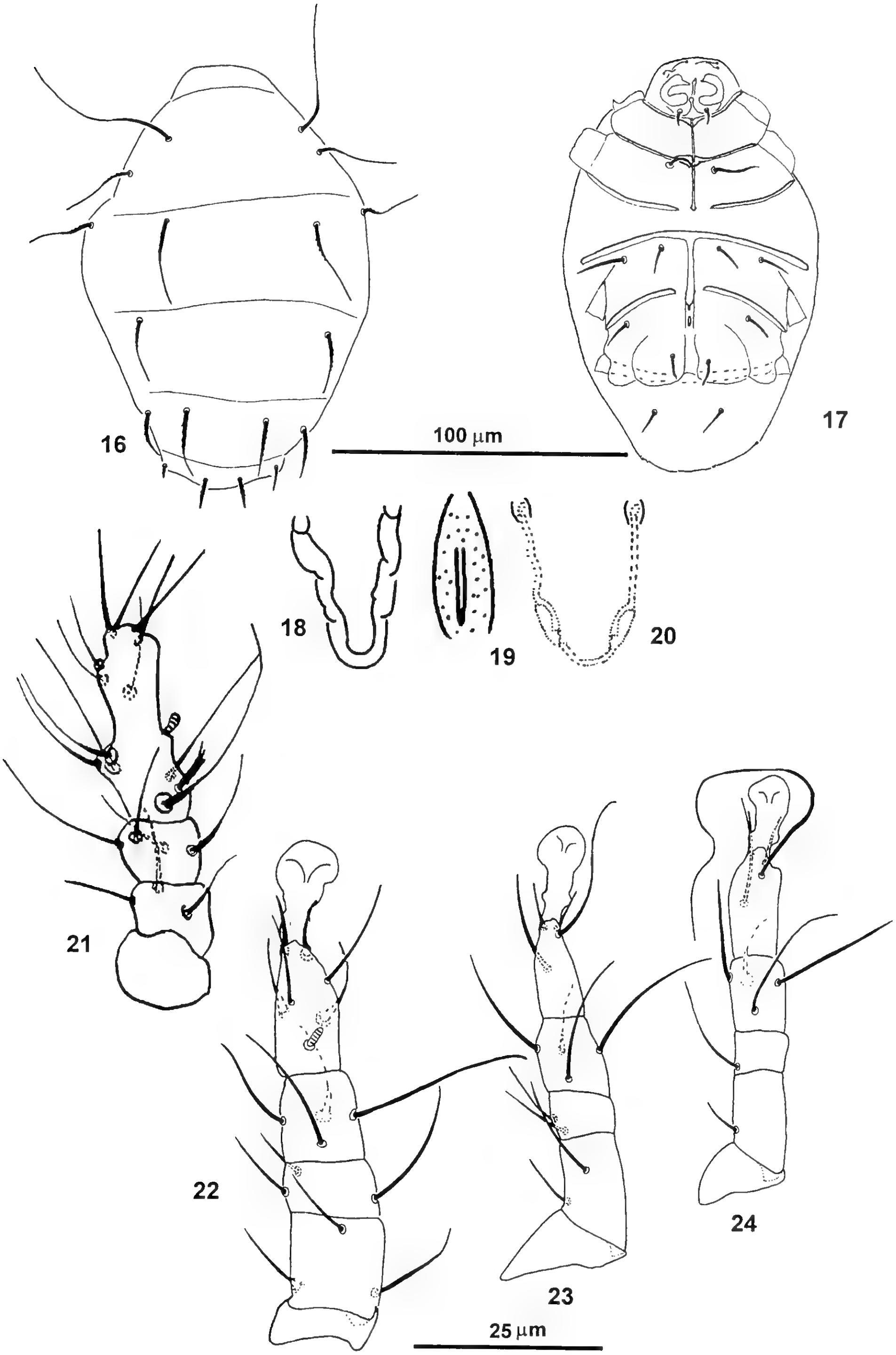
Adactylidium moundi Goldarazena, Jordana, and Zhang 1997: 261 (in part).

Diagnosis.—The female of *A. moundi* is distinguished by the combination of two characters: lobes on the gnathosomal apodeme and the presence of two setae on genu III.

Description.—*Female:* Idiosoma (Figs. 16–17) oval, length of holotype and range of twelve specimens 154 (143–154), width 86 (83–90). Gnathosoma with dorsal and ventral subcapitular setae, and palpal tibiotarsal setae conspicuous. Cheliceral stylets thick and curved. Pharynx very long, dense, with thin muscular walls (Fig. 19). Gnathosomal apodeme lobed, without projections (Fig. 18). Stigma located inside the podocephalic opening, main tracheal trunks with unsclerotized atria, and with undivided broad postatrial structures (Fig. 20).

Dorsum (Fig. 16). Prodorsal shield subtriangular. Prodorsal setae sc_1 50 (50–58) and sc_2 30 (26–30) slender and simple. Base of sc_1 anteromedial of sc_2. Tergite C with setae c_1 26 (25–28) and setae c_2 20 (17–20) simple, and slightly serrate; bases of c_1 and c_2 nearly transversally aligned. Tergite C and D similar in length, wider than long. Tergite D with setae *d* 27 (25–28) simple and serrate. Tergite E–F with setae *e* 22 (19–22) and setae *f* 26 (24–27) simple and serrate. Tergite H with two pairs of subequal, short, stout serrate setae; h_1 10 (9–10), h_2 8 (8–9). Body without reticulate sculpturing pattern.

Venter (Fig. 17). Apodemes I well developed, united with prosternal apodeme;



Figs. 16–24. *Adactylidium moundi,* female. 16, Dorsal. 17, Ventral. 18, Gnathosomal apodeme. 19, Pharynx. 20, Tracheal trunks. 21–24, Legs I–IV.

prosternal apodeme uninterrupted and slender; apodemes II well developed, united with prosternal apodeme. Prosternal apodeme not united with sejugal apodeme; sejugal apodeme divided in two equal curved sections. Apodemes III longer than apodemes IV, conspicuous and curved, united with poststernal apodeme. Apodemes IV not united with poststernal apodeme. Poststernal apodeme fragmented distally. Apodemes V reduced. Setae *1b* absent; *2a* 16 (14–16); coxal fields III with two pairs, *3a* 16 (14–16) and *3c* 14 (14–15), and coxal fields IV with two pairs of setae, *4b* 12 (11–12) and *4c* 14 (12–14). One pair of *ag* setae present 14 (12–14), aggenital plate smooth.

Legs (Figs. 21–24). Leg I 40 (38–40), leg II 60 (57–60), leg III 71 (68–72), and leg IV 68 (67–72). Number of setae and solenidia on femur, genu, tibia, and tarsus, respectively: leg I: 3–4–6+7 (*pv′*, *pv″* absent) (ω); leg II: 3–3–4–6 (ω); leg III: 2–2–4–4; leg IV: 1–1–4–4. Solenidion ω of tibiotarsus I slightly shorter and wider than solenidion ω of tarsus II, both stout and rodlike. Tibiotarsus I with a ventral subapical indentation; setae *ft′*, *ft″*, *tc′*, and *tc″* stout, cylindrical, and subequal in length.

Male: Unknown.

Material examined.—Holotype and 7 paratype ♀ (one on slide and 6 on SEM stubs) collected from the abdomen of *Compsothrips albosignatus* (Reuter) on *Quercus rotundifolia* Lam. branches with lichens, SPAIN: Navarra, Tafalla, 12 March 1995, A. Goldarazena (MZUNAV); 3 ♀ from *C. albosignatus*, same locality, 25 January 1995 (MZUNAV).

Remarks.—Goldarazena et al. (1997) confused two different species in their original description of *A. moundi*. Subsequent analysis has allowed us to distinguish these taxa, one of which is described below as *A. lindquisti*.

Adactylidium nicolae (Krczal)
(Figs. 25–34, 139)

Acarophenax nicolae Krczal 1959: 553.
Adactylidium nicolae (Krczal): Cross 1965: 142.

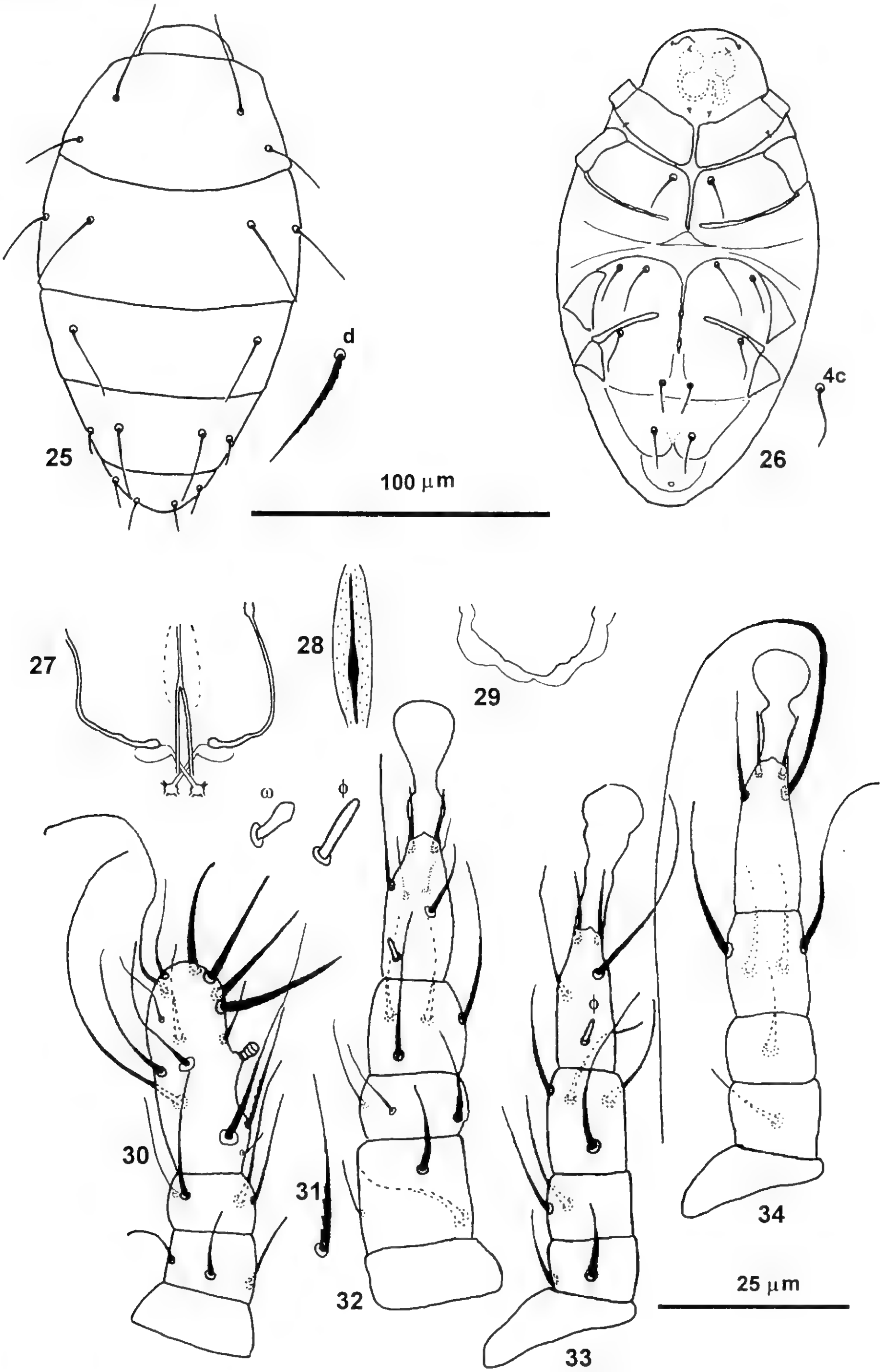
Diagnosis.—The female of *A. nicolae* is distinguished by the presence of a solenidion (ω) on tarsus III.

Description.—*Female:* Idiosoma (Figs. 25–26) elongate ovoid, length 138–140, width 74–76. Gnathosoma with dorsal and ventral subcapitular setae, and palpal tibiotarsal setae. Cheliceral stylets curved. Pharynx very long, dense, with thin porous walls (Fig. 28). Gnathosomal apodeme without medial projections, lobed distally (Fig. 29). Stigma located inside the podocephalic opening, main tracheal trunks with long unsclerotized atria, and broad, divided postatrial structures (Fig. 27).

Dorsum (Fig. 25). Prodorsal shield subquadrate. Prodorsal setae sc_1 (35–36) and sc_2 (21–22) slender and simple. Base of sc_1 anteromedial of sc_2. Tergite C wider than long, with setae c_1 (24–25) longer than c_2 (14–15) simple; base of c_1 on the same transverse line as c_2. Tergite C longer than D. Tergite D longer than wide, with setae *d* (23–24) slightly serrate. Tergite E–F with setae *f* (20–21) longer than e (11–12). Tergite H with two pairs of short setae; setae h_1 (8–9), setae h_2 (7–8). Setae *c*, *d* and *f* slightly serrate (Fig. 25), remaining dorsal setae simple and setiform.

Venter (Fig. 26). Apodemes I present, fused with prosternal apodeme; prosternal apodeme uninterrupted and extending slightly beyond sejugal apodeme; apodemes II conspicuous and curved, united with prosternal apodeme. Sejugal apodeme reduced to two lateral fragments and not united with prosternal apodeme. Apodemes III well developed fused with poststernal apodeme; apodemes IV well sclerotized not united with poststernal apodeme. Poststernal apodeme present, uninterrupted posteriorly. Apodemes V reduced. Setae *1b* present (4); *2a* (12–13); coxal fields III with two pairs *3a* (12–13) and *3c* (11–12), and coxal fields IV with two pairs, seta *4b* (10–11) and *4c* (12–14). One pair of *ag* setae present (10–13), aggenital plate smooth.

Legs (Figs. 30–34). Leg I (40–41), leg II (54–56), leg III (73–74), and leg IV (70–



Figs. 25–34. *Adactylidium nicolae,* female. 25, Dorsal. 26, Ventral. 27, Tracheal trunks. 28, Pharynx. 29, Gnathosomal apodeme. 30–34, Legs I–IV.

71). Number of setae and solenidia on femur, genu, tibia, and tarsus, respectively: leg I: 3–4–6+9 (ω); leg II: 3–3–4–6 (ω); leg III: 2–2–4–4 (ϕ); leg IV: 1–1–4–4. Solenidion ω of tibiotarsus I, slightly clavate, shorter than solenidion ω of tarsus II. Solenidia on tarsi II and III, rodlike. Tibiotarsus I with a ventral subapical indentation; setae *ft′*, *ft″*, *tc′*, and *tc″* stout, cylindrical, and subequal in length.

Male: Unknown

Material examined.—Two ♀ on single slide ("Typus" No. 126) deposited at ZIZM. The slide does not bear collection information other than the date, 11-6-53, but the original description indicates the mites were collected in moss on wood. The published type locality is given only as "Franken." Krczal (personal communication 1998) informed us that the full locality is: GERMANY: Bayern (Franken), Nürnberg, Zoological Garden. Additional material: 2 ♀ from *Hoplothrips ulmi* (Fabricius) under bark of *Ulmus* sp., SPAIN: Basque Country, Hondarribia (Guipuzcoa), 12 June 1995, A. Goldarazena (MZUNAV).

Remarks.—The two specimens in the slide can be considered syntypes. We here designate one specimen as lectotype. The lectotype specimen is the more sclerotized individual on the left side of the slide (with the original determination label to the left). This specimen is further identifiable because one leg III is broken. This specimen is here designated lectotype so as to fix and stabilize the current concept of the name and has been so labeled.

The females of *Adactylidium nicolae* are unique among Acarophenacidae in bearing a solenidion on tarsus III. The homology of this structure is uncertain. Although it is possible the solenidion is the ω that is present in early derivative trombidiform mites, this solenidion is apparently not present ancestrally in Heterostigmata (Lindquist 1986). It is present as an apparently derived reversal in males, but not females, of some Pygmephoridae and Scutacaridae (Lindquist 1986). An alternative hypothesis is that the solenidion represents the tibial ϕ which has migrated onto the tarsus. A tibial solenidion is present ancestrally in Heterostigmata and is retained in most taxa, being lost in Heterocheylidae, Tarsonemidae and Acarophenacidae. Furthermore, solenidial migration between tibia and tarsus is known to occur in some heterostigmatic mites, but most cases involve migration of the tarsal ω onto the tibia, as in *Petalomium krczali* (Cross) (Cross 1965, Lindquist 1986). If it is true that both solenidia are ancestrally absent in the Acarophenacidae, then the appearance of this structure in *A. nicolae* must be the result of an evolutionary reversal. Until more information can be gathered on the ontogeny and sexual dimorphism, as well as the taxonomic distribution of such reversals, we take a conservative approach and regard the solenidion in question here as the tarsal ω.

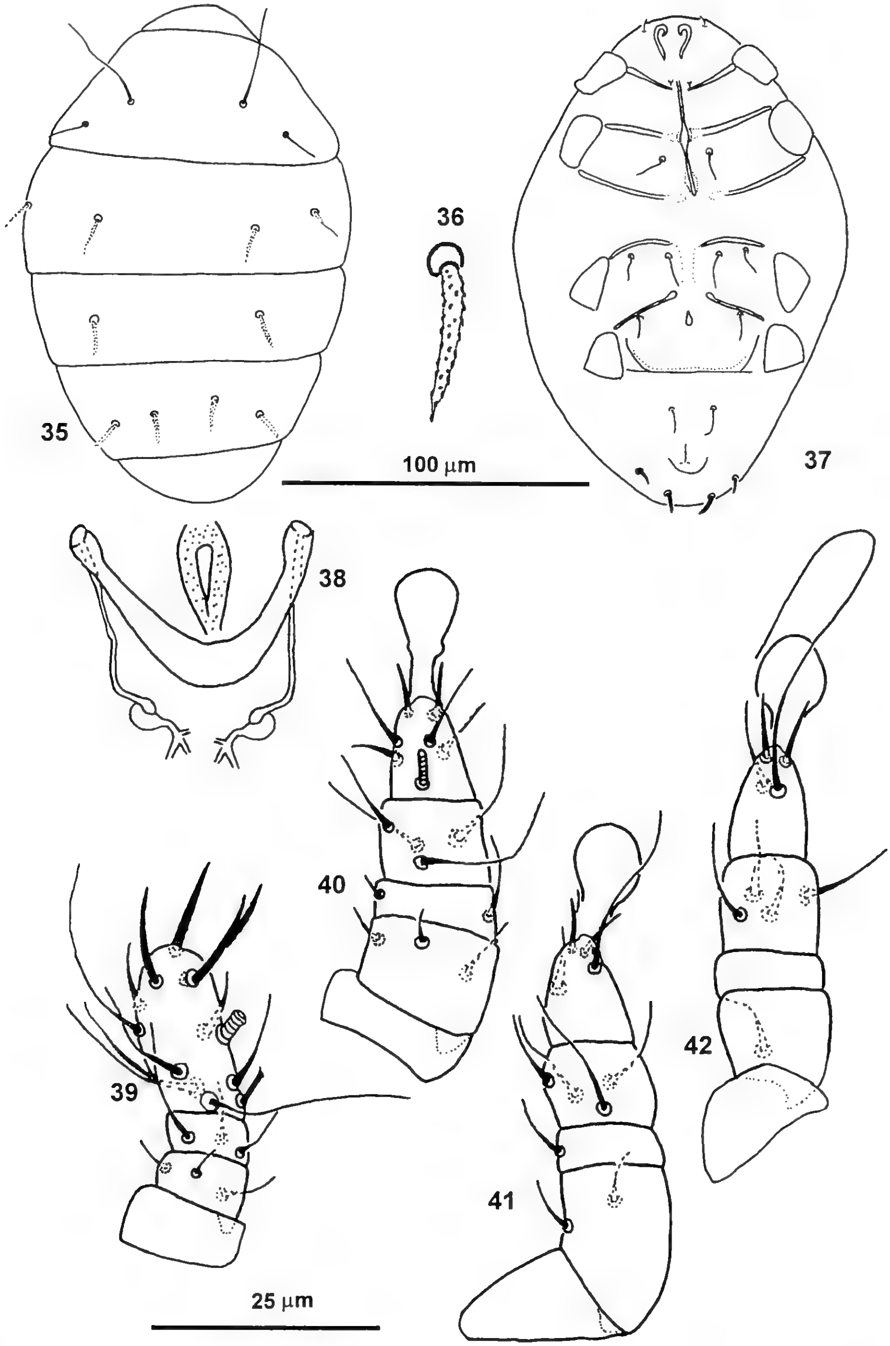
Adactylidium brasiliensis Goldarazena and Ochoa, new species

(Figs. 35–42, 136)

Diagnosis.—The female of *Adactylidium brasiliensis* is distinguished by the lack of tarsal setae *pv″*, *pv′*, and *u″* on tibiotarsus I and the presence of distinctly barbed dorsal setae (Fig. 36).

Description.—*Female:* Idiosoma (Figs. 35–37) oval, length of holotype and range of three paratypes 129 (129–143), width 87 (81–95). Gnathosoma with dorsal and ventral subcapitular setae reduced and setiform; palptibiotarsal setae inconspicuous. Cheliceral stylets thick and curved. Pharynx long, dense, with thin muscular walls. Gnathosomal apodeme without median projections. Stigma located inside the podocephalic opening, main tracheal trunks with unsclerotized divided atria and divided broad postatrial structures (Fig. 38).

Dorsum (Fig. 35). Prodorsal setae sc_1 25 (25–30) and sc_2 11 (11–16) slender and simple. Base of sc_1 anteromedial of sc_2. Tergite C with setae c_1 10 (10–12) and c_2 (8–12) simple and subequal in length; base of c_1 anteromedial of c_2. Tergite D with setae



Figs. 35–42. *Adactylidium brasiliensis,* female. 35, Dorsal. 36, Serrate dorsal seta. 37, Ventral. 38, Pharynx, tracheal trunks and gnathosomal apodeme. 39–42, Legs I–IV.

d 9 (9–11). Tergite E–F with setae *e* 8 (8–10) and setae *f* 9 (9–11) short, and subequal in length. Tergite H with two pairs of subequal, short, stout setae, h_1 8 (6–8), setae h_2 6 (6). Setae c_1, c_2, *d, e, f,* h_1, and h_2 barbed. (Fig. 36)

Venter (Fig. 37). Apodemes I not united with prosternal apodeme; prosternal apodeme not fragmented distally; apodemes II conspicuous and curved, united with prosternal apodeme. Prosternal apodeme not united with sejugal apodeme; sejugal apodeme divided in two equal curved sections and less sclerotized than prosternal apodeme. Apodemes III as longer as apodemes IV, conspicuous and curved, not joining poststernal apodeme. Poststernal apodeme reduced to a small ellipsoidal nodule. Apodemes V reduced. Setae *1b* absent; *2a* 10 (10–11); coxal fields III with two pairs *3a* 12 (12) and *3c* 11 (10–11), and coxal fields IV with one pair *4c* 10 (10–11), *4b* absent. One pair of *ag* setae present 11 (9–11), aggenital plate smooth.

Legs (Figs. 39–42, 136). Leg I: 31 (31–32), leg II 46 (46–50), leg III 49 (49–53), and leg IV 47 (47–51). Number of setae and solenidia on femur, genu, tibia, and tarsus, respectively: leg I: 3–3 (*v′* absent)–6+7 (*pv′*, *pv″* absent) (ω); leg II: 3–2 (*v′* absent)–4–6 (ω); leg III: 2–1 (*l′* absent)–4–4; leg IV: 1–0 (*v′* absent)–4–4. Solenidion ω of tibiotarsus I slightly shorter and wider than solenidion ω of tarsus II, both stout and rodlike. Tibiotarsus I with setae *ft′*, *ft″*, *tc′*, and *tc″* stout, cylindrical, and subequal in length and lacking *pv″*, *pv′*, and *u″* setae (Fig. 39). Remaining setae slightly barbed; ventral subapical indentation not observed.

Male: Unknown.

Type, host, and locality data.—Holotype ♀ and 9 paratype ♀ collected from *Gynaikothrips ficorum* (Marchal), BRAZIL: São Paulo, Iracemápolis, 4 November 1983, F. D. Bennet, ESALQ No. 1594. Holotype and 5 paratypes deposited in ESALQ, three paratypes in USNM, two paratypes in FSCA.

Etymology.—This species is named for the country where the species was collected.

Adactylidium crespii Goldarazena and OConnor, new species

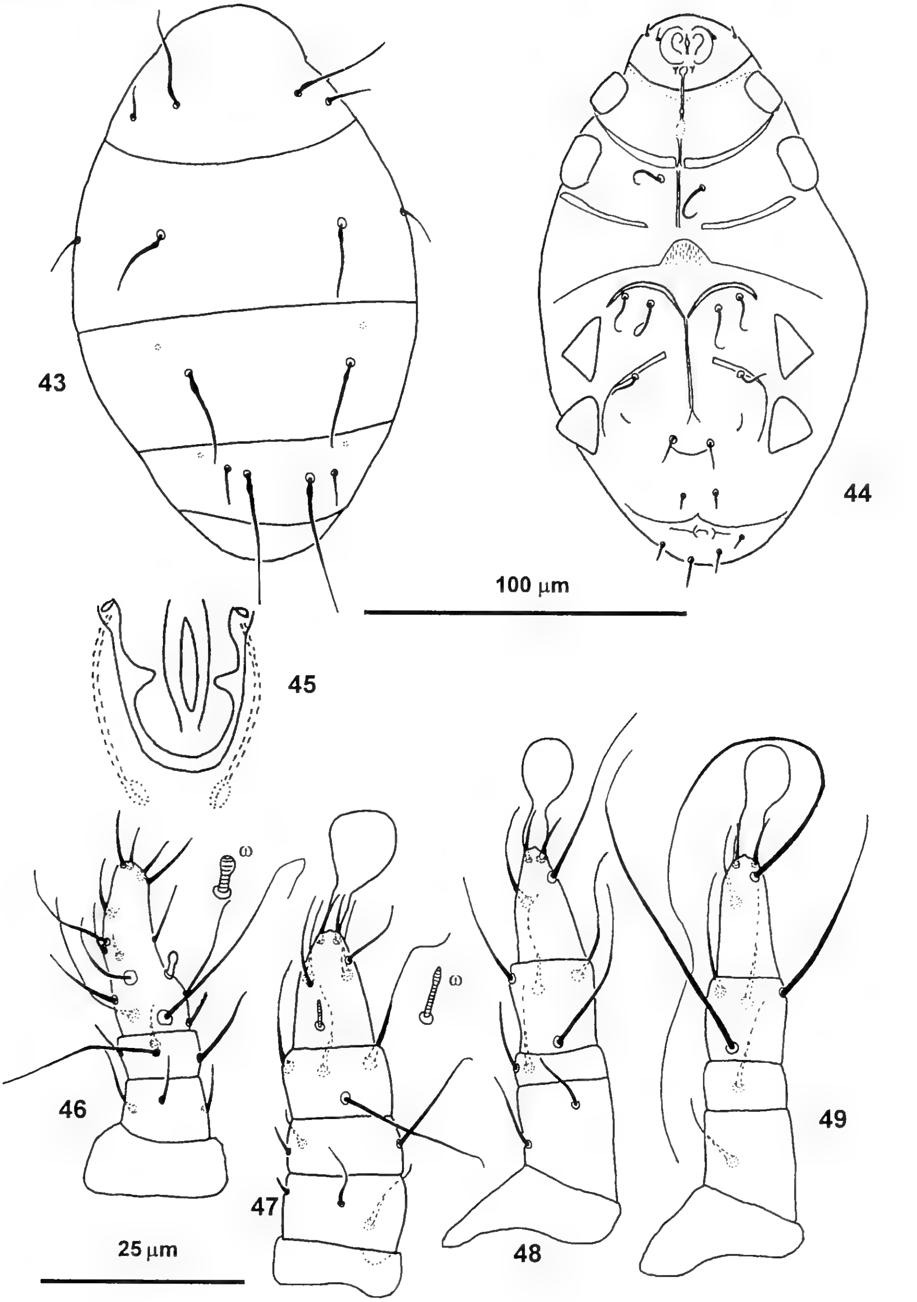
(Figs. 43–55, 137–138)

Diagnosis.—Adult females of *A. crespii* can be distinguished by a combination of characters: palpal tibiotarsal seta are present, setae *1b* are absent, apodemes V are reduced and tergite C is wider than it is long.

Description.—*Female* (Fig. 43–49): Idiosoma (Figs. 43–44) elongate, ovoid, length of holotype and six paratypes 160 (159–168), width 91 (90–93). Gnathosoma with dorsal and ventral subcapitular setae, and palpal tibiotarsal setae present, proximal pair inconspicuous. Cheliceral stylets curved. Pharynx longer than wide, walls thinner than in other species. Gnathosomal apodeme with medial projections (Fig. 45). Stigma located inside the podocephalic opening, main tracheal trunks with long unsclerotized divided atria, and with undivided broad postatrial structures.

Dorsum (Fig. 43). Prodorsal shield subtriangular. Prodorsal setae sc_1 44 (44–46) and sc_2 10 (10–12) slender and simple. Base of sc_1 anteromedial of sc_2. Tergite C wider than long, with setae c_1 27 (26–31) and setae c_2 10 (9–12) simple; base of c_1 on the same transverse line to c_2. Tergite D wider than long, with setae *d* 34 (34–38). Tergite E–F with setae *f* 52 (50–53) three times longer than setae *e* 10 (7–11). Tergite H with two pairs of subequal, short setae, h_1 8 (8–9), h_2 6 (6–7) slightly serrated. Body with reticulate sculpturing pattern. All dorsal setae simple, broadened basally, setiform (Fig. 43).

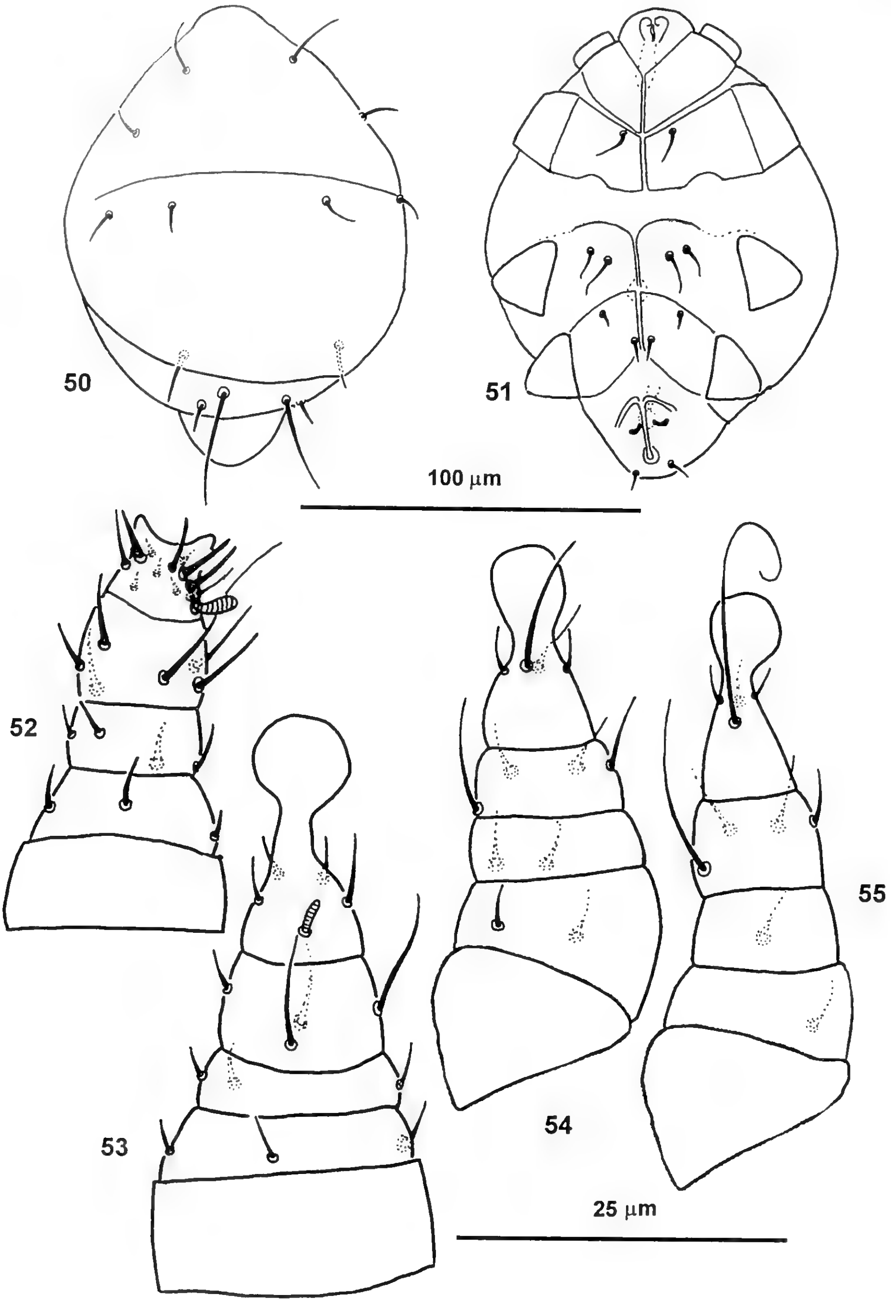
Venter (Fig. 44). Apodemes I inconspicuous; prosternal apodeme interrupted anteriorly and not extending to sejugal apodeme; apodemes II conspicuous and curved, united with prosternal apodeme. Sejugal apodeme divided into two equal, curved sections and not united with prosternal apodeme. Apodemes III well developed joining



Figs. 43–49. *Adactylidium crespii,* female. 43, Dorsal. 44, Ventral. 45, Pharynx, tracheal trunks and gnathosomal apodeme. 46–49, Legs I–IV.

with poststernal apodeme; apodemes IV well sclerotized not united with poststernal apodeme. Poststernal apodeme entire. Apodemes V reduced. Setae *1b* absent; *2a* 15 (14–16); coxal fields III with two pairs *3a* 17 (15–17) and *3c* 12 (11–12), and coxal fields IV with two pairs, seta *4b* 6 (6–7) and *4c* 10 (9–11). One pair of *ag* setae present 6 (6–7), aggenital plate smooth.

Legs (Figs. 46–49). Leg I 40 (40–43),



Figs. 50–55. *Adactylidium crespii,* male. 50, Dorsal. 51, Ventral. 52–55, Legs I–IV.

leg II 63 (62–66), leg III 80 (79–82), and leg IV 75 (74–76). Number of setae and solenidia on femur, genu, tibia, and tarsus, respectively: leg I: 3–4–6+9 (ω); leg II: 3–3–4–6 (ω); leg III: 2–2–4–4; leg IV: 1–1–4–4. Solenidion ω of tibiotarsus I clavate and slightly shorter than solenidion ω of tarsus II. Solenidion on tarsus II rodlike. Tibiotarsus I with a ventral subapical indentation; setae *tc′* and *tc″* stout, cylindrical; *ft′* and *ft″* two times longer than *tc′* and *tc″*.

Male (Figs. 50–55, 137–138): Idiosoma

oval, length 127, width 69. Gnathosoma and chelicerae reduced.

Dorsum (Fig. 50). Prodorsal two pair of setae, sc_1 (18–19) longer than sc_2 (8–9). Tergite C with two pairs of setiform setae, c_1 (16–17) and c_2 (11–12). Tergite D and E–F fused. Setae *d* (21–22), *f* (31–32) and *e* (6–7) setiform and smooth. Segment H with one pair of setae *h* (4–5). Body without reticulate sculpturing pattern.

Venter (Fig. 51). All apodemes present, well developed. Prosternal apodeme not extending beyond sejugal apodemes. Coxal fields I without setae, coxal fields II with one pair *2a* (10–11), coxal fields III with two pairs *3a* (11–12) and *3c* (7–8), and coxal fields IV with two pairs *4b* and *4c* (3–4). Setae *ag* absent.

Legs (Figs. 52–55, 119–120). Leg I (32–33), leg II (53–55), leg III (53–55) and leg IV (56–58). Number of setae and solenidia on femur, genu, tibia, and tarsus, respectively: leg I: 3–4–6–11 (ω); leg II: 3–3–4–4 (ω); leg III: 2–2–4–4: leg IV: 1–1–4–4. Setae *pv′* and *pv″* of tarsus II absent in male, although present in female. Tarsus I with a distal notch. Tarsi I–IV without claws. Solenidion ω of tarsus I wider than solenidion of tarsus II, both rodlike.

Type, host, and locality data.—Holotype ♀, 10 paratype ♀ and allotype ♂ collected from *Elaphrothrips tuberculatus* (Hood), USA: Michigan, Livingston Co., E. S. George Reserve, 7–17 May 1985, B. Crespi, BMOC #85-0522-1; 1 paratype ♀, same host and locality, 7 July 1985, BMOC 85-0724-1. Holotype, allotype and 6 paratypes deposited in UMMZ, one paratype in MZUNAV, 2 paratypes in USNM, one in ESALQ, one in OSAL.

Etymology.—This species is dedicated to its collector, Dr. Bernard Crespi, Simon Fraser University, in recognition of his contribution to the knowledge of Thysanoptera.

Adactylidium ficorum Goldarazena and Ochoa, new species

(Figs. 56–72, 140–141)

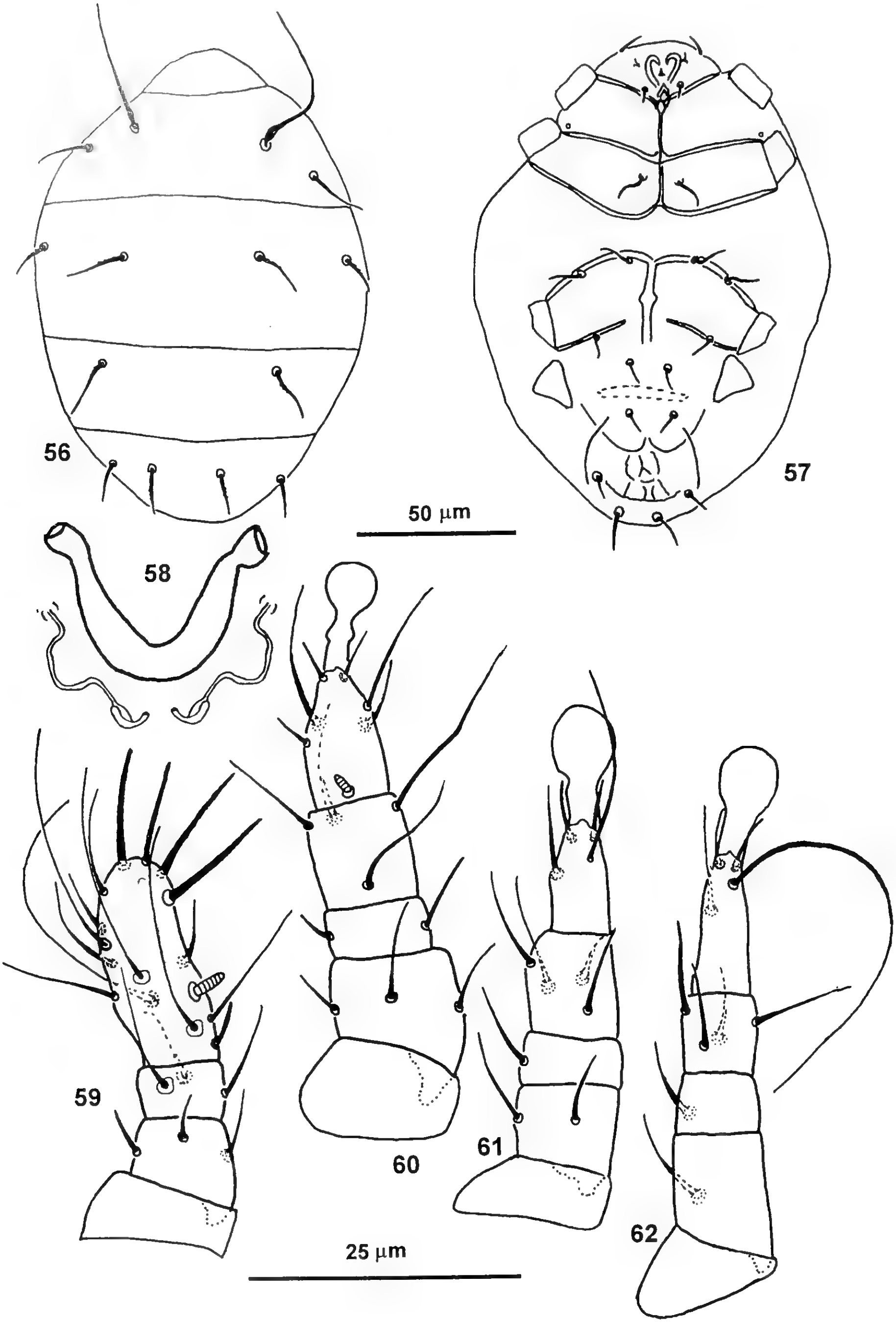
Adactylidium sp.: Elbadry and Tawfik 1966: 458; Abreu 1982: 310.

Diagnosis.—The female of *A. ficorum* can be distinguished by the combination of a fully developed sejugal apodeme and the presence of three setae on genu I.

Description.—*Female:* Idiosoma (Figs. 56–57) oval, length of holotype and range of eight non-physogastric paratypes 127 (124–133), width 92 (86–95); range of four physogastric females, length (310–353), width (240–275). Body of physogastric females with 6 to 9 eggs, some containing larvae. Gnathosoma with dorsal and ventral subcapitular setae, and palpal tibiotarsal setae present and setiform. Cheliceral stylets thick and curved. Pharynx longer than wide, dense, with thin muscular walls. Gnathosomal apodeme without lateral projections (Fig. 58). Stigma located inside the podocephalic opening, main tracheal trunks with unsclerotized divided atria, and with undivided broad postatrial structures.

Dorsum (Fig. 56). Prodorsal setae sc_1 36 (28–41) and sc_2 17 (16–21) slender and simple, sc_1 broadened at its basis. Base of sc_1 anteromedial of sc_2. Tergite C with setae c_1 17 (16–20) and setae c_2 12 (11–14) simple; base of c_1 and c_2 nearly transversally aligned. Tergite C longer than D. Tergite D with setae *d* 16 (13–16), longer than half the length of segment. Tergite E–F with setae *e* 12 (9–12) and *f* 14 (12–16) short, setiform. Tergite H with two pairs of subequal, short, stout setae, setae h_1 7 (6–10), setae h_2 6 (5–7). All dorsal setae from C to H are simple and serrate.

Venter (Fig. 57). Apodemes I present united with prosternal apodeme; apodemes II conspicuous and curved, united with prosternal apodeme. Prosternal apodeme present, uninterrupted, fused with sejugal apodeme posteriorly, not extending posterior to sejugal apodeme; sejugal apodeme curved laterally and less sclerotized than prosternal apodeme. Apodemes III longer than apodemes IV, conspicuous and curved, fused with poststernal apodeme; apodemes IV not united with poststernal apodeme. Poststernal apodeme thicker and not inter-



Figs. 56–62. *Adactylidium ficorum,* female. 56, Dorsal. 57, Ventral. 58, Gnathosomal apodeme and tracheal trunks. 59–62, Legs I–IV.

rupted. Apodemes V reduced. Setae *1b* absent but alveoli visible; *2a* 11 (6–13); coxal fields III with two pairs *3a* 11 (10–12) and *3c* 8 (8–10), and coxal fields IV with two pairs *4a* 8 (6–9) and *4b* 7 (7–10). One pair of *ag* setae present 6 (6–10), aggenital plate smooth.

Legs (Figs. 59–62). Leg I 32 (31–36), leg II 51 (48–53), leg III 54 (52–54), and leg IV 53 (49–53). Number of setae and solenidia on femur, genu, tibia, and tarsus, respectively: leg I: 3–3–6+9 (ω); leg II: 3–2 (*v′* absent)–4–6 (ω); leg III: 2–1 (*l′* absent)–4–4; leg IV: 1–1–4–4. Solenidion ω of tibiotarsus longer than solenidion ω of tarsus II, both stout and rodlike. Tibiotarsus I with a flat, tapering projection ventroapically; setae *ft′*, *ft″*, *tc′*, and *tc″* stout, cylindrical, and subequal in length.

Male (Figs. 63–69, 140–141): Idiosoma rounded, length 95, width 47. Gnathosoma reduced and with one pair of dorsal setae, ventral setae inconspicuous. Chelicerae reduced.

Dorsum (Fig 63). Prodorsal two pairs of setae: sc_1 (24–25) and sc_2 (16–18). Tergite C with two pairs of subequal setae, c_1 11–12, c_2 9–10. Tergite D with one pair of setae *d* weakly serrated (9–10). Tergite E–F with a pair of setae, *e* (6–7), *f* (7–8) subequal in length and serrated (Fig. 64). Tergite H reduced and with one pair of setiform setae *h* (3) ventrally. Body without reticulate sculpturing pattern.

Venter (Fig. 65). All apodemes well developed. Prosternal apodeme extending slightly beyond sejugal apodeme. Coxal fields I without setae, coxal fields II with one pair *2a* (5–6), coxal fields III with two pairs *3a* (5–6) and *3c* (4–5) and coxal fields IV with two pairs *4b* (3) and *4c* (3–4). Setae *ag* absent.

Legs (Figs. 66–69, 140–141). Leg I (26–27), leg II (42–44), leg III (43–45) and leg IV (41–42). Number of setae and solenidia on femur, genu, tibia, and tarsus, respectively: leg I: 0–2–5–11 (ω); leg II: 3–0–4–4 (ω); leg III: 2–0–4–4; leg IV: 1–0–4–4. Tarsus I knoblike. Tarsi I–IV without claws. Solenidion ω of tarsus I longer than solenidion ω of tarsus II, both stout and rodlike.

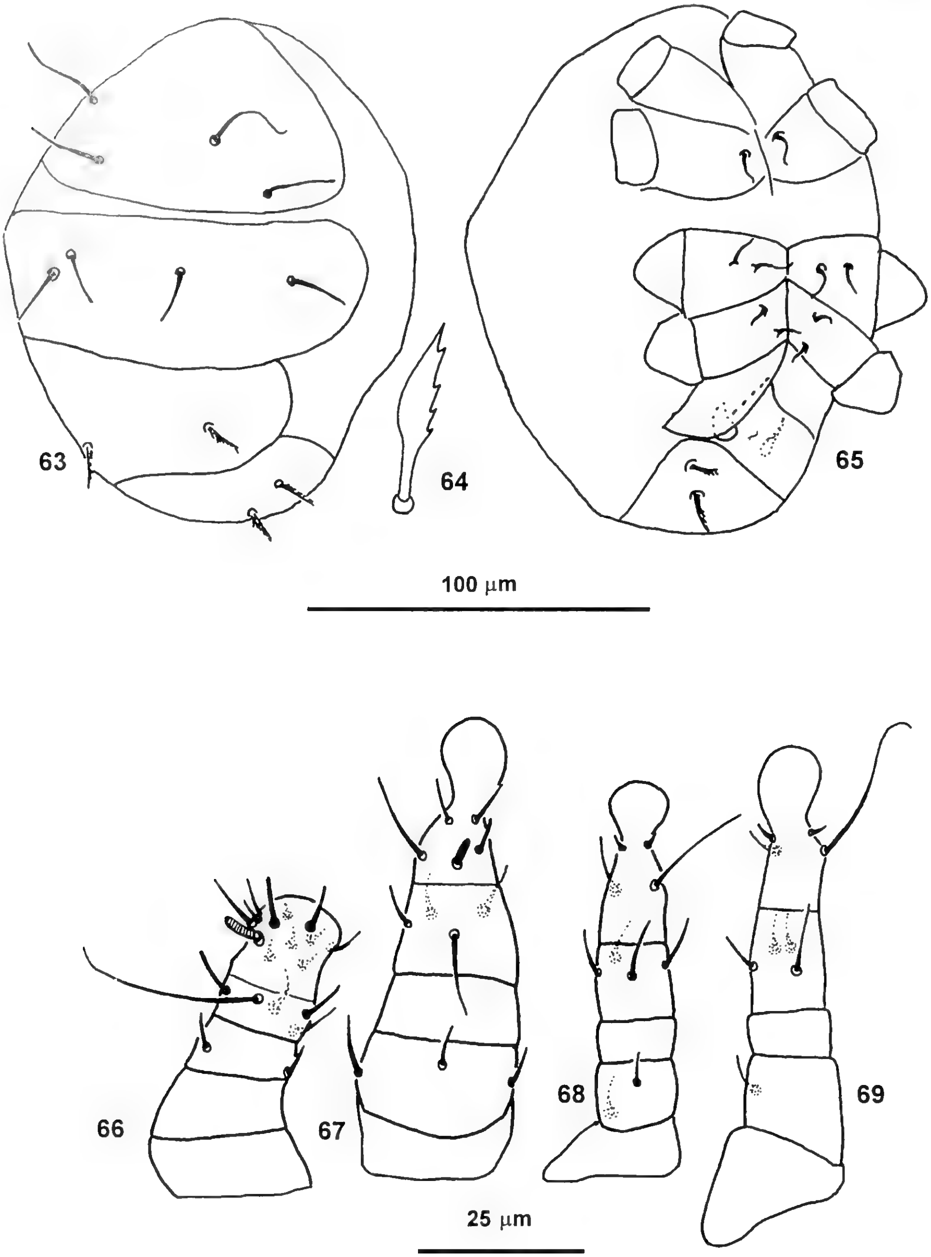
Larva (Fig. 70–72): Idiosoma elongate ovoid, with segment H narrower, directed distally; length of six specimens (110–130), width (60–90). Gnathosoma reduced, positioned ventrally. Stylets present but reduced. Idiosoma with discrete tergites but without setae. Venter with apodeme I visible, apodeme II fused with prosternal apodeme, prosternal apodeme reduced anteriorly, sejugal apodeme present, fused with prosternal apodeme, not extending beyond sejugal apodeme. Apodeme III present, fused medially; poststernal apodeme not observed. Coxal fields without setae. Legs I–III strongly reduced with telescoped segments, lengths (16–23), without setae but with two claws distally.

Type, host, and locality.—Holotype ♀, allotype ♂, and 15 paratype ♀ collected from *Gynaikothrips ficorum* (Marchal) and its eggs on *Ficus microcarpa* L., PUERTO RICO: Mayaguez, 19 April 1976, E. Abreu-Rodriguez (AL-5333) (OSUAL 0000119); 12 paratype ♀ collected from *G. ficorum* on *Ficus nitida* Thunberg, EGYPT [United Arab Republic] (no further locality), from studies of E. A. Elbadry and M. S. F. Tawfik. Holotype, allotype and 7 paratypes deposited in the OSAL, 11 paratypes deposited in the FSCA, 4 paratypes deposited in the USNM, 2 paratypes deposited in the UMMZ, 2 paratypes deposited in the MZUNAV, and 1 paratype deposited in the ESALQ.

Etymology.—This species is named for the host of the thrips on which the mite was collected.

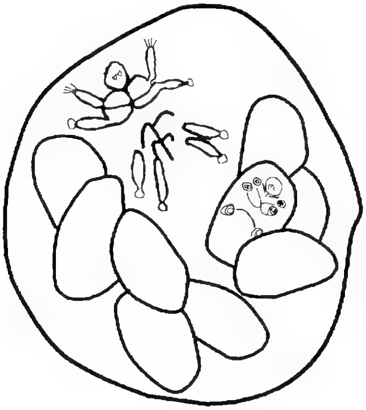
Remarks.—Specimens from Egypt differed from those from Puerto Rico in having setae sc_1 slightly shorter (range 28–32 vs. 36–41). We regard this difference as intraspecific variation.

Elbadry and Tawfik (1966) reported on



Figs. 63–69. *Adactylidium ficorum*, male. 63, Dorsal. 64, Serrate seta on D. 65, Ventral. 66–69, Legs I–IV.

the life cycle of this species and gave brief descriptions of female, male and larva, but they did not name the species. Those authors also referred to "nymphs," however, their figure 5B, indicated as a nymph, is a pharate male within a larval cuticle. Specimens examined in this study were vouchers from the studies of Elbadry and Tawfik (1966) located in the collection of the late Dr. E. A. Cross, now housed in FSCA, and that of Abreu (1982) deposited in OSAL. The specimens of Elbadry and Tawfik in-



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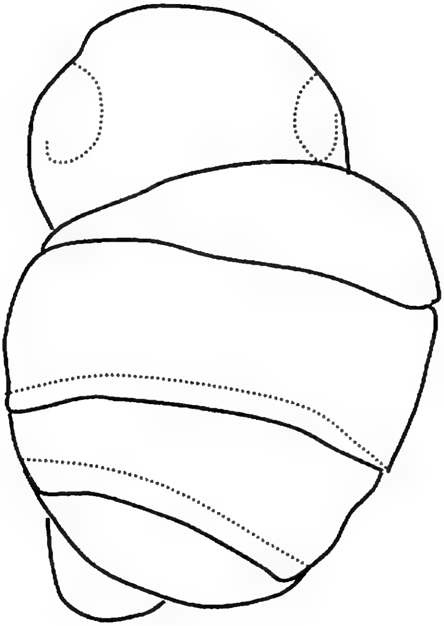

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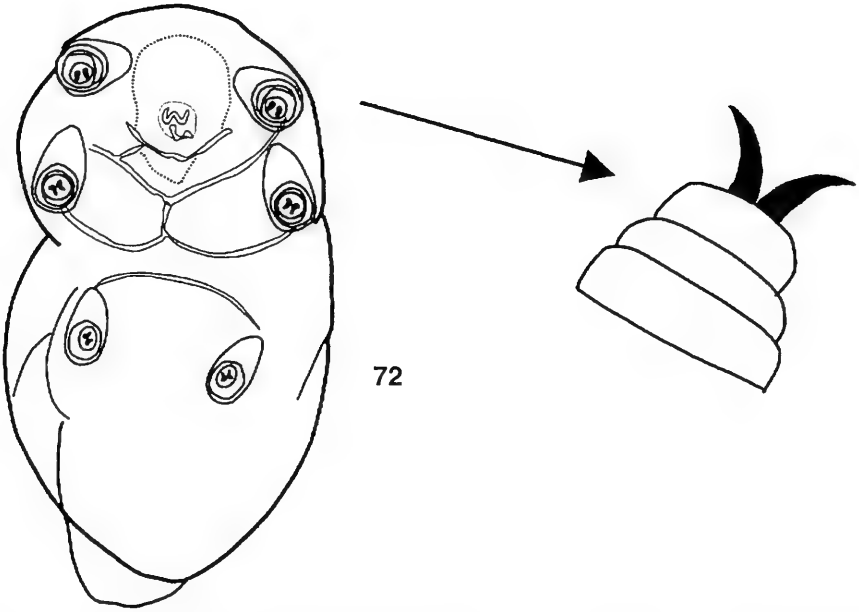

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Figs. 70–72. *Adactylidium ficorum.* 70, Physogastric female. 71, Larva, dorsal. 72, Larva, ventral, with detail of leg I.

cluded non-physogastric females as well as five physogastric females with larvae inside. No males were found on the slides, each of which bore multiple specimens. The slides do not bear specific locality information, nor is such information indicated in their publication on the biology of the species.

Adactylidium flechtmanni Goldarazena and Ochoa, new species

(Figs. 73–81)

Diagnosis.—The female of *A. flechtmanni* can be distinguished by the presence of seta *1b* and the absence of seta *4b*.

Description.—*Female:* Idiosoma (Fig. 73–75) oval, length of holotype and range of four paratypes 135 (132–144), width 91 (91–100). Gnathosoma with dorsal and ventral subcapitular setae, and palpal tibiotarsal setae short, setiform. Cheliceral stylets thick and curved. Pharynx long, dense, with thin muscular walls. Gnathosomal apodeme without medial projections. Stigma located inside the podocephalic opening, main tracheal trunks with unsclerotized atria and with undivided broad postatrial structures (Fig. 77).

Dorsum (Fig. 73). Prodorsal setae sc_1 22 (20–23) and sc_2 15 (14–16) slender and simple. Base of sc_1 anteromedial of sc_2. Tergite C with setae c_1 15 (15–16) and setae c_2 14 (14–15) simple, slender and subequal in length; base of c_1 and c_2 nearly transversally aligned. Tergite D with setae *d* 17 (16–18) slender, simple, serrate, longer than half the length of segment (Fig. 74). Tergite E–F with setae *e* 16 (14–16) and setae *f* 17 (14–17) slender, simple and subequal in length. Tergite H with h_1 7 (7–8) and h_2 7 (7) short, stout and subequal in length. All dorsal setae are shorter than length of each segment.

Venter (Fig. 75). Apodemes I short, not united with prosternal apodeme; prosternal apodeme fragmented distally; apodemes II conspicuous and curved, not united with prosternal apodeme. Prosternal apodeme not united with sejugal apodeme; sejugal apodeme divided in two equal curved sections and less sclerotized than prosternal apodeme. Apodemes III as long as apodemes IV, conspicuous and curved, weakly united with poststernal apodeme; apodemes IV not united with poststernal apodeme. Poststernal apodeme weak, divided distally, with a very small separate posterior fragment. Apodemes V present, fused medially. Setae *1b* 3 (3–5) shorter than *2a* 10 (10–13); coxal fields III with two pairs *3a* 14 (14–16) and *3c* 15 (14–16), and coxal fields IV with one pair *4c* 13 (13–14). One pair of *ag* setae present 11 (11–13), aggenital plate smooth.

Legs (Figs. 78–81). Leg I 37 (36–37), leg II 55 (55–57), leg III 60 (57–60), and leg IV 57 (56–59). Number of setae and solenidia on femur, genu, tibia, and tarsus, respectively: leg I: 3–4–6+9 (ω); leg II: 3–3–4–6 (ω); leg III: 2–1 (*l′* absent)–4–4; leg IV: 1–1–4–4. Solenidion ω of tibiotarsus I slightly shorter and wider than solenidion ω of tarsus II, both rodlike. Tibiotarsus I with setae *ft′*, *ft″*, *tc′*, and *tc″* stout, cylindrical, and subequal in length. A few specimens bear a small, spine-like, ventroapical projection.

Male: Unknown.

Type, host, and locality data.—Holotype ♀ and one paratype ♀ (ESALQ Zool. No. 26), collected from *Gynaikothrips ficorum* Marchal on *Ficus microcarpa,* BRAZIL: Recife, Pernambuco October 1966, G. P. Arruda, and 11 paratype ♀, same host and locality, 30 November 1966, C. H. W. Flechtmann, November 30, 1966. The holotype and one paratype are mounted on a single slide. The holotype is the lower specimen when the slide is viewed with the labels upright. Holotype and two paratypes deposited in ESALQ and ten paratypes (on 3 slides) deposited in FSCA.

Etymology.—This species is dedicated to Dr. Carlos H. W. Flechtmann, Universidade de São Paulo, in recognition of his contributions to the knowledge of mites in Latin America.

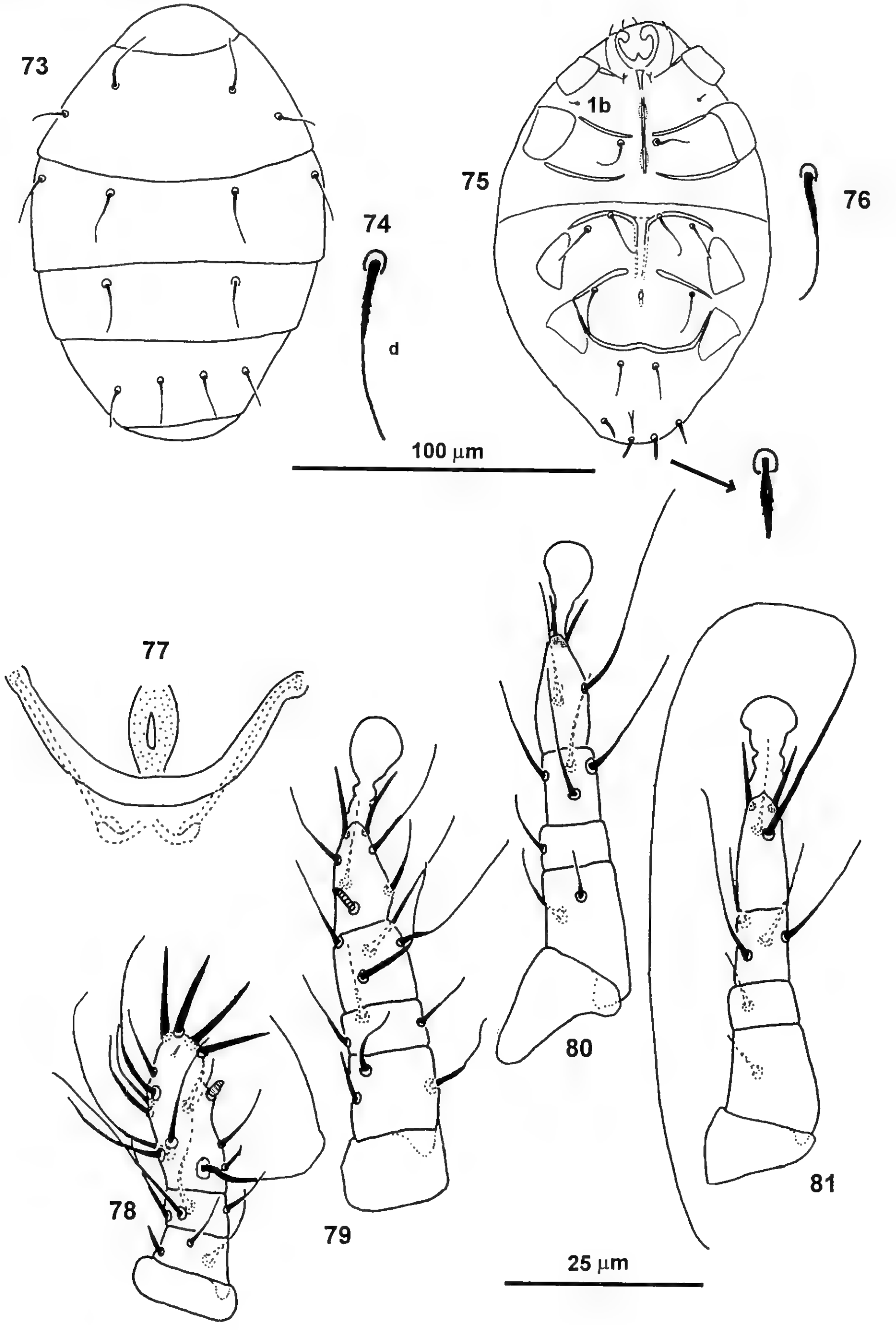
Remarks.—These specimens were misidentified as *A. beeri* by Cross in 1967 (Flechtmann, 1976), probably because of the similarities in body and dorsal setae shape.

Adactylidium irregularis Goldarazena and Ochoa, new species

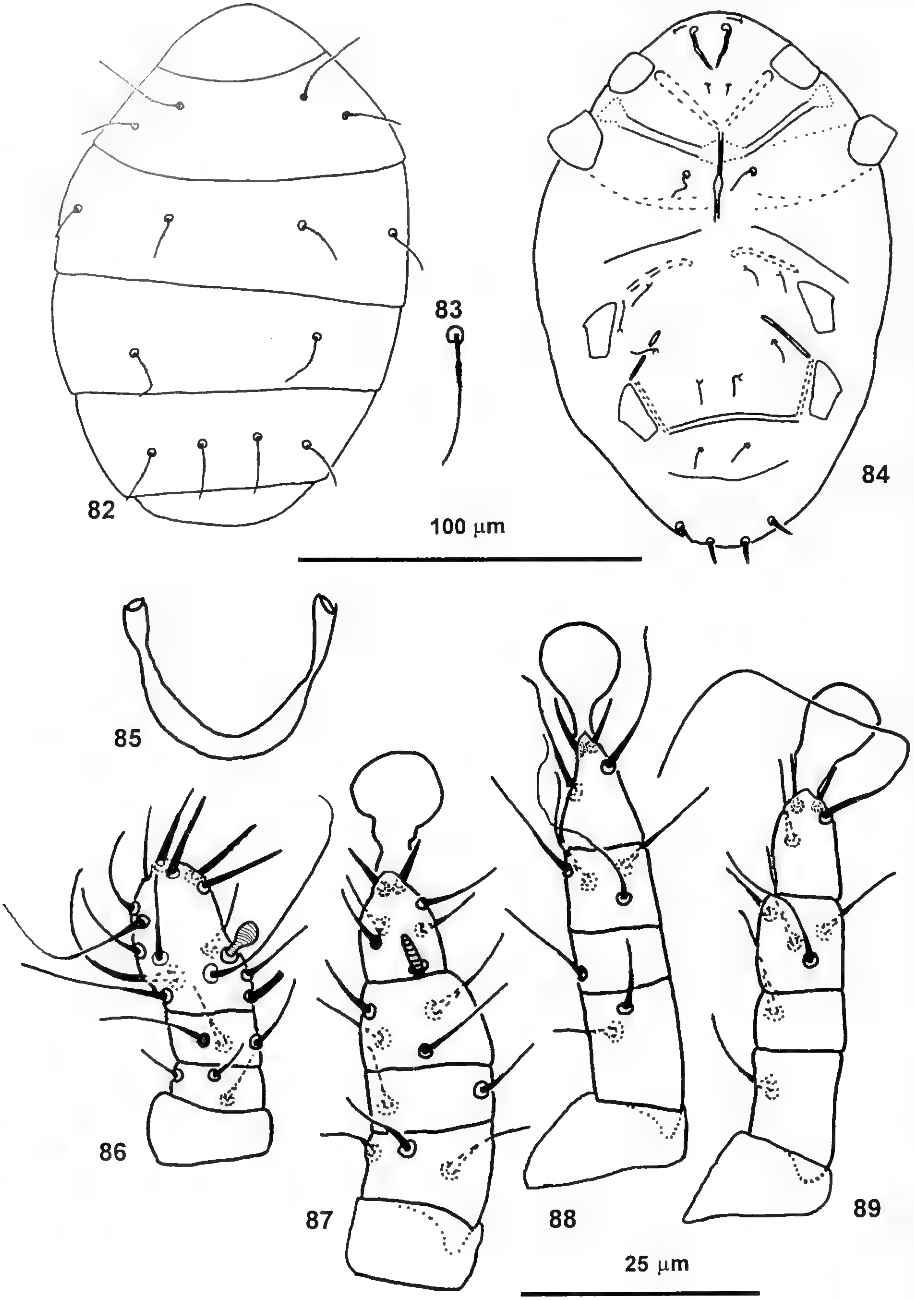
(Figs. 82–89)

Diagnosis.—The female of *A. irregularis* can be distinguished by the presence of seta *4b* and slightly serrate dorsal setae.

Description.—*Female:* Idiosoma (Figs.



Figs. 73–81. *Adactylidium flechtmanni,* female. 73, Dorsal. 74, Dorsal seta on D. 75, Ventral. 76, Ventral seta. 77, Pharynx, tracheal trunks and gnathosomal apodeme. 78–81, Legs I–IV.



Figs. 82–89. *Adactylidium irregularis,* female. 82, Dorsal. 83, Dorsal seta. 84, Ventral. 85, Gnathosomal apodeme. 86–89, Legs I–IV.

82–84) oval, length of holotype and range of two paratypes 153 (150–158), width 90 (85–93). Gnathosoma reduced with dorsal and ventral subcapitular setae, proximal pair inconspicuous, palpal tibiotarsal seta not observed. Cheliceral stylets relatively straight. Pharynx long, dense, with thin muscular walls. Gnathosomal apodeme without medial projections (Fig. 85). Stigma located inside the podocephalic opening, main tracheal trunks and atria inconspicuous.

Dorsum (Fig. 82). Prodorsal setae sc_1 24 (23–28) and sc_2 23 (20–26) slender and simple. Base of sc_1 anteromedial of sc_2. Tergite C wider than long, with setae c_1 11 (9–13) and setae c_2 13 (10–14) simple, and subequal in length; base of c_1 and c_2 nearly transversally aligned. Tergite C and D subequal. Tergite D wider than long, with setae *d* 15 (13–15). Tergite E–F with setae *e* 9 (9–11) and *f* 10 (9–12) short, and subequal in length. Tergite H with two pairs of subequal, short, stout setae; h_1 7 (6–7), h_2 7 (6–7). Dorsal setae of C, D, E and F are setiform, slightly serrate basally (Fig. 83).

Venter (Figs. 84). Apodemes difficult to observe in strongly cleared specimens. Following structures were observed: Apodemes I united with prosternal apodeme; prosternal apodeme uninterrupted; apodemes II conspicuous and slightly curved, united with prosternal apodeme. Sejugal apodeme curved. Apodemes III reduced apparently less sclerotized than apodemes IV; apodemes IV short and well sclerotized. Poststernal apodeme not observed. Apodemes V present. Setae *1b* absent; *2a* 6 (6–7); coxal fields III with two pairs *3a* 9 (8–10) and *3c* 9 (8–10), and coxal fields IV with two pairs *4b* 9 (9–10) and *4c* 9 (9–10). One pair of *ag* setae present 8 (8–9), aggenital plate smooth.

Legs (Figs. 86–89). Leg I 30 (30–32), leg II 51 (50–51), leg III 58 (53–58), and leg IV 56 (52–56). Number of setae and solenidia on femur, genu, tibia, and tarsus, respectively: leg I: 3–3 (*v′* absent)–6+9 (ω); leg II: 3–2 (*v′* absent)–4–6 (ω); leg III: 2–1 (*l′* absent)–4–4; leg IV: 1–1–4–4. Solenidion ω of tibiotarsus I capitate, slightly shorter than solenidion ω of tarsus II. Solenidion ω of tarsus II rodlike. Tibiotarsus I with setae *ft′*, *ft″*, *tc′*, and *tc″* stout, cylindrical, and subequal in length, ventral subapical indentation not observed.

Male: Unknown.

Type, host, and locality data.—Holotype ♀ and three paratype ♀ collected from unidentified thrips on *Cattleya* sp. (Orchidaceae) COLOMBIA: intercepted at Washington D.C., USA, 25 June 1937, Limber & Wood coll., E. Q.-A 42303, Lot. 37-19412. Holotype and one paratype deposited in USNM, two paratypes deposited in FSCA.

Etymology.—This species is named for the variation in the shape of the solenidia and sclerotization of the ventral apodemes.

Remarks.—All specimens of *A. irregularis* were remounted in October 1959 and are overly cleared, making observation of internal sclerotization difficult.

Adactylidium lindquisti **Jordana and Goldarazena, new species**

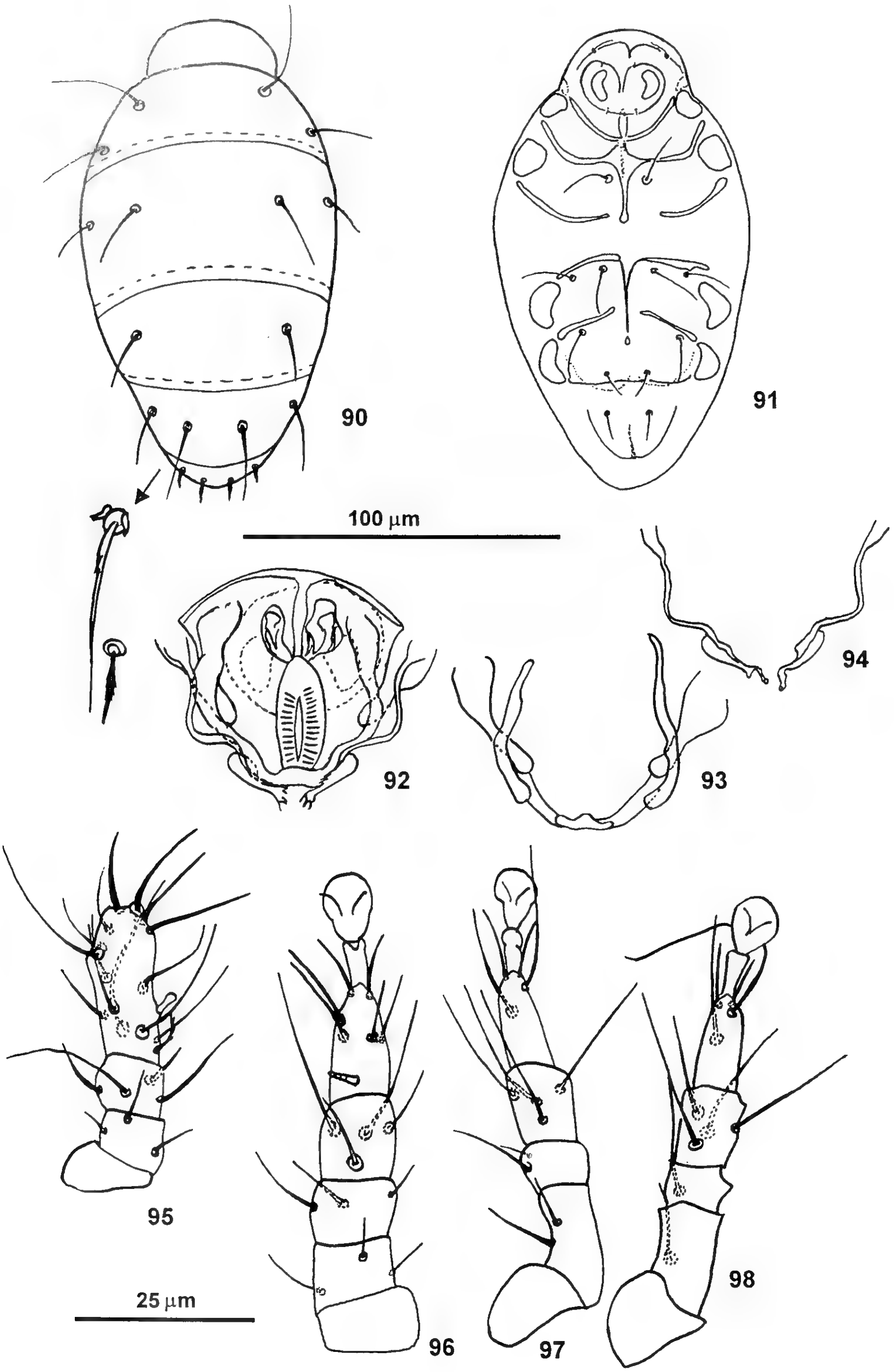
(Figs. 90–98, 142–145)

Adactylidium moundi: Goldarazena, Jordana, and Zhang 1997: 261 (in part).

Diagnosis.—The female of *A. lindquisti* can be distinguished by the absence of setae *pv′* and *pv″* on tibiotarsus I.

Description.—*Female:* Idiosoma (Figs. 90–91) elongate, ovoid, length of holotype and paratype 145–150, width 82–100. Gnathosoma with dorsal and ventral subcapitular setae, and palpal tibiotarsal setae conspicuous (Fig. 144). Cheliceral stylets thick. Pharynx very long, dense, with striated walls (Fig. 92). Gnathosomal apodeme with medial projections (Figs. 92–93). Stigma located inside the podocephalic opening, main tracheal trunks with unsclerotized atria, and with divided broad postatrial structures (Fig. 94).

Dorsum (Figs. 90, 143). Prodorsal setae sc_1 (40–41) and sc_2 (20–21) slender and slightly serrate basally. Insertion of sc_1 anteromedial of sc_2. Tergite C with setae c_1 (26–27) and setae c_2 (15–16) similar in form to sc_2. Insertion of setae c_1 and c_2 nearly transversally aligned. Tergite D shorter than tergite C, wider than long with setae *d* (18). Tergite E–F with setae *e* 24 and setae *f* (27–30). Tergite H with two pairs of subequal, short and stout setae; h_1 (7–10), h_2 (5). All dorsal setae are slightly



Figs. 90–98. *Adactylidium lindquisti,* female. 90, Dorsal. 91, Ventral. 92, Pharynx, gnathosomal apodeme and tracheal trunks. 93, Gnathosomal apodeme. 94, Tracheal trunks. 95–98, Legs I–IV.

serrate basally. Body without reticulate sculpturing pattern but with fine punctation.

Venter (Fig. 91). Apodemes I well developed, united with prosternal apodeme; prosternal apodeme uninterrupted and slender; apodemes II well developed, united with prosternal apodeme. Prosternal apodeme not united with sejugal apodeme; sejugal apodeme divided in two equal curved sections. Apodemes III longer than apodemes IV, conspicuous and curved, united with poststernal apodeme. Apodemes IV not united with poststernal apodeme. Poststernal apodeme fragmented distally. Apodemes V reduced. Seta *1b* absent; *2a* (16); coxal fields III with two pairs *3a* (18) and *3c* (14), and coxal fields IV with two pairs of setae *4b* (11) and *4c* (16). One pair of *ag* setae present (11), aggenital plate smooth.

Legs (Figs. 95–98, 142, 145). Leg I (37–39), leg II (65–70), leg III (65–72), and leg IV (65–72). Number of setae and solenidia on femur, genu, tibia, and tarsus, respectively: leg I: 3–4–6+9 (ω); leg II: 3–3–4–6 (ω); leg III: 2–2–4–4; leg IV: 1–1–4–4. Solenidion ω of tibiotarsus I slightly clavate, shorter and wider than rodlike solenidion ω of tarsus II. Tibiotarsus I with ventroapical indentation; setae *ft′*, *ft″*, *tc′*, and *tc″* stout, cylindrical, and subequal in length.

Male: Unknown.

Type, host, and locality date.—Holotype ♀ and one paratype ♀ collected from the abdomen of *Megalothrips bonannii* Uzel on dead branch of *Quercus rotundifolia* Lam., SPAIN: Navarra, Olleta, 16 March 1995, A. Goldarazena, deposited at MZUNAV.

Etymology.—This species is dedicated to Dr. Evert E. Lindquist, Agriculture and Agri-Food Canada for his contribution to the knowledge of mite systematics.

Remarks.—These specimens were misidentified as *A. moundi* by Goldarazena et al. (1997); in *A. moundi* setae *pv′* and *pv″* on tibiotarsus I are present.

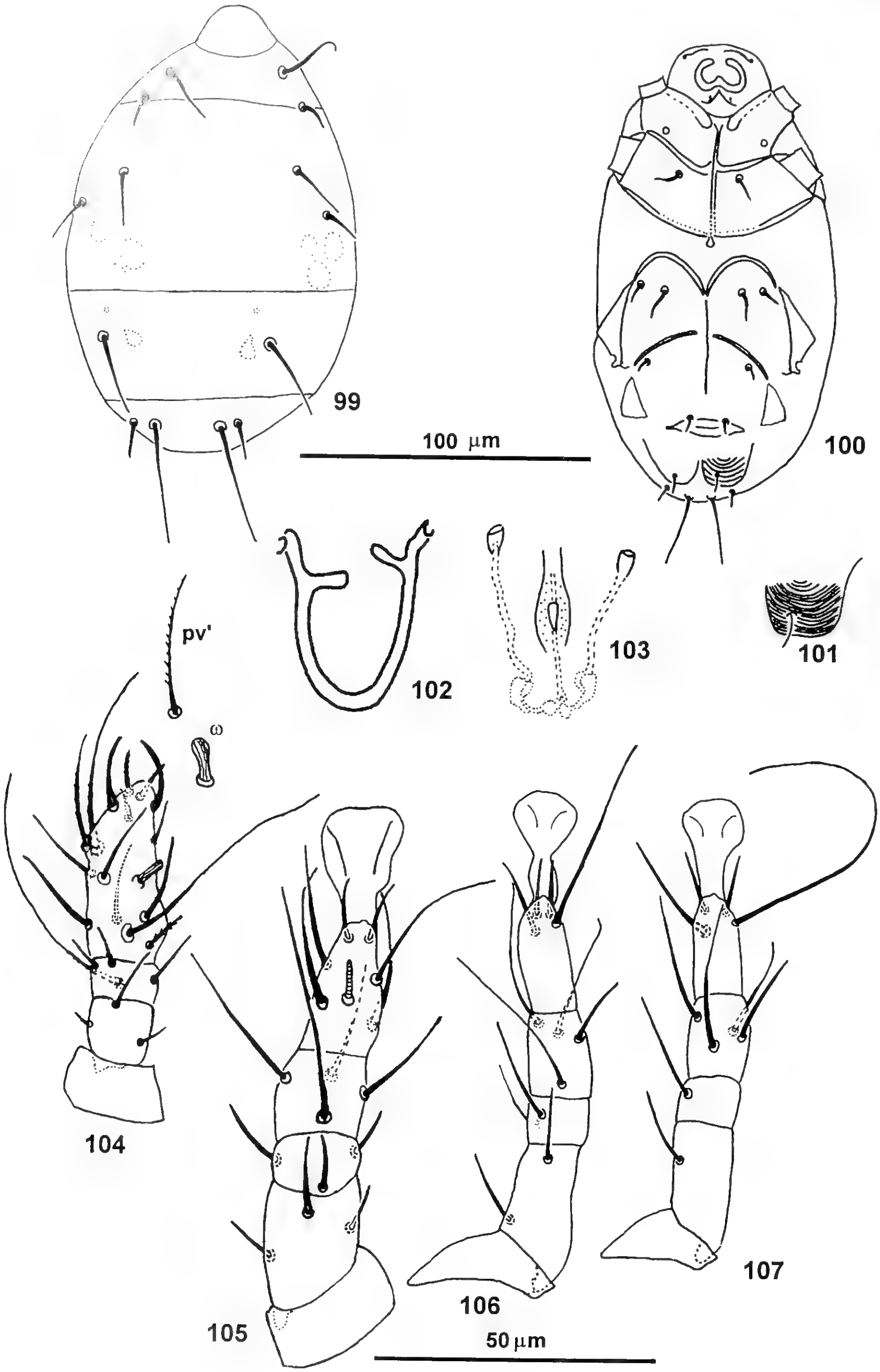
Adactylidium mooniensis Goldarazena and Jordana, new species
(Figs. 99–110)

Diagnosis.—Adult females of *A. mooniensis* can be distinguished by having setae h_1 about three times longer than h_2 and striations on the aggenital plate.

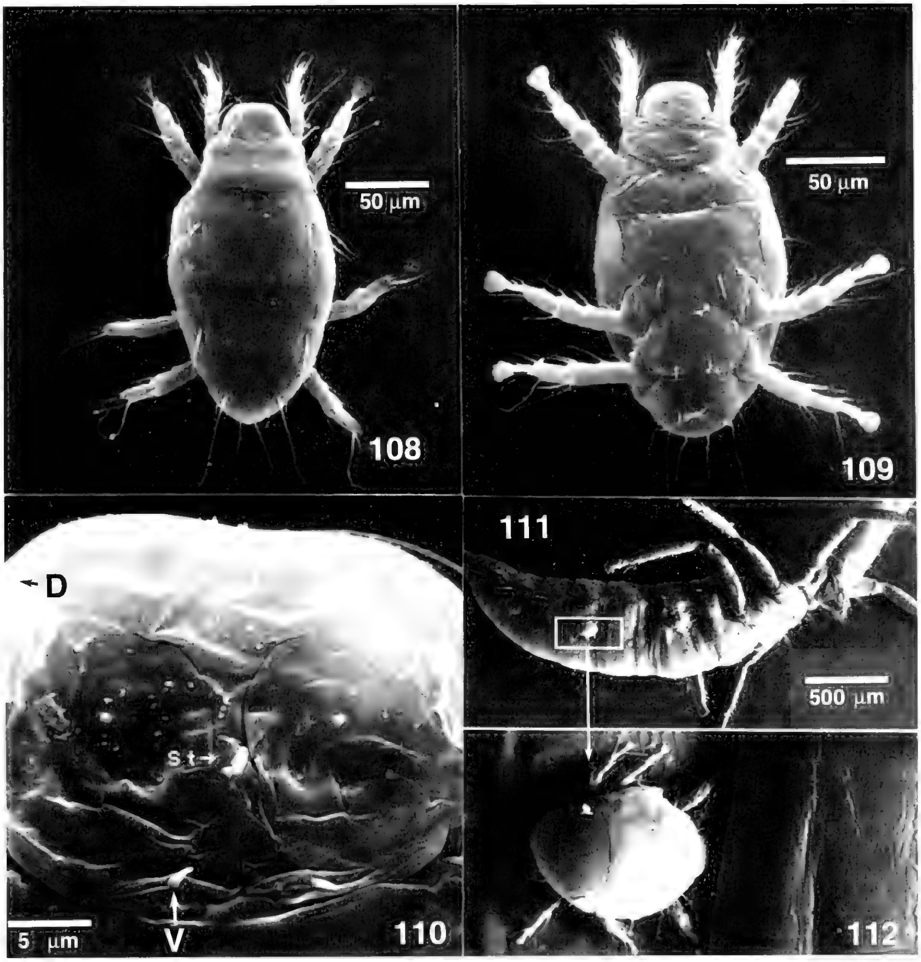
Description.—*Female:* Idiosoma (Figs. 99–100, 108–109) elongated, ovoid, length of holotype and range of three paratypes 165 (165–172), width 92 (89–94). Gnathosoma with dorsal and ventral subcapitular setae (Figs. 100, 110), palpal tibiotarsal setae inconspicuous. Cheliceral stylets curved. Pharynx very long, dense, with thin muscular walls. Gnathosomal apodeme with medial projections (Fig. 102). Stigma located inside the podocephalic opening, main tracheal trunks with long, kidney shaped unsclerotized atria, and undivided broad postatrial structures (Fig. 103).

Dorsum (Figs. 99, 108). Prodorsal setae sc_1 35 (35–38) and sc_2 16 (16–18) slender and simple. Base of sc_1 anteromedial of sc_2. Tergite C as long as wide, with setae c_1 28 (28–30) and setae c_2 22 (22–23) simple; base of c_1 anteromedial to c_2. Tergite D wider than long, with setae *d* 25 (25–27) setiform. Tergite E–F with setae *e* 15 (15–17) shorter than setae *f* 42 (42–45). Tergite H with two pairs of setae, h_1 25 (25–28) three times longer than h_2 7 (6–7). All dorsal setae simple and setiform. Body with reticulate pattern.

Venter (Figs. 100, 109). Apodemes I present, not fused with prosternal apodeme; apodemes II conspicuous and curved, united with prosternal apodeme. Sejugal apodeme united with prosternal apodeme; prosternal apodeme uninterrupted and extending beyond sejugal apodeme. Apodemes III well developed weakly fused with poststernal apodeme; apodemes IV well sclerotized not united with poststernal apodeme. Poststernal apodeme slender, uninterrupted distally. Apodemes V reduced. Setae *1b* absent but alveoli visible; *2a* 11 (10–11); coxal fields III with two pairs *3a* 9 (8–10) and *3c*



Figs. 99–107. *Adactylidium mooniensis,* female. 99, Dorsal. 100, Ventral. 101, Striation on aggenital plate. 102, Gnathosomal apodeme. 103, Pharynx and tracheal trunks. 104–107, Legs I–IV.



Figs. 108–110. Scanning electron micrographs of female *Adactylidium mooniensis*. 108, Dorsal. 109, Ventral. 110, Detail of gnathosoma; st = stylets, D = dorsal palpal setae, V = ventral palpal setae. 111–112, Females of *A. moundi* on host thrips, *Compsothrips albosignatus*.

11 (11–12), and coxal fields IV with two pairs, seta *4b* 6 (6–7) and *4c* 8 (8–9). One pair of *ag* setae present 5 (5–6), aggential shield striate (Fig. 101).

Legs (Figs. 104–107). Leg I (53–55), leg II (66–69), leg III (86–88), and leg IV (77–79). Empodium of leg II very long and expanded similar in length to the tarsus. Number of setae and solenidia on femur, genu, tibia, and tarsus, respectively: leg I: 3–4–6+9 (ω); leg II: 3–3–4–6 (ω); leg III: 2–2–4–4; leg IV: 1–1–4–4. Solenidion ω of tibiotarsus I clavate and slightly shorter than solenidion ω of tarsus II, both thin. Solenidion on tarsus two rodlike. Tibiotarsus I with setae *tc′* and *tc″*, *ft′* and *ft″* stout, and cylindrical; *ft′* and *ft″* twice as long as *tc′* and *tc″*; ventroapical indentation not observed (Figs. 104).

Male: Unknown.

Type, host, and locality data.—Holotype, a non-gravid ♀, and ten paratype ♀ (5 on slides in Hoyer's medium, and 5 on SEM stubs), from *Lichanothrips* sp., AUSTRALIA: Queensland, Moonie, 28 September 1997, L. A. Mound and A. Goldarazena; two paratype ♀ ex *Idolothrips spectrum* Haliday male on dead branch of *Eucalyptus* sp., same data. Additional material: one ♀ collected from *Mecynothrips hardyi* Priesner, female, in dead hanging leaves of a branch of *Acacia harpophylla* Benth., same locality, 3 October 1997 L. A. Mound and A. Goldarazena, deposited in Australian National Insect Collection, CSIRO Entomology, Canberra. Holotype and one paratype deposited in CSIRO, one paratype deposited in USNM, one paratype BMNH and three paratypes on slides and five on SEM stubs in MZUNAV.

Etymology.—This species is so named for the town, Moonie, Australia, where it was collected.

Adactylidium morazae Goldarazena and Ochoa, new species

(Figs. 113–119)

Diagnosis.—The female of *A. morazae* can be distinguished by the combination of the presence of setae *1b* on coxal fields I, posterior indentations on the gnathosomal apodeme, and reduction of the poststernal apodeme to a small ellipsoidal nodule.

Description.—*Female:* Idiosoma (Figs. 113–114) oval, length of holotype and range of three paratypes 125 (121–132), width 76 (73–79). Gnathosoma reduced with dorsal and ventral subcapitular setae, proximal pair inconspicuous, palp tibiotarsal seta not observed. Cheliceral stylets curved. Pharynx long, dense, with thin muscular walls. Gnathosomal apodeme with a pair of indentations basally (Fig. 115). Stigma located inside the podocephalic opening, main tracheal trunks with sclerotized atria and undivided broad postatrial structures (Fig. 115).

Dorsum (Fig. 113). Prodorsal setae sc_1 26 (25–30) and sc_2 20 (20–25) slender and simple. Base of sc_1 anteromedial of sc_2. Tergite C longer than wide, with setae c_1 22 (22–24) and c_2 20 (19–21) simple, and subequal in length; base of c_1 and c_2 nearly transversally aligned. Tergite C wider than D. Tergite D longer than wide, with setae *d* 30 (30). Tergite E–F with setae *e* 26 (25–28) and *f* 24 (21–28) subequal in length. Tergite H with two pairs of subequal, long setae h_1 11 (10–12), h_2 14 (10–14). All dorsal setae setiform and simple.

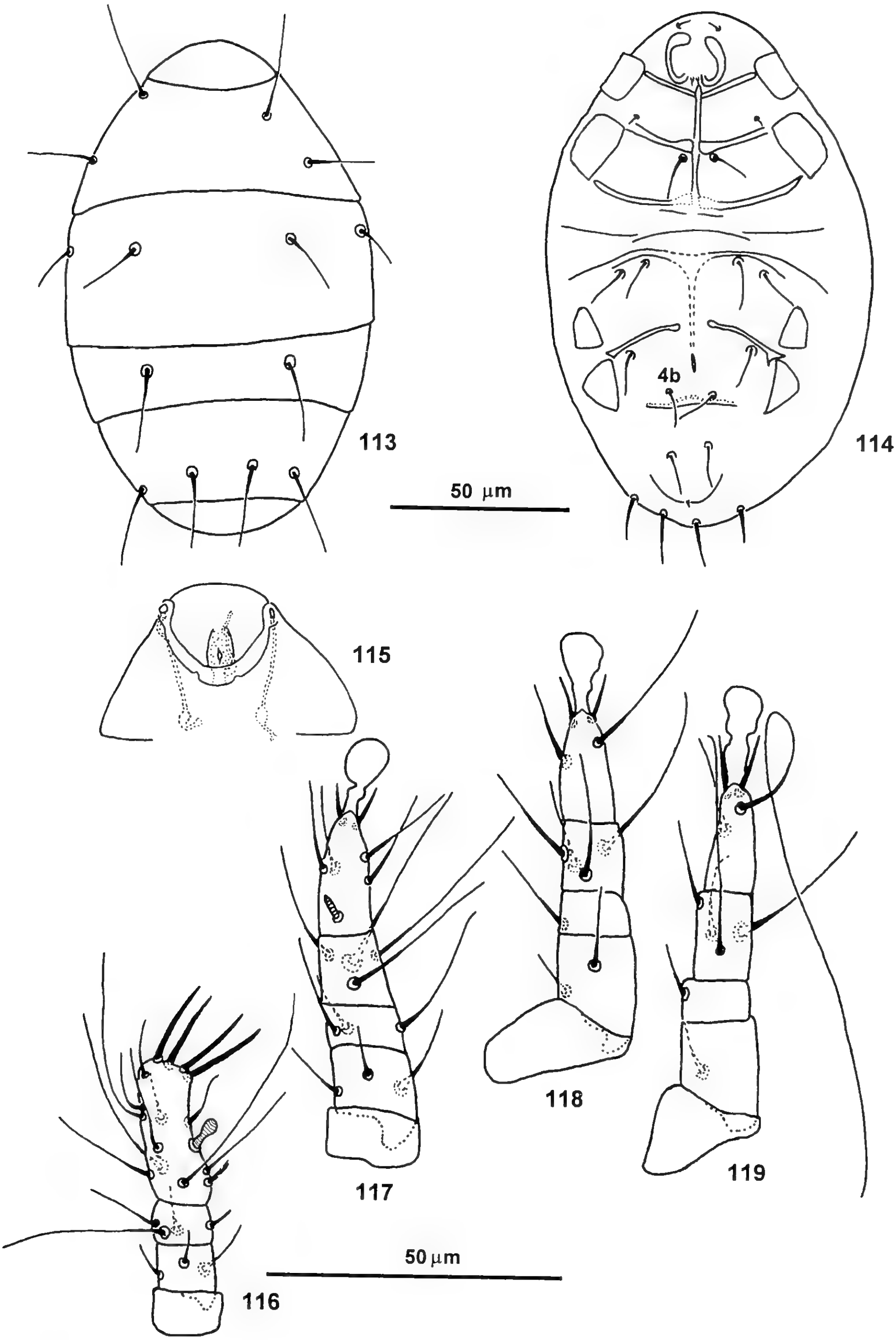
Venter (Fig. 114). Apodemes I present, united with prosternal apodeme; prosternal apodeme uninterrupted; apodemes II conspicuous and curved, united with prosternal apodeme. Prosternal apodeme not extending posteriorly. Sejugal apodeme weakly joined with prosternal apodeme and reduced to two sclerotized lateral fragments. Apodemes III well developed forming a weak juncture with poststernal apodeme; apodemes IV well sclerotized not united with poststernal apodeme. Poststernal apodeme reduced to a small ellipsoidal nodule distally. Apodemes V reduced. Setae *1b* present 2 (2–3); *2a* 15 (14–16); coxal fields III with two pairs *3a* 15 (15–16) and *3c* 15 (10–15), and coxal fields IV with two pairs *4a* 11 (10–11) and *4c* 13 (13–15). One pair of *ag* setae present 13 (12–14), aggenital plate smooth.

Legs (Figs. 116–119). Leg I 32 (30–34), leg II 54 (50–53), leg III 56 (55–57), and leg IV 55 (53–55). Number of setae and solenidia on femur, genu, tibia, and tarsus, respectively: leg I: 3–4–6+9 (ω); leg II: 3–3–4–6 (ω); leg III: 2–1 (*l′* absent)–4–4; leg IV: 1–1–4–4. Solenidion ω of tibiotarsus I capitate, slightly shorter than rodlike solenidion ω of tarsus II. Tibiotarsus I with ventroapical indentation, and setae *ft′*, *ft″*, *tc′*, and *tc″* stout, cylindrical, and subequal in length.

Male: Unknown.

Type, host, and locality data.—Holotype ♀ and 2 paratype ♀ from *Leptothrips distalis* (Hood) on *Artemisia tridentata* Nutt., USA: California, Alpine Co. Markleeville, Carson River Bridge, 13 September, 1969 T. Kono and M. S. Wasbauer, No 69J18-28, and one paratype ♀ on thrips, USA: California, Inyo Co., Benton, 13 September, 1969, T. Kono and M. S. Wasbauer, No 69J3-8. Holotype and two paratypes deposited in FSCA, one paratype deposited in USNM.

Etymology.—This species is dedicated to



Figs. 113–119. *Adactylidium morazae,* female. 113, Dorsal. 114, Ventral. 115, Pharynx, tracheal trunks and gnathosomal apodeme. 116–119, Legs I–IV.

Dr. M. L. Moraza, University of Navarra, for her contribution to Spanish acarology.

Adactylidium rumanicus Jordana and Goldarazena, new species
(Figs. 120–128)

Diagnosis.—The female of *A. rumanicus* can be distinguished by the presence of 2 setae on femur II and 3 triangular projections on the pseudanal plate.

Description.—*Female:* Idiosoma (Figs. 120, 122) oval, length of holotype 160, width 110. Gnathosoma rounded, with dorsal and ventral subcapitular setae conspicuous, palp tibiotarsal setae not observed. Cheliceral stylets thick. Pharynx very long, dense, with punctate walls (Fig. 123). Gnathosomal apodeme with small projections (Fig. 123). Stigma located inside podocephalic opening, main tracheal trunks with unsclerotized atria, and with divided broad postatrial structures (Fig. 123).

Dorsum (Fig. 120). Prodorsal setae sc_1 (40) and sc_2 (30) slender. Insertion of sc_1 anteromedial of sc_2. Tergite C distinctly wider than long, with setae c_1 (30) and setae c_2 (20) slender. Insertion of setae c_1 and c_2 nearly transversally aligned. Tergite D wider than long with setae *d* (20). Tergite E–F with setae *e* (17) and setae *f* (20). Tergite H with four, short, stout serrated setae; h_1 (7), h_2 (5) (Fig. 121). All other dorsal setae smooth. Body without reticulate sculpturing pattern but with punctation.

Venter (Fig. 122). Apodemes I poorly developed, not united with prosternal apodeme; prosternal apodeme uninterrupted and slender; apodemes II well developed, united with prosternal apodeme. Prosternal apodeme not united with sejugal apodeme; sejugal apodeme divided in two equal curved sections. Apodemes III slightly longer than apodemes IV, conspicuous and curved, united with poststernal apodeme. Apodemes IV not united with poststernal apodeme. Poststernal apodeme not fragmented distally. Apodemes V reduced. Setae *1b* absent; *2a* (12); coxal fields III with two pairs *3a* (15) and *3c* (12), and coxal fields IV with two pairs of setae *4b* (16) and *4c* (20). One pair of *ag* setae present (10). Anal plate (Fig. 124) with 3 triangular projection distally.

Legs (Figs. 125–128). Leg I (42), leg II (64), leg III (64), and leg IV (64). Number of setae and solenidia on femur, genu, tibia, and tarsus, respectively: leg I: 3–4–6+9 (ω); leg II: 2 (*l′* absent)–3–4–6 (ω); leg III: 2–2–4–4; leg IV: 1–1–4–4. Solenidion ω of tibiotarsus I clavate, shorter and wider than rodlike solenidion ω of tarsus II. Tibiotarsus I with a scale-like ventroapical projection and with setae *ft′*, *ft″*, *tc′*, and *tc″* stout, cylindrical, and subequal in length.

Male: Unknown.

Type, host, and locality data.—Holotype ♀ collected from the abdomen of a male *Megathrips lativentris* (Heeger) on green grasses, ROMANIA: Mehedinti judet, Potile di Fieri (44°41′N, 22°31′E), 21 April 1996, Liliana Vasiliu-Oromulu, deposited in MZUNAV.

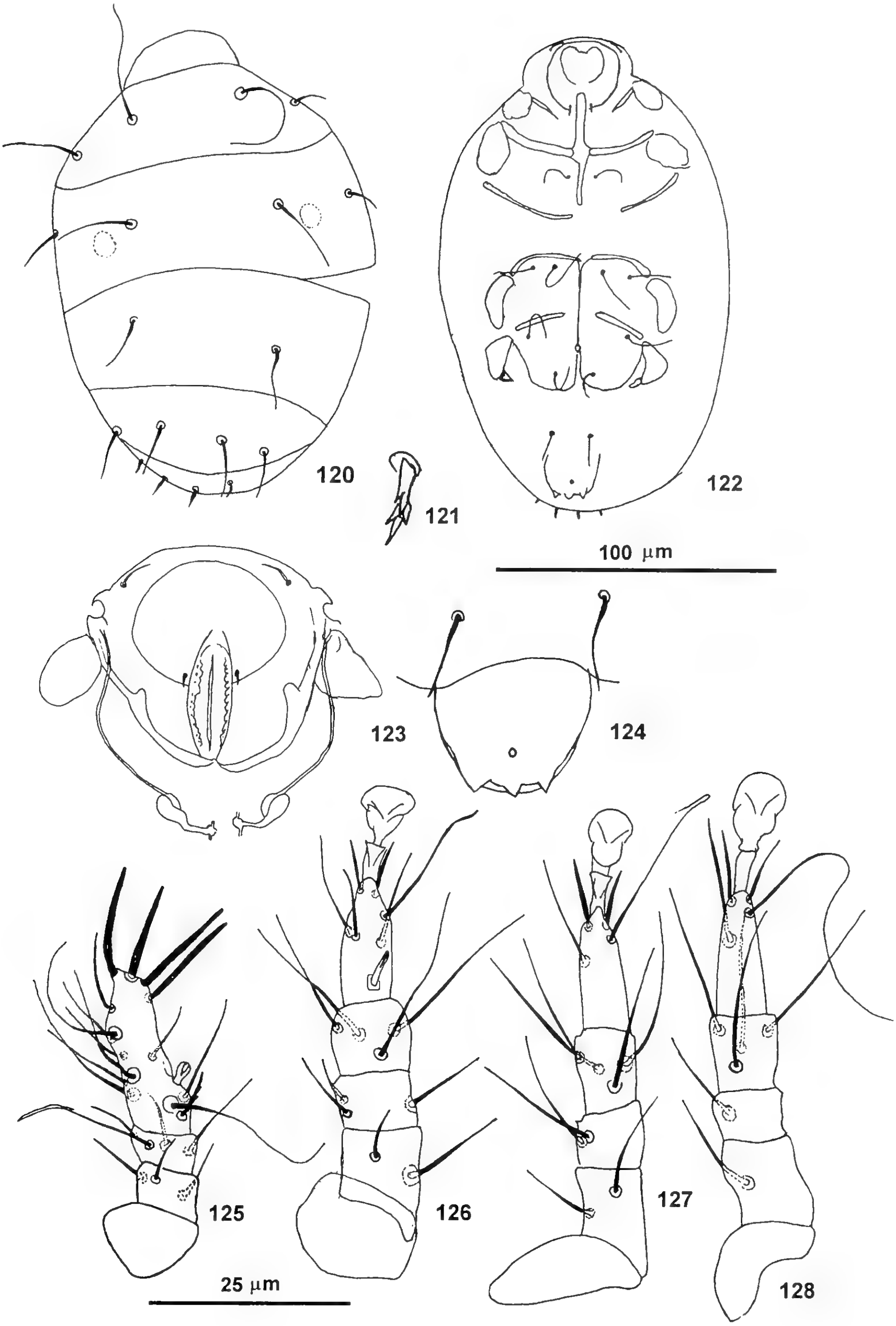
Etymology.—This species is so named for the Country, Romania, where it was collected.

Adactylidium smileyi Goldarazena and Ochoa, new species
(Figs. 129–134)

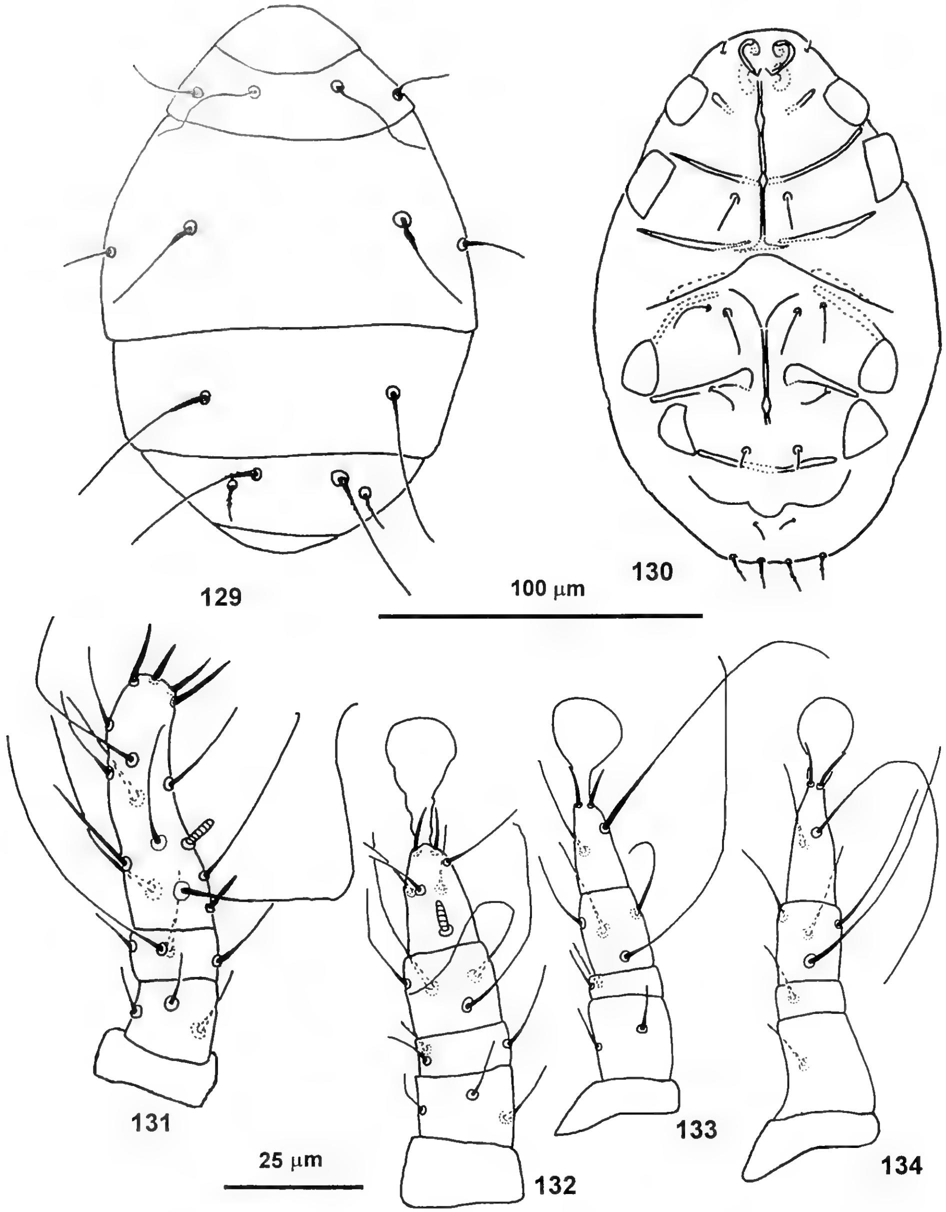
Diagnosis.—The adult female of *A. smileyi* can be distinguished by having setae sc_1 as long as sc_2 and having apodemes V present and well sclerotized.

Description.—*Female:* Idiosoma (Figs. 129–130), oval, length of holotype 170, width 104. Gnathosoma reduced with three pairs of setae, dorsal and ventral subcapitular setae short, palpal tibiotarsal setae inconspicuous. Cheliceral stylets curved. Pharynx longer than wide, with thin striate walls. Gnathosomal apodeme with small medial projections. Stigma located inside the podocephalic opening, main tracheal trunks with rounded unsclerotized atria, and with broad, undivided postatrial structures.

Dorsum (Fig. 129). Prodorsal setae sc_1 (17) and sc_2 (20) slender and simple. Base of sc_1 on the same transverse line as sc_2.



Figs. 120–128. *Adactylidium rumanicus,* female. 120, Dorsal. 121, Seta h_1. 122, Ventral. 123, Pharynx, gnathosomal apodeme and tracheal trunks. 124, Pseudanal segment. 125–128, Legs I–IV.



Figs. 129–134. *Adactylidium smileyi*, female. 129, Dorsal. 130, Ventral. 131–134, Legs I–IV.

Tergite C wider than long, with setae c_1 (35) broadened basally and setae c_2 (17) simple; base of c_1 on the same transverse line to c_2. Tergite D wider than long, with setae *d* (47) setiform. Tergite E–F with setae *f* (62–64) five times longer than serrate setae *e* (12). Tergite H with two pairs of setae subequal in length, h_1 (9), h_2 (7) and serrate. Body with reticulate sculpturing pattern.

Venter (Fig. 130). Apodemes I present, not united with prosternal apodeme; prosternal apodeme uninterrupted barely extending to sejugal apodeme; apodemes II conspicuous and curved, united with prosternal apodeme. Sejugal apodeme reduced to a lateral fragment on each side, not united with prosternal apodeme. Apodemes III present and not united with poststernal apodeme; apodemes IV well sclerotized not united with poststernal apodeme. Poststernal apodeme uninterrupted distally. Apodemes V reduced. Setae *1b* absent; *2a* (14); coxal fields III with two pairs of setae *3a* (15) and *3c* (15), and coxal fields IV with two pairs, seta *4a* (7) and *4c* (9–10). One pair of *ag* setae present (5–6).

Legs (Figs. 131–134). Leg I (48), leg II (69), leg III (88), and leg IV (79). Empodium of leg II as long and wide distally as tarsus II. Number of setae and solenidia on femur, genu, tibia, and tarsus, respectively: leg I: 3–4–6+9 (ω); leg II: 3–3–4–6 (ω); leg III: 2–2–4–4; leg IV: 1–1–4–4. Solenidion ω of tibiotarsus I slightly shorter and wider than solenidion ω of tarsus II, both thin and rodlike. Tibiotarsus I with ventroapical indentation and setae *tc′*, *tc″*, *ft′*, and *ft″* stout and cylindrical; *ft′* and *ft″* longer than *tc′* and *tc″*. Seta *tc″* longer than *tc′*.

Male: Unknown.

Type, host, and locality data.—Holotype ♀, collected from *Megalothrips spinosus* Hood, USA: New York, Tompkins Co., Ithaca, 16 July 1950, deposited in USNM.

Etymology.—This species is dedicated to Mr. Robert L. Smiley, Systematic Entomology Laboratory, USDA, ARS for his contribution to the knowledge of mites.

PHYLOGENETIC ANALYSIS

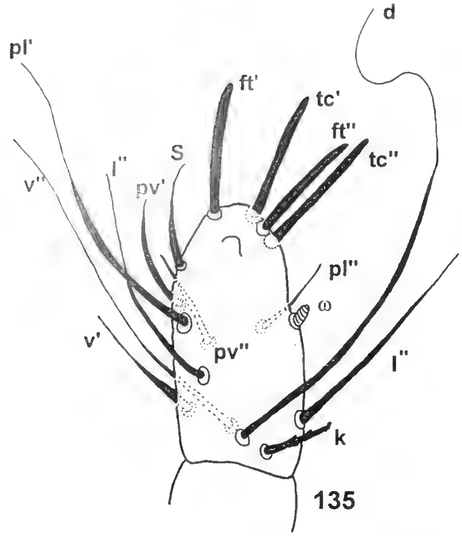
Data for phylogenetic analysis were derived from the external morphology of non-physogastric females. Thirty-seven characters, coded as either binary or multistate, were included in the analysis (Appendix A). In order to polarize character states, we investigated several other genera in the family Acarophenacidae as potential outgroups. Preliminary analyses of acarophenacid phylogeny suggested that the genus *Paradactylidium* was closely related to *Adactylidium*. For the analysis of species relationships within *Adactylidium,* we included both known species of *Paradactylidium, P. micrangulatum* Mahunka, 1975, and *P. oconnori* Goldarazena, Ochoa and Jordana, 1999, as outgroups.

Phylogenetic analysis was performed using PAUP version 4.0b4a for Macintosh (Swofford 2000), a computerized algorithm that produced cladograms on the basis of parsimony. The number of characters and taxa necessitated a branch and bound search.

The analysis produced two shortest trees of length 39.95 (CI: 0.85; RI: 0.87; RC: 0.75), the consensus of which is presented in Fig. 146; character changes are indicated at each internode. The genus *Paradactylidium* is the sister-group of a clade containing all the species of *Adactylidium.* The genus *Adactylidium* is diagnosed by the following derived character states: palps rounded (1.1), palpal tibiotarsal solenidion reduced (2.1), palpal tibiotarsal solenidia anterior to cheliceral opening (3.1), gnathosomal apodeme thickened basally (4.1), vertical setae v_1 absent (5.1), setae c_1 on the same transverse line as c_2 (8.1), setae h_1 as long as h_2 (12.1), apodeme III present (18.0), apodemes V reduced (19.1), claw on leg I absent (26.1), setae *u′* and *u″* absent (29.1), seta *pv′* on tarsus III absent (34.1).

Within the genus *Adactylidium, A. nicolae* is the sister-group of the remaining species. The latter inclusive clade is diagnosed by the following states: seta *f* as long as seta *e* (11.1), seta *l′* on genu III absent (36.1). Within this clade, *A. morazae* and *A. flechtmanni* form a trichotomy with a clade containing the remaining eleven species. These eleven species are characterized by the loss of seta *1b* (23.1) and a rounded tarsal apex (25.2). Within this clade, the lineage comprising *A. ficorum, A. irregularis* and *A. brasiliensis* is sister to the clade comprising the remaining eight species. These three species share the loss of seta *v′* of genu I (31.1), and seta *v′* of genu II (32.1). *Adactylidium irregularis* and *A. brasiliensis* are sister taxa and share the following states: apodemes I not joined with prosternal apodeme (13.1), apodeme III not joined with poststernal apodeme (18.1).

The remaining eight species are characterized by the fragmentation of the post-



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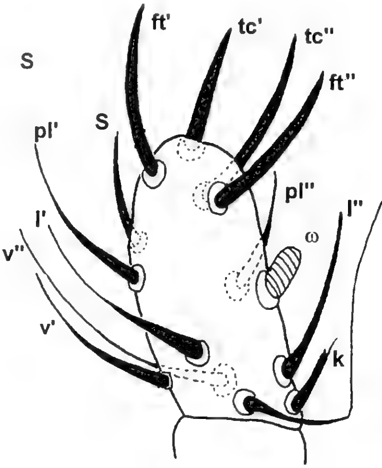

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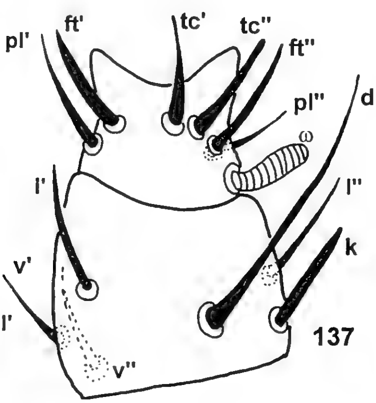

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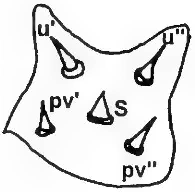

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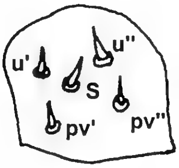

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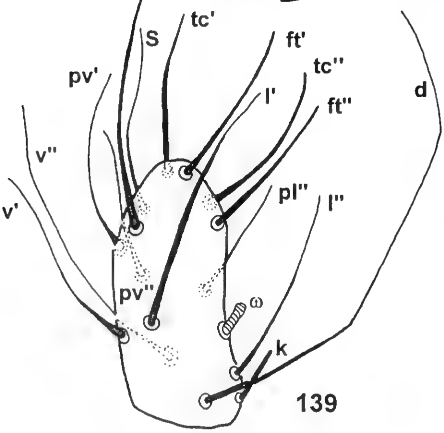

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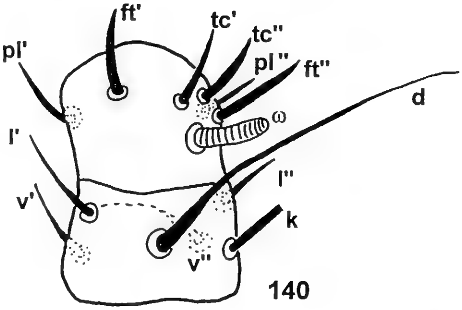

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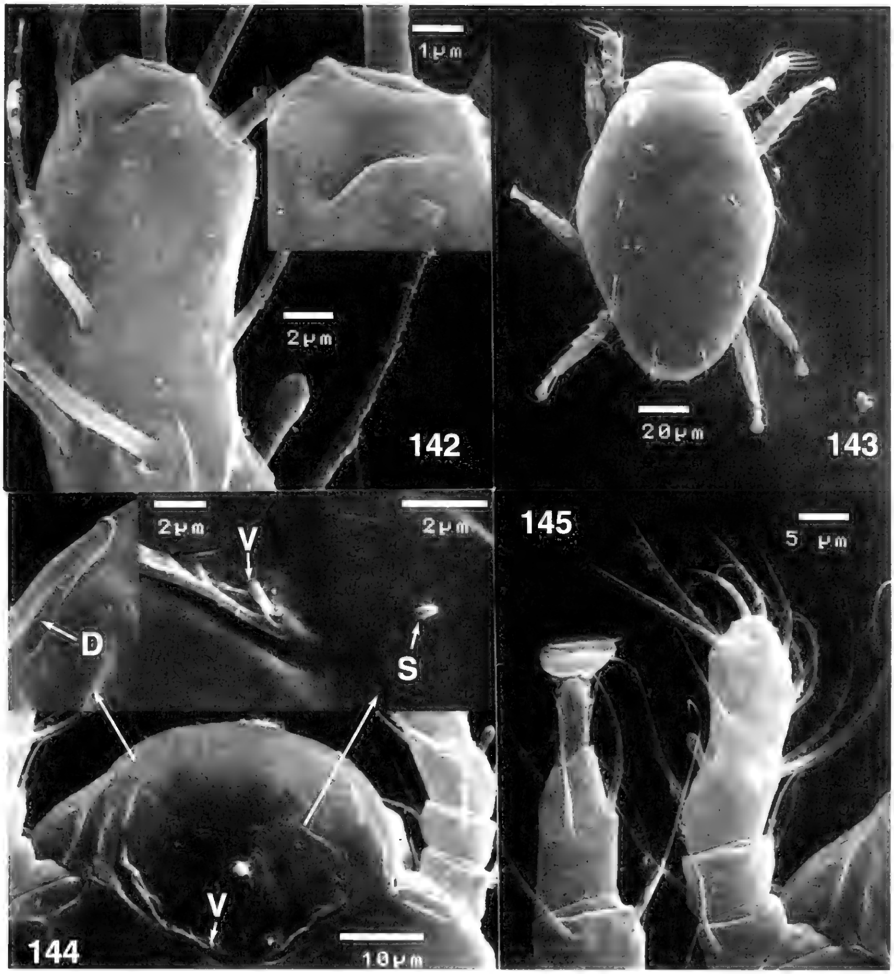
Fig. 135. *Adactylidium. beeri,* female tibiotarsus I, dorsal. 136, Female tarsus I of *Adactylidium brasiliensis.* 137, *Adactylidium crespii,* male tibia-tarsus I, dorsal. 138, *Adactylidium crespii,* male tarsus I, ventral. 139, *Adactylidium nicolae,* female tibiotarsus I, dorsal. 140, *Adactylidium ficorum,* male tibia-tarsus I, dorsal. 141, *Adactylidium ficorum,* male tarsus I, ventral.



Figs. 142–145. SEM of *Adactylidium lindquisti*, female. 142, Ventral view of distal part of tibiotarsus I with detail of subapical indentation. 143, Female, dorsal. 144, Gnathosoma, ventral; D = dorsal palpal seta, V = ventral palpal seta, S = palpal tibiotarsal solenidion. 145: Legs I–II, ventral.

sternal apodeme (20.2). Within this clade, *A. beeri* is sister to the remaining seven species. These seven species are characterized by the blunt apices on the tarsi (25.0) and presence of seta *l′* of genu III (36.0). *Adactylidium moundi* is sister to the remaining six taxa. These six taxa share the following states: gnathosomal apodeme with lateral projections (4.2), and solenidion ω clavate (28.2). *Adactylidium lindquisti* is sister to the remaining five species. The five taxa share the following states: apodeme I not joined with prosternal apodeme (13.1), poststernal apodeme interrupted (20.1), and tarsal apices are pointed (25.1). *Adactylidium rumanicus* is sister to the remaining four species. The remaining four species form a clade characterized by seta *f* at least three times longer than seta *e* (11.0), anterior ventral metapodosomal lobe present (21.1) and setae (*tc*) of tibiotarsus I shorter than setae (*ft*) (27.1). These species form two clades. *Adactylidium crespii* and *A. smileyi* share the position of seta sc_1 on the same transverse line as sc_2 (7.0). The final species, *A. costarricensis* and *A. moonienensis,* share five character states: the position of seta c_1 is well anterior to c_2 (8.2), tergite

Table 1. List of *Adactylidium* species with hosts and localities.

Species	Host	Locality	Reference
A. beeri	Unknown	Michigan, USA	Cross, 1965
A. beeri	*Leptothrips distalis*	California, USA	new record
A. nicolae	Unknown	Bavaria, Germany	Krczal, 1959
A. nicolae	*Hoplothrips ulmi*	Basque Country, Spain	new record
A. moundi	*Compsothrips albosignatus*	Navarre, Spain	Goldarazena et al., 1997
A. costarricensis	*Zactinothrips* sp.	Costa Rica	Goldarazena et al., 1997
A. costarricensis	*Elaphrothrips laevicollis*	Costa Rica	Goldarazena et al., 1997
A. costarricensis	*Actinothrips* sp.	Costa Rica	Goldarazena et al., 1997
A. costarricensis	*Pristothrips albipunctatus*	Costa Rica	Goldarazena et al., 1997
A. costarricensis	*Psalidothrips* sp.	Costa Rica	Goldarazena et al., 1997
A. brasiliensis	*Gynaikothrips ficorum*	Brazil	Flechtmann & De Arruda Pereira, 1967[a]
A. crespii	*Elaphrothrips tuberculatus*	Michigan, USA	new record
A. ficorum	*Gynaikothrips ficorum*	Puerto Rico	Abreu-Rodriguez, 1982[b]
A. ficorum	*Gynaikothrips ficorum*	Egypt	Elbadry & Tawfik, 1966[b]
A. flechtmanni	*Gynaikothrips ficorum*	Brazil	Flechtmann & De Arruda Pereira, 1967[a]
A. irregularis	Unidentified thrips	Colombia	Cross, 1965[b]
A. lindquisti	*Megalothrips bonannii*	Navarre, Spain	Goldarazena et al., 1997[a]
A. mooniensis	*Lichanothrips* sp.	Queensland, Australia	new record
A. mooniensis	*Idolothrips spectrum*	Queensland, Australia	new record
A. mooniensis	*Mecynothrips hardyi*	Queensland, Australia	new record
A. morazae	*Leptothrips distalis*	California, USA	new record
A. rumanicus	*Megathrips lativentris*	Romania	new record
A. smileyi	*Megalothrips spinosus*	New York, USA	Cross, 1965[b]

[a] Some specimens misidentified in original.
[b] Mite species unidentified in original.

C is wider than it is long (9.1), the prosternal apodeme is interrupted or fragmented (15.1), the end of the prosternal apodeme extends posteriad to sejugal apodeme (16.1), and there are striations on aggenital plate (22.1).

DISCUSSION

In contrast to the extensive literature on the biology of some other heterostigmatic mites, relatively little is known about the biology of Acarophenacidae. Females of *Adactylidium* species feed on eggs of thrips belonging to the Suborder Tubulifera, family Phlaeothripidae. Most known hosts are sporophagous, but some are phytophagous, with one host species, *G. ficorum*, a well known pest of *Ficus* species. Host specificity is not well documented in *Adactylidium* species. Some species (*A. costarricensis, A. mooniensis*) are known from several different genera of hosts, while most others are known only from single collections. Similarly, some thrips species are known to host several species of *Adactylidium* (e.g., *Gynaikothrips ficorum*). All known host associations are summarized in Table 1.

The phylogenetic hypothesis can be used to test the degree of historical association between the mites and their hosts. Early derivative mite lineages are associated with hosts in the subfamily Phlaeothripinae (*A. nicolae, A. morazae, A. flechtmanni, A. ficorum, A. brasiliensis,* and *A. beeri*). Note that the host of *A. irregularis* is unknown). Hosts is this subfamily are phytophagous (*G. ficorum, Lichanothrips* sp.), predaceous (*L. distalis*) or fungivorous (*H. ulmi, P. albipunctatus*). The more derived clade containing the remaining *Adactylidium* species is associated primarily with hosts in the subfamily Idolothripinae, all of which are

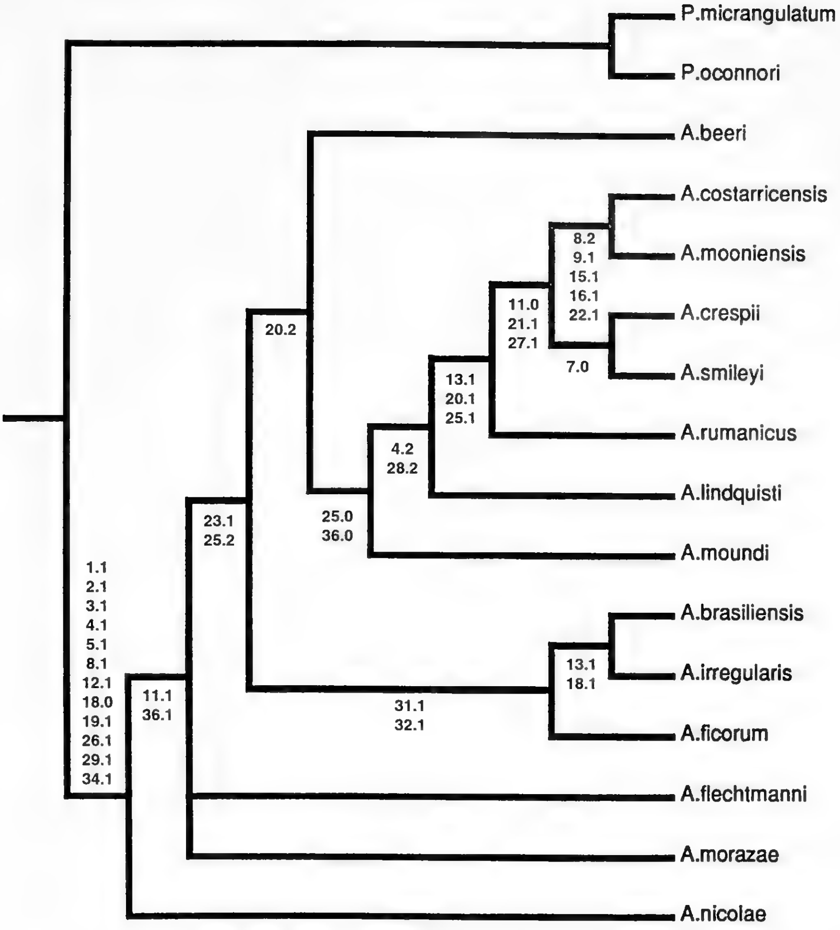


Fig. 146. Phylogenetic relationships among species of *Adactylidium* and related genus. Character changes are indicated at each internode.

specialized sporophagous species. Exceptional is the most derived clade comprising *A. costarricensis* and *A. mooniensis.* Both species are unusual in being reported from multiple host species belonging to both host subfamilies.

When examining the geographic distribution of these species, few patterns are apparent. The only clades showing geographic consistency are the Neotropical clade comprising *A. brasiliensis, A. irregularis* and *A. ficorum,* and the Nearctic clade comprising *A. smileyi* and *A. crespii.* Although *A. ficorum* has also been collected in Egypt, the host plant of the thrips, *Ficus nitida,* is a Neotropical species widely introduced in other areas. The final clade, comprising the very closely related species *A. costarricensis* and *A. mooniensis* shows a striking geographical disjunction, with the former being Neotropical and the latter Australian.

Most species of *Adactylidium* are known only from non-gravid females, and few species have been studied alive (Elbadry and Tawfik 1966). Elbadry and Tawfik (1966) first described the development of the species described above as *A. ficorum.* The life cycle consists of egg, larva, and adult. The "nymph" reported by Elbadry and Tawfik (1966) is actually the adult male. After piercing the chorion of a thrips egg, females feed and become physogastric. Larvae develop inside the mother's body and receive all their nourishment from the egg. Each physogastric female of *A. ficorum* produced 6–9 offspring. Elbadry and Tawfik (1966) also observed one male which did not feed but copulated with the females and died within a few hours of emergence. The fertilized females emerge by breaking through the integument of the physogastric female, then disperse on adult thrips hosts until eggs are found. In our observations on *A. crespii,* we also found one male attached to a host thrips.

Sampling in the Mediterranean area of Navarre by one of us (A. G.) has shown that females of *A. moundi* and *A. lindquisti* parasitize only females of sporophagous thrips, not the males. *Adactylidium* species have been collected mostly from the host's body (Figs. 111–112) where they attach by their stylets while sucking the host's haemolymph (Goldarazena et al. 1997). As such, the mites can be considered to be ectoparasites of the adult thrips. When they feed on the thrips eggs the mites can also be considered to be parasitoids (Kaliszewski et al. 1995).

Different mite species have been collected from the same attachment sites on their hosts, the abdominal pleurotergites (Figs. 102–103) and sternites. In contrast, one specimen of *A. costarricensis* was found attached to the lateral side of its host's head and one specimen of *A. mooniensis* at the base of the right forewing. All collections of *Adactylidium* were from adult thrips (Table 1); none have been found on immature stages. Until eggs of their host are available as food, the non-gravid females apparently feed on their adult hosts during their dispersal phase. Immature thrips may also colonize habitats other than those of the adults, e.g., leaf litter (Goldarazena and Mound 1999), and not deliver mites to egg resources.

Lindquist (1967) noted that few data were available on the effects of Acarophenacidae on insect hosts. Species of *Paracarophenax* and *Acarophenax* are egg predators of beetles (Cross 1965, Rack 1959, Redikortsev 1947), but their role as regulatory agents had not been explored until recently. Faroni et al. (2000) demonstrated significant reduction in egg viability and population growth of the stored product pest, *Rhizopertha dominica* (F.) when attacked by *Acarophenax lacunatus* Cross and Krantz in the laboratory. *Adactylidium* species might be able to exert similar pressure on populations of thrips species that induce leaf galls, such as *G. ficorum,* by destroying their eggs. Elbadry and Tawfik (1966) reported a very short life cycle for *A. ficorum,* with a new generation produced every 4 days at 30°C. Such short life cycles potentially allow a rapid increase in the parasitoid populations. More studies on the life cycles and host associations of *Adactylidium* species are needed in order to demonstrate the effectiveness of these mites as potential biological control agents against phytophagous thrips pests.

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Appendix A. Character matrix.

Taxon	1234567890	1234567890	1234567890	1234567
Paradactylidium				
P. micrangulatum	0000001000	0200101203	0000000000	0000000
P. oconnori	0000011000	0200001203	0000000000	0000000
Adactylidium				
A. beeri	1111111100	1100001012	0010210010	0001010
A. brasiliensis	1111111100	1110001113	0011210011	1101011
A. costarricensis	1112111221	0120111021	1110111210	0001000
A. crespii	1112110100	0120001011	1010111210	0001000
A. ficorum	1111111100	1100000010	0010210010	1101010
A. flechtmanni	1111111100	1111101023	0001010010	0001010
A. irregularis	1111111100	1110002124	0010210210	1101010
A. lindquisti	1112111100	1100011012	0010010210	0001000
A. mooniensis	1112111210	0010110011	0110111110	0001000
A. morazae	1111111100	1100001013	0000010110	0001010
A. moundi	1111111100	1100001012	0010010011	0001000
A. nicolae	1111111100	0100011011	1000210010	0001100
A. rumanicus	1112111100	1110001011	0010110210	0011000
A. smileyi	1112110100	0110001111	1010011110	0001000

Appendix B Character analysis, adult females.

Gnathosoma

1. Palp shape:
    - (0) Elongated
    - (1) Rounded
2. Palpal tibiotarsal solenidion:
    - (0) Well-developed
    - (1) Reduced
3. Position of palpal tibiotarsal solenidions relative to cheliceral opening:
    - (0) Lateral
    - (1) Anterior
4. Gnathosomal apodeme
    - (0) Looped basally
    - (1) Thickened basally
    - (2) With lateral projections

Prodorsum

5. Vertical setae, v_1
    - (0) Present
    - (1) Absent
6. Vertical setae, v_2
    - (0) Present
    - (1) Absent
7. Position of sc_1 seta relative to sc_2 bases:
    - (0) On the same (or almost) transverse line
    - (1) Well anterior

Hysterosoma

8. Position of c_1 seta relative to c_2 bases:
    - (0) Well posterior
    - (1) On the same (or almost) transverse line
    - (2) Well anterior
9. Length of tergite C:
    - (0) As long as wide
    - (1) Wider than long
10. Length of tergite D:
    - (0) Wider than long
    - (1) As long as wide
    - (2) Longer than wide
11. Length of seta *f*:
    - (0) Two to three times longer than seta e
    - (1) As long as seta e
12. Length of seta h_1:
    - (0) Three times longer than seta h_2
    - (1) As long as seta h_2
    - (2) Shorter than h_2

Venter

13. Apodemes I:
    - (0) Present, joined with prosternal apodeme
    - (1) Present, not joined with prosternal apodeme
    - (2) Absent
14. Apodemes II:
    - (0) Joined with prosternal apodeme
    - (1) Not joined with prosternal apodeme
15. Prosternal apodeme:
    - (0) Uninterrupted
    - (1) Interrupted or fragmented
16. End of prosternal apodeme:
    - (0) Not extending posteriad to sejugal apodeme
    - (1) Extending posteriad to sejugal apodeme
17. Sejugal apodeme:
    - (0) Fully developed, without interruptions
    - (1) Reduced to a lateral fragment on either side
    - (2) Absent
18. Apodemes III:
    - (0) Present, joined with poststernal apodeme
    - (1) Present, not joined with poststernal apodeme
    - (2) Absent
19. Apodemes V:
    - (0) Absent
    - (1) Reduced
    - (2) Present, well developed
20. Poststernal apodeme:
    - (0) Present, thick
    - (1) Interrupted, thin
    - (2) Fragmented
    - (3) Reduced to a nodule
    - (4) Absent
21. Anterior ventrometapodosomal lobe:
    - (0) Absent
    - (1) Present
22. Striations on aggenital plate:
    - (0) Absent
    - (1) Present
23. Seta *1b*:
    - (0) Present
    - (1) Absent
24. Seta *4b*:
    - (0) Present
    - (1) Absent

Legs

25. Tarsus apex:
    - (0) Blunt
    - (1) Pointed
    - (2) Rounded
26. Claw on leg I:
    - (0) Present
    - (1) Absent
27. Setae (*tc*) on tibiotarsus I:
    - (0) As long as (*ft*)
    - (1) Smaller than (*ft*)
28. Solenidion ω on leg I:
    - (0) Stout, rod-like
    - (1) Thin, rod-like
    - (2) Clavate
29. Setae μ' and μ'' of tibiotarsus I:
    - (0) Present
    - (1) Absent
30. Setae pv' and pv'' of tibiotarsus I:
    - (0) Present
    - (1) Absent

Appendix B Continued.

31. Seta v' of genu I:
    - (0) Present
    - (1) Absent
32. Seta v' of genu II:
    - (0) Present
    - (1) Absent
33. Seta l' of femur II:
    - (0) Present
    - (1) Absent
34. Seta pv' of tarsus III:
    - (0) Present
    - (1) Absent
35. Solenidion ω on tarsus III:
    - (0) Absent
    - (1) Present
36. Seta l' of genu III:
    - (0) Present
    - (1) Absent
37. Seta v' of genu IV:
    - (0) Present
    - (1) Absent

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LIFE HISTORY AND DESCRIPTION OF ADULTS AND IMMATURE STAGES OF *PROCECIDOCHARES BLANCI*, N. SP. (DIPTERA: TEPHRITIDAE) ON *ISOCOMA ACRADENIA* (E. GREENE) E. GREENE (ASTERACEAE) IN SOUTHERN CALIFORNIA

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Abstract.—***Procecidochares blanci*, n. sp.** is described as eggs, first-, second- and third-instar larvae, puparia, and adults. Adults are readily distinguished from all North American congeners, for which a preliminary key is provided, by the absence of dark pigmentation on the anterior abdominal segments or portions thereof. The first instar has a dorsally grooved, anterior mouthhook; the mouthhook of the second instar has four teeth, the most reported to date among nonfrugivorous tephritids. The anterior spiracles of the second and third instars are flattered and recessed. The oral ridges increase from none in the first instar, to one in the second instar, to two in the third instar. *Procecidochares blanci* is a true monophage on *Isocoma acradenia* (E. Greene) E. Greene, on which it produces two annual generations, one florivorous, which alternates with a longer generation that spends most of the winter, spring, and summer as a first instar inside a slowly developing, axillary bud/branch gall. The florivorous generation feeds within chambers excavated from adjacent, hypertrophied ovules. *Mesopolobus* sp. (Hymenoptera: Pteromalidae), *Eurytoma veronia* Bugbee (Hymenoptera: Eurytomidae), and *E.* sp. nr. *tumoris* are reported as primary, solitary, larval-pupal endoparasitoids of *P. blanci.*

Key Words: Insecta, *Procecidochares,* Asteraceae, *Isocoma, Haplopappus,* nonfrugivorous Tephritidae, new species, adult taxonomy, key, biology, taxonomy of immature stages, flower-head feeding, galls, aggregative life cycle, seed predation, parasitoids

Until recent taxonomic revision of the California flora (Hickman 1993), the genus *Haplopappus* (Asteraceae) represented one of our most prominent and widespread native plant genera, yet one on which after a decade and a half of careful examination by RDG and his coworkers, they had failed to detect any galls formed by fruit flies (Diptera: Tephritidae). Finally, in 1995, Jeff Teerink and RDG found the galls of the new species described herein, but by that time, the genus of this host plant and all of its former congeners had been changed (Hickman 1993)! This paper is dedicated to the late F. L. (Louie) Blanc who passed away in 1999 and who first introduced RDG to the fruit flies of California and encouraged his studies of the previously neglected, native, nonfrugivorous species among them.

MATERIALS AND METHODS

The present study was based in large part on dissections of samples of flower heads and galls on *Isocoma acradenia* (E. Greene) E. Greene (formerly *Haplopappus acradenius,* Hickman 1993) (Asteraceae) mainly collected along the westernmost portion of the secondary road connecting Interstate Highway 10 at the Whitewater exit with State Highway 111 near West Palm Springs (hereafter called the Whitewater site) at the eastern end of the San Gorgonio Pass at 390-m elevation, Riverside Co., from 1995 to 1999. One-liter samples of excised, immature and mature flower heads containing eggs, larvae, and puparia, as well as basal portions of branches sampled monthly from non-flowering, gall-bearing plants during 1998 and 1999 were transported in cold-chests in an air-conditioned vehicle to the laboratory and stored under refrigeration for subsequent dissection, photography, description, and measurement. Three eggs, six first-, 14 second-, and 15 third-instar larvae and seven puparia dissected from flower heads were preserved in 70% EtOH for scanning electron microscopy (SEM). Additional 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, and studied and 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. Twenty-two pairs of virgin flies, each consisting of one or two males and a female obtained from emergence cages, also were held in clear-plastic, petri dishes 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.

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 Blanc and Foote (1961) and Goeden and Teerink (1997a). Terminology and telegraphic format used to describe the immature stages follow Goeden (2000a, b, c, d, 2001), Goeden and Headrick (1999), Goeden and Teerink (1997a, b, 1999a, b), Teerink and Goeden (1999), and earlier works cited therein. Means ± SE are used throughout. The holotype, allotype, and 23 reared paratypes of each sex of this new species are deposited in the National Museum of Natural History, Smithsonian Institution, Washington, DC (USNM). The holotype, allotype, and 22 paratypes used for measurements to describe *P. blanci* originated from one collection on 23.X.1996 at the Whitewater site. All remaining paratypes and voucher specimens not designated as paratypes and all reared parasitoids reside in RDG's research collections.

RESULTS AND DISCUSSION

TAXONOMY

The following key written by ALN incorporates several species described since the publication of the most recent key to *Procecidochares* north of Mexico (Foote et al. 1993), as well as some additional characters. It is provided as a provisional key until this genus can be revised comprehensively. Users should be aware that several additional, undescribed species are already known.

PRELIMINARY KEY TO THE SPECIES OF *PROCECIDOCHARES* OF THE UNITED STATES AND CANADA

1. Wing with crossvein between costa and vein R_{2+3} about midway between apices of R_1 and R_{2+3} (Foote et al. 1993, fig. 172). Anterior notopleural and postsutural supra-alar setae usually absent. Anepisternum with small anterodorsal nonmicrotrichose shiny area. A cluster of 2–4 setae in normal position of anterior orbital seta (Foote et al. 1993, fig. 33). Facial ridge and parafacial with numerous white, lanceolate setulae. Scutum with row of postsutural intra-alar setulae. Scutellum with white setulae near basal seta. Hosts *Ambrosia* spp. Canada (Nova Scotia) & eastern USA west to Iowa & Texas . . . . . . *P. gibba* (Loew)

– Wing without crossvein to costa between apices of R_1 and R_{2+3}, rarely a stump present on vein R_{2+3}. Anterior notopleural and postsutural supra-alar setae present. Anepisternum either entirely microtrichose or with large nonmicrotrichose shiny area covering at least anterodorsal and anteroventral sections. Usually only a single anterior orbital seta. Facial ridge setulae often yellow or white, but rarely lanceolate. Parafacial usually nonsetose; setulae, if present, acuminate. Row of intra-alar setulae and scutellar setulae present or absent . . 2

2. Anepisternum and notopleuron entirely microtrichose (Fig. 1D). Katepisternum entirely microtrichose except in *P. pleuralis*. Scutum with 1 or a cluster of several white, laneolate setulae immediately anterior to postsutural supra-alar seta. Scutellum without white setulae basally. Cell r_{2+3} with marginal hyaline area variable in shape, but often broadest near midpoint or subapically, absent or narrow bordering apex of vein R_{4+5} (Foote et al. 1993, figs. 342, 344) 3

– Anepisternum with large nonmicrotrichose shiny area, at least anterodorsally and anteroventrally (Fig. 1C). Anterior half of notopleuron mostly or entirely nonmicrotrichose and shiny. Katepisternum with large nonmicrotrichose shiny area. Scutum usually without white lanceolate setulae immediately anterior to postsutural supra-alar seta. Scutellum often with 1 to several white setulae near basal scutellar seta (Fig. 1A). Cell r_{2+3} with marginal hyaline area absent or narrowest near middle, broader bordering apex of vein R_{4+5} (Foote et al. 1993, figs. 346–350), sometimes not quite touching vein apex in *P. australis* Aldrich (Foote et al. 1993, fig. 351) 5

3. Katepisternum and postpronotal lobe entirely microtrichose (Fig. 1D). Cell r_{2+3} with marginal hyaline area broadest near midpoint or subapically, absent or narrow bordering apex of vein R_{4+5} (Foote et al. 1993, figs. 342, 344). Scutum with cluster or row of setulae extending to or towards presutural supra-alar seta anteromesal to it (Fig. 1B) (*P. utilis* group) 4

– Katepisternum with large nonmicrotrichose shiny area. Postpronotal lobe with dorsomesal nonmicrotrichose shiny area. Cell r_{2+3} with marginal hyaline area absent or narrowest near middle, broader bordering apex of vein R_{4+5} (Foote et al. 1993, fig. 345). Scutum without setulae anteromesal of presutural supra-alar seta. Host "sunflower". USA (Arizona), Mexico (Durango). . . . . *P. pleuralis* Aldrich

4. Posterior orbital seta very small, but present (Foote et al. 1993, fig. 42). Femora often largely brown. Wing bands generally brown (Foote et al. 1993, fig. 342). Apical and subapical bands not connected. Hosts *Brickellia* spp. USA (California, New Mexico), Mexico (Baja California) . . . . *P. flavipes* Aldrich

– Posterior orbital seta absent. Legs entirely yellow. Wing bands generally yellow or pale brown (Foote et al. 1993, fig. 344). Apical and subapical bands sometimes connected along vein R_{4+5}. Hosts unknown. USA (Montana, Colorado) . . . . *P. montana* (Snow)

5. Basal and discal bands connected at least in cells r_1 and br or br and bm (Fig. 2; Foote et al. 1993, fig. 346; this character should be observed carefully with transmitted light). Scutum with one postsutural dorsocentral seta; usually with row of setulae from transverse suture to or towards intra-alar seta along intra-alar line (Fig. 1A) (absent in *P. kristinae* Goeden, variable in *P. stonei* Blanc & Foote). Scutellum usually with 1 to several white setulae near basal scutellar seta (Fig. 1A) (often absent in *P. stonei*) 6

– Basal and discal bands separate or narrowly connected only in cell br (rarely only in cell bcu). Scutum with 1–2 dorsocentral setae, the second presutural if present; with or without row of intra-alar setulae. Scutellum with or

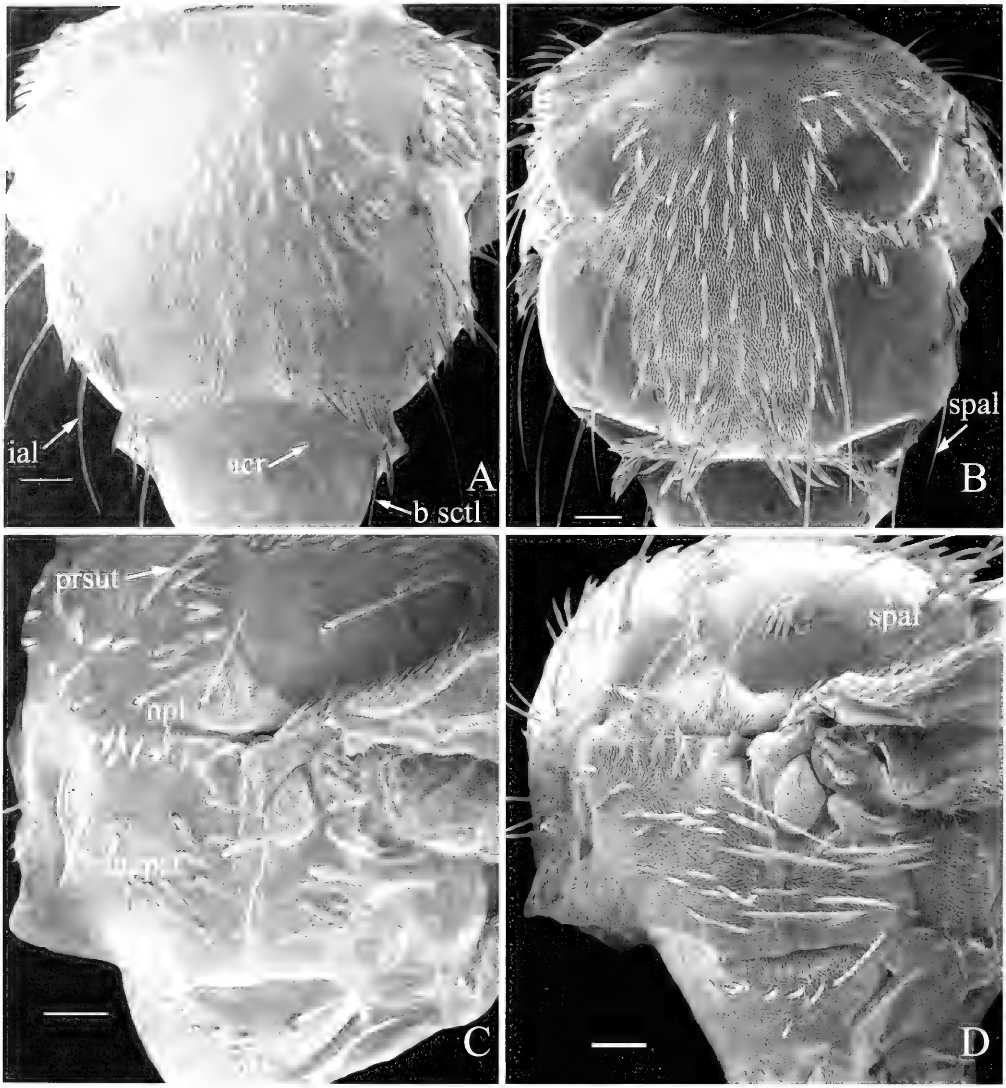

Fig. 1. Thoraces of *Procecidochares blanci*: (A) dorsal view; (C) lateral view; and *P. flavipes*: (B) dorsal view; (D) lateral view. anepst - anepisternum, b sctl - basal scutellar seta, ial - intra-alar seta, kepst - katepisternum, npl - notopleuron, prsut - presutural supra-alar seta, spal - postsutural supra-alar seta.

without white setulae near basal scutellar seta 9

6. Abdomen partially yellow, at least basolaterally. Gena without brown spot. Scutum with medial areas of white setulae and microtrichia relatively narrow, neither entirely enclosing acrostichal seta (Fig. 1A). Pterostigma entirely brown (Fig. 2). Apical band usually connected to subapical band in cell r_{2+3} and sometimes cell r_1. In lateral view (Fig. 1C), lateralmost setulae in ring of presutural lateral scutal setulae closer to anterior notopleural seta than to presutural supra-alar seta or midway between them. Host *Isocoma acradenia*. USA (California) . . . . *P. blanci* Goeden and Norrbom, n. sp.

– Abdomen entirely brown. Gena often with large brown spot bordering eye. Scutum with area of medial white setulae and medial microtrichose area relatively broad, acrostichal seta within area of white setulae and at lateral border of or within microtrichose area. Pterostigma often with yellow or paler brown area basally. Apical band connected to or separate

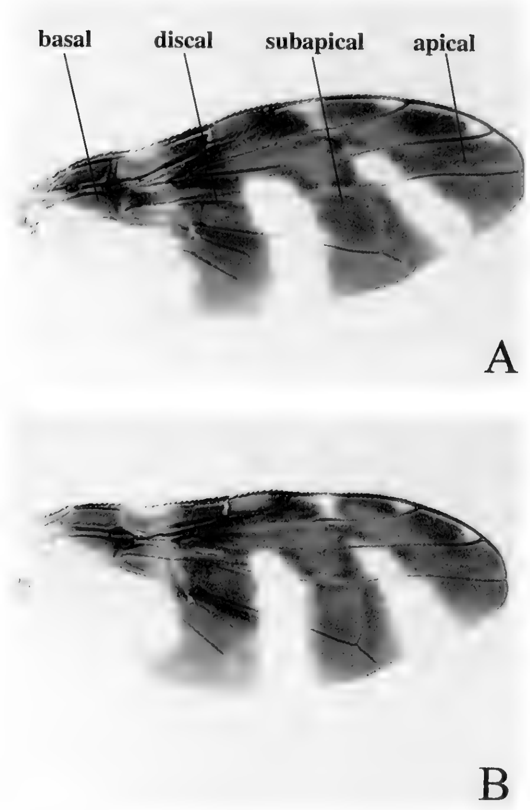

Fig. 2. Right wings of *Procecidochares blanci*: (A) female with bands labelled; (B) male.

from subapical band. In lateral view, lateralmost setulae in ring of presutural lateral scutal setulae often closer to presutural supra-alar setae than to anterior notopleural seta or surrounding it 7

7. Gena without large brown spot. Scutum without row of setulae from transverse suture to or towards intra-alar seta along intra-alar line; with 1 or a cluster of serveral white lanceolate setulae immediately anterior to postsutural supra-alar seta. Scutellum with 1 to several white setulae near basal scutellar seta. Pterostigma usually with yellow or paler brown area basally (Goeden and Teerink 1997, fig. 1). Apical band usually connected to subapical band in cell r_{2+3} and sometimes cell r_1. Host *Ambrosia dumosa* (Gray) Payne. USA (California, Nevada, Arizona) . . . . *P. kristineae* Goeden (in part)

– Gena usually with large brown spot bordering eye. Scutum with or without intra-alar and supra-alar setulae (*P. lisae* Goeden with intra-alars, without supra-alars; both variable in *P. stonei*). Scutellum with or without 1 to several white setulae near basal scutellar seta. Pterostigma with or without yellow or paler brown area basally. Apical band usually separate from subapical band 8

8. Discal band reduced, in male not extended beyond vein A_1+Cu_2, in female at most narrowly reaching posterior wing margin, but if so, part posterior to A_1+Cu_2 much paler than rest of band (Goeden & Teerink 1997, fig. 2). Cell c entirely brown or at most yellow medially. Pterostigma usually with yellow or paler brown area basally. Scutellum with 1 to several white setulae near basal scutellar seta. Host *Ambrosia eriocentra* (Gray) Payne. USA (California) . . . . *P. lisae* Goeden

– Discal band not reduced, broadly and distinctly reaching posterior wing margin in both sexes (Foote et al. 1993, fig. 346). Cell c with large medial hyaline area. Pterostigma evenly brown. Scutellum with or without white setulae near basal scutellar seta. Hosts *Viguiera* spp. USA (California) . . . . *P. stonei* Blanc and Foote

9. Legs entirely yellow. Scutum with 1 postsutural dorsocentral seta. Scutellum with 1 to several white setulae near basal scutellar seta. Apical and subapical bands not connected (Foote et al. 1993, fig. 343). Hosts *Solidago* spp. USA (Massachusetts south to Florida, Mississippi) . . . . *P. polita* (Loew)

– Femora usually mostly brown, if yellow, scutum with 2 dorscentral setae (1 presutural) or scutellum without white setulae. Apical and subapical bands sometimes connected 10

10. Scutum with row of setulae from transverse suture to or towards intra-alar seta along intra-alar line; with 2 dorsocentral setae (1 presutural) 11

– Scutum rarely with partial row of intra-alar setulae, if present, with only 1 dorsocentral seta 12

11. Scutum with presutural microtrichia extended laterally no more than one fourth distance from dorsocentral line to presutural supra-alar seta. Acrostichal seta usually at margin of medial microtrichose area of scutum. Subapical and apical bands separate (Foote et al. 1993, fig. 350). Hosts *Grindellia* spp. USA (California, Colorado) . . . . . . *P. grindeliae* Aldrich

– Scutum with presutural microtrichia extended laterally more than half distance from dorsocental line to presutural supra-alar seta, usually reaching it. Acrostichal seta usually within medial microtrichose area of scutum. Subapical and apical bands sometimes connected in cell r_{2+3}, Hosts *Heterotheca* spp. USA (Texas), Mexico . . . . *P. australis* Aldrich

12. Hyaline triangular area between discal and

subapical bands distinctly broader along posterior wing margin than hyaline area between subapical and apical bands (Foote et al. 1993, fig. 347). Acrostichal seta usually at margin of or within medial microtrichose area of scutum. Scutellum without white setulae. Subapical and apical bands sometime connected in cell r_1. Hosts *Solidago* spp. Southeastern Canada, northern and eastern USA . . . . *P. atra* (Loew)

– Hyaline triangular area between discal and subapical bands at most slightly broader than hyaline area between subapical and apical bands. Other characters variable 13

13. Scutum with 1 or a cluster of several white, lanceolate setulae immediately anterior to postsutural supra-alar seta; area of medial white setulae relative broad, including acrostichal seta; medial microtrichose area also broad but short, enclosing acrostichal seta laterally, but bare area sometime touching it posteriorly. Pterostigma usually with yellow or paler brown basal area (Goeden & Teerink 1997, fig. 1). Scutellum with 1 to several white setulae near basal scutellar seta. Host *Ambrosia dumosa.* USA (California, Nevada, Arizona) . . . . *P. kristinae* Goeden (in part)

– Scutum without white setulae immediately anterior to postsutural supra-alar seta; area of medial white setulae usually narrower, acrostichal seta usually lateral to or at its border; medial microtrichose area usually narrower and longer, usually at most partially enclosing acrostichal seta (the latter sometimes within indentation of bare area). Pterostigma without paler basal area. Scutellum usually without white setulae basally 14

14. Scutum with presutural microtrichia extended laterally at least half distance from dorsocentral line to level of presutural supra-alar seta, at least along anterior part of ring of white setulae 15

– Scutum with presutural microtrichia extended laterally no more than one fourth distance from dorsocentral line to presutural supra-alar seta 16

15. Scutum usually with 2 dorsocentral setae, 1 presutural; without intra-alar setulae; medial areas of white setulae and microtrichia sometimes including acrostichal seta. Scutellum without white setulae basally. Body usually redbrown; postpronotal lobe and propleuron usually partially yellow. Apical and subapical bands separate or connected along vein R_{4+5}. Hosts *Heterotheca* and *Conyza* spp. USA (Florida, South Carolina, Maryland?) . . . . sp. 1 near *P. australis*

– Scutum with 1 dorsocentral seta; often with partial row of white intra-alar setulae; medial areas of white setulae and microtrichia rarely including acrostichal seta. Scutellum often with 1 or 2 white setulae near basal scutellar seta. Apical and subapical bands connected along vein R_{4+5}. Body, including postpronotal lobe and propleuron dark brown. USA (Texas) . . . . sp. 2 near *P. australis*

16. Scutum usually with 2 dorsocentral setae, 1 presutural. Apical and subapical bands sometimes connected in cell r_1 only. Host *Solidago californica* Nuttall. USA (Oregon & Montana south to California, Arizona & Colorado) . . . . *P. anthracina* (Doane)

– Scutum with 1 postsutural dorsocentral seta. Apical and subapical bands not connected in cell r_1, or if so, also more broadly connected in cell r_{2+3}. (*minuta-blantoni* complex, which appears to include at least several additional cryptic species) 17

17. Parafacial less than half as wide as first flagellomere. Hosts various. USA (Washington & Montana south to California & Texas) . . . . *P. minuta* (Snow)

– Parafacial about half as wide as first flagellomere. Hosts *Heterotheca* spp. USA (Oregon) . . . . *P. blantoni* Hering

Procecidochares blanci Goeden and Norrbom, new species

(Figs. 1A, C, 2–8)

Adult female.—*Head:* Generally pale colored except occiput and often ocellar tubercle and orbital plates brown, entirely microtrichose. In profile 0.6–0.7 times as long as high, face and frons meeting at about 120° angle; parafacial about 0.8 times as wide as first flagellomere; gena about 0.2 times as high as eye; eye 0.5–0.6 times as wide as high; frons ocherous brown to yellow, at vertex 1.2–1.4 times as wide as eye in lateral view, 1.2–1.4 times as wide as length from vertex to lunule; lunule about 0.7 times as high as wide; face and lunule white, paler than frons, face concave with moderate carina; antenna short, yellow, sometimes white or ocherous brown, microtrichose, arista ocherous brown to brown, extreme base yellow. Usually 2 brown frontal setae, occasionally 3 on one side, or rarely 3 on both sides, or 1 on one side. 1 brown orbital seta, posterior seta absent. Ocellar and medial vertical setae brown, well developed. Lateral vertical seta yellow to white, slightly to distinctly lanceolate, 0.5–0.7 times as long as medial vertical seta. Postocular and postocellar setae white, lanceolate. Facial ridge setulae yellow or white, acuminate. Gena without distinct brown spot bordering eye, genal seta brown.

Thorax (Figs. 1A, C): Mostly dark brown to black, posterodorsal corner of anepisternum and posterior half of notopleuron yellow. Mostly shining, microtrichose only on propleuron, scutum medially (between dorsocentral lines anteriorly, slightly wider at level of transverse suture, then narrowing posteriorly; at level of acrostichal setae slightly narrower than distance between setae) and on extreme lateral margin (at or below level of postpronotal seta), on posterior half of notopleuron, posterodorsally on anepisternum, dorsally on anepimeron, medial or ventral margin of katepisternum, part or most of katatergite, most of anatergite, dorsal half of mediotergite, most or all of subscutellum, and underside of scutellum. Postpronotal, 2 notopleural, pre- and postsutural supra-alar, intra-alar, postalar, 1 postsutural dorsocentral (approx. midway between suture and level of supra-alar seta), acrostichal, 2 scutellar setae well developed, brown. Mesonotal setulae relatively large, stout, lanceolate, white, in pattern as follows: large medial area of continuous setulae between dorsocentral setae, with unpaired medial and paired dorsocentral rows extending anteriorly, the latter joining row along anterolateral margin, margin of notopleuron and anterior margin of transverse suture to form circular arrangement (in lateral view, lateralmost setulae midway between anterior notopleural and presutural supra-alar setae or slightly closer to one of those setae); rarely with 1 to several setulae anteromesal to presutural supra-alar seta; another row extending laterally along posterior margin of transverse suture, curving posteriorly and extending to intra-alar seta and sometimes laterally to postalar seta; main medial area of setulae narrowing posteriorly, between acrostichal setae dividing into paired submedial rows that curve laterally and then extend to posterior margin; rarely 1 to several setulae immediately anterior to postsutural supra-alar seta. Postpronotal lobe with several additional lanceolate white setulae. Scutellum with 1 to several lanceolate white setulae near base of basal scutellar seta. Anepisternum with 1 brown seta and 1–2 large lanceolate white setulae posteriorly, and numerous smaller white lanceolate setulae. Anepimeron with only several large lanceolate white setulae. Katepisternum with a few lanceolate white dorsal setulae and 1 white or brown seta. Scutellum stout in vertical and horizontal planes, rounded. Legs mostly yellow to ocherous.

Wing (Fig. 2): With base and 3 broad bands brown. Basal band (usually isolated in other *Procecidochares* species) extended posteriorly to base of vein Cu, broadly connected to discal band in cells, sc, r_1, and br, and almost always in bm, sometimes also in cell c or rarely in cell bcu, although area connecting bands often paler than bands. Discal, subapical, and apical bands extended to posterior wing margin. Discal and subapical bands connected anteriorly in pterostigma and cells r_1 and r_{2+3}. Subapical and apical bands usually broadly, sometimes narrowly connected in cell r_{2+3} and to lesser extent in cell r_1, rarely narrowly separated in both cells. Apical band broad, with small marginal hyaline spots at apices of veins R_{2+3} and R_{4+5} and often a very narrow hyaline area connecting them. Pterostigma about 2–3 times as long as wide and evenly brown. Distance between crossveins R-M and DM-Cu about equal to length of R-M. Haltere shaft ocherous yellow, knob pale yellow.

Abdomen: Partially to entirely yellow, non-yellow areas dark brown. Syntergite 1+2 yellow laterally, often brown medially. Tergites 3–4 usually yellow laterally and often medially. Tergite 5 and especially tergite 6 usually brown at least medially. At least sternites 1, 2, and usually 3 yellow.

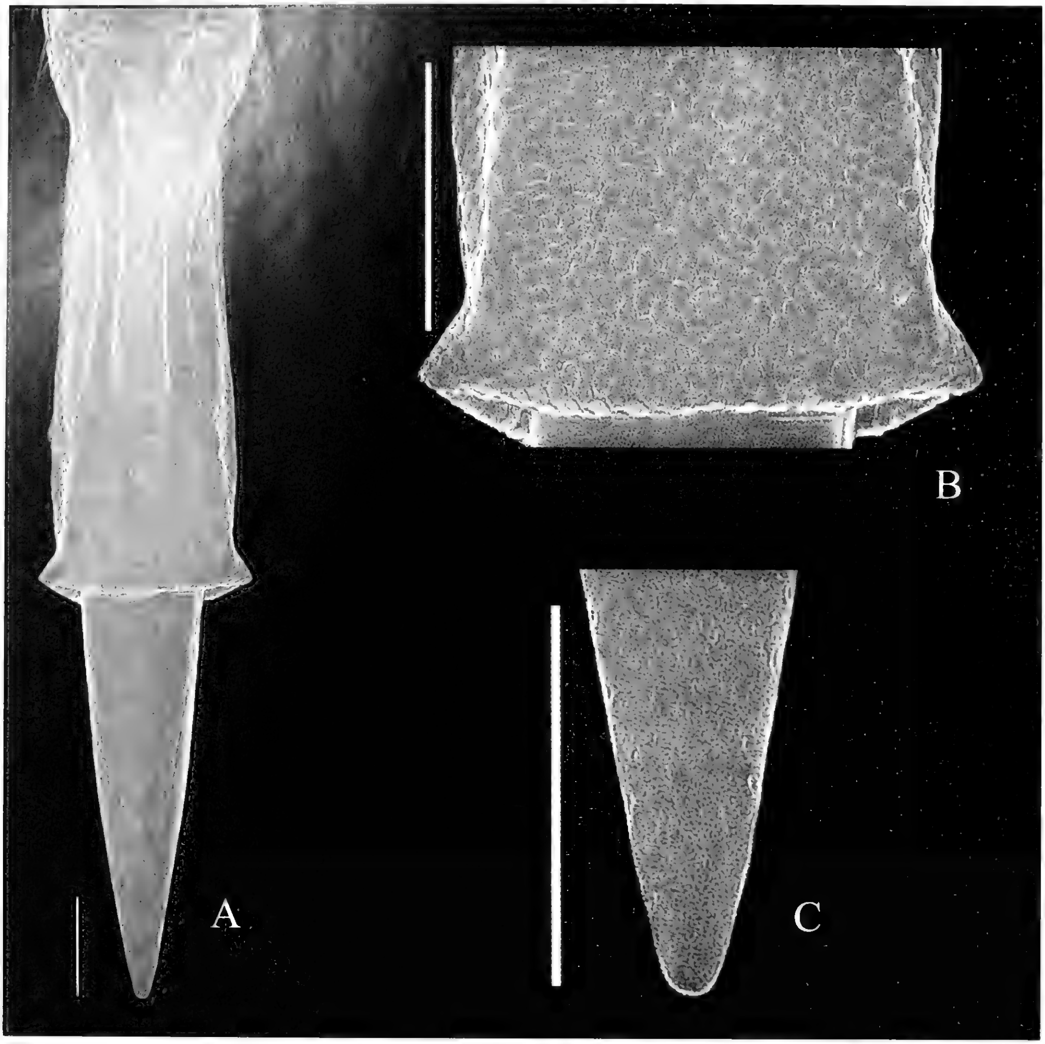

Fig. 3. Eversible membrane and aculeus of *Procecidochares blanci*, dorsal view. (A) partially everted; (B) middle of eversible membrane, enlarged; (C) aculeus tip.

Setulae more or less evenly covering tergites, mostly white and lanceolate, often more acuminate and/or yellow laterally. Syntergite 1+2 except posterior corner, tergite 3 except laterally, usually broad basomedial area of tergite 4, and often narrow basomedial area of tergite 5 microtrichose. Oviscape, in dorsal view, 2/3 length of rest of abdomen; brown, nonmicrotrichose, shiny; setulae acuminate. Aculeus tip acute, simple (Fig. 3).

Male.—*Head:* Similar to female, but parafacial about 0.8 times as wide as first flagellomere; gena 0.13–0.20 times as high as eye; frons at vertex 1.0–1.3 times as wide as eye in lateral view, 1.1–1.3 times as wide as length from vertex to lunule; lunule 0.4–0.5 times as high as wide. *Thorax:* Similar to female. *Wing* (Fig. 2B): Similar to female. Basal band usually connected to discal band in cell c. *Abdomen:* Color and vestiture similar to female. Tergite 5 nonmicrotrichose. Epandrium and surstyli brown.

Variation.—Examination of reared *P.*

Table 1. Variation in number and color of frontal setae of *P. blanci*. b = black, w = white.

No. Setae/Side	Females No.	Females %	Males No.	Males %
2b:2b	98	81.7	84	74.3
1b1w:1b1w	1	0.8	2	1.8
2b:1b1w	2	1.7	5	4.4
2w:1b1w	0	0	1	0.9
1b:1b	1	0.8	1	0.9
1b:0	0	0	1	0.9
1b:3b	0	0	1	0.9
2b:1b	8	6.7	8	7.1
2b:3b	3	2.5	5	4.4
2b:2b1w	1	0.8	0	0
2b:4b	0	0	1	0.9
3b:3b	3	2.5	3	2.7
2b1w:2b1w	2	1.7	1	0.9
3b:2b1w	1	0.8	0	0

blanci specimens with intact setation indicated that the number of frontal setae varies from one to six, even greater than the variation from two to five noted for the genus by Foote et al. (1993). The variation in frontal seta color and number is summarized in Table 1.

Diagnosis.—Adults of *P. blanci* can be distinguished from those of most other species of *Procecidochares* known from north of Mexico by their partially yellow abdomen. This character otherwise appears to occur only in some specimens from Florida that have been regarded as *P. australis* (see Foote et al. 1993), but they are readily distinguished from *P. blanci* by the presence of presutural dorsocentral setae, which are always absent in *P. blanci*. In other characters *P. blanci* most closely resembles *P. kristineae, P. gibba, P. lisae,* and *P. stonei* which also have the basal and discal bands broadly connected (usually less broadly in *P. kristineae*). These species differ in having broader medial areas of white setulae and microtrichia on the scutum. Several other useful diagnostic characters include: the gena without a large brown spot; thoracic microtrichia generally reduced (e.g., postpronotal lobe, anterior half of notopleuron, most of anepisternum and katepisternum bare); scutum with a row of white postsutural intra-alar setulae (absent in *P. kristineae*); scutellum with one to several small white setulae near basal scutellar seta; pterostigma without a yellow or paler brown basal area; and the apical band usually connected to the subapical band in cell r_{2+3} and sometimes cell r_1. This is the only *Procecidochares* species known to infest *Isocoma acradenia.*

Types.—Holotype, ♀ (USNM); along Whitewater Rd. SW of Whitewater, S of I-10, N of Hwy 111, 1270 ft, Riverside Co., CA; 23.x.1996; R. D. Goeden, coll. (hereafter RDG)/J. A. Teerink, coll. (hereafter JAT); reared from flower *head of Isocoma* (= *Haplopappus*) *acradenia* on 6.xi.1996. Allotype, ♂; same data as holotype (USNM). Paratypes: CALIFORNIA: 65 ♂ and 60 ♀; same data as holotype (24 ♂ and 23 ♀ to USNM). 1 ♂ and 3 ♀; Coyote Wells, Imperial Co., 6.xi.1986; RDG. 2 ♂ (1 missing abdomen), E of Ocotillo, CA at Coyote Wells, SW Imperial Co., 140 ft elevation, 15.xi.1990, reared from flower head of *I. acradenia* (as *H. acradenius*). 8 ♂ and 4 ♀; Coyote Wells, 140 ft, Imperial Co., 17.xi.1994, RDG/JAT; reared 22.xi.1994. 14 ♂ and 31 ♀; same location as holotype, 26.x.1995; RDG/JAT. 2 ♂ and 1 ♀; Frontage road to In-Koh-Pah Tower, N of Interstate Hwy 8, 2880 ft, San Diego Co., 2.x.1997; RDG/JAT. 18 ♂ and 18 ♀; same location as holotype, 29.x.1997; RDG/JAT.

Etymology.—*Procecidochares blanci* is named in honor of the late F. L. (Louie) Blanc, noted California tephritologist, who first introduced RDG to the Tephritidae, previewed all of RDG's manuscripts on nonfrugivorous fruit flies prior to Louie's death, and served as a constant source of encouragement for RDG's studies of these flies.

Egg.—Sixty-two eggs dissected from field-collected flower heads were white, opaque, smooth, elongate-ellipsoidal, 0.55 ± 0.004 (range, 0.48–0.64) mm long, 0.16 ± 0.002 (range, 0.12–0.20) mm wide,

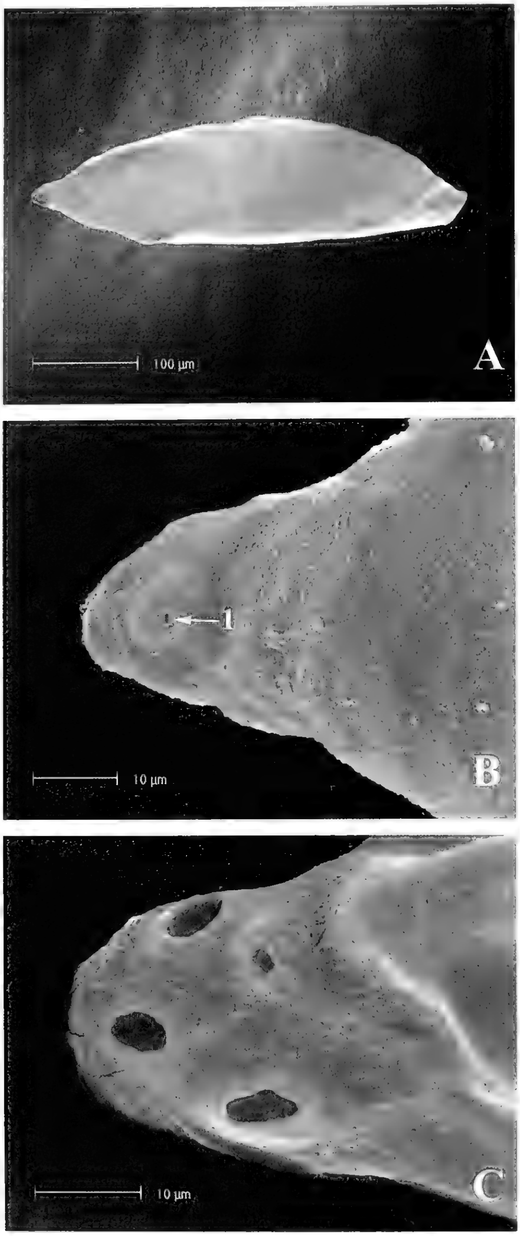

Fig. 4. Egg of *Procecidochares blanci*: (A) habitus, anterior end to left; (B) pedicel showing 1- small aeropyle; (C) pedicel of a different egg with aeropyles.

smoothly rounded at tapered basal end (Fig. 4A); pedicel nipple-like, 0.03 mm long, circumscribed by few, very small (Fig. 4B-1) to several larger, oval (Fig. 4C) aeropyles scattered around the pedicel (Fig. 4C).

The egg of *P. blanci* is similar in general shape to that of *P. stonei,* which also has few small aeropyles on a less pronounced pedicel (Green et al. 1993); however, the pedicel with the sole, tiny aeropyle shown in Fig. 4B probably was an aberration or the result of plugging during preparation for SEM, as suggested by the circular areas anterior to the arrow. The egg of *P. kristineae* was described as navicular by Silverman and Goeden (1994), which agrees with photos in Goeden and Teerink (1997a), with a prominent pedicel circumscribed ± in a row by a few small subcircular aeropyles. In contrast, the prominent pedicel of the egg of *P. anthracina* has only a few, large aeropyles (Goeden and Teerink 1997b). The eggs of *P. flavipes* are slightly larger and wider on average (Goeden et al. 1994) than those of *P. blanci* (Fig. 4A), as are those of *P. lisae* (Goeden and Teerink 1997a), all three of which are longer and wider on average than those of *P. kristineae* (Silverman and Goeden 1980), *P. anthracina* (Goeden and Teerink 1997b), and *P. stonei* (Green et al. 1993).

First-instar larva.—White, cylindrical and bluntly rounded anteriorly and posteriorly when newly hatched, becoming subglobose (Fig. 5A); body segments well defined, finely wrinkled (probably as a result of preparation for SEM), free of minute acanthae; gnathocephalon finely wrinkled, flattened (Fig. 5B), dorsal sensory organ a well-defined, flat pad (Figs. 5B-1, C-1); anterior sensory lobe (Figs. 5B-3, C-2) bears terminal sensory organ (Figs. 5B-4, C-3); lateral sensory organ (Fig. 5C-4), supralateral sensory organ (Fig. 5C-5), and pit sensory organ (Fig. 5B-2); stomal sense organ poorly defined, reduced to two pore sensilla, ventrolaterad of terminal sensory organ (Fig. 5C-6); mouthhook bidentate (Fig. 5B-5), apical tooth grooved dorsally (Figs. 5B-6, C-7); median oral lobe laterally compressed, apically rounded (Figs. 5B-7, C-8); anterior spiracle absent; lateral spiracular complexes not seen; caudal segment with two stelex sensilla, dorso- and ventrolaterad

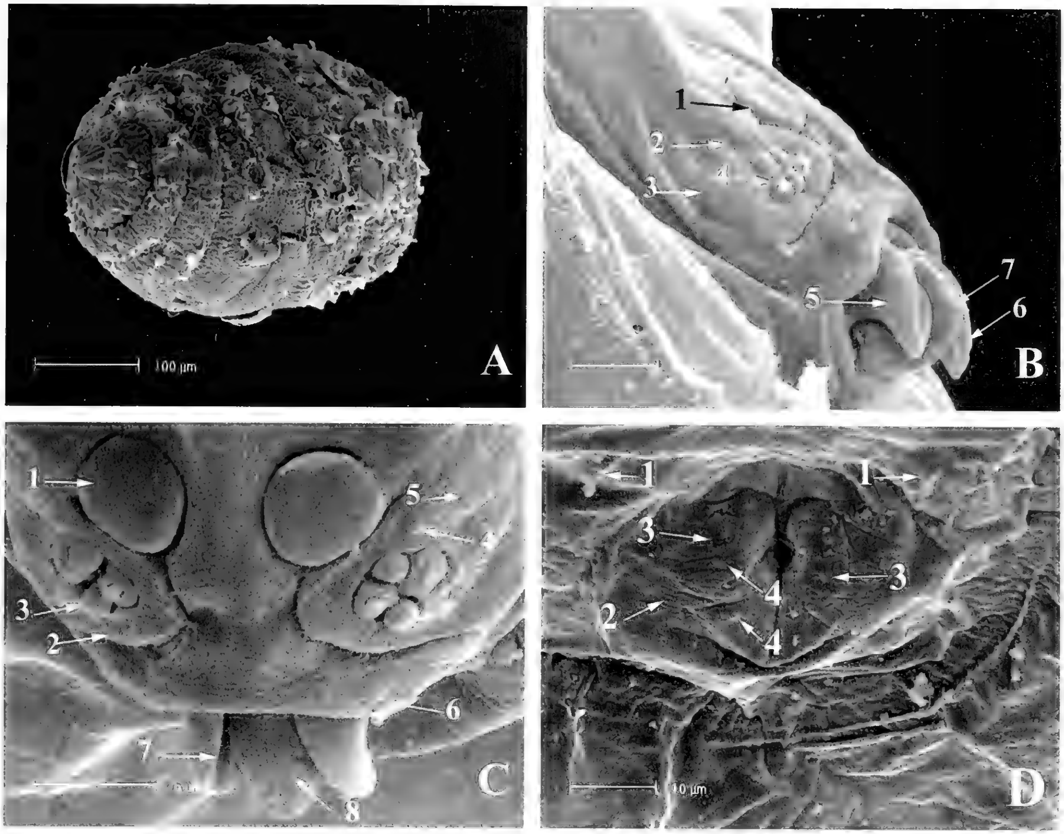

Fig. 5. First instar of *Procecidochares blanci*: (A) habitus, anterior to left; (B) gnathocephalon, lateral view, 1- dorsal sensory organ, 2- pit sensory organ, 3- anterior sensory lobe, 4- terminal sensory organ, 5- mouthhook, 6- dorsally grooved, apical tooth of mouthhook, 7- median oral lobe; (C) gnathocephalon, dorsal 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- dorsally grooved apical tooth of mouthhook, 8- median oral lobe; (D) caudal segment, 1- dorsolateral stelex sensillum, 2- posterior spiracular plate, 3- rima, 4- interspiracular process.

(Fig. 5D-1) of posterior spiracular plate (Fig. 5D-2); posterior spiracular plate bears two elliptical rimae, ca. 0.01 mm in length (Fig. 5D-3), and four, small, hemispherical, much reduced, unbranched, interspiracular processes (Fig. 5D-4); no intermediate sensory complex observed.

The first instar habitus shortly after eclosion has the cylindrical form ascribed to *P. anthracina* (Goeden and Teerink 1997b) and *P. lisae* (Goeden and Teerink 1997a), but later during this long stadium more closely assumes the barrel shape ascribed to *P. stonei* (Green et al. 1993) and *P. kristineae* (Goeden and Teerink 1997a) with this change of shape with growth probably accounting for these reported, apparent differences. No minute acanthae circumscribe the intersegmental lines as reported for *P. kristineae, P. lisae* (Goeden and Teerink 1997a), and *P. anthracina* (Goeden and Teerink 1997b). The dorsal sensory organ of the first instar of *P. blanci* is well-defined (Figs. 5B-1, C-1), but flattened, not dome-shaped, as reported for *P. kristineae, P. lisae* (Goeden and Teerink 1997a) and *P. anthracina* (Goeden and Teerink 1997b), nor as pictured for *P. stonei* (Green et al. 1993). The apical tooth of the two-toothed mouthhook of *P. blanci* is dorsolaterally grooved

(Figs. 5B-6, C-7), and this tooth appears grooved dorsomedially in *P. kristineae* and *P. lisae* (Goeden and Teerink 1997a). In these three species, this character provides a ready means of separating the first from the second instars, which lack dorsal grooves. However, photos of this anterior tooth in the first instar of *P. stonei* (Green et al. 1993) show no such groove, nor was such a groove reported in the description of the first instar of that species. The mouthhook of the first instar of *P. anthracina* (Goeden and Teerink 1997b) was not observed for comparison. Evaluation of the locations and presence or absence of this character among first instars of *Procecidochares,* a character not seen in other genera of Tephritidae that we have studied (i.e., *Aciurina, Neaspilota, Trupanea*), awaits descriptions of first instars of additional *Procecidochares.*

Two stelex sensilla dorso- and ventrolaterad of each posterior spiracular plate are reported in the first instar of *P. blanci* (Fig. 5D-1); however, in the first instar of *P. lisae* (Goeden and Teerink 1997a), these sensilla are verruciform and "compound" (i.e., paired verruciform), respectively. The caudal segment of *P. anthracina* (Goeden and Teerink 1997b) was reported to be circumscribed by stelex "sensilla", thus, presumably by at least two pairs. In the first instar of *P. kristineae,* only a ventrolateral pair of stelex sensilla was seen, photographed, and reported (Goeden and Teerink 1997a). The first instars of *Neaspilota wilsoni* (Goeden and Headrick 1999), *N. footei* (Goeden 2001), *N. aenigma* (Goeden 2000b), and *N. appendiculata* (Goeden 2000c) also have four (two pairs of) stelex sensilla reported to ring the caudal segment; however, these stelex sensilla characteristically are ringed by different-shaped, minute acanthae, unlike *P. blanci,* which lacks a basal ring of minute acanthae.

Second instar larva.—White, elongate-ovoidal, rounded anteriorly, truncated posteriorly (Fig. 6A), body segments well-defined, prothorax circumscribed by many round, oval or elliptical, flattened, rugose pads of different size (Fig. 6B-1), few rugose pads on gnathocephalon (Fig. 6B), rugose pads absent from remaining thoracic and abdominal segments; dorsal sensory organ well-defined, flattened (Figs. 6B-2, C-1); anterior sensory lobe (Fig. 6C-2) with terminal sensory organ (Fig. 6C-3), lateral sensory organ (Fig. 6C-4), supralateral sensory organ (Fig. 6C-5), and pit sensory organ (Fig. 6C-6); oral ridge (Figs. 6B-3, C-7) with entire margins, lateral to terminal sensory organ, and separate from stomal sense organ (Figs. 6B-4, C-8), which lies ventrolaterad of anterior sensory lobe; mouthhook (Figs. 6B-5, C-9) with four teeth (Fig. 6D); median oral lobe laterally compressed, apically rounded (Figs. 6B-6, C-10); anterior thoracic spiracle recessed in body fold, with three, indistinct, flattened "papillae" (Fig. 6E); lateral spiracular complexes not seen; each posterior spiracular plate bears three ovoid rimae (Fig. 6F-1), ca. 0.009 mm long, and four, unbranched spiniform interspiracular processes (Fig. 6F-2) 0.006 mm long; sensilla lateral to spiracular plate and intermediate sensory complex not seen.

The habitus of the second instar of *P. blanci* (Fig. 6A) probably actually differs little in shape from the "barrel-shaped" (doliform) second instars of *P. stonei* (Green et al. 1993) and *P. kristineae* (Goeden and Teerink 1997a) or the cylindrical shape ascribed to *P. anthracina* (Goeden and Teerink 1997b) and *P. lisae* (Goeden and Teerink 1997a). However, only *P. blanci* among them has the prothorax circumscribed by the numerous, different sized, rugose pads described above (Fig. 5B-1). The dorsal sensory organ is well-defined in the first and second instars of all six congeneric species (Figs. 6B-2, C-1; Green et al. 1993; Goeden et al. 1994; Goeden and Teerink 1997a, b), unlike certain *Neaspilota* spp. in which the definition of this character differs between these instars and can be used to separate them (Goeden 2001). The single oral ridge present in *P. blanci* (Figs.

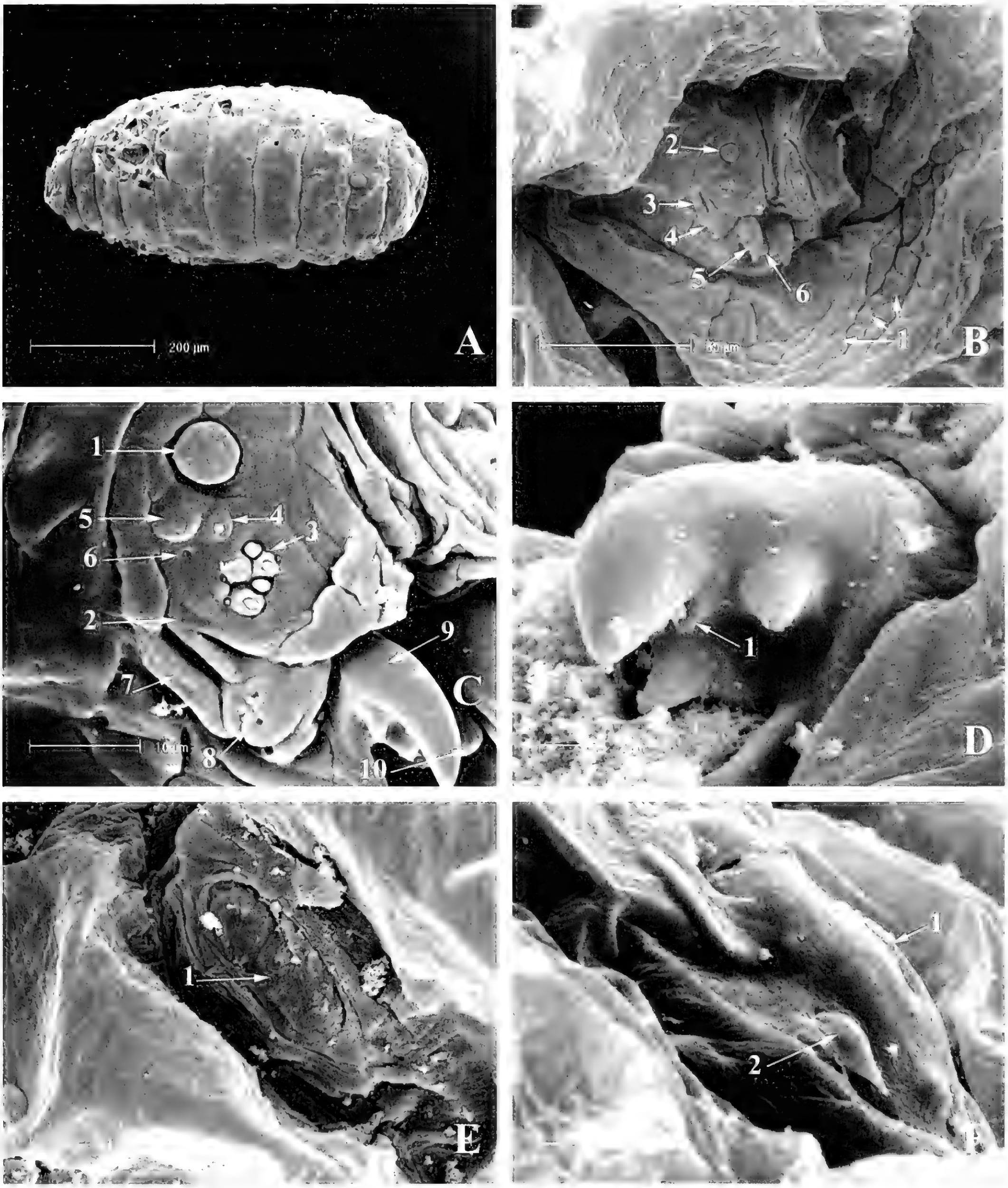

Fig. 6. Second instar of *Procecidochares blanci*: (A) habitus, anterior to left; (B) gnathocephalon, anteriolateral view, 1- rugose pads, 2- dorsal sensory organ, 3- oral ridge, 4- stomal sense organ, 5- mouthhook, 6- median oral lobe, (C) 1- dorsal sensory organ, 2- anterior sensory lobe, 3- terminal sensory organ, 4- lateral sensory organ, 5- supralateral sensory organ, 6- pit sensory organ, 7- oral ridge, 8- stomal sense organ, 9- mouthhook, 10- median oral lobe; (D) ventral view of mouthhook with four teeth; 1- small inner tooth; (E) anterior thoracic spiracle; (F) posterior spiracular plate, 1- rima, 2- interspiracular process.

6B-3, C-7) went unmentioned and uncounted in second instars of *P. anthracina, P. kristineae, P. lisae* (Goeden and Teerink 1997a, b) and *P. stonei* (Green et al. 1993). Only in *P. anthracina* (Goeden and Teerink 1997b) could the distinct separation of the stomal sense organ from adjacent oral ridges in *P. blanci* (Figs. 6B-4, C-8) also be seen from published illustrations compared to those other congeners. The discovery of a mouthhook with four teeth in the second instar of *P. blanci* (Fig. 6D) is especially noteworthy, not only as the sole example of this many teeth in this instar, but also of any instar of other tephritids examined by RDG and coworkers to date. Because of the usually hidden, central, ventral location of this small fourth tooth, it posits the question of whether such a tooth or teeth may have been overlooked in other larvae. The view in Figure 6D is not usually obtained with specimens prepared for scanning electron microscopy, because much of the gnathocephalon all-too-often is withdrawn inside the prothorax.

Third instar larva.—Pale yellow or white, elongate-ellipsoidal, tapering anteriorly, truncated posteriorly, distinctly segmented (Fig. 7A), rugose pads circumscribe anterior halves of pro-, meso- and metathorax (Fig. 7B-1), but not abdominal segments, which are finely, smoothly wrinkled; gnathocephalon conical, flattened dorsally and anteriorly (Fig. 7B-2); dorsal sensory organ well-defined, flattened (Fig. 7C-1); anterior sensory lobe (Fig. 7C-2) bears terminal sensory organ (Fig. 7C-3), lateral sensory organ (Fig. 7C-4), supralateral sensory organ (Fig. 7C-5), and pit sensory organ (Fig. 7C-6); two oral ridges (Fig. 7C-7) laterad and ventrolaterad of anterior sensory lobe, entire, and separated from stomal sense organ (Fig. 7C-8) ventrad of anterior sensory lobe; mouthhook (Fig. 7B-3) tridentate (Fig. 7D-1); median oral lobe, thickened basally, smoothly rounded apically (Fig. 7D-2); anterior thoracic spiracle recessed on posterior margin of prothorax with two, flattened "papillae" (Fig. 7E); lateral spiracular complexes not seen; each posterior spiracular plate (Fig. 7F) bears three ovoid rimae, ca. 0.022 mm in length (Fig. 7F-1), and four, unbranched, single or paired spiniform interspiracular processes, each 0.007 mm long (Fig. 7F-2); stelex sensilla dorsolaterad and ventrolaterad of spiracular plate, a verruciform sensillum lateral of spiracular plate.

Although the general appearances of the third instars of *Procecidochares* spp. are similar, the habitus of the third instar of *P. blanci* (Fig. 7A) most closely approximates that of *P. flavipes* (Goeden et al. 1994) among the six species studied in California to date (Green et al. 1993, Goeden and Teerink 1997a, b). The gnathocephala of *P. blanci* and *P. flavipes* are flattened dorsally and anteriorly (Fig. 7B-2), whereas those of the others are more or less conical. Both species have rugose pads on the thoracic segments; however, these fully circumscribe the anterior half of these segments in *P. blanci* (Fig. 7B), but circumscribe the prothorax only and cover the lateral and ventral surfaces of the meso- and metathorax in *P. flavipes* Aldrich (Goeden et al. 1994). The dorsum and intersegmental membranes of the abdomen of *P. flavipes* bear clawlike minute acanthae, absent in *P. anthracina, P. blanci, P. kristineae, P. lisae* (Goeden and Teerink 1997a, b) and *P. stonei* (Green et al. 1993). *Procecidochares anthracina* (Goeden and Teerink 1997b) has rugose pads anteriorly circumscribing its prothorax only.

The dorsal sensory organ is prominent in the third instar of all six species of *Procecidochares* that we have studied; however in *P. flavipes,* this organ is verruciform (Goeden et al. 1994), protruding and dome-shaped in *P. stonei* (Green et al. 1993), *P. anthracina* (Goeden and Teerink 1997b), *P. lisae,* and *P. kristineae* (Goeden and Teerink 1997a), but is flattened in *P. blanci* (Fig. 7C-1). Two oral ridges (rugose pads) are present in the third instar of *P. blanci* (Fig. 7C-7), one more than in the second instar (Figs. 7B-3, C-7). However, as no

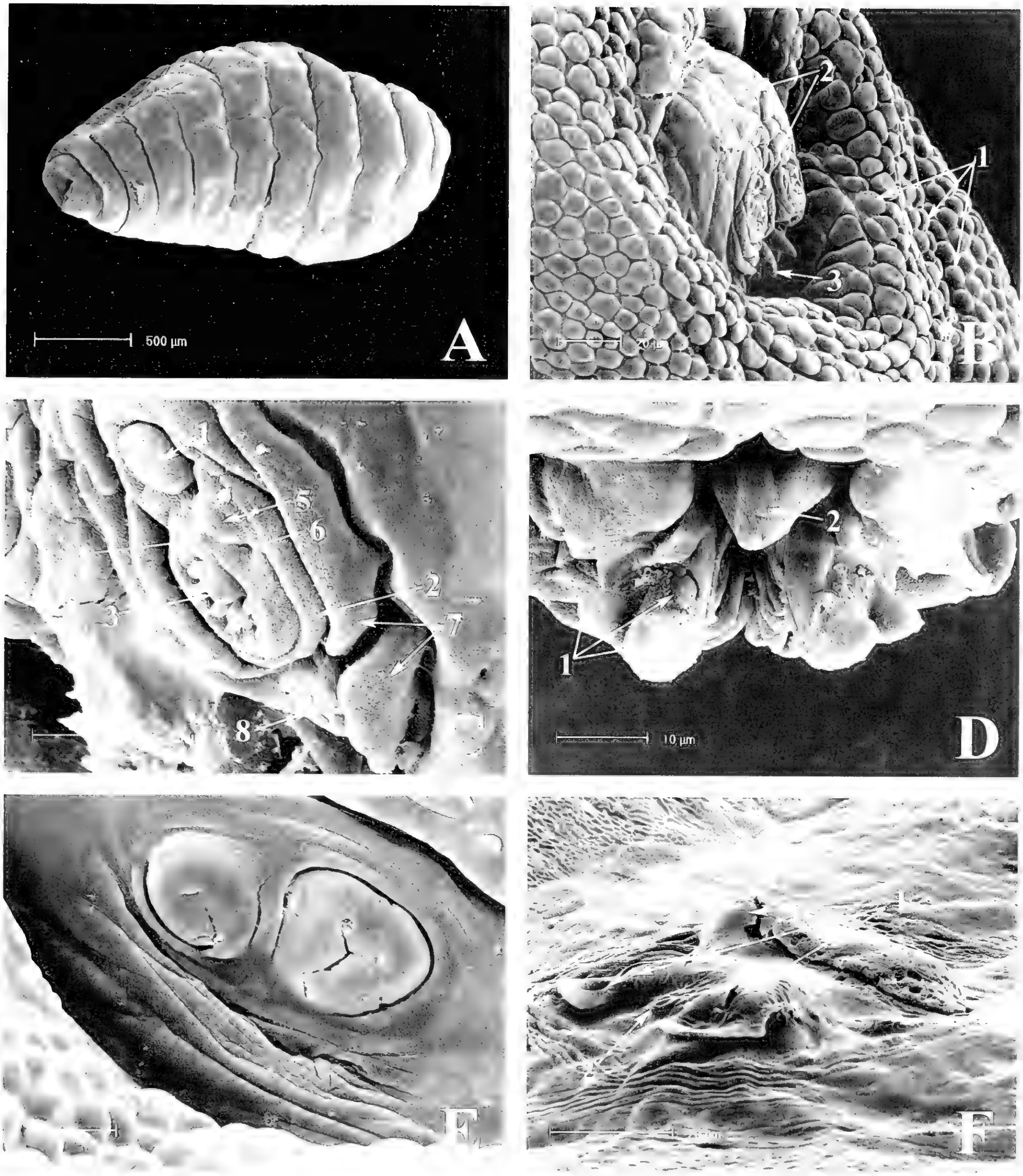

Fig. 7. Third instar of *Procecidochares blanci*: (A) habitus, anterior to left; (B) gnathocephalon, anteriolateral view, 1- rugose pads, 2- gnathocephalon, 3- mouth hook; (C) gnathocephalon, 1- dorsal sensory organ, 2- anterior sensory lobe, 3- terminal sensory organ, 4- lateral sensory organ, 5- supralateral sensory organ, 6- pit sensory organ, 7- oral ridges, 8- stomal sense organ; (D) oral cavity, ventral view, 1- three teeth of mouthhook, 2- median oral lobe; (E) anterior thoracic spiracle; (F) posterior spiracular plate; 1- three rimae, 2- interspiracular process.

oral ridges were reported as present in third instars of *P. stonei* (Green et al. 1993), *P. flavipes* (Goeden et al. 1994), *P. kristineae* and *P. lisae* (Goeden and Teerink 1997a), the following comparisons are now made. The third instar gnathocephalon of *P. flavipes* pictured in Goeden et al. (1994) shows at least six oral ridges laterad of the anterior sensory lobe, one such oral ridge in *P. kristineae* and *P. lisae* (Goeden and Teerink 1997a), at least two are seen in *P. anthracina* (Goeden and Teerink 1997b), but none are discernable in *P. stonei* (Green et al. 1993). The lateral margins of the rugose pads of *P. anthracina* (Goeden and Teerink 1997b) approach being serrate, or are at least, uniquely strigosely margined. The number, arrangement, and serrated margins of these oral ridges are prime taxonomic characters for larvae of *Neaspilota* spp. (Goeden 2001).

The progression of teeth on each mouthhook of *P. blanci* from two teeth in the first instar (Figs. 5B-5, C-7), to four teeth in the second instar (Fig. 6D), to three teeth in the third instar (Fig. 7D-1) is noteworthy, as usually this progression is from fewer to greater numbers of teeth among the larvae of Tephritinae that we have studied. Accordingly, and more conventionally, the number of oral ridges in *P. blanci* increased from none in the first instar, to one in the second instar (Figs. 6B-3, C-7), to two in the third instar (Fig. 7C-7). However, like the number of teeth on the mouthhook, starting with the usual lack of anterior spiracles in the first instar, the number of papillae is three in the second instar (Fig. 6E), but decreases to two in the third instar (Fig. 7E), the number of papillae also helps one to distinguish these instars in *P. blanci.*

The recessed location and flattened nature of the anterior spiracle of *P. blanci* in both the second (Fig. 6E) and third instars (Fig. 7E) apparently is unique so far to this species of *Procecidochares;* in other larvae of California Tephritinae this organ is not recessed and projects above the surrounding integument. However, this recessed condition also could be an artifact of specimen preparation for SEM.

The spiniform interspiracular processes on the posterior spiracular plate of the third instar of *P. blanci* (Fig. 7F-2) match those reported for this instar of *P. stonei* (Green et al. 1993), *P. kristineae* and *P. lisae* (Goeden and Teerink 1997a), *P. anthracina* (Goeden and Teerink 1997b), and *P. flavipes* (Goeden et al. 1994). The stelex sensilla reported dorsolaterad and ventrolaterad of the posterior spiracular plate of *P. blanci* apparently are unique for this species compared to other congeners examined to date. Stelex sensilla surround the caudal segment of *P. flavipes* (Goeden et al. 1994) in a four-dorsal, six ventral arrangement (or two-dorsal, three-ventral arrangement relative to each posterior spiracular plate). Additionally, the caudal segment of *P. flavipes* reportedly bears "compound sensilla" or a pair of stelex sensilla ventrad of each posterior spiracular plate (Goeden et al. 1994); however, the "compound sensilla" in this position on the third instars of *P. kristineae* and *P. anthracina* consist of a verruciform sensillum and a stelex sensillum (Goeden and Teerink 1997a, b), but in *P. lisae,* two verruciform sensilla (Goeden and Teerink 1997a). These so-called compound sensilla may be homologous with the intermediate sensory complexes reported in larvae of California *Trupanea* spp. (Goeden and Teerink 1999a, b, and citations therein) and *Neaspilota* spp. (Goeden 2001 and citations therein). No additional sensilla were reported lateral or dorsal of the spiracular plates of *P. stonei, P. kristineae,* or *P. lisae* (Green et al. 1993, Goeden and Teerink 1997a).

Puparium.—Ellipsoidal, mostly translucent white, with elliptical or ovoidal (Fig. 8A), irregularly margined, dark brown to black spot (n = 14), 1.11 ± 0.07 (range, 1.0–1.25) mm long, 0.70 ± (range, 0.55–0.95) mm wide on abdominal tergites A3 or A4 to A7 (Fig. 8D); anterior half to all of mesothorax also dark brown or black in about one in ten puparia; anterior end bears the small, somewhat protuberent, invagination scar (Fig. 8B-1), anterior thoracic spiracles not discernable; caudal segment bears posterior spiracular plates, each with three broadly elliptical, raised rimae (Fig. 8C-1), and four, single or paired, spiniform, interspiracular processes (Fig. 8C-2). Ninety-three puparia averaged 2.56 ± 0.03

(range, 1.78–3.42) mm in length; 1.34 ± 0.02 (range, 0.91–2.00) mm in width.

DISTRIBUTION AND HOSTS

Procecidochares blanci is a true monophage, with *Isocoma acradenia* as its only known host plant. The distribution of *P. blanci* may coincide wholly or in part with that of its host plant, which as a desert subshrub inhabits sandy or clay soils in alkaline or gypsum flats or slopes below 1,300 m in California, Arizona, and Nevada, and Baja California, Mexico (Hickman 1993). 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

Procecidochares blanci is a bivoltine species in southern California in which a flower-head-infesting (F_1) generation alternates with a gall-forming generation (F_2) on the same host plant. Accordingly, the biology of each generation differs considerably and is treated separately as follows.

Florivorous (F_1) generation.—*Egg:* In each of 17, closed, preblossom, immature flower heads of *Isocoma acradenia* an average of 5.5 ± 1.0 (range, 1–15) eggs of *P. blanci* were inserted separately, or more commonly side-by-side, in groups of three or more, pedicel-last, between the phyllaries (Fig. 9A). All 93 eggs rested with their long axes parallel to the long axes of the flower heads (Fig. 4A). Only one egg (1%) penetrated an outer ovule adjacent to an inner phyllary; otherwise, no other ovules were damaged by oviposition. The receptacles of these preblossom heads that contained eggs averaged 0.79 ± 0.05 (range, 0.28–1.14) mm in diameter.

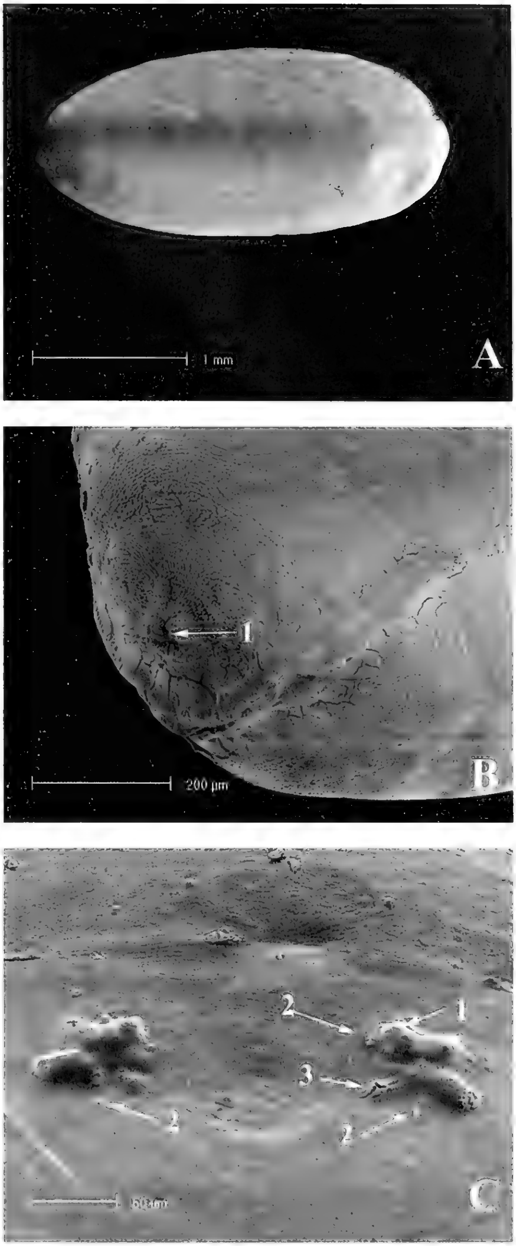

Fig. 8. Puparium of *Procecidochares blanci*: (A) habitus, anterior to left; (B) anterior end, 1- invagination scar; (C) caudal segment, 1- rima, 2- interspiracular process, 3- ecdysial scar.

Larva: Upon eclosion, the 88 first instars found in 32, closed, preblossom flower heads moved to an ovule (Fig. 9B) or between two adjacent ovules on which they fed from an external position (Fig. 9B). Thus, an average of 2.75 ± 0.3 (range, 1–8) first instars were found in these 32 heads. Usually the attacked ovules were located on the periphery of a head (Fig. 9B), and each larva fed independently of the other larvae

Fig. 9. Life stages of the F_1 florivorous generation of *Procecidochares blanci* in *Isocoma acradenia*: (A) three eggs (arrows) in closed, preblossom flower head; (B) first instar (arrow) feeding on ovule; (C) second instar (arrow) feeding in cell in expanded ovule; (D) two puparia (note black spots on dorsa) in cells formed from expanded achenes; (E) female fly on open flower head; (F) male fly on open flower head. Lines = 1 mm.

in a flower head, although the same ovule sometimes was attacked from opposite sides by different larvae. The receptacles averaged 1.02 ± 0.03 (range, 0.85–1.42) mm in diameter and an average of 3.2 ± 0.4 (range, 1–7) ovules were attacked in these 32 flower heads, or about 21% of an average total of 15 ± 0.3 (range, 7–21) ovules/achenes counted in 99 preblossom and blossom flower heads. No receptacle was abraded or pitted by larval feeding.

Second instars (Fig. 9C) continued feeding on the ovules in preblossom flower heads which remained closed. They fed with their bodies ± perpendicular to, but always well above the receptacles, scraping away with their mouthhooks from a position between adjacent sides of two, or sometimes three ovules, which began to enlarge, the excavation forming a cell within which each larva developed separately (Fig. 9C). Receptacles of eight flower heads containing 12 second instars averaged 1.21 ± 0.04 (range, 1.14–1.42) mm in diameter. Thus, these flower heads each contained an average of 1.5 ± 0.5 (range, 1–5) larvae that had collectively damaged an average of 3 ± 1 (range, 2–10) ovules, or about 20% (range, 13–66%) of the average total of 15 ovules per flower head.

Third instars continued to feed mainly on the expanded ovules in preblossom and blossom flower heads. Twenty-five flower heads that averaged 1.5 ± 0.03 (range, 1.4–1.99) mm in diameter each contained an average of 1.8 ± 1.1 (range, 1–5) third instars. An average of 3.4 ± 4.2 (range, 1–8) of the soft achenes therein were expanded and damaged, or about 23% (range, 7–53%) of the average total of 15 ovules/soft achenes per flower head. Third instars in flower heads fed within their individual cells formed from two or three excavated, enlarged ovules (Fig. 9D). No receptacles were abraded or pitted. Upon completing their feeding, the larvae oriented with their anterior ends away from the receptacles, retracted their mouthparts, and pupariated (Fig. 9D).

Pupa: The receptacles of 45 overwintered flower heads that contained 95 puparia, or an average of 2.1 ± 0.2 (range, 1–6) puparia per head, each averaged 1.7 ± 0.05 (range, 1.28–2.85) mm in diameter (Fig. 9D). An average of 4.3 ± 0.4 (range, 2–12) soft achenes therein had expanded and were damaged, or about 29% (range, 13–80%) of the average total of 15 ovules/soft achenes per flower head.

Adult: Adults (Figs. 9E, F) are short-lived. Under insectary conditions, 31 unmated males lived an average of 6.6 ± 0.7 (range, 3–19) days, and 36 virgin females averaged 5.1 ± 0.4 (range, 3–15) days. The flies mate shortly after their emergence from flower heads (Fig. 7F) and soon thereafter begin oviposition; description of mating behavior is deferred until after the biology of the immature stages of the gall-forming (F_2) generation is described next.

Gallicolous (F_2) generation.—*Egg:* In each of 18 axillary buds on basal, woody, previous year's branches of *Isocoma acradenia* an average of 2.3 ± 0.3 (range, 1–6) eggs of *P. blanci* were inserted separately, or more commonly, side-by-side, in pairs or groups of three, pedicel-last, usually between the leaves at the base of the bud (Fig. 10A). Most eggs were found in axillary buds on basal branches an average of 10.5 ± 1.3 (range, 0–21) cm above the branch juncture with a stem. All 41 eggs rested with their long axes parallel to the long axes of the axillary bud (Fig. 10A). Three and one (10% of total) eggs were inserted into the centers of two separate buds, but none of the 41 eggs penetrated any plant tissue, thus no buds were damaged by oviposition. The diameters of these buds bearing eggs averaged 1.06 ± 0.08 (range, 0.56–1.54) mm.

Monthly samplings of branch segments at the Whitewater location showed that the embryos remained within the egg chorions for as long as 2 months, eclosion apparently occurring along with the onset of axillary bud growth triggered by winter rainfall. From one to four first instars were found in eight infested buds out of hundreds of buds sampled at random during the first three months following oviposition, as nothing distinguished axillary buds bearing eggs or newly eclosed larvae. The newly eclosed first instars moved to the base of the bud where they entered the central pith below the apical meristem and began to excavate a single open chamber in which they fed singly or gregariously (Fig. 10B). Furthermore, the larvae remained as first instars during subsequent months as the galls slowly developed and grew to full size (Fig. 10C). Each gall represented a foreshortened axillary branch circumscribed by up to 20 ranks of scale-like, lanceolate, entire-margined leaves demarking stunted internodes. Eventually, the gall-bearing branches elon-

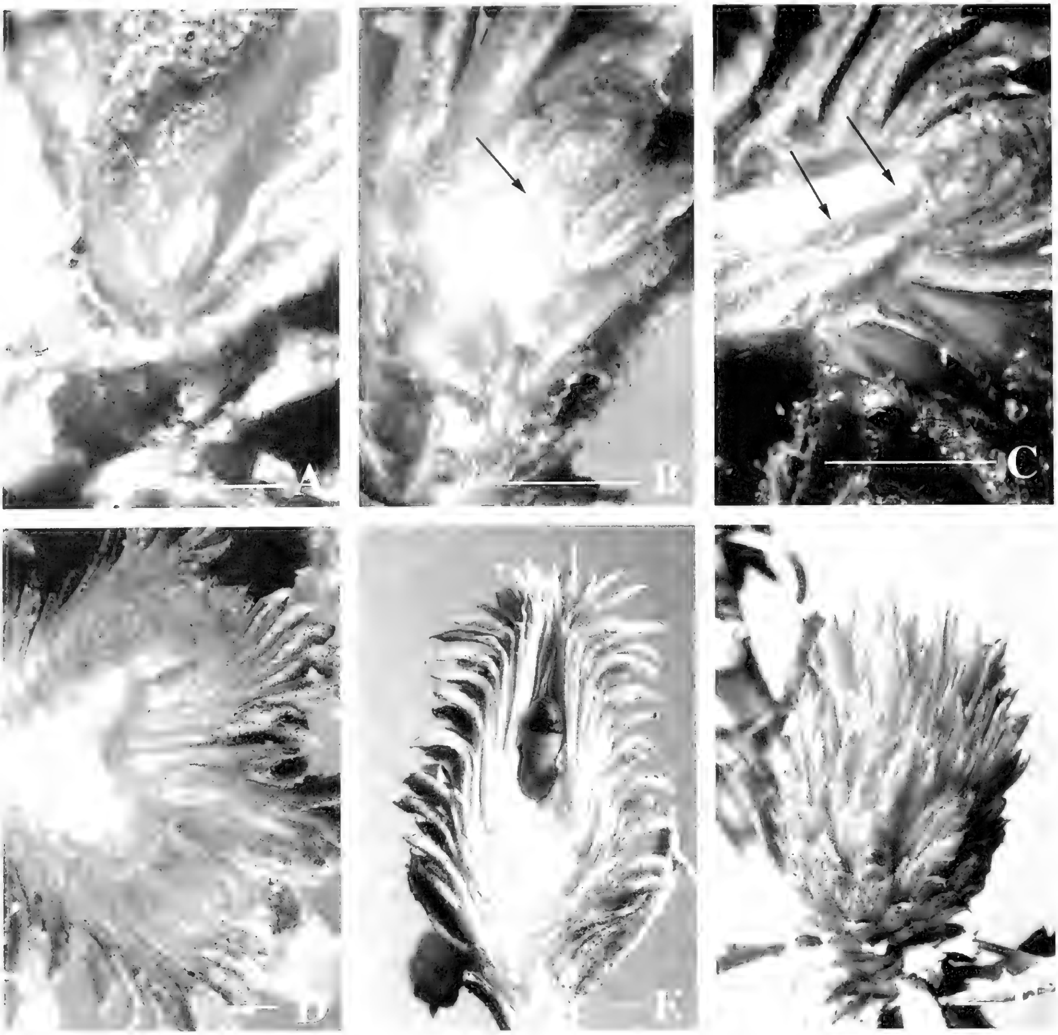

Fig. 10. Life stages of the F_2 gallicolous generation of *Procecidochares blanci* in *Isocoma acradenia*: (A) two eggs (arrows) in axillary bud; (B) first instar (arrow) feeding in cell in pith beneath apical meristem of expanding axillary bud in saggital section; (C) first instar (arrow) continuing to feed in cell in pith of stunted axillary branch comprising gall; (D) saggital section through gall showing two branches formed as two first instars in gall separated; (E) empty puparium in open, mature gall, (F) intact mature gall. Lines = 1 mm.

gated noticeably more slowly than uninfested axillary branches and thus were detected and sampled much more readily. The first instars fed in open, linear cells in the center of the expanded pith of the galled branches (Figs. 10B, C). However, at some indeterminate point from 2 to 10 mm above the gall base, multiple larvae within single galls separated and split off from their common chamber and began individual branch tunnels (Fig. 10D). These first instars continued to extend their separate tunnels, feeding just below the apical buds topping each gall branch (Fig. 10D). As the gall grew apically, the parenchyma lining the gall cavity grew together basally sealing the tunnel behind each apically feeding larva (Fig. 10E). The basal leaves died and desiccated while the upper leaves remained green, and as these dead leaves abscissed, and the galls added growth apically, each gall became seated on a stalk of varying length. Gall growth ceased when the larva, still in the first instar, consumed the gall meristem and nipped off the terminal leaf-bracts at their bases, forming a bundle that plugged the future exit tunnel of the gall. The larva then molted to the second instar and rapidly passed through the second and third stadia as it expanded the gall chamber to accomodate its larger size, leaving no frass, only the discarded cephalopharyngeal skeleton of the second instar at the bottom of this cell. The second and third stadia plus pupariation and the pupal period ending in adult emergence altogether lasted about 1 month. The adult emerged from the puparium by pushing outward the aforementioned plug of basally-excised terminal bracts and exiting through the exit tunnel so formed (Fig. 10E). Mature galls ranged in shape from ovoidal to cylindrical to flattened-obovoidal (Fig. 10F). Galls from which adults emerged were denoted by browned apices, with the entire gall subsequently dying and turning from blue- to yellow-green to brown. Twenty-six mature galls contained an average of 1.5 ± 0.1 (range, 1–3) puparia. They were borne on pedicels that averaged 5.8 ± 0.9 (range, 3–18) mm in length, and measured 12.6 ± 0.4 (range, 8–15) mm long by 9.1 ± 0.4 (range, 6–13) mm wide. Thus, the stunted axillary branches comprising these galls, including pedicels, averaged 18 ± 0.6 (range, 15–22) mm in length.

Mating behavior.—The premating, mating, and postmating behaviors of *P. blanci* 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 of *Procecidochares* 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, Headrick and Goeden 1994). Moreover, both sexes displayed wing supination blending into rapid wing enantion during copulation if agitated, especially the females, just prior to postcopulatory separation.

Mating behavior of *P. blanci* was similar to that reported for *P. kristineae* by Silverman and Goeden (1980) and Goeden and Teerink (1997a). Males tracked females slowly from behind and mounted females by jumping onto their dorsa, either headfirst or from behind. Once mounted, males clasped the dorsolateral anterior margins of the dorsum of the females with their foretarsal claws; the middle tarsi grasped the base of the oviscape laterally, and the hindtarsi were crossed under the oviscape (Fig. 11C). The wings of the female were parted at 80 to 90° (Figs. 11A–B), those of the male at 30 to 40° (Figs. 9A–B), with both pairs of wings more or less centered over the midlines of both flies. The mouthparts of the male were held above the scutellum of the female. The oviscape of the female was elevated about 30° above the horizontal, with the rest of her body more or less parallel to the substrate (Fig. 11C); the body of the males was angled upward 30° (Fig. 11C). The male generally maintained no contact with the substrate during copulation (Fig. 11C).

Eleven copulations (Figs. 11A–C) averaged 94 ± 13 (range, 19–158) minutes in duration and usually occurred after midday, when the flies were most active in bright sunlight. Males mounted females perfunctorily and aggressively initiated copulation, sometimes wrestling the females into submission on the substrate. This strong male sex drive was also demonstrated by one male persistantly attempting coitus with a dead female and commonly by males wedging themselves between a copulating pair (Fig. 11D) or attempting to mate by climbing onto a male already in copula. This latter behavior often caused the male to extend the time the pair remained in copula and to remain atop the female after copulation and

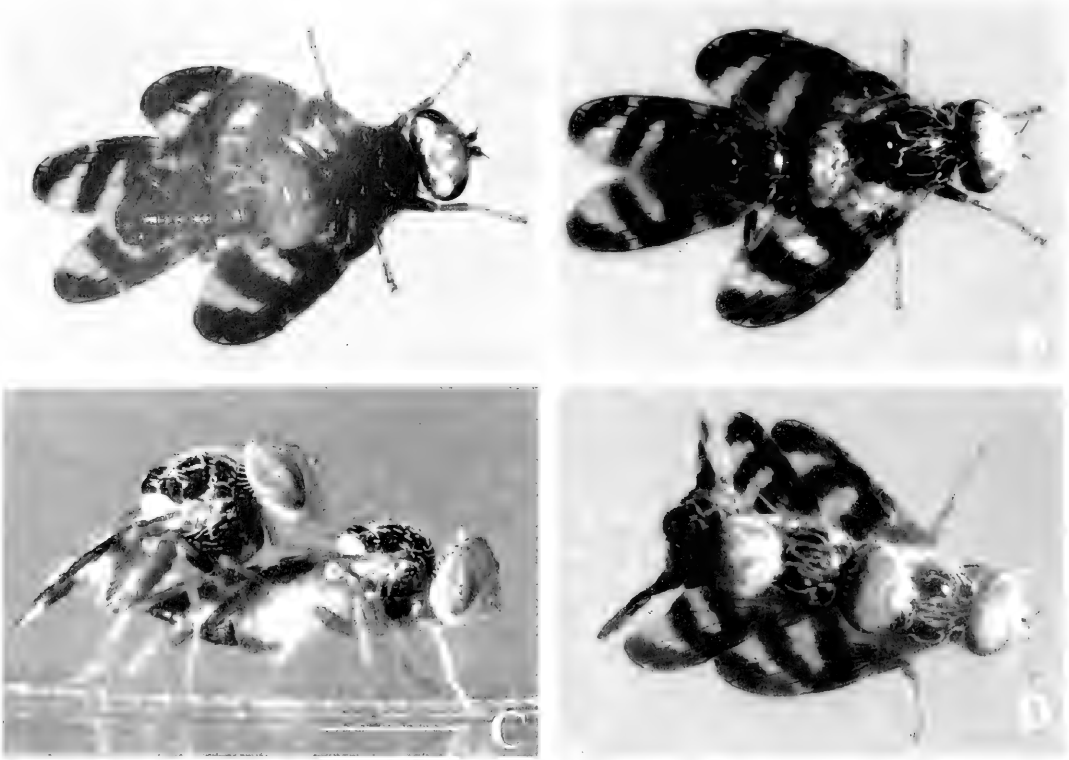

Fig. 11. Mating pairs of *Procecidochares blanci*: (A) ventral view; (B) dorsal view; (C) lateral view; (D) second male has inserted itself between mating pair (see text). Lines = 1 mm.

reattempt, and sometimes successfully resume, copulation. Four 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; three such uncouplings lasted less than 10 seconds, and the fourth 12 seconds.

Seasonal history.—*Procecidochares blanci* is a bivoltine, circumnatal species (Headrick and Goeden 1994, 1998) on *Isocoma acradenia* in southern California. Reproduction by the florivorous F_1 generation parallels flower head development by its host plant. Eggs are laid in flower heads in late summer (September) and the larval and pupal stages are completed by early fall (November), when the F_1 adults emerge, mate and oviposit in axils of axillary buds on last year's branches. As noted above, these eggs remain unhatched with the slowly developing embryos inside until January when larval eclosion and gall initiation coincide with axillary bud growth stimulated by the resumption of winter rainfall. The gallicolous, F_2 generation larvae remain as first instars throughout the remainder of the winter, the spring, and summer, as the galls slowly reach their full size about August. Then, within a month, the F_2 generation rapidly passes through the second and third stadia, pupariates, and the adults emerge from galls to repeat the reproductive cycle.

Natural enemies.—Many individual *Mesopolobus* sp. (Hymenoptera: Pteromalidae), *Eurytoma veronia* Bugbee (Hymenoptera: Eurytomidae), and *E.* sp. nr. *tumoris* were reared from puparia of *P. blanci* as solitary, larval-pupal endoparasitoids.

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TWO NEW SPECIES OF *LEPIDOSTOMA* RAMBUR (TRICHOPTERA: LEPIDOSTOMATIDAE) FROM THE WESTERN UNITED STATES

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Abstract.—Two new species of *Lepidostoma* (Trichoptera: Lepidostomatidae) from the western United States are described and illustrated. ***Lepidostoma apache*, n. sp.**, is known from eastern Arizona and appears related to *L. xolotl* in the *L. (Nosopus) mexicanum* species group. ***Lepidostoma uinta*, n. sp.**, is known from central Utah and appears related to *L. verodum, incertae sedis* within the subgenus *Nosopus.*

Key Words: Trichoptera, *Lepidostoma,* new species, Arizona, Utah

The nearly cosmopolitan genus *Lepidostoma* Rambur (Lepidostomatidae) contains 80 known species from North and Central America; of these, 28 are found from the United States west of the Great Plains (Weaver 1988, Morse 2000). *Lepidostoma* larvae usually occur in areas of low current velocity within a wide variety of lotic habitats, but are occasionally found in lakes as well (Denning 1958, Wiggins 1996). Larval cases are typically quadrate in shape and composed of a variety of materials, including stones, leaf pieces, and woody debris (Weaver 1988, Wiggins 1996). Weaver (1988) provided descriptions and keys to the fauna of North America including Mexico. Additional species have recently been described from the eastern United States, Costa Rica, Guatemala, Mexico, and Panama (Flint and Harp 1990, Holzenthal and Strand 1992, Bowles et al. 1994).

The caddisflies of the western United States are not particularly well known; for example, a 1995 collecting trip to seven western states organized in conjunction with the 8th International Symposium on Trichoptera documented 20 new state species records (Ruiter 1996). Recent collecting by the author in the Apache National Forest in eastern Arizona has yielded an undescribed species of *Lepidostoma.* A second undescribed *Lepidostoma* species was collected in 1994 from the Uinta National Forest, central Utah, by K. M. Kjer, Rutgers University, and R. W. Holzenthal, University of Minnesota. These two species are described and illustrated herein. Type material has been deposited in the National Museum of Natural History, Smithsonian Institution, Washington, DC (NMNH), and in the University of Minnesota Insect Museum, Saint Paul, MN (UMSP).

Lepidostoma apache Houghton, new species
(Fig. 1)

This species, typical of the *L.* (*Nosopus*) *mexicanum* group as defined by Weaver (1988), appears most similar to *L. xolotl* Holzenthal and Strand known from eastcentral Mexico (Holzenthal and Strand 1992). It differs from *L. xolotl* in having posterior elongate processes on segment X and in having lateral flanges on the phallus.

Male.—Known only from holotype, stored in EtOH, abdomen cleared. Head

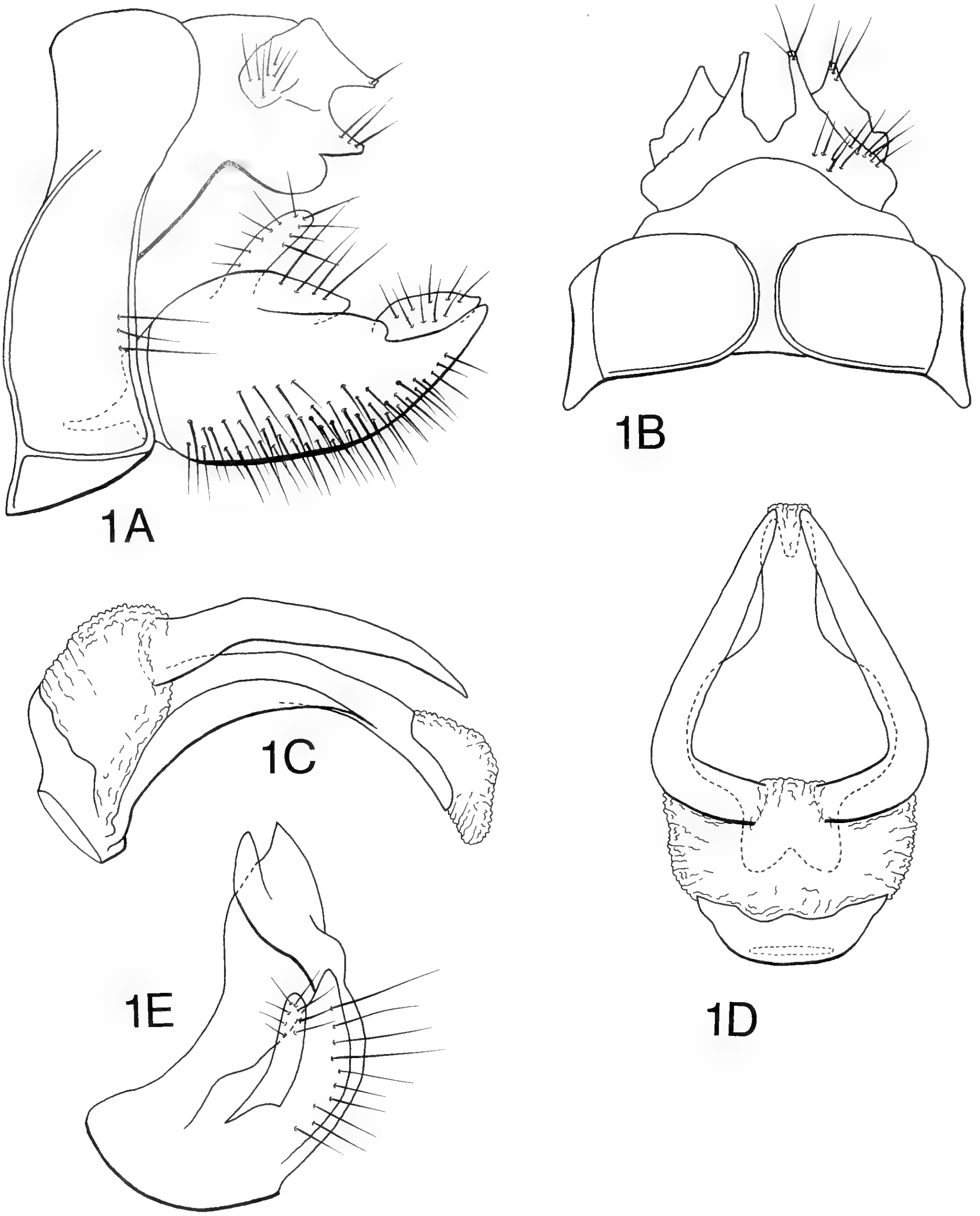

Fig. 1.—*Lepidostoma apache,* male genitalia. A, Segments IX, X, inferior appendages, lateral. B, Segments IX, X, dorsal. C, Phallus, lateral. D, Phallus, dorsal. E, Inferior appendage, dorsal.

golden brown. Maxillary palp one-segmented, fused together mesally into a single tongue-like structure for virtually their entire length, acuminate apically, lateral region densely covered with silky brown setae, medial portion with sparse short brown setae on dorsal and ventral surface. Scape long and cylindrical, subequal to interocular

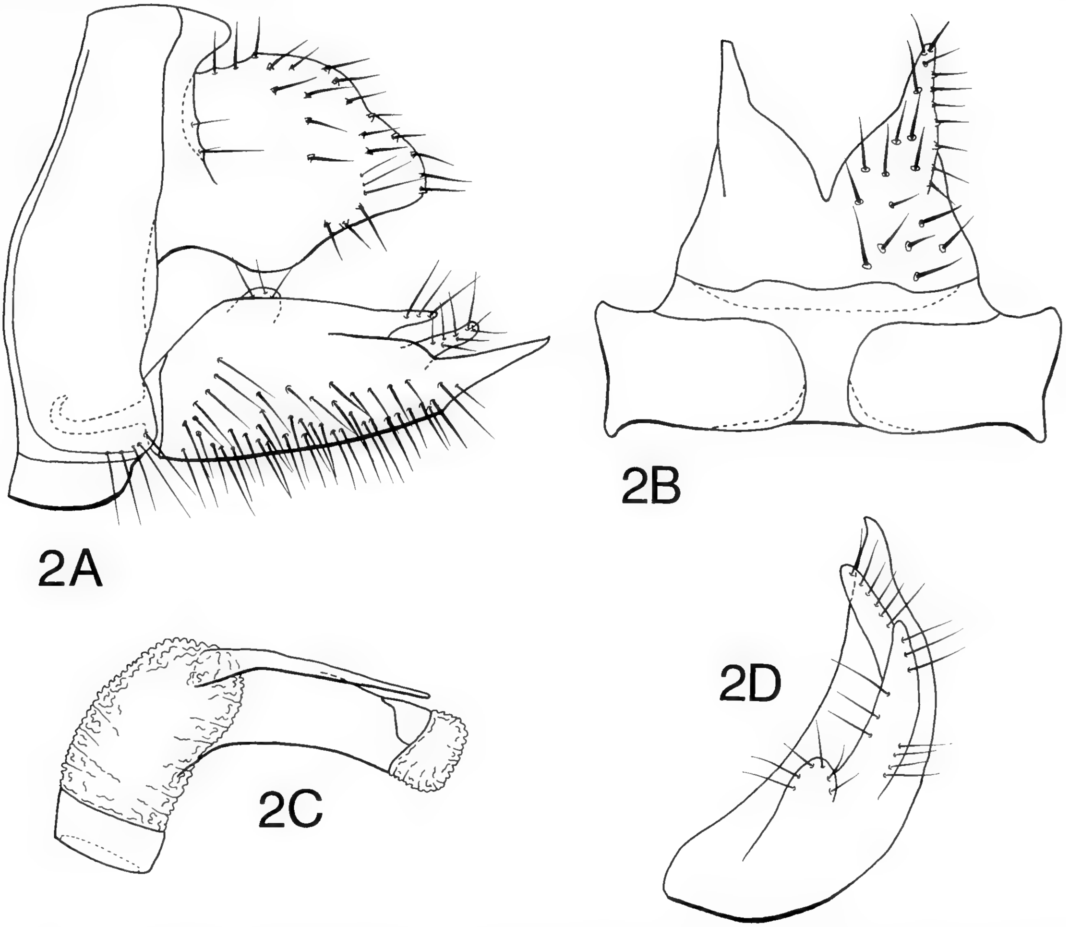

Fig. 2.—*Lepidostoma uinta,* male genitalia. A, Segments IX, X, inferior appendages, lateral. B, Segments IX, X, dorsal. C, Phallus, lateral. D, Inferior appendage, dorsal.

distance, anteromesal surface covered with pale yellow setae. Flagellomeres pale yellow, posteromesal surface with flattened tufts of short light brown setae. Body golden brown. Forewing length 9 mm, golden brown, sparsely covered with short light brown setae. Hindwing 7 mm, pale golden brown, sparsely covered with short light brown setae. Legs pale yellow. Tibial spur formula 2–4–4.

Male genitalia: Segment IX annular, parallel-sided. Segment X in lateral view with short setae, median ridge extending anteroventrad, posteriorly with two elongate processes separated dorsoventrally by u-shaped notch, rounded process below these two processes; in dorsal view cleft mesally, elongate median processes on either side of cleft separated from rest of tergum by v-shaped notch. Inferior appendages similar to *L. xolotl*; in lateral view broad basally, setose on ventral half, with long, cylindrical basodorsal process bearing short setae and thumb-like middorsal processes bearing long setae, apex acuminate, with oval-shaped apicodorsal process bearing setae. Phallobase with apical margin jagged; phalicata tubular, slightly longer than parameres, with basal lateral flanges extending to apical 1/3; paramere glabrous; phallotremal sclerite, if present, difficult to discern.

Female.—Unknown

Holotype.—♂, ARIZONA: Greenlee Co., Blue River, Forest Road 281, near Upper Blue Campground, Apache-Sitgreaves National Forest, 33.6635°N, 109.0917°W, 1,768 m, 20.vi.1999, D.C. Houghton (UMSP).

Etymology.—Named for the type locality, the Apache National Forest.

Lepidostoma uinta Houghton, new species

(Fig. 2)

This species appears most similar to *L. verodum* Ross, placed as *incertae sedis* in the subgenus *Nosopus* and known from northern California, Oregon, and Washington (Weaver 1988). It differs from *L. verodum* in having a posteriorly protrusive segment X and in having less modification of the male scape and maxillary palpi.

Male.—Holotype pinned, abdomen cleared, wings removed and mounted separately. Head golden brown. Maxillary palp one-segmented, fused mesally into cylindrical structure, slightly widening apically into knob, covered with silky brown setae. Scape brown, long, cylindrical, slightly widening apically, subequal to interocular distance, tufts of dark brown and pale yellow setae on anteromesal margin. Flagellomeres pale yellow, posteromesal surface with flattened tufts of short light brown setae. Body golden brown. Forewing length 7.5 mm, golden brown, covered with yellow setae. Hindwing 6 mm, pale golden brown, covered with light yellow setae. Legs pale yellow. Tibial spur formula 2–4–4. Anterodorsal surface of abdominal segments III–VIII with pair of setal warts sometimes subdivided into two pairs.

Male genitalia: Segment IX annular, parallel-sided. Segment X in lateral view approximately quadrate, protruding posterad, with many scattered spinose projections and short thick setae; in dorsal view cleft mesally. In lateral view inferior appendages slightly elongate, longer than segment X, setose on ventral half; basodorsal process short, barely reaching dorsal aspect of inferior appendage; middorsal process slender and elongate, bearing setae; apex acuminate with subapical slender dorsal process upturned apically. Phallobase approximately quadrate; phalicata short, stout, slightly longer than parameres; paramere glabrous; phallotremal sclerite present.

Female.—Unknown

Holotype.—♂, UTAH: Utah Co., Uinta National Forest, tributary of South Fork Creek, Hwy 92, 40°26.268′N, 111°37.943′ 2,146 m, 5.ix.1994, K. M. Kjer and R. W. Holzenthal (UMSP).

Paratypes.—Same data as holotype, 2 ♂ (UMSP), 1 ♂ (NMNH).

Etymology.—Named for the type locality, the Uinta National Forest.

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DISCOVERY OF THE FEMALE OF *PARASIMULIUM* (*ASTONEOMYIA*) *MELANDERI* STONE (DIPTERA: SIMULIIDAE) IN A CAVE IN BRITISH COLUMBIA, WITH A DISCUSSION OF ITS PHYLOGENETIC POSITION

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Abstract.—Two females of *Parasimulium* (*Astoneomyia*) *melanderi* Stone were collected from a cave on Vancouver Island, British Columbia and these are described for the first time. The presence of elongate, thickened setae on various body parts are possibly adaptations to subterranean existence. Further phylogenetic interpretation supports earlier hypotheses that the subgenus *Astoneomyia* Peterson is the sister group of *Parasimulium s. str.* and that together they form the sister group of all other Simuliidae.

Key Words: black fly, Nearctic, aquatic

The genus *Parasimulium* Malloch is an intriguing group of black flies restricted to the Pacific Northwest of North America (Peterson 1977, Borkent 1992). This taxon, with only four species, is the sister group of all remaining Simuliidae and therefore has the potential of shedding substantial light on the diversification of the family.

For years *Parasimulium* was known from only eight male specimens. Wood and Borkent (1982) rediscovered a substantial population of *P. crosskeyi* Peterson from the type locality at Wahkeena Creek, Oregon, and were able to report, for the first time, on the females of this genus. Subsequently, viable eggs were obtained from a female of *P. stonei* Peterson and these and the resultant first and second instar larvae were described (Borkent and Wood 1986). Courtney (1986) discovered the larvae and pupae of *P. crosskeyi* in the seepages at Wahkeena Creek and briefly described these stages.

Although previous authors considered *Parasimulium* to hold a primitive position within the family, Wood and Borkent (1982) were the first to provide cladistic evidence that the group represented the earliest lineage within the family. Subsequently, Borkent and Wood (1986) suggested that three larval character states indicated that the genus may actually belong within the Prosimuliini and recognized that there was a conflict in the interpretation of adult and larval character states.

Currie (1988), based on cladistic analysis of larvae, pupae and adult characters, supported Wood and Borkent's (1982) hypothesis that *Parasimulium* is indeed the monophyletic sister taxon of all other simuliids. This interpretation was recently supported by Moulton's (2000) molecular systematic analysis of the Simuliidae.

Parasimulium is currently divided into two subgenera, with *P.* (*Parasimulium*) including three species (*P. crosskeyi, P. stonei, P. furcatum* Malloch) and *P.* (*Astoneo-*

myia Peterson) with the single species *P. melanderi* Stone, previously known only from the male holotype collected on Mt. Baker, Washington in 1925. In this paper we report the first females of *P.* (*Astoneomyia) melanderi* and provide further analysis of its phylogenetic position and the cladistic relationship of *Parasimulium* to other Simuliidae.

MATERIALS AND METHODS

Two female specimens of *P.* (*Astoneomyia*) were collected with an aspirator in Pellucidar Cave, 20 km SW of Port McNeill, British Columbia (elevation—200 m) on August 13, 1997 by Patrick Shaw. The cave has only one known natural exit, which ends after a short section of air-filled passage in a sump, completely filled with flowing water. A dry, second entrance was recently excavated by hand and is now reinforced with a culvert that is completely covered to recreate a naturally reduced airflow. Even before excavation there was a moderate air flow through the obstructing rocks. This dry portion of the cave was open in the distant past (probably about 8,000 years ago) as is evidenced by the presence of a wide array of bird and mammal bones inside the cave.

The two females were collected about 10 m from this dry entrance, well into the dark zone of the cave. The passage is less than 1 meter high for approximately the first 20 meters from the dry entrance but has a few taller (less than 2.5 m) bells in the ceiling. The females of *P. melanderi* were retrieved from damp walls at the top of these bells.

There is a substantial cave stream (about 2.5 meters wide, ½ meter deep) about 165 meters down-passage from the dry entrance and small wall-seeps en route, starting about 20m from the sample site. The main stream enters the explored portion of the cave through a sump that has been dived for more than 200m, and only two small air bells were found. From the in-cave spring, the stream flows through about 220 meters of air-filled passage before disappearing, resurfaces in a downstream portion of the cave after about 30 meters and flows about 100 meters to the exit. It is the 220 meter portion of the stream that provides access to the dry portion of the cave where the *P. melanderi* females were collected.

The nearest surface lotic habitat to the dry entrance is the stream which exits the natural entrance of the cave, 218 meters from the dry, excavated entrance. There are no other lotic habitats nearby (not within several kilometers).

Both females were originally collected into ethylene glycol and transferred soon thereafter to isopropanol. One female was mounted on a microscope slide according to the methods in Borkent and Bissett (1990) and is deposited in the Royal British Columbia Museum (Victoria). The other female was dissected, the head and abdomen cleared in lactic acid and stored in glycerine in a vial under the critical point dried body glued on a pin, and is deposited in the Royal Ontario Museum (Toronto).

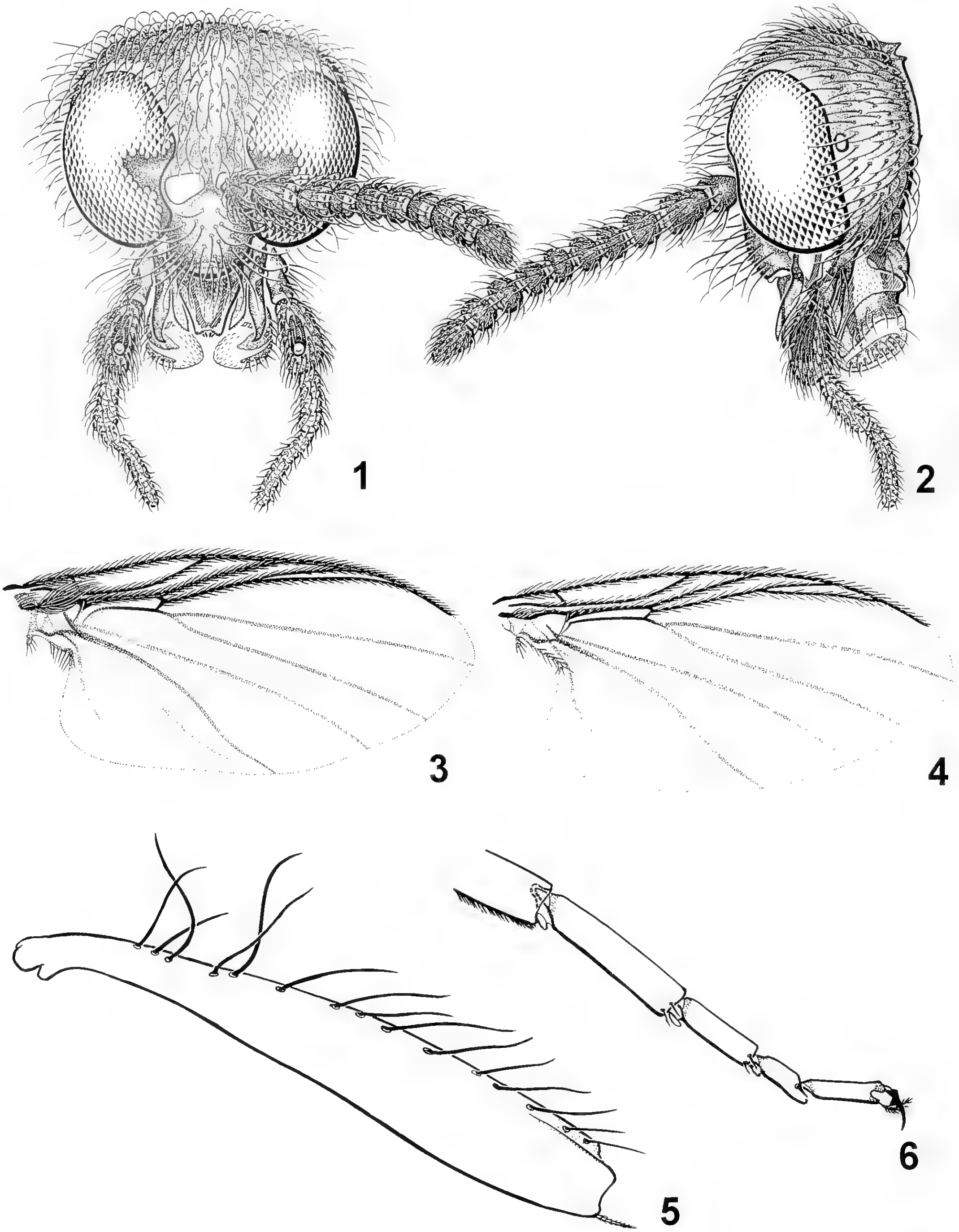
Terms for structures follow those used in the Manual of Nearctic Diptera (McAlpine 1981). Wing length was measured from the arculus to the wing apex.

DESCRIPTION

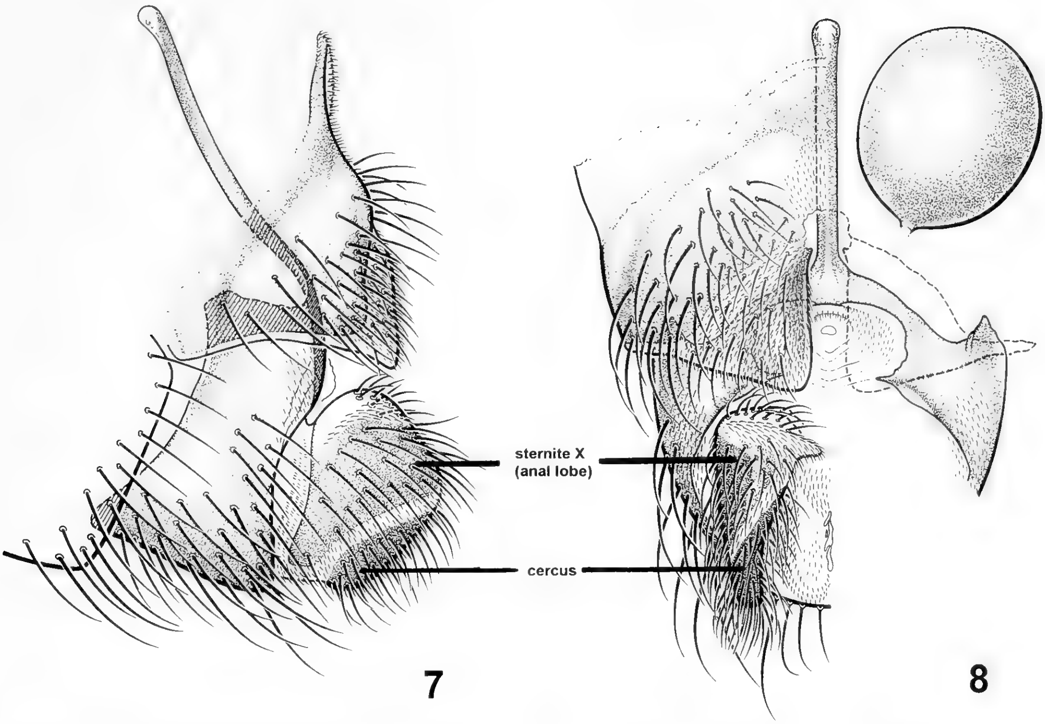
Parasimulium melanderi Stone
(Figs. 1–3, 5–8)

The following description gives only those features different from those of other species of *Parasimulium* (see Peterson, 1977, Wood and Borkent 1982, Peterson and Courtney 1985).

Female.—*Pigmentation and chaetotaxy*: Entire body dark brown to black but with apical half of bulb of halter pale, stemmatic bulla pale. Chaetotaxy similar in distribution to those of other *Parasimulium* but with the following bearing strikingly elongate, thicker setae, many of these strongly curved: ventral region of frons (not clearly shown in Figs. 1–2), clypeus (not clearly shown in Figs. 1–2), antepronotum, posteromedial region of scutum, lateral margin



Figs. 1–6. *Parasimulium melanderi.* 1, Anterior view of head of female. 2, Lateral view of head of female. 3, Wing of female. 4, Wing of male. 5, Hind tibia of female. 6, Tarsomeres 2–5 of hindleg of female.



Figs. 7–8. *Parasimulium melanderi.* 7, Lateral view of terminalia. 8, Ventral view of terminalia.

of scutum, scutellum, stem vein, ventroapical 0.7 of fore femur with 8 long setae, ventroapical 0.4 of mid femur with 6 long setae, ventroapical 0.4 of hind femur with 11–12 long setae, base of hind tibia with 2–3 long setae (Fig. 5).

Head (Figs. 1–2): Capsule with pair of dorsal occipital crests on either side of midline. Well-developed stemmatic bulla present. Antenna with eight flagellomeres. Labrum well developed, elongate, projecting well beyond base of palpal segment III, with nearly parallel sides, with well-developed medial cuticular rod, small nosepiece, three apical sensilla associated with somewhat reduced prestomal tooth (possibly bearing 2 small cusps). Mandible slender, about same length as labrum, tapering to curved, pointed apex, without teeth. Lacinia about same length as labrum, with spicules subapically, apically. Hypopharynx well-developed, about same length as labrum, with abundant apical spicules. Sensory vesicle on palpal segment III about ⅘ length of segment, with short neck, broad mouth. Palpal segment V short, markedly less than twice length of palpal segment IV.

Thorax: Supra-alar notch shallow. Empodium hairlike, plumose, extending to near apex of claws (Fig. 6).

Wing (Fig. 3): Length = 2.45–2.46 mm. Rs forking just proximal to point where R_1 meets costa; length Rs/R_{4+5} = 0.81–0.85. False vein (m-cu fold) ill-defined, evanescent well before wing margin.

Abdomen: Tergites, sternites well developed. Apparently completely developed eggs present in one female, similar in shape to those of other black flies, with a swollen dorsal transverse bulge.

Terminalia (Figs. 7–8): Arm of genital fork (sternite 9) with large subquadrate terminal plate bearing short, pointed medial process. Anal lobes (sternite 10) closely approximated anteromedially; in lateral view not extended beyond cercus. Cercus small, situated apicomedially on anal lobe, with only faint line of demarcation. Spermatheca without unsclerotized ring around apex of spermathecal duct.

DISCUSSION

There are presently two species of *Parasimulium* (*Astoneomyia*) known: *P. melanderi* from Mt. Baker, Washington and an undescribed species from Oregon (a single male) which differ from each other in details of the male genitalia (Currie and Courtney in prep.). On the basis of geographical proximity we consider it more likely that the two females described here are those of *P. melanderi* although there is a possibility that they are conspecific with the male from Oregon or perhaps even represent a third species. The males of *P. melanderi* and the undescribed species have unicolourous, brown halters and the presence of a pale area on the apical half of the bulb of the halter of the females here may indicate their distinctiveness. Furthermore, the wing of the females described here have a comparatively shorter Rs (compared to the length of R_{4+5}) than the male of *P. melanderi* (Figs. 3–4). Regardless, we have conservatively recognized the females here as those of *P. melanderi*.

Peterson (1977, 1981) keyed the two subgenera of *Parasimulium*. However, the length of Rs/R_{4+5} is actually quite similar between the two groups and the other wing characters are, at best, difficult to see clearly. Furthermore, female *P. melanderi* have only a partially pigmented halter, requiring further modifications of the key. The following adequately distinguishes the two groups and may replace couplet 2 in Peterson (1981):

– Body uniformly dark brown with only halter, in some, at least partially pale . . . . *Parasimulium* (*Astoneomyia*)

– At least some parts of body lightly pigmented, including antenna, palpus, much of thorax (scutum may be light brown), at least abdominal tergite 1 . . . . *Parasimulium* (*Parasimulium*)

Recent descriptions and redescriptions of adults of species of *Parasimulium* also requires some changes in the diagnosis of adults of this genus, as follows:

Diagnosis.—R_1 joined to C slightly beyond middle of wing; branches of Rs conspicuously separated by membrane, with posterior branch (R_{4+5}) ending well before apex of C. Costa, Sc and branches of R with elongate macrotrichia dorsally and ventrally; differentiated macrotrichia absent. Basal section of R short, less than one-fourth distance from base of Rs to apex of wing. Bm cell absent. False vein (m-cu fold) not forked apically. CuA_2 only slightly sinuous. Mesepimeral tuft absent. Katepisternum tapered ventrally; katepisternal sulcus absent. Calcipala and pedisulcus absent. Empodium elongate, spiculose. Gonostylus without apical peglike seta. Paramere with strap-like connection to the anterolateral arms of the ventral plate; without apical spines or other accessory structures. Anal lobes (sternite 10) closely approximated anteromedially. Spermatheca spherical and without pattern; with or without an unsclerotized ring around apex of spermathecal duct.

Wood and Borkent (1982) discussed the phylogenetic relationships between the subgenera of *Parasimulium* and provided evidence that the genus was the sister group of all remaining Simuliidae. Borkent and Wood (1986) on the basis of limited information of some larval features suggested that the genus might actually belong within the Prosimuliini. Our investigation of the female of *P. melanderi* provides some further phylogenetic information and our knowledge of the relationships within the genus is summarized in the cladogram in Fig. 9, based on the following character states.

1. Katepisternum rounded, convex in lateral view (plesiomorphic); katepisternum greatly reduced, almost pointed ventrally (apomorphic).
   This feature was discussed by Wood and Borkent (1982).
2. Mesepimeral tuft present (plesiomorphic); mesepimeral tuft absent

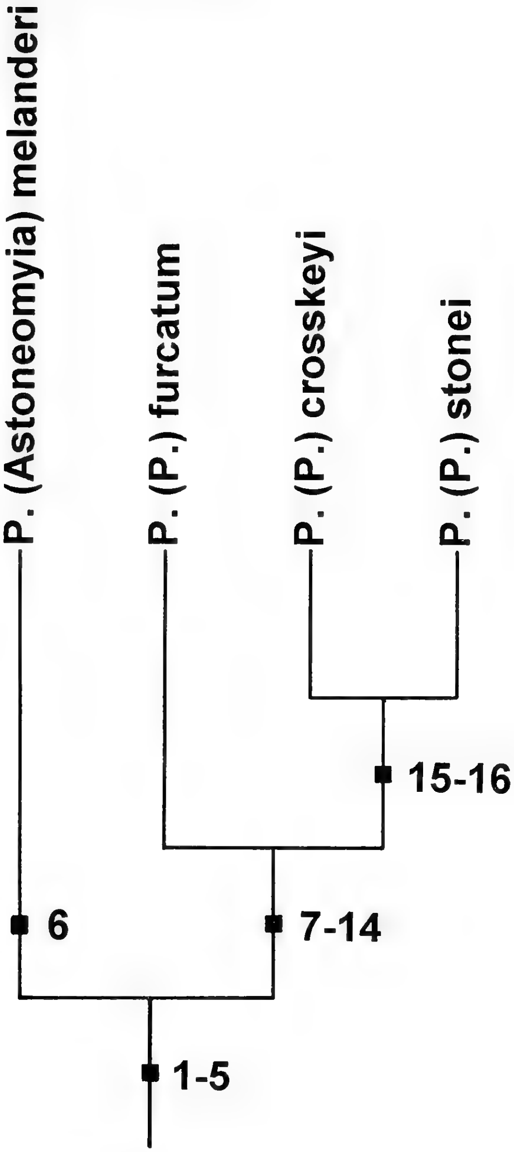


Fig. 9. Cladogram showing relationships between species of *Parasimulium.* Numbers refer to character states discussed in the text.

(apomorphic).
This feature was discussed by Wood and Borkent (1982).

3. Peg-like seta at apex of gonostylus present (plesiomorphic); peg-like seta at apex of gonostylus absent (apomorphic).
This feature was discussed by Wood and Borkent (1982).
4. Basal medial cell present (plesiomorphic); basal medial cell absent (Fig. 3) (apomorphic).
This feature was discussed by Currie (1988).
5. Basal radial cell long (plesiomorphic); basal radial cell short (Fig. 3) (apomorphic).
This feature was discussed by Currie (1988).
6. Body without elongate, stout, strongly curved setae (plesiomorphic); body with elongate, stout, strongly curved setae (apomorphic).
Thick, elongate and strongly curved setae are present on the following body parts of *P. melanderi*: ventral region of frons, clypeus (not shown in Figs. 1–2), antepronotum, posteromedial region of scutum, lateral margin of scutum, scutellum, fore femur, and hind tibia (Fig. 5). Such setae are present in a few other Simuliidae (e.g., *Gymnopais* Stone) but are never as strongly curved as they are in *P. melanderi.* Such setae are not present in other Chironomoidea (and likely not in any other Culicomorpha). Furthermore, the distinct distribution of setae described above seems to be unique and therefore an autapomorphy of the species.

7–11. Five features were recognized by Wood and Borkent (1982) as synapomorphies of *Parasimulium s. str.* These are (in the apomorphic state): (7) Supra-alar notch narrow and deep, with sharp supra-alar crest and narrow lateral opening; (8) Gonocoxite with apicolateral finger-like extension and row of setae along adjacent edge; (9) Ventral plate with forked apex, the apicolateral prongs immobilized by "inner gonostylus"; (10) Medial sclerite long and strap-like, with apically widened portion; (11) Gonostylus with subapical cusp on dorsal side.

12. Female labrum well-developed (ple-

siomorphic); labrum triangular, apically narrow (apomorphic).
Female *P. melanderi* have a well-developed labrum (Fig. 1) (see description above for details) which they share with all other Simuliidae (Colbo et al. 1979, Sutcliffe and McIver 1982). The reduced, apically slender labrum of females of species of *Parasimulium s. str.* is therefore apomorphic (lacking medial cuticular rod, nosepiece and prestomal teeth). Further outgroup comparison indicates that other members of the Chironomoidea have variable character states present. *Archaeochlus* Brundin, the only Chironomidae with biting mouthparts and Ceratopogonidae which feed as female adults (virtually all) all have well-developed labra.

13. Tergite 1 with same pigmentation as more posterior tergites (plesiomorphic); tergite 1 yellow, contrasting with at least tergite 3 (apomorphic).
All members of *Parasimulium s. str.* have a yellow tergite 1. Other Simuliidae and virtually all other Chironomoidea have either unicolourous abdominal tergites or with other pigmentation patterns.
14. Female cercus situated posteriorly on segment 10 (plesiomorphic); cercus arising from a subapical notch on the anal lobe (sternite 10) (apomorphic).
The cercus of *P. melanderi* is situated apically on the anal lobe (Fig. 8). Those of *Parasimulium s. str.* arise from a subapical notch on the dorsal side of the anal lobe. The cerci of other Chironomoidea are situated apically in virtually all members (including all early lineages) and is also the condition in all other Simuliidae (so that the cercus is not obscured by the anal lobe in ventral view).
15. Scape brown (plesiomorphic); scape yellow (apomorphic).
This feature was discussed by Currie (1988).
16. Tergite 1–2 and sternites 1–3 brown (plesiomorphic); tergite 1–2 and sternites 1–3 yellow (apomorphic).
This feature is unique within the Chironomoidea, although a few derived lineages of Chironomidae approximate the derived condition.

Wood and Borkent (1982) discussed three synapomorphies grouping all Simuliidae other than *Parasimulium.* One other feature has now come to our attention. *Parasimulium* adults (both males and females) have an elongate, spiculose empodium (Fig. 6) and all other Simuliidae have only a short empodium. Outgroup comparisons indicate variable character states. However, early lineages of Ceratopogonidae (*Austroconops* Wirth and Lee, Forcipomyiinae) and most Chironomidae have a well developed empodium. Thaumaleidae have a small empodium. This character state distribution suggests to us that the small empodium of Simuliidae other than *Parasimulium* is likely synapomorphic.

The reduced mandibles and laciniae of female *P. melanderi* (Fig. 1) indicate that these, like females of other species in the genus, are unable to feed on vertebrate blood.

The collection of two females from a cave habitat provides intriguing possibilities for obtaining further information about *P. melanderi.* The larvae of two other species of *Parasimulium* have been described (Borkent and Wood 1986, Courtney 1986) and both are striking in having reduced eyes and lack of pigmentation. In the only collection of immatures from nature, Courtney (1986) reported the presence of larvae and pupae of *P. crosskeyi* in the interstitial spaces between cobble-sized stones from a seep that was excavated by hand 1 meter into a bank side, close to a stream in northern Oregon. These larvae exhibited features often present in cave dwelling organisms. The recovery of *P. melanderi* from a cave suggests to us the strong possibility that this species also is associated with subterranean lotic habitats. The strikingly elongate stout hairs on the front of the head and legs suggests that adults may be able to move around in the dark and the lack of nearby surface lotic habitats indicates that *P. melanderi* are truly associated with a cave habitat. It seems likely that *P. melanderi* adults mate outside the cave and enter the dry entrance to lay their eggs in the cave stream (or seeps). It certainly warrants searching this and other wet caves for further material of this fascinating genus.

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LECTOTYPE DESIGNATIONS OF TWO SPECIES OF LACHNINAE DESCRIBED BY H. F. WILSON (HEMIPTERA: APHIDIDAE)[1]

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Abstract.—Examination of the National Museum of Natural History, Smithsonian Institution, Aphidoidea Collection confirmed the presence of two species of Lachninae previously described by H. F. Wilson. The types of one species were thought to have been lost but have been rediscovered. Lectotypes and paralectotypes are designated for *Eulachnus thunbergii* Wilson and *Lachniella thunbergii* Wilson. *Cinara thunbergii* (Wilson) represents a **new combination** for *Lachniella thunbergii* Wilson.

Key Words: Aphididae, Lachninae, *Eulachnus thunbergii* Wilson, *Cinara thunbergii* (Wilson), *Lachniella thunbergii* Wilson, lectotype, paralectotype, new combination

The status of two aphid species, *Eulachnus thunbergii* Wilson and *Lachniella thunbergii Wilson = Cinara thunbergii* (Wilson) **n. comb.**, described by H. F. Wilson in 1919 has been a source of confusion for more than 80 years. This situation arises from the fact that both species were given the same specific name, the descriptions for both were published in the same month and year, and apparently the original specimens were collected or submitted for identification in the same lot of material in 1905. Even in the two most recent aphid catalogs (Eastop and Hille Ris Lambers 1976, Remaudière and Remaudière 1997) the combination used is *Eulachnus thunbergii* (Wilson). Cook (1982) recorded that the type specimens of *Cinara thunbergii* were not in the National Museum of Natural History (USNM), Smithsonian Institution, and probably were lost. However, Cook (1982) also commented that notes written by T. Pergande indicated that there were two collections of material involved and Pergande thought there were two species.

While examining the type series of aphids in the USNM Aphidoidea Collection, it was discovered that specimens on five slides filed as part of the type series for *Eulachnus thunbergii* (Wilson) were not congeneric with the specimens on one of the other slides in the type series. The specimens on those five slides were determined to be members of *Cinara.* After closer examination of both the specimens and label data, it was determined that the series evidently represented the two different species described by Wilson (1919a, b).

The specimens here designated lectotypes are to fix and stabilize the current concept of the names, and the specimens have been labeled so as to identify the lectotypes.

Eulachnus thunbergii Wilson
(Fig. 1)

Eulachnus thunbergii Wilson 1919a:3.
Eulachnus thunbergii (Wilson) (*Lachniella*), Eastop and Hill Ris Lambers 1976:

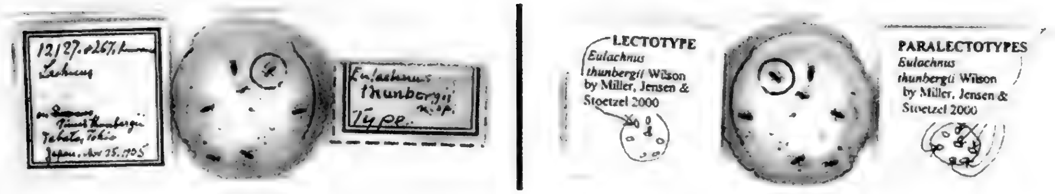

Fig. 1. Lectotype and paralectotypes of *Eulachnus thunbergii* Wilson illustrating front side (left) and reverse side (right).

195; Remaudière and Remaudière 1997: 201(misinterpretation in part).

Seven specimens, 1 alate male and 6 apterous oviparae, mounted in balsam on a single slide, were located. This is the same number of specimens and sex ratio that Wilson (1919a) listed in his original description. There is no doubt that the single slide in the USNM Aphidoidea Collection is the one Wilson (1919a) used for his species description. First, a label attached to the right side of the slide reads, "*Eulachnus thunbergii* n.sp. Type." Second, the left label is with numbers and script as follows: "12127. = 267 Kuwana *Lachnus* on [the next word is marked through and is illegible] *Pinus thunbergii* Tabata, Tokio Japan, Nov. 25, 1905" (Fig. 1). This information is also reflected in Wilson's (1919a) description. His description of *E. thunbergii* also included a quoted reference to Pergande's 1906 notes. Pergande's note cards, which are located with the USNM Aphidoidea Collection literature, were checked and verified against the Wilson (1919a) description. Third, Wilson (1919a) gave a single series of measurements for the apterous female. Only one specimen out of the 6 apterous oviparae had a terminal antennal segment that was measurable. Its length (0.16 mm) was exactly as published and other measurements were comparable. In addition, his mention of the alate male as "the only available [male] specimen" and its nearly identical measurements to the specimen described, serve to reinforce the type status of the slide. We have added to the slide, on its reverse side, labels designating the lectotype, paralectotypes, and an accompanying map illustrating the location of each (Fig. 1). The left label reads: "LECTOTYPE *Eulachnus thunbergii* Wilson by Miller, Jensen & Stoetzel 2000." The right label reads: "PARALECTOTYPES *Eulachnus thunbergii* Wilson by Miller, Jensen & Stoetzel 2000." The lectotype (Fig. 1), which best reflects the measurements in Wilson's (1919a) description, is located in the one o'clock position on the front side of the slide and the 11 o'clock position from the reverse side (Fig. 1). A circle is drawn around the specimen. The positioning map reflects the view from the reverse side. All other specimens are paralectotypes. As a side note, Wilson (1919a) did mention the word "slides" in his original description. Considering the overwhelming evidence that this slide contains the syntypes, this was probably a typographical error or the remaining slides are lost.

The lectotype and paralectotypes of *E. thunbergii* are deposited in the USNM Aphidoidea Collection at Beltsville, Maryland, USA.

Cinara thunbergii (Wilson), **n. comb.**
(Fig. 2)

Lachniella thunbergii Wilson 1919b:19.
Eulachnus thunbergii (Wilson) (*Lachniella*), Eastop and Hill Ris Lambers 1976: 195; Remaudière and Remaudière 1997: 201(misinterpretation in part).

Twenty-two specimens, 1 alate male and 21 apterous oviparae, mounted in balsam on five slides, were located. This is the same number of slides that Wilson (1919b) recorded in his original description. Additionally, Wilson (1919b) stated that "three of

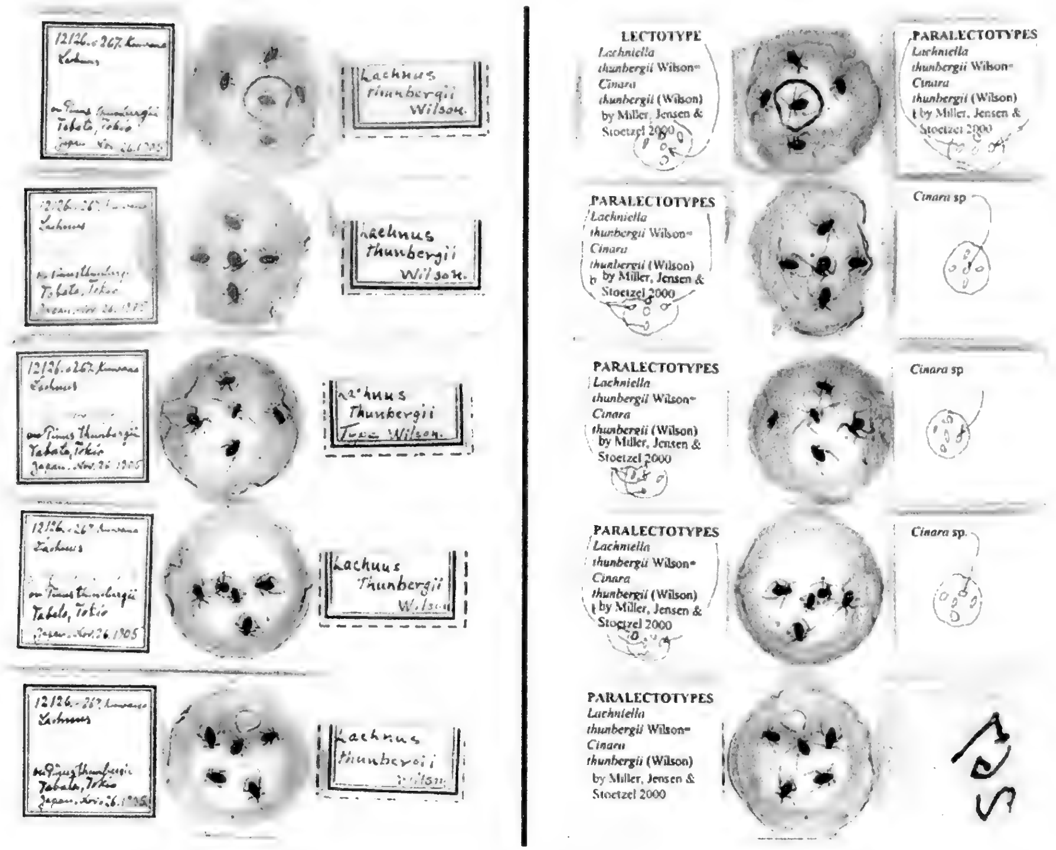

Fig. 2. Lectotype and paralectotypes of *Cinara thunbergii* (Wilson) illustrating front side (left) and reverse side (right).

the slides also contain apterous specimens of another species" but, he did not describe or make a determination for those specimens. Three of the slides in the USNM Aphidoidea Collection contain three specimens each of another *Cinara* species. Although Wilson (1919b) stated that Pergande's notes for *C. thunbergii* were furnished by Baker (A. C. Baker, U.S. Bureau of Entomology), they evidently were not used in their entirety. This may have been done because Wilson realized that the sample contained more than one species. Pergande's original note cards for *C. thunbergii,* dated March 1906 and also located with the literature at the USNM Aphidoidea Collection, were examined. Pergande received the specimens from S. I. Kuwana of the Imperial Agricultural Experiment Station, Tokyo, Japan, and recorded the following information that accompanied the material: "On the twigs of *Sciadopytis verticillata* S.et Z., and *Pinus.* Winged form:—I. Head, black. Eyes, red. Antenna, black. Prothorax, dark. Dorsal aspect, of meso metathorax, black. Abdomen, blackish green. Honeytubes black. Wingless form:—I. Body, purple but the dorsal-middle line and the posterior part of the body, covered with white hairs. Honeytubes, black. Antennae, pale yellow." An additional last line was added to the note card, "On *Pinus thunbergii* Parl., Tabata, Tokio, Nov. 26, 1905." Pergande's notes also listed his acquisition number (12126) and a submittal number (267). Both of these numbers appear on the slide label for the type series. Pergande's notes also included the statement saying, "This [either *C. thunbergii* or *Cinara* sp. since Pergande did not distinguish the two species] appears to be a new species, near *L. grossus* Kalt. [*Lachnus grossus* Kaltenbach = *Cinara piceae* (Panzer)]." There is no doubt that this series of slides represents Wilson's type series. Added to the slides (Fig. 2) on the reverse side is a label designating the lectotype, paralectotypes, and an accompanying map illustrating the location of each specimen. A circle is drawn around the lectotype. The label reads: "LECTOTYPE *Lachniella thunbergii* Wilson = *Cinara thunbergii* (Wilson) by Miller, Jensen and Stoetzel 2000." The positioning map reflects the view of the type specimens from the reverse side. All other specimens are paralectotypes and are designated as such with a label: "PARALECTOTYPES *Lachniella thunbergii* Wilson = *Cinara thunbergii* (Wilson) by Miller, Jensen and Stoetzel 2000." The position maps drawn for the paralectotypes also reflect the view from the reverse side. Labels that include the positions of the three other specimens of another species of *Cinara* that are not *C. thunbergii* are also attached to the reverse side (Fig. 2).

Cinara thunbergii is likely to prove to be a synonym of *Cinara pinidensiflorae* (Essig and Kuwana 1918), however this cannot be confirmed until autumnal forms of this group are available from both *Pinus densiflora* and *P. thunbergii* (V. F. Eastop, personal communication).

The lectotype and paralectotypes of *C. thunbergii* are deposited in the USNM Aphidoidea Collection at Beltsville, Maryland, USA.

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BUCHANANIELLA CONTINUA (WHITE) (HEMIPTERA: HETEROPTERA: ANTHOCORIDAE) FROM CALIFORNIA, WITH NEW SYNONYMY

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Abstract.—*Buchananiella continua* (White), originally described from the island of Madeira, now is known from many widely separated localities around the world. *Cardiastethus cavicollis* Blatchley, 1934, was described from southern California, and is synonymized with *B. continua* (**n. syn.**). Recent collections of this bug were taken from plant litter and shrubs infested with psocids, white flies, and mites. Details leading to the identification of *B. continua* and subsequent synonymy of *C. cavicollis* are given, and a diagnosis of the adult and pertinent other characters are provided to assist in recognition.

Key Words: Hemiptera: Heteroptera, Anthocoridae, non-indigenous species, California

F. Buchanan White (1879) described *Cardiastethus continuus* from the island of Madeira—an unlikely prospect to be discovered in California (Los Angeles, 1928; San Francisco, 1998 and 1999; and Oceanside, 1999). *Buchananiella* Reuter (1884) was described to include three species: *Cardiastethus sodalis* White from Hawaii, *Cardiastethus continuus* White from Madeira, and *Buchananiella whitei,* new species, from "Vandiemeus Land." No type of the genus was designated. Subsequently, Kirkaldy (1906) designated *Cardiastethus continuus* White as the type species. Herring (1965) clarified the position of *Buchananiella* with the type *B. continua* (White), and other included species, *annulata* (Carayon), *crassicomis* Carayon, *sodalis* (White), and *whitei* Reuter. He (Herring) later made *Buchananiella sodalis* (White) the type of the genus *Alofa* Herring in 1976. Hiura (1966) illustrated the adult and the male capsule of *B. continua* based on specimens from Picton, New Zealand, and for the first time showed the pair of large punctures on the scutellum. His drawing of the genital clasper agrees with the earlier illustration by Carayon (1957) of *B. continua.*

Carayon (1972) published a drawing of *Buchananiella continua* that closely resembled the specimens we examined from California; again, the pair of large punctures on the scutellum are very distinct. Péricart (1972) provided an excellent review of *B. continua* in his treatise on the Anthocoridae, Cimicidae, and Microphysidae. His drawing of the adult and a figure showing details of the male capsule, apex of the female abdomen, ostiolar canal, antennae, rostrum, and the outline of the head and pronotum provided our basis for positive identification of *Buchananiella continua.*

The key characters are small size (2.2–2.7 mm); dark color (lighter in color in southern California specimens); dorsum with distinct, pale, rather dense, decumbent setae; antennal segments one and two greater in diameter than segments three and four, second segment slightly enlarged apically; pronotum with sides tapered anteriorly, collar narrow, posterior margin concave, calli well developed, posteriorly defined by distinct transverse impression, posterior half with distinct median impression, ostiolar canal distinct, almost straight and then broadly curved anteriorly; scutellum with two large, distinct punctures arranged transversely; hemelytra with indistinct punctations on clavus, membrane with three distinct veins, innermost vein branched at base to form small cell; male genital segment distinctive (see Péricart 1972); female with omphalophore at center of anterior margin of sternite VII.

Blatchley (1934) described *Cardiastethus cavicollis* from two specimens, one from Griffith Park, Los Angeles (21 February 1928) (the holotype) and another from Santa Monica Beach (13 January 1928). The description contained many of the characters eventually compiled from the specimens from San Francisco and Los Angeles, although no mention was made of the scutellum or the very distinct pair of large punctures on it. Ultimately, we examined the holotype through the courtesy of Arwin Provonsha. The specimen had the exact information of date and place and showed the distinct pair of large punctures on the scutellum. *Cardiastethus cavicollis* Blatchley proved to be identical to *Buchananiella continua* (White), **new synonomy**. We also note that the holotype is a female, not a male. Blatchley indicated that this specimen was a male, as he did for the "paratype." Upon examination of the holotype, however, the specimen turned out to be a female—an easy mistake since the females of *Buchananiella* have greatly reduced external female genitalia and appear to lack the characteristic ovipositor found on many Anthocoridae. Further, the characteristic female omphalophore, just before the apex of the abdomen, is not generally visible in dry specimens. The paratype "male" cited but not seen here also may be a female for the same reason.

Carayon (1958a) reported *B. continua* from Atlantic islands, "La Réunion," oriental Africa (Kenya) and South America (Argentina). Péricart (1972) considered it to be pantropical. Péricart (1996) gave the known distribution of *B. continua* as Europe (France, Italy, Poland, Spain), North Africa (Azores, Madeira), Asia (Turkey, Israel), tropical Africa, tropical America, Australia, and Reunion. It is known from Continental United States, and it was reported from the Hawaiian Islands (Brenner and Lattin 2001). The wide-spread occurrence of this species makes it difficult to determine its native range.

Blatchley (1934) collected specimens in southern California from ". . . leaves of a dead oak . . ." and ". . . beneath a bunch of weeds just above high water line . . ." in January and February 1934 (as *Cardiastethus cavicollis* Blatchley). Péricart (1972) found *B. continua* in dry grass in France where he believed their food likely consisted of associated Psocoptera. He also reported Daumal and Carayon's observation that specimens had been taken with the hibernating larvae of the pyralid moth *Myelois ceratoniae* Zell. Elsewhere, Carayon (1958b) reported *B. crassicomis* from the nests of weaver birds in the Ivory Coast.

Contemporary collection details of *Buchananiella continua* in California follow. It was collected on two occasions in Golden Gate Park, San Francisco, California. On July 30, 1998, females were beaten from *Acacia* sp. litter with old blossoms and dead vine leaves. On July 28, 1999, several females, two males, and a large nymph were beaten from an unidentified ornamental shrub. Leaves of the shrub were covered with a black sooty mold and were infested with psocids and mites. On April 6, 1999, at Newport Beach, Los Angeles County, females were beaten from an unidentified ornamental hedge that was heavily infested with whitefly and mites. Leaves of the hedge were covered with a black sooty mold. On May 21, 1999, a male was beaten from the flowering head of a thistle in Dawson Canyon near Oceanside, San Diego County, California.

Two generations of *B. continua* were successfully reared in the Wapato, WA, laboratory on pear seedlings infested with spider mites and with eggs and nymphs of the pear psylla, *Cacopsylla pyricola* (Förster). Females deposited reddish-pink eggs (~0.65 mm in length) on plant and container surfaces. Young nymphs were red, darkening to brown in later instars. Development time from egg to adult was about four weeks at 23°C.

Extensive movement of plant materials of all types enhance the possibilities of discovering additional non-indigenous species. All seasons of the year could produce specimens, particularly around ports in warmer climates. We now know of at least 21 non-indigenous species of Anthocoridae in Canada and the continental United States.

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GALL MIDGES (DIPTERA: CECIDOMYIIDAE) INFESTING *SUAEDA MONOICA* (CHENOPODIACEAE) IN ISRAEL

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Abstract.—Six new species of gall midges are described from the salt marsh plant *Suaeda monoica* Gmelin in Israel, the first cecidomyiid species to be described from this host. Five of the new species, ***Baldratia occulta*, n. sp.**, ***Izeniola obesula*, n. sp.**, ***Stefaniola siliqua*, n. sp.**, ***S. defoliata*, n. sp.**, and ***S. rufa* n. sp.**, are leaf or twig gallers belonging to a large group of Old World Lasiopterini which is restricted to Chenopodiaceae. ***Asphondylia acinata*, n. sp.**, is a fruit galler belonging to the Asphondyliini. Descriptions of adults, galls, and larval stages, as available, as well as biological remarks are given for each species. The terminology of female genitalia in the Lasiopterini and the significance of characters of immature stages in this tribe are discussed.

Key Words: Cecidomyiidae, gall midges, Lasiopterini, *Suaeda monoica,* galls, Israel

With about 100 species, *Suaeda* is one of the dominant genera in the family Chenopodiaceae. *Suaeda* spp. are well adapted to harsh environmental conditions (high salinity and aridity) and occupy the saltiest niches in wet saline and sandy soils (Waisel 1972). While most *Suaeda* species are annuals, semi-shrubs or shrubs, *Suaeda monoica* is a bushy tree that may grow to 6 m high. It is a thermophilic, salt-requiring, Sudanian species that is mainly distributed along the tropical coasts of East Africa, Arabia and India, where it dominates halophitic plant communities (Boulos 1991, El-Demerdash et al. 1994, Waisel 1972). The Dead Sea and Arava Valley in Israel are the northernmost localities of its distribution. Although locally abundant in Israel, *S. monoica* habitats are subject to intensive development endangering its existence to the point of possible extinction. This unfortunate situation has also been reported to prevail elsewhere (e.g. Arabia, El-Demerdash et al. 1994).

Supporting more than 300 cecidomyiid species, the Chenopodiaceae form one of the most important host families of gall midges (Dorchin 1998). However, only 25 cecidomyiid species are known to infest *Suaeda* spp., and no gall midges have been described from *S. monoica* prior to this study. Houard (1922) referred to four types of galls on this plant, based on information and, possibly, galls conveyed to him by Stefani (1909), but in both Houard (1922) and Stefani (1909) these galls were merely attributed to "cecidomyiids" or "insects."

In this study, I describe six new species that gall leaves, twigs and fruit of *S. monoica* in Israel. Five of the species belong to the tribe Lasiopterini, which mostly comprises Old World chenopod-infesting genera (subtribe Baldratiina). The sixth species belongs to *Asphondylia,* a large (ca. 260 species), cosmopolitan genus, of which only three species are known to infest *Suaeda.* The six species described here form only a small part of the rich Israeli fauna of chenopod-infesting cecidomyiids, including at least five additional undescribed *Suaeda*-infesting species. It is noteworthy that adults of five of the six species described here are found almost throughout the year. This phenomenon appears to be exceptional for gall systems studied so far, as almost all of these show strong seasonality. The unclear seasonality in the *S. monoica* complex, especially that exhibited by *Izeniola obesula* n. sp., is probably due to the availability of growing plant tissues at all times, which is a common phenomenon in Sudanian plants.

METHODS

The field work for this study was conducted in four main locations in the Dead Sea area and Arava Valley, Israel, during 1995–2000: Qalia, at the northern part of the Dead Sea; 'En Boqeq and Newe Zohar, in its southern part; Ne'ot HaKikkar in the northern Arava Valley, and Elot, near the city of Elat (Fig. 1). Galls were also observed on plants about 20 km north of Nuweiba, Sinai, but no collections were made in this location. Galls and other plant parts were collected and held in rearing cages or small plastic vials until adult emergence. Some of the galls were dissected to obtain larval stages. Specimens were killed and preserved in 70% ethanol. Adults and larvae were slide mounted in euparal according to the method described by Gagné (1989, 1994). Larvae of some species were also prepared for SEM examination. Pupae and pupal exuviae were temporarily mounted for study in glycerol gel and then stored in 70% ethanol. Eggs were obtained upon oviposition by females introduced into cages containing potted *S. monoica* plants. Terminology for adult morphology follows McAlpine et al. (1981). Additional terms specific to female Lasiopterini are suggested below. Description of the scale pattern on the adult abdomen refers to fresh specimens; this conspicuous pattern is lost in pinned or alcohol stored specimens. Terminology of larval and pupal morphology essentially follows Gagné (1989), but the pupal descriptions refer to the pupa as horizontal and lying face down, rather than upright. Specimens used in this study, including gall samples, were collected by the author unless otherwise indicated. All holotypes and most paratypes and associated material are deposited in the National Collection of Insects, Zoological Museum, Tel Aviv University. Some paratypes were donated to The Natural History Museum (formerly British Museum of Natural History), London, UK and the National Museum of Natural Histroy, Smithsonian Institution, Washington, DC, USA. Holotypes are mounted on slides; paratypes are either mounted on slides or stored in 70% alcohol. The species are treated below in alphabetical order.

TERMINOLOGY OF FEMALE GENITALIA IN THE LASIOPTERINI

Most of the synapomorphic characters of Lasiopterini are in the female ovipositor, which exhibits great variability, and therefore offers the best characters for discrimination of genera and species. However, many of these characters have not been given specific terms, as they are unique to this tribe. Furthermore, different taxonomists have been using various terms for similar body parts, even in the same publication, making it hard to interpret their descriptions. In the following overview I offer standardized terms for lasiopterine female genitalia, with reference to the work of B. M. Mamaev and Z. A. Fedotova, who have contributed much to the knowledge of the Old World Lasiopterini (for a list of references see Mamaev 1972 and Fedotova 1999). The terminology discussed here (demonstrated in Fig. 51) is also applicable to lasiopterine genera that are not associated with Chenopodiaceae (e.g., *Lasioptera* Meigen).

Tergites and sternites 2–7 of the female abdomen are usually rectangular. Tergite 8 is frequently much shorter than preceding tergites, and shows variable degree and pattern of sclerotization. Sternite 8 is either di-

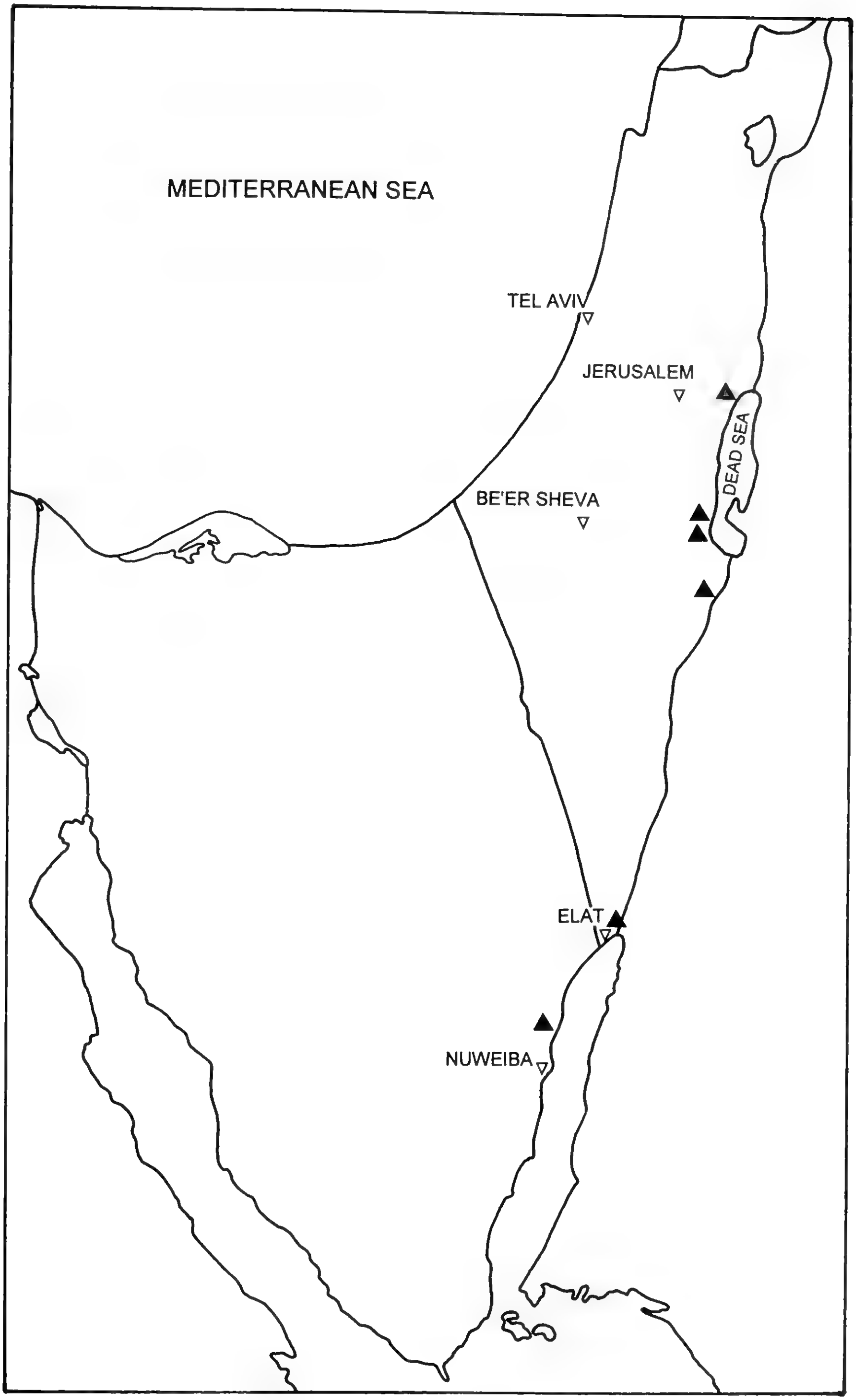


Fig. 1. Collection sites of *Suaeda monoica* galls in Israel and Sinai (marked as ▲).

vided, or much shorter than the preceding sternites, or completely unsclerotized (Figs. 25, 38, 49). The group of strong and usually curved setae on each side distal to tergite 8 is referred to here as the "lateral group of setae" (Fig. 51, S). These may be straight, curved or S-shaped, and are sometimes useful as a taxonomic character. The two sclerotized rods that run along segment 9 ("inner sclerotized longitudinal arms" in Mamaev 1972; "longitudinal sclerotized rods" in Fedotova (1991)) are apparently the arms of the genital fork, which is derived from sternite 9 (McAlpine et al. 1981), and are referred to here as "genital fork" (Fig. 51, GF). These rods join a pair of sclerotized lateral plates ("lateral plates" in Fedotova 1992; "lateral sclerites" or "area of spines proximal from the stylus" in Mamaev 1972), which vary in shape, dimensions and sclerotization and bear several straight, curved, hooked or split setae (Fig. 51, LP). These plates may form the extensions of a dorsal plate, but in some species (e.g., *Baldratia occulta*) they are separated from each other dorsally, and are only joined by the aculeus (see below). I interpret these plates as at least analogous, if not homologous, to the acanthophorites of some orthorrhaphous Brachycera (e.g., Dolichopodidae) that are a pair of spine-bearing hemitergites 10 used for digging during oviposition. Similarly, the spiny lateral plates in the Lasiopterini may serve for scratching or piercing plant tissue onto which the eggs are to be laid. Conversely, it is possible that the lateral plates are derived from the cerci (i.e., tergite 11), in which case they resemble pseudacanthophorites as described in Tethinidae by Freidberg and Beschovski (1996). The plates extend distally to form a single spike referred to here as the aculeus ("aculeus" in Fedotova 1992; "stylus" in Mamaev 1972), which may bear several strongly curved or hooked setae (Fig. 51, A). In some species of *Baldratia* Kieffer the aculeus bears an additional, shorter spine, which is directed posteriorly ("accessory spine" in Fedotova 1991). The shape of the lateral plate, the aculeus, and the setae they bear provide valuable taxonomic characters both on the generic and species level. The apical membranous part of the ovipositor, posterior or ventral to the aculeus ("fleshy lobe" in Mamaev (1972); "apical lobe" or "apical part" in Fedotova (1991, 1993)), is derived from the cerci which are fused into a single lamella and are referred to here as "apical lamella" (Fig. 51, AL). The shape of the apical lamella sometimes also provides a good taxonomic character.

EVALUATION OF CHARACTERS OF IMMATURE STAGES IN CHENOPOD-INFESTING LASIOPTERINI

The only comprehensive investigation of larval stages of Lasiopterini was conducted by Möhn (1966–1971) who based this work on larval characters alone. However, apart from the presence or lack of a spatula in the third instar larva, I find lasiopterine larvae from Chenopodiaceae to be generally uninformative, exhibiting only slight interspecific differences even when inspected in SEM, a fact that renders Möhn's keys extremely hard to use.

While most workers have ignored pupal characters in their descriptions, Möhn designated pupal paratypes for some of the species he described, but no pupae were actually described. Lasiopterine pupae do possess several distinct characters that can readily be used for identification, sometimes with better results than those obtained with adult characters. The best pupal characters are the number and shape of cephalic horns, which are usually well developed in this group. In addition to the antennal horns, which are commonly prominent in other groups as well, baldratiine pupae usually possess 1–4 facial horns that are single or paired and pointed or ridge-like in various combinations (e.g., Fig. 43). These characters are sometimes informative enough to enable positive identification of certain species. It is therefore unfortunate that pupae were overlooked in previous taxonomic works conducted on chenopod Lasiopterini.

TREATMENT OF SPECIES

Asphondylia Loew 1850

Asphondylia Loew 1850: 21, 37.
Type species: *Cecidomyia* (*Asphondylia*) *sarothamni* Loew 1850. By subsequent designation of Karsch 1877.

Asphondylia is a cosmopolitan genus with about 260 described species whose adults have very few specific diagnostic characters. Larvae and pupae better serve to discriminate species from one another (e.g., Möhn 1959, Hawkins et al. 1986, Gagné and Waring 1990), but since larval stages of many Old World species were not described, the descrimination of new species greatly relies on gall characters and host identity.

***Asphondylia acinata* Dorchin, new species**

(Figs. 2, 8–18)

Adult.—*Head:* Eye facets hexagonal. Flagellomeres: 10, cylindrical, bearing two relatively straight whorls of circumfila in female (Fig. 8), sinuous circumfila in male (Fig. 9), and setae at least 0.5 as long as flagellomere. Palpus three segmented, first segment much shorter than each of second and third segments (Fig. 10).

Thorax: Wing: length 2.5–2.6 in males (n = 4), 2.9–3.3 in females (n = 7); C, Sc and R_5 much stronger than remaining veins; R_5 only slightly curved, joining C at wing apex; M present as a weak fold; Cu forked. Legs covered by hairs and dark, elongated, striped scales; claws untoothed, thick, evenly curved (Fig. 11); empodia about as long as claws.

Female abdomen (Figs. 12, 14): Tergites 1–7 rectangular, with posterior row of setae; first tergite about 0.6 as long as second; tergite 8 band-like, about 0.3 as long as preceding; second to fourth sternites shorter ventrally than dorsally; tergites and sternites without anterior pair of trichoid sensilla. Ovipositor short: distal protrusible half 1.4–1.6 as long as sternite 7 (n = 7).

Male abdomen (Fig. 13): Eighth tergite and sternite shorter and lower than preceding, only second, and sometimes third, sternites shorter ventrally than dorsally; other tergite and sternite characters similar to female. Genitalia (Fig. 15): Cercus globular; hypoproct distally with shallow notch; paramere absent; aedeagus cylindrical, rounded apically. Arms of epandrium straight proximally, arched distally. Gonocoxite wide and short, somewhat protruding apically, setulose as shown. Gonostylus carried dorsally on gonocoxite, almost rounded, evenly setulose; tooth divided in two, or almost to its base.

Pupa (Figs. 16–17).—Prothoracic spiracles short. Antennal horn dorsoventrally flattened. One short anterofrontal horn present, pointed anteriorly. Clypeus anteriorly with two tapered projections (Fig. 16). Abdominal tergites bear rows of spines, more pronounced on posterior segment.

Larva (third instar).—Orange. Integument rugose. Spatula rectangular, without shaft, quadridentate, lateral teeth longer than median teeth. Three setose lateral papillae on each side of spatula, situated as in Fig. 18.

Egg.—Unknown.

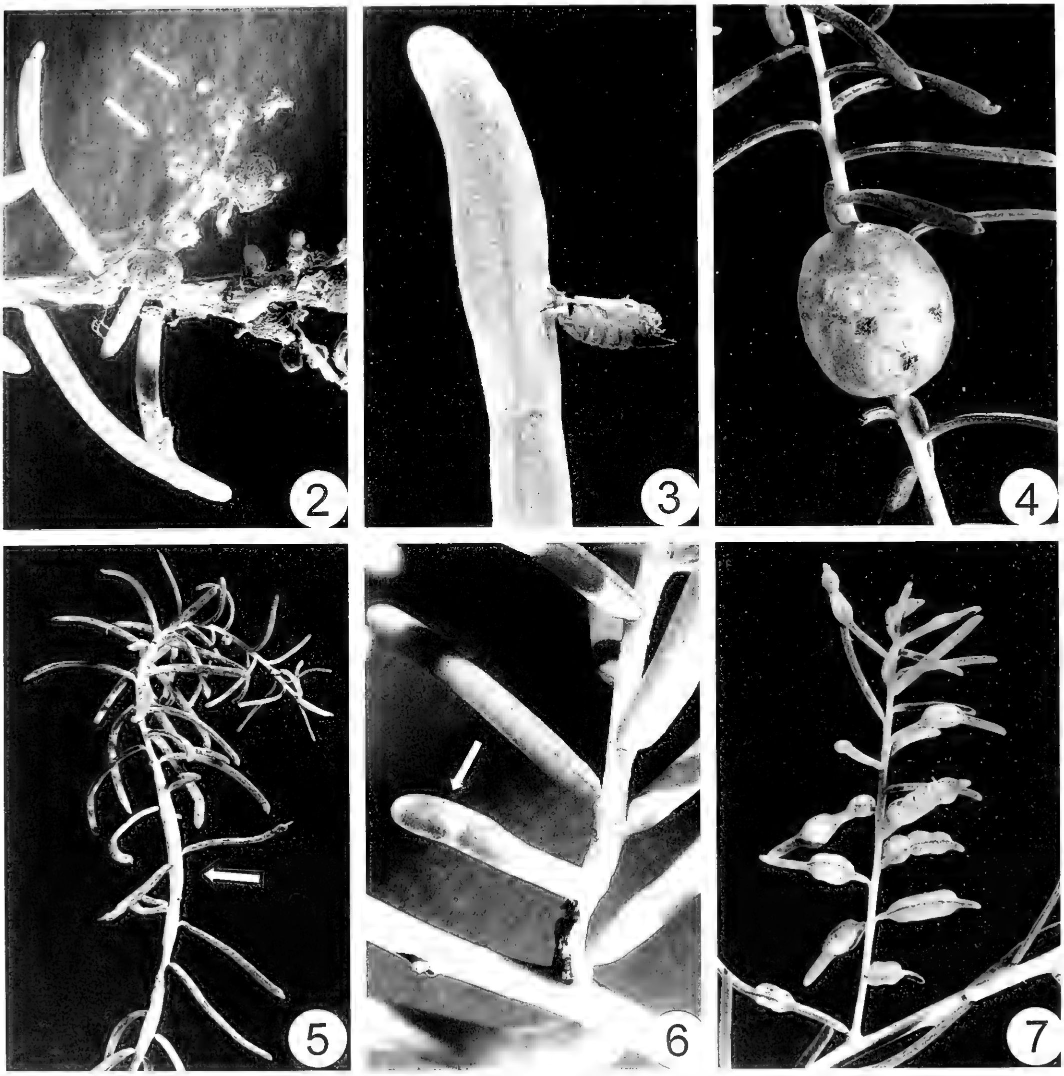
Distribution.—Israel (Dead Sea area and Arava Valley); Eritrea (Houard 1922).

Holotype.—♂ reared from *Suaeda monoica* fruit gall. Israel, Ne'ot HaKikkar, 4.IV.1998, N. Dorchin (slide).

Paratypes.—All specimens reared from *Suaeda monoica* fruit galls: 14 ♀, 12 ♂, same data as holotype; 3 ♀, Newe Zohar, 8.IV.1996; 1 ♀, 2 pupae 1 larva, Newe Zohar, 12.III.1998; 1♀ Newe Zohar 15.III.1999

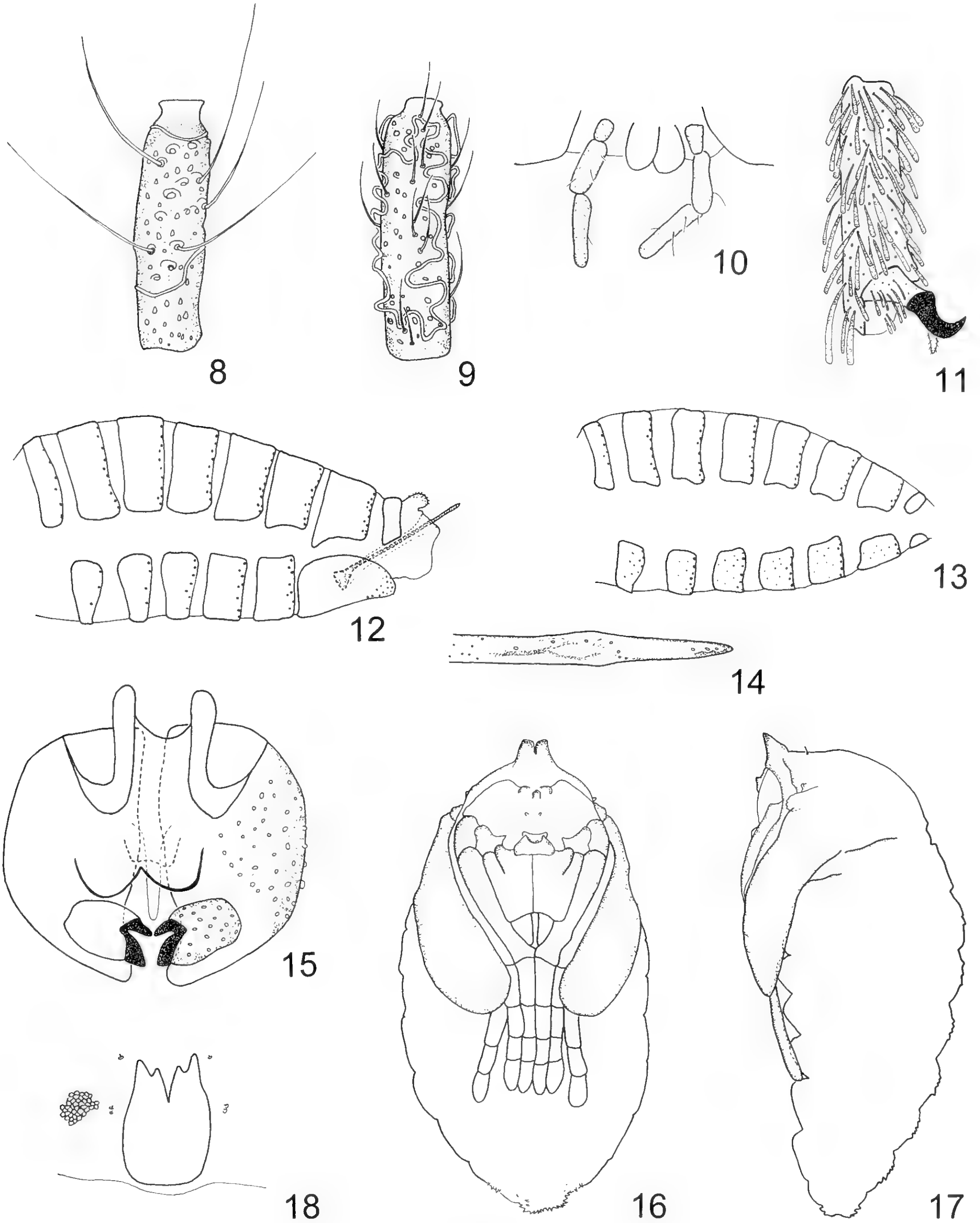
Etymology.—The name *acinata* is an adjective derived from the Latin acinus ("berry") with reference to the shape of the gall.

Biology.—Each larva induces a spherical, monothalamous fruit gall resembling a small berry, ca. 0.5 cm in diameter (Fig. 2). The gall contains a single, round larval chamber in which only one larva is found.



Figs. 2–7. Cecidomyiid galls on *Suaeda monoica.* 2, Fruit galls induced by *Asphondylia acinata.* 3, Exuviae of *Baldratia occulta* protruding from an infested leaf. 4, Twig gall induced by *Izeniola obesula.* 5, Twig gall induced by *Stefaniola defoliata.* 6, Leaf galls induced by *S. rufa.* 7, Leaf galls induced by *S. siliqua.*

When mature, the gall is gray externally, light green internally, and its internal walls are covered by white mycelium. Galls are usually found in aggregations of 5–20 and are frequently associated with thickening and deformation of the twig on which they are formed. The length of the deformed section may reach up to 20 cm, depending on the number of galled fruit it carries. The species is univoltine. Gall formation is initiated in spring (March–May), when the plant is in bloom, and the gall reaches its final dimensions in October–November, when the larva inside it is still a first instar. The larva overwinters in the gall as a first instar, advances quickly through the second and third instars in late winter, pupates in March, and adults emerge during March–April. Galls containing first instar larvae were found in early March, indicating that development from first instar larva to adult occurs during a very short time period.



Figs. 8–18. *Asphondylia acinata.* 8, Female, 5th flagellomere. 9, Male, 5th flagellomere. 10, Mouthparts. 11, Distal tarsomere. 12, Female abdomen, lateral view. 13, Male abdomen, lateral view. 14, Tip of female ovipositor, lateral view. 15, Male terminalia, dorsal view. 16, Pupa, ventral view. 17, Pupa, lateral view. 18, Larva, spatula and papillae.

Fungal mycelium was not found in galls containing first instar larvae, which possibly feed on the plant tissue at this stage. Although the plant flowers from October to May, adult emergence and gall initiation only occur during spring. This is the only species on *Suaeda monoica* showing clear seasonality.

Remarks.—Eleven New World and nine Old World *Asphondylia* species have been described so far from Chenopodiaceae, most of them from galls on *Atriplex* species (Houard 1922; Gagné 1989, 1994). *Asphondylia acinata* differs from the *Atriplex*-infesting species in lacking a posterofrontal horn in the pupa. Only three described *Asphondylia* species infest *Suaeda: A. swaedicola* Kieffer and Jörgensen and *A. dondiae* Felt from bud galls in the Americas (Gagné 1989, 1994), and *A. suaedae* Kieffer from fruit galls on *Suaeda vermiculata* in Europe (Kieffer 1909). The description of the latter was based on its gall only, which is notably hairy and contains an elongated larval chamber; the insect itself was not described. The gall of *A. acinata* is bare, and the larval chamber is round. This resembles the fruit gall described by Houard (1922) from *Suaeda monoica* in Eritrea, which I therefore believe is that of *A. acinata.*

Baldratia Kieffer 1897

Baldratia Kieffer 1897: 7.

Type species: *Baldratia salicorniae* Kieffer 1897. By monotypy.

This Old World genus comprises about 35 species, mostly known from Central Asia. It is characterized by the larger, slender body and relatively longer legs than those of the related genera *Stefaniola* Kieffer and *Careopalpis* Marikovskij. The female aculeus is always ventrally curved (convex), the apical lamella is almost always fusiform to ovoid. The lateral plate and the distribution and form of its setae vary among species and may serve to subdivide the genus, as was tentatively done by Fedotova (1991). The new species described below belongs to a large group within the genus whose lateral plate possesses split setae—a character unique to *Baldratia.*

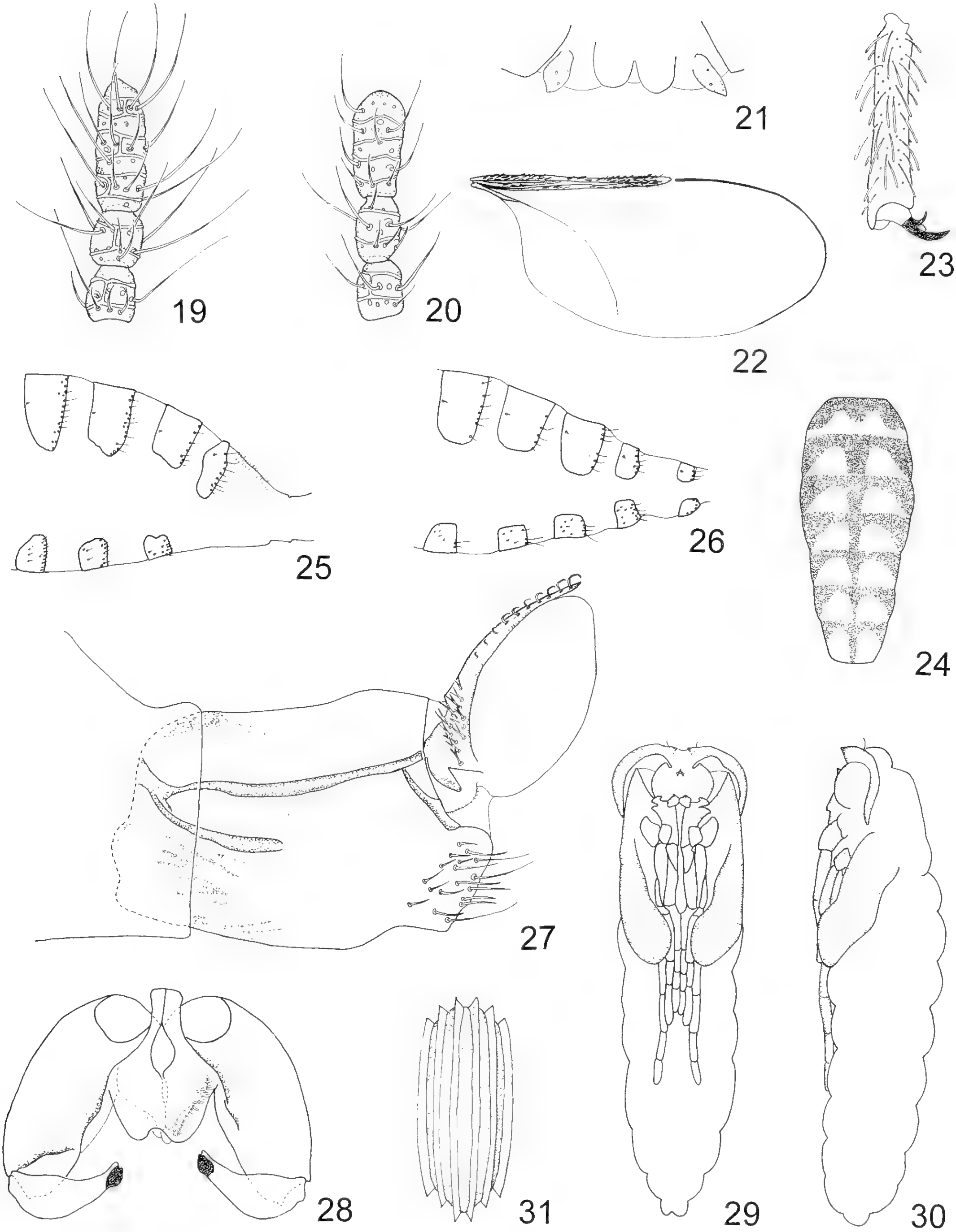
***Baldratia occulta* Dorchin, new species**

(Figs. 3, 19–31)

Adult.—*Head:* Eye facets round; gap between eyes on vertex 1–2 facets wide. Occiput, gena and postgena covered by white scales. Antennal scape with white scales; flagellomeres 13–14 in female, 12 in male; number sometimes variable in same (female) individual; each with two closely appressed circumfila with longitudinal links; the 2–3 distalmost flagellomeres fused or partially fused to form a distinctly longer segment with several whorls of setae and circumfila (Figs. 19–20). Palpus one segmented, covered by white scales (not shown), usually cylindrical with tapered tip, sometimes globular (Fig. 21).

Thorax: Dorsum and pleura covered by white scales. Wing (Fig. 22) length, 2.06–2.18 mm. in males (n = 4), 2.1–2.6 in females (n = 14); C, Sc and R_5 light orange, with sparse, delicate black scales, denser near juncture of R_5 and C; rest of wing transparent; M present; Cu unforked; posterior margin with long, fine hairs up to juncture of M with C (not shown). Stem of halter light orange, knob white. Legs: Coxae covered by white scales; femora, tibiae and tarsi covered by dark scales, with few white scales; tarsal claws evenly curved, with strongly curved tooth (Fig. 23); empodia much shorter than claws.

Female abdomen: Overall appearance more elongate and slender than that of other Lasiopterini on this host. General color pink, covered by black and white scales that form a pattern on dorsum as in Fig. 24. Eighth tergite shorter than preceding, eighth sternite completely unsclerotized (Fig. 25); tergites 1–7 anteriorly with a pair of trichoid sensilla. Ovipositor (Fig. 27) Lateral group of setae on eighth segment hyaline, visible only in dorsal view (not shown);



Figs. 19–31. *Baldratia occulta.* 19, Female distalmost flagellomeres. 20, Male distalmost flagellomeres. 21, Mouthparts. 22, Wing. 23, Distal tarsomere. 24, Scale pattern on abdomen, dorsal view. 25, Female postabdomen, lateral view. 26. Male postabdomen, lateral view. 27, Female ovipositor, lateral view. 28, Male terminalia, dorsal view. 29, Pupal exuviae, ventral view. 30, Pupal exuviae, lateral view. 31, Egg.

ninth segment anteriorly with dark, sclerotized patches, posteriorly with few long setae; lateral plate relatively short, bearing 10–15 straight, split setae; aculeus as long as ovoid apical lamella, curved posteroventrally, with few curved, thin setae.

Male abdomen (Fig. 26): Color pattern as in female. Eighth tergite greatly reduced, up to 0.5 times as long as preceding; tergites with anterior pair of trichoid sensilla. Genitalia (Fig. 28): Cercus wide, rounded at apex, with many tiny setae; hypoproct almost entire, distally with a shallow notch; paramere apically divided in two longitudinal lobes, sheathing almost entire length of aedeagus dorsally, narrowing abruptly from mid-length apically on ventral part, densely covered by short setae; aedeagus rounded apically; gonocoxite cylindrical, almost same width throughout its length, medially with longitudinal sclerotized ridges on dorsal part; mediobasal lobe not prominent, setulose; gonostylus with flattened setae on distal half.

Pupa (Figs. 29–30, based on exuviae).—Body elongated. Antennal horn pointed anteroventrally, relatively small. One small frontal horn, pointed anteriorly.

Larva (first instar).—Bright orange, smooth integument. Second and third instars unknown.

Egg (Fig. 31).—Orange, cylindrical, with longitudinal white ridges perpendicular to egg surface.

Distribution.—Israel (Dead Sea area and Arava Valley).

Holotype.—♀ reared from *Suaeda monoica* normal-looking leaf, Israel, Newe Zohar, 15.III.1999, N. Dorchin (slide).

Paratypes.—All specimens reared from *Suaeda monoica* normal-looking leaves: 14 ♀, 2 ♂, same data as holotype; 1 ♀, Newe Zohar, 19.IV.1995; 1 ♂, 1 ♀, Ne'ot HaKikkar, 29.III.1996; 3 ♀, 1 ♂, Newe Zohar, 8.IV.1996; 2 ♀, 1 ♂ Ne'ot HaKikkar, 3.II.1998; 1 ♀ Newe Zohar, 27.X.1998; 2♂ Newe Zohar 24.X.1999; 1 exuviae Newe Zohar 15.XII.1999; 1 exuviae 22.XII.1999; 2 ♀, 2 exuviae Newe Zohar 2.III.2000; 1 ♀ Newe Zohar 21.III.2000.

Etymology.—The name *occulta,* an adjective, is Latin for "hidden," referring to the lack of any external signs of infestation prior to adult emergence.

Biology.—Eggs are glued individually on leaves, 1–2 on a leaf. The larva penetrates the leaf directly through the egg shell, leaving the empty white shell on the leaf for several more days. Larvae develop inside normal-looking leaves and the presence of the cecidomyiid is apparent only after adult emergence when the exuviae are found protruding from the leaf (Fig. 3). Adults of this species were scarce during summer (May–September), but relatively abundant during the rest of the year.

Remarks.—This species belongs to a group within *Baldratia* whose lateral plate carries split spines—a character unique to this genus. Fedotova (1991) divides this group into the salicorniae and climacopterifolia subgroups (each with two species). Species of the climacopterifolia subgroup (*B. nitraricarpa* Fedotova and *B. climacopterifolia* Fedotova) are distinguished by the apical lamella that is positioned in a right angle relative to segment 9, and by lateral plates that only partially embrace the apical lamella. The salicorniae subgroup (*B. salicorniae* Kieffer and *B. suaedifolia* Fedotova) is distiguished by the apical lamella that is positioned at an obtuse angle relative to segment 9 and by the relatively large lateral plates that embrace the entire base of the apical lamella. According to this division, *B. occulta* belongs to the climacopterifolia subgroup. However, this species lacks the distinctive spine at the base of the aculeus which is present in both subgroups mentioned by Fedotova.

Baldratia suaedifolia and *B. climacopterifolia* infest leaves (of *Suaeda acuminata* and *Climacoptera obtusifolia*, respectively, in Kazakhstan) without causing any external deformation (Fedotova 1991), similar to infestations of *B. occulta* on *Suaeda monoica. Baldratia salicorniae* and *B. nitrari-*

carpa, however, differ greatly from *B. occulta* with regard to their hosts and life history: the former species induces twig galls on *Salicornia fruticosa* (Kieffer 1912), the latter develops in seeds of *Salsola nitrariae* (Fedotova 1991).

Two other *Baldratia* spp. that may be considered related to *B. occulta* are *B. aellenii* Möhn and *B. suaedae* Möhn, which are known only from larvae (Möhn 1969). Both species form distinctive leaf swellings on *Suaeda* species. *Baldratia aellenii* infests *S. microphylla,* which does not occur in Israel, and *B. suaedae* infests *S. vera,* which occurs in Israel in biotopes that do not overlap with those of *S. monoica.*

Izeniola Fedotova 1985

Izeniola Fedotova 1985: 46.

Type species: *Stefaniola potanini* Fedotova 1982 (in Taranov and Fedotova 1982).
= *Stefaniola deserta* Fedotova 1982 (synonymized by Fedotova 1985). By monotypy.

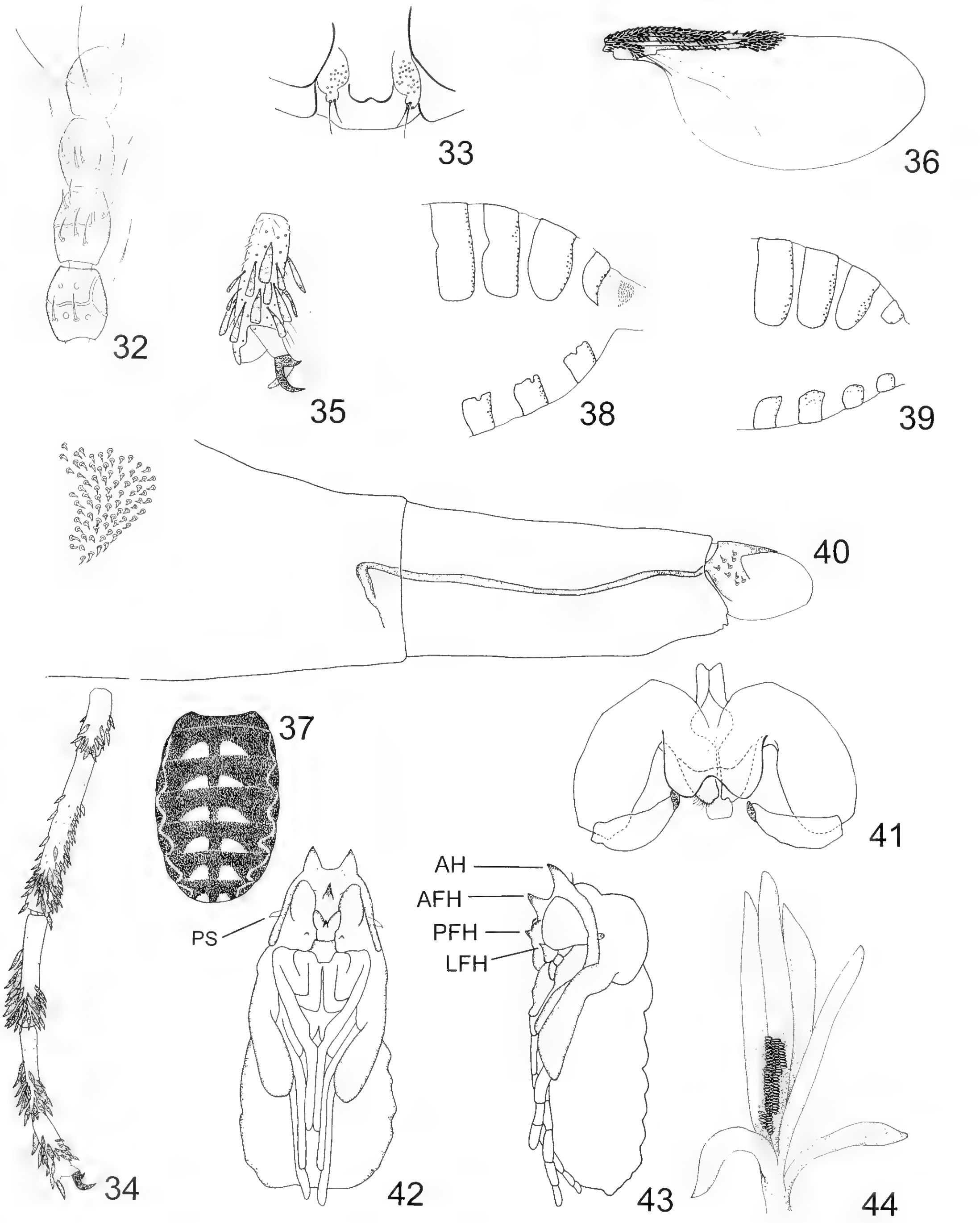
This genus currently contains two species: *I. potanini* Fedotova from Kazakhstan and *I. bassiae* Fedotova from Turkmenistan; both induce minute stem swellings on their hosts (*Kochia prostrata* and *Bassia hyssopifolia,* respectively). The new species matches the generic concept that is mainly based on female ovipositor characters (relatively long ovipositor and reduced lateral plates and aculeus). However, a comparison with the type material of the Central Asian species has not been possible so far, and the conclusions are therefore based on their original descriptions alone. Furthermore, larval stages of the two Central Asian species are unknown, and when found and described could lead to the conclusion that the species described here is not congeneric with the other two.

***Izeniola obesula* Dorchin, new species**
(Figs. 4, 32–44)

Adult.—*Head:* Eye facets round, more spaciously arranged on vertex; gap between eyes on vertex 0.5–2 facets wide. Vertex with few long setae. Occiput with white scales and hairs. Gena and postgena with dark scales and few long setae; frons with white scales and few long setae. Antennal scape conical, wider distally; pedicel globular, wider than long, about twice as large as first flagellomere; scape and pedicel densely covered by dark scales; flagellomeres (Fig. 32) 10 in both sexes, barrel-shaped, necks barely evident, light orange, without scales, evenly covered by microtrichia, each with 1, occasionally partial second circumfilum; one row of strong setae on each side of circumfilum; apical flagellomere usually shorter than preceding, rounded distally. Palpus one segmented, with short apical projection bearing 2–3 long setae (Fig. 33).

Thorax: Dorsum covered by sparse, white scales. Pleura without scales, light brown to orange. Wing (Fig. 36)length, 1.5–1.8 mm in male (n = 9), 1.7–2.2 mm (n = 21) in female; light brownish orange, evenly covered by microtrichia; basal half of R_5 and junction of R_5 and C covered by dark scales with short break separating these two sections; M present; Cu unforked; posterior wing margin with long, fine hairs up to junction of M and C (not shown). Knob of halter covered by short, dark scales. Legs: Basal part of fore coxa with a group of white scales; coxae and trochanters otherwise without scales, only with few long setae; femora and tibiae densely covered by short, dark scales, irregularly speckled with white, with several very long setae; each tarsomere with fine, hyaline hairs and scales on proximal two thirds and a dense group of dark scales on distal third, which creates impression of striped tarsi (Fig. 34); tarsal claws thick, evenly curved, with short, thick tooth; empodia about as long as claw (Fig. 35).

Female abdomen: Densely covered by dark scales; white scales on dorsum form a pattern as in Fig. 37. Pleura with a pattern of 2–3 white patches on dark background. Tergites without trichoid sensilla; eighth



Figs. 32–44. *Izeniola obesula.* 32, Female distalmost flagellomeres. 33, Mouthparts. 34, Tarsus. 35, Distal tarsomere. 36, Wing. 37, Scale pattern on abdomen, dorsal view. 38, Female postabdomen, lateral view. 39, Male postabdomen, lateral view. 40, Female ovipositor, lateral view. 41, Male terminalia, dorsal view. 42, Pupa, ventral view. 43, Pupa, lateral view. 44, Egg batch. AFH = anterofrontal horn, AH = antennal horn, LFH = laterofrontal horn, PFH = posterofrontal horn, PS = prothoracic spiracle.

tergite shorter than preceding; sternite 8 completely unsclerotized (Fig. 38). Ovipositor (Fig. 40): Setae of lateral group on eighth segment short, wide and curved; ovipositor 0.4–0.5 times as long as abdomen; arm of genital fork almost evenly wide throughout its length; lateral plate reduced, rectangular, with deep, posterior notch, bearing 5–10 straight or slightly curved setae; aculeus much shorter than apical lamella, straight, tapering distally, without setae; apical lamella cylindrical, setulose, almost twice as long as aculeus.

Male abdomen (Fig. 39): Color pattern as in female. Eighth tergite much smaller than preceding. Genitalia (Fig. 41): Cercus wide, rounded at apex, with many tiny setae; hypoproct almost entire, with very shallow depression distally; paramere bulbous, slightly longer than cercus, sheathing about 0.75 of aedeagus length dorsally, narrowing abruptly from mid-length posteriorly in ventral view, covered by many proclinate spine-like setae; aedeagus robust, rectangular, truncate apically; gonocoxite robust, cylindrical, widest at midlength; mediobasal lobe prominent, setulose; gonostylus evenly setulose.

Pupa (Figs. 42–43).—Prothoracic spiracle about five times as long as wide, tapered abruptly at tip. Antennal horn well developed, pointed anteriorly. Anterofrontal horn prominent, pointed anteriorly. Small posterofrontal horn, pointed ventrally between two wing-like ridges. Small laterofrontal horns, pointed anteroventrally posterior to eyes. Dorsum of abdomen with minute, dense, blunt spines (only discernible in SEM). Color changes from very light orange to dark orange, and finally to dark brown as the adult develops within.

Larva.—Cylindrical, color changes from very light orange to darker orange as the larva matures. Third instar integument smooth, spatula absent, papillae not observed.

Egg.—Orange during first 24 hours, then dark brown, resembling rice grain in shape (Fig. 44).

Distribution.—Israel (Dead Sea area and Arava Valley); Egypt (Sinai); Eritrea (Houard 1922).

Holotype.—♀ reared from *Suaeda monoica* round twig gall, Israel, Newe Zohar, 15.III.1999, N. Dorchin (slide).

Paratypes.—All specimens reared from *Suaeda monoica* round twig galls: 7 ♀, same data as holotype; 1 ♀, 1 ♂, 18.III.1995, Elot; 22 ♀, 4 ♂, 3 pupae, Newe Zohar, 19.IV.1995; 4 ♀, Newe Zohar, 11.V.1995; 10 ♀, 3 ♂ Elat, 30.III.1996; 4 ♂, 10 pupae, 2 larvae, Ne'ot HaKikkar, 30.III.1996; 38 ♀, 3 pupae, 17 larvae, Newe Zohar, 8.IV.1996; 3 pupae, Newe Zohar 27.X.1998; 8 pupae, 7 larvae, 'En Boqeq, 1.III.1999; 4 larvae, 1 pupa, Qalia 2.II.1999; 1♀, Newe Zohar, 15.IV.1999; 16 ♀, 10 ♂, 'En Boqeq, 13.V.1999; 12 ♀, 7 ♂, Newe Zohar, 22.IX.1999.

Etymology.—The name *obesula* is an adjective derived from the word obesa, which is Latin for "fat," with reference to the bulky appearance of the adult midges.

Biology.—Eggs are laid between leaves of young twig tips in densely packed batches comprising 90–130 eggs (n = 3) (Fig. 44). Batch size 3–5 mm. Larvae form globular, asymmetrical, polythalamous galls on young growing twigs (Fig. 4). Galls may reach more than 2 cm. in diameter and contain more than 50 individuals each. They are smooth and shiny green. A mature gall contains many interconnected larval chambers embedded in tough, woody tissue surrounded by soft tissue. Each mature larva is encapsulated in a separate chamber surrounded by sclerenchymatic tissue. Old galls dessicate, blacken, and may remain on the plant after eclosion of the midges for more than one year. The part of the twig distal to the gall usually dies after the midges emerge. Galls are frequently infested by a lepidopteran inquiline (*Pammene megalocephala* Diakonoff: Tortricidae) and the midges are parasitized by several species of parasitic Hymenoptera (mainly Platygasteridae). Galls are formed throughout the year, with a peak during winter and spring (December–May). During the summer months (June–September), mature galls are much scarcer and considerably smaller than at other times of the year.

Remarks.—This species shares with its two congeners, *I. potanini* and *I. bassiae,* the markedly long ovipositor and an aculeus that is shorter than the apical lamella. It differs from them by having a greatly reduced lateral plate, with a notch at the base of the aculeus, and an aculeus that is straight rather than dorsally curved and that lacks hooked setae. *Izeniola obesula* males differ from the males of *I. potanini* in having a massive, rectangular aedeagus that does not narrow towards its tip.

Galls induced by this species are very common and conspicuous, and are probably identical to those described by Houard (1922) from Eritrea. They greatly differ from galls of the two other *Izeniola* spp. which, although induced on twigs, constitute very small and shallow swellings that are barely visible.

Stefaniola Kieffer 1913

Stefaniola Kieffer 1913: 45.
Type species: *Stefaniola salsolae* (Tavares 1904). By monotypy.

This Old World genus, comprising about 110 species, is the largest in the tribe Lasiopterini. It is characterized by a short, bulky body and short ovipositor with dorsally curved (concave) aculeus. Aculei and apical lamellae vary greatly in shape and can readily serve to subdivide the genus. Larvae lack a spatula. The majority of the species are known from Central Asia, and some are known from the Mediterranean Basin. The three new species described here match well the generic concept.

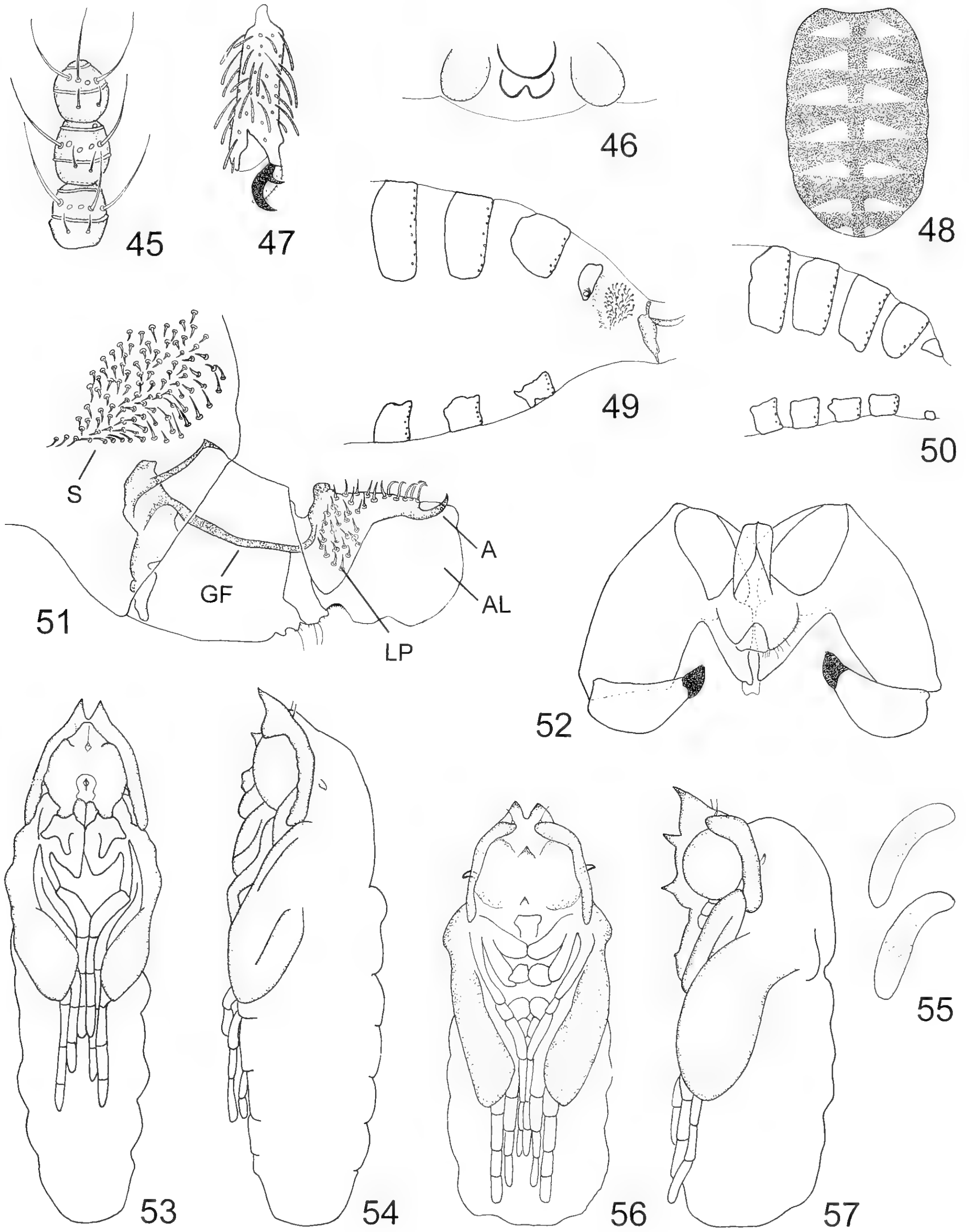
Stefaniola defoliata **Dorchin, new species**
(Figs. 5, 45–55)

Adult.—*Head:* Eye facets round; gap between eyes on vertex 0–1 facets wide. Occiput, frons, gena and postgena covered by white scales and hairs. Antenna: scape bare, light orange; pedicel covered by dark scales; flagellomeres 10 in both sexes (in one female flagellomeres 6–7 were fused to form one, long flagellomere), light orange, without scales, each with two whorls of circumfila (Fig. 45). Palpus one segmented, globular, covered by white scales and hairs (not shown) (Fig. 46).

Thorax: Dorsum black, covered by sparse, white scales and hairs. Pleura light brown to orange, with white scales. Wing: Light brownish orange, evenly covered by microtrichia; length, 1.8–1.9 in males (n = 2), 1.1–2.1 mm. in females (n = 12); anterior edge with black and white scales from basal portion to juncture of R_5 and C; juncture with a patch of dark scales; M present; Cu unforked; posterior wing margin with long, fine hairs up to junction of M and C. Stem of halter light orange, without scales, knob white with few dark scales. Legs: coxae and trochanters with white scales; femora, tibiae and tarsi dorsally covered by dark scales, ventrally by white scales; claws evenly curved, with thin tooth at base; empodia almost as long as claws (Fig. 47).

Female abdomen (Fig. 49): General color pink, covered by white scales. Eighth tergite much shorter than preceding, with round, socket-like area; tergites and sternites without trichoid sensilla; sternite 8 completely unsclerotized. Scale pattern on dorsum as in Fig. 48. Ovipositor (Fig. 51): setae of lateral group on eighth segment at least five times as long as wide; peripheral setae directed towards center, central and ventral setae directed ventrally; arm of genital fork widens distally into lateroventral plate; lateral plate bearing straight or slightly curved, strong setae, proximally with dorsal, saddle-like projection; aculeus almost as long as apical lamella, strongly recurved only in distal half, proximal half bears few posteriorly curved, thin setae; apical lamella globular to rectangular.

Male abdomen (Fig. 50): General color dull gray, evenly covered by white scales; scale pattern on dorsum as in female; eighth



Figs. 45–57. 45–55, *Stefaniola defoliata*. 45, Distalmost flagellomeres. 46, Mouthparts. 47, Distal tarsomere. 48, Scale pattern on abdomen, dorsal view. 49, Female postabdomen, lateral view. 50, Male postabdomen, lateral view. 51, Female ovipositor, lateral view. 52, Male terminalia, dorsal view. 53, Pupa, ventral view. 54, Pupa, lateral view. 55, Eggs. 56–57, *S. siliqua*. 56, Pupa, ventral view. 57, Pupa, lateral view. A = aculeus, AL = apical lamella, GF = genital fork, LP = lateral plate, S = lateral group of setae.

tergite and sternite greatly reduced, almost unsclerotized. Genitalia (Fig. 52): Cercus triangular; hypoproct distally with shallow depression, almost rectangular; paramere triangular, narrower than aedeagus throughout its length, setulose; aedeagus truncate, with a small apical notch; gonopod bearing several long, recurved setae (not shown); gonocoxite robust, rectangular; mediobasal lobe not prominent, setulose; gonostylus entirely setulose.

Pupa (Figs. 53–54).—Prothoracic spiracles about three times as long as wide, tapered at tip. Antennal and anterofrontal horn pointed anteriorly. Posterofrontal horn laterally flattened, crest-like. Dorsum of abdomen with minute spines.

Larva (third instar).—Light orange. SEM reveals a group of minute triangular spines situated on each side of thoracic and abdominal segments. Dorsum of abdomen with rows of minute, flattened, blunt spines.

Egg (Fig. 55).—Orange, cylindrical, slightly curved.

Distribution.—Israel (Dead Sea area and Arava Valley); Egypt (Sinai).

Holotype.—♀ reared from *Suaeda monoica* elongated twig gall, Israel, Ne'ot HaKikkar, 1.V.1997, N. Dorchin (slide).

Paratypes.—All specimens reared from *Suaeda monoica* elongated twig galls, Israel, Ne'ot HaKikkar: 13 ♀, 1 ♂, 9 pupae, 7 larvae, same data as Holotype; 1 ♀, 1 ♂, 1 larva, 30.III.1996; 1 ♀, 4 ♂, 2 pupae, 2 larvae, 29.III.1996; 10 larvae, 2.II.1999; 1 ♀ Newe Zohar 7.XI.1999.

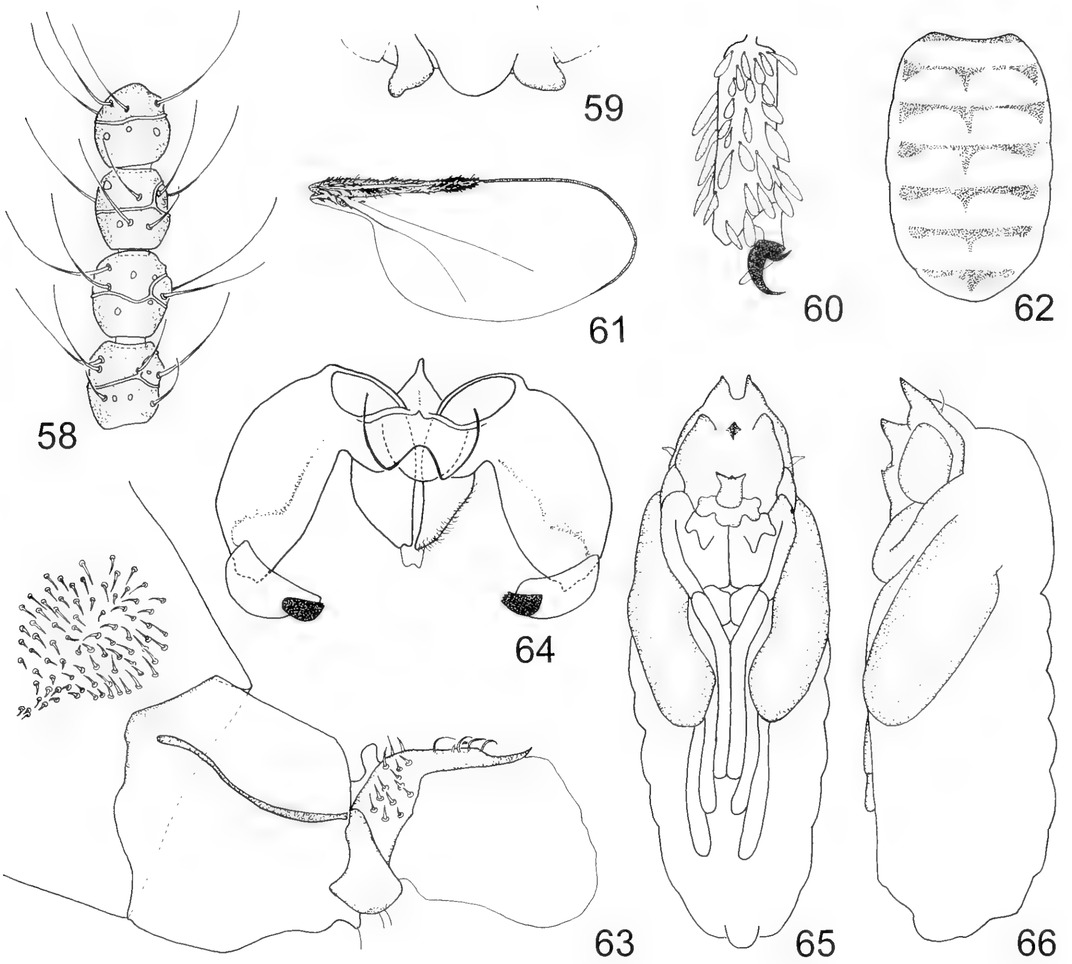
Etymology.—The name *defoliata* is an adjective derived from the Latin folium ("leaf") with the prefix 'de', with reference to the effect large galls induced by this species have on shoots.

Biology.—Eggs are scattered individually on young leaves and twigs. Larvae induce elongated, polythalamous twig galls (Fig. 5). Gall dimensions depend on the number of occupant larvae. When only 3–5 larvae are present, the gall is about 1.5 times wider than a normal twig, no more than 3 cm long, and is difficult to detect. Galls containing 20–30 larvae are 3–4 times as wide as a normal twig and up to 20 cm long. Merging of two or more adjacent galls on the same or on branching twigs is common. Large, fully mature galls are conspicuous for causing defoliation of the twig on which they develop. Twigs sometimes desiccate and die after eclosion of the midges. Small galls are mainly found from October to May in all localities. Much larger and more conspicuous galls were mainly found in one location (Ne'ot HaKikkar) during spring (March–May). The reason for this difference between localities is unclear.

Remarks.—While females of almost all *Stefaniola* species have a typical elongate, dorsally curved (concave) aculeus with several curved setae, the aculeus of this species is short, strongly curved on its distal third only, and does not bear any setae. The apical lamella is about as long as the aculeus, whereas in other species with a short aculeus (e.g., *S. nitrariae* Fedotova and *S. orientalis* Fedotova), the apical lamella is 2–3 times longer. Adults of *S. defoliata* could not be distinguished from those of *S. siliqua*. This resemblance is perplexing when considering the remarkably different galls induced by these species. The pupa of *S. siliqua* has a pointed posterofrontal horn and a small projection on the fore coxa, whereas the posterofrontal horn of *S. defoliata* is in the form of a laterally flattened ridge, and the fore coxa lacks any projection. The phenology of the two species differs as well. While galls of *S. siliqua* are found throughout the year, those of *S. defoliata* are not formed during summer, and their dimensions vary according to season.

***Stefaniola rufa* Dorchin, new species**
(Figs. 6, 58–66)

Adult.—*Head:* Eye facets round; gap between eyes on vertex 0–1 facets wide. Occiput, gena and postgena covered by white scales and hairs; frons densely covered by white scales. Antenna: scape conical, bare, light orange; pedicel globular, covered by



Figs. 58–66. *Stefaniola rufa.* 58, Distalmost flagellomeres. 59, Mouthparts. 60, Distal tarsomere. 61, Wing. 62, Scale pattern on abdomen, dorsal view. 63, Female ovipositor, lateral view. 64, Male terminalia, dorsal view. 65, Pupa, ventral view. 66, Pupa, lateral view.

dark scales; flagellomeres (Fig. 58): 10 in both sexes, barrel-shaped, necks not evident, light orange, without scales, evenly covered by microtrichia, each with one, occasionally partial second circumfilum and one row of strong setae on each side of circumfilum; apical flagellomere shorter than preceding, rounded distally. Palpus one segmented (Fig. 59), bearing few long setae (not shown).

Thorax: Dorsum black, covered by sparse, white scales and hairs. Pleura light brown to orange, with white scales. Wing (Fig. 61): light brownish orange, evenly covered by microtrichia; length, 1.25 mm in male (n = 1), 1.47–1.75 mm in females (n = 9); basal half of C covered by dark hairs; patch of dark scales situated proximal to junction of R_5 and C; M present, Cu unforked; posterior wing margin with long, fine hairs reaching juncture of M and C (not shown). Halter light orange, without scales. Legs: coxae and trochanters with white scales; femora, tibiae and tarsi dorsally covered by dark scales, ventrally by white scales; tarsi covered by wide, clavate scales (Fig. 60); tarsal claws evenly curved, with pronounced, strongly curved tooth; empodia about 0.75 as long as claws.

Female abdomen: General color pink,

covered by white scales. Tergites and sternites similar to *S. defoliata.* Dark scales on dorsum form a pattern as in Fig. 62. Ovipositor (Fig. 63): Setae of lateral group on eighth segment form a circle, directed towards the center, except for several short, ventral spines directed ventrally; most setae at least five times as long as wide, slightly and evenly curved; arm of genital fork widens distally into lateroventral plate bearing short setae; lateral plate bearing straight or slightly curved, strong setae, dorsoproximally with blunt, saddle-like projection which is much less sclerotized than rest of plate; aculeus notably shorter than apical lamella, slightly dorsally curved, bearing a few strongly curved, thin setae; apical lamella bulbous, somewhat extended towards posterad.

Male abdomen: General color light brownish orange, covered by white scales; tergites and sternites basically similar to *S. defoliata.* Dark scale pattern on dorsum duller than in female. Genitalia (Fig. 64): Cercus triangular; hypoproct rounded and entire; paramere bulbous, densely covered by curved setae, distally with small notch, narrowing from mid-length apically on ventral side; aedeagus rectangular, with small apical notch; gonocoxite bulbous, widest at midlength, more sclerotized laterally than medially; mediobasal lobe prominent, setulose; gonostylus entirely setulose.

Pupa (Figs. 65–66).—Prothoracic spiracles tapered at tip. Antennal horn well developed, pointed anteriorly. Anterofrontal horn prominent, pointed anterodorsally. Posterofrontal horn much smaller, pointed anterodorsally, with two lateral flat ridges on anterior part of clypeus. Pupa color light orange.

Larva (third instar).—Light orange, integument smooth, papillae not observed.

Egg.—Unknown.

Distribution.—Israel (Dead Sea area and Arava Valley); ?Eritrea (Houard 1922).

Holotype.—♀ reared from *Suaeda monoica* red leaf gall, Israel, Newe Zohar, 1.III.1999, N. Dorchin (slide).

Paratypes.—All specimens reared from *Suaeda monoica* red leaf galls, Israel, Newe Zohar: 7 ♀, 2 pupae, 2 larvae, same data as Holotype; 3 ♀, 13.V.1999; 3 ♀, 1 ♂, 24.X.1999; 7 ♀, 1 ♂, 7.XI.1999 N. Dorchin and Y. Malihi; 12 ♀, 5 exuviae 22.XI.1999; 2 pupae 15.XII.1999; 4 ♀, 4 ♂ 2.III.2000.

Etymology.—The name *rufa,* an adjective, is Latin for "red," with reference to the distinct color of the gall.

Biology.—Larvae induce conspicuously red colored leaf galls (Fig. 6), that barely differ in shape from an unaffected leaf. The only sign of infestation is the red color that is limited to the infested part of the leaf. During summer, when galls are scarce, their color is much duller than during winter and spring, when they are easily located due to the dark red pigmentation. Each gall contains 1–4 larvae, in individual larval chambers. Each chamber is surrounded by rigid sclerenchymatic tissue and can be externally seen as a light yellowish area against the red background of the gall. The galls are heavily parasitized by internal hymenopteran parasitoids (sometimes up to 95% parasitization). Galls are abundant during winter and spring (October–June) but are very difficult to find during summer (July–September).

Remarks.—The closest relatives of this species are probably *S. siliqua* and *S. defoliata,* which share with it the general shape of the ovipositor. In *S. rufa* the aculeus is only slightly curved, and the apical lamella is distinctly longer than the aculeus. The adult colors are lighter and duller than those of *S. siliqua* and *S. defoliata,* and it is usually smaller than them, although size ranges of these species overlap. The galls induced by this species can sometimes be mistaken for young galls of *S. siliqua*; however they are usually much smaller, never occupy the entire surface of the leaf, and cause only slight swelling of the leaf, if at all. Moreover, *S. rufa* galls contain only 1–4 larvae while those of *S. siliqua* usually contain 6–10. The two species also differ with regard to seasonality; while *S. siliqua* galls are abundant in great numbers throughout the year, those of *S. rufa* are rarely found during the hot season.

Galls induced by this species may be similar to those described by Houard (1922) from Eritrea, although according to Houard's description the galls resemble small bulges on the leaf blade, while *S. rufa* galls only rarely protrude above the leaf surface.

Stefaniola siliqua Dorchin, new species
(Figs. 7, 56–57)

Adult.—*Head:* Eye facets round; gap between eyes on vertex 0–2.5 facets wide. Occiput, frons, gena and postgena covered by white scales and hairs. Antenna: scape light orange, with white scales; pedicel covered by dark scales; flagellomeres 10 in both sexes, barrel-shaped, light orange, without scales; apical flagellomere rounded at tip. Palpus globular, one segmented, covered by white scales and hairs.

Thorax: Wing length: 1.1–1.9 mm in male (n = 5), 1.3–1.7 mm in female (n = 7). Other characters similar to *S. defoliata.*

Female abdomen: Similar to *S. defoliata* (Figs. 48, 49, 51).

Male abdomen: Similar to *S. defoliata* (Figs. 48, 50, 52).

Pupa (Figs. 56–57).—Prothoracic spiracles about three times as long as wide, tapered at tip. Antennal horn pronounced, pointed anteroventrally. Frontal horns smaller, pointed ventrally. Antennal and posterofrontal horns with small bulge at base. Fore coxa bearing small, nipple-like projection. Dorsum of abdomen with minute blunt bulges (only discernible in SEM).

Larva.—Third instar: light orange, integument covered by minute flattened spines (only discernible in SEM); papillae not observed.

Egg.—Unknown.

Distribution.—Israel (Dead Sea area and Arava Valley); Eritrea (Houard 1922).

Holotype.—♀ reared from *Suaeda monoica* pod-like leaf gall, Israel, Newe Zohar, 1.III.1999 (slide).

Paratypes.—All specimens reared from *Suaeda monoica* pod-like leaf galls: 11 ♀, 1 ♂ same data as Holotype; 3 ♂, Elot 18.III.1995; 1 ♀, 1 ♂, 1 larva, Newe Zohar 19.IV.1995; 3 ♀, Newe Zohar 9.I.1996; 1 ♂, Elot 30.III.1996; 2 ♀, 1 ♂, Newe Zohar, 14.X.1997; 15 ♀, 11 ♂, 12 pupae, 14 larvae, Elot 29.X.1997, A. Freidberg; 4 pupae, Newe Zohar, 27.X.1998; 2 ♀, 4 ♂, 'En Bogeg, 13.V.1999; 2♀, 2♂, Newe Zohar, 24.VIII.1999; 1 ♀, Ne'ot Hakinnar, 22.XII.1999; 8 ♀, 2 pupae, Newe Zohar, 2.III.2000.

Etymology.—The name *siliqua,* a noun in apposition, is Latin for "pod," referring to the shape of the gall and the position of the larvae in it, which resemble the fruit of legumes.

Biology.—Larvae induce polythalamous, pod-like leaf galls (Fig. 7), usually green, sometimes with a touch of red. Each gall contains 4–15 cells which form early during gall development (first instar larvae), and are situated in 1–2 rows, similar to seeds in a legume pod. The gall varies greatly in size according to the number of larvae it contains; it may occupy the entire leaf or only a part of it. Galls are abundant throughout the year, with a peak during winter and spring (November–May).

Remarks.—*Stefaniola siliqua* is closely related to the other two *Stefaniola* species infesting *Suaeda monoica* (see above), as well as to a yet undescribed *Stefaniola* species that infests leaves of several other *Suaeda* species in Israel. See differences between these species under *S. defoliata* and *S. rufa.*

Galls of this species are probably similar to these described by Houard (1922) from Eritrea. They resemble several other *Stefaniola* galls on Chenopodiaceae (e.g. *S. aelleniafolia* Fedotova on *Aellenia glauca* and *S. suaedae* Fedotova on *Suaeda physophora* in Central Asia). However, none of these species or their hosts occur in Israel, and their adults can be readily distinguished from those of *S. siliqua.*

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CERATOPHYLLUS ALTUS TIPTON AND MENDEZ (SIPHONAPTERA: CERATOPHYLLIDAE) IN CHILE, WITH NOTES ON THE DISTRIBUTION OF THE GENUS *CERATOPHYLLUS* CURTIS 1832 IN THE SOUTHERN HEMISPHERE

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Abstract: *Ceratophyllus altus* Tipton and Mendez is reported from Huerquehue National Park, Pucón (39°07′40″S, 71°42′01″W), Cautín Province, Chile from the nest of *Campephilus magellanicus* (King). This is the third report of the genus *Ceratophyllus* Curtis occurring in South America and the first record in Chile. Notes are provided on the distribution of the genus *Ceratophyllus* in the Southern Hemisphere.

Key Words: Siphonaptera, Ceratophyllidae, *Ceratophyllus,* Chile

The genus *Ceratophyllus* Curtis 1832, comprised of 82 species (including subspecies), occurs most commonly on birds [subgenera *Ceratophyllus* (51), *Celeophilus* (2), and *Emmareus* (11)] with only 18 taxa [subgenera *Amonopsyllus* (4) *Monopsyllus* (12) and *Rosickyiana* (2)] occurring on mammals. The genus, with few exceptions, is restricted to the Holarctic Region with the majority of species occurring in the more boreal climes. The common European chicken flea, *Ceratophyllus gallinae* (Schrank 1803), and a flea occurring on pigeons in Europe, *Ceratophyllus columbae* (Gervais 1844), have been transported with these domestic birds as far south as New Zealand (Pilgrim 1980, Smit 1965) and an unsubstantiated record of the former species was reported in Australia (Roberts 1952). Only two records of *Ceratophyllus* have been reported in the Neotropics. Smit (1963) reported two females (*Ceratophyllus* sp.) from northwestern Argentina and (1978) described *Ceratophyllus titicacensis* from southern Peru. Recently, Dr. Milton H. Gallardo, Universidad Austral de Chile, Valdivia, Chile, kindly submitted a series of three males, six females, and a single second instar larva for identification. I identified the adults of these specimens as *Ceratophyllus altus* Tipton and Mendez 1966. The male of *C. altus* was described by Tipton and Mendez (1966) and the female by Holland (1971). The morphology, distribution, and host relationships of *C. altus* are discussed in this paper. Institutional depositories for material examined include The Natural History Museum, London (NHM), National Museum of Natural History, Smithsonian Institution, Washington, DC (NMNH), and the Canadian National Collection of Insects, Arachnids and Nematodes, Ottawa, Ontario, Canada (CNCIAN). Avian and mammalian host synonymies follow those of Sibley and Monroe 1990 and Wilson and Reeder 1993, respectively.

Ceratophyllus altus Tipton and Mendez 1966

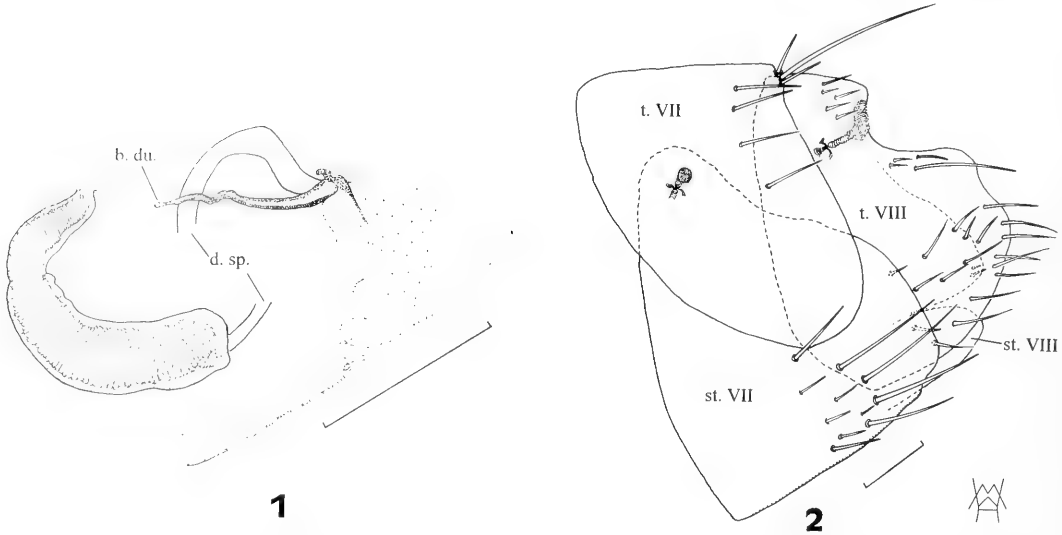
Material examined.—ARGENTINA: *Ceratophyllus* sp., 1 ♀, ex *Colaptes pitius cachinnans* = *Colaptes pitius* (Molina 1782), El

Bolsón (41°59′S, 71°35′W), elevation 600–1,000 m, Rio Negro Province, 22 September 1961, G. Topál and Szabó, (NHM). CHILE: *C. altus,* 3 ♂, 6 ♀, (+1 larva, *Ceratophyllus* sp.), ex nest of *Campephilus magellanicus* (King 1828) in a tree hole 8.2 m high in *Nothofagus pumilio* (Poepp. and Endl. 1896), Huerquehue National Park, Pucón (39°07′40″S, 71°42′01″W), elevation 1,000–1,500 m, Cautín Province, 22 January 1997, Juan Fuentes (U.G. Patrimonio Silvestre, Ministerio de Agricultura). MEXICO: *C. altus,* 4 ♂, 2 ♀, ex "owl nest" (*Glaucidium* sp.), 6 May 1969, 3 ♂, 2 ♀, ex "nest and adult of *Glaucomys volans goldmanni* = *Glaucomys volans* (Linn. 1758)", 13 May 1969, 4 ♂, 4 ♀, ex "wood pecker holes", 15 May 1969, 4 ♂, 4 ♀, ex "sparrow hawk nests" (*Falco sparverius tropicalis* = *Falco sparverius* Linn. 1758), 19 May 1969, all from 9 km E San Cristobal de las Casas, Chiapas, 2 ♂, 4 ♀, ex "owl nest in hollow tree" (*Glaucidium* sp.), 19 May 1969, 13 km E San Cristobal de las Casas, Chiapas, all elevations ~2,135 m, all collected by J.E.H. Martin, (CNCIAN). PANAMA: *C. altus,* male holotype, ex *Glaucidium jardinii* (Bonaparte 1855), Boquete, Chiriqui, elevation 2,380 m, 3 May 1961, Keenan and Tipton, (NMNH). PERU: *Ceratophyllus titicacensis* Smit 1978, 6 ♂, 6 ♀ paratypes, ex *Phalacrocorax olivaceus olivaceus* (Humbolt) = *Phalacrocorax brasilianus* (Gmelin 1789), near Taman (15°38′S, 69°50′W), elevation 3,850 m, Capachica Peninsula, Lake Titicaca, 21 November 1937, G. O. Crawford, (NHM).

Remarks.—Chilean males compared with the holotype male of *C. altus* from Panama and with males of *C. altus* from Chiapas, Mexico, are conspecific. Holland (1971) examined a large series of both sexes from Chiapas. He indicated and illustrated extreme variation in the female st. VII, although he did not discuss the features of this sclerite relative to specific host species. The posterior margin of st. VII of specimens from "woodpecker holes" from Mexico has neither a sinus nor lobes, a feature common to all six Chilean females. Mexican specimens from a "sparrow hawk nest" possess a large dorsal lobe with a deep subtending sinus on margin of st. VII, as do most specimens examined from the "nest and adult of *G. volans*" and the nests of "*Glaucidium* sp." One specimen each, from the latter two hosts has a poorly developed lobe and only a slight indication of a sinus. The st. VII of most material from Mexico resembles that of *Ceratophyllus idius* Jordan and Rothschild 1920 (with dorsal lobe and deep subtending sinus), but the accompanying males are clearly *C. altus.* Because of the unique distribution and need to document the presence of *C. altus* in Chile, an illustration of the spermatheca and st. VII is provided as Figs. 1–2.

The single larva accompanying adults of *C. altus* was submitted to Professor R. L. C. Pilgrim. He placed it in the Ceratophylloidea, Ceratophyllidae, and stated (pers. comm.) "that it has close morphological similarities with larvae of *C. idius* and of *Ceratophyllus niger* C. Fox 1908. The latter two taxa are, as yet, inseparable from each other in the larval stages (Pilgrim and Galloway 2000)." While the larvae of *C. altus* have never been described, Tipton and Mendez (1966) indicated that adults of *C. altus* are very similar to *C. idius.* The only other genus belonging to Ceratophyllidae known to occur in South America that parasitizes only birds is *Dasypsyllus,* whose larvae are sufficiently distinct from those of *Ceratophyllus.* Therefore, evidence suggests that the single larva is the offspring of the *C. altus* adults found in the same nest.

Smit (1963) discussed two females of *Ceratophyllus* sp., however, only one of these could be located in The Natural History Museum, London. The spermatheca and caudal margin of st. VII of this single female from Argentina are indistinguishable from those of the specimens from Chile and from those of *C. altus* females from "woodpecker holes" in Mexico. Ele-



Figs. 1–2. Female *Ceratophylluls altus.* 1, Spermatheca and bursa copulatrix (b. du. = blind duct, d. sp. = duct of spermatheca. 2, Terminal segments (t. VII = tergite VII, t.VIII = tergite VIII, st. VII = sternite VII, st. VIII = sternite VIII).

vation records of *C. altus* range from 600–1,500 m in Chile and Argentina, while records in warmer climates of Mexico (2,100 m) and Panama (2,380 m) occur at higher elevations. Species of *Ceratophyllus* require cool, temperate climates and the occurrence of the genus in South America seems to be limited to higher elevations, which have climatic conditions similar to temperate regions. Although little is known about *C. titicacensis,* its occurrence at such a high altitude (3,850 m) supports the required temperate climatic conditions of species of *Ceratophyllus.* The finding of *C. altus* at lower elevations in Chile and Argentina may be explained by the cool summer climate of the Magellanes. The common use of woodpecker nest cavities by other hosts such as owls (*Glaucidium* sp.), sparrow hawks (*Falco* sp.), and flying squirrels (*Glaucomys*) might explain the presence of this species on these hosts. The introduction of *C. altus* into South America likely occurred via migratory birds, but evidence of propagation in the nest of *C. magallanicus* in Chile suggests it may be well established in this region, contrary to the dearth of records. *Falco sparverius* has the broadest range of all the potential migrating host species, occurring from Alaska south to the islands of the Diego Ramírez Archipelago. This is the most plausible host for distributing *C. altus* from its northern distribution in Chiapis, Mexico, south to Chile and Argentina. Species of *Campephilus* may well be a common host of *C. altus* throughout this woodpecker's range. Additional collecting of fleas from woodpecker nest cavities from the northern range of *C. altus* from Chiapis, Mexico, to the southern limits of Cautín Province, Chile, and Rio Negro Province, Argentina, at elevations above 1,500 m will likely yield many more records of *C. altus.* Beaucournu and Gallardo (1991) document 91 species of fleas in Chile. This new Chilean record of *C. altus* increases the country's total number of species to 92.

Two pairs of *C. altus* are deposited in the Museo Nacional de Historia Natural, Santiago, Chile, the larva in the collection of R. L. C. Pilgrim, and the remainder in the author's collection.

ACKNOWLEDGMENTS

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LIFE HISTORY AND DESCRIPTION OF IMMATURE STAGES OF *TEPHRITIS JOANAE* GOEDEN (DIPTERA: TEPHRITIDAE) ON *ERICAMERIA PINIFOLIA* (A. GRAY) H. M. HALL (ASTERACEAE) IN SOUTHERN CALIFORNIA

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Abstract.—*Tephritis joanae* Goeden is a univoltine or bivoltine, oligophagous fruit fly (Diptera: Tephritidae) producing a single, annual, fall generation in the flower heads of *Ericameria pinifolia* (A. Gray) H. M. Hall (Asteraceae) belonging to the subtribe Solidagininae of the tribe Astereae in southern California. It also has been reared from fall-blooming flower heads of *E. cuneata* (A. Gray) McClatchie and *E. ericoides* (Lessing) Jepson in the same subtribe and from *Senecio flaccidus* Lessing belonging to the subtribe Senecioninae of the tribe Senecioneae. The egg, second- and third-instar larvae and puparium are described and figured, and these immature stages are compared with those of other southern California *Tephritis*. The egg is covered by a smooth, membraneous sheath of unknown function. The integumental petals of the second instar are described and figured for the first time for the genus *Tephritis*, as are the anterior spiracles, the lateral spiracular complexes of the metathorax and the first abdominal segment, and the posterior spiracular plate with its rimae and interspiracular processes. The most ventral oral ridges of the third instar are bluntly toothed along their ventral margins. A stelex sensillum lies dorsolaterad and ventrolaterad, but apparently not mediolaterad of each posterior spiracular plate. One or two, annual generations are produced in southern California; it is unknown if there is a spring generation on still-unknown, spring-flowering, alternate hosts, or if there is solely a generation in the fall on *E. pinifolia*, *E. ericoides*, and *S. flaccidus*. The life cycle is of the aggregative type and overwintering occurs as long-lived, sexually immature adults. *Eurytoma* sp. nr. *bigloviae* Ashmead, *E. veronia* Bugbee (Hymenoptera: Eurytomidae), and *Pteromalus* sp. (Hymenoptera: Pteromalidae) were reared from puparia of *T. joanae* as solitary, larval-pupal endoparasitoids. Additional, *E. veronia*, *E. obtusiventrus* Gahan, and *Pteromalus* sp. were reared from mature flower heads containing *T. joanae* as probable solitary primary parasitoids, as were *Torymus* sp. (Hymenoptera: Torymidae) and *Bresema* sp. (Hymenoptera: Eupelmidae).

Key Words: Insecta, *Tephritis*, *Ericameria*, Asteraceae, nonfrugivorous Tephritidae, biology, taxonomy of immature stages, flower-head feeding, aggregative life cycle, seed predation, parasitoids

To date, the life histories and immature stages of two species of *Tephritis* have been described in detail from southern California: *T. arizonaensis* Quisenberry (Goeden et al. 1993) and *T. baccharis* (Coquillett) (Goeden and Headrick 1991). The former species annually produces a florivorous generation and a branch-tip-mining generation (Goeden et al. 1993); whereas, the latter species is a multivoltine, obligate gall-former (Goeden and Headrick 1991). A third species, *T. stigmatica* (Coquillett), is both florivorous and gallicolous (Tauber and Toschi 1965, Goeden 1988a). This paper describes the life history and immature stages of the obligate, flower head-infesting species, *T. joanae* Goeden (1993).

MATERIALS AND METHODS

The present study was based in large part on dissections of samples of flower heads of *Ericameria pinifolia* (A. Gray) H. M. Hall (Asteraceae) mainly collected at three locations during 1992 to 1996: (1) along La Posta Road, S of Interstate Highway 8 at 1,052-m elevation, San Diego Co.; (2) at the junction of State Highway 79 and Palomar Divide Road at 890 m, Cleveland Nat. Forest, San Diego Co.; and (3) Bautista Canyon near Cottonwood Canyon below road to Thomas Mountain at 1,097 m, San Bernardino Nat. Forest (S Section), Riverside Co. 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, six second- and 16 third-instar larvae and seven puparia dissected from flower heads were preserved in 70% EtOH for scanning electron microscopy (SEM). Additional 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, and 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. Twenty-one arenas each consisted of a clear-plastic, petri dish provisioned with a flattened, water-moistened pad of absorbant cotton spotted with honey (Headrick and Goeden 1994) and each arena contained two virgin males and a 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). Terminology and telegraphic format used to describe the immature stages follow Goeden (1993, 2001), Goeden et al. (1993), Goeden and Headrick (1999), Goeden and Teerink (1999a, b), Teerink and Goeden (1999), and our earlier works cited therein. Means ± SE are used throughout this paper. Voucher specimens of *T. joanae* immature stages, adults, and parasitoids reside in my research collections. Digitized photographs used to construct text figures were processed with Adobe Photoshop® Version 5.

RESULTS AND DISCUSSION

TAXONOMY

Adult.—*Tephritis joanae* was described by Goeden (1993), who pictured right wings of a male and a female.

Immature stages.—The egg, second- and third-instar larvae, and puparium are described below for the first time.

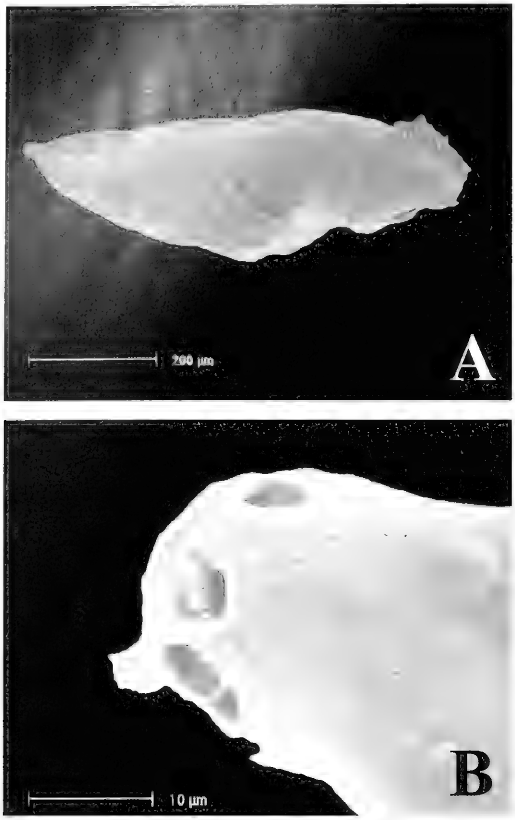

Fig. 1. Egg of *Tephritis joanae*: (A) habitus, anterior end to left; (B) pedicel showing pattern of aeropyles.

Egg: Thirteen eggs measured *in situ* in field-collected, preblossom flower heads were white, opaque, smooth, elongate-ellipsoidal, 0.70 ± 0.006 (range, 0.66–0.72) mm long, 0.19 ± 0.003 (range, 0.18–0.20) mm wide, smoothly rounded at tapered basal end (Fig. 1A); pedicel button-like, 0.02 mm long, circumscribed apically by different-sized, semicircular or elliptical, sometimes partitioned aeropyles, arranged in a single row parallel to the long axis of the egg (Fig. 1B).

The egg of *T. joanae* 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. Except for the pedicel (Fig. 1B), the egg of *T. joanae* is covered by a smooth, membraneous sheath (Fig. 1A), which remains intact and is not partly shed and peeled back during oviposition as in the other two species. In *T. arizonaensis* (Goeden et al. 1993), this membraneous sheath is prominently, longitudinally striated, but it is only very slightly striated anteriorly in *T. joanae* (Fig. 1A). 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 three species of *Tephritis.*

Second instar: White, cylindrical, body segments well-defined; gnathocephalon conical (Fig. 2A); dorsal sensory organ well-defined, flattened (Figs. 2A-1, B-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. 2A-2, B-7) ventrolaterad of anterior sensory lobe; mouthhook bidentate (Figs. 2A-3, B-8); median oral lobe not seen; three, flattened papilliform, integumental petals dorsad of each mouthhook (Figs. 2A-4, B-9), three or four more pairs of integumental petals also in vertical series in medial groove between anterior sensory lobes (Fig. 2B-10); at least three complete, oral ridges (Fig. 2B-11) laterad of anterior sensory lobe, and three incomplete oral ridges dorsad of the aforementioned oral ridges (Fig. 2B-12); prothorax circumscribed anteriorly by at least two rows of minute acanthae (Fig. 2A-5); anterior thoracic spiracle with three, doliform papillae (Fig. 2C); lateral spiracular complex of metathorax consists of a spiracle (Figs. 2D-1, E-1) and two verruciform sensilla (Fig. 2D-2), one dorsal to other, and upper one posteriorad of spiracle (Figs. 2D, E-2); lateral spiracular complex of first abdominal segment (A-I) also consists of a spiracle, apparently closed (Fig. 2D-3), and two verruciform sensilla (Fig. 2D-4), one dorsal to other, and upper one posteriorad of spiracle (Fig. 2D); posterior

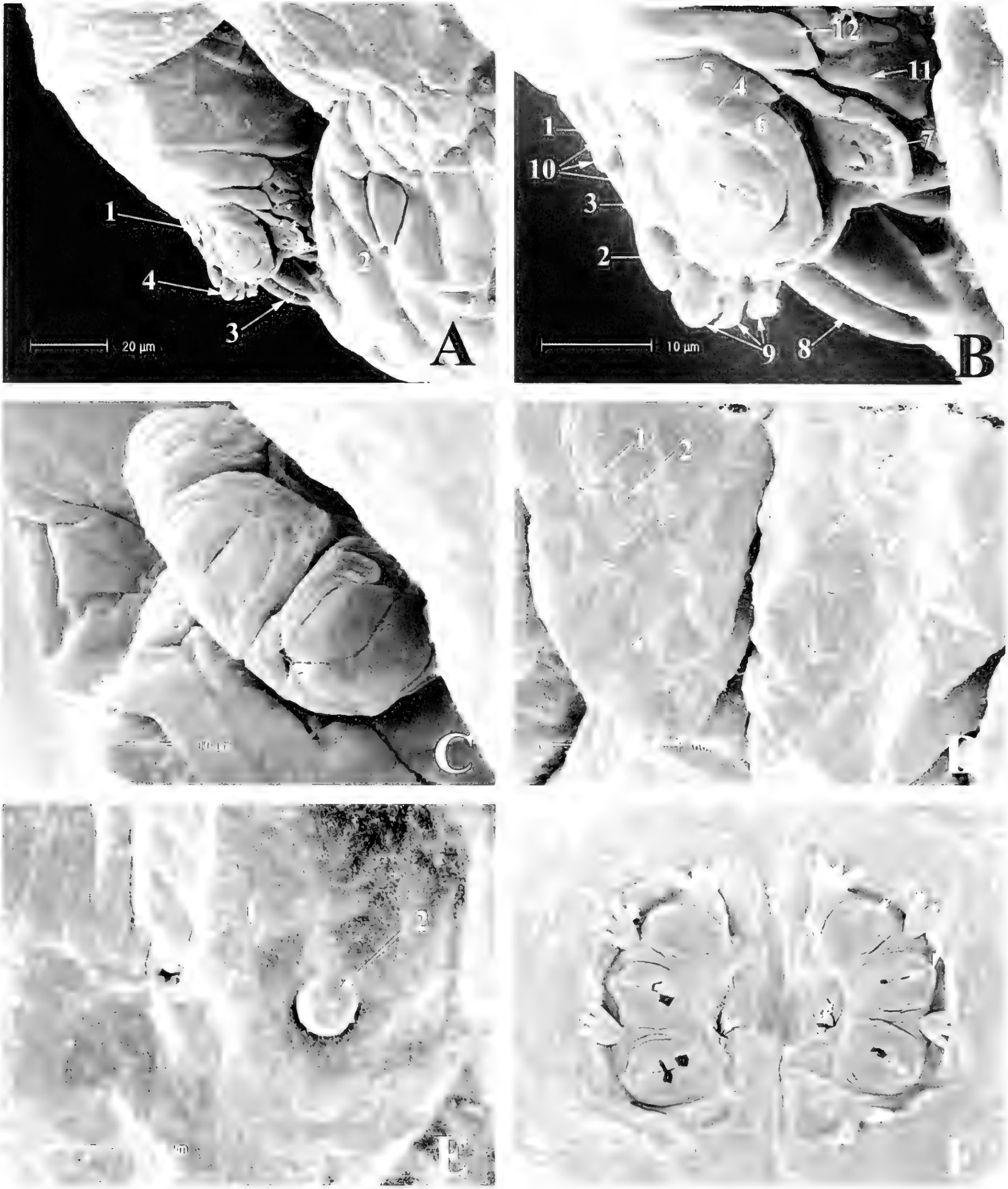

Fig. 2. Second instar of *Tephritis joanae*: (A) gnathocephalon, lateral view, 1- dorsal sensory organ, 2- stomal sense organ, 3- mouthhook, 4- integumental petal, 5- minute acanthae; (B) 1- dorsal sensory organ, 2- anterior sensory lobe, 3- terminal sensory organ, 4- lateral sensory organ, 5- supralateral sensory organ, 6- pit sensory organ, 7- stomal sense organ, 8- mouth hook, 9- integumental petals, 10- integumental petals, 11- oral ridge (complete), 12- oral ridge (incomplete); (C) anterior spiracle; (D) lateral spiracular complexes of metathorax (left) and abdominal segment 1 (right), 1- metathoracic spiracle, 2- metathoracic verruciform sensilla, 3- spiracle of, 4- verruciform sensilla of abdominal segment 1; (E) close-up of 1- metathoracic spiracle, 2- verruciform sensillum; (F) posterior spiracular plate, 1- rimae, 2- interspiracular processes.

spiracular plate bears three ovoid rimae (Fig. 2F-1), ca. 0.02 mm long, and four interspiracular processes (Fig. 2F-2), each with two to four, foliose branches with one to three, apical teeth, longest branch measuring 0.01 mm.

The habitus of the second instar of *T. joanae* approximates those of *T. baccharis* (Goeden and Headrick 1991) and *T. arizonaensis* (Goeden et al. 1993). The dorsal sensory organ is well-defined in the second instar of *T. joanae* (Figs. 2A-1, B-1); it also is well defined in *T. baccharis* (Goeden and Headrick 1991), and it was pictured, though not specifically mentioned as occurring in *T. arizonaensis* (Goeden et al. 1993). The integumental petals of *T. joanae* (Figs. 2A-4, B-9, -10) are described and figured here for the first time for a second instar in this genus, as are the anterior spiracle (Fig. 2C), the lateral spiracular complexes of the metathorax (Figs. 2D-1, -2; 2E-1, -2) and abdominal segment 1 (Fig. 2D-3, -4), and the posterior spiracular plate with its rimae and interspiracular processes (Figs. 2F-1, -2).

Third instar: White, ovoidal, distinctly segmented, superficially smooth, tapered anteriorly, truncated posteriorly (Fig. 3A); gnathocephalon conical, anteriorly flattened, and medially cleaved by a vertical suture (Figs. 3B, C): one or two rows of posteriorly directed, spinose, minute acanthae incompletely circumscribe prothorax and mesothorax anteriorly (Fig. 3B-1); dorsal sensory organ well-defined, hemispherical (Figs. 3C-1, D-1, E-1), with dorsolateral pair of basal pores (Fig. 3E-2); anterior sensory lobe (Figs. 3C-2, D-2, E-3) bears terminal sensory organ (Figs. 3C-3, D-3, E-4), lateral sensory organ (Figs. 3C-4, D-4, E-5), supralateral sensory organ (Figs. 3C-5, D-5, E-6), and pit sensory organ (Figs. 3C-6, D-6, E-7); six papilliform or spatulate, integumental petals in two rows above each mouthhook (Figs. 3C-7, D-7, E-8), plus two more pairs of integumental petals dorsal to the aforementioned petals (Figs. 3C-8, E-9) and to each side of vertical medial suture, topped by a single, dorsocentral petal (Fig. 3E-10); at least 10 oral ridges (Figs. 3C-9, D-8) dorsolateral to oral cavity, the ventral six oral ridges bluntly toothed ventrally, the dorsal four oral ridges with a single ventral tooth, the uppermost oral ridge incomplete dorsally; stomal sense organ (Figs. 3C-10, D-9) ventrolaterad of anterior sensory lobe; mouthhook (Figs. 3B-2, C-11, E-11) tridentate; median oral lobe (Figs. 3C-12, E-12) laterally flattened, bluntly pointed anteriorly; anterior thoracic spiracle on posterior margin of prothorax bears three (Figs. 3F, 4A-1) or four (Figs. 3B-3, 5B-2) doliform papillae; mesothoracic lateral spiracular complex with five verruciform sensilla (Fig. 4A-2) and metathoracic lateral spiracular complex with five verruciform sensilla (Fig. 4A-3), sensilla of both complexes aligned vertically (Fig. 4A), mesothoracic spiracle greatly reduced (not shown), metathoracic spiracle open (Figs. 4A-4, B-1) and just anteriorad of upper verruciform sensillum (4A-3, B-2); lateral spiracular complex of abdominal segment 1 with a spiracle (Fig. 4A-5) and three verruciform sensilla (Fig. 4A-6), one dorsoposteriorad and one ventroposteriorad of the spiracle (Figs. 4A-5, C), the third well ventral to and aligned vertically with the other two sensilla (Fig. 4A-6); one stelex sensillum dorsolaterad (Figs. 4D-1, F-1) and one ventrolaterad (Fig. 4D-2) of posterior spiracular plate (Fig. 4E), each stelex sensillum sits within a raised circular area (Fig. 4F-1); each posterior spiracular plate (Figs. 4D-3, 4E) bears three ovoid rimae, ca. 0.05 mm in length (Figs. 4D-4, E-1), and four, two- to three-branched, single- or bifurcately-tipped, interspiracular processes, each ca. 0.016 mm long (Figs. 4D-5, E-2); intermediate sensory complex (Figs. 4D-6, F-2) with a stelex sensillum (Fig. 4F-3) and a medusoid sensillum (Fig. 4F-4).

The habitus of the third instar of *T. joanae* is similar to that described for *T. baccharis* (Goeden and Headrick 1991) and *T. arizonaensis* (Goeden et al. 1993). The gnathocephalon, or at least the anterior sen-

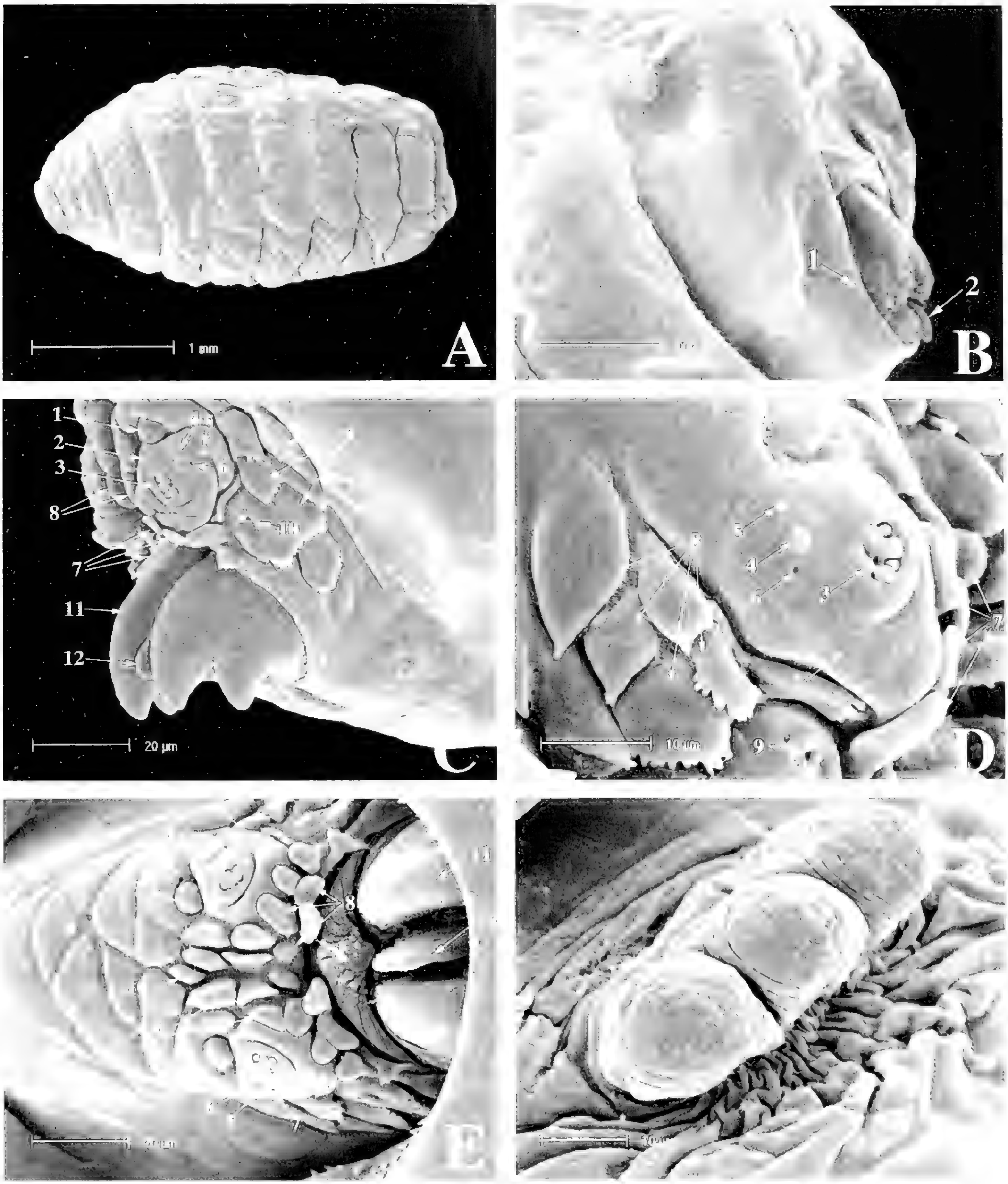

Fig. 3. Third instar of *Tephritis joanae*: (A) habitus, anterior to left; (B) gnathocephalon and prothorax, frontolateral view, 1- minute acanthae, 2- mouthhook, 3- anterior spiracle; (C) gnathocephalon, frontolateral view, 1- dorsal sensory organ, 2- anterior sensory lobe, 3- terminal sensory organ, 4- lateral sensory organ, 5- supralateral sensory organ, 6- pit sensory organ, 7- integumental petals, 8- integumental petals, 9- oral ridges, 10- stomal sense organ, 11- mouthhook, 12- median oral lobe; (D) close-ups, 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- integumental petals, 8- oral ridges, 9- stomal sense organ; (E) gnathocephalon, frontal view, 1- dorsal sensory organ, 2- pair of dorsolateral, basal pores, 3- anterior sensory lobe, 4- terminal sensory organ, 5- lateral sensory organ, 6- supralateral sensory organ, 7- pit sensory organ, 8- integumental petals, 9- integumental petals, 10- dorsocentral, unpaired, integument petal, 11- mouthhook, 12- median oral lobe; (F) anterior thoracic spiracle.

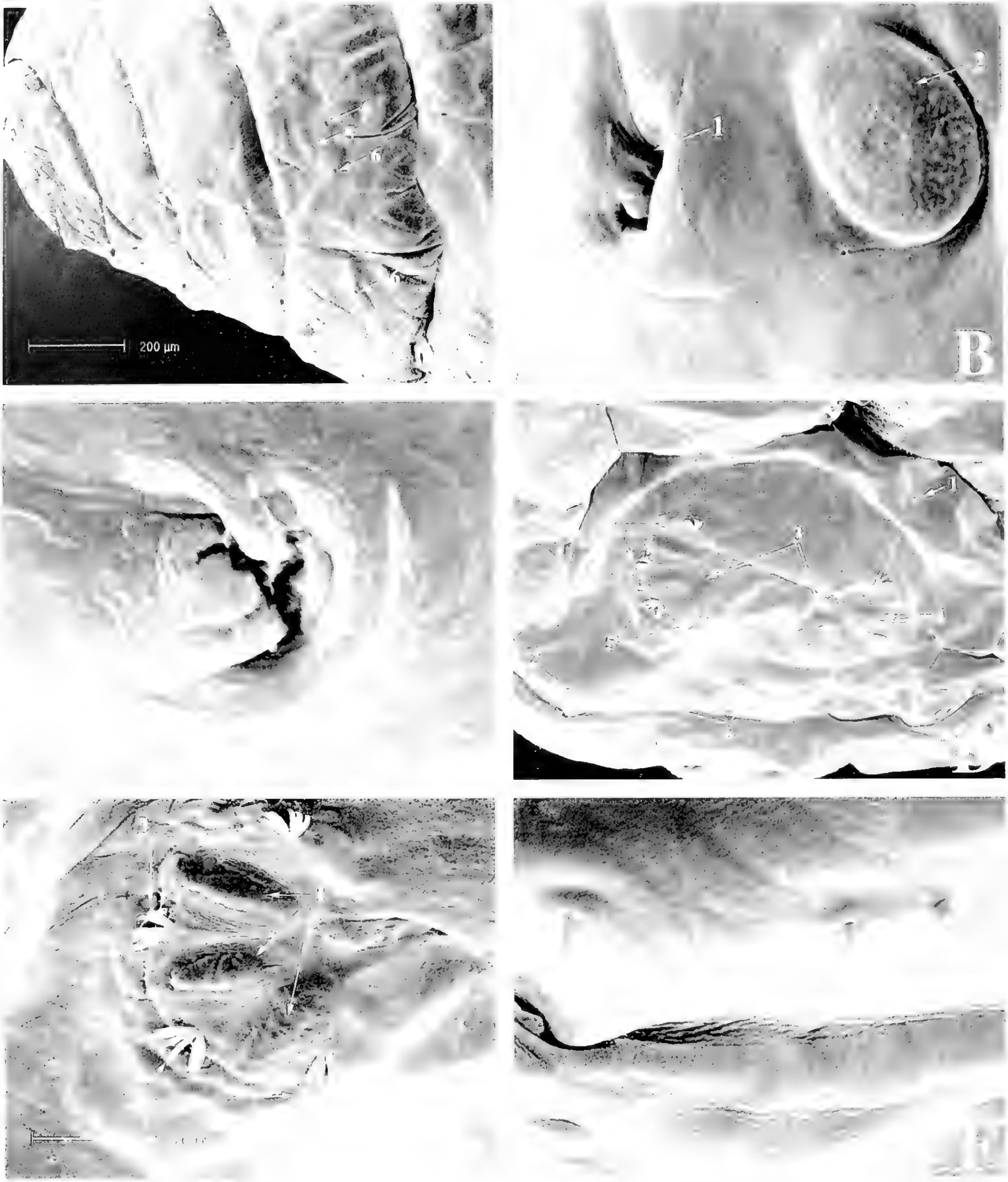

Fig. 4. Third instar of *Tephritis joanae*, continued: (A) mesothoracic, metathoracic, and A-I, lateral spiracular complexes, 1- anterior spiracle, 2- mesothoracic verruciform sensilla, 3- metathoracic verruciform sensilla, 4- metathoracic spiracle, 5- spiracle of abdominal segment 1, 6- verruciform sensilla of abdominal segment 1; (B) close-up of 1- metathoracic spiracle, 2- verruciform sensillum; (C) close-up of spiracle of abdominal segment 1; (D) caudal segment, 1- dorsolateral stelex sensillum, 2- ventrolateral stelex sensillum, 3- posterior spiracular plates; 4- rimae, 5- interspiracular processes, 6- intermediate sensory complexes; (E) posterior spiracular plate, 1- rimae, 2- interspiracular processes; (F) 1- ventrolateral stelex sensillum, 2- intermediate sensory complex with 3- stelex sensillum, 4- medusoid sensillum.

sory lobes of all three species are separated by a vertical medial suture (Goeden and Headrick 1991, Goeden et al. 1993; Fig. 3B). Far fewer minute acanthae anteriorly circumscribe the thoracic and abdominal segments of the third instars of these three species of *Tephritis* (Goeden and Headrick 1991, Goeden et al. 1993; Fig. 3B-1) than those of *Neaspilota* spp. (Goeden 2001 and references therein) and *Trupanea* spp. (Goeden and Teerink 1999 and references therein). Most other comparisons of *Tephritis* with *Neaspilota, Trupanea,* and *Procecidochares* spp. are deferred until the paper on *T. araneosa,* the fifth and probably the last species of *Tephritis* on which I intend to report.

The integumental petals in the third instars of all three congeners examined to date are arranged in a double row above each mouthhook, and additional integumental petals are found in a vertical double row above these papillae, one pair to each side of the medial depression separating the anterior sensory lobes (Goeden and Headrick 1991, Goeden et al. 1993; Figs. 3C-7, -8, D-7, E-8, -9). The integumental petals differ in number among the third instars of the three species of *Tephritis* (Goeden and Headrick 1991, Goeden et al. 1993; Figs. 3C-7, -8, D-7, E-8, -9), and increase in number between the last two instars of *T. joanae* (Figs. 2A-4, B-9, -10).

The six ventral-most oral ridges of the third instar of *T. joanae* have bluntly toothed ventral margins (Figs. 3C-9, D-8) not found in the second instars (Fig. 2B-11, -12), nor in third instars of *T. baccharis* (Goeden and Headrick 1991) or *T. arizonaensis* (Goeden et al. 1993).

The mouthhooks of the third instars of all three *Tephritis* spp. studied to date are tridentate (Goeden and Headrick 1991, Goeden et al. 1993; Figs. 3B-2, C-11, E-11); whereas, those of the second instar are bidentate (Goeden and Headrick 1991; Goeden et al. 1993; Figs. 2A-3, B-8).

The lateral spiracular complexes of the mesothorax, metathorax and abdominal segment 1 of the third instar of *T. joanae* (Fig. 4A) differ from those of the second instar in the number of component verruciform sensilla (Fig. 2D), i.e., two versus five in the metathorax and two versus three in abdominal segment 1, respectively, of the second versus third instars.

The number of stelex sensilla surrounding the posterior spiracular plate apparently differ among the three *Tephritis* species examined to date. Ten stelex sensilla reportedly surround the margin of the caudal segment of *T. arizonaensis* (Goeden et al. 1993) in a four-dorsal, six-ventral arrangement, not including the two intermediate sensory complexes ventrad of the spiracular plates. The medusoid sensilla in the intermediate sensory complex was described as tuberculate, being topped by what appear to be only two, short papillae. On the other hand, the caudal segment of the third instar of *T. baccharis* is ringed by three pairs of stelex sensilla, one pair each at dorsal, medial, and ventral positions, and a pair of medusoid sensilla inaccurately reported by Goeden and Headrick (1991) as associated with the dorsal pair of stelex sensilla. This should have read ". . . ventrally each closely paired with a separate stelex sensillum . . ." to constitute the intermediate sensory complex as pictured in Goeden and Headrick (1991). Here, the medusoid sensillum was described as a dome with a raised crown bearing several open pores, and thus, either having extremely short apical papillae, or lacking same. In contrast, the caudal segment of the third instar of *T. joanae* apparently is surrounded by only a dorsolateral and ventrolateral pair of stelex sensilla (Fig. 4D-1, -2) as well as a ventral pair of intermediate sensory complexes, the medusoid sensilla of which each bears two or three short apical papillae (Fig. 4F-4) more typical of this type of chemosensillum (Goeden 2001; Goeden and Teerink 1999, and references therein).

Further interspecific, intraspecific, and intergeneric comparisons of larval taxonomy are deferred until the next two papers on *T. ovatipennis* and *T. araneosa.*

Puparium: Dull black, ellipsoidal, and smoothly rounded at both ends (Fig. 5A); anterior end bears the invagination scar (Fig. 5B-1) and anterior thoracic spiracles (Fig. 5B-2); posterior spiracular plate bears three broadly elliptical rimae (Fig. 5C-1), and four, two- to three-branched, single- to bifurcately-tipped, interspiracular processes (Fig. 5C-2). Seventy-one puparia averaged 2.99 ± 0.021 (range, 2.28–3.27) mm in length; 1.64 ± 0.014 (range, 1.28–1.85) mm in width.

Distribution and Hosts

To date, *T. joanae* is only known from California (Goeden 1993). Two locations in southern California, other than the study sites reported above, from which adults of *T. joanae* were reared from samples of mature flower heads of *Ericameria pinifolia* and not reported by Goeden (1993) were: S of Aquanga along State Highway 79 at 616-m elevation, Riverside Co., 13.x.1993; N of Granite Mountain at 1847 m, Angeles National Forest, Los Angeles Co., 16.x.1996. The 23 specimens identified and reported by Goeden (1993) as *T. araneosa* reared from *E. cuneata* (A. Gray) McClatchie (as *Haplopappus cuneatus* Gray), upon re-examination are re-identified and confirmed with other reared specimens from three other locations as *T. joanae* Goeden, as suggested by A. L. Norrbom (in litt. 1994). Thus, *T. joanae* is now known from three congeneric hosts (Goeden 2001b).

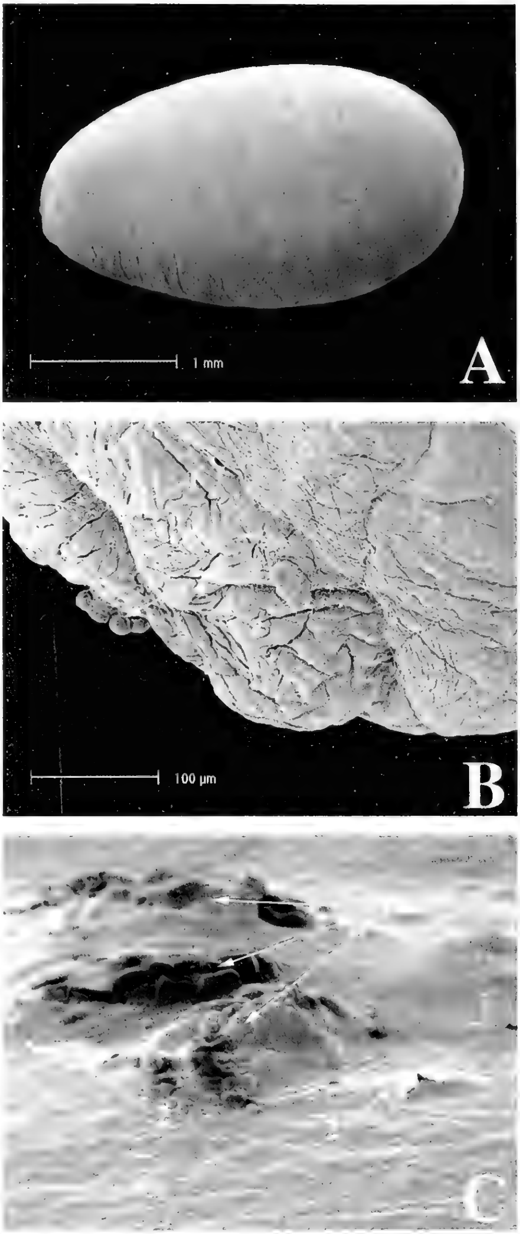

Fig. 5. Puparium of *Tephritis joanae*: (A) habitus, anterior to left; (B) anterior end, 1- invagination sear, 2- anterior thoracic spiracle; (C) posterior spiracular plate, 1- rimae, 2- interspiracular processes.

All four hosts plants from which Goeden (1993) reported *T. joanae* are of widespread occurrence in California (Hickman 1993): *E. cuneata* (as *T. araneosa*), *E. pinifolia* (as *Haplopappus pinifolius* deCandolle), *E. ericoides* (Lessing) Jepson [as *Haplopappus ericoides* (Lessing) Hooker and Arnott], and *Senecio flaccidus* Lessing (as *S. douglasii* deCandolle). *Ericameria cuneatus, E. ericoides* and *E. pinifolia* belong to the subtribe Solidagininae of the tribe Astereae, and *S. flaccidus* belongs to the subtribe Senecioninae of the tribe Senecioneae (Bremer 1994). Moreover, *E. ericoides* and *E. pinifolia,* together with *E. palmeri* (A. Gray) H. M. Hall, may be a single, highly variable species (Hickman 1993). The distribution of *S. flaccidus* extends into Mexico (Hickman 1993), as may that of *T. joanae.* Because the confirmed host plants of *T. joanae* belong to two, separate, large tribes of Asteraceae (Bremer 1994), this presumably widespread tephritid is classed as an oligophagous species (Headrick and Goeden 1998) for which additional hosts probably remain to be found.

BIOLOGY

Egg.—In each of 20, closed, preblossom, immature flower heads of *Ericameria pinifolia* a single egg of *T. joanae* was inserted pedicel-last, between or within two adjacent phyllaries or between an inner phyllary and outer floret (Fig. 6A). Thus, the aculeus may or may not have penetrated a phyllary during oviposition. Fifteen eggs (75%) rested with their long axes parallel to the long axes of the flower heads. The remaining eggs rested at an angle of 45° relative to the surface of the receptacle (Fig. 6A), but no ovules were damaged by oviposition. The receptacles of preblossom heads that contained eggs averaged 1.09 ± 0.06 (range, 0.85–1.71) mm in diameter.

Larva.—Upon eclosion, single first instars found in each of 15 closed, preblossom flower heads tunneled immediately into an ovule and then continued to feed parallel to the receptacle on one or more ovules (Fig. 6B). The receptacles averaged 1.26 ± 0.06 (range, 1.14–1.96) mm in diameter and an average of 2.9 ± 1.1 (range, 0–7) ovules was damaged in these 15 flower heads. No receptacle was abraded or pitted by larval feeding. Thus, about 20% (range, 0-47%) of an average total of 15 (range, 10–27) ovules/soft achenes counted in 154 infested and uninfested, preblossom, blossom, and postblossom flower heads were damaged by the first instars.

Second instars continued feeding on ovules in closed, preblossom flower heads. They fed with their bodies parallel to the receptacles, but always well above the receptacles (Fig. 6C). Receptacles of nine flower heads containing second instars averaged 1.29 ± 0.07 (range, 1.14–1.68) mm in diameter. These nine flower heads each contained a single larva that had damaged an average of 7.6 ± 1.12 (range, 4–15) ovules, or about 50% (range, 27–100%) of the average total of 15 ovules/soft achenes per flower head counted for the above-mentioned, 154 flower heads.

Third instars (Fig. 6D) initially continued to feed mainly on ovules and soft achenes in preblossom, blossom, or postblossom flower heads. Forty-one flower heads that averaged 1.91 ± 0.09 (range, 1.42–3.19) mm in diameter each contained a single third instar. An average of 12.5 ± 0.6 (range, 6–18) of the ovules or soft achenes therein were damaged, or about 83% (range, 40–100%) of the average total of 15 ovules/soft achenes per flower head.

Third instars in flower heads fed with their long axes oriented perpendicular to the receptacles (Figs. 6D, E), with their mouthparts commonly directed towards (Fig. 6D) or less commonly, away from the receptacles (Fig. 6E). The receptacles were abraded or pitted in 18 of 41 (44%) flower heads containing third instars, and the central feeding areas were moist, suggesting that sap apparently constituted at least part of the diet of third instars of *T. joanae.* 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 (Headrick and Goeden 1998).

Pupa.—The receptacles of 72 flower heads each of which contained a single puparium (Fig. 6G) averaged 2.30 ± 0.09 (range, 1.14–3.63) mm in diameter. The receptacles were abraded or pitted in 67 of 72 (93%) flower heads containing puparia, fur-

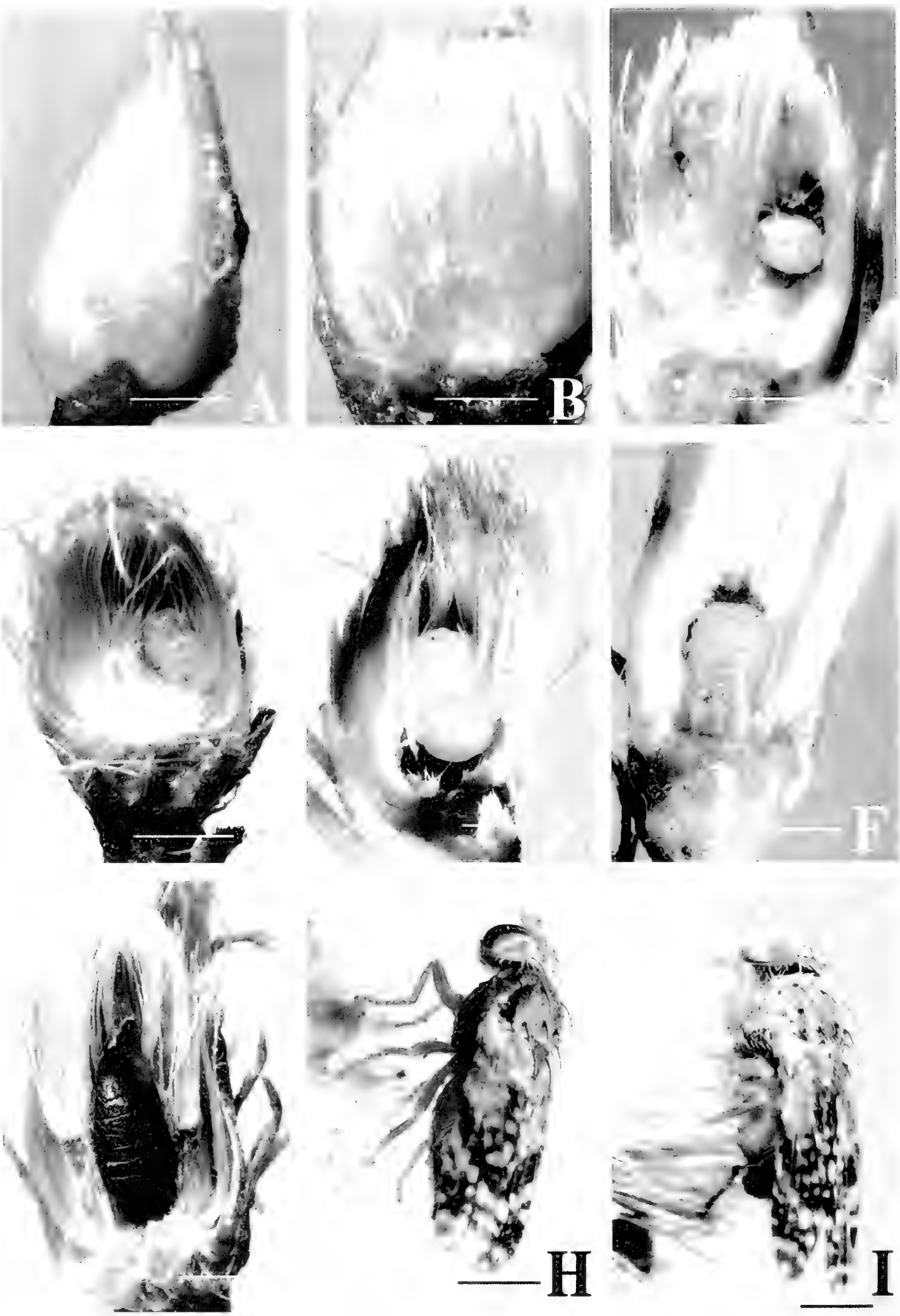

Fig. 6. Life stages of *Tephrits joanae* in flower heads of *Ericameria pinifolia*: (A) egg (arrow) on periphery of closed, preblossom flower head with phyllaries removed; (B) first instar (arrow) feeding on ovules in preblossom flower head; (C) second instar preblossom flower head, (D) third instar feeding on aborted achenes while facing receptacle; (E) early third instar feeding on soft achenes while facing away from receptacle; (F) third instar feeding on receptacle in center of flower head surrounded scored achenes; (G) puparium in flower head, (H) adult female, (I) adult male. Lines = 1 mm.

ther confirming that sap constituted part of the diet of the third instars. An average of 14.2 ± 0.3 (range, 11–18) of the ovules or soft achenes within these flower heads were damaged, or 95% (range, 74–100%) of the average total of 15 ovules/soft achenes per flower head.

Adult.—Adults (Figs. 6H, I) are long-lived and apparently constitute the only overwintering stage in southern California. Under insectary conditions, 29 unmated males (Fig. 6I) lived an average of 109 ± 10 (range, 30–278) days, and 28 virgin females (Fig. 6H) averaged 101 ± 5 (range, 58–149) days. Such 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. joanae* 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). Premating behaviors occasionally observed with *T. joanae* were abdominal pleural distension and side-stepping by males and stilting and swaying by both sexes while tracking their opposite sexes (Headrick and Goeden 1994). Droplet formation (Fig. 7A) also was observed for both sexes (Headrick and Goeden 1994, 1998). 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). Asynchronous supination, like that reported for *T. arizonaensis* (Goeden et al. 1993), was either irregular, i.e., one wing was extended more than once, and often held extended for several seconds; or regular, i.e., each wing was extended in turn without pause. Sometimes asynchronous supinations ended in a few wing enantions, i.e., synchronous wing extensions without supination (Goeden et al. 1993; Headrick and Goeden 1994, 1999). Agonistic behavior by unreceptive females involved rushing at males while synchronously supinating both wings. Another indication of an unreceptive female was a depression of her oviscape before and after being mounted by a male. Males did not exhibit any of the common tephritid courtship displays, including regular, abdominal pleural distension, although as mentioned above, such distensions were occasionally noted, possibly with replete males that had just imbibed (Fig. 7A). A male ready to initiate courtship stalked a female and attempted to jump on her dorsum, or did so without stalking as opportunity arose, as noted with *T. arizonaensis* (Goeden et al. 1993). Consequently, the rapid initiation of copulation was rarely observed with *T. joanae,* e.g., one male was observed to jump atop a receptive female and attain coitus in less than 2 minutes, whereas, three males attempting to copulate with different, nonreceptive females took 30, 150, and 160 minutes, respectively, to affect coitus.

Potentially at least, males are polygamous, females are polyandrous; although, what happens under unconfined conditions in nature remains unanswered. Females mated (Figs. 7B, C) in 21 cagings at least 40 days after their emergence. Pairs mated repeatedly, but usually only once, and no more than twice per day, unless some disturbance prematurely aborted copulation. One female mated at least 25 times between 19.xii.1995, and 2.ii.1996, including on the latter date when she died; another female mated at least 20 times between 8.xii.1995 and 2.ii.1996, when both males died. Copulatory induction behavior (CIB) (Headrick and Goeden 1994, 1999), other copulation behaviors, and copulatory positions attained by each sex (Figs. 7B, C) generally were as described for *T. arizonaensis* (Goeden et al. 1993). Minor differences from *T. arizonaensis* observed with *T. joanae* included the elevation of the female's oviscape about 20° (not 45°) above the horizontal and a recurving downward of the male's abdomen up to 90° when engaging the aculeus with his surstyli. Also, the wings of females were parted from 60 to 80° (not 45°) during copulation; whereas, those of the males

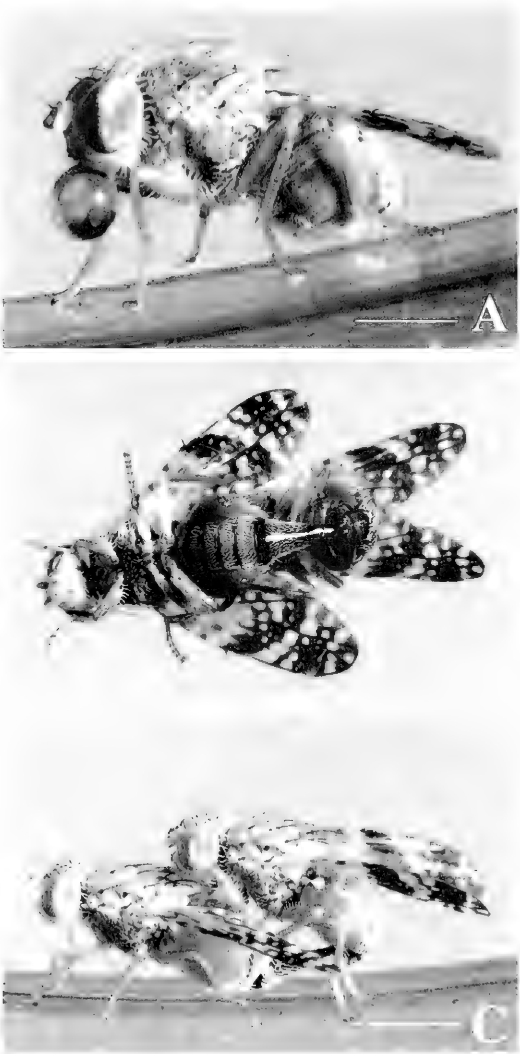

Fig. 7. Behaviors of *Tephritis joanae* adults: (A) droplet forming by male; (B) ventral view pair in copula; (C) lateral view of pair in copula. Lines = 1 mm.

were parted 10 to 30° (not mostly overlapped), while those of both species similarly were held unmoving, nonsupinated, and centered equidistant from their body midlines. Twice, different males disturbed while in copula by an approaching male, rapidly vibrated and lofted their wings for a few seconds, and once this same male behavior apparently was used in resumed CIB in response to female agitation. Twenty-eight matings with an average duration of 511 ± 20 (range, 193–860) min were recorded, that usually began between late morning and early afternoon. None of these matings were viewed completely from beginning to end, as termination of mating and separation of the male and female apparently also proceed very rapidly (Headrick and Goeden 1994, 1999). This average mating duration for *T. joanae* compared with an average duration of 5.5 h (330 min) (range, 2.5–8 h; 150–480 min) reported for *T. arizonaensis* (Goeden et al. 1993).

Seasonal history.—The life cycle of *T. joanae* in southern California follows an aggregative pattern (Headrick and Goeden 1994, 1998) in which the adult is the principal overwintering stage. However, it is unknown whether this tephritid is univoltine (see below) or bivoltine like *T. stigmatica* (Tauber and Toschi 1965, Goeden 1988a), *T. arizonaensis* (Goeden et al. 1993), and conceivably, *T. baccharis* (Goeden and Headrick 1991). Consequently, if bivoltine, in the spring (April–May), overwintered adults probably aggregate on preblossom shoots of still undetermined, early blossoming, alternate hosts to mate 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 to begin a second generation either on additional, unknown alternate hosts and on the known, fall-blooming hosts, *Ericameria cuneatus, E. pinifolia, E. ericoides,* and *Senecio flaccidus,* on which another generation is completed. The adults emerge in late fall (October-November) and overwinter. Or, *T. joanae* is univoltine on each of its three known hosts, and the long-lived adults not only overwinter, but also oversummer.

Natural enemies.—A single *Pteromalus* sp. (Hymenoptera: Pteromalidae) was reared from a puparium of *T. joanae* as a solitary, larval-pupal endoparasitoid, and six additional specimens were reared from mature flower heads as probable parasitoids. One *Eurytoma* sp. nr. *bigloviae* Ashmead and six *E. veronia* Bugbee (Hymenoptera: Eurytomidae) also were reared from individual puparia as solitary, larval-pupal endoparasitoids and 29 additional specimens of *E. veronia* and three *E. obtusiventrus* Gahan were reared from mature flower heads as probable solitary primary parasitoids, as were nine *Torymus* sp. (Hymenoptera: Torymidae) and five *Bresema* sp. (Hymenoptera: Eupelmidae).

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THE *YUGUS BULBOSUS* COMPLEX, WITH A COMMENT ON THE PHYLOGENETIC POSITION OF *YUGUS* WITHIN THE EASTERN PERLODINI (PLECOPTERA: PERLODIDAE: PERLODINAE)

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Abstract.—*Yugus bulbosus* (Frison) is found to be a complex of three closely similar species. Descriptions, illustrations, and SEM photomicrographs of ***Y. kondratieffi*, n. sp.**, ***Y. kirchneri*, n. sp.**, as well as the two previously known species of *Yugus, Y. bulbosus* (Frison) and *Y. arinus* (Frison), are presented. A preliminary cladistic analysis was undertaken to determine the position of *Yugus* within an eastern Nearctic generic complex comprising species belonging to *Malirekus, Hydroperla, Helopicus* and *Isogenoides.* Also included were representatives from *Diura, Oconoperla, Cultus* and *Megarcys.* The analysis identified four equally parsimonious trees of 132 steps and indicated that *Yugus* and *Helopicus* are grouped together in the same clade.

Key Words: Plecoptera, stoneflies, Perlodidae, Perlodinae, Perlodini, *Yugus,* eastern Nearctic, cladistic analysis

Yugus was established as a subgenus of *Isogenus* by Ricker (1952) for three southern Appalachian Perlodinae species; *I. arinus* (Frison), *I. bulbosus* (Frison), and *I. innubilis* (Needham and Claassen). This group was later raised to generic status by Illies (1966). Subsequently *Y. innubilis* was removed from *Yugus* and placed in a monotypic genus *Oconoperla* (Stark and Stewart 1982, Stark 1985). Recent collecting efforts by colleagues have yielded additional material of *Yugus* that reveals *Yugus bulbosus* to be a complex of three closely related species.

Much of our understanding of the relationship of *Yugus* with other perlodid genera comes from the thoughtful contributions of Stark and his co-workers. Stark and Ray (1983) hypothesized that *Yugus, Malirekus, Hydroperla, Helopicus* and *Isogenoides* were members of an eastern Nearctic generic complex. Within this complex these workers considered that *Helopicus* was most closely related to *Hydroperla.* Egg, nymphal and male genitalic characteristics suggested to Stark and Stewart (1982) and Stark (1985) that *Oconoperla* was a specialized sister group of eastern Nearctic complex members *Yugus* and *Malirekus.* However, this relationship was considered a distant one. Later Stark and Szczytko (1984), based on the triangular-shaped cross section of the egg, forward location of the subapical tooth of the nymphal lacinia, and modification of the male S7 posterior margin, included the genera of this eastern Nearctic complex and ten other Nearctic and Palearctic genera in the tribe Perlodini.

One objective of this study is to describe the two species of the *Y. bulbosus* complex that are new to science and compare them to the known species, *Y. bulbosus* and *Y.*

arinus. A second objective is to attempt to clarify the relationship of *Yugus* with the other members of the Perlodini eastern Nearctic generic complex of Stark and Ray (1983).

MATERIALS AND METHODS

Specimens were obtained from the following collections: Colorado State University (CSU), Brigham Young University (BYU), R. F. Kirchner Collection (RFK), Charles H. Nelson Collection (CHN), Bill P. Stark Collection (BPS) and Virginia Polytechnic Institute and State University (VPI).

A preliminary analysis of the phylogenetic position of *Yugus* relative to the other members of the eastern Nearctic generic complex, *Malirekus, Hydroperla, Helopicus* and *Isogenoides,* used the exemplar approach (Yeates 1995) instead of a single hypothetical genus. Each of the five genera of the eastern Nearctic generic complex were represented by at least two species. *Diura* and monotypic *Oconoperla* also belong to the Perlodini and have species found in the eastern Nearctic region and representative species from these genera were included as well. The outgroup comprised two exemplar species selected from one genus in the tribe Diploperlini, *Cultus,* and two from one genus in the tribe Arcynopterygini, *Megarcys.* Arcynopterygini is considered to be the sister group of Diploperlini + Perlodini (Stark and Szczytko 1984).

Cladistic analysis was undertaken using the branch and bound option in PAUP* 4.0b4a (Swofford 1998). In order to confirm the monophyly of the ingroup, the outgroup taxa were treated in the same manner as the ingroup taxa. Bootstrap values were calculated for clades from 500 replicates of the data matrix, with the heuristic search option, random addition sequence (10 replicates) and a 'MaxTrees' setting of 200 used for each replicate. Bremer support values (Bremer 1994) for clades were estimated by identifying the cladograms of shortest length in which a clade fails to appear. The cladograms were constructed using the heuristic search option, random addition sequence (10 replicates), and a 'MaxTrees' setting of 200.

SYSTEMATICS

Genus *Yugus* Ricker 1952

Isogenus (*Yugus*) Ricker 1952: 123 (type species, *Diploperla bulbosa* Frison = *Isogenus* (*Yugus*) *bulbosus* (Frison)).
Yugus: Illies 1966: 380.

The genus *Yugus* can be characterized by the following combination of features:

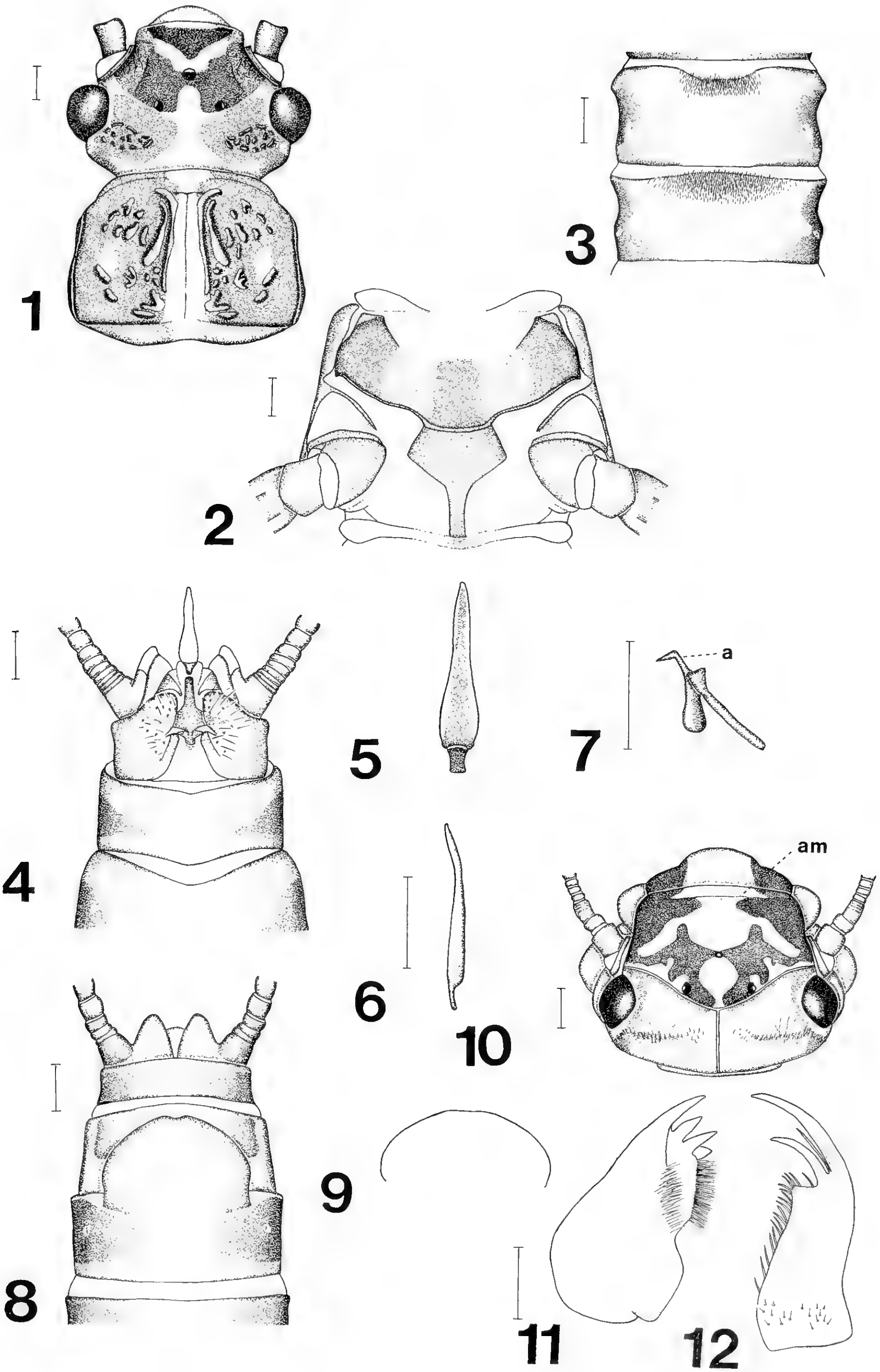
Adult: Discernible mesal lobe on posterior margin of male S7, lobe on male S8 indistinct (Figs. 3, 15); male S7 and S8 posterior marginal areas each exhibiting a mesal concentration of setae (Figs. 3, 15); male 10 hemitergal lobes broad, with broadly rounded apical margins and clothed with long setae and short, stout peg-like setae (Figs. 4, 16, 25, 36); dorsal section of male epiproct with sclerotized caudal band, membranous area bearing spinulae, lateral stylets absent (Figs. 4, 5, 16, 18, 25, 27, 36, 37); female subgenital plate moderately produced, posterior margin slightly to greatly excavated mesally (Figs. 8, 21, 30, 41).

Nymph: Submental gills absent or present as diminutive nubs, labrum with mesal longitudinal light band (Figs. 10, 23, 32, 43); mandible bearing four or five teeth; lacinia bidentate, tufted low marginal knob present, inner margin bearing setae, ventral basal region with transverse setal band (Figs. 12, 34).

Egg: Length 3.9–4.6 mm; width 2.4–3.0 mm. General shape oval; cross section triangular; collar stalked; chorionic surface bearing upraised scales or smooth (Figs. 48–51).

Yugus arinus (Frison)
(Figs. 1–12, 44, 48)

Diploperla arina Frison 1942: 309, figs. 82, 83 (orig. description, adult, ♂, ♀,



Figs. 1–12. *Yugus arinus.* 1, Head, dorsal. 2, Mesothoracic sterna, ventral. 3, Male S7 and S8, ventral view. 4, Male terminalia, dorsal. 5, Male epiproct dorsal section, caudal. 6, Male epiproct dorsal section, lateral. 7, Male epiproct anchor plate, lateral. 8, Female genitalia, ventral. 9, Female subgenital plate variant, ventral. 10, Nymphal head, dorsal. 11, Nymphal right mandible, ventral. 12, Lacinia maxillus, ventral. Abbreviations: a = anterior arms of epiproct anchor plate; am = anterior margin of fronto-clypeal region. Scale = 0.5 mm.

nymph), holotype ♂, Balsam, North Carolina.

Isogenus (*Yugus*) *arinus*: Ricker 1952: 124.

Yugus arinus: Illies 1966: 380—Kondratieff and Voshell 1982: 770, figs. 18–21 (description, adult ♂, ♀).

Description.—*Male:* Forewing length 15.0–17.0 mm, body length 15.0–19.0 mm. General color dark brown to black patterned with yellow. Dorsum of head (Fig. 1) with mesal brown patch on anterior frons; dark brown pigment bands extending from antennal base to lateral ocellus of each side; interocellular area semi-circular and lightly pigmented; occiput with large dark brown region behind compound eyes that extends mesad. Meso- and metasternum (Fig. 2) with mesal and lateral areas darkly pigmented. T10 completely divided into two hemitergites (Fig. 4). Paraprocts apically membranous. Epiproct dorsal section lanceolate (Figs. 4–6); membranous area bearing slender spinulae (Fig. 44); caudal band gradually tapering to apex (Fig. 5). Anterior arms of epiproct anchor plate lateral braces (Figs. 4, 7, a) weakly developed, posterior arms well developed.

Female: Forewing length 16.0–21.0 mm, body length 14.0–24.0 mm. General body color similar to male. Subgenital plate broadly rounded, covering ⅔ of S9, posterior margin mesally not noticeably indented or very slightly indented (Figs. 8–9).

Nymph: Body length 15.0–21.0 mm. Anterior margin of frontoclypeal region with lateral dark areas separated by a mesal longitudinal light band (Fig. 10, am). Ocelli connected by dark M-shaped pigment bands extending laterally to antennal bases and then expanding anteriorly and mesally; interocellular area light (Fig. 10). Light area in front of median ocellus forming an incomplete M band. Occiput between compound eyes with two incompletely enclosed oval regions patterned with indistinct darker lines. Mandible (Fig. 11) bearing four teeth; serrations scarcely distinct. Lacinia (Fig. 12) bearing two teeth; apex of low knob located at a distance from subapical tooth equivalent to approximately 2× width of base of the subapical tooth; inner marginal row of setae and transverse band of basal ventral setae present.

Egg: Chorionic surface bearing clusters of upraised scales (Fig. 48).

Specimens examined.—NORTH CAROLINA: Haywood Co., Cataloochee Creek Rd 284, Great Smoky Mountains National Park, 16 May 1983, 16 exuviae, B. C. Kondratieff (VPI); East Fork Pigeon River, Rt. 276, Shining Rock W A, 17 May 1983, B. C. Kondratieff, 1 ♀ (VPI); VIRGINIA: Giles Co., Little Stony Creek, Rt. 460, Pembroke, 22 April 1978, D. Gray, 1 nymph (VPI); 28 March 1980 (adult emerged 21 April 1980), B. C. Kondratieff, 1 ♀, 1 exuvium (VPI); 11 April 1980, B. C. Kondratieff, 1 ♀, 1 exuvium (VPI); 19 April 1980 (adult emerged 26 April 1980), B. C. Kondratieff, 1 ♂, 1 exuvium (VPI); 7 May 1980, B. C. Kondratieff, 4 ♂, 14 ♀, 12 exuviae (VPI); 12 May 1980, B. C. Kondratieff, 1 ♂, 1 exuvium (VPI); Little Stony Creek, Rt. 623, Cascades, 19 June 1978, B. C. Kondratieff, 1 ♀ (VPI).

Remarks.—Characteristics that distinguish this species from its congeners include the darkly pigmented mesal longitudinal pigment band of the adult meso- and metasternum (Fig. 2), male T10 completely divided into two hemitergites (Fig. 4), lancoleate shape of the dorsal section of the male epiproct (Figs. 5, 6), weakly developed anterior arms of epiproct anchor plate lateral braces (Figs. 4, 7, a), membranous apical area of male paraprocts (Fig. 4), female S8 with posterior margin slightly indented mesally or not indented at all (Figs. 8–9), nymphal mandible bearing four teeth (Fig. 11), nymphal frontoclypeal region with an incomplete light M band in front of the anterior ocellus (Fig. 10), nymphal occiput between the compound eyes with two incompletely enclosed oval regions (Fig. 10), and egg chorionic surface bearing clusters of upraised scales (Fig. 48).

Yugus bulbosus Complex

The *Yugus bulbosus* complex consists of three similar species that can be distinguished from *Y. arinus* by the absence of a dark longitudinal mesal pigment band on the adult meso- and metasternum (Fig. 14), male T10 incompletely divided into two hemitergites (Figs. 16, 25, 36), dorsal section of the male epiproct apically expanded (Figs. 16, 25, 36), apical area of male paraprocts bearing a dorsal sclerotized band (Figs. 16, 25, 36), female subgenital plate with mesal posterior margin broadly excavated (Figs. 21, 30, 41), nymphal frontoclypeal region with a light M band forward of the median ocellus (Figs. 23, 32, 43), nymphal occiput between the compound eyes with two enclosed oval areas patterned with indistinct darker lines (Figs. 23, 32, 43), nymphal mandibles bearing five teeth (Fig. 33), nymphal lacinia with apex of low knob located at a distance from subapical tooth equivalent to approximately the width of the subaptal tooth (Fig. 34), and egg chorionic surface smooth (Figs. 49–51).

Yugus bulbosus (Frison)
(Figs. 13–23, 45, 49)

Diploperla bulbosa Frison 1942: 308, figs. 80, 81 (orig. description, adult ♂, ♀, nymph), holotype ♂, Great Smoky Mountains National Park, Greenbrier Cove, Tennessee.

Isogenus (*Yugus*) *bulbosus*: Ricker 1952: 124.

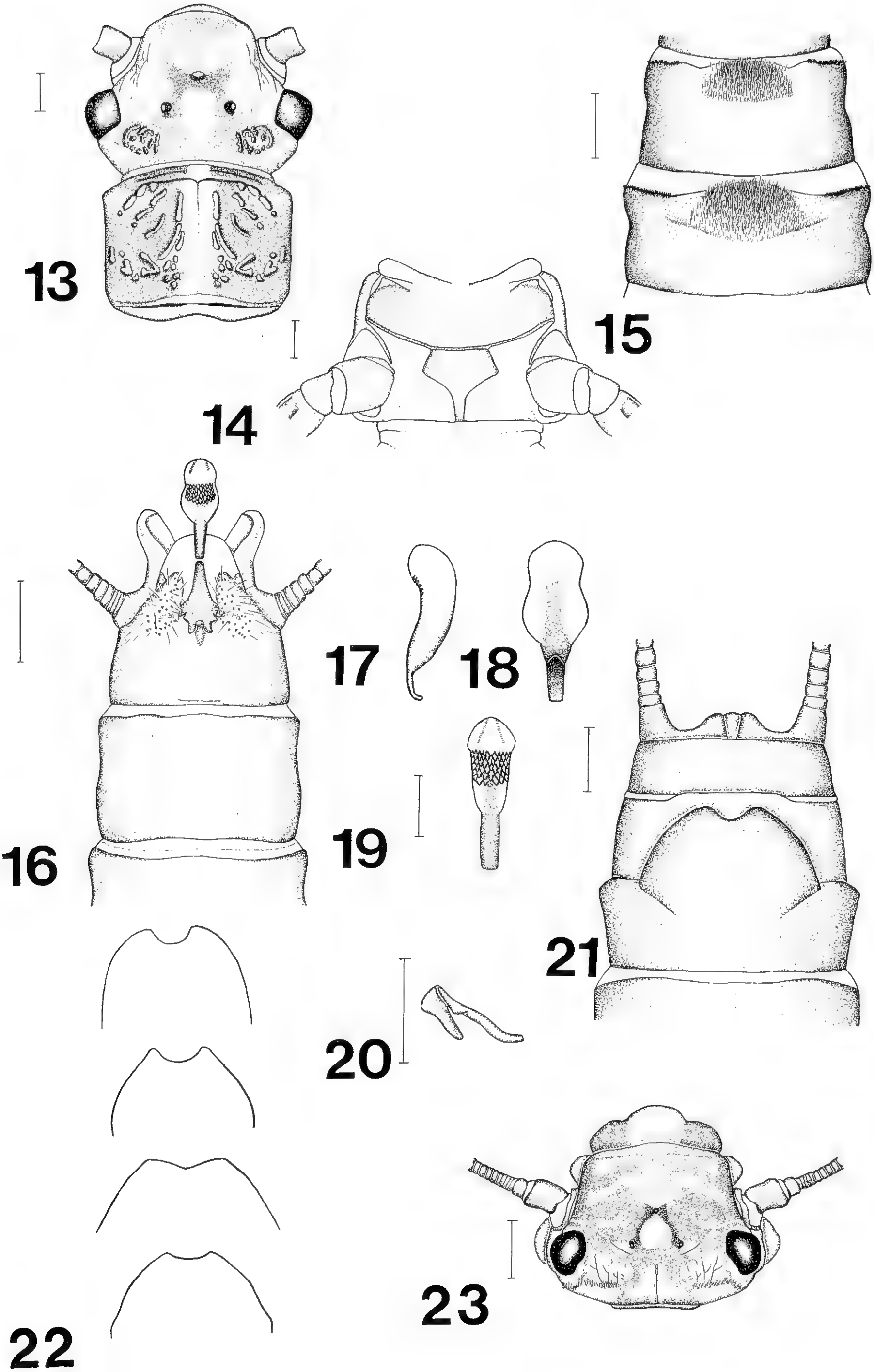
Yugus bulbosus: Illies 1966: 380.

Description.—*Male:* Forewing length 11.5–14.0 mm, body length 9.5–14.0 mm. General color light yellow-brown to dark brown patterned with yellow. Dorsum of head (Fig. 13) with mesal brown patch on anterior frons; X-shaped pigment band connecting the ocelli; interocellular area semicircular and lightly pigmented; occiput with large brown area behind each compound eye that extends mesad. In some specimens head pattern faint or absent. Paraprocts dorsally with a weakly sclerotized band not quite reaching apex (Fig. 16). Dorsal section of epiproct in frontal view with narrow and straight sided basal section and expanded figure eight shaped bulbous tip (Figs. 16, 18), but in some individuals sides of tip compressed (Fig. 19); in lateral view sausage-shaped (Fig. 17). Frontal surface of dorsal section bearing conspicuous patch of triangular spinulae approximately 2× longer and wider than adjacent spinulae (Figs. 16, 45); caudal band not extending to apex (Fig. 18). Anterior arms of epiproct anchor plate lateral braces rudimentary (Figs. 16, 20), posterior arms well developed.

Female: Forewing length 13.0–17.0 mm, body length 11.5–16.5 mm. General body color similar to male. Subgenital plate rounded covering much of S9 (Fig. 21), posterior margin mesally broadly but not deeply excavated, usually ⅕ length or less of the distance of the plate to the posterior sternal margin, variation shown in Fig. 22.

Nymph: Body length 10.0–13.0 mm. Anterior margin of frontoclypeal region with lateral brown areas separated by a mesal longitudinal light band (Fig. 23). Head interocellular area light; two ovoid light spots on each side of ocellular triangle; two small light spots forward of the ecdysial line each connecting to a lateral ocellus (Fig. 23).

Specimens examined.—GEORGIA: Union Co., Chattahoochee National Forest, Soapstone Creek, Rt. 180 near junction of Owl Creek Road, 2 June 1994, C. H. Nelson, 1 ♂ (CHN); White Co., Chattahooche National Forest, Andrews Creek, Andrews Cove Campground, Rts. 75/17, 2 June 1994, C. H. Nelson, 1 ♂, 2 ♀ (CHN), same location but 8 June 1994, C. H., C. P., and B. A. Nelson, 2 ♀ (CHN). NORTH CAROLINA: Haywood Co., Great Smoky Mountains National Park, Tributary of Sterling Creek, Gov. Rd. 1397, 5 August 1982, B. C. Kondratieff, 1 ♀ (VPI); Cove Creek, near Maggie Valley, 22 May 1990, B. C. Kondratieff and R. F. Kirchner, 1 ♀, 1 exuvium (CSU); Right Fork of Cove Creek, County Road 1395, 23 May 1993, B. C. Kondratieff and R. F. Kirchner, 2 ♂ (CSU);



Figs. 13–23. *Yugus bulbosus.* 13, Head, dorsal. 14, Mesothoracic sterna, ventral. 15, Male S7 and S8, ventral view. 16, Male terminalia, dorsal. 17, Male epiproct dorsal section, lateral. 18, Male epiproct dorsal section, caudal. 19, Male epiproct dorsal section, frontal. 20, Male epiproct anchor plate, lateral. 21, Female genitalia, ventral. 22, Female subgenital plate variation, ventral. 23, Nymphal head, dorsal. Scale = 0.5 mm.

Great Smoky Mountains National Park, Sterling Creek, Rt. 32 (Rd 1397), 10 July 1993, B. C. Kondratieff, 2 ♂, 3 ♀ (CSU); Jackson Co., Mull Creek, Rd. 1737, Nantahala National Forest, 23 May 1993, B. C. Kontratieff and R. F. Kirchner, 1 ♀ (CSU); Macon Co., Nantahala River Gorge, Nantahala National Forest, Tributary of Nantahala River, Rts. 19 & 74, 25 May 1992, C. H. and C. P. Nelson, 1 ♂ (CHN); Swain Co., Great Smoky Mountains National Park, Taywa Creek, 10 June 1976, B. Trumpf, 1 ♂, 3 ♀ (CHN); Great Smoky Mountains National Park, Collins Creek, Collins Creek Picnic Area, 5 June 1988, C. H., E. S., B. A., and C. P. Nelson, 1 ♂ 1 ♀ (CHN); same but 13 June 1991, C. H., E. S., and C. P. Nelson, 2 ♂, 3 ♀ (CHN); Nantahala River Gorge, Nantahala National Forest, Ledbetter Creek, Rts 19 & 74, 25 May 1992, C. H. and C. P. Nelson, 2 ♂ (CHN); same location but 23 May 1993, 1 ♂, 1 exuvium (CHN). TENNESSEE: Blount Co., Great Smoky Mountains National Park, Sams Creek below Starkey Creek, 21 May 1986, C. R. Parker, 1 ♂ (VPI).

Diagnosis.—Males of *Y. bulbosus* can be most easily distinguished from *Y. kondratieffi* and *Y. kirchneri* by the figure eight shape of the tip of the epiproct dorsal section (Fig. 16), and the presence of large, stout, triangular spinuale on its frontal surface (Fig. 45). Females of *Y. bulbosus* are closely similar to *Y. kondratieffi* differing from that species in that the X-shaped pigment band of the head, when distinct in the ocellular region, does not extend from the anterior ocellus to the antennal bases (Fig. 13).

Yugus kondratieffi Nelson, new species

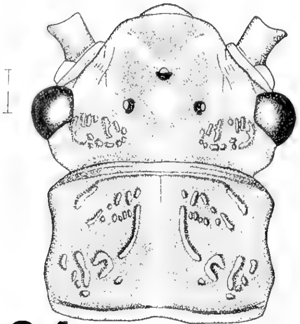
(Figs. 24–34, 46, 50)

Description.—*Male:* Forewing length 12.5–15.5 mm body length 10.5–16.0 mm. General body color brown to dark brown patterned with yellow. Dorsum of head (Fig. 24) with mesal brown patch on anterior frons; X-shaped pigment band connecting ocelli and antennal bases; interocellular area semi-circular and lightly pigmented; occiput with large brown area behind each compound eye that extends mesad. In some specimens head pattern faint or absent. Paraprocts dorsally each with a distinct sclerotized band extending to apex (Fig. 25). Dorsal section of epiproct expanding apically to a subglobate tip (Figs. 25, 27) but in some individuals sides of tip may be somewhat compressed (Fig. 28); in lateral view, club-shaped (Fig. 26). Frontal surface of dorsal section bearing uniform moderately sized triangular spinulae (Fig. 46); caudal band not extending to apex (Fig. 27). Anterior arms of epiproct anchor plate lateral braces absent (Figs. 25, 29), posterior arms well developed.

Female: Forewing length 12.5–15.5 mm, body length 12.0–16.0 mm. General body color similar to male. Subgenital plate rounded covering much of S9 (Fig. 30), posterior margin mesally is broadly but not deeply excavated, usually ⅕ length or less of the distance of the plate to the posterior sternal margin, variation shown in Figure 31.

Nymph: Body length 10.0–13.0 mm. Anterior margin of frontoclypeal region with lateral brown areas separated by a mesal longitudinal light band (Fig. 32). Frontoclypeal region mostly brown with light M band in front of median ocellus; interocellular area light; two ovoid light spots on each side of ocellular triangle; two small light spots forward of the ecdysial line each connecting to a lateral ocellus.

Types.—Holotype, ♂; North Carolina, Watauga Co., Blue Ridge Parkway, 18 May 1994, B. C. Kondratieff and R. F. Kirchner. Paratypes: NORTH CAROLINA: same location data as holotype, 6 ♂, 3 ♀ (CSU); Transylvania Co., South Fork Mills River, Yellow Gap Road, 24 August 1979, P. Porter, 1 ♂, 1 ♀ (CHN); Yances Co., Tributary to Cane River, 1 mi. off pavement, 2 mi S of Munchison, Rt 1100, 18 May 1994, B. C. Kondratieff and R. F. Kirchner, 1 ♂ (CSU). VIRGINIA: Floyd Co., Shooting



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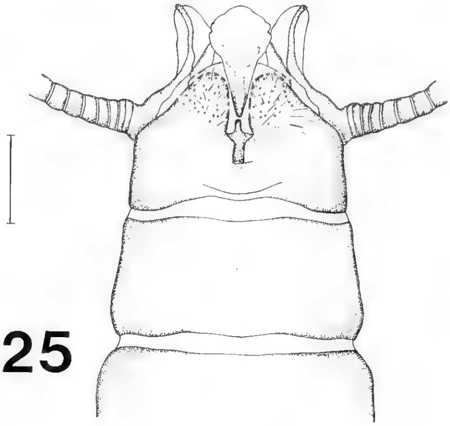

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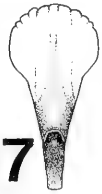

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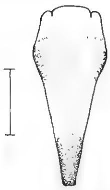

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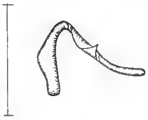

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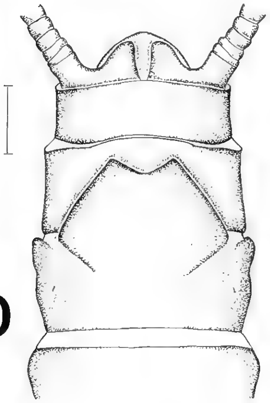

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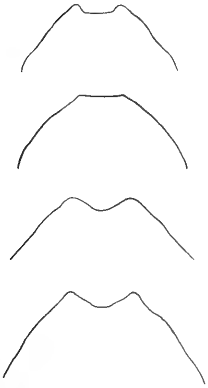

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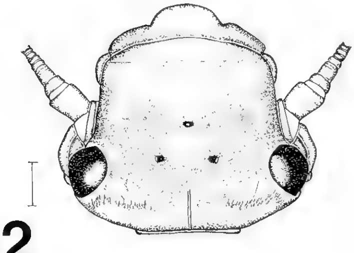

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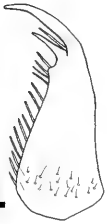

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Figs. 24–34. *Yugus kondratieffi.* 24, Head, dorsal. 25, Male terminalia, dorsal. 26, Male epiproct dorsal section, lateral. 27, Male epiproct dorsal section, caudal. 28, Male epiproct dorsal section frontal. 29, Male epiproct anchor plate, lateral. 30, Female genitalia, ventral. 31, Female subgenital plate variation, ventral. 32, Nymphal head, dorsal. 33, Nymphal right mandible, ventral. 34, Lacinia maxillus, ventral. Scale = 0.5 mm.

Creek, Highway 860 E of Floyd, 22 May 1988, R. L. Hoffman, 1 ♂ (CSU); Grayson Co., Lewis Fork Rt. 603, 11 July 1981, B. C. Kondratieff, 1 ♂, 2 ♀ (VPI); Patrick Co., Rockcastle Creek, Rt. 605 off Rt. 8, 13 May 1978, B. C. Kondratieff, 1 ♂ (VPI); Little Rockcastle Creek, Rt. 605 off Rt. 8, 13 May 1979 emerged 25 May 1979, B. C. Kondratieff, 1 ♀ (VPI); Smyth Co., Lewis Fork, NT, Lewis Fork Trail, Rt. 603, 14 August 1979, J. R. Voshell, 1 ♀ (VPI); Big Laurel Creek, Rt. 603, 18 May 1990, B. C. Kondratieff, R. F. Kirchner and J. Welch, 1 ♂ (CSU).

The holotype will be deposited in the National Museum of Natural History, Smithsonian Institution, Washington, DC (USNM), paratypes in the collections of CSU, CHN, and VPI.

Other material.—Nymphs and exuviae of this species were collected from the following location: VIRGINIA: Grayson Co., Lewis Fork, Rt. 603.

Diagnosis.—Males are best distinguished from *Y. bulbosus* and *Y. kirchneri* by the shape of the expanded tip of the epiproct dorsal section resembling a single scoop of ice cream on a cone (Fig. 16) and paraprocts each with a distinct dorsal sclerotized band extending to apex (Fig. 25). Females are closely similar to those of *Y. bulbosus* differing in the head color pattern (Fig. 24).

Etymology.—This patronym honors Dr. Boris C. Kondratieff for his many substantive contributions to the knowledge of North American Plecoptera and who collected and made available material of this species for this study.

Yugus kirchneri Nelson, new species
(Figs. 35–43, 47, 51)

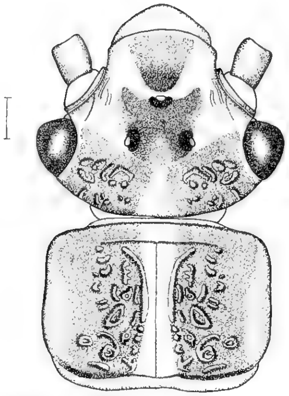
Yugus bulbosus: Kondratieff and Voshell 1982: 771, figs. 22–24, (description adult ♂, ♀).—Stewart and Stark 1988: 417, figs. 14.57, 14.58 (A–J) (description, nymph).

Description.—*Male:* Forewing length 12.3–15.1 mm, body length 10.3–15.1 mm. General body color brown to dark brown patterned with yellow. Dorsum of head with mesal brown patch on anterior frons; dark brown X-shaped pigment band connecting ocelli; on each side light brown band extends from M band to antennal base; interocellular area exhibiting medium brown pigmentation and not well contrasted from M band; occiput with large brown area behind each compound eye that extends mesad (Fig. 35). In some specimens head pattern faint or absent. Paraprocts dorsally with a discernible sclerotized band not quite reaching apex (Fig. 36). Dorsal section of epiproct with narrow, elongate, straight sided, anteroposteriorly compressed basal section leading to a subglobate tip; base and tip together resembling a lollipop (Figs. 36, 38), but in some individuals sides of subglobate tip somewhat compressed (Fig. 39); in lateral view, mace-shaped (Fig. 37). Frontal surface of dorsal section bearing uniform moderate sized triangular spinulae (Fig. 47); caudal band extends to apex (Fig. 38). Anterior arms of epiproct anchor plate lateral braces absent (Figs. 36, 40), posterior arms well developed.

Female: Forewing length 13.4–18.4 mm, body length 13.9–18.7 mm. General body color similar to male. Subgenital plate rounded covering much of S9 (Fig. 41), posterior margin mesally deeply excavated, usually greater than ⅕ length the distance of the plate to the posterior sternal margin, variation shown in Fig. 42.

Nymph: Body length 12.0–16.0 mm. Anterior margin of frontoclypeal region dark (Fig. 43). Frontoclypeal region mostly brown with light M band in front of median ocellus; interocellular area light; two ovoid light spots on each side of ocellular triangle; two small light spots forward of the ecdysial line each connecting to a lateral ocellus. Labrum expanded mesally; with lateral dark areas on either side of the light mesal band not extending to posterior margin.

Types.—Holotype, ♂; West Virginia, Logan Co., Frogtown Hollow near Holden, 7



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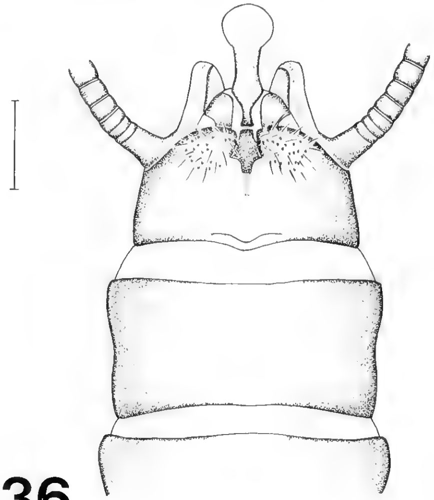

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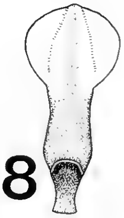

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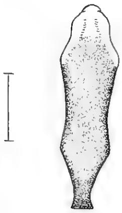

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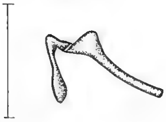

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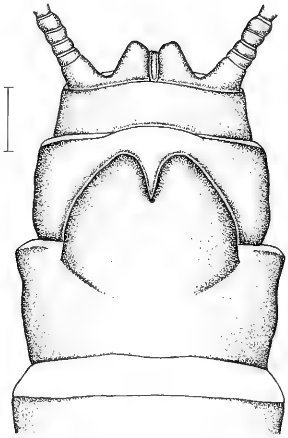

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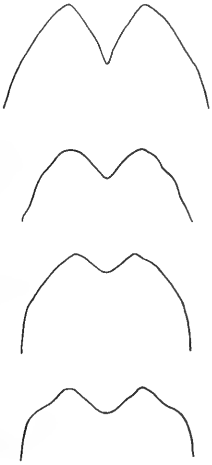

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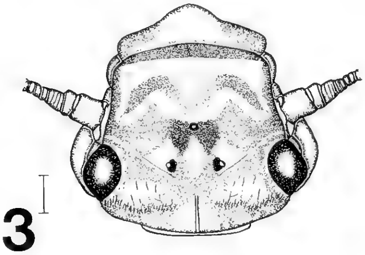
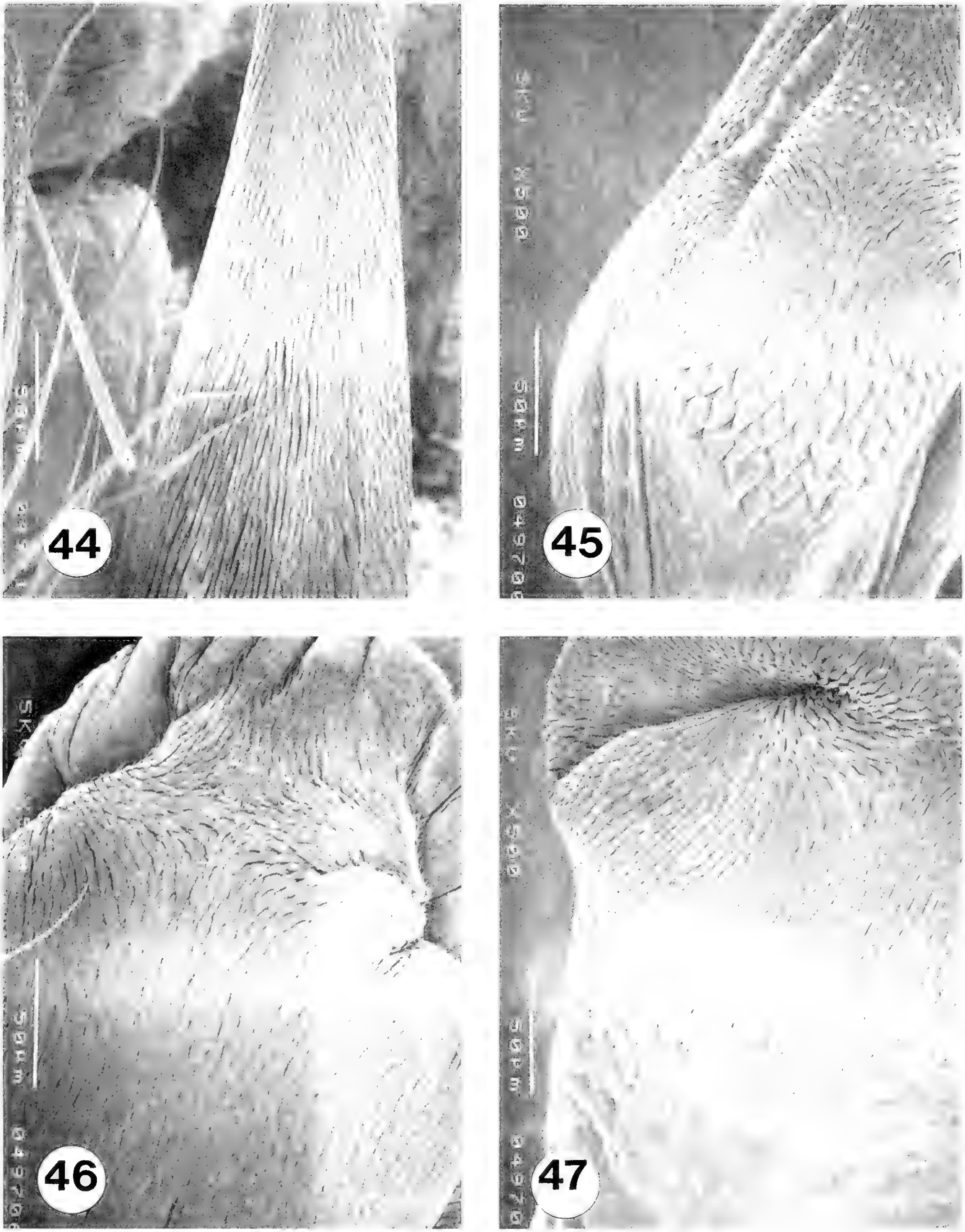


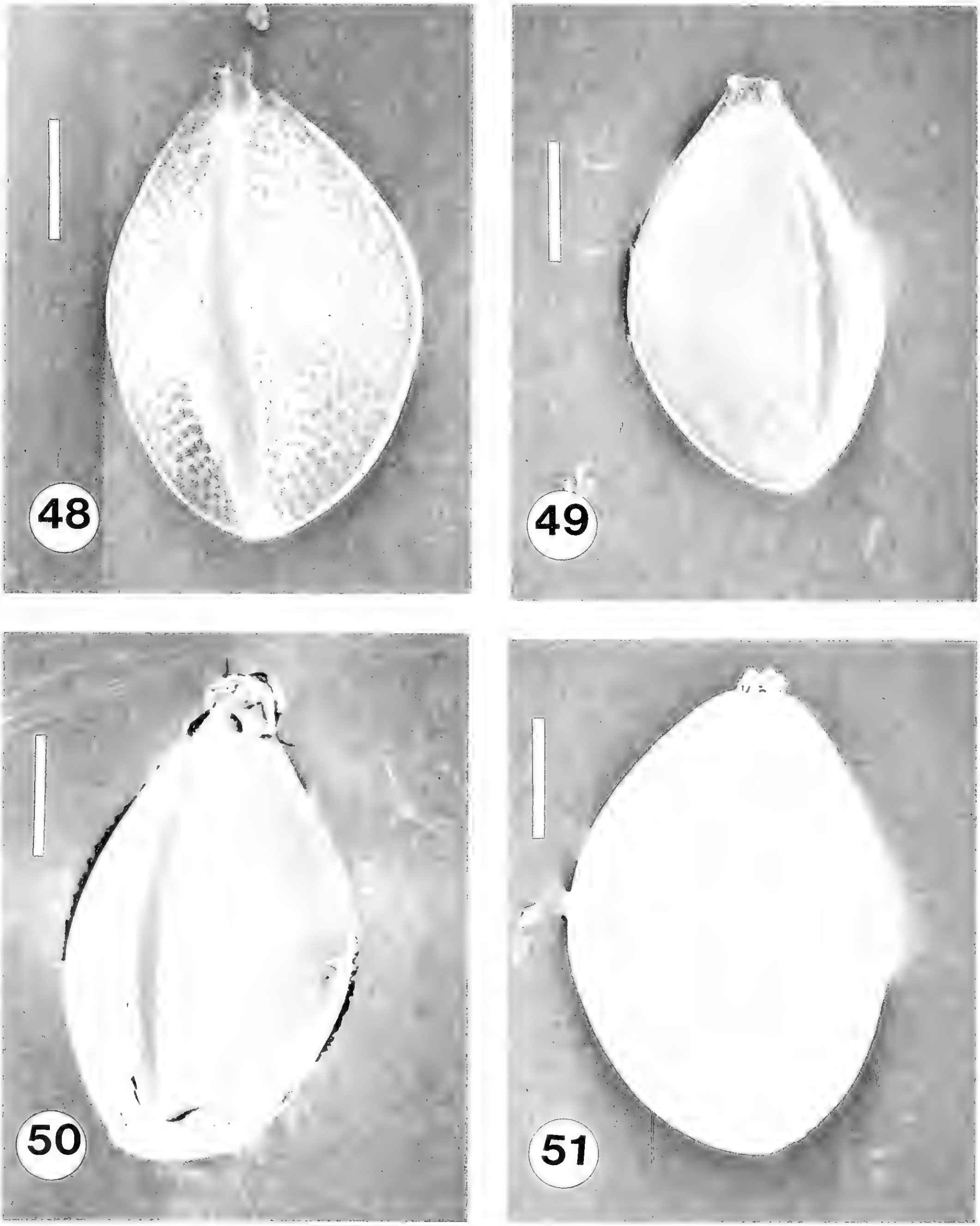
43

Figs. 35–43. *Yugus kirchneri.* 35, Head, dorsal. 36, Male terminalia, dorsal. 37, Male epiproct dorsal section, lateral. 38, Male epiproct dorsal section, caudal. 39, Male epiproct dorsal section, frontal. 40, Male epiproct anchor plate, lateral. 41, Female genitalia, ventral. 42, Female subgenital plate variation, ventral. 43, Nymphal head, dorsal. Scale = 0.5 mm.



Figs. 44–47. Male epiproct tip. 44, *Yugus arinus*. 45, *Y. bulbosus*. 46, *Y. kondratieffi*. 47, *Y. kirchneri*.

May 1975, R. F. Kirchner. Paratypes: KENTUCKY: Floyd Co., Shade Branch, Jenny Wiley State Park near May Lodge, 13 May 2000, B. C. Kondratieff and R. F. Kirchner, 2 ♂, 2 ♀ (CSU). PENNSYLVANIA: Westmoreland Co., Powdermill Run, Laurel Mts., 11 June 1993, S. Grubbs, 1 ♂, 1 ♀ (CSU). VIRGINIA: Tazewell Co., Springs



Figs. 48–51. Eggs. 48, *Yugus arinus*. 49, *Y. bulbosus*. 50, *Y. kondratieffi*. 51, *Y. kirchneri*. Scale = 0.25 mm.

into Station Spring Creek, Burkes Garden, 18 May 1979, B. C. Kondratieff, 1 ♂, 1 ♀ (VPI); Spring-fed stream into Station Spring Creek, Burkes Garden, 18 May 1979 emerged 27 May 1979, B. C. Kondratieff, 1 ♂, 1 ♀ (VPI); same but emerged 2 June 1979, 1 ♂, 1 ♀ (VPI); Station Spring Creek, MB Ranch, 28 May 1992, B. C.

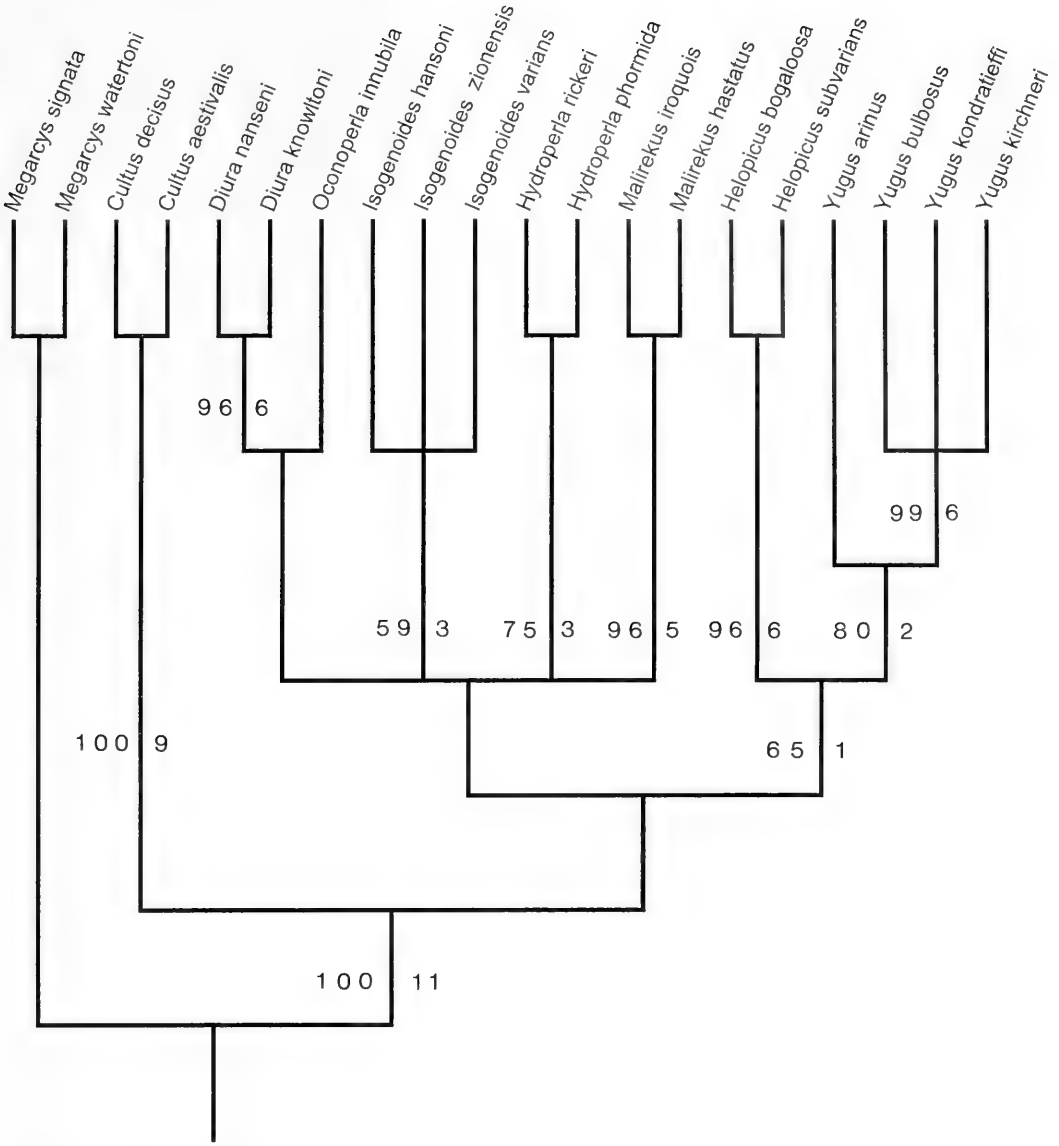


Fig. 52. Strict consensus tree of the four most parsimonious trees, with bootstrap values (left side clade branch) and Bremer indices (right side of clade branch) indicated.

Kondratieff, 4 ♂, 3 ♀ (CSU). WEST VIRGINIA: Greenbrier Co., Coats Run, Rt. 39, 16 June 1993, B. C. Kondratieff, 1 ♂ (CSU); Kanawha Co., Buzzard Branch, 4 mi. S of Pratt, CR 83, 28 May 1992, B. C. Kondratieff and R. F. Kirchner, 3 ♂, 4 ♀ (CSU); Buzzard Branch, I-64/77, 16 May 1994, B. C. Kondratieff and R. F. Kirchner, 3 ♂, 2 ♀ (CSU); Buzzard Branch, 1 mi. S Standard, CR 83, 24 May, 1999, B. Stark and R. F. Kirchner, 2 ♂ (BPS); Logan Co., same location data as holotype, 26 April 1975 emerged 27 April 1975, R. F. Kirchner, 1 ♂ (RFK); same but 2 May 1975 emerged 4 May 1975, 1 ♂, 1 ♀ (RFK); same but 7 May 1975, 1 ♂, 1 ♀ (RFK); at Holden, Frogtown Hollow of Copperas Mine Fork, 6 May 1979, R. F. Kirchner, 1 ♀ (RFK); Mingo Co., Laurel Fork of Pigeon Creek, 6 May 1975 emerged 8 May

Table 1. List of characters and character states used in the phylogenetic placement of *Yugus*.

1. Interocellular area: (0) bearing light pigmented area, (1) somewhat darkly pigmented not well contrasted from the darkly pigmented transverse band that incorporates the ocelli.
2. Submental gills: (0) absent, (1) present.
3. Meso- and metasternal pigmentation: (0) entirely darkly pigmented, (1) with some light pigmentation.
4. Meso- and metasternal pigmentation: (0) lightly pigmented between lateral and mesal dark pigment bands, (1) lightly pigmented between lateral dark pigment bands or entirely lightly pigmented.
5. Meso- and metasternal pigmentation: (0) some dark pigmentation, (1) entirely lightly pigmented.
6. Mesosterna with median longitudinal ridge connecting forks of the Y arms: (0) absent, (1) present.
7. Y arms: (0) reaching posterior corners of furcal pits, (1) reaching anterior corners of furcal pits.
8. Tarsal claws bearing setae: (0) absent, (1) present.
9. Mesal lobe on S7: (0) absent, (1) present.
10. Mesal lobe on S7: (0) weakly developed, outline demarked by pigment, (1) moderately to strongly developed.
11. Mesal lobe on S7: (0) moderately developed, (1) strongly developed.
12. Mesal lobe on S8: (0) absent, (1) present.
13. Mesal lobe development on S8: (0) demarked by pigment, (1) distinct but small.
14. Mesal concentration of setae on S7 and S8: (0) absent, (1) present.
15. Mesal excavation of female S8 subgenital plate: (0) absent, (1) present.
16. Mesal excavation of female S8 subgenital plate: (0) slight, (1) shallow to deep.
17. Mesal excavation of female S8 subgenital plate: (0) shallow, (1) moderate to deep.
18. Mesal excavation of female S8 subgenital plate: (0) moderate, (1) deep.
19. Male T10 hemitergites: (0) widely separated mesally (1) narrowly separated mesally.
20. Male T10 hemitergites: (0) not joined anteriorly (1) joined anteriorly.
21. Male 10 hemitergal lobes: (0) present, (1) absent.
22. Male 10 hemitergal lobe shape: (0) long, narrow, recurved forward and upward, bluntly pointed or rounded at apices, (1) broad, broadly rounded at apices.
23. Male 10 hemitergal lobes: (0) peg-like setae present, (1) peg-like setae absent.
24. Male epiproct: (0) present, (1) absent.
25. Male epiproct: (0) dorsal and ventral sections not separated, (1) dorsal and ventral sections separated.
26. Dorsal section of male epiproct: (0) not lanceolate, (1) lanceolate.
27. Lanceolate dorsal section: (0) subapically expands slightly then tapers to tip, (1) tapers along entire length to tip.
28. Dorsal section of male epiproct: (0) largely sclerotized with frontal knife-like edge and a caudally protruding membranous structure, (1) largely membranous typically with frontal and caudal sclerites.
29. Frontal sclerite of dorsal section of male epiproct: (0) present, (1) absent.
30. Frontal sclerite: (0) unitary, (1) divided into lateral and mesal sclerites.
31. Frontal lateral epiproct sclerites: (0) joined to rest of frontal sclerite, (1) separated from rest of frontal sclerite.
32. Narrow frontal sclerite: (0) recurved over apex, (1) not recurved over apex.
33. Frontal surface of apex of dorsal section of male epiproct: (0) not excavated, (1) excavated.
34. Apical third of dorsal section of male epiproct: (0) not covered with elongate, reddish-brown spinulae, (1) covered with elongate, reddish-brown spinulae.
35. Conspicuous mesal patch of triangular spinulae present on apical third of anterodorsal surface and approximately 2× longer and wider than adjacent spinulae: (0) absent, (1) present.
36. Paired downward directed teeth on frontal surface of dorsal section of male epiproct: (0) absent, (1) present.
37. Paired barbs on caudal surface of dorsal section of male epiproct: (0) absent, (1) present.
38. Caudal sclerite of dorsal section of male epiproct: (0) stopping well before apex, (1) extending to, near, or over apex.
39. Caudal sclerite of dorsal section of male epiproct: (0) extends to or near apex, (1) extends over apex.
40. Caudal sclerite of dorsal section of male epiproct at apex: (0) does not form a sclerotized process, (1) forms a sclerotized process.
41. Caudal sclerite apical process tip: (0) rounded apically, (1) pointed apically.
42. Caudal sclerite apical process: (0) projects dorsally, (1) decurved posteriorly.
43. Lateral braces of male epiproct anchor plate: (0) undivided, (1) divided into an anterior and posterior arms.
44. Anterior arms of lateral braces: (0) well developed, equivalent or nearly equivalent to the posterior arms, (1) weakly developed, rudimentary, or absent.

Table 1. Continued.

45. Anterior arms of lateral braces: (0) weakly developed, (1) rudimentary or absent.
46. Anterior arms of lateral braces: (0) rudimentary, (1) absent.
47. Lateral stylets: (0) present, (1) absent.
48. Lateral stylet: (0) attached basal portion strongly sclerotized, (1) attached basal portion weakly sclerotized.
49. Lateral stylet: (0) free apical portion pronounced, claw-like or blade-shaped, (1) free apical portion not prominent, flattened and somewhat rounded.
50. Dorsal sclerotized band of male paraprocts: (0) absent, (1) present.
51. Amount of sclerotization of dorsal sclerotized band of male paraprocts: (0) weakly sclerotized, not reaching apex, (1) strongly sclerotized reaching apex.
52. Lateral sclerotized bar of male paraprocts: (0) absent, (1) present.
53. Nymphal labrum pigmentation pattern: (0) relatively uniformally pigmented, (1) contrasting dark brown and yellow areas.
54. Nymphal labrum pigmentation pattern: (0) mesal longitudinal yellow band between lateral dark brown areas, (1) mesal tip yellow, remainder dark brown.
55. Nymphal labrum pigmentation pattern: (0) mesal yellow band posteriorly not extending behind lateral dark brown areas, (1) mesal yellow band posteriorly extending behind the lateral dark brown areas.
56. Anterior margin of nymphal frontoclypeal region pigmentation pattern: (0) uniformally light, (1) with some dark pigmentation.
57. Anterior margin of nymphal frontoclypeal region pigmentation pattern: (0) mesal light band between lateral dark areas, (1) uniformally dark.
58. Darkly pigmented transverse M-band of nymphal frontoclypeal region: (0) interrupted by 3 light spots, (1) or not interrupted.
59. Darkly pigmented transverse M-band of nymphal frontoclypeal region: (0) with anterior margin M-shaped, (1) with anterior margin straight.
60. Nymphal occipital spinulae row: (0) present, (1) absent.
61. Nymphal occipital spinulae row: (0) abundant, (1) sparse.
62. Oval light spots of nymphal occiput: (0) present, (1) absent.
63. Oval light spots of nymphal occiput: (0) enclosed, (1) not enclosed.
64. Nymphal inner lacinia margin below subapical tooth: (0) with pronounced shoulder or with low knob, (1) lacking pronounced shoulder or low knob.
65. Nymphal inner lacinial margin below subapical tooth: (0) with pronounced shoulder, (1) with low knob.
66. Nymphal lacinia apical and subapical teeth: (0) distinctly separated, (1) close together.
67. Nymphal inner lacina margin: (0) with a fringe of setae along part or most of its distance, (1) with only a small cluster of setae.
68. Setae of nymphal inner lacinia margin: (0) extending from subapical tooth to near base, (1) restricted to apical area below subapical tooth.
69. Nymphal lacinia with median ventral setal patch: (0) absent, (1) present.
70. Nymphal lacinia with transverse setal band: (0) no, (1) yes.
71. Number of teeth nymphal left mandible: (0) six, (1) less than six.
72. Number of teeth nymphal left mandible: (0) five, (1) four.
73. Nymphal mandible ventral tooth: (0) serrated, (1) serrations absent.
74. Nymphal mandible ventral tooth nature of serrations: (0) serrations distinct, (1) serrations shallow.
75. Nymphal pronotum: (0) margined with setae, (1) setae restricted to corners.
76. Egg shape cross-section: (0) circular, (1) not circular.
77. Egg shape: (0) cross-section triangular, (1) turtle-shell shaped.
78. Egg collar: (0) present, (1) absent.
79. Egg collar: (0) not fingernail-like, (1) fingernail-like.
80. Egg collar with 3 rib-like processes: (0) absent, (1) present.
81. Egg collar rib-like processes: (0) not pronounced, (1) pronounced.
82. Egg with erect scales: (0) absent, (1) present.
83. Erect scales of egg: (0) forming hexagonal pattern, (1) organized into patches.

Table 2. Data matrix of exemplar species selected for determining the phylogenetic placement of *Yugus* (? = inapplicable, a = 01).

	11111111112222222222333333333344444444445555555555666666666677777777778888 12345678901234567890123456789012345678901234567890123456789012345678901234567890123
Megarcys signata	0110?0100??0?0111100000000?0????00000????0???0000?00??000000000?000000?0000?000?0?
Megarcys watertoni	0110?0100??0?0110?00000000?0????00000????0???0000?00??000000000?000000?0000?000?0?
Cultus decisus	000??0011110?00???00010010?100?10000010???0???0000?00??00001?001101?00101?111010?0?
Cultus aestivalis	000??0011111100???00010010?100?10000010???0???0000?00??00001?001101?00101?111010?0?
Diura nanseni	000??0010??0?00???101??1??????????????????????1??0??0??0000010010101000?1?010000?0?
Diura knowltoni	001100010??0?00???101??1??????????????????????1??0??0??0000010011101000?1?010000?0?
Isogenoides hansoni	010??1011100?00???00010010?1010?100001111110000000?10??0000000010100000?0001000110?
Isogenoides varians	111101011100?00???00010010?1011?10011110??10000000?00??0000000010100000?0001000110?
Isogenoides zionensis	110??1010??0?00???00010010?100?01000110??10000010?00??0000000010100000?0001000110?
Helopicus bogaloosa	010??00110?1000???000100110100?00000010???11001??0?011?0010001?1010010100001000100?
Helopicus subvarians	0110?00110?0?00???000100110100?00000010???10001??0?011?0011001?1010010100001000100?
Hydroperla phormida	0110?0010??0?00???00010010?100?010001110010000010?00??000000011010000111?010000?0?
Hydroperla rickeri	0110?0010??0?00???00010010?100?0100111110110001??0?00??000000011010010111?010000?0?
Oconoperla innubila	001100010??0?00???00011010?100??10010110??10000000?10??00001?1?0?000000?1?0101???10
Malirekus hastatus	010??0011100?0110?00010010?1010?01000110??100001?0?10??000000001010010101?010000?11
Malirekus iroquois	000??0011100?0110?00010010?1010?01000110??100001?0?10??000000001010010101?010000?0?
Yugus arinus	0a10?0011100?110??000100111110?00000010???11001??0?0100100000011010001111?010000?11
Yugus bulbosus	0a1110011100?1110?01010010?100?0001000????11101??1001001000000010100011001010000?0?
Yugus kondratieffi	0a1110011100?1110?01010010?100?0000000????11111??1101001000000010100011001010000?0?
Yugus kirchneri	1a1110011100?1111001010010?100?00000010???11111??1001011100000010100011001010000?0?

1975, R. F. Kirchner, 1 ♂ (RFK); Laurel Fork, Laurel Fork Public Fishing Area, 27 May 1993, B. C. Kondratieff and R. F. Kirchner, 2 ♂ (CSU); Nicholas Co., Jims Branch of Panther Creek, 6 mi. W of Richwood, Rt. 39, 29 April 1983 emerged 16 May 1983, B. C. Kondratieff, 1 ♂, 4 ♀ (VPI); Pocahontas Co., Hills Creek, Hills Creek Falls, Rt. 39, 16 June 1983, B. C. Kondratieff, 2 ♀ (VPI); Longs Run, Hwy 28, Island Campground junction East Fork Greenbriar River, 15 May 1990, B. C. Kondratieff and R. F. Kirchner 1 ♂ 1 ♀ (CSU); Longs Run, Hwy 28, Junction East Fork Greenbriar River, 15 May 1990, R. W. Baumann, R. F. Kirchner, and B. C. Kondratieff, 3 ♂ (BYU); same, 1 ♂, 1 ♀ (BYU); small creek into Charles Creek, Cranberry Glades, 24 May 1994, B. C. Kondratieff and R. F. Kirchner, 1 ♂ (CSU); Tucker Co., Wilson Hollow Run, Fernow Experimental Forest, Monongahela National Forest, 18 May 1994, R. M. Duffield, 1 ♂ (CHN); Watershed No. 3, Fernow Experimental Forest, Monongahela National Forest, 18 May 1994, R. M. Duffield, 2 ♂ (CHN).

Other material.—Nymphs and exuviae of this species were collected from the following locations: VIRGINIA: Tazewell Co., Station Spring Creek, MB Ranch; Springs into Station Spring Creek, Burkes Garden. WEST VIRGINIA: Logan Co., Frogtown Hollow near Holden; Mingo Co., Laurel Fork of Pigeon Creek; Nicholas Co., Jims Branch of Panther Creek, 6 mi. W of Richwood, Rt. 39.

The holotype will be deposited in the USNM, paratypes in the collections of CSU, BYU, RFK, CHN, BPS, and VPI.

Diagnosis.—Males are best distinguished from *Y. bulbosus* and *Y. kondratieffi* by the lollipop shaped dorsal section of the male epiproct (Fig. 36), narrow caudal band reaching the apex (Fig. 38), and paraprocts each with a moderately demarked dorsal sclerotized band not quite extending to the apex (Fig. 36). Females are distinguished by the combination of head color pattern

(Fig. 35) and the deeply excavated mesal region of the subgenital plate posterior margin (Figs. 41, 42). Nymphs are distinguished by the entirely dark anterior margin of the frontoclypeal region (Fig. 43).

Etymology.—Named in honor of Ralph F. Kirchner in recognition of his many substantive contributions to the knowledge of North American Plecoptera and who collected and made available material of this species for this study.

KEY TO *YUGUS* SPECIES

1. Meso-and metasternum with mesal longitudinal dark pigment band (Fig. 2); male epiproct dorsal section lanceolate (Figs. 4–6); posterior margin of female subgenital plate mesally not indented or only slightly indented (Figs. 8, 9); ova chorionic surface covered with upraised scales (Fig. 48) . . . . *arinus*

– Meso- and metasternum lacking mesal longitudinal dark pigment band (Fig. 14); male epiproct dorsal section not lanceolate, expanded apically (Figs. 16, 25, 36); posterior margin of female subgenital plate mesally broadly excavated (Figs. 21, 30, 41); ova chorionic surface smooth (Figs. 49–51) 2

2. In profile epiproct dorsal section with expanded subglobate tip abruptly arising from transversely flattened base (Fig. 37), caudal band reaching apex (Fig. 38); posterior margin of subgenital plate deeply excavated, usually greater than ⅕ plate length (Fig. 41) . . . . *kirchneri*

– In profile epiproct dorsal section sausage shaped (Fig. 17) or mace-shaped (Fig. 26), caudal band not reaching apex (Figs. 18, 27); posterior margin of subgenital plate broadly excavated usually ⅕ or less of plate length . . 3

3. Dorsal band of each male paraproct weakly sclerotized, not quite reaching apex (Fig. 16); epiproct dorsal section in frontal view bearing a mesal cluster of conspicuous spinulae 2 × longer and wider than adjacent spinulae (Figs. 16, 45), in profile sausage-shaped (Fig. 17); head X-shaped pigment band, if distinct in ocellular region, not reaching antennal bases . . . . *bulbosus*

– Dorsal band of each male paraproct distinct, extending to apex (Fig. 25); epiproct dorsal section in frontal view bearing uniform moderate sized spinulae (Figs. 25, 46), in profile mace-shaped (Fig. 26); head X-shaped pigment band, if distinct in ocellular region, reaching antennal bases (Fig. 24) . . . . *kondratieffi*

CLADISTIC ANALYSIS

The eighty-three two-state characters used in the cladistic analysis are listed in Table 1. Analysis of the character data matrix of Table 2 yielded four minimum length cladograms each with 132 steps and CI of 0.6591, HI of 0.3712, RI of 0.7321, and RC of 0.4825. A strict consensus of these four cladograms is shown in Figure 52. Next a successive weighting analysis on the four cladograms using the rescaled consistency index and a base weight of 1,000 was conducted. It yielded two cladograms (length = 68,378) which were identical to two of the four 132 step cladograms produced in the initial analysis. One of these cladograms is shown in Figure 53. These cladograms indicate that the eastern Nearctic generic complex of Stark and Ray (1983) is apparently not a monophyletic clade. Moreover, Bootstrap and Bremer analyses do not strongly support the monophyly of the Perlodini clade (Bootstrap <50%, Bremer 0) which provides added support for Zwick and Weinzierl's (1995) observation that this clade might be paraphyletic. Bootstrap and Bremer indices, however, do support the monophyly of a clade comprising genera from both Diploperlini and Perlodini (Bootstrap 100%, Bremer 11) and they provide support for the monophyly of *Cultus* (Bootstrap 100%, Bremer 9), *Diura* (Bootstrap 96%, Bremer 6), *Isogenoides* (Bootstrap 59%, Bremer 3), *Hydroperla* (Bootstrap 75%, Bremer 3), *Malirekus* (Bootstrap 96%, Bremer 5), *Helopicus* (Bootstrap 96%, Bremer 6), and *Yugus* (Bootstrap 80%, Bremer 2). Also supported is a clade consisting of *Yugus* and *Helopicus* (Bootstrap 65%, Bremer 1) countering previous hypotheses of a *Helopicus* + *Hydroperla* clade and *Yugus* + *Malirekus* clade. However, this clade is only supported by two apomorphies and one of these, absence of lateral stylets, has occurred several times independently. At best, therefore, this analysis represents a very early approximation at estimating the position of *Yugus* within

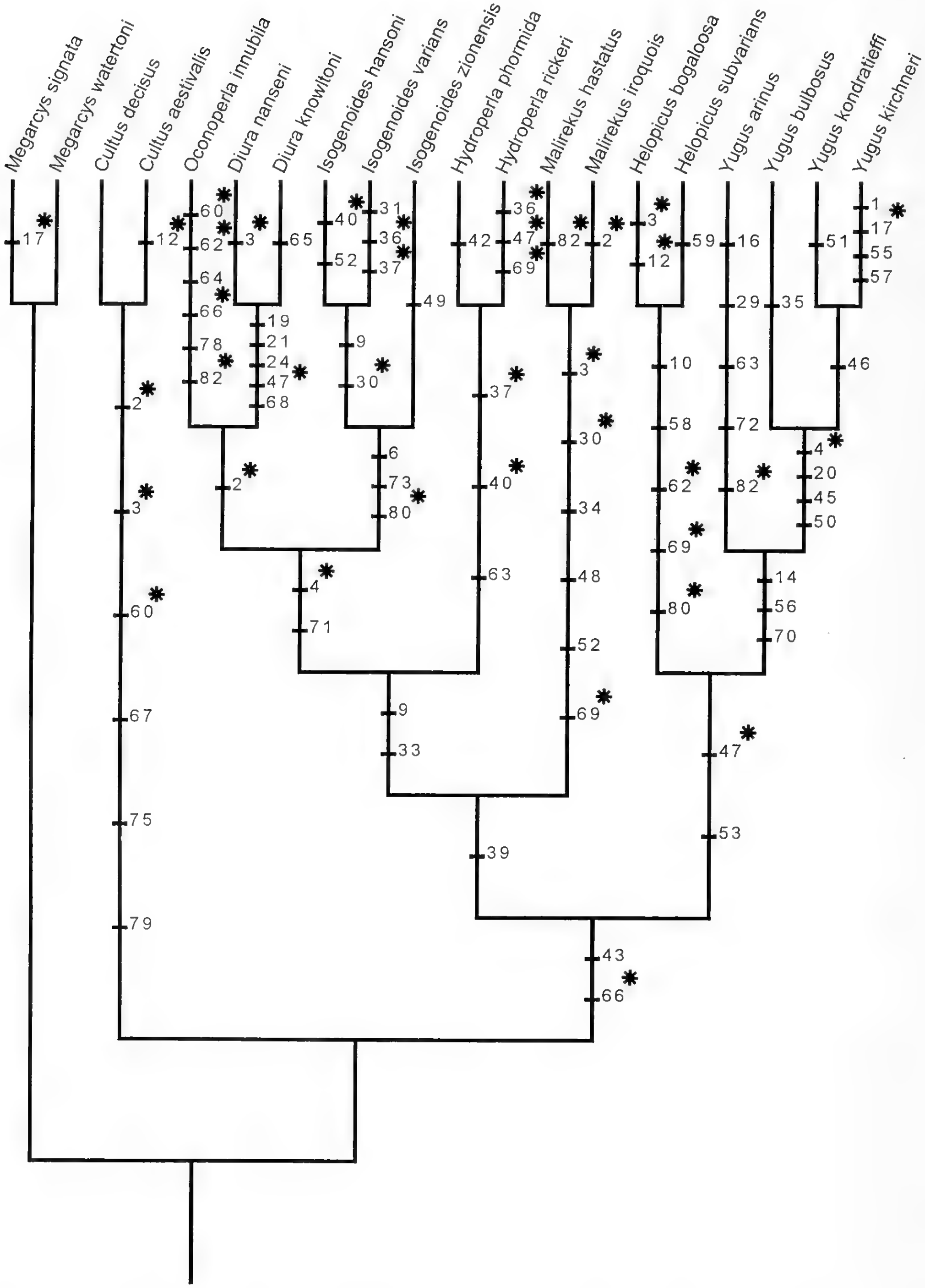


Fig. 53. One of the four equally parsimonious 132 step trees and also identical to one of the two trees resulting from successive weighting of the dataset. Unambiguously placed apomorphies are noted along the branches (* denotes a change on more than one branch).

the complex of eastern Nearctic genera that, in part, comprise the Perlodini. A more complete understanding of the phylogenetic relationships among the Perlodinae genera will have to await the inclusion of representatives of the western Nearctic and Palearctic genera in subsequent analyses.

ACKNOWLEDGMENTS

In addition to those colleagues earlier acknowledged, I am indebted to Dr. Richard Baumann (Monte L. Bean Life Science Museum), Dr. Richard Duffield (Howard University), and Dr. Bill P. Stark (Mississippi College) for the gift or loan of specimens. I also thank Dr. Gene Van Horn for reading an early version of the manuscript.

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SEPEDON MCPHERSONI, N. SP., KEY TO NORTH AMERICAN *SEPEDON,* GROUPS IN *SEPEDON S.S.,* AND INTRA- AND INTERGENERIC COMPARISON (DIPTERA: SCIOMYZIDAE)

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Abstract.—***Sepedon mcphersoni*, new species**, from southern Illinois, U.S.A., is described and illustrated, and a key to the 20 North American species of *Sepedon* is presented. The classification of the genus *Sepedon* and six related genera is discussed. All known species of *Sepedon* are classified in nine groups including the subgenus *Parasepedon* Verbeke 1950 as the *Trichrooscelis* group, the subgenus *Mesosepedon* Verbeke 1950 as the *Dispersa* group, and the genus *Sepedomyia* Verbeke 1950 as the Nasuta group. A character matrix of the groups of *Sepedon* and related genera is included. Publications on the life cycles and/or immature stages of *Sepedon* and related genera are summarized.

Key Words: snail-killing flies, taxonomy, classification, biocontrol agents

The classification of snail-killing flies of the genus *Sepedon* Latreille in the Western Hemisphere was last revised by Steyskal (1951), who included 12 North American species and one subspecies. Since then, nine North American species have been described or their status has been changed (Steyskal 1960, 1965b; Fisher and Orth 1969, 1972, 1974; Orth 1986; Manguin 1990). Herein we describe a new species of *Sepedon* from Illinois, present a revised key to the species of North America, propose taxonomic groups for the species of *Sepedon* worldwide, compare these groups with six related genera, and present a list of publications on the life cycles and/or immature stages.

The cosmopolitan genus *Sepedon* and related genera are of special interest to evolutionary and behavioral studies of Sciomyzidae because certain species represent some of the most derived lineages within the family and because some are prime candidates as biological control agents of disease-carrying snails. Study of these genera is beginning to afford an opportunity to understand the evolution of diverse modes of feeding behavior—from obligate parasitoids to predators—by correlating feeding behavior with phylogenetic position established on the basis of morphological character systems. As discussed below, indications of the degree of relatedness and generic and supra-generic characterizations have been provided in a few earlier studies of "*Sepedon.*" A cladistic analysis of the family by Marinoni and Mathis (2000) confirms or rejects some of those proposals and provides a more comprehensive basis for comparisons.

Sepedon mcphersoni Knutson and Orth, new species
(Figs. 1–4)

Male.—Gross aspect tawny brown. Head with broadly excavated frons with moderate para-orbital and median ridges. Medifacies with a few, scattered, fine black setae. Orbito-antennal spot and fronto-orbital spot rounded, black, velvety pruinose, separated from eye margin by whitish pruinosity. One (posterior) fronto-orbital bristle. Ocellar bristles absent. Postocellar bristle well developed. Angle of face with oral margin in profile about 90°, rostrum not extended. Palpus present. Scape about ⅓ as long as wide. Pedicel about 2¼ times as long as wide. Arista densely furnished with short, white hairs.

Thorax tomentose dorsally with 4 longitudinal brown stripes, median pair coalescing before mesonotal suture. Mesonotum not angulate anteriorly, transverse mesonotal suture incomplete. Prosternum with a few scattered setae in lower ½. Pleura with sparsely scattered setae, denser on anepisternum. Anterior and posterior notopleural bristles present. Presutural bristle absent. Katatergite (= metapleural) callus dark brown tomentose, with cluster of black setae. Scutellum with pair of apical bristles.

Fore coxa light brown, whitish tomentose; middle and hind coxae slightly darker. Sternal-coxal bridge absent. Legs mostly yellowish; fore femur with brownish area midway on external surface. No strong, erect dorsal bristle on fore femur. Hind femur simple, without midventral notch. Fore and middle tibae brownish at distal ends; hind femur brownish in distal ⅓, hind tibia with straw-colored area in distal ⅓, contrasting with brown before and after; fourth and fifth tarsal segments brownish.

Wing length 4.7 mm. Membrane brownish, hyaline; costal margin and wing veins brownish. Crossveins clouded. Halter, calypter, and calyptral fringe brown.

Abdominal segments brownish. Terminalia as in Figs. 1 and 4. Cochleate vesicle absent, posterior surstylus and epandrium not fused, cerci not fused together, epandrium not closed below cerci, aedeagal filaments present.

Female.—Similar to holotype male except for terminalia. Wing length 5.1 mm.

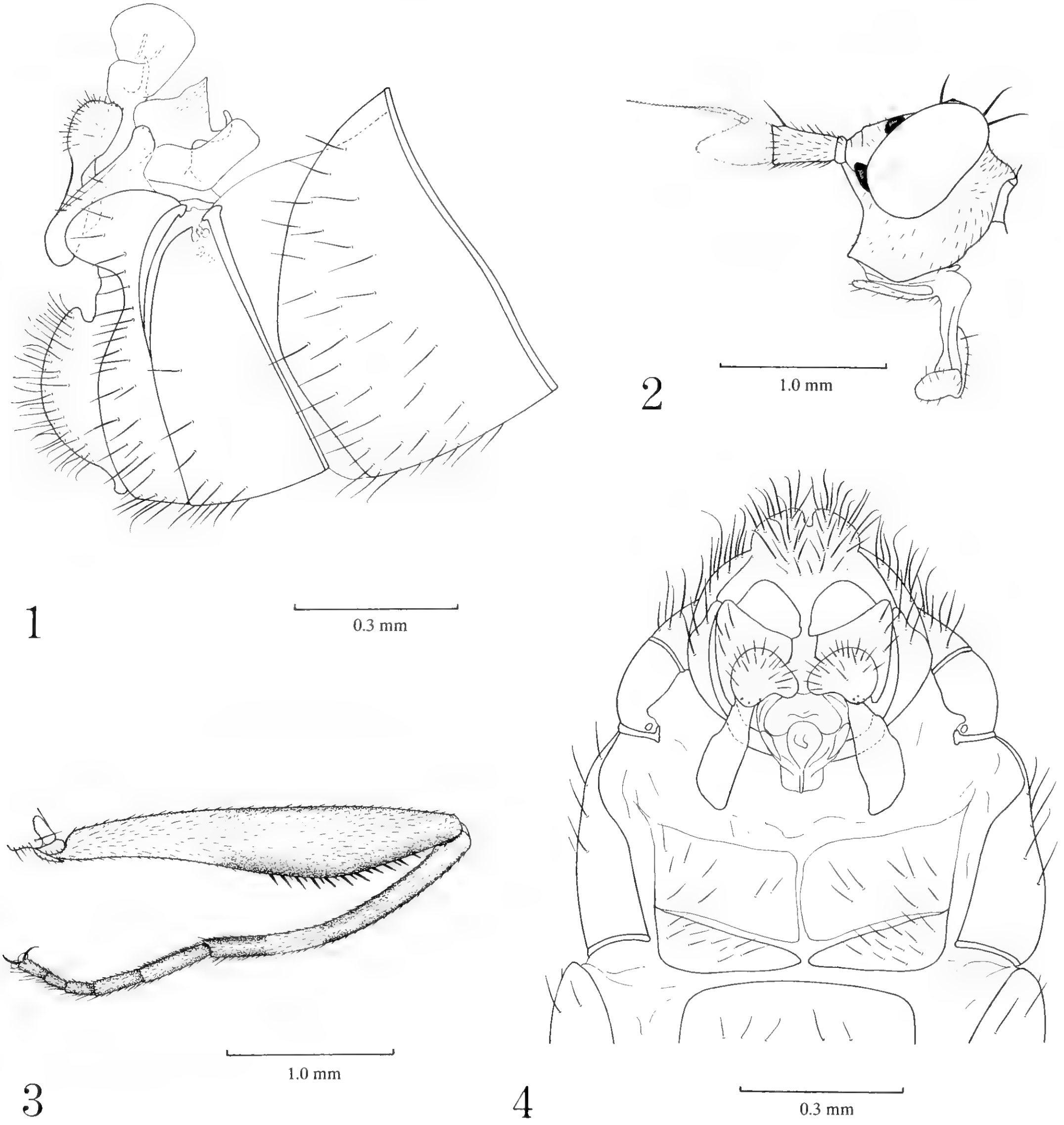
Holotype.—♂, USA, Illinois, Union Co., Pine Hills, 1 mi E LaRue, March 15, 1977, D. W. Webb. In Illinois Natural History Survey (INHS).

Allotype.—♀, USA, Illinois, Union Co., Pine Hills, September 28, 1965, collector not recorded. In INHS.

Paratypes.—All from USA, Illinois, Union Co., Pine Hills: September 25, 1965, J. M. Nelson (1 ♂) INHS; September 28, 1965, collector not recorded (1 ♂) INHS; September 29, 1972, R. W. Vangeison (1 ♀) SIU (Southern Illinois University); March 2, 1973, J. E. McPherson (1 ♂) SIU. Winters Pond, 9 km N Wolf Lake: September 24, 1996, D. W. Webb (2 ♂, 1 ♀) INHS.

Diagnosis.—*Sepedon mcphersoni* is a member of the *S. sphegea* group, which includes 7 Nearctic, 2 Palearctic, and 1 Palearctic-Oriental species. It may be placed in the *S. pusilla* subgroup, which includes *S. borealis* Steyskal, *S. lignator* Steyskal, *S. neili* Steyskal, and *S. pusilla* Loew. All five are North American, north temperate to boreal species and have been found only north of 37°N latitude. Members of this subgroup are identified by their (1) simple, not notched, hind femur (2), evenly arcuate hind tibia (3), small size (wing length less than 5.2 mm), and (4) frequently almost black abdomen with bluish reflections.

Externally, *S. mcphersoni* is distinct from other members of the *S. pusilla* subgroup. The hind femur and tibia are more or less uniformly brown in all species of the subgroup, except *S. mcphersoni.* The hind femur of *S. mcphersoni* is straw colored proximally and brown distally. The hind tibia has a straw colored area in the distal ⅓, contrasting with brown before and after, thus giving the appearance of a yellowish band. The color pattern of the hind leg of *S. mcphersoni* closely resembles that of *S.*



Figs. 1–4. *Sepedon mcphersoni.* 1, Paratype male, postabdomen (sinistral view, inverted). 2, Holotype male, head. 3, Paratype male, sinistral hind leg. 4, Paratype male, postabdomen (ventral view).

floridensis Steyskal, a much larger Nearctic species in the *S. fuscipennis* group (see Orth 1986). The abdominal segments of *S. mcphersoni* are not as dark as other members of the subgroup, with the exception of *S. pusilla.* The terminalia of the male of *S. mcphersoni* (Figs. 1, 4) show no close similarity to other members of the subgroup.

Distribution and habitat.—*Sepedon mcphersoni* is known only from the LaRue-Pine Hills Ecological Area, Shawnee National Forest, Union County, southernmost Illinois. The two specific localities according to the specimen labels, 1 mi. E LaRue and Winters Pond, are about 3.6 km apart, near the southern edge and at the northern edge, respectively, of the Area. D. W. Webb, (in litt.) noted that "all of the *Se-*

pedon were collected along the edges of swamps." The Area, comprising 1,996 acres, has been described by Evers and Page (1977). It is bordered on the west, in part, by the Big Muddy River, a tributary of the Mississippi River, and on the east, in part, by the up to 33 m high, cherty limestone bluffs of the Pine Hills. The swamps are in an old channel of the Big Muddy River below the mostly west facing bluffs. Evers and Page (1977) noted: "The swamps are of interest botanically for the occurrence of several species that are rare in Illinois. Several species of duckweeds, including *Wolffiella floridana,* live in the water of this swamp, as do frog-bit and swamp loosestrife, the last a species more common much farther north. Here can also be found the rare grass, *Glyceria pallida.*—Especially unusual invertebrates at LaRue-Pine Hills are an endemic scud, *Gammarus minus pinicollis* (Cole 1970); the dwarf crayfish, *Cambarellus shufeldtii*; the scorpionflies, *Boreus brumalis, Merope tuber,* and *Bittacus punctiger*; the stonefly, *Hastaperla brevis*; the thrips, *Heterothrips azaleae* and *Oxythrips divisus*; the grasshoppers, *Schistocera obscura* and *Neotettix femoratus*; and the butterflies, *Amblyscirtes carolina, Autochton cellus,* and *Atlides halesus.*"

Other species of Sciomyzidae that we have identified from the Area are *Atrichomelina pubera* Loew, *Pherbellia nana* Fallén, *Sepedon floridensis* Steyskal, *S. f. fuscipennis* Loew, *S. tenuicornis* Cresson, *Dictya stricta* Steyskal, *Trypetoptera canadensis* Macquart, and *Limnia septentrionalis* Melander.

Biology and immature stages.—Unknown.

Etymology.—This species is named after Dr. Jay E. McPherson, Department of Zoology, Southern Illinois University, Carbondale, Illinois, in recognition of his studies of the LaRue-Pine Hills Area and of his efforts to maintain and preserve this important habitat.

ANNOTATED KEY TO SPECIES OF *SEPEDON* OF NORTH AMERICA

1\. Katatergite callus with black setae 2

– Katatergite callus without black setae, completely bare (*S. fuscipennis* group of Orth 1986) 17

2\. Medifacies with or without fine black setae; if without, katatergite callus densely setose 3

– Medifacies without fine black setae; katatergite callus sparsely setose. Male genitalia with apical process of aedeagus a large, recurved crest; as figured in Steyskal 1951: 294 (Alaska, widespread in Canada, Washington south to northern California, east to Maine south to Ohio) .... *S. spinipes americana* Steyskal

3\. Large species; wing length 5.8–8.9 mm; hind femur of male without midventral notch ... 4

– Smaller species; wing length 3.6–5.5 mm; hind femur of male with or without midventral notch 5

4\. Face yellowish to amber, with or without scattered fine black setae on medifacies; wing length: male 5.8–7.2 mm, female 6.3–7.3 mm; hind femur usually less than 4 mm long. Male genitalia with apical plate of aedeagus truncate in anterior view; as figured in Fisher and Orth 1972: 9 (Nebraska, Kansas, Colorado, Utah, Arizona, New Mexico, Mexico (highlands to Oaxaca)) .... *S. praemiosa* Giglio-Tos

– Face amber to brownish, medifacies with fine black setae scattered to moderately dense; wing length; male 7.2–8.9 mm, female 7.0–8.0 mm; hind femur usually greater than 4 mm long. Male genitalia with apical plate of aedeagus bilobed in anterior view; as figured in Fisher and Orth 1972: 10 (British Columbia east to Saskatchewan, USA west of Mississipi River, Baja California Norte) .... *S. pacifica* Cresson

5\. Male hind femur emarginate ventrally; female hind femur simple; hind tibia distinctly more curved in distal third; abdomen brown with little more than a trace of bluish reflection; oral margin usually raised, forming a right angle in profile (Canada, USA, Mexico) (*S. armipes* group of Steyskal 1951) 6

– Hind femur of both sexes simple; hind tibia more or less evenly arcuate; abdomen frequently almost black with bluish reflections; oral margin usually low, angle with face frequently forming a somewhat acute angle in profile (north of 37°N. latitude) (S. *pusilla* subgroup of Steyskal 1951) 13

6\. Frons with no more than a trace of black fronto-orbital spots 7

Frons with distinct, velvety black fronto-orbital spots 8

7. Vein M slightly turned anteriad at apex; hind tibia with median dark brown band. Male genitalia with processes of hypandrium strongly curved mesad, sharply pointed, with bimucronate anterior branch and 2 small subsidiary teeth; as figured in Steyskal 1960: 41 as *S. haplobasis* (Mexico, D.F., Hidalgo, Michoacán) . . . . *S. relicta* Wulp

– Vein M not turned anteriad at apex; hind tibia without median band. Male genitalia with expanded and irregularly toothed surstylus; as figured in Steyskal 1951: 281 (California, Baja California Norte) . . . . . . *S. bifida* Steyskal

8. Fronto-orbital black spots very large, extending nearly to vertex. Male genitalia with quadrangular cercus with apical tooth; as figured in Steyskal 1951: 281 (Washington (Snoqualmie Pass)) . . . . *S. melanderi* Steyskal

– Fronto-orbital black spots smaller, extending ⅔ or less of distance to vertex 9

9. Fronto-orbital spots extending approximately ⅔ of distance to vertex, intense dull black, oval; central area of anterior dorsum with pinkish-orange hue. Male genitalia with knoblike process ventrally near base of aedeagus; as figured in Fisher and Orth 1974: 293 (Oregon) . . . . . *S. cascadensis* Fisher and Orth

– Fronto-orbital spots extending halfway or less to vertex. Male genitalia with fanlike crest on ventral surface or flat 10

10. Ventral surface of aedeagus with fanlike crest; as figured in Steyskal 1956: 86 (Alaska, south to Utah, east to Minnesota, north to Manitoba) . . . . *S. anchista* Steyskal

– Ventral surface of aedeagus flat 11

11. Apex of aedeagus not at right angle to base; as figured in Fisher and Orth 1969: 155, 156 (western USA) . . . . *S. capellei* Fisher and Orth

– Apex of aedeagus at right angle to base . . 12

12. Distance between gonopore and basal anterior process of aedeagus short; as figured in Fisher and Orth 1969: 155, 156 (widespread in Canada, USA, south to northern Sonora, Mexico, not far western USA) . . . . . . *S. armipes* Loew

– Distance between gonopore and basal anterior process of aedeagus twice as long as in *S. armipes;* as figured in Fisher and Orth 1969: 155, 156 (British Columbia and northwestern USA) . . . . . . *S. pseudarmipes* Fisher and Orth

13. Median stripe of pruinosity on face extending in a point to oral margin 14

– Median stripe not extending to oral margin, blunt at apex 15

14. Oral margin usually low, in profile angle with face acute. Male genitalia with strongly lobate cercus; as figured in Steyskal 1951: 284 (Idaho east to Manitoba and Quebec, south to Georgia, west to Utah) . . . . . . *S. neili* Steyskal

– Oral margin raised, in profile angle with face approximately right angle. Male genitalia with cerci small, placoid; as figured in Steyskal 1951: 284 (widespread in southern Canada and northern USA) . . . *S. lignator* Steyskal

15. Hind tibia with straw colored area in distal ⅓, contrasting with light brown basad and dark brown apicad. Genitalia with aedeagus keel-like but not extended as in *S. spinipes;* as figured in text, Figs. 1, 4 (known only from southern Illinois) . . . . . . *S. mcphersoni,* n. sp.

– Hind tibia more or less uniform in color . . 16

16. Darker-colored species; fronto-orbital black spots large, intensely pigmented. Male genitalia with surstylus much longer than cercus, simple and tapering to a point but somewhat twisted, ultimate sternites without protuberances; as figured in Steyskal 1951: 284 (widespread in North America north of 37°N. latitude) . . . . *S. borealis* Steyskal

– Lighter-colored species; fronto-orbital black spots of moderate size, not intensely pigmented. Male genitalia with surstylus shorter than cercus, narrow, with rectangular pre-apical prong; ultimate sternite with 2 pairs of protuberances; as figured in Steyskal 1951: 284 (Indiana east to District of Columbia, south to Georgia, west to Mississippi) . . . . *S. pusilla* Loew

17. Pedicel approximately 2½ times as long as wide in lateral view 18

– Pedicel 4 or more times as long as wide in lateral view 20

18. Hind tibia with straw colored area in distal ½, contrasting with dark brown before and after; male hind tibia with short setae on dorsal surface. Male genitalia with basal process of aedeagus narrowed apically, directed anteriorly; as figured in Orth 1986: 67, 68 (Illinois and Maryland south to Louisiana and Florida) . . . . *S. floridensis* Steyskal

– Hind tibia without contrasting area, more or less uniform brown; male hind tibia with setae on dorsal surface as long as width of tibia 19

19. Frons with distinct, velvety black, fronto-orbital spot. Male genitalia with 2 long, subequal, parallel processes; as figured in Orth 1986: 67, 68 (Illinois east to New Jersey, south to Florida, west to Texas) . . . . *S. fuscipennis fuscipennis* Loew

– Frons usually with no more than a trace of black fronto-orbital spot in specimens from Canada and western USA, eastern specimens with darker spot. Male genitalia with apical process of aedeagus shorter and narrower than basal process; as figured in Orth 1986: 67, 68 (Alaska, Canada, USA generally north of 40°N. latitude; also New Mexico) . . . . *S. fuscipennis nobilis* Orth (Electrophoretic studies by Manguin (1990) suggest that *S. fuscipennis* is a single species.)

20. Pedicel approximately 4 times longer than wide. Male genitalia with apical process of distiphallus long, narrowly tapered; basal process tapered (lateral view); as figured in Orth 1986: 67, 68 (Minnesota east to southern Ontario and Quebec: Maine south to Pennsylvania and west to Iowa) . . *S. gracilicornis* Orth

– Pedicel approximately 5 times longer than wide. Male genitalia with apical process of distiphallus shorter, broadly tapered; basal process strongly lobate, reflexed (lateral view); as figured in Orth 1986: 67, 68 (New York and Massachusetts southwest to Texas and Oklahoma) . . . . *S. tenuicornis* Cresson

Character Analysis and Classification of *Sepedon* and Related Genera

The modern suprageneric classification of the family Sciomyzidae has been discussed by Verbeke (1950, 1961), Hennig (1965), Steyskal (1965), Griffiths (1972), Berg and Knutson (1978), Barnes (1979a, b, 1981), Vala (1984, 1989), McAlpine (1989), and a preliminary, computer-based cladistic analysis of 50 of the 58 genera has recently been completed (Marinoni and Mathis, 2000). *Sepedon,* with 74 species is the second largest genus, after *Pherbellia* Robineau-Desvoidy, in the family, and it and at least 6 related genera include some of the most derived forms in the family. Extensive life cycle information gained over the past years on *Sepedon* and some of the related genera has generated renewed interest in their phylogenetic placement.

Although almost all authors since Enderlein (1939) have placed *Sepedon* and related genera in Tetanocerini *sensu* Steyskal (1965) (= Tetanocerinae of authors), seven, especially the earlier authors, placed at least *Sepedon* in a separate tribe or subfamily. Interestingly, this historically represents the most concerted agreement on the status of a suprageneric category in Sciomyzidae, other than the more recent widely held recognition of Phaeomyiidae, Salticellinae, and Sciomyzinae, with 2 tribes. It is over 100 years since Acloque (1897) designated the tribe Sepedonini. Cresson (1920) used the tribe Sepedontini for 5 North American species of *Sepedon* s.s. (plus *Thecomyia* and "probably" *Dichetophora*) along with 2 other tribes in his subfamily Euthycerinae (= modern Tetanocerini). Hendel (1923) used the tribe Sepedonina for *Sepedon* and *Dichetophora.* Malloch (1928) included *Sepedon, Thecomyia,* and *Dichetophora* in his Sepedonini. Crampton (1944) in a simple list grouping families of Acalyptrata based on the male terminalia listed "Tetanoceratidae, or Sciomyzidae" and "Sepedonidae (possibly merely a subfamily of the Tetanoceratidae)." Verbeke (1950) created the subfamily Sepedoninae for *Sepedon* and his new Afrotropical genera *Sepedomyia, Sepedoninus,* and *Sepedonella.* In describing the Neotropical genera *Sepedomerus* and *Sepedonea,* Steyskal (1973) did not recognize that subfamily, considering it not sufficiently distinct from more typical Tetanocerini, especially from such genera as *Hedria* and *Dichetophora,* and preferred to call it the *Sepedon* group. He recognized *Sepedoninus* as a genus and under *Sepedon* he included Verbeke's subgenera *Mesosepedon* and *Parasepedon* and genus *Sepedomyia,* noting the latter is very doubtfully more than subgenerically distinct on the basis of the elongate scape. Notably, Hennig (1965) analyzed the subfamily and tribe classifications of Steyskal (1965) and Verbeke (1950) in detail and recognized Sepedoninae Verbeke as a subfamily and monophyletic group. Marinoni and Mathis (2000) placed *Sepedon* and related genera in the Tetanocerini, subfamily Sciomyzinae.

Until now, there has been no overall proposal of subgeneric categories for the genus *Sepedon* on a world basis. Groups have been designated for 17 of the 20 North American species (*Armipes* and *Pusilla* groups, [Steyskal 1951] and *Fuscipennis* group, [Orth 1986]); the 3 known Central-South American species (*Macropus* group, Steyskal, 1951), placed in the new genus

Table 1. Matrix of characters of adults in groups of *Sepedon sensu strictu* and related genera.

Taxa	1 medifacial setae	2 katatergite setae	3 fronto-orbital bristles (1)	4 postocellar bristles	5 ant. notopleural bristle	6 presutural bristle	7 scutellar bristles	8 dors. bristle fore femur	9 palpi
Groups in *Sepedon s.s.*									
1. *Sphegea* — P, O, Na	±	+	1	+	+	−	+	−	+
2. *Neanias* — P, O	+	+	1	+	+	−	+	−	+
3. *Spinipes* — P, Na	−	+	1	+	+	+	+	−	+
4. *Fuscipennis* — Na	±	−	1	+	+	−	+	−	+
5. *Armipes* — Na	+	+	1	+	+	−	+	−	+
6. *Trichrooscelis* — Af, O, AO	−	−	1	+	−	±	+	+	+
7. *Dispersa* — Af	−	−	1	+	−	±	+	+	+
8. *Lobifera* — O	−	−	0	+	−	−	−	−	+
9. *Nasuta* — Af	−	−	1	+	−	+	+	+	+
Related Genera									
1. *Sepedomerus* — Na, Nt	−	+	1	−	+	−	+	−	+
2. *Sepedonea* — Nt	−	−	1,2	+	+	+	+	+	+
3. *Thecomyia* — Nt	−	−	0,1	−	−	−	+	−	−
4. *Sepedonella* — Af	−	−	1	−	−	−	+	−	+
5. *Sepedoninus* — Af	−	−	0,2	+	−	±	+	−	+
6. *Sepedonites* — F	−	−	2	+	+	+	+	?	+

(1) Usual number present given first.
(2) Distinct and continuous across middle of mesonotum.
(3) Rudimentary.
(+) present, (−) absent.
Abbreviations: P = Palearctic; Na = Nearctic; Nt = Neotropical; Af = Afrotropical; O = Oriental; AO = Australian-Oceanian; F = Fossil.

Sepedomerus by Steyskal 1973; and the subgenera *Parasepedon* with 7 species groups (24 species) and *Mesosepedon* (2 species) for the Afrotropical species known at the time (Verbeke 1950). Steyskal and Knutson (1975), in their study of the highly apomorphic cochleate vesicle (sperm pump), listed 28 Afrotropical, Oriental, and Australian species as to presence or absence of this structure, which is not present in any Nearctic, Palearctic, or Neotropical species of *Sepedon* or in any of the related genera.

Steyskal in Steyskal and Verbeke (1956) noted a few species do not fit well in any group, and preferred not to use groups. Verbeke (1961) provided a key to and new arrangement of eight groups of *Parasepedon.* Groups of Afrotropical *Sepedon* were not recognized subsequently. *Sepedomyia* with *S. nasuta* and *S. alaotra* Verbeke, 1962, *Mesosepedon* with 5 species, and *Parasepedon* with 33 species, were presented as subgenera of *Sepedon* in the catalog of Afrotropical Diptera (Knutson 1980). Barraclough (1985) noted that Verbeke's (1950) subgenera *Mesosepedon* and *Parasepedon* were established primarily on genitalic differences (*Mesosepedon* with sixth and seventh abdominal terga poorly developed, aedeagus without spiral filament, and presutural seta usually strong; *Parasepedon* with genital segments well developed, aedeagus with spiral filament, and strong presutural bristle present in some species, absent in others). *Mesosepedon,* unlike *Parasepedon,* lack a cochleate vesicle. Barraclough (1985: 484) stated "Subgeneric status appears to be valid, because *Sepedomyia* species are clearly distinguished from other *Sepedon* species by the longer first antennal segment, the presence of a humeral seta, and a distinct hypopygial structure. . . . It thus appears that only aedeagal characters can separate *Mesosepedon* from *Parasepe-*

Table 1. Extended.

10 fronto-orbital spot	11 orbito-antennal spot	12 scape elongate	13 rostrum extended	14 hind femur modified	15 sternal-coxal bridge	16 complete mesonotal sut. (2)	17 mesonotum angulate anter.	18 cerci fused	19 epand. closed below cerci	20 post. surst. & epand. fused	21 cochleate vesicle	22 aedeagal filaments	23 aqua. predaceous larvae	24 terrest. parasitoid larvae
−	+	−	−	−	−	−	−	±	−	−	−	+	+	−
+	+	−	−	−	−	−	−	+	+	+	−	−	+	−
+	+	−	−	−	−	−	−	−	−	−	−	+	+	−
±	+	−	−	−	−	−	−	−	−	−	−	+	+	−
±	+	−	−	+	−	−	−	−	−	−	−	−	+	−
±	−	−	−	−	−	−	−	−	−	−	±	±	+	+
+	−	−	−	−	−	−	−	−	−	±	−	−	?	?
+	−	−	−	−	−	−	−	−	−	−	+	−	?	?
+	−	+	−	−	−	+	+	−	−	+	−	+	?	?
−	+	−	−	−	−	−	−	−	−	−	−	−	+	−
−	−	−	−	−	−	−	−	−	+	−	−	−	+	−
+	−	−	+	−	+	−	−	−	−	+	−	−	+	−
−	−	−	−	−	−	−	−	−	−	−	−	−	+	−
+	−	−	−	−	−	+	+	−	−	+	+(3)	−	?	?
?	?	?	?	−	?	?	?	?	?	?	?	?	?	?

Table 2. Explanation of Characters. The presumed plesiomorphic (P) condition within the tribe Tetanocerini is indicated for each character below by a + (present) or − (absent) sign or the number 2 for number of fronto-orbital bristles. The genus *Tetanocera* was used as the outgroup for comparison.

1. medifacial setae (P = +)
2. katatergite callus setae (P = +)
3. number of fronto-orbital bristles (P = 2)
4. postocellar bristles (P = +)
5. anterior notopleural bristle (P = +)
6. presutural bristle (P = +)
7. scutellar bristles (P = +)
8. dorsal bristle on fore femur (P = +)
9. palpi (P = +)
10. fronto-orbital spot (P = +)
11. orbito-antennal spot (P = +)
12. scape elongate (P = −)
13. rostrum extended ventrally (P = −)
14. hind femur modified (P = −)
15. sternal-coxal bridge (P = −)
16. complete mesonotal suture (P = −)
17. mesonotum angulate anteriorly (P = −)
18. cerci fused (P = −)
19. epandrium closed below cerci (P = −)
20. posterior surstyli and epandrium fused (P = −)
21. cochleate vesicle (P = −)
22. aedeagal filaments (P = −)
23. aquatic predacious larvae (P = +)
24. terrestrial parasitoid larvae (P = −)

don, and that these two subgenera should at best be considered species groups."

Miller (1995) noted that the "subgeneric categories will have to be modified or may fall away, because several species do not possess both the cochleate vesicle and aedeagal spiral filament (Steyskal and Knutson 1975), yet appear to fall into *S.* (*Parasepedon*)."

Herein we do not recognize subgenera of *Sepedon.* We recognize the *Armipes* group as proposed by Steyskal, but place his *Pusilla* group as a subgroup with the *Sphegea* subgroup in the *Sphegea* group (stem group). We propose the *Dispersa* group for the subgenus *Mesosepedon* and the *Trichrooscelis* group for the subgenus *Parasepedon* plus 11 Oriental and Australian species having a cochleate vesicle. We propose the *Nasuta* group for the genus *Sepedomyia* and 3 other new groups: *Spinipes* - 1 Holarctic species; *Neanias* - 1 Palearctic and Oriental species; and *Lobifera* - 1 Oriental species. Characters of the groups are shown in Table 1. Members of groups are listed in Table 3.

Genera that seem to be related to *Sepe-*

Table 3. Groups of *Sepedon sensu stricto*, with characters apomorphic in relation to the *Sphegea* group (compare numbers in parentheses after the characters to Table 1).

1. *Sphegea* group — Nearctic, Palearctic, Oriental Regions.
   Stem group, without apomorphic characters in relation to other groups, except for characters 3, 6, 8, 18 (in *S. noteoi* and *S. oriens*), and 22.
   - a. *Sphegea* subgroup
     - *aenescens* Wiedemann 1830 — P, O
     - *femorata* Knutson & Orth 1984 — P
     - *noteoi* Steyskal 1980 — O
     - *oriens* Steyskal 1980 — O
     - *pacifica* Cresson 1914 — Na
     - *praemiosa* Giglio-Tos 1893 — Na (medifacial setae present or absent)
     - *sphegea* Fabricius 1775 — P
   - b. *Pusilla* subgroup
     - *borealis* Steyskal 1951 — Na
     - *lignator* Steyskal 1951 — Na
     - *mcphersoni* Knutson & Orth, n. sp. — Na
     - *neili* Steyskal 1951 — Na
     - *pusilla* Loew 1859 — Na
2. *Neanias* group — Palearctic and Oriental Regions
   - cerci fused — (18)
   - epandrium closed below cerci — (19)
   - posterior surstyli and epandrium fused — (20)
     - *neanias* Hendel 1913 — P, O
3. *Spinipes* group — Nearctic and Palearctic Regions
   - medifacial setae absent — (1)
     - *spinipes* Scopoli 1763 — H
4. *Fuscipennis* group (Orth 1986) — Nearctic Region
   - medificial setae absent — (1)
   - katatergite setae absent — (2)
     - *floridensis* Steyskal 1951 — Na
     - *fuscipennis* Loew 1859 — Na
     - *gracilicornis* Orth 1986 — Na
     - *tenuicornis* Cresson 1920 — Na
5. *Armipes* group (Steyskal 1951) — Nearctic Region
   - hind femur modified — (10)
     - *anchista* Steyskal 1956 — Na
     - *armipes* Loew 1859 — Na
     - *bifida* Steyskal 1951 — Na
     - *capellei* Fisher & Orth 1969 — Na
     - *cascadensis* Fisher & Orth 1974 — Na
     - *melanderi* Steyskal 1951 — Na
     - *pseudarmipes* Fisher & Orth 1969 — Na
     - *relicta* Wulp 1897 — Na
6. *Trichrooscelis* group — Afrotropical, Oriental, Australian-Oceanian Regions
   - medifacial setae absent — (1)
   - katatergite setae absent — (2)
   - anterior notopleural bristle absent — (5)
   - dorsal bristle present on fore femur — (8)
   - orbito-antennal spot absent or weak — (11)
   - cochleate vesicle usually present — (21)
   - aedeagal filaments usually present — (22)
   - = subgenus *Parasepedon* Verbeke, 1950 and the following species:
     - *costalis* Walker 1858 — O
     - *crishna* Walker 1849 — O
     - *ferruginosa* Wiedemann 1824 — O
     - *lata* Bezzi 1928 — AO
     - *plumbella* Wiedemann 1830 — O, AO
     - *senex* Wiedemann 1830 — O
     - *spangleri* Beaver 1974 — O

Table 3. Continued.

7. *Dispersa* group — Afrotropical Region
    medifacial setae absent — (1)
    katatergite setae absent — (2)
    anterior notopleural bristle absent — (5)
    dorsal bristle on fore femur present — (8)
    orbito-antennal spot absent — (11)
    posterior surstyli and epandrium usually fused — (20)
    = subgenus *Mesosepedon* Verbeke 1950
        convergens Loew 1862
        dispersa Verbeke 1950
        ethiopica Steyskal 1956
        knutsoni Vala, Gbedjissi, & Dossou 1994
        pleuritica Loew 1862
        schoutedeni Verbeke 1950
        tuckeri Barraclough 1985
8. *Lobifera* group — Oriental Region
    medificial setae absent — (1)
    katatergite setae absent — (2)
    fronto-orbital bristles absent — (3)
    anterior notopleural bristle absent — (5)
    scutellar bristles absent — (7)
    orbito-antennal spot lacking — (12)
    cochleate vesicle present — (21)
        lobifera Hendel 1911
9. *Nasuta* group — Afrotropical Region
    medifacial setae absent — (1)
    katatergite setae absent — (2)
    anterior notopleural bristle absent — (5)
    orbito-antennal spot absent — (11)
    scape elongate — (12)
    complete mesonotal suture — (16)
    = genus *Sepedomyia* Verbeke 1950
        alaotra Verbeke 1962
        nasuta (Verbeke) 1950

don are included in Table 1 for comparison. As Steyskal (1951) noted, other genera such as *Tetanoptera* and *Dichetophora* show a relationship with *Sepedon*. In describing the male of *Tetanoptera*, Knutson and Vala (1999) compared the genus with *Sepedon* and related genera, along with *Elgiva, Hedria, Oligolimnia, Verbekaria, Dichetophora* and *Neosepedon*, in a matrix of characters including characters 2–6, 9, 20, 21 as in Table 1, but also 16 other characters. They concluded that *Tetanoptera* appears to be related to *Dichetophora*, and intermediate in an evolutionary lineage between the primitive *Tetanocera* and the advanced *Thecomyia*.

Because information on the life cycles and immature stages of *Sepedon* is so dispersed we have listed in Table 4 the more important publications for each species, for which information has been presented.

Shortly after this manuscript was completed, we received a copy of Marinoni and Mathis' (2000) cladistic analysis of the family. Their analysis of 50 of the 58 genera was based on study of the type species of each genus, and thus does not speak to the groups within *Sepedon s.s.*, but it is of interest to compare their comprehensive analysis of the generic relationships to our Table 1. The 36 morphological characters they used included only characters 5, 6, and

Table 4. Publications on the life cycles and/or immature stages of *Sepedon* and related genera. The literature prior to 1966 was summarized by Neff and Berg 1966.

	Neotropical Region
Sepedomerus	
caeruleus (Melander)	Neff & Berg 1966; Neff 1964
macropus (Walker)	Neff & Berg 1966; Neff 1964; Chock et al. 1961
Sepedonea	
barbosai Knutson & Bredt	Freidberg et al. 1991; Bredt & Mello 1978
guatemalana Steyskal	Neff & Berg 1966
guianica (Steyskal)	Freidberg et al. 1991
isthmi (Steyskal)	Knutson & Valley 1978
lagoa (Steyskal)	Freidberg et al. 1991
lindneri (Hendel)	Freidberg et al. 1991
telson (Steyskal)	Freidberg et al. 1991
Thecomyia	
limbata (Wiedemann)	Abercrombie & Berg 1975
	Palearctic Region
Sepedon	
hispanica hispanica Loew	Knutson et al. 1967
sphegea Fabricius	Gercke 1876; Neff & Berg 1966; Knutson et al. 1973; Tirgari & Massoud 1981; Ghamizi 1985; Vala & Manguin 1987; (summarized by Knutson & Orth 1984)
spinipes americana Steyskal	Neff & Berg 1966
spinipes spinipes Scopoli	Gercke 1876; Beaver 1972, 1973, 1974a, b; Neff & Berg 1966; Vala & Manguin 1987
	Nearctic Region
Sepedon	
anchista Steyskal	Neff & Berg 1966
armipes Loew	Neff & Berg 1966
bifida Steyskal	Neff & Berg 1966
borealis Steyskal	Neff & Berg 1966
fuscipennis Loew	Neff & Berg 1966; Needham & Betten 1901; Neff 1964; Eckblad & Berg 1972; Peacock 1973; Eckblad 1973; Barnes 1976; McCoy & Joy 1977; Arnold 1978; Juliano 1981, 1982; Berg et al. 1982; Manguin 1990; Manguin & Hung 1991
neili Steyskal	Neff & Berg 1966
praemiosa Giglio-Tos	Neff & Berg 1966
pusilla Loew	Neff & Berg 1966
relicta van der Wulp	Neff & Berg 1966 (as *S. haplobasis*)
spinipes americana Steyskal	Neff & Berg 1966
tenuicornis Cresson	Neff & Berg 1966; Geckler 1971
	Oriental Region
Sepedon	
aenescens Wiedemann	Nagatomi & Kushigemachi 1965; Nagatomi & Tanaka 1967; ChannaBasavanna & Yano 1969; ChannaBasavanna & Prasad 1971; Beaver et al. 1977; Yano 1978; (summarized by Knutson & Orth 1984)
ferruginosa Wiedemann	Beaver et al. 1977
plumbella Wiedemann	Beaver et al. 1977; Bhuangprakone & Areekul 1973
senex Wiedemann	Beaver et al. 1977; Beaver 1989
spangleri Beaver	Beaver et al. 1977; Chandavimol et al. 1975

Table 4. Continued.

	Afrotropical Region
Sepedon	
hispanica ruhengeriensis Verbeke	Knutson 2000
neavi Steyskal	Barraclough 1983
ruficeps Becker	Knutson et al. 1967; Gbedjissi 1997
scapularis Adams	Knutson et al. 1967; Maharaj et al. 1992
testacea Loew	Barraclough 1983
trichrooscelis Speiser	Vala et al. 1995; Knutson 2000
Sepedonella	Vala et al. 2000
Sepedoninus	No published biological data.

7 in our Table 1, but their analysis was for broader purposes and thus included many characters of importance to genera other than *Sepedon* and related genera. Their analysis agreed with Steyskal's (1973) *Sepedon* group of genera (*Sepedon, Sepedonella, Sepedoninus, Sepedomerus,* and *Sepedonea*), but with the addition of *Ethiolimnia* (8 Afrotropical species) and *Teutoniomyia* (2 Neotropical species). The Afrotropical genera *Tetanoptera* and *Verbekaria* were not included in their analysis. They found 5 groups of genera within the Tetanocerini, with the monophyletic *Ethiolimnia* to *Sepedonea* subgroup in the fourth group, along with 7 other genera (*Guatemalia, Elgiva, Dichetophora, Hedria, Coremacera, Dictyacium,* and *Euthycera*). The monophyly of their *Ethiolimnia* to *Sepedonea* subgroup was established by 8 characters ("6-anterior surstylus absent, 9-pedicel approximately twice the length of first flagellomere, 28-prominent eyes, 30-ocellar setae absent, 31-post pronotal setae absent, 32-one pair of scutellar setae, 33-one notopleural seta, and 35-head sutures indistinct"), and they concluded it was the most "corroborated" lineage in their analysis.

We consider it appropriate to utilize somewhat disparate sets of characters when making non-numerical phylogenetic analyses of limited groups of genera, for example the analysis of *Sepedon* and relatives presented here, for *Tetanoptera* and relatives (Knutson and Vala 1999), and for *Verbekaria* (Vala, Greve, and Knutson 2000). But for either a numerical or non-numerical analysis of the family as a whole, obviously a comprehensive set of characters is needed. The analyses of *Sepedon, Tetanoptera, Verbekaria,* and relatives are steps in the preparation of a comparative anatomy comprising all species of the family (Knutson, in prep.). This will indicate for which species, genera, and higher categories the character might be appropriately used, and the historical use of the character by others, but will not include minor characters of use only in distinguishing between closely related species, except as they might be useful in higher level distinctions. Further analysis of the *Ethiolimnia* to *Sepedonea* subgroup, including *Tetanoptera,* will be of interest after the many undescribed species known to us, K. Elberg (in litt.), R. M. Miller (in litt.), C. Kassebeer (in litt.) and possibly others are published. Characters used by Marinoni and Mathis (2000) along with some of the characters in Table 1 should be considered.

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SYSTEMATICS AND BIOLOGY OF A NEW, POLYPHAGOUS SPECIES OF *MARMARA* (LEPIDOPTERA: GRACILLARIIDAE) INFESTING GRAPEFRUIT IN THE SOUTHWESTERN UNITED STATES

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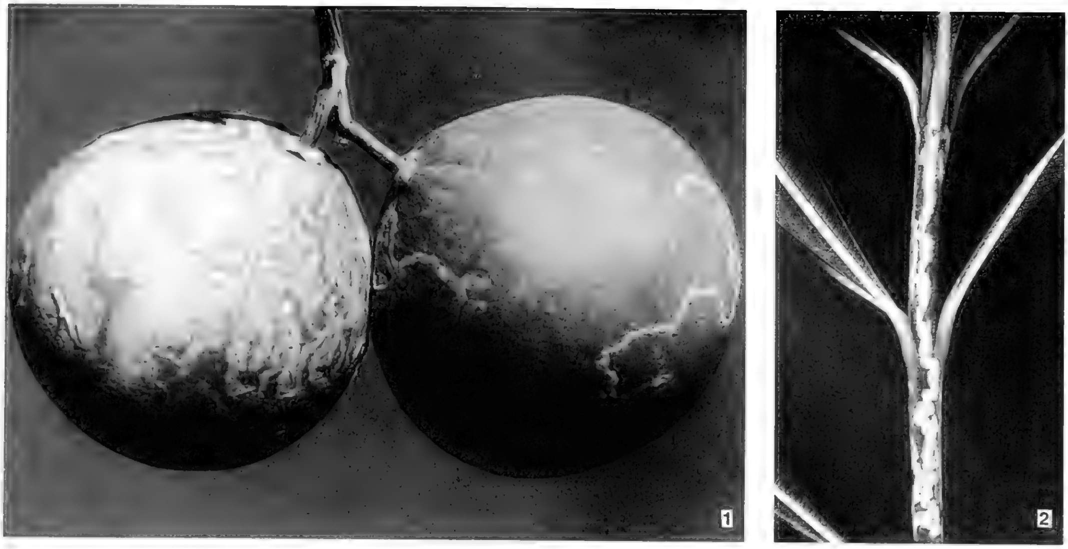
Abstract.—A new species of *Marmara* (Lepidoptera: Gracillariidae), ***M. gulosa* Guillén and Davis**, from the southwestern United States, is described and illustrated. This species, the citrus peelminer, which was previously misidentified as *M. salictella* Clemens, is a cyclical pest in xeric areas of California and Arizona. Larvae mine the surface of citrus fruits, with grapefruit, *Citrus paradisi* Macfadyen, as a preferred host, and with oleander, *Nerium oleander* L., cotton, *Gossypium hirsutum* L., and avocado, *Persea americana* Mill., as alternate hosts. *Salix lasiolepis* Benth is probably the primary host. Based on two nuclear gene regions, 28S-D2 and ITS2, almost no genetic differences were found between populations of peelminer on oleander and grapefruit (0–0.4%), whereas both populations had a 6.8–9.2% divergence from an undescribed, sympatric species of *Marmara* on tree tobacco. Thus at the morphological and genetic level the populations on oleander and grapefruit appear to be panmictic. On grapefruit in the laboratory, females laid 48.5 ± 7.2 eggs and developmental time (egg-adult) at 26°C was 28.8 ± 0.4 days.

Key Words: citrus, cotton, avocado, oleander, willow, *Marmara,* peelminer, biology, hypermetamorphosis, morphology, 28S-D2, ITS2

The citrus peelminer has been reported mining the peel of citrus fruits in the southwestern United States since the early part of the twentieth century (Vinal 1917; Essig 1926; Lockwood 1933; Quayle 1938; Woglum 1948; Anonymous 1960; Atkins 1961, 1971; Chong and La Rosa 1986; Reeves 1995; Gibson et al. 1997). The earliest known collection of this insect consists of a mined orange (*Citrus sinensis* Osbeck) peel collected 23 July 1915 at Pasadena, California (USNM). It has been reported as an economic pest in California (Atkins 1961, 1971; Reeves 1995), Arizona (Anonymous 1960, Gibson et al. 1997) and Cuba (Chong and La Rosa 1986). It also reputedly occurs in very low numbers in Texas and Florida (H. Browning, Manners, in litt.), although no adults from citrus collected outside of California have been examined. Citrus fruit mines from Texas and Florida could also be the result of the citrus leafminer, *Phyllocnistis citrella* Stainton (Gracillariidae), which has become well established along the southern United States and through much of the Neotropical citrus growing regions after 1993, and now in California (Heppner 1993, 1995; Heppner and Dixon 1995; Hoy and Nguyen 1997; JMH unpublished). Larvae of the citrus peelminer form long serpentine mines (Fig. 1) that disfigure the epidermal surface of the fruit (Atkins 1961), and under heavy infestations, the entire fruit surface may be-



Figs. 1–2. *Marmara gulosa,* larval mines. 1, On grapefruit, *Citrus paradisi.* 2, On oleander, *Nerium oleander* (photo courtesy of E. L. Reeves).

come blistered (Reeves 1995). The damage is cosmetic because the internal quality of the fruit is not affected, however the fruit is rendered unacceptable for the fresh fruit market (Atkins 1961, Reeves 1995).

Citrus peelminer was first identified as a western form of *Marmara salictella* Clemens (Lepidoptera: Gracillariidae), a miner on young twigs of willow in the Atlantic states (Woglum 1948), and since, has been reported as this species (Lockwood 1933, Woglum 1948, Anonymous 1960, Atkins 1961, Chong and La Rosa 1986, Reeves 1995, Gibson et al. 1997). Although morphologically closely allied to *M. salictella,* citrus peelminer adults reared from citrus fruit from the Coachella Valley, California, represent a distinct, previously undescribed species.

Besides *Citrus* (Rutaceae), other plants previously reported as hosts for the citrus peelminer include willow (*Salix* sp.) in California (Woglum 1948, Atkins 1971); oleander (*Nerium oleander* L.) in California (Atkins 1961, Reeves 1995) and Arizona (Gibson et al. 1997); watermelon (*Citrullus vulgaris* Schrad.) in California (Atkins 1971); cotton (*Gossypium hirsutum* L.) in Arizona (Atkins 1971); mesquite (*Prosopis* sp.) and grape (*Vitis vinifera* L.) in Arizona (Gibson et al. 1997). On citrus, citrus peelminer mines the peel of fruits, with grapefruit as a preferred host, although tangerines, oranges, lemons and limes are also mined (Atkins 1961, 1971, Gibson et al. 1997). Less frequently, larvae mine the green shoots of lemon, tangerine (Atkins 1971, Gibson et al. 1997), grapefruit and tangelo cultivar Minneola (Gibson et al. 1997). On oleander (Fig. 2), shoots and leaves are mined (Atkins 1961, Reeves 1995, Kerns, in litt.); on watermelon, fruits are mined (Atkins 1971), and on mesquite, grape and cotton, stems are mined (Gibson et al. 1997, D. Kerns, personal communication). All of the above host plants have been previously considered as alternate hosts for the citrus peelminer because they grow in close proximity to peelminer-infested citrus.

Information on alternate host plants for the citrus peelminer is essential to identify sources of citrus infestation of this pest. Oleander plants are abundant in the Coachella Valley, being present as hedges surrounding groves or houses, serving as windbreaks, as ornamental planting or as individual plants. In Arizona, cotton and citrus are grown in close proximity in several areas where oleander is also abundant.

The genus *Marmara* is endemic to the New World. Including *M. gulosa,* 22 species have been described. Seventeen occur in North America north of Mexico (Clemens 1860, 1863; Chambers 1875; Busck 1906, 1909; Braun 1909; Vinal 1917; Forbes 1923; DeGryse 1943; Fitzgerald 1973, 1975; Davis 1983), with at least 12 additional, undescribed species known (D. R. Davis and D. Wagner, unpublished). Six species (including *M. opuntiella* Busck) have been reported from South America (Bondar 1939; Meyrick 1915, 1918; Davis 1984). Recent fieldwork in Costa Rica by Wagner and Davis (unpublished) has revealed the presence of a rich Neotropical gracillariid fauna from the La Selva Biological Reserve, Costa Rica. *Marmara* from this area are especially prevalent on the monocot families Araceae and Heliconiaceae. Alibert (1951) mistakenly reported one species from Africa, but his illustration of the adult and, more importantly, his description of the last instar larva "cinq paires de fausses pattes" indicates another, more atypical, possibly oecophyllembiine genus with four pairs of abdominal prolegs.

Of the North American species of *Marmara,* two occur in Canada (British Columbia) (Clemens 1860, Fitzgerald 1975) and eleven in the northern United States (Clemens 1860, 1863; Chambers 1875; Braun 1909; Busck 1909; Vinal 1917; Forbes 1923; Fitzgerald 1973, 1975). Only two of the described species occur in southern areas, *M. guilandinella* Busck (Vinal 1917) from Florida and *M. opuntiella* (Busck 1906) from southern Texas, ranging also into the northern neotropics (Mann 1969). In southern California, unidentified species of *Marmara* have been found on different host plants in five different families: leaves of *Umbellularia californica* Nutt. (Umbelliferae), stems of *Rhamnus californica* Esch. (Rhamnaceae), stems of *Prunus ilicifolia* D. Dietr. and *Heteromeles arbutifoliella* M. Roemer (Rosaceae), and stems of *Acer macrophyllum* Pursh (Aceraceae) (D. Frack, in litt.). Another undescribed species of *Marmara* is sympatric in distribution with *M. gulosa* in southern California but mines the leaves and stems of tree tobacco, *Nicotiana glauca* Graham (Solanaceae). The only described species in southern California is *Marmara arbutiella* Busck, mining *Arbutus menziesii* Pursh and *Arctostaphyllos andersonii* A. Gray (Wagner et al. 2000), neither of which occur in the desert region of California.

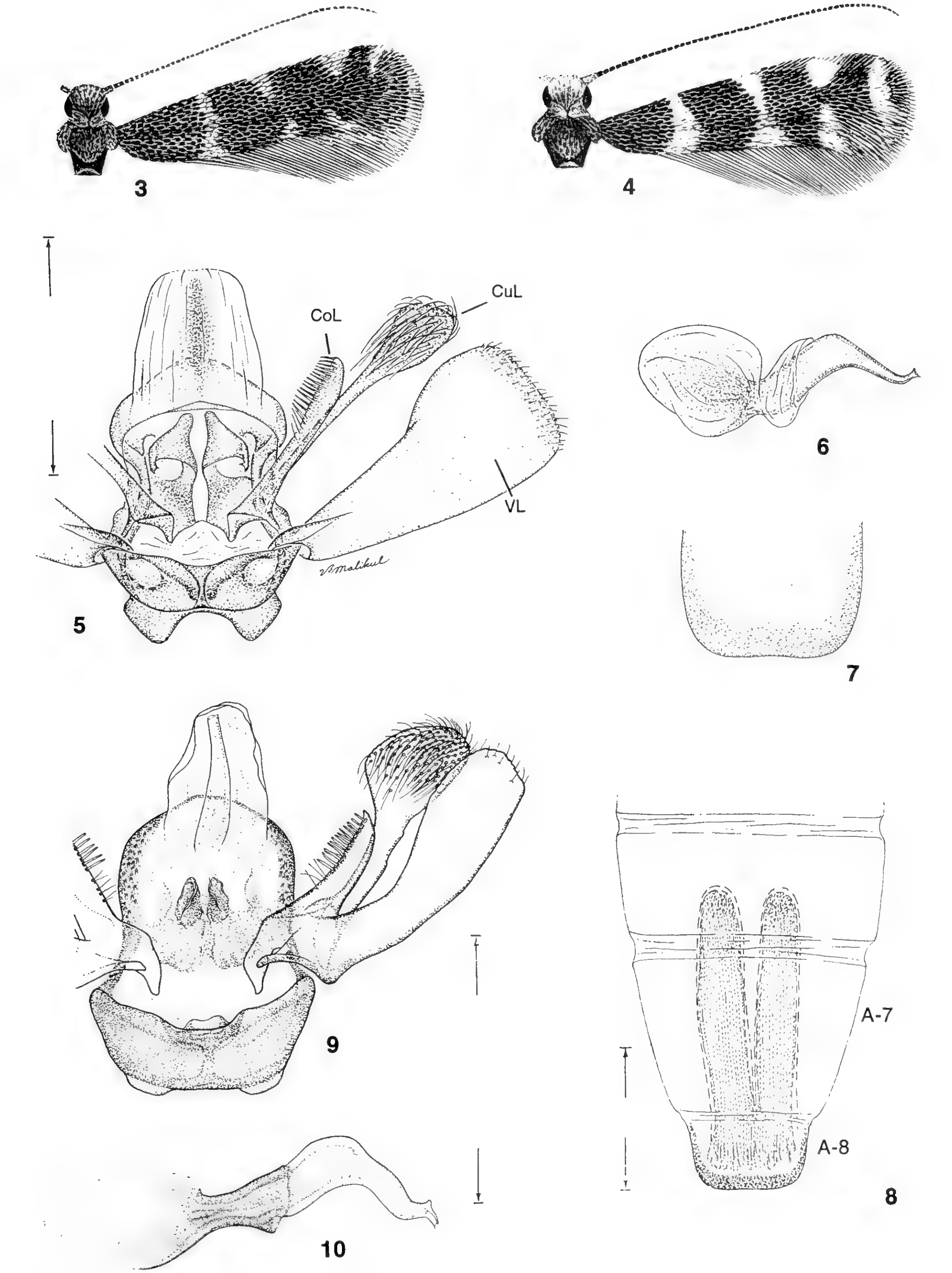
In this study, the citrus peelminer is described and alternate host plants are investigated. We focused on *Marmara* found on citrus and oleander, although miners discovered on avocado, cotton, and willow were also investigated. Specimens from these host plants were collected and compared with the citrus peelminer by utilizing external morphology of adults and, where possible, immature stages. As a means for testing conclusions derived from morphological studies, genetic comparisons of two nuclear genes from moths reared from grapefruit, oleander, and tree tobacco were also examined.

Marmara gulosa Guillén and Davis, new species

(Figs. 1–3, 5–10, 11–47)

Adult (Fig. 3).—Forewing length: 2.3–2.6 mm.

Head: Vestiture smooth, scales curving down over frons; scales on vertex mostly silvery gray with brown tips; frons mostly silvery white with brown-tipped scales adjacent to mouthparts; a broad band of grayish brown scales across back of head. Antenna about 0.8 × length of forewing; flagellum with a single annulus of slender, usually brown scales; scape brown dorsally, cream ventrally. Ocellus absent. Length of maxillary palpus about half vertical diameter of eye; cream dorsally, dark brown ventrally and laterally and with brown distal end. Haustellum elongate, about 2.0 ×



Figs. 3–10. *Marmara* adults. 3, *M. gulosa* from grapefruit, (2.4 mm). 4, *M. salictella,* from *Salix* sp. (2.7 mm). Length of forewing in parentheses. 5–10, Male genitalia and abdominal morphology. 5, *M. gulosa* from grapefruit, ventral view, (0.25 mm; CoL = costal lobe, CuL = cucullar lobe, VL = valvular lobe). 6, Aedeagus, lateral view. 7, Eighth sternum. 8, Coremata inside abdominal segments A6–8, (0.5 mm). 9, *M. salictella,* ventral view, (0.25 mm). 10, Aedeagus, lateral view. (Scale lengths in parentheses.)

length of labial palpus, coiled in repose. Labial palpus elongate, about 1.5 × vertical diameter of eye, cream with distal ends of 2nd and 3rd segments brown.

Thorax: Dorsum with brown-tipped silvery gray scales; venter cream over coxa. Forewing with scales dark gray with brown apices, 4 cream striae crossing the wing at ¼, ½ and ¾ length of wing and at subapex; 2nd stria usually narrower at middle but sometimes interrupted; 3rd stria usually interrupted medially; subapical stria usually extending from the apical cilia midway across wing (Fig. 3); fringe gray with white patch dorsally at apex. Hindwing uniformly with gray scales with brown apices, lighter in color than forewings. Female frenulum consisting of 2 bristles, male of 1 bristle. Tibiae dark brown, and usually cream ventrally, with white scales at distal end; middle tibia with 2 white bands, one near middle and one closer to proximal end of segment; with two black spurs at distal end, with white scales at distal end of each spur; hind tibia with white scales where proximal spurs are attached; proximal and distal spurs cream with the largest of the 2 proximal spurs with a narrow brown band near middle and sometimes brown at tip. Fore and mid femora dark brown with white band near distal end; hind femur white with black tip laterally. Tarsi white with dark brown scales dorsally at distal end of each tarsus. Coxae white with black-tipped scales at distal end.

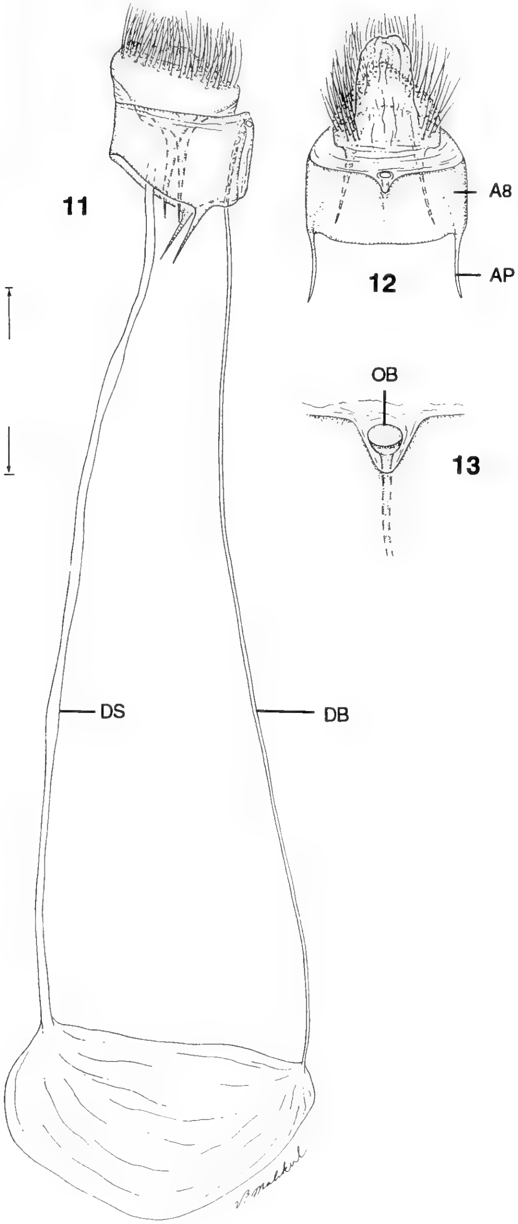
Abdomen: Silvery gray dorsally, mostly cream to white ventrally, with 6 slender, dark brown, oblique bands laterally across segments A2–7. Male with a moderately long pair of coremata (Fig. 8) ~ 1.25 × length of valva, and normally withdrawn completely within abdomen; sternum 7 (Fig. 7) a narrow, U-shaped sclerite.

Male genitalia (Figs. 5–6): Uncus absent. Tegumen a moderately broad, rounded, dorsal band. Vinculum a moderately broad, ventral band with a pair of small round lobes protruding from anterior margin. Gnathal arms separate, stout, and tapering distally. Valva separated nearly from base into three distinct lobes: a moderately short, slender, acute, costal lobe bearing a subapical row of ~ 10–12 short spines; an elongate, slender, more lateral, cucullar lobe that expands distally to form a setose clavate pad, and the largest, most ventral, valvular lobe that expands abruptly along costa near apex. Aedeagus sinuate, with phallobase inflated, globular, nearly as long as tubular portion of aedeagus.

Female genitalia (Figs. 11–13): Ovipositor shortened. Posterior apophyses moderately short, slightly longer than anterior pair. Eighth segment a moderately broad band with anterior apophyses directed slightly dorsad, short, slightly shorter than length of segment; sternum with a shallow cleft at sinus vaginalis. Ductus bursae extremely long and filamentous, only ~ 11 μm in diameter; caudal end abruptly flared at ostium bursae (Fig. 13); diameter of ostium ~ 27–30 μm; corpus bursae a moderately large, elliptical, membranous sac; signum absent. Ductus seminalis arising from opposite end of corpus bursae from ductus bursae and approximately twice the diameter of ductus bursae.

Egg (Fig. 14).—Elongate and flat against the epidermis of the host plant; average length 0.41 mm, width 0.28 mm (n = 30). Dorsal surface finely reticulated.

Larva.—Hypermetamorphic with three distinct forms. Sapfeeding (mining) larva (Fig. 38): a highly specialized form with a semitransparent-yellowish, depressed body adapted to mining beneath epidermis of host plants; maximum length, 4.4 mm. Spinning larva (Fig. 37): more generalized caterpillar form with red-banded, orange, cylindrical body in final phase; maximum length, 4.2 mm; body width, 1.0 mm; maximum head width, 0.4 mm. Between both forms exists a largely inactive, non-feeding transitional form which does not molt but remains within cuticle of last mining instar (DeGryse 1916; Vinal 1917; Fitzgerald and Simeone 1971; Fitzgerald 1973, 1975; Kumata 1978; Davis 1987, 1998; Wagner et



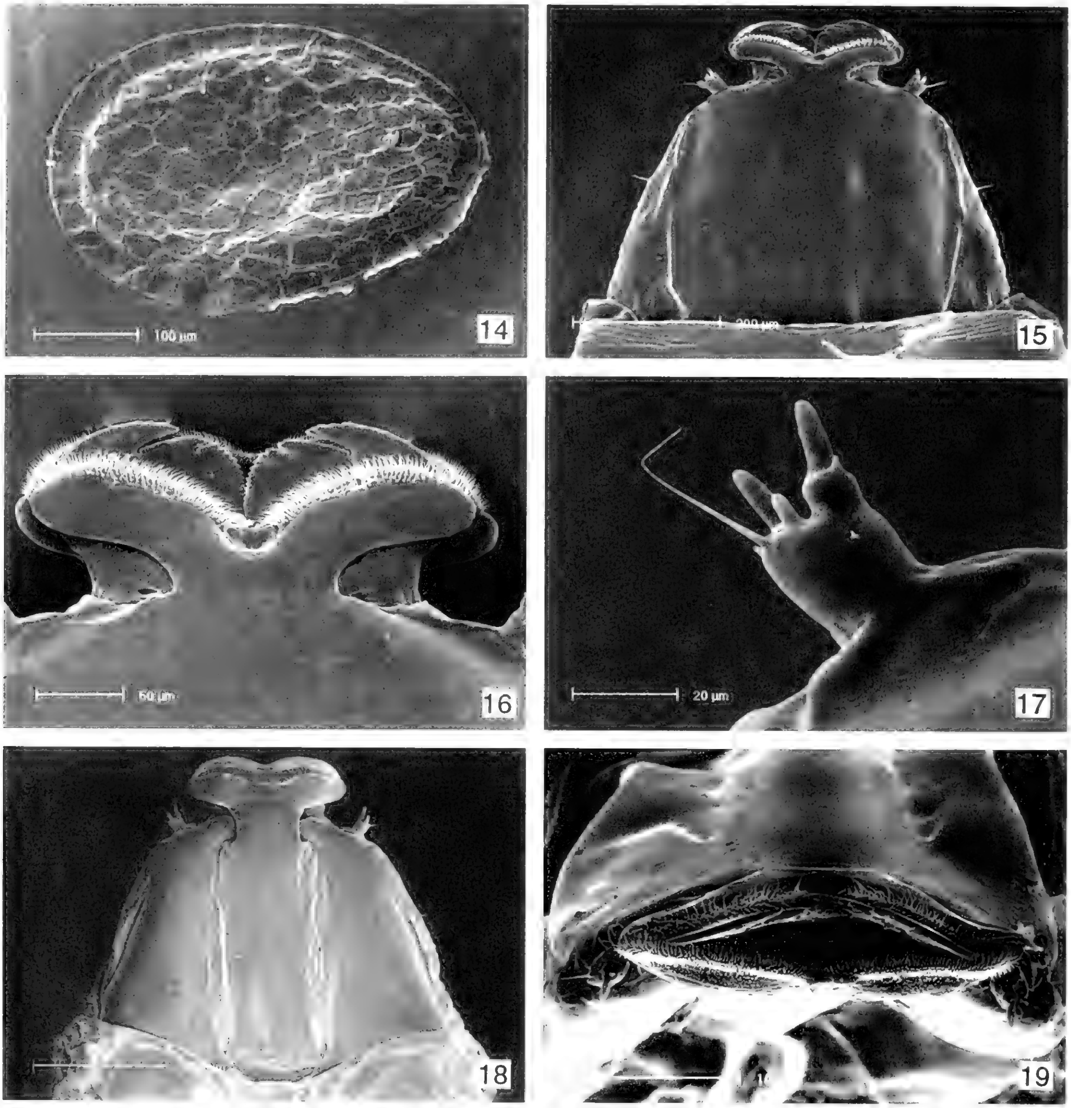
Figs. 11–13. *Marmara gulosa* from grapefruit, female genitalia. 11, Lateral view (0.5 mm). 12, Ventral view, segments 8, 9+10. 13, Enlarged view of sinus vaginalis and ostium bursae. (A8, eighth abdominal segment; AP, anterior apophysis; DB, ductus bursae; DS, ductus spermathecae; OB, ostium bursae. Scale length of Figs. 11–12 in parentheses.)

al. 2000). When succeeding final, spinning instar emerges, it proceeds to shed cuticles of both last spinning and transitional instars.

Sapfeeding larva.—*Head:* Greatly depressed and triangular (Figs. 15, 20). Most setae lost or reduced: dorsal cranium with 10 pairs of setae preserved, A1, A2, A3, L1, P1, P2, MD1, MD2 and MD3. Labrum strongly constricted at base then flaring to form two, broadly curved, lateral lobes; anterior and ventral margins with dense concentration of short epipharyngeal spines (Fig. 16). Mandible large, greatly flattened, with three apical cusps; innermost cusp broad with a serrated margin; outermost cusp with serrated outer and inner margins (Fig. 16). Labial lobe with anterior margin depressed at middle and densely covered with short hypopharyngeal spines (Figs. 18–19). Maxillary and labial palpi absent. Ventral cranium with only a single pair of setae (S2). Antenna two-segmented with a relatively stout sensillum basiconicum and two smaller sensilla on apex of much smaller distal segment (not always well-developed); basal segment with one elongate seta and three sensilla basiconica: a relatively stout one, a smaller one, and a minute one at edge of segment, and a small seta on the dorsal surface of segment (Fig. 17). Three black stemmata present, of irregular shape and size.

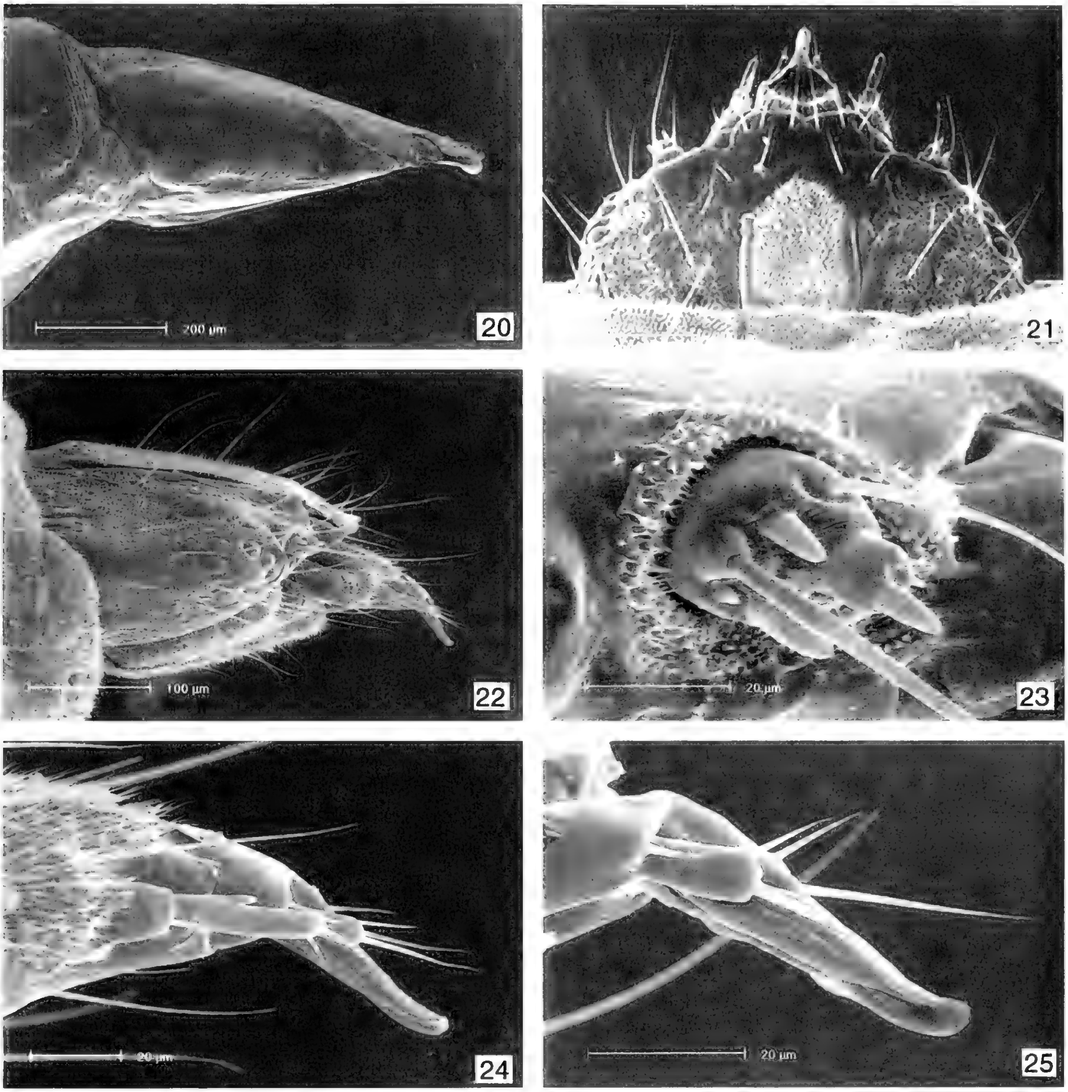
Body: Setae extremely reduced. Legs, prolegs and crochets absent. A1–9 banded near the dorsoanterior margin with small spines.

Spinning larva.—*Head:* More rounded than preceding, poorly sclerotized, with distinct, dense patches of minute spines, broadly angular in lateral view, and with full complement of mouthparts (Figs. 21–22). Chaetotaxy relatively complete (Figs. 33–35): three anterior setae (A1, A2, A3), three stemmatal setae (S1, S2, S3), three substemmatal setae (SS1, SS2, SS3), one lateral seta (L1), two posteriodorsal setae (P1, P2) and three dorsal setae (MD1, MD2, MD3) present; frontal and adfrontal



Figs. 14–19. *Marmara gulosa* from grapefruit, egg and sapfeeding larva. 14, Egg. 15, Head, dorsal view. 16, Labrum and mandibles, dorsal view. 17, Antenna, ventral view. 18, Head, ventral view. 19, Anterior view of mouthparts.

setae absent. Six stemmata arranged in a semicircle, with sixth usually greatly reduced, indistinct (Fig. 35). Antenna similar to mining larva but both setae of segment II considerably longer (Fig. 23). Labrum reduced, largely fused to cranium, and notched at center, with three pairs of setae (Figs. 21, 33). Mandible with five cusps, two distal and distinct, and three smaller; with two setae on lateral surface (Fig. 36). Maxillary palpus well-developed and composed of three distinct segments; proximal segment with three long setae (including dorsal seta of reduced mesal lobe); middle segment with seta at apex; distal segment elongate with two setae, plus one short and two very small setae at apex, and an elongate sensillum digitiformium mid-dorsally; mesal lobe (laciniogalea, in Grimes and Neunzig 1986) indistinct, with single stout,



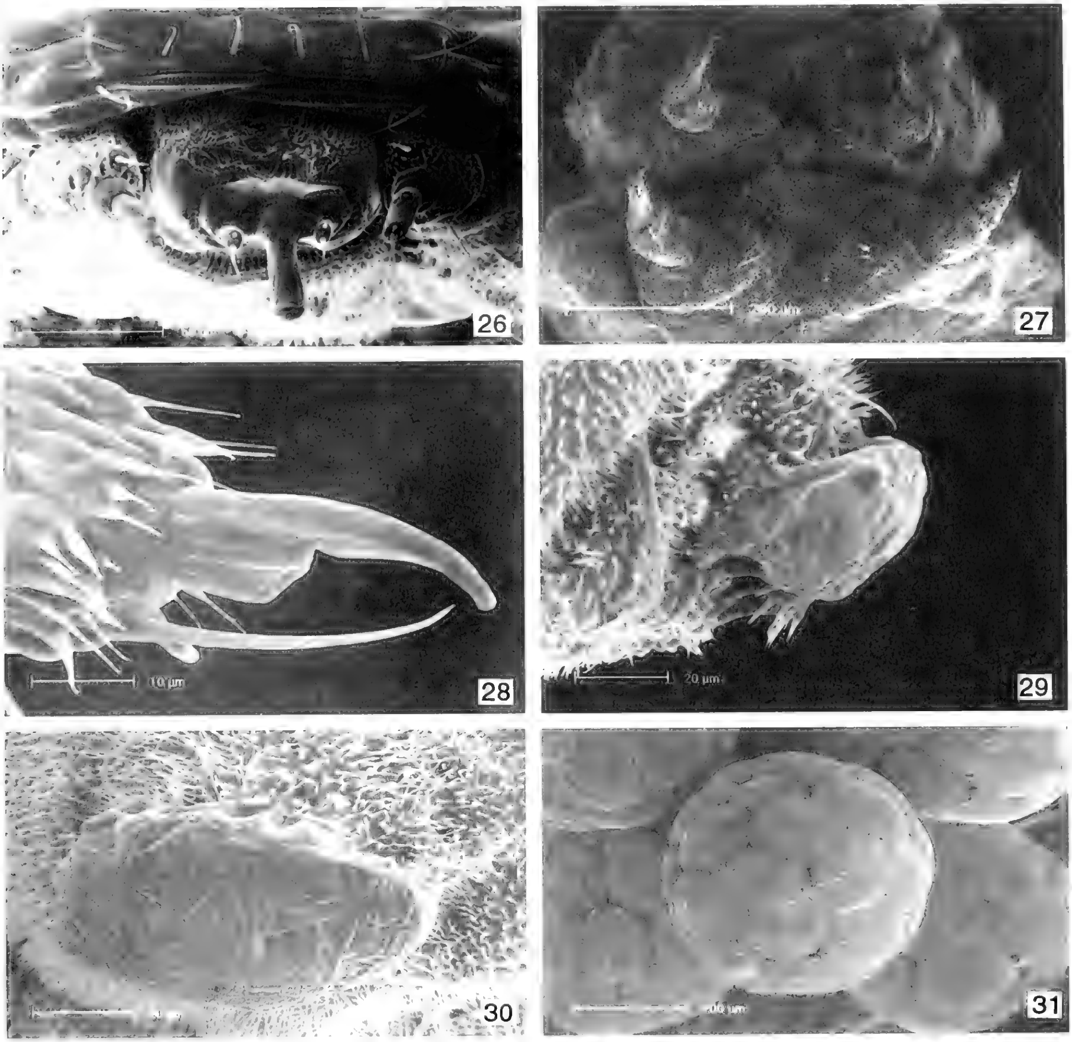
Figs. 20–25. *Marmara gulosa* from grapefruit larva. 20, Sapfeeding larva, lateral view of head. 21–25, Spinning larva, 21, Dorsal view of head. 22, Head, lateral view. 23, Antenna, lateral view. 24, Maxilla and labium, lateral view. 25, Labial palpi and spinneret, lateral view.

dorsal seta (Fig. 24). Labium with prominent spinneret; labial palpus moderately short, two-segmented, with two setae at apex of distal segment and a shorter seta at base (Figs. 25, 34).

Thorax: Setae more conspicuous than in sapfeeding larva. MD1 present on T2–3. D group bisetose on T1–3. XD1 present on T1; XD2 absent. SD bisetose on T1–3. L group bisetose on T1, unisetose on T2–3 (Fig. 32).

Abdomen: MD1 present on A1–9. D group bisetose on A1–9. SD and L group unisetose on A1–9. SV bisetose on A1–8, absent on A9. V group unisetose on A1–7, absent on A8–9 (Fig. 32). Rudimentary prolegs on A3–5 and 10 (Figs. 29, 30); ventral prolegs with anterior row of 4–7 crochets (Fig. 29). Anal plate with dorsal, lateral, subventral and ventral setae; anal prolegs devoid of crochets.

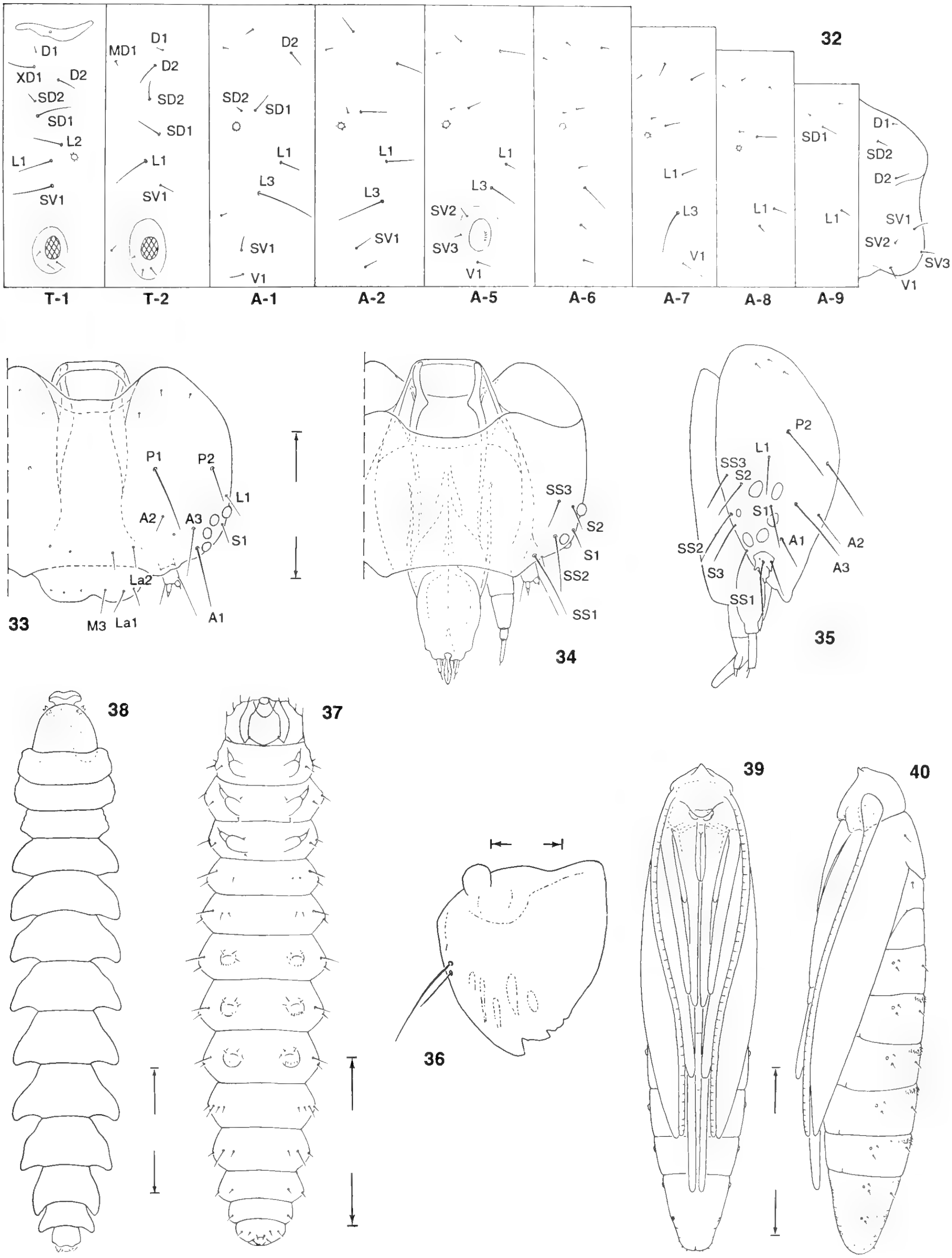
Pupa (Figs. 39–46).—Maximum length:



Figs. 26–31. *Marmara gulosa* from grapefruit, spinning larva and cocoon. 26, Labial palpi and spinneret. 27, Thorax, ventral view. 28, Pretarsus, lateral view. 29, Abdominal proleg, lateral view. 30, Abdominal proleg, ventral view. 31, Cocoon globules.

2.9 mm; width: 0.7 mm. Light brown in color. Vertex with broadly triangular, minutely serrated apical process (cocoon cutter) (Figs. 41–42) which appears ridge-like, viewed laterally. Setae absent from frontal area. Mandible visible as a small sclerite partially covered by the labrum (Fig. 41). Maxilla extend to A4. Sheath for antenna approximately same length or slightly longer than wings and usually extending to A7. Foreleg slightly shorter than maxilla. Midleg usually extends to A5. Hindleg usually reaching A9–10 (Fig. 39). Chaetotaxy as in Fig. 40; all setae extremely short. Spiracles well developed on A2–8. Anterior fifth of dorsum of A3–7 with dense concentration of small, stout spines mostly arranged into 4–5 scattered rows (Figs. 40, 43); tergal spines more reduced and scattered over A8–9. A10 with three pairs of similar, short, stout, cremasteral spines; one pair dorsally and two pairs laterally (Figs. 44–46).

Cocoon.—Consists of a firm sheet of white silk over some crevice in bark or on



Figs. 32–40. *Marmara gulosa* from grapefruit, morphology of larva and pupa. 32, Spinning larva, chaetotaxy of pro- and mesothorax, abdominal segments 1, 2, 5, 6–10. 33, Head, dorsal view (0.2 mm). 34, Head, ventral view. 35, Head, lateral view. 36, Mandible (0.2 mm). 37, Spinning larva, ventral view (1 mm). 38, Sapfeeding larva, ventral view (1 mm). 39, Pupa, ventral view (1 mm). 40, Lateral view. (Scale length in parentheses.)

ground among leaf litter; ornamented externally by 20–40 minute, frothy, compartmentalized balls approximately 1 mm in diameter; a sinuate row of minute spines meandering over surface of ball (Fig. 31).

Holotype.—♂; UNITED STATES: California: Riverside Co:, Oasis Ranch, 14 km S of Coachella, 26 Aug 1998, M. Guillén, ex *Citrus paradisi.* (USNM).

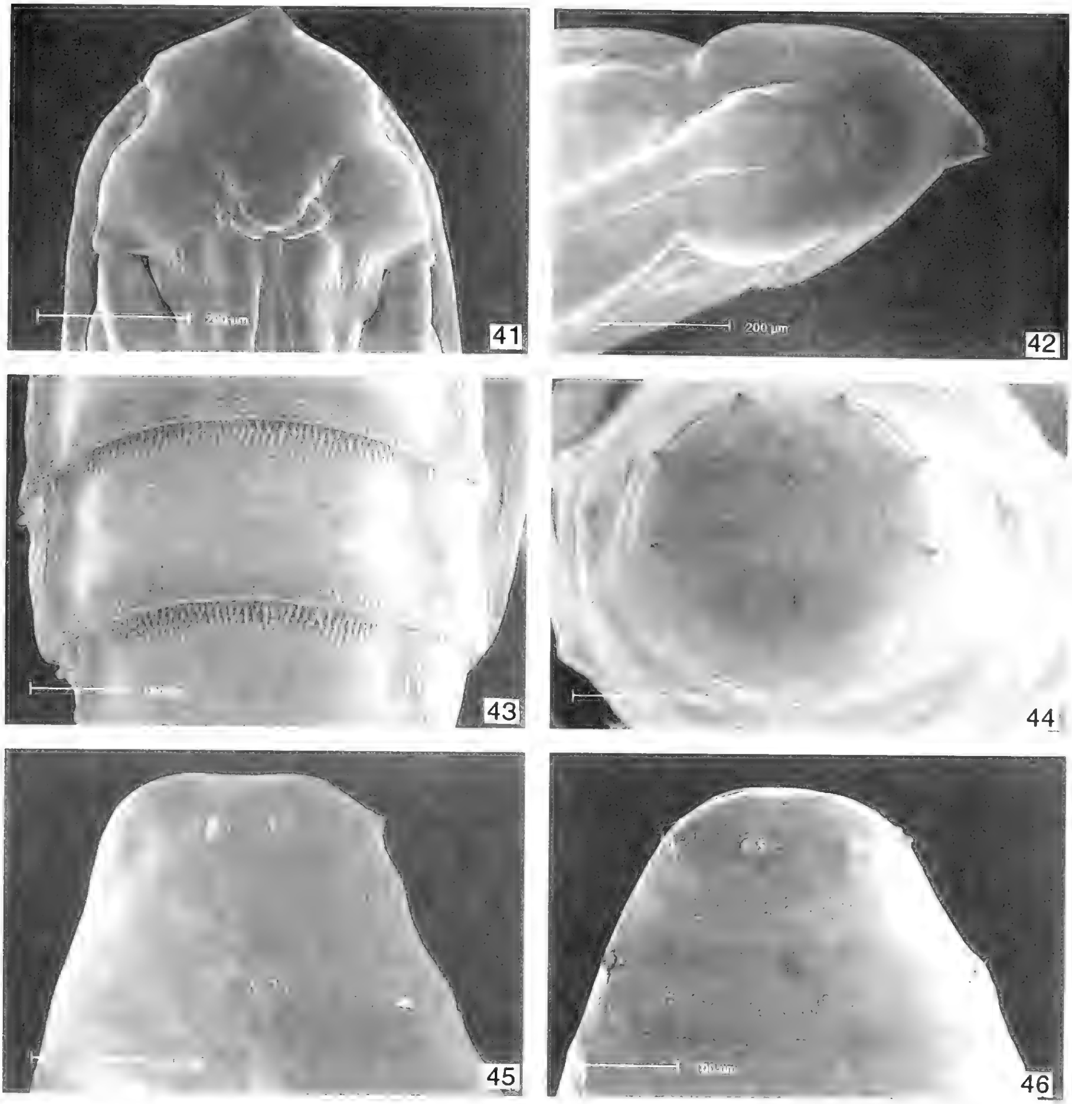
Paratypes.—UNITED STATES: California: Contra Costa Co: Antioch: 15 Mar 1985, em. 17 Apr–2 May 1985, D. L. Wagner, DLW 85C17, ex *Salix lasiolepis,* slides DRD 4085, USNM 32196 (1 ♂, 4 ♀, DLW, USNM). Riverside Co: Coachella Valley: Shogun Ranch, 16 km S of Coachella: 18 Jul 1997, ex *Citrus paradisi,* M. Guillén (1 ♂, 1 ♀, UCR); 29 Apr 1996, ex *Nerium oleander,* M. Guillén (2 ♂, UCR); 18 Jul 1996, ex *Nerium oleander,* M. Guillén (1 ♂, USNM); 25 Jul 1996, ex *Nerium oleander,* M. Guillén (8 larvae, 1 pupa, UCR); 8 Jul 1996, ex *Nerium oleander,* M. Guillén (1 pupa, UCR); 25 Aug 1998, ex *Citrus paradisi,* M. Guillén (3 larvae UCR). Coachella Valley: Tierra del Mar Ranch, 1 km N of Oasis: 29 Apr 1997, ex *Citrus paradisi,* M. Guillén (1 ♂, 3 ♀, UCR); 11 Sep 1996, ex *Citrus paradisi,* M. Guillén (6 pupae, UCR). Coachella Valley: Oasis Ranch, 14 km S of Coachella: 26 Jul 1998, ex *Citrus paradisi,* M. Guillén (2 ♀, USNM); 9 Sep 1998, ex *Citrus paradisi,* M. Guillén (1 ♂, 1 ♀, UCR, 2 ♂, USNM). Coachella Valley: Thermal Plaza Ranch, 10 km S of Coachella: 20 Aug 1996, ex *Citrus paradisi,* M. Guillén (3 larvae, UCR); Dec 1997, M. Guillén, ex *Citrus paradisi,* slide 32194 (5 larvae, USNM). Coachella Valley: 5 km E of Mecca: 10 Apr 1997, ex *Nerium oleander,* M. Guillén (1 ♂, UCR); 8 May 1997, ex *Nerium oleander,* M. Guillén (1 ♀, USNM); 29 Apr 1996, ex *Nerium oleander,* M. Guillén (1 ♂, USNM). Indio: Oct–Nov, 1960, L. Atkins, ex *Citrus paradisi,* slides USNM 32191, 32192, (1 ♂, 1 ♀, USNM); 14 Mar 1971, L. Atkins, ex *Citrus paradisi,* (1 ♀, USNM). Orange Co: Irvine:, 18 Oct 1997, ex *Persea americana,* J. Barcinas (1 ♂, USNM). Arizona: Yuma Co.: Yuma: Yuma Valley Agricultural Center: 19 Aug 1997, ex *Gossypium hirsutum,* D. Kerns (2 ♂, UCR; 2 ♀, USNM).

Distribution.—Southwestern United States (as far north as Contra Costa Co. and Bakersfield, Kern Co., California, and east to Maricopa Co. and Yuma Co. in Arizona); reported also from Texas, Florida (Browning, M. Manners, in litt.) and Cuba (Chong and La Rosa 1986). Records from Bakersfield represent field observations of mine damage on citrus and on citrus and cotton in Maricopa Co.

Etymology.—The specific name is derived from the Latin *gulosus* (gluttonous, greedy) in reference to the broad host range of this species.

Diagnosis.—Morphologically and biologically *Marmara gulosa* appears most allied to *M. salictella,* which supports our current belief that the eastern and western willow miners are probable sister species. The basic forewing pattern of *M. gulosa* (Fig. 3)—dark gray to fuscous with 1–2 basal fascia, 2–3 costal and 1–2 dorsal strigulae—is generally similar to that of several North American species. Four species, *M. fraxinixola* Braun, *M. corticola* Fitzgerald, *M. elotella* Ely and *M. fulgidella* (Clem.) have dominantly pale wings with the black background reduced by the much broader pale striae, allowing them to be readily separated from *M. gulosa.* The white markings on the forewing of *M. gulosa* are generally smaller or more narrow than in *salictella* (Fig. 4). In particular, the second fascia traversing the middle of the wing is often constricted or interrupted medially in *M. gulosa,* compared to the broader, normally intact condition in *M. salictella.*

Male genital morphology of *M. gulosa* is also similar to that of most North American species in possessing a deeply divided, trilobed valva (Fig. 5). Within this group the smaller, costal lobe of the valva bears a row of stout spines; the mediolateral cucullar lobe is slender and spatulate; and the ven-



Figs. 41–46. *Marmara gulosa* from grapefruit, pupa. 41, Head, ventral view. 42, Head, lateral view. 43, Dorsal view of A4. 44, Caudal view of A10. 45, Lateral view of A9–10. 46, Dorsal view of A9–10.

tral, valvular lobe is the broadest and most diagnostic in form. The valvae of *M. gulosa* differ from that of *M. salictella* (Fig. 9) in possessing a more reduced apex of the cucullar lobe, and from virtually all other *Marmara* by the expanded subapical costal margin of the valvular lobe (Fig. 5).

The female genitalia of *M. gulosa* and *salictella* are similar in possessing a shallow median cleft in the caudal margin of sternum 8 as well by the greatly reduced, abruptly flared ostium bursae (Figs. 12–13). The sternal cleft in *salictella* is approximately twice that of *gulosa*. *Marmara pomonella* Bsk., currently represented only by the female holotype from Oregon but also reported from California (Essig 1926), superficially resembles *gulosa* in wing pattern. The female genitalia of *M. pomonella* differ in sternum 8 being deeply excavated, with the ostium bursae heavily sclerotized and more than 3× the diameter of that of *gulosa*.

Table 1. Genetic differences between populations of *Marmara gulosa* on oleander (OL; n = 2), grapefruit (GR; n = 2) and an undescribed species on tree tobacco (TT; n = 1) based on pairwise comparisons of ITS2 (513–557 shared bp) and 28S-D2 rDNA (602–608 shared bp) sequences. Multiple clones sequenced for *M. gulosa* are included in the total number of sequences (t) compared below.

		ITS2		28S-D2	
	t	Bases Differing	Percent Difference	Bases Differing	Percent Difference
within OL/GR	6	0–2	0–0.4	0–2	0–0.3
between OL/GR	6	0–2	0–0.4	0–2	0–0.3
between OL-GR/TT	7	46–47	9.0–9.2	41–42	6.8–7.0

Few larval characters were useful for distinguishing known species. The mandibles in the last sapfeeding instar of *M. gulosa* have three cusps dorsally. The innermost cusp has a series of minute serrations along the outer margin, and the lateral cusp is minutely serrated along both the outer and inner margins (Fig. 16). The inner cusp is serrated in *M. arbutisella,* but the lateral cusp is smooth. The mandibles of the last sapfeeding instars of *M. fraxinicola* and *M. basidendroca* are entirely smooth. In both *M. gulosa* and *arbutisella* the epipharyngeal spines extend across the entire anterior margin of the labrum (Fig. 16); these spines are present only along the basal half of the anterior margin of each labral lobe in *M. fraxinicola* and *M. basidendroca* (Fitzgerald 1973). The labrum in the spinning larvae of *M. gulosa* and *arbutisella* has a median notch, which is reportedly lacking in *M. elotella* (Vinal 1917). Prolegs are also reputedly absent in *elotella*, but this needs further confirmation.

Pupal descriptions are available for only two other species in this genus. *Marmara gulosa* has a single pair of dorsal abdominal setae (D1) and two pairs of shorter setae (SD1,2) located near the spiracles, in segments one through eight (Fig. 40). *Marmara fraxinicola* supposedly lacks SD1 and 2, and *M. elotella* has retained only SD1 and 2.

GENETIC DIFFERENCES

Because of the extreme differences in host plant choice within *M. gulosa,* an additonal test of population structure was made by comparing sequences of two nuclear genes demonstrated to exhibit differences at the species level: the non-coding interspacer region (ITS2; Forward primer: 5′ TCT AAg Cgg Tgg ATC ACT Cg 3′, Reverse primer: 5′ TAT gCT TAA ATT CAg ggg gT 3′ [reverse primer from Campbell et al. 1993]) and the D2 variable transcript region of 28S rDNA (primers from Campbell et al. [2000]). Extraction and sequencing protocols are outlined in Babcock and Heraty (2000). Sequences were obtained from fresh frozen adults reared from oleander (2 individuals: Shogun Ranch, 10 km S of Coachella, 9 Oct 1997 and 23 Oct 1997), grapefruit (2 individuals: Tierra del Mar Ranch, 1 km N of Oasis, 9 Oct 1997 and Laboratory Colony, Oct 1997 [adults collected from various localities in the Coachella Valley]), and tree tobacco (1 individual: Riverside, 9 Sep 1996). Specimens from willow were not available. Multiple clones were sequenced for some of the individuals for a total of six clones for each of the oleander and grapefruit samples. Sequences are deposited in GENBANK under accession numbers AF280424–AF280430 (285) and AF284564–AF284570 (ITS2).

Few differences were found for either gene between *M. gulosa* reared from grapefruit or oleander (0–0.4%). By contrast, *M. gulosa* and the easily recognized different species from tree tobacco (6.8–9.2%) differed considerably (Table 1). Some variation was observed within the populations, but this was not consistent nor enough to

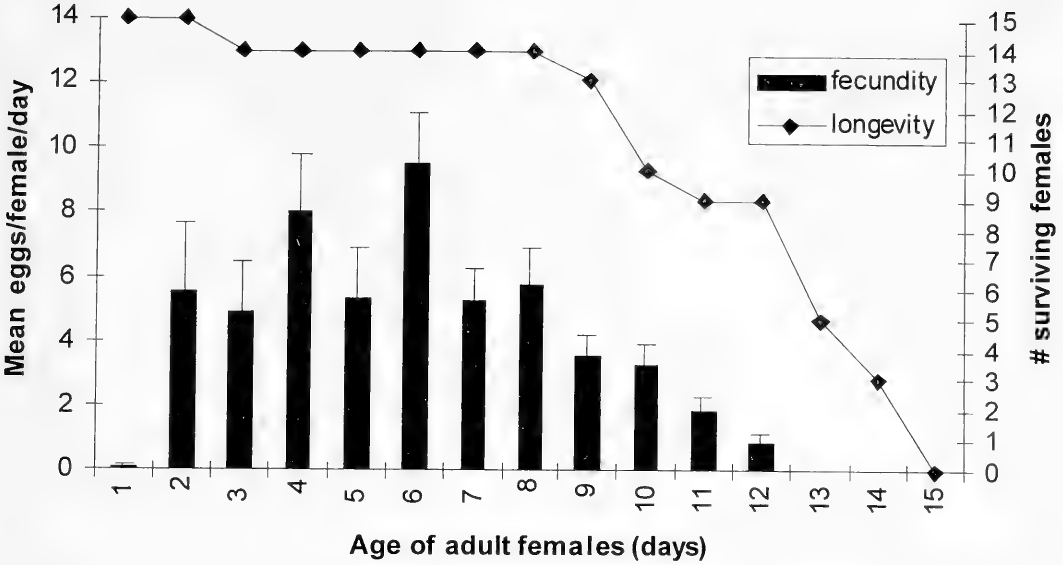


Fig. 47. Age-specific fecundity and survival of *Marmara gulosa* females from grapefruit.

suggest any divergence between populations at this level of analysis.

BIOLOGY

Rearing methods.—Grapefruits with live peelminer larvae were collected in the Coachella Valley, and adults emerged in the laboratory. A colony was started and maintained on grapefruit at room temperature and under natural light. Field-collected fruits were placed in small clear-plastic containers (49.5 × 20.3 × 22.2 cm), and the bottom of each cage was covered with paper towel as a pupation site. Cocoons were cut from the paper towel and placed in small glass vials (15 × 45 mm) closed with a piece of cotton and then placed in a humidified 750 ml clear-plastic container. Relative humidity was maintained at 75% by use of a saturated NaCl solution (Winston and Bates 1960). Newly-emerged adults were released daily into a cage (74 × 46 × 46 cm with wooden walls, the floor and top covered with glass, and the back wall with fine fabric mesh) with grapefruits for oviposition. Food was provided via cotton wool dipped into a 35 ml plastic vial of 10% sucrose solution.

Biological studies.—Studies were carried out in constant temperature cabinets (Percival Scientific Inc., IA) at 26 ± 0.5°C, 75 ± 10% RH and a 14:10 photoperiod. Virgin females and males were paired in individual cages with Rio Red grapefruits. The number of eggs/female/day and longevity of adults were measured. Egg incubation time, larval development, and duration of pupal stage were recorded. The number and duration of each larval instar was recorded by marking the position of the larvae every day and identifying molting periods by larval inactivity.

Eggs were deposited singly on the surface of the fruit. Total fecundity per female was 48.5 ± 7.2 (n = 15) with an average of 4.5 ± 0.8 eggs laid per female per day. Oviposition started 2.9 ± 0.1 days after release of adults in the cages and lasted an average of 7.8 ± 0.7 days with a decline observed after day eight. Little female mortality was observed until day nine (Fig. 47). Adult females survived an average of 10.9 ± 0.8 days (n = 15) and males lived an average of 9.3 ± 1.4 days (n = 14). Eggs hatched after 4.2 ± 0.1 days. Larvae left the eggs by boring directly through the lower surface of the egg into the epidermis of the fruit. Larvae fed in the epidermis, form-

Table 2. Duration of development (days) of *Marmara gulosa* on grapefruit at 26 ± 0.5°C.

Stage	x ± SE (n)	
Egg	4.2 ± 0.1 (42)	
Feeding larva		
	Four feeding instars	Five feeding instars
1st instar	3.5 ± 0.1 (16)	4.2 ± 0.4 (5)
2nd instar	2.9 ± 0.1 (16)	2.2 ± 0.2 (5)
3rd instar	2.6 ± 0.2 (16)	2.8 ± 0.2 (5)
4th instar	3.1 ± 0.2 (16)	3.4 ± 0.2 (5)
5th instar		2.0 ± 0.3 (5)
Pseudopupa + spinning larva	1.0 ± 0.0 (21)	
Pupa	10.6 ± 0.1 (21)	
Total life cycle	28.8 ± 0.4 (21)	

ing long, serpentine mines which often intersected (Fig. 1). The number of sapfeeding instars was variable with most larvae developing through four and a few through five (Table 2), and with males and females present in both groups. After feeding, the final sapfeeding instar became quiescent as the penultimate, nonfeeding transitional instar formed without shedding the cuticle of the former. Appearance of the final, nonfeeding spinning instar thus resulted in shedding of both the last sapfeeding cuticle and that of the transitional instar. The last instar spinning larva then exited the mine, lowered itself from the fruit by a silken thread, and pupated in a slender cocoon in the paper towel provided. The outside of the cocoon was ornamented with small, white, frothy balls. These balls were first discharged from the anus of the spinning larva. Using its mouthparts and legs, the larva then placed the balls on the outside of the cocoon through previously cut slits (as described by Wagner et al. 2000). The slits were then covered with additional silk, and the larva changed to the prepupal stage. The whole larval period lasted 14.1 ± 0.4 days. Adults emerged 10.6 ± 0.1 days after pupation. The entire life cycle required 28.8 ± 0.4 days (Table 2).

The general life cycle is probably the same on oleander, cotton and avocado, as it is in grapefruit, although developmental times will probably be affected by the host plant. Additionally, mines on stems of oleander have been observed to be more linear than those on grapefruit (Fig. 2). Another gracillariid, the citrus leafminer, *Phyllocnistis citrella* (Gracillariidae), mines leaves of *Citrus* spp., although it will occasionally mine the fruit epidermis (Heppner 1995). *Marmara gulosa* will also occasionally mine shoots of citrus (Atkins 1971, Gibson et al. 1997). The citrus leafminer occurs on citrus in most regions of the world (Heppner 1993, 1995; Garrido 1995), including California. The main difference between mines by *M. gulosa* and *P. citrella* is in the deposition of frass, with that of *P. citrella* forming a slender, brownish black trail down the middle of the mine; a distinct frass trail is not present in *M. gulosa*. Both species form a serpentine mine, but that of *M. gulosa* consists of a wandering, more convoluted gallery that often intersects (Fig. 1). The mine of *P. citrella* tends to be more compact and does not intersect.

Discussion.—*Marmara gulosa* may be one of the most polyphagous species of Gracillariidae. Most species of Gracillariidae are either monophagous or oligophagous, usually restricting their feeding to a single plant family. More general feeders include two species of the southeastern Asian genus *Conopomorpha,* which mine as many as five plant genera belonging to three families in as many orders (Bradley 1986). As has been observed with other introduced insects, a few Gracillariidae have expanded their host range following introduction. A few years after its intial discovery in New Zealand in 1950, the European oak leaf moth, *Phyllonorycter messaniella* (Zeller), mined 12 plant genera of six families and four orders within two subclasses (Wise 1953, Common 1976). In Europe this species occurs on Fagaceae (*Quercus, Fagus*) and less commonly on Betulaceae (*Betula, Carpinus*) and Rosaceae (*Malus, Prunus*) (Watkinson 1985). An even greater degree of increased polyphagy was documented for the tortricid *Platynota stultana* (Walsingham) when it expanded both its geographical and ecological range from Mexico northward into California (Atkins et al. 1957, Powell 1983). *Marmara gulosa* is apparently native, because it is morphologically similar to other indigenous *Marmara* and feeds on native *Salix.*

Within *Marmara,* species are usually host plant specific or even specific to a particular structure on the same host plant (Fitzgerald 1973, Davis and Feller, unpublished). Of those species occurring in North America, each species feeds on a single host species, or if present on more than one, the plants at least belong to the same genus or family. Additionally, when a *Marmara* species occurs on more than one species of host plant, usually the same structure of the plant is attacked (Table 3). *Marmara gulosa* is unusual in being broadly polyphagous, with verified rearing records from five families in four of the six recognized subclasses of dicotyledonous plants (Heywood 1993) (Table 4), including *Citrus* (grapefruit, etc.), *Gossypium* (cotton), *Nerium* (oleander), *Persea* (avocado), and *Salix* (willow). Moreover, larvae of this species have been observed to mine different structures of their hosts; e.g., fruit peel and shoots of citrus, shoots and leaves of oleander, stems of cotton, fruits and shoots of avocado, and shoots of willow. Notably, except for *Salix lasiolepis,* none of these species is native to California. *Persea americana* and *G. hirsutum* are probably neotropical in origin; *Nerium oleander* is from the Mediterranean region, and *Citrus* is native to subtropical Asia (Bailey 1957).

A cultural practice for control of the citrus peelminer has been the removal of oleander plants near citrus groves (Reeves 1995). The fact that miners on citrus and oleander are the same species would support this method. However, it now appears that native species of *Salix* are the original source of secondary infestations of *Marmara* on citrus and oleander as well as on cotton and avocado. Also, not all citrus groves with oleander in proximity have had important citrus peelminer infestations and some of the infested citrus groves do not have oleander nearby. More studies are necessary to better understand the movement of the moth from *Salix* to other secondary plant hosts.

In Arizona, the citrus peelminer mines stems of cotton during the summer, presumably without causing important damage to the plants (D. Kerns, personal communication). Cotton is harvested in these areas in September when increasing populations of peelminer on citrus have been reported (Gibson et al. 1997). The deterioration in quality of cotton as it senesces may lead to a shift by emerging adults to citrus. This may also be the case with oleander, on which larvae mine only fresh new shoots. A shift to citrus may correlate with the absence of fresh growth in the early summer.

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Table 3. Host and tissue specificity of *Marmara* species.

Marmara Species	Host Plant	Family	Part Mined	References
		Three species share one host species		
M. basidendroca Fitzgerald	*Fraxinus pennsylvanica* Marsh.	Oleaceae	Stem: base of tree, root collar	Fitzgerald 1971
M. corticola Fitzgerald	*Fraxinus pennsylvanica* Marsh.	Oleaceae	Stem: branches (periderm and cortex)	Fitzgerald 1971
M. fraxinicola Fitzgerald	*Fraxinus pennsylvanica* Marsh.	Oleaceae	Stem: branches (periderm)	Fitzgerald 1971
		Species reported from a single plant genus/species		
M. elotella Busck	*Malus* sp.	Rosaceae	Twigs	Vinal 1917
M. fasciella Chambers	*Pinus strobus* Ehrh.	Pinaceae	Stems	DeGryse 1943
M. isortha Meyrick	*Theobroma cacao* L.	Sterculaceae	Pods	Bondar 1939, Meyrick 1915
M. opuntiella Busck	*Opuntia* sp.	Cactaceae	Leaves	Busck 1906, Forbes 1923
M. pomonella Busck	*Malus* sp.	Rosaceae	Fruit	Clemens 1860
M. salictella Clemens	*Salix vitellina* L.	Salicaceae	Bark	Clemens 1863
M. serotinella Busck	*Prunus serotina* L.	Amygdalaceae	Stems	Forbes 1923
		Species reported from two plant genera within same family		
M. arbutiella Busck	*Arbutus* sp.	Ericaceae	Leaves	Vinal 1917
	Arbutus menziesii Pursh.	Ericaceae	Leaves	Wagner et al. 2000
	Arctostaphylos andersonii Gray	Ericaceae	Leaves	Wagner et al. 2000
M. auratella Braun	*Rudbeckia lacinata* L.	Asteraceae	Stems	Forbes 1923
	Dahlia sp.	Asteraceae	Stems	Forbes 1923
M. fulgidella Clemens	*Quercus* sp.	Fagaceae	Twigs	Clemens 1860
	Castanea sp.	Fagaceae	Twigs	Clemens 1860
M. smilacisella Chambers	*Smilax glabra* Roxb.	Liliaceae	Leaves	Chambers 1875
	Smilax hispida Muhl. ex Torr.	Liliaceae	Leaves	Braun 1923
M. oregonensis Fitzgerald	*Pseudotsuga menziesii* (Mirb.) Franco	Pinaceae	Bark	Fitzgerald 1975
	Abies grandis (Dougl. ex D. Don) Lindl.	Pinaceae	Bark	Fitzgerald 1975

Table 4. Classification of Plant Hosts of *Marmara gulosa.*

Subclass	Order	Family	Genus
Magnolidae	Laurales	Lauraceae	*Persea*
Dilleniidae	Malvales	Malvaceae	*Gossypium*
Dilleniidae	Salicales	Salicaceae	*Salix*
Rosidae	Sapindales	Rutaceae	*Citrus*
Asteridae	Gentianales	Apocynaceae	*Nerium*

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SUBMERGED *STILOBEZZIA RABELLOI* LANE (DIPTERA: CERATOPOGONIDAE) PUPAE OBTAIN OXYGEN FROM THE AQUATIC FERN *SALVINIA MINIMA* BAKER

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Abstract.—Pupae of the predaceous midge *Stilobezzia rabelloi* Lane have sharply pointed, anteriorly directed respiratory organs which they insert into the underside of floating leaves or into the dangling submerged leaves of *Salvinia minima* Baker. They also have extremely elongate body setae and apicolateral processes which help them to insert their respiratory organs and to remain immobile amongst the highly branched submerged leaves once they have pierced the plant tissue. These features are shared by the African *Stilobezzia poikiloptera* (Ingram and Macfie) and are synapomorphic character states. Sharply pointed respiratory organs and elongate apicolateral processes are known in more distantly related Ceratopogonidae and these represent instances of homoplasy.

Resumen.—Las pupas de *Stilobezzia rabelloi* Lane presentan órganos respiratorios puntiagudos dirigidos hacia adelante, los que insertan en la faz inferior de las hojas flotantes o dentro de la hojas sumergidas de *Salvinia minima* Baker. También presentan setas corporales extremadamente elongadas y procesos apicolaterales, los que ayudan a insertar los órganos respiratorios, así como a permanecer inmóviles entre las hojas sumergidas una vez que han perforado el tejido vegetal. Estas características son compartidas por la especie africana *Stilobezzia poikiloptera* (Ingram & Macfie), y son estados sinapomórficos del caráácter. Tanto órganos respiratorios puntiagudos como procesos apicolaterales elongados son conocidos para Ceratopogonidae más lejanamente emparentados, y estos representan instancias de homoplasia.

Key Words: biting midges, immatures, behavior, phylogeny, morphology, Costa Rica, Neotropical, *Dasyhelea*

While collecting Ceratopogonidae in Costa Rica in 1993, the senior author was puzzled to discover adults of a species of *Stilobezzia* Kieffer emerging from samples of a floating fern (*Salvinia minima* Baker) even though these had been previously checked for free floating pupae on a repeated basis. Thinking that the pupae remained submerged for most of their development, as do those of a few species of *Dasyhelea* Kieffer and *Culicoides* Latreille (Dyce and Murray 1966, Lee and Chan 1985), samples of *Salvinia minima* were more carefully examined and it was discovered that the pupae had their respiratory organs firmly embedded in the underside of the floating leaves or in totally submerged leaves (which look like dangling roots). This paper is the first report of the immatures of a ceratopogonid species using an aquatic plant as a source of air and describes the pupa of this species, including the modifications which are likely associated with this adaptation.

MATERIALS AND METHODS

The samples of *Salvinia minima* Baker were collected at Carara Biological Preserve (about 5 km NE of Tarcoles) in Costa Rica during July 1993. This park includes several trails and the floating ferns were sampled at the lagoon approximately 1.5 kilometers from the entrance of the north trail. The lagoon is closely associated with, and is occasionally flooded by, the Tarcoles River. Samples of *S. minima* were transported to the laboratory, placed in small buckets and covered with fine mesh. Each container was checked daily (generally in the morning) for adults. Specimens were preserved in 70% ethanol and later mounted on microscope slides using the method described by Borkent and Bissett (1990).

Members of *Salvinia* Séguier have three leaves, two of which float, while the third is completely submerged, hangs down into the water and is highly branched, very much like dangling roots (Tryon and Tryon 1982). We refer to these herein as floating and submerged leaves, respectively. The submerged leaf sometimes bears sori (for the developing sporangia), which look like small balls supported on a separate axis amongst the branches of the submerged leaf.

Specimens were examined, measured and drawn using a Wild M3 dissecting microscope and a Zeiss Jenaval compound microscope. Two pupae were coated with gold and studied at 5 kV and 20 kV with a scanning electron microscope (a JEOL 6301 FXV). Terms for structures follow those used in the Manual of Nearctic Diptera (McAlpine, et al. 1981) and Lawson (1951).

RESULTS

Fourteen adult *Stilobezzia rabelloi* Lane were reared from samples of *S. minima* during July 1993. All of the adults emerged from samples in which no pupae were floating at the water surface the previous day. Examination of *S. minima* under the dissecting scope revealed seven pupae which had one (most common) or both of their respiratory organs firmly imbedded in the underside of the floating leaves, in the bases of the submerged leaves or in the submerged sori. When in this position, the pupae were completed motionless. Removal of a pupa from its position resulted in it becoming agitated, curving its abdomen and using the long abdominal setae and apicolateral processes to move its body until it found a location where it could push one or more of its respiratory organs into the plant's tissues by straightening its bent abdomen. Clearly, the very long abdominal setae and apicolateral processes of this species help to anchor the pupa when pushing its respiratory organs into the plant. The pupae often took 10–15 minutes to reembed their respiratory organs after being artificially separated from the plants (when in a petri dish with a small mat of the fern). The removal of the pupa from a leaf was done repeatedly with four individuals and the results were identical each time. The respiratory organs were often embedded to about ½ their total length, which was the maximum they could penetrate before the head of the pupa was restrained by the trichomes on the leaves. Other pupae had just the tips of the respiratory organs embedded. One pupa was separated from its attachment to a fern and left overnight without any plants. It floated at the surface with most of the upper surface of the swollen basal portion of the respiratory organ emergent (this surface appearing hydrophobic and probably taking in air through the basal pores) but with the apical portion of the respiratory organ remaining under water. Afterwards, when placed in a fern mat, this pupa embedded its respiratory organ once again. Just before emergence, the pupae released their attachment to the plants and floated to the surface of the water and all adults emerged during the night.

There are structural modifications of the pupa which are related to their ability to use air from submerged leaves and the pupa is therefore described below.

Pupa.—Length 2.9 mm (not including apicolateral processes). General coloration uniformly medium brown, with apical portion of segment 7, all of segments 8, 9 slightly darker. Body surface smooth except for fine spicules on anterior margin of abdominal sternites 3–9 with well developed abdominal tubercles. Operculum (Fig. 1A) with well-developed anteromarginal seta located on tubercle, with pore at tubercle base. One slender anterodorsal seta, with additional basal pore (Figs. 1C, 3A). Two elongate dorsomedial setae of more or less equal size on short tubercle (Figs. 1D, 3A). Two long, basally thick dorsolateral setae, with additional short sensilla near their bases (Figs. 1F, 3A). Five dorsal sensilla, i, ii, iv elongate, slender setae, i on very short tubercle, v, vi pores; iii absent (Figs. 1E, 3A). Ventromedian setae elongate, slender (Fig. 1B). Two ventrolateral setae elongate, thick basally (Fig. 1B). Thorax with medial crest (in which adult scutal spine develops) extending from between respiratory organs to level of dorsal setae; with short protuberance posterior to base of respiratory organ (against which posterior base of respiratory organ abuts) (Fig. 3A). Respiratory organs (Figs. 1G, 2D, 3A–E) directed anteriorly, parallel to one another; bases closely approximated, separated by swollen medial ridge; each with swollen base, narrowing gradually to pointed apex, with groove extending from most apical of basal pores to lateral margin at apex; with basal row of about five dorsal pores, apical half with medially-facing row of about 15 pores; tracheal tube thick at base of respiratory organ, dividing in basal portion to each pore. Metathorax completely divided medially, with medial protuberance from scutum protruding to posterior margin of metathorax. Abdomen with setae elongate, thick basally, separate from one another (none on common tubercle), each born on a well-developed, bifurcate, elongate spicule. Segment 4 sensilla pattern (Fig. 2A) with 2 d.a.s.m., 5 d.p.m., 1 l.a.s.m., 3 l.p.m., 3 v.p.m.; d.a.s.m. ii, d.p.m. ii, iii, pores; all others with elongate setae, d.p.m. i, iv, v, vn ii, iii bifurcating with plumose apices, l.a.s.m., l.p.m. i, ii, iii simple with plumose apices, vn i simple, with plumose apex or bifurcating with plumose apices. Anal segment (segment 9) (Fig. 2B) with apicolateral process directed posteriorly to posterolaterally, very elongate, slender, with fine spicules along length; base of apicolateral process with both dorsal, ventral thick spine, with small patch of clear cuticle on medial margin, outer margin with small area of bent cuticle just anterior to spine.

CONCLUSIONS

There are several features of the pupa of *S. rabelloi* which appear to be related to its capacity to obtain air from the leaves of *S. minima.* The most obvious is the dagger-like, sharply pointed respiratory organ which undoubtedly is important in piercing the plant surface (Figs. 1G, 2D, 3A–E). The respiratory organ has two rows of pores. When the respiratory organ is in position in the plant tissue, the medial row (Figs. 3D, E) is inside the plant and these almost certainly function to obtain air from the plant. The basal row of pores (Figs. 3B, C) is used to obtain air from the water surface when the pupa is either dislodged from the plant tissue or is ready to emerge. When at the surface, the medial row of pores remains below the water surface.

The elongate groove on the apical half of the respiratory organ (Fig. 3B) is of unknown function. However, at least two possibilities come to mind. One is that the groove likely strengthens the more narrow apical portion of the respiratory organ to allow this structure to successfully puncture

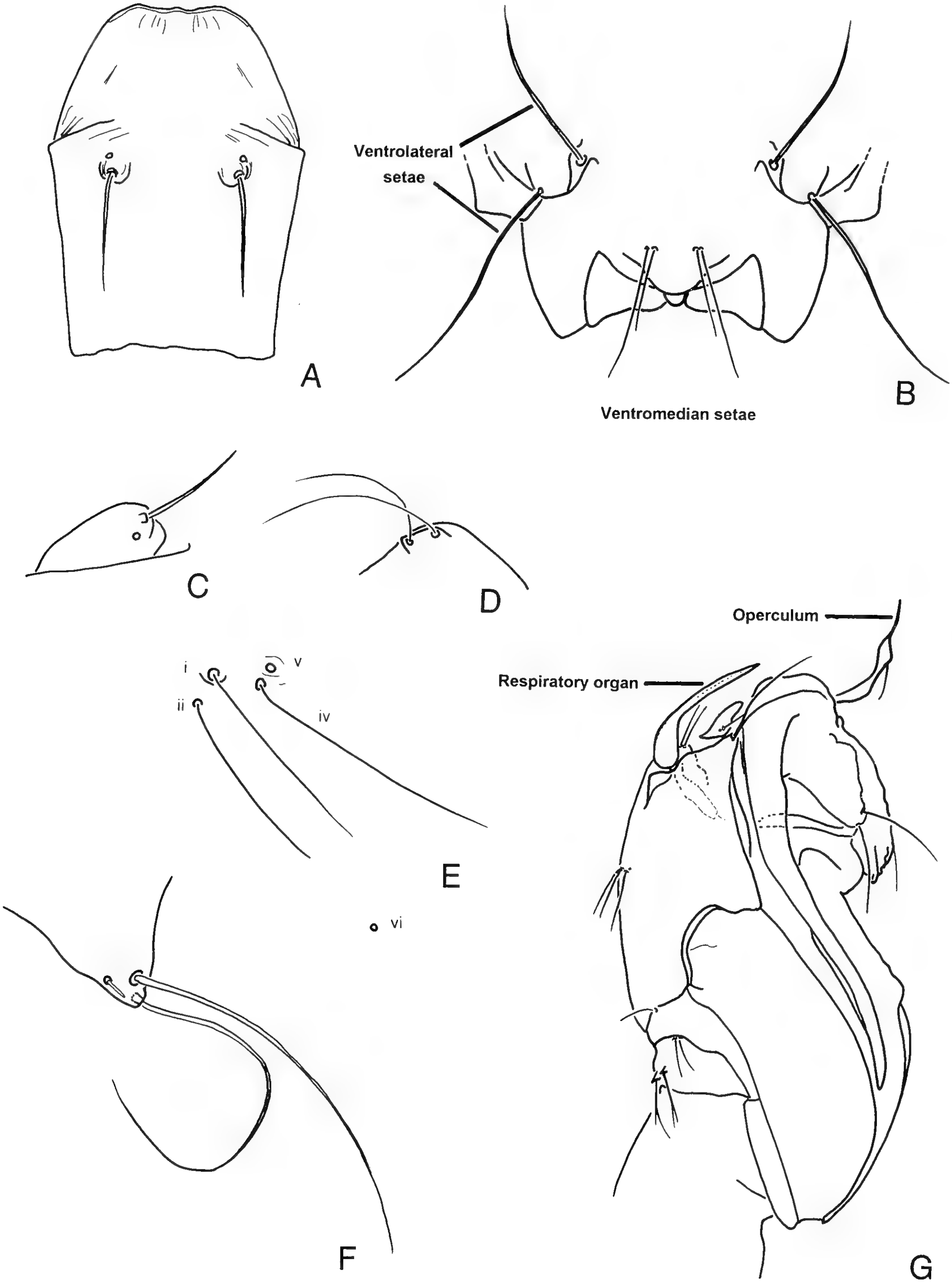

Fig. 1. Structures of the pupa of *Stilobezzia rabelloi*. A, Operculum. B, Mouthpart sheath in ventral view. C, Anterodorsal seta. D, Dorsomedial setae. E, Dorsal setae. F, Dorsolateral setae. G, Thorax of exuviae in lateral view.

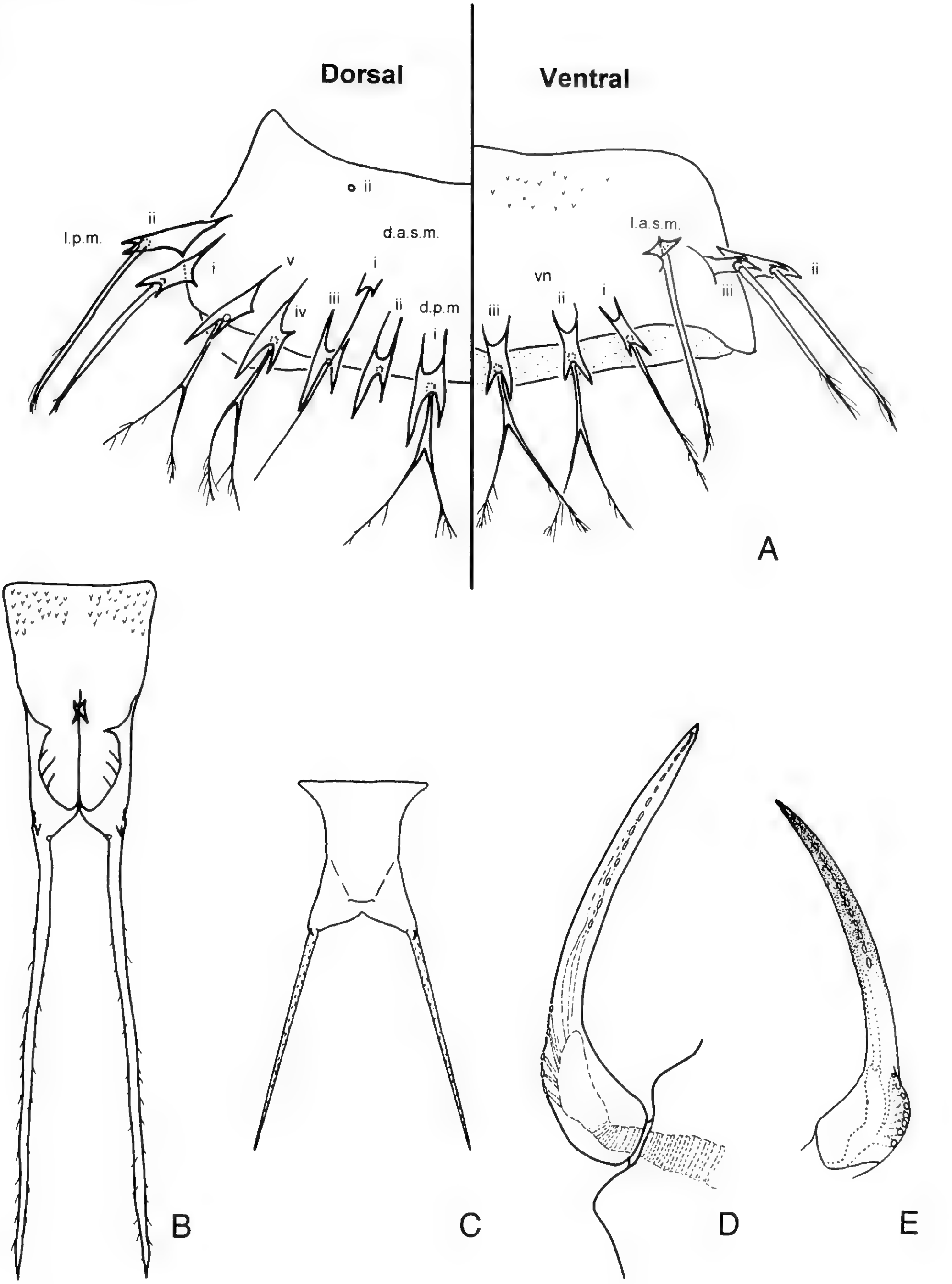

Fig. 2. Structures of pupae of *Stilobezzia rabelloi.* A, Fourth abdominal segment of *Stilobezzia rabelloi.* B, Segment 9 of *S. rabelloi* in ventral view. C, Segment 9 of *S. poikiloptera* (from Ingram and Macfie, 1922). D, Left respiratory organ of *S. rabelloi* in medial view. E, Respiratory organ of *S. poikiloptera* (from Ingram and Macfie 1922).

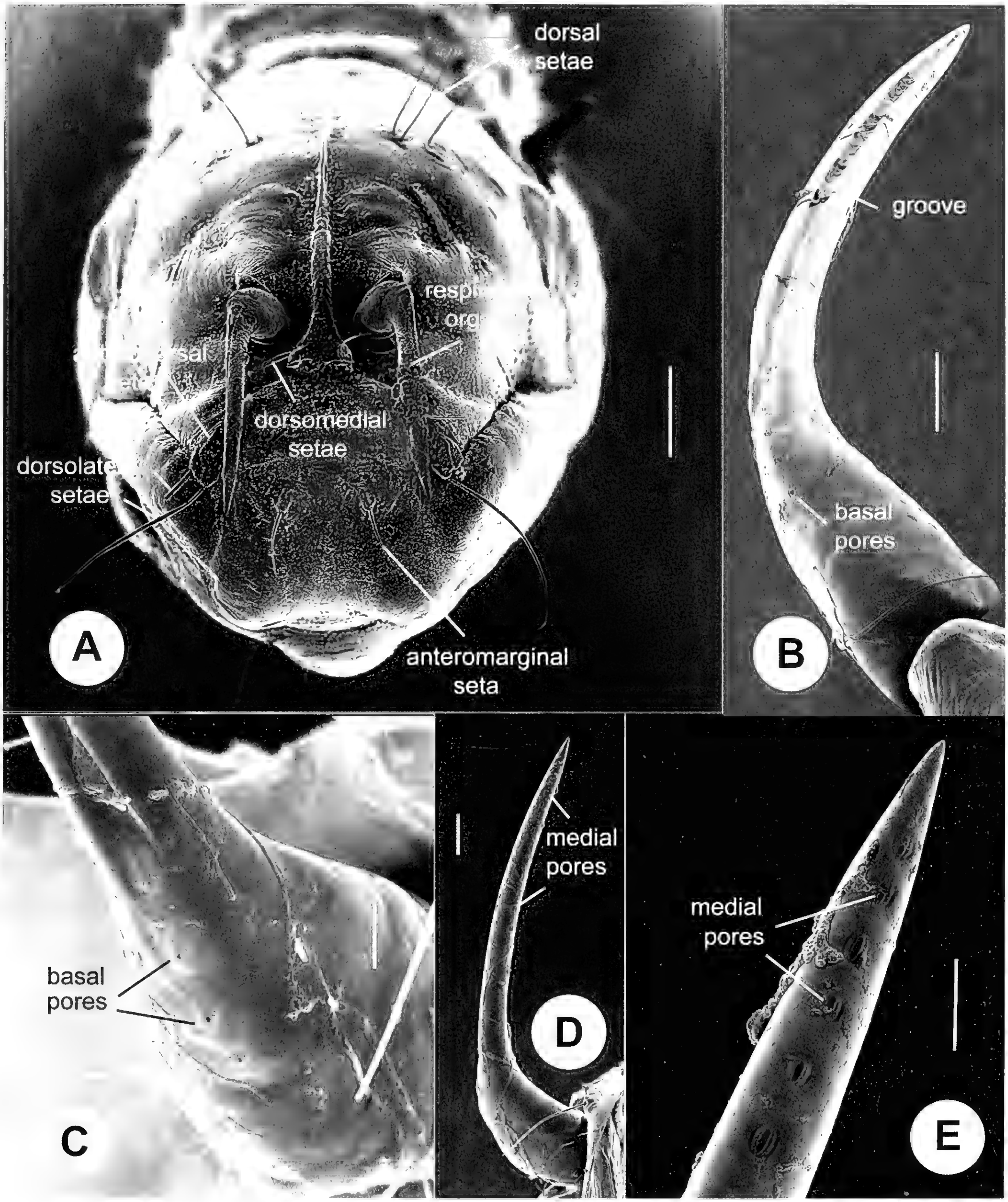

Fig. 3. Structures of pupae of *Stilobezzia rabelloi*. A, Cephalothorax in anterodorsal view. Scale bar = 100 μm. B, Right respiratory organ in lateral view. Scale bar = 20 μm. C, Base of right respiratory organ, in dorsolateral view. Scale bar = 10 μm. D, Left respiratory organ in medial view. Scale bar = 20 μm. E, Apex of respiratory organ, in medial view. Scale bar = 10 μm.

the plant surface; the groove may also allow the structure to bend without undue stress. The other possibility is that the groove serves to reduce pressure on the inserted portion of the respiratory organ by providing an escape for surrounding fluids when the respiratory is being inserted or extracted from the plant.

The respiratory organs are directed in an anterior direction and are parallel to one another (i.e., directed along the longitudinal axis of the body) (Figs. 1G, 3A) and this probably makes it easier for the pupa to lodge these into plant tissue. All other Ceratopogonidae pupae the senior author has examined have respiratory organs which are in a more oblique angle relative to the body (generally in a dorsoanterolateral position). The short protuberance directly posterior to the base of the respiratory organ, and possibly the medial thoracic crest, may serve to limit the movement of the respiratory organs, ensuring that these can be successfully directed into the plant tissue.

The presence of strikingly long, bifurcating and/or plumose setae, supported by strong basal spicules, and the extremely long apicolateral processes likely helps the pupa of *S. rabelloi* anchor itself amongst the submerged leaves. This allows it to effectively apply pressure when twisting and straightening out its abdomen (to push the respiratory organs into position) and, once the respiratory organs are in position, to ensure that the pupa remains in a fixed position amongst the leaves. The apicolateral processes of segment 9 can be bent from a nearly posterior to a posterolateral position. The base of each has a clear, medial patch of cuticle and a lateral patch of bent cuticle and these serve to permit this movement. Such mobility likely allows the pupa to move more effectively, without being caught in the mat of submerged leaves.

Of the 313 species of *Stilobezzia* presently named, only 26 are known in the pupal stage (including the species described here) and virtually all of these have a respiratory organ with a rounded apex. However, the pupa of *S. rabelloi* is very similar to that of the African *S. poikiloptera* Ingram and Macfie, described and illustrated by Ingram and Macfie (1922). Both share the same, highly modified, respiratory organ (Figs. 2D, E), very elongate setae on the body and a very elongate apicolateral process (Figs. 2B, C). It seems certain that the pupa of *S. poikiloptera* also obtains oxygen from below the surface; indeed, Ingram and Macfie (1922) point out that their material was reared from floating vegetation (*Pistia stratiotes* Linnaeus).

Stilobezzia diversa (Coquillett), from the eastern United States, also has a pointed respiratory organ (Wirth and Grogan 1981) but it is not nearly as slender and dagger-like as those of *S. rabelloi* and *S. poikiloptera*; neither does it have a swollen base with a row of pores.

There are some other Ceratopogonidae with sharply pointed respiratory organs, all restricted to the genus *Dasyhelea. Dasyhelea traverae* Thomsen, from eastern United States, (Waugh and Wirth 1976), *D. pollinosa* Wirth, from western and eastern United States (Wirth 1952), *D. chani* Wirth and Linley, from Florida (United States), *D. paulistana* Forattini and Rabello, from Brazil (Forattini and Rabello 1957), and three unnamed species from Sumatra, Indonesia (as *Holoconops* Kieffer sp. in Mayer 1934), from Australia (pers. obs.) and from Costa Rica (pers. obs.) respectively, all have virtually identical respiratory organs; these are thick at the base to about midlength and taper to a sharp apex. The respiratory organs of the pupae from Costa Rica are somewhat more elongate than those of the other species of *Dasyhelea* noted here. The larvae of this species mine the floating leaves of *Salvinia minima* (ms in prep.) and the pupae stick their respiratory organs through the upper surface of the mine to obtain oxygen from the exposed surface of the leaf. These observations show that at least the Costa Rican species uses its respiratory organs to pierce plant tissue.

Because *Dasyhelea* is distantly related to *Stilobezzia* (Borkent 1995, 2000), it is clear that such pointed respiratory organs must have evolved independently from those in *Stilobezzia.*

Observations of movement of the pupa of *S. rabelloi,* showed that the elongate apicolateral processes were important in negotiating the maze of branches of the sub-

Table 1. Species of Ceratopogonidae whose pupae exhibit very elongate apicolateral processes (at least as long as the remainder of segment 9) and the type of habitat from which they were collected. The semiaquatic or terrestrial genus *Forcipomyia* was not completely surveyed.

Taxon	Reference	Habitat
Forcipomyia dominicana	de Meillon and Wirth 1979	*Heliconia*
F. falcifera	Saunders 1959	Epiphytic bromeliad
F. longispina	Saunders 1956	Under wet leaves
F. setigera	Saunders 1959	Rotting leaves
F. varicolor	Saunders 1956	Moist, rotting wood
Dasyhelea chani	Wirth and Lindley 1990	Leaves of *Pistia stratiotes*
D. paulistana	Forattini and Rabello 1957	Not given
D. pollinosa	Wirth 1952	Creek margin
D. traverae	Waugh and Wirth 1976	Algal mat; sandy margin of ponds
Dasyhelea sp. (as *Holoconops* sp.)	Mayer 1934	*Sphagnum*
Culicoides dicrourus	Wirth and Soria 1981	Liquid in flowers of *Calathea*
Stilobezzia poikiloptera	Ingram and Macfie 1922	*Pistia stratiotes*
S. rabelloi	This paper	*Salvinia minima*
Heteromyia clavata	Wirth and Grogan 1977	*Cabomba* (Nymphaceae)
H. pratti	Wirth and Grogan 1979	*Sphagnum*
H. wokei	Wirth and Grogan 1977	Not given
Dibezzia debenhamae	Wirth and Ratanaworabhan 1981a	Treehole
Bezzia biannulata	Wirth 1983b	Pond
B. bicolor	Wirth 1983b	*Spirogyra*
B. collessi	Wirth and Ratanaworabhan 1981b	Surface of weedy pond; open grassy pool, swamp
B. fascispinosa	Wirth et al. 1984	Pond weeds
B. glabra	Wirth 1983b	Pond weeds, algae
B. pruinosa	Wirth 1983a	Not given
B. pulchripes	Spinelli and Wirth 1989	Algal mats
B. xanthogaster (as a *Probezzia*)	Thienemann 1928	*Ceratophyllum*

merged leaves of *S. minima.* There are pupae of some other species of Ceratopogonidae with a similar extreme elongation of the apicolateral processes; Table 1 lists these and the type of habitat from which they were collected. Members of *Forcipomyia* Meigen are semi-terrestrial and there seems to be no correlation between the long apicolateral processes of some species in this genus and the need to move through a maze of any sort (the literature survey of this genus was not complete). Other species of Ceratopogonidae with elongate apicolateral processes, all of which are aquatic, have been reared from such plant material as algae, *Sphagnum* or pond weeds. Although it is clear that it is not universal, there appears to be a general correlation between species with elongate apicolateral processes and living in a maze of plant material. There are, however, a number of other Ceratopogonidae species whose pupae live in mazes of roots, algae or weeds but which do not have such elongate apicolateral processes.

The abdominal setae of the pupae of *S. rabelloi* and *S. poikiloptera* are the longest of any ceratopogonid species, other than those of a few species in the Forcipomyiinae (with semi-terrestrial pupae). Likewise the pupal abdominal setae of other Ceratopogonidae are generally simple (again, except for in some Forcipomyiinae). The pupa of *Pellucidomyia leei* Wirth, from Australia, is the only other member of the family to have bifurcating abdominal setae (Elson-Harris and Kettle 1986); these are elongate but not as long as in *S. rabelloi* and *S. poikiloptera.*

The pupae of the species of *Dasyhelea*

listed in Table 1 have both pointed respiratory organs and elongate apicolateral processes which suggests that the pupae of these species might also obtain oxygen from submerged plants. Two of these species have already been recorded as associated with plants: *D. chani* and the unnamed *Dasyhelea* species from Indonesia. Wirth and Linley (1990) in describing *D. chani,* pointed out the convergent similarity of the respiratory organ and apicolateral processes between this species and *S. poikiloptera,* and suggested that these character states must serve a biological function, perhaps "to aid in climbing or moving around on plants". The discovery here that *S. rabelloi* pupae use these modifications to move through a maze of submerged leaf branches to insert its respiratory organs into an aquatic plant suggests that these *Dasyhelea* species may do the same. The only *Dasyhelea* species which has been studied in detail is *D. chani.* Chan and Linley (1991) reported that most pupae of this species were found below the water surface on leaves of *Pistia stratiotes.* Although most *Dasyhelea* pupae keep their respiratory organs in contact with the water surface when at rest, there is at least one species in which the pupae may remain submerged for long periods of time (Lee and Chan 1985). Chan and Linley (1991) did not, in their examination of the leaves, find any pupae with respiratory organs embedded in the *P. stratiotes*; perhaps they were dislodged when the plants were being dissected.

In the present study the pupae were described on the basis of reared adults which keyed out close to *S. rabelloi* in Lane and Forattini (1961) and they match the available descriptions fairly well (Lane 1947, Wirth 1953, Wirth and Grogan 1981). However, the adults here have lighter leg coloration and it appears likely that they are actually of an undescribed species (in a species complex). The senior author has initiated a revision of Central American *Stilobezzia* and this material will obviously be included in that study.

We considered the possibility that *S. rabelloi* and *S. poikiloptera* were conspecific but the pupa of *S. poikiloptera* differs as follows: 1) abdominal segment four d.p.m. i has an associated forked spicule arising from the cuticle; all other sensilla have a single pronged spicule, 2) d.p.m. i are broadly separated from one another medially, 3) vn iii are broadly separated from one another medially, 4) the pigmented portions of the abdomen are covered with a reticulate pattern. Further details of wing pigmentation and the male genitalia confirms that the *S. rabelloi* and *S. poikiloptera* are distinct species.

The respiratory organ shape of *S. rabelloi* and *S. poikiloptera,* with a sharp apex and two separate rows of pores, is unique within the Ceratopogonidae and clearly a derived feature indicating that these two species are closely related. *Stilobezzia poikiloptera* from Africa has been placed in the *poikiloptera* species group within the subgenus *Stilobezzia s. str.* with several others: *S. inermipes* Kieffer from India to Micronesia and the Ryukyu Islands, *S. chasteli* Clastrier from India to the Philippines to Cambodia and *S. quatei* Das Gupta and Wirth from Vietnam and Thailand (Das Gupta and Wirth 1968). The characterization of this group by Das Gupta and Wirth (1968) and Clastrier (1976) was based on a large complex of character states, all of which occur in different combinations in other species of *Stilobezzia.* As noted above only 26 of 131 species of *Stilobezzia* are known as pupae. It is therefore presently impossible to gauge the character state distribution of the peculiar respiratory organ shared by *S. rabelloi* and *S. poikiloptera* within most of the genus.

The shared presence of bifurcating abdominal setae between *S. rabelloi* and *S. poikiloptera* is virtually unique within the Ceratopogonidae and therefore also a synapomorphy. Such setae are also found in *Pellucidomyia leei* but, considering the distant relationship between *Stilobezzia* and *Pellucidomyia* (Borkent 1995, 2000), this is a clear instance of homoplasy. A cladistic study of the genus *Stilobezzia* is needed to further analyze these character states; interpretation of pupal features, as shown here, will certainly help to accomplish that task.

Although this is the first report of a ceratopogonid using an aquatic plant as a source of oxygen, the phenomena is known for the pupae of a few other families of Diptera such as Culicidae (*Mansonia* Blanchard, *Coquillettidia* Dyar, *Mimomyia* Theobald), Tipulidae (some *Erioptera* Meigen) and Ephydridae (*Notiphila* Fallén) (Clements 1992, Houlihan 1969).

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CHECKLIST AND DISTRIBUTION OF THE PEIRATINAE (HETEROPTERA: REDUVIIDAE) OF MEXICO

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Abstract.—Five genera, 14 species, and one subspecies of Peiratinae (Reduviidae) from Mexico are listed. Collection records and distribution are given for each species.

Key Words: true bugs, Heteroptera, Reduviidae, Peiratinae, taxonomy, Mexico

Information on the Peiratinae of Mexico is scattered throughout the literature. The purpose of this publication is to present a checklist of the Peiratinae species known to occur in Mexico. The information comes mainly from the material deposited in the Universidad Nacional Autónoma de México.

Synonymic and distributional information can be obtained from revisionary contributions of the genus *Melanolestes* (Coscarón and Carpintero 1994), *Rasahus* (Coscarón 1983a, b), *Sirthenea* (Willemse 1985), *Thymbreus* (Coscarón 1994), and *Tydides* (Lent 1955, Lent and Jurberg 1967)

All are new records except for *Sirthenea stria stria* (F.) that is confirmed for Veracruz.

Peiratinae

Melanolestes argentinus (Berg 1879) (Fig. 2)

CHIAPAS: ♂ San Rafael 10 km S. Comitán, 20-V-1952.

Melanolestes morio (Erichson 1848) (Fig. 1)

CHIHUAHUA: ♂ Nueva Ciudad de las Casas, Laguna Fierro, 14-VII-85, E. Barrera. TAMAULIPAS: 2 ♂ 20 km. S. E. de Soto la Marina, 24-X-85, J. Bueno. E. de Soto la Marina. SAN LUIS POTOSI: ♂ Ciudad Valles, Río Micos, 5-XI-80, H. Pérez. JALISCO: ♂ Estación de Biología Chámela, 30-IX-77, col. Nocturna. VERACRUZ: 2 ♂ Km. 20 carretera Sayula-Ciudad Alemán, 20-V-85, H. Velasco; ♂ Los Tuxtlas, Sierra de Santa Marta, Ocotal Chico, 17-18-VII-82; ♂ 26-IX-81, H. Pérez, R. Sánchez; ♀ San Andres Tuxtla, 10-XII-84, A. Ibarra; ♂ Estación de Biología Tropical Los Tuxtlas, 17-VI-89, L. Colín, H. Rojas; ♂ Río Maquinas, 19-II-84, M. García. GUERRERO: 3 ♂ Mochiltlan, Acahuizotla, alt. 950 m. bosque tropical bajo caducifolio, VI-90, L. Delgado. OAXACA: ♂ Francisco Sarabia, 28-V-51; ♂ Chacahua, 31-V-87, F. Arias; ♂ Monte Flor, 21-V-57; ♂ Bethania, Río Coapan, 24-V-81, J. Bueno. CHIAPAS: ♂ Agua Azul, 22-V-79, L. Rivera. QUINTANA ROO: ♂ Puerto Morelos, Rancho San Isidro, 12-VIII-82, M. García; ♂ Chunyaxche, 19-VI-84, Z. Cano; ♂ 19-VI-84, H. Heredia; ♂ 20-VI-84, H. Hernandez. Tulúm, 3-VIII-81, E. Pech.

Melanolestes picipes (Herrich-Schaeffer 1848) (Fig. 1)

DURANGO: 3 ♂ Mapimi, 8-IX-85, P. Aguilar; ♀ Romita, 22-VI-72. NUEVO-

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Fig. 1. Distribution of *Melanolestes morio* ▼, *M. picipes* ♦, *Rasahus. albomaculatus* ●, and *R. biguttatus* ✪.

LEON: 2 ♂ Monterrey, Potrero Redondo, 28-III-78, H. Pérez; ♂ 21-III-78, S. Zaragoza. TAMAULIPAS: ♂ 20 Km. S. E. De Soto La Marina, 24-X-85, S. Tufinio.

Rasahus albomaculatus (Mayr 1865)
(Fig. 1)

VERACRUZ: ♀ San Andrés Tuxtla, 23-V-76; ♀ Estación de Biología Tropical Los Tuxtlas, 14-16-76, R. Terrón; 2 ♂, ♀ 19-20-X-88. CHIAPAS: ♀ Reserva de Bonampak, 3-V-78, E. Barrera; ♀ Km 10 carretera Villa Flores-Sierra Morena, 600 m, 11-VII-88, A. Cadena, L. Cervantes.

Rasahus biguttatus (Say 1832)
(Fig. 1)

BAJA CALIFORNIA SUR: ♀ 26 millas al sur de Loreto, 1-I-77, C. Griswold y L. Vicent. SONORA: ♀ Navojoa, 18-X-82, C. Beutelspacher. COAHUILA: 2 ♀, 6 ♂ San Pedro, IX-75. SINALOA: 2 ♂ Culiacán, 2-III-75, E. Bayliss; 2 ♀ Mazatlán, 17-X-82, C. Beutelspacher. DURANGO: ♂ Vicente Guerrero. NUEVO LEÓN: ♀ Aramberri, 24-IX-83, M. García. SAN LUIS POTOSI: ♀ Ciudad Valles, Río Micos, 21-X, XI-78, H. Pérez; ♀ Chapulhuacanito. GUANAJUATO: ♀ 8-VII-53; ♂ Acámbaro, XI; ♀ Irapuato, 10-II-80, W. López; ♀ Actopan, 19-VI-74, E. Bayliss. HIDALGO: ♀ Tasquillo, 28-XII-69, H. Brailovsky. MICHOACÁN: La Piedad, 2-IV-87, H. Brailovsky. VERACRUZ: ♂ Chicontepec, 14-IV-71, H. Brailovsky; ♀ Cot. 30-III-71, H. Tatuya. OAXACA: ♂ Tehuantepec, 30-V-51, H. Brailovsky.

Rasahus flavovittatus Stål 1872
(Fig. 2)

PUEBLA: ♂ San Diego, 16-V-53.

Rasahus guttatipennis (Stål 1862)
(Fig. 2)

VERACRUZ: ♀ Estación de Biología Tropical Los Tuxtlas, 23-25-X-88, E. Me-

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Fig. 2. Distribution of *Melanolestes argentinus* ■, *R. flavovittatus* ●, *R. guttatipennis* ★, *R. hamatus* ✹, and *R. sulcicollis* ☆.

jorada y M. A. Pérez.; 2 ♀ 3-15-XII-88, E. Mejorada; ♀ 17-IV-89, E. Barrera y J. L. Colín; ♀ 17-V-1989, E. Barrera, J. L. Colín; ♀ 23-25-X-88.

Rasahus hamatus (Fabricius 1781)
(Fig. 2)

SAN LUIS POTOSÍ: ♀ Tamuín, 13-IV-75, H. Brailovsky. PUEBLA: 4 ♂, 2 ♀ Rancho Alegre, 25-I-52. VERACRUZ: ♂ Paraje Nuevo, 3-II-52, C. N; 2 ♂ Ocotal Chico, 25-X-81, H. Pérez R. Sánchez; ♀ Estación de Biología Tropical Los Tuxtlas, 17-IV-89, E. Barrera; ♀ 5-II-90, G. Ortega; ♀ 23-30-V-79, R. Zurbia; ♂ Monte Flor, 19-IV-56, L. Vásquez; ♂ 22-V-56, L. Vásquez. CHIAPAS: ♂ El Lechugal, 17-I-53; ♂ Bonampak, 2-V-78, H. Brailovsky; ♂ 23-25-V-84, M. García; ♂ San José Comitan 21-V-52; ♂ Tapachula, Puente Colorado, 14-III-85, F. Arias; ♂ Río Mixcon, 23-III-85, H. Velasco.

Rasahus sulcicollis (Serville 1831)
(Fig. 2)

JALISCO: ♂ Estación de Biología Chámela, 22-VII-76, H. Brailovsky. HIDALGO: 2 ♂ Otongo, 14-VI-89, L. Rivera. PUEBLA: ♂ El Agengibre, 26-I-52; 3 ♂ San Diego, 15-V-53. VERACRUZ: 2 ♂, ♀ Los Tuxtlas, Las Cabañas, 11-I-72, H. Brailovsky; ♂ Los Tuxtlas, 18-I-80, H. Brailovsky; ♂ 14-16-IV-76, R. Terrón; ♂ 19-V-74, L. Vázquez; 2 ♂ 20-26-II-85, A. Ibarra; ♂ 3-VI-89, J. L. Colín; ♂ 15-II-78, Johsep; ♂ Catemaco, 17-IX-53; ♂ 19-IV-69, C. Beutelspacher; ♂ San Andrés Tuxtla, 10-IX-90; ♂ 12-IV-75, L. Vázquez; ♂ 22-VI-72; ♀ 19-V-74, L. Vázquez; ♀ Las Choapas, 5-V-78, H. Brailovsky; ♂ Los Tuxtlas, 22-VII-72; ♂ 9-V-75, H. Pérez; ♂ Paraje Nuevo, Ojo de Agua Grande, 2-V-53; ♂ Los Tuxtlas, La Palma, 27-IX-77, E. González; ♂ 18-I-80, H. Brailovsky; ♂ Estación de Biología Tropical Los Tuxtlas, 12-VI-89, H.

Rojas; 3 ♂ Río Maquinas, 19-II-84, H. Delfin; ♂ 17-IX-87, F. Arias; ♂ 31-VII-89, A. Villegas; 2 ♂ 1-IX-84, A. Villegas; ♂ 31-VIII-89, A. Villegas; ♂ 2-VII-84, M. A. Pérez; ♂ 15-20-XI-86, E. Mejorada; ♂ 14-17-VI-89, J. L. Colín, M. Rojas; ♂ A. Villegas; ♂ 19-IX-89, J. L. Colín; ♂ 3-VI-89, J. L. Colín. TABASCO: ♂ Tlapa, Puyacatenango, 9-XII-85, R. Barba; ♂ Cárdenas, 29-V-79, R. Ramírez. GUERRERO: ♂ Venta Vieja, 25-VI-60; ♂ Acahuizotla, 8-VI-66, G. Ruíz. OAXACA: ♀ Temascal, 19-II-75, E. Barrera; ♂ Camelia Roja, 2-V-75, J. Butze; ♀ Pochutla, Finca Concordia, 2-VI-87, F. Arias; ♂ Monte Flor, 23-V-57, L. Vázquez; 2 ♀, 3 ♂ Piedra de Lumbre, 3-XI-87, F. Arias, R. Barba, E. Barrera; ♂ Toltepec, 30-V-87, F. Arias. CHIAPAS: ♂ Bonampak, 20-V-80, H. Brailovsky; ♀ Comitan, 17-V-61; ♂ 4-V-78, H. Brailovsky; ♂ Corozal, 25-V-84; ♀ Bonampak, 23-25-V-84, E. Barrera; 8 ♂, ♀ Ocosingo, Chajul, Reserva Montes Azules, 10-16-VII-87, F. Arias, R. Barba; 3 ♂, ♀ Boca Lacantun, 24-V-84, M. García; ♂, ♀ Acahuacan, Unión Juárez km 3 San José, 24-III-85, F. Arias; ♂ Tapachul a, Río Monte Perla, 19-III-85, F. Arias; ♀ Betel, Selva Lacandona, 4-VII-85, J. Ramos, V. Ocosingo, Chajul; ♂ Ocosingo, 3-IV-85, F. Arias; ♀ Cocachatan, La Victoria, 10-VI-83, M. A. Morón; 2 ♂ Bonampak, 20-22-V-84, A. Ibarra; ♂ 30-IV-86, F. Arias; ♂ 9-11-VII-87, F. Arias; ♂ 28-IV a 5-V-86, L. Cervantes; ♂ 27-VIII-84, Deloya-Villalobos; 3 ♂ 24-X-84, Deloya-Villalobos. CAMPECHE: ♂ Escárcega, IX-61, G. Gutiérrez. QUINTANA ROO: ♂ km 146 carretera Chetumal-Cancun, 3-V-82, M. García; ♂ Acacho, 21-24-II-84, G. Montoya.

Rasahus surinamensis Coscarón 1983b
(Fig. 3)

VERACRUZ: ♂ Las Choapas, Cerro Pelón, 16-17-VIII-80, H. Pérez, R. Sánchez. QUINTANA ROO: ♂ Km. 146 carretera Chetumal-Puerto Juárez, 17-VI-84, V. Hernández.

Rasahus thoracicus Stål 1872
(Fig. 3)

NUEVO LEÓN: 2 ♂, ♀ Aramberri, 24-IX-83, M. García. Monterrey; ♂ 4-X-44. TAMAULIPAS: ♀, ♂ La Pesca, 8-X-85, F. Arias; ♀ 8-X-85, L. Cervantes; ♂ 8-X-85, M. García; ♂ V. Alnova, 8-VI-79, T. Carmona NAYARIT; ♂ Rincón de Guayavitos, 7-XII-77, R. Surbia. SAN LUIS POTOSÍ: Tamuín, 13-IV-75, H. Brailovsky; ♂ Ciudad Valles, 7-IV-75, H. Pérez; ♂ 13-VII-90, E. Ramírez; ♂ 7-IV-78; ♀ 21-XI-78, H. Pérez; ♀ -Chapulhuacanito, 3-V-76, E. Barrera; ♂ 17-IX-50; ♂ 3-V-76, J. Butze; ♂ Tamazunchale, 3-V-76, T. Carmona; ♀ Tamuín, 13-IV-75, H. Brailovsky; ♂ 5-V-50. JALISCO: 3 ♂ Atitic, 10-VI-75, B. Kolhmann; ♀ Ayotla, 21-I-66, C. Beutelspacher; ♂ Chamela, Estación de Biología, 17-IV-75, H. Brailovsky; ♂ 24-II-89, E. Ramírez.; ♀ 18-III-89, E. Ramírez; ♀ 24-II-89, E. Ramírez; ♂ Km 99 carretera Barra de Navidad-Puerto Vallarta, río San Nicolás, 28-IV-89, E. Barrera; ♀ 29-III-88, E. Ramírez; 8 ♀, 6 ♂ 18-22-XII-87, H. Brailovsky; ♂ Chamela, 1-VII-77, M. A. Gurrola; ♀ 2-XII-77, H. Brailovsky; ♀ 6-10-IV-81, A. Pescador; ♂ 30-IV-77, H. Brailovsky; ♂ 9-II-80, H. Brailovsky; ♂ 8-9-II-80, H. Brailovsky; ♂ 30-IX-77, H. Brailovsky; ♂ Zapotlaneio, 21-VII-82, H. Brailovsky; ♂ I-77, M. A. Gurrola; ♂ Río Cuitzmala, 31-VII-90, E. Ramírez; ♀ 2-IV-81, A. Pescador; 3 ♂ San Patricio, 12-I-75; ♂ Puerto Vallarta, río Cuitzmala, 26-VI-90, J. Villa Ramírez. GUANAJUATO: 2 ♂ Acambaro, Bresel, N; ♀ Actopan, 19-VI-74. COLIMA: ♂ Tecoman, 2-II-83, H. Brailovsky. HIDALGO: ♂ Tasquillo, 28-XII-76, H. Brailovsky. MICHOACÁN: ♂ Coahuayana, 17-VII-85, F. Arias. Apatzingan, 12-VIII-71; ♂ 19-VII-71; ♀ Zamora, 13-VIII-50; ♂ 2-VII-71; ♂ 29-VIII-71; ♂ 19-VII-71; ♂ Popogitla, 25-XI-79, W. López; ♂ La Piedad, 13-V-85, H. Brailovsky; ♀ 27-V-88, A. Cadena, L. Cervantes; 2 ♂ La Piedad, 13-VIII-85, H. Brailovsky; ♀ Felipe Carrillo Puerto, El Tamarindo, 27-

3

Fig. 3. Distribution of *Tydides rufus* ✣, *Rasahus surinamensis* ☆, *Rasahus thoracicus* ✱, *Sirthenea stria stria* ✦, and *Thymbreus crocinopterus* ●.

VII-88, A. Cadena, L. Cervantes Pedernales; ♂ El Salitre, 19-IX-87, R. Barba. MORELOS: ♂ Terpalcingo, 20-VI-83, L. Cendrero; 2 ♀ Ticumán, 2-II-84, E. Mariño; 9 ♂ 7-II-81, E. Mariño; ♂ Villa de Ayala, 22-VII-71, H. Pérez; ♂ Alpuyeca, 6-IX-80, E. Barrera; 2 ♂ 3-III-81, E. Mariño; 2 ♂ 13-III-81, E. Mariño; 4 ♂ 6-II-81, E. Mariño; ♂ 9-I-81, E. Mariño; ♂ 8-I-81, E. Mariño; ♂ Cuautla, 29-XII-79, H. Brailovsky. Sin abdomen. Villa de Ayala, 25-III-71, H. Pérez; ♂ Alpuyeca, 30-X-81, A. Ibarra; ♀ 20-I-72, H. Pérez; ♂ El Polvorín 21-I-72, H. Pérez; ♂ 25-III-71, H. Pérez; ♀ 8-IV-72, H. Pérez; 2 ♂, 17 ♀ 22-IV-71, ♀ 6-V-72, H. Pérez; 2 ♂ 22-VII-71, H. Pérez; ♂ Cuautla, 10-IX-82-II; ♀ 10-VIII-89, O. Maldonado, H. Brailovsky; ♂ Amacuzac, 1-VI-74; ♂ Villa de Ayala, Rancho Abundes, 27-VII-70, H. Pérez. PUEBLA: ♂ Tehuacán, 16-VII-39. VERACRUZ: ♂ Los Tuxtlas, 16-V-72; ♂ Coatzacoalcos, 30-II-71, R. M. Tantoia; ♂ Isla, 13-VI-67; ♂ Apuapán de Cabañas, 2-IV-53; ♂ Catemaco, Dos Amates, 12-XI-66; ♂ Jesús Carranza, 2-IV-56, F. Islas; ♂ Río Tonalá, 4-XII-80, R. Sánchez; 10 ♂ Sierra de Santa Marta, Los Tuxtlas, Ocotal Chico, 25-26-X-81, R. Sánchez. TABASCO: ♂ Cárdenas, VI-81, La Cedelli. GUERRERO: ♂ Colotlipa, 15-I-86; ♀, ♂ Tecpan, 12-VIII-71; ♂ Ciudad Altamirano, 8-II-84, H. Brailovsky; ♂ El Ocotito, 7-V-82, H. Brailovsky; 2 ♀ Huayacán, 12-II-75; ♀ Ixtapa, 17-IV-74, Pletsch; ♂ Venta Vieja, 24-V-60; 2 ♂ Juxtlahuaca, 16-I-86, H. Brailovsky; ♂ Zihuatanejo, Ixtapa, 25-29-XII-89, H. Brailovsky; ♂ 16-I-86, E. Barrera; ♂ Acahuizotla, Nochistlán, 24-VIII-85, F. Arias. OAXACA: ♂ Sierra de Juárez, V-83; ♂ Candelaria Loxicha, 10-II-82, Ibarra; ♂ Mitla, 21-V-70; ♂ Guelatao, 14-X-79, H. Brailovsky; ♂ Tehuantepec, 30-V-51; ♂ 26-V-70; ♂ 16-XII-58; ♂ Mitla, 21-V-70; 2 ♂ Candelaria Loxicha, 10-II-82, A. Ibarra, M. Garcia; ♂ Pochutla, Finca Progreso, 2-VI-87, A. Cervantes; ♂ 2-VI-87, E. Barrera; ♂ Juchitán, 20-VII-72, J. Silva; ♂ Monteflor, 20-V-56, L. Vázquez. CHIAPAS: ♂ Jaltenango, Finca Prusia, 8-V-85; ♂ Huitiupan, 17-III-87, F. Arias; ♂ Bonampak, 20-22-V-84, E. Barrera; 4 ♂ Palenque, 31-I-81, M. García; ♂ Caguaré, 14-IX-80, C. Beutelspacher; ♂ 31-I-85, M. Gracia; 2 ♂ 31-I-85, M. Garcia; 24 ♂ Ocozocoautla, 17-III-76, A. Espinoza; 6 ♂ 15-30-XII-75, A. Espínoza; 5 ♂ 12-XII-75, A. Espínoza; 4 ♂ Cahuare, 14-IX-80, C. Beutelpacher; ♂ Bonampak, 4-V-78, H. Brailovsky; ♂ 2-V-7; ♂ 20-22-V-84; ♂ El Sumidero, 14-VII-73, H. Pérez. CAMPECHE: ♂ 10-VII-71; ♀, ♂ Escarcega, 4-VI-89, O Canul; ♀ Champoton, El Zapote, 19-VI-89. A. Cadena. L. Cervantes; ♂ 2-VIII-71, H. Brailovsky; ♂ Kalkini, 27-IV-82, M. Garcia; ♂ 2-VIII-77, M. García; ♂ 27-IV-82, A. Ibarra; 2 ♀ Escarcega, El Tormento, 18-VI-89, A. Cadena, L. Cervantes. QUINTANA ROO: ♂ km 146 carretera Chetumal-Puerto Juárez, 17-IV-82, M. García; ♂ Tulum, Playa Aventuras, X-81, E. Petch.

Sirthenea stria stria (Fabricius 1794)
(Fig. 3)

TAMAULIPAS: ♂ Río Guayalejo, 25-X-85, R. Barba. JALISCO: 2 ♂ Chámela, Estación de Biología, 9-VIII-75, H. Brailovsky; ♂ Km 44 carretera Barra de Navidad-Puerto Vallarta, 28-IV-89, E. Barrera; ♀ 16-VII-75. MICHOACÁN: 2 ♂ Pedernales, El Salitre, 19-IX-87, R. Barba. MORELOS: Vicente Aranda, 18-IX-82, H. Vélasco. VERACRUZ: ♂ Los Tuxtlas, 27-IX-79, J. Padilla; ♂ 14-VI-89, J. Colín, H. Rojas; ♂ río Las Palmas, 30-XI-77, E. Ríos; ♂ San Isidro, 29-I-82, L. Torres; ♀ Los Tuxtlas, 16-V-72; ♂ 1-13-V-81, G. Ortega. GUERRERO: ♂ Tecpán, 17-VIII-71, H. Brailovsky. OAXACA: ♀ S. E. de Sarabia, 28-V-51, L. Vázquez. CHIAPAS: ♀ km 3 carretera Tapachula-Talismán, 5-III-85, H. Vélasco; ♀ Boca Lacantún, 24-V-84, M. García; ♀ Ocosingo, Reserva Montes Azules, 10-16-VII-87, L. Cervantes; ♂ Huitiupan, 17-II-87, C. Beutelspacher, ♂ 18-II-87, V. Hernández; ♂ Chajul, 3-V-84, J. Villalobos. QUINTANA ROO: ♂ km 146 carretera Chetumal-Cancun, 5-IV-82, A. Ibarra.

Thymbreus crocinopterus Stål 1863
(Fig. 3)

SINALOA: ♀ Culiacan, 19 millas al sur, 22-VI-63, J. Doyen. CHIAPAS: ♀ Ocosingo, Chajul, Reserva Montes Azules, 28-IV/5-V-86, F. Arias, R. Barba, L. Cervantes.

Tydides rufus (Serville 1831)
(Fig. 3)

VERACRUZ: ♀ Estación de Biología Tropical Los Tuxtlas, 28-XI-76, R. Terrón, Noct; ♀ 18-IV-89, E. Barrera, J. Colin; ♂ río Las Palmas, 30-XI-77, E. Ríos. CHIAPAS: ♂ Betel Selva, La Candona, 4-VII-85, J. Ramos.

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SPECIES TURNOVER IN THE LEAFROLLERS (LEPIDOPTERA: TORTRICIDAE) OF PLUMMERS ISLAND, MARYLAND: ASSESSING A CENTURY OF INVENTORY DATA

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Abstract.—During the period 1900 through 1999, 119 species of tortricid moths (leafrollers) have been present at one time or another on Plummers Island and the adjacent northern shore of the Potomac River, Maryland. The number of species of leafrollers documented has declined over the last century from 71 in the decade 1900–1909 to 59 in the decade 1990–1999—a reduction of 17% in species richness. Of 71 species recorded from the turn of the century, only 30 are still present. With 41 apparent species extinctions and 29 apparent species colonizations, species turnover is 54%. Because of potential differences in sampling methods (e.g., equipment, diurnal vs. nocturnal, and frequency) between the two decades, "inventories" for the two decades are not strictly comparable. Hence these calculations do not represent precise measurements of changes in the fauna. Nonetheless, it is highly likely that they reflect the overall trend. Of six species described from Plummers Island just after the turn of the century, only one was detected during recent survey work. The most likely explanation for changes in the species composition of the site is faunal response to plant community succession. Since the turn of the last century, vegetation of the island has changed from an open juniper grassland to a submature hickory-maple-oak woodland. The adjacent northern shore, likewise, has undergone considerable succession. The hypothesis that changes in the fauna are the result of succession is consistent with the proposal that habitat maturation is the mechanism behind regional declines of several bird and mammal species that require early successional habitat in the northeastern United States.

Key Words: species inventory, species discovery curve, succession, local extinction, habitat management, conservation

The species composition of any site is dynamic, constantly changing in response to varying biotic and abiotic factors. Such changes may be driven by slow, long-term events, such as plate movements (hundreds of millions of years) or major shifts in regional or global climatic patterns (thousands of years), by more rapid processes such as community succession (tens to hundreds of years), or by short-term, localized environmental perturbation or ecological catastrophes (days to months). This concept of change is so fundamental to biogeography that it was a major, although rarely tested, component of MacArthur and Wilson's (1967) classic equilibrium theory of island biogeography, and it is referred to as species turnover. While species turnover can be estimated for some taxa at a coarse level (e.g., adjacent layers in fossil beds or

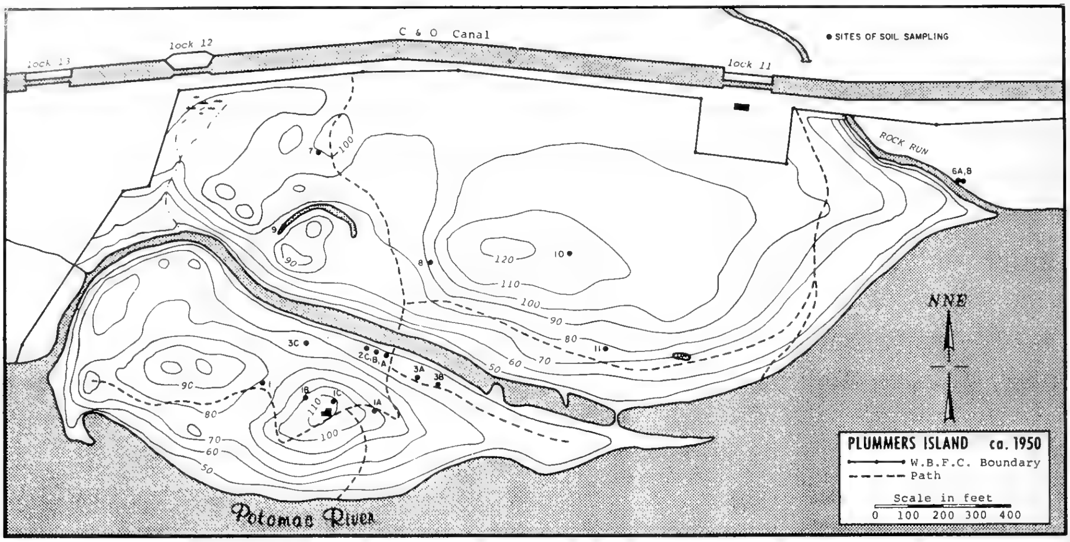

Fig. 1. Map of Plummers Island (from Erwin 1981).

changes in frequency of pollen of different plant species in core samples from lakes or shallow seas), contemporary or fine level turnover rates are unknown for most taxa. Obtaining such data typically requires long-term monitoring of the particular biotic element being evaluated.

Plummers Island, a small land feature situated along the northern shore of the Potomac River near Washington, D.C., has been a focal point of biological investigations for nearly a century. The natural history collections accumulated since 1900 represent a wealth of biological data. The moth family Tortricidae (leafrollers) is well represented in these collections, providing a unique opportunity to examine changes in the species composition of this family since 1900. I used historical specimens and data accumulated through field work in 1998–1999 to compile a cumulative species inventory of the site and examine species turnover and change in species richness, focusing on the decades 1900–1909 and 1990–1999. I also follow the fate of six species of Tortricidae described from Plummers Island during the first decade of the 20th century.

MATERIALS AND METHODS

Study site.—The study site is Plummers Island (about 3.6 hectares) and a section of the immediately adjacent northern shore of the Potomac River (about 15.6 hectares) south of the C&O Canal, Montgomery County, Maryland (Fig. 1; also see TopoZone 2000), at 39.969°N, 77.177°W. The site is situated immediately east of Interstate Highway 495 (the Capitol Beltway) and approximately 14.5 km northwest of The Mall, Washington, D.C. Erwin (1981) describes the soils, topography, and vegetation of the area and presents a brief review of historical land use. In general, the flora of the island has changed from an open juniper grassland at the turn of the century, to a submature hickory-maple-oak woodland today. Portions of the adjacent northern shore were cleared either for agriculture or timber before the turn of the 20th century, and these areas now support a rather homogeneous subclimax woodland. The study site has existed in a protected state since about 1907, under the ownership of the Washington Biologists' Field Club.

Data sources.—Information on the leafrollers of Plummers Island was accumulated from three sources: (1) label data from specimens in the collection of the National Museum of Natural History (USNM), Smithsonian Institution, Washington, D.C.; (2) data from specimens accumulated during field work conducted in 1998–1999; and (3) historical literature on North American leafrollers. For each species of the family Tortricidae documented from the study area, the first year of capture was recorded; also, for each decade, the number of specimens examined and the number of species recorded were tallied.

The Lepidoptera collection at the USNM was examined thoroughly for specimens from Plummers Island. Owing to a longstanding interest in the site, the collection is rich in material gathered throughout the century, particularly during the first two decades.

During 1998, field work was conducted one night per week from early May through the end of September (n = 23 sampling nights) by the author and Michael G. Pogue (USDA, Systematic Entomology Laboratory), alternating weekly between collecting at a sheet and using a blacklight trap. Sheet collecting was conducted with a 15-watt UV (ultra-violet) light hung in front of a white sheet supported by a rope tied between two trees. On alternate weeks, a blacklight trap was deployed in the evening and retrieved the following morning. The blacklight trap consisted of an aluminum box, ca. 0.5 m × 0.5 m, with a large funnel and a baffle ca. 0.5 in height, using a 15-watt black light to attract insects. The trap was placed on the ground. In 1999, field work was conducted approximately one night per week from the first of April through the first of November (n = 30 sampling nights), using one or two blacklight traps (n = 38 samples). All specimens of Tortricidae were pinned, labeled, identified, and incorporated into the collection of the USNM.

It was impossible to determine the number of sampling dates for the first decade of the century because of the lack of precision in the data that accompanies the specimens (e.g., usually only the month and year are given, sometimes only the year), and because there is no way to determine how many sampling efforts resulted in no specimens. However, based on specimens with unambiguous label data, a minimum of 23 sampling dates can be determined with certainty: July 1902, August 1902, April 1903, May 1903 (three dates), June 1903, July 1903, August 1903, September 1903, March 1905, April 1905, May 1905, August 1905, September 1905, May 1906, June 1906, July 1907, September 1907, March 1908, May 1908, April 1909, and May 1909. Approximately 65% of the specimens from this decade are from the single year 1903. It is likely that samples included diurnal collecting (e.g., larvae from vegetation) as well as collecting with a lantern at night. A cursory review of the late August Busck's (USDA) field notes revealed no additional information (M. Epstein, pers. comm.).

Historical and contemporary sources of information on the family Tortricidae were reviewed for information regarding the Tortricidae of Plummers Island, including Heinrich's (1923, 1926) revisions of the Olethreutinae and taxonomic treatments by Kearfott (1907) and Busck (1906, 1907).

Data analyses.—The years of capture of each species were pooled by decade (i.e., 1900–1909, 1910–1919, 1920–1929, etc.), and a histogram was constructed using these data. A table of capture records for each species by decade was compiled, and the number of species and specimens recorded for each decade was tallied. Changes between the decades 1900–1909 and 1990–1999 were evaluated by comparing species richness and calculating species turnover. Percent change in species richness was calculated by the following equation: $R = b - d/b$, where "b" is the number of species documented from the first decade and "d" is the number of species documented from the last decade. When the number is negative, species richness has declined. Species turnover was calculated by the equation popularized by Diamond (1969): T = (e + c)/(b + d), where "e" is the number of apparent extinctions, "c" is the number of apparent colonizations, "b" is the number of species present at the first date, and "d" is the number of species present at the second date.

The first and last decade were chosen for comparison for two reasons: (1) they represent the greatest time interval and therefore provide the highest likelihood of detecting changes in the fauna; and (2) they are the two most thoroughly sampled decades.

The fate of six species of Tortricidae described around the turn of the century from material collected on Plummers Island was followed: *Ecdytolopha islandana* (Kearfott, 1907), *Proteoteras crescentana* Kearfott, 1907, *Saphenista foxcana* (Kearfott, 1907), *Saphenista plummeriana* (Busck, 1907), *Talponia plummeriana* (Busck, 1906), and *Thyralia gunniana* (Busck, 1907).

RESULTS

A total of 1,095 specimens of Tortricidae from the study area was examined, including 595 historical specimens (pre-1990) in the USNM collection and 500 specimens acquired through field work in 1998–1999. Based on the specimen evidence, during the period 1900 through 1999, 119 species of Tortricidae have been present in the study area at one time or another (see Appendix). This number represents over 60% of the Tortricidae recorded from the entire state of Maryland (i.e., 195 species) (Brown unpubl.). The histogram of number of species by decade (Fig. 2) reflects relative collecting effort by decade. For example, in the first two decades of the century, several entomologists (e.g., C. Heinrich, A. Busck, E. Schwartz, W. Warren, and R. Shannon) were active on Plummers Island, followed by four decades of little activity. In the 1960s and 1970s Ronald W. Hodges and Donald R. Davis, respectively, repeatedly sampled microlepidoptera on Plummers Island, followed by little collecting in the 1980s.

A comparison of the decades 1900–1909 and 1990–1999 revealed that 71 species of leafrollers were present in the study area at the turn of the century (1900–1909) and only 59 today (1990–1999)—a reduction of 17% in species richness. Of the 71 species present at the turn of the century, only 30 are still there. With 41 apparent extinctions and 29 apparent colonizations, there is a species turnover of 54%. Actual species turnover is considerably higher than this value because between the two decades evaluated an additional 19 species were recorded and subsequently disappeared. Because of potential differences in sampling methods (e.g., equipment, diurnal vs. nocturnal, frequency) between the two decades, inventories for the two decades are not strictly comparable. Hence these calculations do not represent precise measurements of changes in the fauna. Nonetheless, it is highly likely that they reflect the overall trend. The status of the six species of leafrollers described from Plummers Island is detailed below.

Ecdytolopha islandana Kearfott (1907) was described from two worn males collected by August Busck in May, probably 1903; it has not been collected since. Although Heinrich (1926) indicated that "it [the only specimen of *E. islandana* he examined] looks like a runted specimen of [*E.*] *insiticiana,*" both specimens lack the male secondary structures characteristic of *E. insiticiana* Zeller. The two specimens of *E. islandana* are nearly identical to *E. mana* (Kearfott), which occurs across the southern U.S. from Alabama to Arizona, and it is likely that the two are conspecific (*E. mana* has priority). *Ecdytolopha mana* has been reported to make galls on the leaves and petioles of *Celtis* sp. (Ulmaceae) in Texas (Brown et al. 1983).

Proteoteras crescentana Kearfott (1907) was described from seven specimens from Iowa, western Manitoba, Ohio, Illinois, and Maryland (Plummers Island). Its known

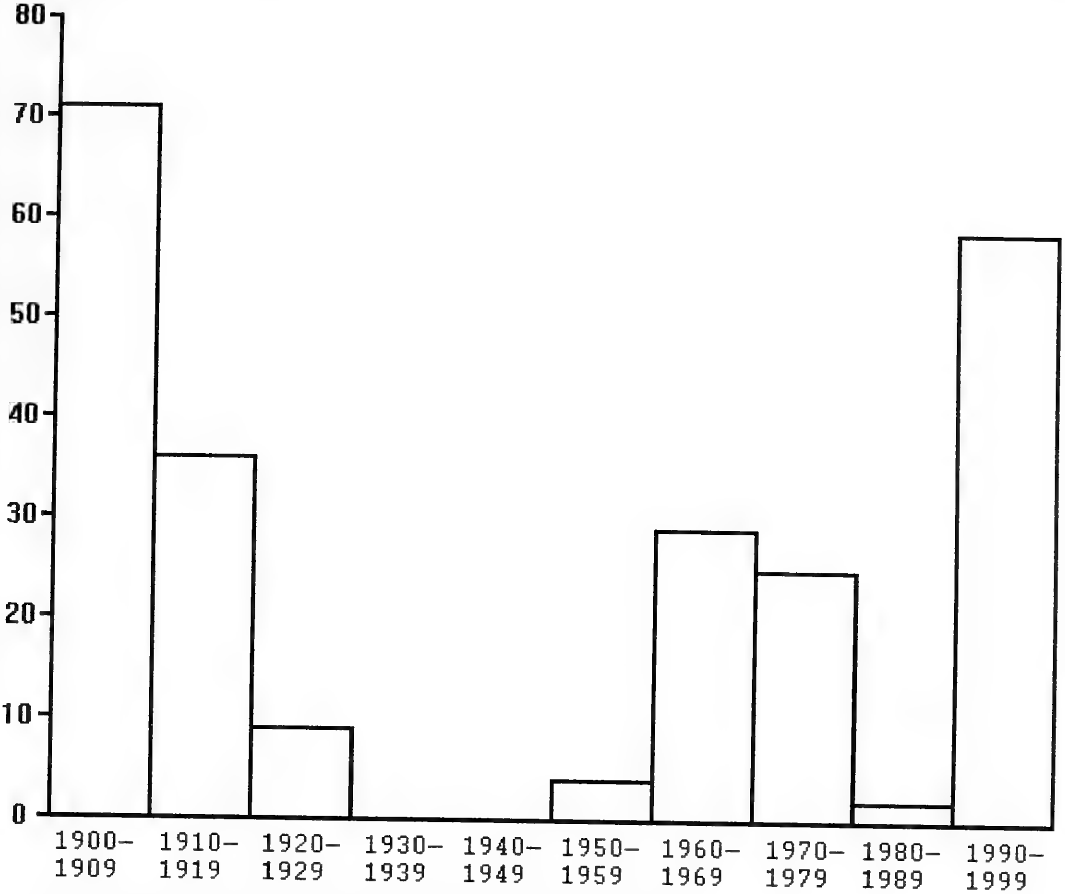

Fig. 2. Histogram of number of species documented (y-axis) by decade (x-axis).

range extends from Maryland west through the mid-western U.S., and north to Manitoba, Canada (Henirich 1923, USNM collection). Of the six species described from Plummers Island, it was the only one that we detected during recent survey work. With 19 specimens captured, it was among the most common species in 1998–1999. The recorded larval host plant is *Acer negundo* (Aceraceae) (Heinrich 1923).

Saphenista foxcana Kearfott (1907) was described from three specimens from Cincinnati, Ohio, and Plummers Island, Maryland. No additional specimens have been documented from the island or elsewhere. The larval host plant is unknown.

Saphenista plummeriana Busck (1907) was described from a single male from Plummers Island collected in May 1903. Two additional specimens were collected from the site in 1914, but it has not been recorded since. This species ranges throughout much of the central Atlantic States from Massachusetts to North Carolina, and west to Illinois and Wisconsin. The larval host plant is unknown, but related Cochylini utilize annual Asteraceae.

Talponia plummeriana Busck (1907) was described from a single male collected on Plummers Island in May 1906. Two additional specimens were collected in 1909, three in 1910, and 101 in 1914; all but the original male were collected as larvae on pawpaw (*Asimina triloba*; Annonaceae). Although the species is now known from Delaware, Kentucky, Maryland, Ohio, Alabama, and Mississippi, it has not been collected on Plummers Island since 1914. It is highly likely that this species is still present but that adults are not attracted to light (R. Brown, in litt.). Hence a thorough search of pawpaw, which is common in the area, is required to determine its presence/absence.

Thyralia gunniana Busck (1907) was described from a single specimen collected on Plummers Island in 1903. No subsequent specimens are known from Plummers Island or any other locality. The larval host plant is unknown, but it is suspected to be an herbaceous Asteraceae.

Of the six species discussed above, all but *P. crescentana* may to be locally extinct, although it is likely that *T. plummeriana* is present but not attracted to lights. While less than convincing, these observations suggests that leafrollers that utilize (or are suspected to utilize) herbs or shrubs as larval food plants have declined, while the only species that feeds on a tree species has not (but see discussion below regarding relative abundance).

Discussion

Explanations for the high species turnover and decline in species richness can be assigned to one of two major categories: sampling error or environmental change. Sampling error may include differences in study area boundaries or in sampling methodologies between the turn of the century and now. Alternatively, observed species turnover and decline may be a real phenomenon resulting from environmental change. Although there are virtually no "hard data" that reliably support arguments for or against these explanations, circumstantial evidence provides a context for briefly exploring each of the hypotheses below.

Shapiro (1998) concluded that species turnover in butterflies rarely can be evaluated using older species lists because of differences or ambiguities between the historical and current boundaries of study sites, and changing taxonomy. Using the example of the butterflies of Truckee, California, he showed that the historical study site of "Truckee" was clearly much larger than the city limits of the current town itself. In contrast, there is considerable evidence that the "Plummers Island" locality of early collectors is the same size as the current study area. Erwin (1981) discusses the history of early collecting and ownership of the area, and it is apparent that other field investigations defined the study area to include both the island and the adjacent shore. Additionally, the current work relied entirely on the examination of specimens, not on older species lists that may have been "biased" by the taxonomy of the era.

Another possible sampling error is that current survey methods may not have been as thorough or effective as those used at the turn of the century. However, one would expect the opposite to be true owing to improved collecting equipment (e.g., blacklight traps that run all night on portable batteries) and improved access to the site, the latter greatly facilitating frequent trips to the area. It is assumed that collecting around the turn of the century was accomplished both diurnally (e.g., larval collections) and nocturnally; the term "at light" on a few older specimen labels indicates that at least some collecting was conducted at night, presumably with kerosene lamps. It is possible that additional years of sampling, expanded seasonal work (i.e., sampling earlier in year), and searching for larvae would result in the documentation of a few additional species, but it seems unlikely that such increases would alter significantly the overall trends. The total of 59 species for 1990–1999 is the second highest decade, and the total of 500 specimens is over twice that of the next highest decade (see Appendix).

Because it is unlikely that observed changes in the fauna are entirely an artifact of sampling error, changes in the environment seem to provide the most likely explanation. The two most conspicuous changes in the landscape between 1900 and the present are the American Legion Memorial Bridge, spanning the Potomac River to the immediate west of the site (completed between 1963–1965), and the dramatic overall change in the plant community. Although the general area undoubtedly has suffered from habitat fragmentation through modest urbanization, an extensive national park that parallels the Potomac River has ensured the continued presence of at least a corridor of native vegetation for potential dispersal and colonization.

Traffic on the American Legion Memorial Bridge probably is responsible for some habitat degradation via air pollution (e.g., Lawrey and Hale 1979, Lawrey 1993), noise pollution, and light pollution, but the impacts of these perturbations are difficult or impossible to quantify because we have no data on these parameters prior to construction of the bridge. Because most leafrollers are nocturnal and attracted to lights, the large number of lights associated with the bridge may possibly interrupt dispersal. Potential leafroller colonists, particularly from the west, may be attracted to the nearby lights of the bridge, become disoriented, and never arrive on the site. However, in one of the few published reviews on the subject, Frank (1988) concluded that disruption of the dispersal of moths by lights is likely to have only a local affect (i.e., 10s of meters). I conclude that the bridge itself probably does not represent a significant barrier to the dispersal of moths, but features associated with the bridge, such as light pollution (potentially disrupting dispersal) and air pollution (potentially diminishing host plant quality in the vicinity) (e.g., Lawrey 1993) may exert a limited, localized affect.

More conspicuous than the bridge is the dramatic change in the vegetation of the study site as a result of plant community succession. When the Washington Biologists' Field Club first leased Plummers Island in 1901, the vegetation was described as an open juniper grassland (Erwin 1981). Approximately 3 hectares of the adjacent northern shore had been cleared for agriculture or timber. Owing to the protected status of the site over the last century, activities that degrade the habitat were ceased (starting in about 1907), and plant community succession has proceeded unabated. Today nearly the entire study area supports a rather homogeneous submature hickory-maple-oak woodland, with scattered tuliptrees (*Liriodendron tulipifera*; Magnoliaceae) and a moderately depauperate understory.

Because the larvae of all leafrollers are phytophagous (plant-feeding) and many are fairly host specific, it is logical to assume that changes in floral composition associated with plant community successional would lead to changes in leafroller species composition. Although succession represents the likely mechanism behind species turnover, the decline in species richness is more difficult to explain, given that the site continuously has supported native vegetation. It is possible that diminished habitat heterogeneity on the site, increased habitat fragmentation in the general area, and lowered habitat quality from pollution all have contributed to the overall decline in species numbers.

Changes in relative abundance of the most common species are summarized in Table 1. Of the 10 most common species in 1900–1909 (based on number of specimens), four are still among the most common (i.e., *Choristoneura rosaceana, Clepsis peritana, Platynota idaeusalis,* and *Coelostathma discopunctana*), five are still present but apparently in lower relative abundance, and two apparently are locally extinct. All four of the species that are still common are general feeders (polyphagous) as larvae; of the five still present but at lower relative abundance, two are general feeders and three specialists; and the two species that are extinct are both specialists—*Bactra furfurana* on *Cyperus* sp. (Cyperaceae) and *Ecdytolopha insiticiana* on *Robinia pseudoacacia* (Fabaceae). The most abundant species of the decade 1990–1999 (i.e., *Endothenia hebesana*) is highly polyphagous. Based on this small data set, there appears to be a positive correlation

Table 1. Most common species 1900–1909 and 1990–1999 (based on number of capture records).

1900–1909 (number of specimens 1900–1909—number of specimens 1990–1999)
1. *Clepis peritana* (15-77)
2. *Choristoneura rosaceana* (15-36)
3. *Coelostathma discopunctana* (14-14)
4. *Argyrotaenia velutinana* (13-3)
5. *Platynota idaeusalis* (10-14)
6. *Ecdytolopha insiticiana* (10-0)
7. *Eucosma derelicta* (9-2)
8. *Olethreutes concinnana* (8-2)
9. *Eucosma sombreana* (7-2)
10. *Bactra furfurana* (7-0)

1990–1999 (number of specimens 1990–1999—number of specimens 1900–1909)
1. *Endothenia hebesana* (95-5)
2. *Clepsis peritana* (77-15)
3. *Choristoneura rosaceana* (36-15)
4. *Notocelia trimaculana* (23-1)
5. *Proteoteras aesculana* (19-1)
6. *Proteoteras crescentana* (19-1)
7. *Acleris negundana* (16-1)
8. *Olethreutes fasciana* (16-4)
9. *Platynota idaeusalis* (14-10)
10. *Acleris semipurpurana* (14-0)
11. *Coelostathma discopunctana* (14-14)

between polyphagy and persistence. Additional support for this relationship can be found in the limacodid fauna (Lepidoptera: Limacodidae) of Plummers Island, which has changed very little over the past 100 years (M. Epstein, unpubl.); i.e., a species turnover of less than 10%. All of the resident limacodids are relatively polyphagous and are considered generalists.

Deviations from the pattern of "persistence by polyphagy" can be found. For example, although *Argyrotaenia velutinana* is a generalist, it has declined in relative abundance. While one might expect any species to persist as long as its larval host plant persists, *E. insiticiana* and *B. furfurana* apparently are locally extinct even though *Robinia* and *Cyperus* (their respective hosts) are still present in the study area.

In two other studies on insects, community succession or habitat change was implicated as the primary cause of changes in the fauna. In a study of the carabid beetles (Coleoptera: Carabidae) of Plummers Island, Erwin (1981) found records of 189 species from the turn of the century and 107 for the decade of 1971–1980, resulting in a turnover of about 45% and a reduction of species richness of about 43%. In a recent study on oecophorid moths (Jensen and Brown unpubl.), turnover was estimated to be about 34%, with a decline in species richness of only about 10%.

Similar patterns of declines in species richness or in populations of specific species as a result of succession or "habitat maturation" have been reported for a variety of bird species (e.g., Karr 1968, Morgan and Freedman 1987, Hunt 1998) and/or bird faunas (e.g., Willis 1974, Willis and Eisenmann 1979, Karr 1982). Litvaitis (1993) proposed that forest maturation was the mechanism behind regional declines of several bird and mammal species that require early successional habitat in the northeastern United States. The findings presented herein, together with those of Erwin (1981) and Jensen and Brown (unpubl.), suggest that this may be true for some invertebrates as well.

Potential implications of the findings of this study in a conservation or habitat management context are few, but include the following. First, caution must be exercised when compiling species inventories for comparing richness between or among sites for purposes of assigning or evaluating conservation priorities. That is, mixing historical and current data may present an extremely biased view of the actual species richness of a site. Although the cumulative data would lead one to believe that 119 species of leafrollers are present on Plummers Island, it is highly unlikely that the island has supported more than about 71 species at any given time over the past 100 years. The common practice of constructing species distribution maps based on cumulative specimen capture records likewise portrays data in a manner that does not reflect reality.

It generally is accepted that an asymptote in a species discovery curve provides a reasonable estimate of the number of species resident at a particular site being sampled (e.g., Caldwell and Coddington 1994). However, if the curve has been generated by sampling efforts spanning many years (e.g., Powell 1995), the asymptote may reflect the number of species that have been present over the sampling period, not the actual number of species present on the site at any given time. Hence, the asymptote may actually over-estimate the fauna. The longer the sampling time, the more likely the asymptote will over-estimate the fauna.

Finally, the "preservation" of Plummers Island (i.e., the interruption of activities that degrade the habitat or maintain some land in a state of early succession) has allowed the habitat to revert slowly to a homogeneous, subclimax community that supports considerably fewer species than were present prior to implementation of this policy. This and other studies (e.g., Morris and Web 1987, Bollinger 1995, Hunt 1998) suggest that the maintenance of at least some successional habitat may be critical for the maintenance of species richness, and that protection or management in the form of "benign neglect" may have significant, negative impacts on the species richness of a local site.

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Appendix. Capture data for Tortricidae of Plummers Island.

	1900 1909	1910 1919	1920 1929	1930 1939	1940 1949	1950 1959	1960 1969	1970 1979	1980 1989	1990 1999	1st Year
OLETHREUTINAE											
Endotheniini											
Endothenia hebesana (Walker)	5	0	0	0	0	0	2	1	0	95	1903
Endothenia nubilana (Clemens)	0	2	0	0	0	0	1	0	0	1	1919
Hulda impudens (Walsingham)	1	1	0	0	0	0	0	0	0	0	1903
Bactrini											
Bactra furfurana (Haworth)	7	0	0	0	0	0	0	0	0	0	1903
Bactra verutana (Zeller)	0	0	0	0	0	0	0	0	0	6	1998
Olethreutini											
Endopiza viteana Clemens	1	0	0	0	0	0	0	0	0	0	1903
Episimus argutanus (Clemens)	1	0	0	0	0	0	0	2	0	2	1903
Eumarozia malachitana (Zeller)	1	0	0	0	0	0	0	0	0	3	1903
Hedya cyanna (Murtfeld)	0	0	0	0	0	0	0	0	0	1	1998
Olethreutes astrologana (Zeller)	1	2	0	0	0	0	0	0	0	4	1903
Olethreutes cespitana (Hübner)	2	0	0	0	0	0	1	0	0	0	1903
Olethreutes clavana (Walker)	0	0	0	0	0	0	0	3	0	1	1971
Olethreutes concinnana (Clemens)	7	0	0	0	0	0	0	4	0	3	1903
Olethreutes coruscana (Clemens)	1	0	4	0	0	0	0	0	0	1	1903
Olethreutes fasciatana (Clemens)	5	7	1	0	0	0	0	0	0	16	1903
Olethreutes inornata (Walsingham)	0	0	0	0	0	0	0	0	0	1	1998
Olethreutes permundana (Clemens)	0	0	0	0	0	0	1	0	0	0	1962
Phaecasiophora confixana (Walker)	2	2	0	0	0	0	1	3	0	4	1903
Phaecasiophora nieveigutana Grote	4	3	0	0	0	0	0	1	0	0	1902
Pristerognatha fuligana (D. & S.)	2	0	0	0	0	0	0	0	0	0	1903
Eucosmini											
Catastega aceriella Clemens	0	0	0	0	0	0	0	0	0	4	1998
Chimoptesis gerulae (Heinrich)	0	0	0	0	0	0	1	0	0	0	1962
Chimoptesis pennsylvaniana (Kearfott)	0	0	0	0	0	0	6	0	0	0	1962
Epiblema boxcana (Kearfott)	1	0	0	0	0	0	0	0	0	0	1903
Epiblema carolinana (Wlsm.)	0	0	0	0	0	0	0	1	0	4	1972
Epiblema otiosana (Clemens)	0	0	0	0	0	0	0	0	0	2	1998
Epiblema strenuana (Walker)	2	1	0	0	0	0	0	0	0	1	1902
Epiblema nr. *abruptana* (Walsingham)	0	0	0	0	0	0	0	0	0	1	1999
Epiblema sp.	0	0	0	0	0	0	0	0	0	5	1998
Epinotia sotipena Brown	0	0	0	0	0	0	3	0	0	2	1962
Epinotia walkerana (Kearfott)	0	1	0	0	0	0	0	0	0	0	1919
Eucosma albiguttana (Zeller)	1	0	0	0	0	0	0	0	0	0	1903
Eucosma cataclystiana (Walker)	2	2	0	0	0	0	0	0	0	0	1903
Eucosma derelicta Heinrich	8	2	1	0	0	1	0	1	0	3	1903
Eucosma dorsisignatana (Clemens)	1	0	0	0	0	0	0	0	0	0	1909
Eucosma gomonana Kearfott	2	0	0	0	0	0	21	0	0	0	1909
Eucosma mandana Kearfott	2	0	0	0	0	0	0	0	0	5	1902
Eucosma similana (Clemens)	0	0	0	0	0	0	0	0	0	3	1998
Eucosma sombreana Kearfott	7	0	0	0	0	0	0	0	0	2	1902
Gretchena deludana (Clemens)	2	0	0	0	0	0	1	0	0	1	1903
Gretchena bolliana (Slingerland)	1	1	0	0	0	0	0	0	0	0	1907
Gretchena delicatana Heinrich	0	1	0	0	0	0	4	1	0	1	1920
Notocelia trimaculana (Haworth)	1	0	0	0	0	0	0	0	0	23	1905
Pelochrista womonana Kearfott	1	0	0	0	0	0	0	0	0	0	1903
Pelochrista zomonana (Kearfott)	1	0	0	0	0	0	0	0	0	0	1906
Phaneta paramatana (Clemens)	7[1]	0	0	0	0	0	0	2	0	6	1903
Proteoteras aesculana Riley	1	0	0	0	0	0	3	1	0	19	1903
Proteoteras willingana (Kearfott)	0	1	0	0	0	0	0	0	0	7	1919
Proteoteras crescentana Kearfott	2	0	1	0	0	0	1	1	0	19	1903

Appendix. Continued.

	1900 1909	1910 1919	1920 1929	1930 1939	1940 1949	1950 1959	1960 1969	1970 1979	1980 1989	1990 1999	1st Year
Pseudexentera spoliana (Clemens)	0	0	0	0	0	0	2	0	0	0	1962
Pseudexentera virginiana (Clemens)	0	0	0	0	0	0	2	0	0	0	1962
Suleima helianthana (Riley)	1	0	0	0	0	0	0	0	0	0	1903
Suleima cinerodorsana Heinrich	1	0	0	0	0	0	0	0	0	0	1908
Enarmoniini											
Ancylis comptana (Frölich)	1	0	0	0	0	0	0	0	0	0	1903
Ancylis diminutana (Haworth)	1	0	0	0	0	0	1	0	0	0	1903
Ancylis divisana (Walker)	0	0	0	0	0	0	2	0	0	0	1962
Ancylis platanana (Clemens)	1	1	1	0	0	0	0	0	0	12	1903
Grapholitini											
Cydia caryana (Fitch)	0	2	0	0	0	0	0	0	0	1	1919
Cydia pomonella (Linnaeus)	0	1	0	0	0	0	0	0	0	0	1919
Dichrorampha bittana (Busck)	0	1	0	0	0	0	0	0	0	0	1919
Dichrorampha leopardana (Busck)	0	0	1	0	0	0	0	0	0	0	1929
Dichrorampha simulana (Clemens)	0	1	0	0	0	0	0	0	0	0	1919
Ecdytolopha punctidiscanum (Dyar)	1	0	0	0	0	0	0	0	0	0	1903
Ecdytolopha insiticiana Zeller	10	0	0	0	0	0	0	0	0	0	1903
Ecdytolopha islandana (Kearfott)	2	0	0	0	0	0	0	0	0	0	1903
Grapholita fana (Kearfott)	1	1	0	0	0	0	0	0	0	0	1903
Grapholita interstinctana (Clemens)	4	0	0	0	0	0	1	0	0	0	1902
Grapholita packardi Zeller	1	0	0	0	0	0	0	0	0	0	1903
Pseudogalleria inimicella (Zeller)	3	0	0	0	0	0	0	0	0	0	1902
Talponia plummeriana (Busck)	3	101	0	0	0	0	0	0	0	0	1906
TORTRICINAE											
Sparganothini											
Amorbia humerosana Clemens	6	1	1	0	0	0	0	0	0	0	1905
Coelostathma discopunctana Clemens	14	2	1	0	0	1	0	0	0	14	1903
Platynota exasperatana (Zeller)	0	1	0	0	0	0	0	1	0	0	1919
Platynota flavedana Clemens	0	1	0	0	0	0	0	1	0	0	1919
Platynota idaeusalis (Walker)	10	8	0	0	0	0	0	1	8	14	1903
Sparganothis diluticostana (Wlsm.)	0	0	0	0	0	0	1	0	0	0	1962
Sparganothis reticulatana (Clemens)	1	1	0	0	0	0	0	0	0	1	1908
Sparganothis sulfureana (Clemens)	0	4	0	0	0	0	0	0	0	0	1919
Sparganothis tristriata Kearfott	1	0	0	0	0	0	0	0	0	0	1908?
Sparganothis xanthoides Walker	0	0	0	0	0	0	0	1	0	0	1971
Tortricini											
Acleris cervinana (Fernald)	1	0	0	0	0	0	0	1	0	0	1905
Acleris chalybeana (Fernald)	2	5	0	0	0	0	2	0	0	0	1907
Acleris curvalana (Kearfott)	0	0	0	0	0	0	0	0	0	2	1998
Acleris flavivittana (Clemens)	0	0	0	0	0	0	0	0	0	1	1999
Acleris negundana (Busck)	1	26	0	0	0	0	3	0	0	16	1908
Acleris nivisellana (Wlsm.)	0	0	0	0	0	0	0	0	0	1	1998
Acleris schalleriana (Linnaeus)	1	0	0	0	0	0	0	0	0	12	1903
Acleris semipurpurana (Kearfott)	0	0	0	0	0	0	0	2	0	14	1971
Archipini											
Archips grisea (Robinson)	0	0	0	0	0	0	0	0	0	1	1999
Argyrotaenia alisellana (Robinson)	0	0	0	0	0	0	0	0	0	4	1998
Argyrotaenia mariana (Fernald)	1	0	0	0	0	0	0	0	0	0	1905
Argyrotaenia tabulana Freeman	0	0	0	0	0	0	1	0	0	0	1963
Argyrotaenia quercifoliana (Fitch)	0	0	0	0	0	0	4	6	0	10	1962
Argyrotaenia velutinana (Walker)	13	1	0	0	0	0	11	2	0	3	1903
Choristoneura fractivittana (Clemens)	0	0	0	0	0	0	0	4	0	5	1972
Choristoneura obsoletana (Walker)	1	0	0	0	0	0	0	0	0	0	1908
Choristoneura rosaceana (Harris)	15	1	1	0	0	0	3	9	0	36	1903
Choristoneura parallela (Robinson)	0	0	0	0	0	0	0	0	1	4	1981

Appendix. Continued.

	1900 1909	1910 1919	1920 1929	1930 1939	1940 1949	1950 1959	1960 1969	1970 1979	1980 1989	1990 1999	1st Year
Clepsis melaleucana (Walker)	2	0	0	0	0	0	0	1	0	4	1903
Clepsis peritana (Clemens)	15	3	0	0	0	0	4	5	0	77	1903
Pandemis lamprosana (Robinson)	0	0	0	0	0	2	0	2	0	10	1957
Pandemis limitana (Robinson)	3	4	0	0	0	0	0	0	0	3	1903
Syndemis afflictana (Walker)	4	0	0	0	0	0	4	0	0	0	1905
Cochylini											
Aethes angustana (Robinson)	5	0	0	0	0	1	0	0	0	1	1903
Aethes argentilimitana (Robinson)	4	0	0	0	0	0	0	0	0	0	1903
Aethes aureana (Busck)	0	0	0	0	0	0	1	0	0	0	1968
Aethes floccosana (Walker)	1	0	0	0	0	0	0	0	0	0	1908
Carolella sp.	0	0	0	0	0	0	0	0	0	1	1999
"*Cochylis*" *oenotherana* (Robinson)	1	1	0	0	0	0	0	0	0	0	1903
Recavicula hoffmanana (Kearfott)	5	0	0	0	0	0	0	0	0	0	1903
Saphenista foxcana Kearfott	2[2]	0	0	0	0	0	0	0	0	0	1903
Saphenista plummeriana (Busck)	1	2	0	0	0	0	0	0	0	0	1906
Saphenista straminoides (Grote)	0	1	0	0	0	0	0	0	0	0	1916
Thyralia bunteana (Robinson)	0	0	0	0	0	0	1	0	0	2	1962
Thyralia gunniana (Busck)	1	0	0	0	0	0	0	0	0	0	1903
Trachysmia baracana (Busck)	1	0	0	0	0	0	0	0	0	0	1903
Trachysmia birdana Busck	0	0	0	0	0	0	0	0	0	3	1998
Trachysmia terminana (Busck)	3	0	0	0	0	0	0	0	0	1	1905
Trachysmia sp.	0	0	0	0	0	0	0	0	0	1	1999
# of spp. by decade	71	36	9	0	0	4	29	25	2	59	
# of specimens	227	196	12	0	0	5	89	57	9	500	

[1] Heinrich (1923) described *Thiodia alterana* (syn. of crispana) from 7 specimens collected on Plummers Island, August 1903.

[2] One specimen in AMNH not examined; cited by Klots 1942.

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REVIEW OF THE NEARCTIC SPECIES OF *LIMOTETTIX* (*SCLERORACUS* VAN DUZEE) LEAFHOPPERS (HEMIPTERA: CICADELLIDAE: DELTOCEPHALINAE)

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Abstract.—Descriptions, illustrations, distributions, host plant records, and an identification key are provided for the 32 Nearctic species of the subgenus *Limotettix* (*Scleroracus*), tribe Athysanini, which includes at least two species (one Nearctic) known to vector phytopathogens. Two **new synonymies** are proposed: *Frigartus* Oman to synonymy under *Limotettix* (*Scleroracus*); and *Ophiola uhleri speculatus* Ball to synonymy under *L.* (*S.*) *uhleri* Ball. One **new combination** is proposed, *L.* (*S.*) *frigidus* (Ball) (from *Frigartus*). A lectotype is designated for *Athysanus frigidus* Ball.

Key Words: *Frigartus,* vector, cranberry, phytopathogen, Membracoidea

The subgenus *Limotettix* (*Scleroracus* Van Duzee) is Holarctic in distribution with most species Nearctic. Species feed on ericaceous plants as well as other families (Table 1). Two species have been reported as vectors of phytopathogens (Nielson 1968): *L.* (*S.*) *flavopictus* (Ishihara), a vector of potato witches' broom virus and Japanese aster yellows virus in Japan, and *L.* (*S.*) *vaccinii* (Van Duzee), a vector of false blossom virus of cranberry (*Vaccinium,* Ericaceae) in the Eastern United States. Other species may also vector phytopathogens, but as yet there is too little known about the biology of most species to be sure.

Although three species were thought previously to be transboreal, Hamilton (1994) ascertained correctly that the Nearctic and Palearctic forms represented separate species. Ossiannilsson (1983) provided descriptions and illustrations of the three species, all under *Ophiola*: *cornicula, russeola,* and *striatula* [under *O. decumana* (Kontkanen)]. The Palearctic Region additionally holds 10 other species.

In most previous, illustrated, descriptive work on the subgenus (Medler 1955b, 1958a, b; Beirne 1956, Hamilton 1994), references to genitalic illustrations have replaced descriptions of most particular features, leading to ambiguous morphological representation (see Morphology, below) and there have been none or few habitus illustrations, which can approximate species identity, especially of female specimens. This revision takes the opposite approach; an abbreviated description of coloration is given, with reference to full habitus digital photographs, and the genitalia are both illustrated and described. Furthermore, the distinction between *L.* (*Scleroracus*) and *Frigartus,* a closely related genus, warranted examination. The objective of the present study is to verify the limits of the subgenus and its Nearctic species, provide identification aids (keys, descriptions, and illustrations) and summarize the distribution and host plants of all Nearctic species.

Table 1. Host plant data for *Limotettix* (*Scleroracus*) species, taken from label data or from literature (footnoted). Some plants may not be true, feeding or breeding hosts.

Plant Family	Plant Genus	*Limotettix* (*Scleroracus*) Species
Amaranthaceae	*Amaranthus*	*arctostaphyli*
Anacardiaceae	*Rhus*	*instabilis*
Asteraceae	*Achillea*	*dasidus*
	Ambrosia	*bullatus*
	Artemisia	*frigidus*
	Solidago	*anthracinus, bullatus, comptonianus, osborni*
	undet. genus	[2]*kryptus,* [2]*uhleri,* [2]*varus*
Caprifoliaceae	*Symphoricarpos*	*finitimus, myralis,* [1]*symphoricarpae,* [2]*melastigmus*
Chenopodiaceae	*Atriplex*	*Fridgidus*
	Beta	*glomerosus*
	Sarcobatus	*glomerosus*
Cyperaceae	*Carex*	*humidus*
Ericaceae	*Arctostaphylos*	*humidus, obesura, osborni,* [1]*arctostaphyli,* [2]*luteolus*
	Chamaedaphne	*humidus, vaccinii*
	Gaylussacia	*vaccinii*
	Ledum	*vaccinii*
	Vaccinium	*vaccinii*
Juglandaceae	*Carya*	*kryptus*
Myricaceae	*Comptonia*	*comptonianus*
Pinaceae	*Pinus*	*comptonianus*
Poaceae	*Festuca*	*finitimus*
Rosaceae	*Fragaria*	*melastigmus*
	Prunus	*instabilis, plutonius, shastus*
	Rubus	*osborni*
Salicaceae	*Populus*	*anthracinus*
	Salix	*arctostaphyli, bullatus, dasidus, instabilis, vaccinii*
Solanaceae	*Solanum*	*plutonius*

[1] Medler 1958b.
[2] Hamilton 1994.

LITERATURE REVIEW

Scleroracus was originally described as a genus (Van Duzee 1894c). Species were added by Osborn (1915a), Ball (1902a, 1928c), and Sleesman (1930). Oman (1949a) characterized the genus and listed Nearctic species and also described a new genus, *Frigartus,* assigning as type a species described by Ball (1899c). Medler (1955b, 1958a) described eight new species in *Scleroracus* and later (1958b) provided the first thorough treatment of the Nearctic species of the genus based on male genitalia, establishing new synonymies with species of other genera and providing an identification key. Hamilton (1994) described six additional species, illustrated many others as well, and referred some previously described species to other subgenera of *Limotettix.*

Since its inception, there has been question of the generic status of *Scleroracus.* Although the concept of the group has remained fairly stable, some workers use the alternative name *Ophiola* Edwards, 1922. Another synonym, *Omaniella* Ishihara, 1953, was synonymized a year after its description. Nielson (1968) and Hamilton (1994) treated *Ophiola* and *Omaniella* as junior synonyms of *Scleroracus.* Furthermore, Ribaut (1952a), Hamilton & Langor (1987) and Hamilton (1994) considered *Scleroracus* to be a subgenus of *Limotettix* Sahlberg. Emeljanov (1999) distinguished *Limotettix* from *Ophiola* on the basis of the orientation of the male pygofer processes, being directed downward in the former and upward in the latter, and the aedeagal processes, being fused in *Ophiola* and "usually" articulated in *Limotettix.* Other taxa, all described as subgenera of *Limotettix,* include *Ophiolix* Ribaut, 1942, *Neodrylix* Emeljanov, 1966, and *Dryola* Hamilton, 1994. All the aforementioned taxa share a sclerotized dorsal apodeme, or dorsal connective, of the aedeagus, which is absent in other Athysanini and a long, narrow, ventral connective, which occurs in few other genera of the tribe, so Hamilton's (1994) generic classification is followed here. The subgenus *Limotettix* (*Scleroracus*) can be distinguished from other Deltocephalinae based on the head coloration (most species) and male terminalia features given in the diagnosis below.

Hamilton (1994) argued for an evolutionary scenario of ecological association of *Limotettix,* arising in swale and fen habitats, colonizing bogs and, finally, by *L.* (*Scleroracus*) transferring to ericaceous hosts that also occur outside of bogs, enabling invasion of and radiation in drier habitats. As delimited by Hamilton (1994), the subgenus *Scleroracus* included 44 species, 31 of which are Nearctic. In the present work, one previously described species is referred to the subgenus and one subspecies is synonymized under its species, being recognized as a simple variant, yielding a total of 32 species. Hosts are unknown for 13 species.

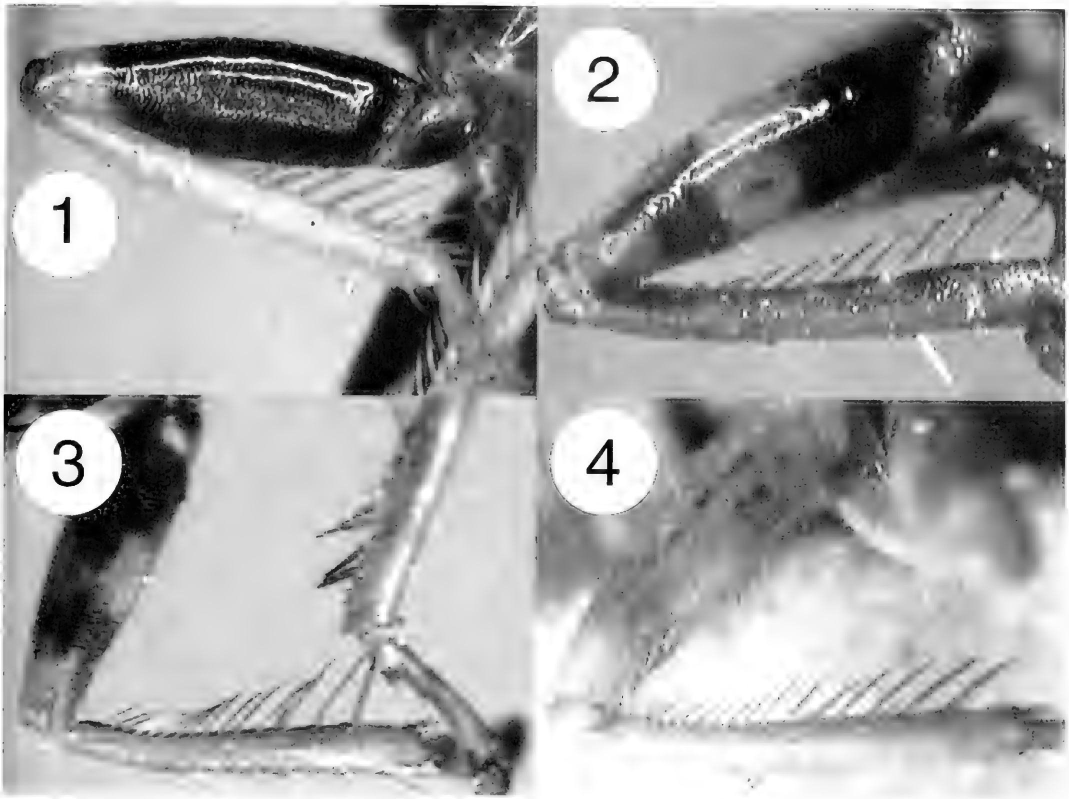
MATERIALS AND METHODS

Literature citations through 1955 are consistent with Metcalf's (1964) bibliography of the Cicadelloidea and are not repeated in the bibliography here.

The entire male genital complex of *L.* (*Scleroracus*) specimens (Fig. 11) is approximately 0.7 mm long and 0.5 mm wide. Extraction for detailed examination, using fine forceps and a minuten-nadeln-tipped wooden applicator stick, was essentially a four-stage operation: preparing the abdomen; exposing the genitalia; isolating the aedeagus; and disconnecting the styles from the subgenital plates. First, the abdomen was dislodged from the rest of the body by inserting the minuten-nadeln-tipped wooden applicator stick between the thoracic and abdominal sterna. The abdomen was then heated in a weak potassium hydroxide (KOH) solution for approximately 45 minutes, rinsed in water, and placed in glycerin. Second, the ninth segment was separated from the rest of the abdomen and the lateral connection between the tergum (the pygofer, Figs. 5–7) and sternum IX plus subgenital plates was severed. Lifting the pygofer was sufficient to tear its connection with the dorsal connective, and exposed the genitalia. Third, the articulated aedeagus was easily dislodged with a lateral force (resulting in Fig. 8). Fourth, the last strong connection between the genitalia and the abdomen was severed by bracing the subgenital plate while pressing the sharpened point of the minuten nadeln between the ventral lobe of the styles (Fig. 10) and the corresponding concavity (Fig. 9) of each subgenital plate. After examination, the aedeagus was pushed into the abdominal cavity and the entire preparation was stored in glycerin in a polypropylene microvial beneath the specimen.

Digital images were captured at 400 dpi resolution by mounting a Sony® DKC5000 digital camera on a Leitz® Diaplan compound microscope (for the genitalia) or at 72 dpi (17 × 13 inch images) using a Fujifilm® Fujix HC-3002 digital camera mounted on a Wild® Heerbrugg M400 stereoscopic microscope.

Specimen depositories are: National Museum of Natural History, Smithsonian Institution, Washington, DC, USA (USNM), Canadian National Collection, Ottawa (CNCI), Snow Entomological Museum, University of Kansas, Lawrence, KS, USA (SEMC), Ohio State University, Department of Entomology, Columbus, OH, USA (OSUC), California Academy of Sciences, San Francisco, CA, USA (CASC), and North Carolina State University, Raleigh,



Figs. 1–4. Prothoracic legs of selected *Limotettix* (*Scleroracus*). 1, *L.* (*S.*) *uhleri*, with the bicolored coloration pattern, also present in *L.* (*S.*) *anthracinus*, *L.* (*S.*) *kryptus*, and *L.* (*S.*) *osborni*. 2–3, *L.* (*S.*) *cachcolus*, and *L.* (*S.*) *vaccinii*, respectively, with the more usual femoral coloration and tibial setal size gradually increasing distally. 4, *L.* (*S.*) *omani*, with tibial setal size bimodal.

NC, USA (NCSU). Primary type specimen data is cited by separating labels by quotation marks and separating individual lines within a label by a vertical line (|).

Morphology

The coloration of *L.* (*Scleroracus*) species can assist in identification, but in some species it is quite variable. The coloration of the pro- and mesothoracic legs is more stable than that of the head, nota, or wings. The bicolored pattern, as used in the key and descriptions below, refers to the femora being shining black or very dark brown to just before apex, then abruptly yellow or orange and concolorous with the tibiae (Fig. 1). The more common pattern is the pro- and mesothoracic femora being twice-banded with fuscous (Figs. 2, 3).

The head varies in degree of protrusion, in dorsal view, and the length of the vertex relative to its width (measured as the minumum width between the eyes, to minimize the effect of measurement error on the ratio). Although most species with a protruding head have a long vertex, some short-vertex species also have protruding heads, epitomized by *L.* (*S.*) *instabilis* (Fig. 99).

Chaetotaxy of the prothoracic tibia falls into two categories: unimodal, in which the basal setae (basal row AV of Rakitov 1998) gradually increase in size distally, lacking a distinct division in size between the basal setae and the distal, larger setae (distal row AV of Rakitov 1998; Figs. 2, 3), and bimodal, in which the size distinction between the two setal groups of row AV is clear (Fig. 4). This feature is included in the descriptions but avoided for the key and diagnoses because the condition can be difficult to ascertain in some specimens (e.g., Fig. 1).

The posterior margin of female sternum VII is a useful diagnostic feature for many leafhopper taxa, but is almost invariable in *L.* (*Scleroracus*), consisting of a broad, shallow excavation, weakly produced posterad in the middle. Suggestions for identifying female specimens are given immediately preceding the key to males.

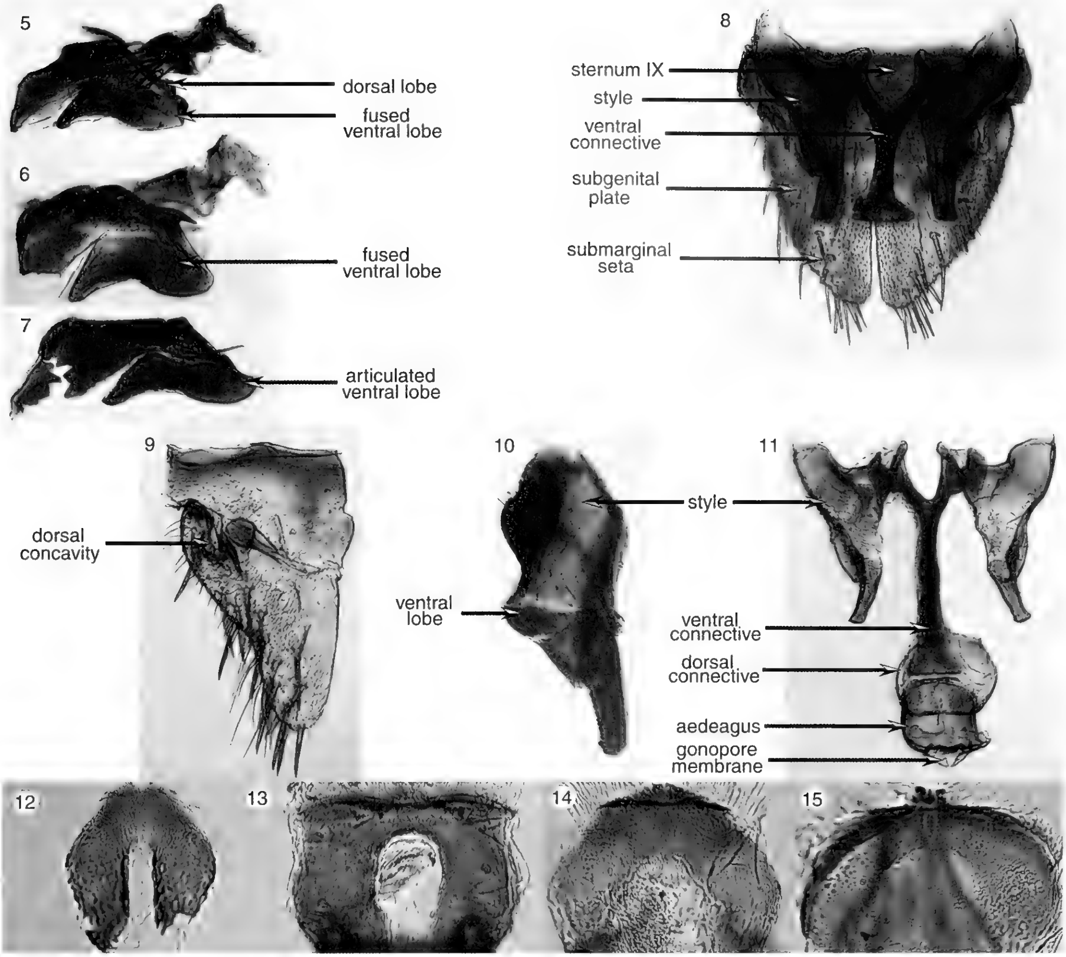
The most reliable character suite for diagnosing species of *L.* (*Scleroracus*) is the male terminalia, i.e., the abdominal segment IX and the genitalia (Figs. 5–15). Most of the features described below are common among species of Deltocephalinae; for example, a Y-shaped ventral connective with an articulated aedeagus occurs in more than half of the Nearctic deltocephaline genera.

The male pygofer (tergum IX) of *L.* (*Scleroracus*) is divided posteriorly into two lobes. The dorsal lobe is most often posteriorly truncate (Fig. 5) but sometimes bears a posterior spine (Fig. 6). The ventral lobe may be fixed-fused (Figs. 5, 6) or articulated-fused (i.e., free anteriorly and posteriorly, and with a weakened line of juncture in the middle, Fig. 7) with the rest of the pygofer. Beneath the pygofer and above the subgenital plates lie the genitalia (Fig. 8).

The male genitalia consist of a pair of lateral parameres, or styles, a ventral connective, aedeagus, and dorsal connective. The styles themselves are, in dorsal view, subtriangular with a robust base (Fig. 11), a ventral lobe at mid length (Fig. 10), and a more slender distal portion that varies slightly in length and width among species. The styles are stabilized laterally by an articulation with the basolateral region of the subgenital plates. Specifically, the articulation is between the ventral lobe of the style and a dorsal, basolateral concavity of the subgenital plate (Fig. 9). The style is stabilized mesially by an articulation with each arm of a Y-shaped ventral connective (Fig. 11) that extends posterad longitudinally and bears, on its apex, an articulation to the ventral lip of the atrium of the aedeagus, which is usually U-shaped in lateral view. The dorsal lip of the aedeagal atrium is articulated with a dorsal connective (Figs. 11–15) that articulates with a fragile membrane to the inner dorsal margin of the pygofer. The U-shape of the aedeagus derives from a constriction of the aedeagal atrium before the shaft, which is plate-like, except in *L.* (*S.*) *frigidus* and *L.* (*S.*) *symphoricarpae,* in which it is tubular.

Arising distally or posteriorly from the aedeagal shaft, between the paired apical processes, is the gonopore, which is usually surrounded by a large membranous tube. Often, however, there is weak sclerotization at the base or sides of the gonopore membrane that in posterior or lateral view can resemble an apical process of the aedeagus. This has led to ambiguous or misleading illustrations, especially for *L.* (*S.*) *beameri, L.* (*S.*) *glomerosus, L.* (*S.*) *kryptus, L.* (*S.*) *luteolus, L.* (*S.*) *vaccinii,* and *L.* (*S.*) *varus* (Figs. 40, 90, 111, 117, 203, 209). In five species [*L.* (*S.*) *finitimus, L.* (*S.*) *frigidus, L.* (*S.*) *shastus, L.* (*S.*) *symphoricarpae,* and *L.* (*S.*) *uhleri*; Figs. 76, 84, 171, 183, 195, respectively], there is strong sclerotization on the sides of the gonopore membrane, and in two of these [*L.* (*S.*) *frigidus* and *L.* (*S.*) *symphoricarpae*] there is some posterior sclerotization as well, with reduction of apical processes, producing a tubular, rather than plate-like, aedeagus (Figs. 84, 185).

The ventral connectives of different species are distinguished in the descriptions in two ratios: the width between the basal arms of the Y-shape compared to its total length, and the length of the distal bar compared to the ventral connective's total length. The ventral connective exceeds the style apices [except in *L.* (*S.*) *frigidus* and *L.* (*S.*) *melastigmus*] and its total length varies from 2.2–4.0 × its width across its anterior arms and 1.6–3.7 × their longitudinal length.



Figs. 5–15. Morphology of male terminalia of *Limotettix* (*Scleroracus*). 5–7, Pygofer of *L.* (*S.*) *comptonianus*, *L.* (*S.*) *shastus*, and *L.* (*S.*) *uhleri*, respectively, lateral aspects. 8, Styles, ventral connective, sternum IX, and subgenital plates of *L.* (*S.*) *melastigmus*, dorsal aspect. 9, Left half of sternum IX and left subgenital plate of *L.* (*S.*) *frigidis*, dorsal aspect. 10, Left style of *L.* (*S.*) *scudderi*, lateral aspect. 11, Styles, ventral connective, aedeagus, and dorsal connective of *L.* (*S.*) *zacki*, dorsal aspect. 12–15, Dorsal connectives of *L.* (*S.*) *bullatus*, *L.* (*S.*) *symphoricarpae*, *L.* (*S.*) *omani*, and *L.* (*S.*) *shastus*, respectively, ventral aspects.

The ventral emargination of sclerotization of the dorsal connective varies in breadth, length, and the lateral shape, usually being narrow (approximately half the width of that shown in Fig. 12), deep (Fig. 12), and parallel-sided (Fig. 12), but can be wide (Figs. 12–13), shallow, or more broadly excavated (Figs. 14–15).

Limotettix (*Scleroracus* Van Duzee)

Scleroracus Van Duzee 1894c: 136. Type species by monotypy *Athysanus anthracinus* Van Duzee 1894c.

Conogonus Van Duzee 1894c: 136. Type species by monotypy *Athysanus anthracinus* Van Duzee 1894c. Objective synonym.

Ophiola Edwards 1922: 206. Type species by sebsequent desigation (Ball 1928c) *Cicada striatulus* Fallén 1806. Synonymy by Oman 1949a.

Limotettix (*Scleroracus*): Ribaut 1952a: 156 [reduced to subgenus].

Omaniella Ishihara 1953: 197. Type species by original designation, *Omaniella fla-*

vopicta Ishihara 1953. Synonymy by Ishihara 1954.

Frigartus Oman 1949a: 150. Type species by original designation, *Athysanus frigidus* Ball 1899c: 172. **New synonymy.**

Diagnosis.—*Limotettix* differs from most Deltocephalinae and all other Athysanini in having a sclerotized dorsal apodeme, or dorsal connective, of the aedeagus. The subgenus *Limotettix* (*Scleroracus*) differs from other Deltocephalinae in having the sclerotization of the dorsal connective ventrally emarginate (Figs. 12–15). Secondary diagnostic features: head black or transversely banded or transversely spotted, in dorsal view anterior margin rounded or subacute, wider than pronotum; male subgenital plates subtriangular with marginal and submarginal setae; male pygofer with dorsal margin thickened, distally narrowed and bifid (though dorsal lobe sometimes posteriorly truncate); ventral connective Y-shaped and extending beyond style apices (except in *L.* (*S.*) *frigidus* and *L.* (*S.*) *melastigmus,* and barely so in *L.* (*S.*) *finitimus*); aedeagus broad, platelike, and strongly recurved (except tubular in *L.* (*S.*) *frigidus* and *L.* (*S.*) *symphoricarpae*).

Remarks.—In color the species are usually some shade of tan brown or black; forewing not extremely long and tapering, cells usually heavily infuscated adjacent to veins, the veins white and prominent (Fig. 22). In the original description of the monobasic genus *Frigartus,* the only feature distinguishing it from *Scleroracus* was the coloration of the maculation on the vertex, that of the former consisting of anterior spots and the latter a dorsal band or bands. A second species of *Frigartus* was described by Knull (1954d), but Medler (1958b) synonymized it under *Scleroracus bullatus.* The diagnostic head shape and genital features of the single remaining species, *frigidus,* suggests that it should also be treated as a species of *L.* (*Scleroracus*). Solid, dorsal transverse bands occur on almost all other species of the subgenus (for exceptions see Figs. 17, 92), and on most species of *Limotettix* outside the subgenus. Nevertheless, the anterior transverse spotting on the head of *L.* (*S.*) *frigidus,* n. comb., resembles that of *L.* (*S.*) *bullatus* (Fig. 48) in that both have a large black macula covering the space between the ocellus and the eye.

Identification of females is problematic for some species. The four species with bicolored prothoracic femora (species listed in legend of Fig. 1) can be readily distinguished from each other by coloration and body robustness (slender and pale in *osborni,* which is the most common species in the genus). The species *bullatus, frigidus, humidus, luteolus, shastus, zacki,* and some *symphoricarpae* are sparsely pigmented on the vertex of the head, and most can be distinguished from each other easily by reference to the figures. *L.* (*S.*) *melastigmus* stands alone as a broad, fuscous species with a subangulate head. *L.* (*S.*) *varus* is unique in the subgenus in having a large, conspicuous pale mark around the first m-cu crossvein of the forewing (Fig. 204). Females of the 20 remaining species closely resemble each other and, if a specimen lacks the aforementioned features, the descriptions and figures should be consulted for identification, relying principally on a comparison of vertex subangulation, size, distribution, and frons maculation. For example, the identity of the female lectotype of *L.* (*S.*) *glomerosus* was ascertained by its large size, moderately subangulate head, and the presence of pigmentation of the dorsum characteristic of the subgenus, but with only a weakly maculate frons.

KEY TO MALES OF NEARCTIC *LIMOTETTIX* (*SCLERORACUS*)

1. Head vertex and frontoclypeus almost entirely stramineous or pale yellow, in dorsal view blunt, but with a large black spot occupying entire space between ocellus and eye and pronotum not black 2

– Head vertex or frontoclypeus, or both, abundantly maculate or, if pale (some *humidus*), then head in dorsal view subangulate; space between ocellus and eye at least partially pale or, if black, then pronotum also black 3

2(1). Head with two dark maculae anteriorly, between ocelli, larger than the lateral maculae (Figs. 80, 81); basal angles of scutellum pale; aedeagus tubular . . . *frigidus*

– Head between ocelli without maculae that are larger than those between ocelli and eyes (Figs. 48, 49); basal angles of scutellum black (Fig. 48); aedeagus platelike with apical processes . . . . *bullatus*

3(1). Aedeagus in posterior view preapically with pair of ventrolaterally produced, acute falcate processes (Figs. 21, 117) . . 4

– Aedeagal processes laterally variable, if laterally produced as acute process, then lateral processes directed dorsolaterad (Fig. 34) 5

4(3). Body almost entirely shining black; aedeagal apical processes attenuate and directed dorsad (Fig. 21) . . . . . . *anthracinus*

– Body almost entirely pale brown; aedeagal apical processes falcate and directed mesad (Fig. 117) . . . . *luteolus*

5(3). Aedeagus bearing two pairs of apical processes (Fig. 34) 6

– Aedeagus bearing one pair of apical processes (Fig. 28) 8

6(5). Aedeagus with lateral processes basally broad and curving anteriorly (Fig. 189), mesal processes touching each other preapically . . . . *taramus*

– Aedeagus with lateral processes basally narrow and directed dorsolaterad (Fig. 32), mesal processes separated from each other (Fig. 34) 7

7(6). Aedeagus with mesal processes converging then diverging distally; head bluntly rounded (Fig. 30) . . . . *balli*

– Aedeagus with mesal processes subparallel then diverging distally; head in dorsal view projecting (Fig. 99) . . . . *instabilis*

8(5). Forewing with broad contrasting spot at first m-cu crossvein, which is usually yellow (Figs. 204, 205) . . . . *varus*

– Forewing without distinctive yellow spot on the first m-cu crossvein, if white or pale yellow, then appearing as other crossveins 9

9(8). Pro- and mesothoracic femora shining black or very dark brown to just before apex, then abruptly yellow or orange and concolorous with tibiae (Fig. 1) 10

– Pro- and mesothoracic femora otherwise, usually twice-banded with fuscous (Fig. 2) 12

10(9). Elongate, pale olive or pale brown; forewing far exceeding abdominal apex . . . . *osborni*

– Robust, black or dark brown; forewing barely exceeding abdominal apex 11

11(10). Aedeagal shaft short and broad in posterior view, apical processes distally robust and laterally convex, apices converging but widely separated from each other (Fig. 111) . . . . *kryptus*

– Aedeagal shaft long and slender in posterior view, apical processes narrow and converging distally, touching each other or nearly so (Fig. 197) . . . . *uhleri*

12(9). Aedeagal apical processes crossing each other (Fig. 46) . . . . *brooksi*

– Aedeagal apical processes not crossing each other 13

13(12). Pygofer dorsal lobe bearing an acute spine that is longer than its width in lateral view (Fig. 6) 14

– Pygofer dorsal lobe not bearing an acute spine or, if so (*zacki*), then spine shorter than its width in lateral view 18

14(13). Pygofer spine of dorsal lobe located dorsally, far removed from ventral lobe (Fig. 6); gonopore membrane heavily sclerotized laterally (Fig. 76) 15

– Pygofer spine of dorsal lobe adjacent to ventral lobe; gonopore membrane not sclerotized or only weakly so 17

15(14). Aedeagus distally tubular, flanked by two small digitate processes (Fig. 185) . . . . *symphoricarpae*

– Aedeagus plate-like throughout, bearing two long apical processes (Fig. 28) . . . 16

16(15). Aedeagal shaft in posterior view laterally concave, apical processes touching each other preapically (Fig. 78) . . . . . . *finitimus*

– Aedeagal shaft in posterior view with lateral margins diverging distally, apical processes minimally separated from each other by approximately twice their width at mid length (Fig. 173) . . . . *shastus*

17(14). Aedeagal shaft in posterior view taller than broad, apical processes as long as shaft and initially directed dorsad (Fig. 129); ventral connective attaining but not exceeding apices of styles (Fig. 128) . . . . *melastigmus*

– Aedeagal shaft in posterior view as broad as tall, apical processes short and directed dorsomesad (Fig. 141); ventral connective exceeding apices of styles (Fig. 140) . . . . *obesura*

18(13). Aedeagal atrium in lateral view weakly or not at all constricted before shaft (Fig. 68); aedeagal apical processes in posterior view short, produced from middle, directed dorsad (Fig. 70) 19

– Aedeagal atrium in lateral view distinctly constricted before shaft (Fig. 26); aedeagal apical processes short or long 20

19(18). Frontoclypeus distinctly and contrastingly maculate (Fig. 67); aeadeagal shaft taller than broad, dorsolaterally convex (Fig. 70) . . . . *dasidus*

– Frontoclypeus weakly maculate (Fig. 87); aedeagal shaft as broad as tall, dorsolaterally angulate (Fig. 90) . . . . . *glomerosus*

20(18). Aedeagal shaft in posterior view as broad as tall; aedeagal apical processes short (Fig. 147) 21

– Aedeagal shaft in posterior view distinctly taller than wide, aedeagal apical processes long (Figs. 28, 40) 23

21(20). Aedeagal apical processes directed mesad (Fig. 203) . . . . *vaccinii*

– Aedeagal apical processes directed dorsad (Fig. 147) 22

22(21). Aedeagal shaft in posterior view with lateral margins strongly diverging distally (Fig. 147); body broad . . . . *omani*

– Aedeagal shaft in posterior view with lateral margins subparallel (Fig. 214); body slender . . . . *zacki*

23(20). Aedeagal apical processes long but distinctly shorter than shaft; shaft in posterior view with margins subparallel or diverging distally 24

– Aedeagal apical processes as long or longer than shaft; shaft in posterior view with margins subparallel 27

24(23). Aedeagus in posterior view vasiform, shaft evenly convex dorsolaterally (Fig. 167) . . . . *scudderi*

– Aedeagus in posterior view variable but not vasiform, if lateral margins diverging distally, then dorsolaterally angled . . . 25

25(24). Aedeagal apical processes straight, subparallel, apices in posterior view directed dorsad (Fig. 40) . . . . *beameri*

– Aedeagal apical processes converging then diverging from each other, apices in posterior view directed dorsolaterad . . 26

26(25). Vertex in dorsal view subangulate, length 0.65–0.71× minimum width between eyes (Fig. 92–93); aedeagal apical processes separated from each other by approximately twice their width . . . . *humidus*

– Vertex in dorsal view projecting but evenly convex, not subangulate, length 0.50× minimum width between eyes (Fig. 119); aedeagal apical processes almost touching, separated from each other by less than their width . . . . *medleri*

27(23). Vertex in dorsal view blunt, length 0.45 × minimum width between eyes (Fig. 54); forewing with most veins and cells infuscate (Fig. 53) . . . . *cacheolus*

– Vertex in dorsal view subangulate, length at least 0.50× minimum width between eyes (Fig. 60); forewing with veins white and contrasting with infuscate cell borders (Fig. 59) 28

28(27). Apical processes of aedeagus broadest at base, gradually narrowing (Fig. 135); ventral connective length 2.4 × width across anterior arms (Fig. 134) . . . . *myralis*

– Apical processes of aedeagus equally broad for most of length (Fig. 161); ventral connective length 2.6–3.5× width across anterior arms 29

29(28). Genital style in dorsal view basolaterally angulate (Fig. 178) 30

– Genital style in dorsal view basolaterally evenly convex (Fig. 160) 31

30(29). Body length with forewings in repose 3.4–3.5 mm; vertex in dorsal view produced but not subangulate, length 0.50× minimum width between eyes (Fig. 175) . . . . *strictus*

– Body length with forewings in repose 3.8–3.9 mm; vertex in dorsal view subangulate, length 0.55–0.57× minimum width between eyes (Fig. 60) . . . . *comptonianus*

31(29). Forewings in repose barely exceeding abdominal apex; body length with forewings in repose 3.1–3.5 mm; pronotum more pale than dark (Fig. 23) . . . . *arctostaphyli*

– Forewings in repose far exceeding abdominal apex, abdominal apex approximately attained by outer apical cell (cell R2+3); body length with forewings in repose 3.6–4.5 mm; pronotum more dark than pale (Fig. 157) . . . . *plutonius*

Limotettix (*Scleroracus*) *anthracinus* (Van Duzee)

(Figs. 16–21)

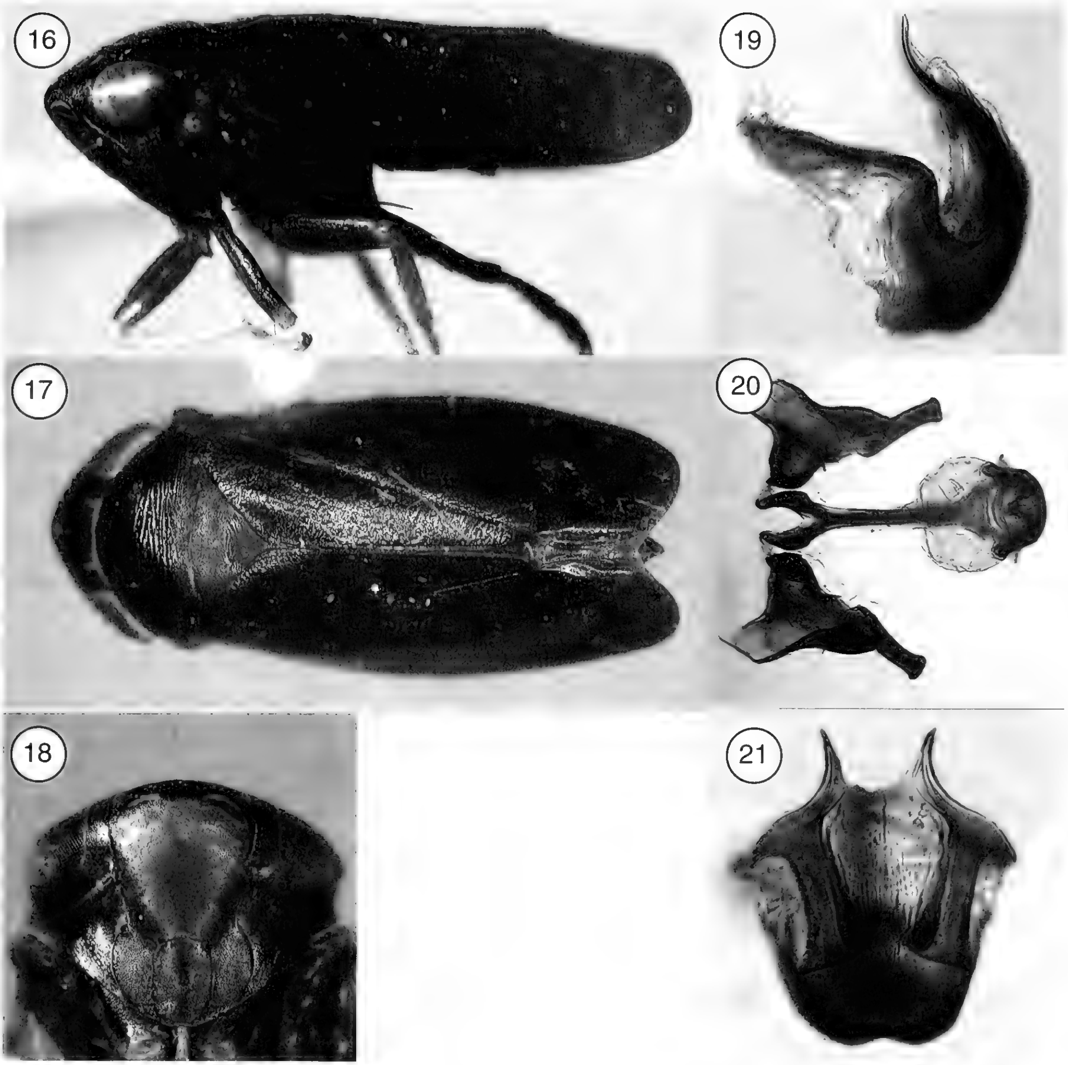
Athysanus anthracinus Van Duzee 1894c: 136 [n. sp.].

Euscelis (*Euscelis*) *anthracinus*: Van Duzee 1916a: 72 [n. comb.].

Ophiola anthracina: Ball 1928c: 185 [n. comb.].

Scleroracus anthracinus: Oman 1947a: 204 [n. comb.].

Limotettix (*Scleroracus*) *anthracinus*: Hamilton 1994: 122 [n. comb.].



Figs. 16–21. *Limotettix* (*Scleroracus*) *anthracinus*. 16–18, Habitus in lateral, dorsal, and ventroanterior aspects, respectively. 19–21, Aedeagus in lateral, dorsal (with connectives and styles), and dorsoposterior aspects, respectively.

Diagnosis.—Almost entirely black, pro- and mesothoracic tibiae and femoral apices yellow; aedeagus apical processes distally attenuate and directed dorsad, with basolateral angles produced lateroventrad, acute.

Measurements (mm). Length with forewings in repose, male 3.9; female 4.0. Width across eyes, male 1.2, female 1.2. *Head:* Vertex in dorsal view subangulate, length 0.40× minimum width between eyes (Fig. 17). *Thorax:* Pronotum in lateral view slightly elevated (Fig. 16). Forewing membrane thickened, veins not clearly demarcated (Fig. 16). Prothoracic tibia with row AV bimodal, basal setae subequal to each other and distinctly shorter than distal macrosetae. *Abdomen:* Male. Pygofer with dorsal lobe posteriorly truncate, ventral lobe articulated. Aedeagal atrium in lateral view strongly constricted before aedeagal shaft (Fig. 19); shaft in posterior view short and broad, lateral margins diverging distally, apical processes distally attenuate and directed dorsad, with basolateral angles produced lateroventrad, acute (Fig. 21); dorsal connective with emargination broad, deep, sides subparallel; ventral connective widest between robust, Y-shaped arms anteriorly, length 3.8× width across anterior arms and 3.5× their longitudinal length (Fig. 20); style moderately long and distally slender, slightly curved laterad, with ventral, rounded preapical lobe not especially prominent.

Coloration. *Head:* Black throughout except yellow on beak (labrum and labium), genae just dorsad of lora, muscle scar arcs on frontoclypeus, ocelli, circular macula in middle just dorsal to interocellar line, and two maculae on posterior margin of head just mesad of ocelli (Figs. 17, 18). *Thorax:* Black throughout except yellow on femoral apices, tibiae and tarsi of pro- and mesothoracic legs (hereafter referred to simply as bicolored; Fig. 1). *Abdomen:* Black throughout.

Hosts.—Label data: *Populus* spp. (aspen; Salicaceae), *Solidago* spp. (goldenrod; Asteraceae).

Specimens examined.—Lectotype ♂ labeled: "Ia.", "Ac. Cat. | 370", "GILLETTE.", "Type", "♂", "Conosanus | gagates Osb." [a *nomen nudum*], "Athysanus | anthracinus | Van Duzee", "LECTOTYPE | Athysanus | anthracinus | Van D. | Oman 1946" [USNM]. Non-type specimens. **CANADA:** Canada, [no date], C. F. Baker (5 ♂) [USNM]. **USA: Arizona.** Kaibab, 26 Jun 1935, E. D. Ball (5 ♂) [USNM]; Long Valley, 5 Aug 1929, E. D. Ball (1 ♂, 1 ♀) [USNM]; **Illinois.** Illinois, [no date], P. R. Uhler (1 ♂) [USNM]; **Iowa.** County #5, 29 Jun 1935, Bill J. (1 ♂), 1 Jul 1933, Bill J. (1 ♀) [USNM]; Ames, 17 Jun 1897, Ames Experiment Station (1 ♂), 1 Jul 1893, E. D. Ball (1 ♀), 1 Jul 1905 (1 ♂), 1 Jul 1895 (1 ♀) [USNM]; **Kansas.** Garnett, 1 Jul 1936, Oman (4 ♀) [USNM]; Garnett, 7 Jul 1933, P. W. Oman, 12 ♀), 20 Jun 1931, P. W. Oman (3 ♀) [USNM]; Onago, [no date] (3 ♂) [USNM]; Riley Co., May [no year], Marlett (2 ♂) [USNM]; **Kentucky.** Rock Haven, 8 Jun 1941, D. A. Young (1 ♀) [USNM]; **Louisiana.** Louisiana, [no date], P. R. Uhler (1 ♂) [USNM]; **Maryland.** Maryland, 1 Jun 1924, E. D. Ball (1 ♀) [USNM]; South River, 4 mi. so. Annapolis, 30 May 1936, Oman (12 ♂, 3 ♀), 11 Jun 1932, P. W. Oman (1 ♂), 10 Sep 1932, P. W. Oman (1 ♀) [USNM]; 24 Jun 1937 (2 ♀) [USNM]; Plummer's Island, 15 Jun 1902, H. S. Barber (1 ♀), 17 Aug 1906, Barber and Schwarz (1 ♀), 20 Jul 1913, W. D. Appel (1 ♀) [USNM]; **Massachusetts.** Woods Hole, 4 Jul 1925, E. D. Ball (1 ♂), 6 Jul 1925, E. D. Ball (2 ♂), 7 Jul 1925, E. D. Ball (4 ♀), 15 Jul–6 Aug 1918, Chris E. Olsen (1 ♀), 26 Jul 1898 (6 ♂) [USNM]; **Mississippi.** Longview, 27 Jun 1920, H. L. Dozier, 27 Jun 1920 (2 ♀) [USNM]; **Missouri.** Oregon Co., 28 May 1937, Turner et al. (1 ♂) [USNM]; **Nebraska.** Nebraska, [no date], C. V. Riley (1 ♂) [USNM]; **New York.** Ithaca, Cornell University, 2 Jul 1895, J. L. Buys (1 ♂) [USNM]; Salem, on Aspen, Jun 1926, E. D. Ball (1 ♂) [USNM]; Roselle, 23 Jun 1924, E. D. Ball (1 ♂, 1 ♀) [USNM]; Cold Spring Harbor, Long Island, 9 Jul 1902 (1 ♂) [USNM]; Green Co., 2500 ft., L. O. Howard, 5 Jul 1899 (1 ♀) [USNM]; Babylon, Long Island, on goldenrod, 26 Jun 1934, F. S. Blanton (1 ♀) [USNM]; White Plains, C. E. Olsen, 20 Jun 1916 (1 ♂) [USNM]; **Nevada.** Nevada, [no date], C. F. Baker (1 ♂) [USNM]; **New Mexico.** Ruidoso, 10 Aug 1941, J. T. Medler (2 ♀, 1 ♂), 21 Sep 1941, J. T. Medler (2 ♂, 1 ♀) [USNM]; **North Carolina.** The Cliffs State Park, 5 Jun 1958, David A. Young (1 ♂) [NCSU]; Looking Glass Rock, Brevard, 19 Jul 1959, W. R. Richards (1 ♀) [CNCI]; Greensboro, 8 Jun 1944, D. A. Young (1 ♂) [USNM]; Greensboro, 11 Jun 1944, D. A. Young (1 ♂) [USNM]; **Tennessee.** Hurricane Mills, 22 Jun 1914, Geo. G. Ainslie (1 ♀) [USNM]; Knoxville, sweep weeds, 28 Jul 1917, W. B. Cartwright (1 ♀) [USNM]; **Virginia.** Great Falls, 30 Jun 1914, A. Wetmore (1 ♀) [USNM]; Arlington, 24 May

1942, Oman (1 ♂) [USNM]; Mountain L., 14 Jul 1938, L. J. and M. J. Milne (1 ♀) [CNCI]; Fairy Stone Park, 1000 ft., 30 May 1962, J. G. Chillcott (2 ♂) [CNCI]; Vienna, [no date] P. W. Oman (1 ♀), 31 May 1932, P. W. Oman (1 ♂) [USNM]; **South Dakota.** Elk Point, 27 Jun 1946, J. A. Lofgreen (1 ♂), 3 Jul 1915, Geo. G. Ainslie (1 ♂) [USNM]; **District of Columbia.** Washington, 23 Jun 1890, Heidemann (1 ♀), 28 Jun 1925, E. D. Ball (5 ♀), 4 Jul 1924, E. D. Ball (2 ♂, 2 ♀), 5 Jul 1920, E. D. Ball (1 ♂, 1 ♀) [USNM]; **Wisconsin.** Gays Mills, 4 Aug 1917, E. D. Ball (1 ♂, 1 ♀) [USNM]; Rich Center, 4 Aug 1917, E. D. Ball (5 ♀) [USNM].

Limotettix (*Scleroracus*) *arctostaphyli* (Ball)

(Figs. 22–28)

Athysanus arctostaphyli Ball 1899c: 172 [n. sp.].

Euscelis (*Euscelis*) *arctostaphyli*: Van Duzee 1916a: 72 [n.comb.].

Ophiola arctostaphyli: Ball 1928c: 185 [n.comb.].

Scleroracus arctostaphyli: Oman 1947a: 205 [n.comb.].

Limotettix (*Scleroracus*) *arctostaphyli*: Hamilton 1994: 122 [n.comb.].

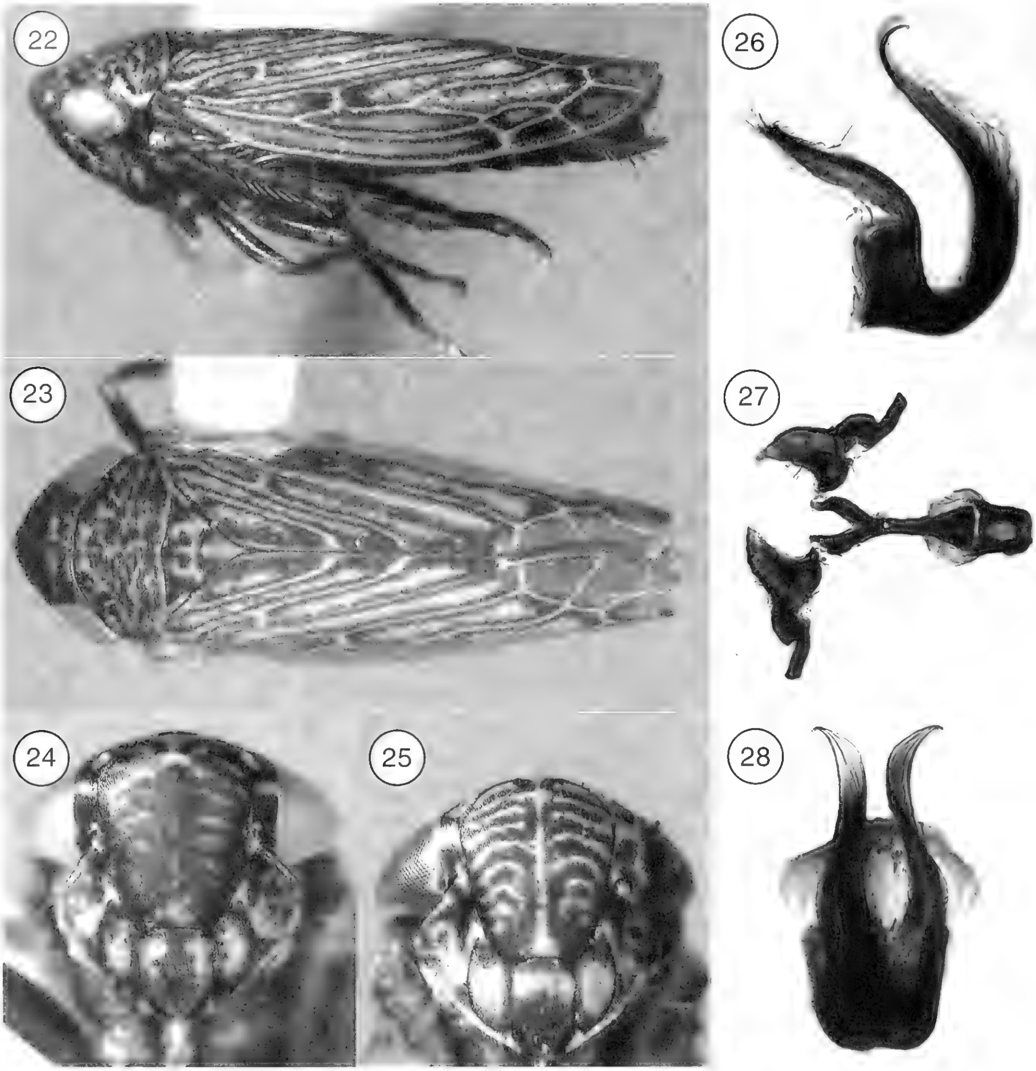
Diagnosis.—Vertex in dorsal view subangulate, length 0.50× minimum width between eyes; forewing short, barely exceeding abdominal apex; ventral connective long and narrow, total length 2.8–3.0 longer than anterior arms.

Measurements (mm). Length with forewings in repose, male 3.1–3.5; female 4.0–4.1. Width across eyes, male 1.1–1.2, female 1.3. *Head:* Vertex in dorsal view subangulate, length 0.50× minimum width between eyes (Fig. 23). *Thorax:* Pronotum in lateral view depressed (Fig. 22). Forewing short, barely exceeding abdominal apex; veins clearly demarcated (Fig. 22). Prothoracic tibia with row AV not distinctly bimodal, basal setae gradually increasing in size distally. *Abdomen:* Male. Pygofer with dorsal lobe posteriorly truncate, ventral lobe fused. Aedeagal atrium in lateral view strongly constricted before aedeagal shaft (Fig. 26); shaft in posterior view taller than broad, lateral margins subparallel, apical processes approximately as long as shaft, distally attenuate and recurved, directed dorsoposterad and laterad (Figs. 26, 28); dorsal connective with emargination somewhat broad basally deep with sides converging evenly; ventral connective widest between robust, Y-shaped arms anteriorly, length vs. width across anterior arms variable, 2.8–3.0 width across anterior arms and 2.7× their longitudinal length (Fig. 27); style moderately long and distally slender, slightly curved laterad, with ventral, rounded preapical lobe not especially prominent.

Coloration. Pro- and mesothoracic legs not bicolored (not as in Fig. 1); otherwise as shown (Figs. 22–25).

Hosts.—Label data: *Salix* sp. (willow; Salicaceae), *Amaranthus* sp. (pigweed, Amaranthaceae). Medler (1958b) recorded bearberry (*Arctostaphylos uva-ursi,* Ericaceae) as a host.

Specimens examined.—Lectotype ♀ labeled: "HpyHollow | Col.7 14 98", "TYPE", "LECTOTYPE", "Athysanus | arctostaphyli | Ball" [USNM]. Paralectotypes. **USA: Colorado.** Rist Canyon, 22 Jul 1898 (1 ♂, 1 ♀) [USNM]; Hpy. Hollow, 14 Jul 1898 (2 ♂) [USNM]; Ft. Collins, 22 Aug 1898 (1 ♀) [USNM]. Non-type specimens. **CANADA: Alberta.** High Prairie, 17 Jul 1961, A. R. Brooks (2 ♂, 2 ♀) [CNCI]; Rycroft, 7 Jul 1961, A. R. Brooks (1 ♂), 21 Jul 1961, A. R. Brooks 1 ♂) [CNCI]; Valleyview, 10 Aug 1961, A. R. Brooks (2 ♂) [CNCI]; Peace River, 10 Jul 1961, A. R. Brooks (2 ♂) [CNCI]; Lac la Biche, 25 Jun 1961, A. R. Brooks (1 ♂) [CNCI]; Grande Prairie, 26 Aug 1961, A. R. Brooks (1 ♂) [CNCI]; **British Columbia.** Upper Carmanah Valley, UTM: 10U CK 803005, 10–29 Sep 1991, N. Winchester 5 ♂, 5 ♀) [CNCI]; Terrace, 25 Jun 1960, W. R. Richards (3 ♀) [CNCI]; Cecil Lake, 15 Jun 1961, A. R. Brooks (1 ♂) [CNCI];



Figs. 22–28. *Limotettix* (*Scleroracus*) *arctostaphyli*. 22–25, Habitus in lateral, dorsal, and ventroanterior aspects (2 variants), respectively. 26–28, Aedeagus in lateral, dorsal (with connectives and styles), and dorsoposterior aspects, respectively. Styles in unnatural position.

Atlin, 22001, 22–23 Jul 1955, B. A. Gibbard (2 ♂) [CNCI]; **Manitoba.** Churchill, 1 Aug 1952, J. G. Chillcott (2 ♂) [CNCI]; **Newfoundland.** Lewis hills, low vegetation, 21 Aug 1986, P. J. Hatcher (1 ♂) [CNCI]; Hebron Lab[rador], 3 Aug 1954, E. E. Sterns (2 ♂) [CNCI]. **Northwest Territory.** 20 miles E Tuktoyaktuk, 6–9 Jul 1971, W. R. M. Mason (1 ♀) [CNCI]; Ennclai L., 28 Jul 1952, H. B. Klots (1 ♂) [CNCI]; Reindeer Depot., McKenzie Delta, 8 Aug 1948, W. J. Brown (1 ♂) [CNCI]; **Ontario.** Amberley, 31 Aug 1988, K. G. A. Hamilton (1 ♀) [CNCI]; Atherton, 11 Aug 1974, K. G. A. Hamilton (1 ♂) [CNCI]; Mer bleue, 9 Aug 1932, G. S. Walley (1 ♂) [CNCI]; Black Stur. Lake, 1–15 Aug 1956, Lindberg (1 ♂) [CNCI]; **Quebec.** La Trappe, 2 Aug 1933, J. Quellet (1 ♀) [USNM]; Indian House L., 7 Jul 1964, W. R. Richards (1 ♂) [CNCI]; Indian House L., 16 Jul 1964, W. R. Richards (1 ♂) [CNCI]; Gt.

Whale R., 3 Aug 1949, J. R. Vockeroth (1 ♂) [CNCI]; **Saskatchewan.** Prince Albert, 23 Jul 1959, A. and J. Brooks (2 ♀) [CNCI]; **Yukon.** Takhini Hot Springs, 2,400 ft., 16 Aug 1962, R. E. Leech (1 ♀), pigweed, 19 Aug 1962, R. E. Leech (1 ♂) [CNCI]; Mile 4 McClintock River Road, 60-7440-10, *Salix* sp., 6 Aug 1960, F. I. S. (1 ♂) [CNCI]. **USA: Alaska.** King Salmon Naknek R., 3 Aug 1952, W. R. Mason (1 ♂) [CNCI]; Fairbanks, 448 ft., 4 Aug 1951, H. C. Severin (1 ♂) [CNCI]; Deering, Seward Peninsula, 28 Jul–2 Aug 1968, J. Matthews (1 ♂) [CNCI]; 5 mi. W Tanacross, GLI 082, 15 Jul 1968, Ross, Ross and Miller (1 ♂) [CNCI]; **Colorado.** Dtch Geo., 11 Aug 1899 (1 ♂), 13 Aug 1899 (1 ♂, 1 ♀) [USNM]; Home, 17 Aug 1899 (1 ♀) [USNM]; Palmer Lk., 13 Jul 1901 (1 ♀) [USNM]; Rist Canon, 13 Jul 1898 (1 ♂, 1 ♀), 22 Jul 1898 (1 ♂) [USNM]; Hpy. Hollow, 14 Jul 1898 (1 ♀) [USNM]; Fort Collins, 9 Jul 1902 (1 ♂) [USNM]; Pingree Park, Alt. 9,000 ft., 18 Aug 1931, D. A. Wilbur (1 ♂, 3 ♀), 21 Aug 1931, E. W. Davis (1 ♂), 14 Jul 1931, E. W. Davis (1 ♀) [USNM]; Near Boulder, Marshall, swept from top of low mesa, 12 Jun 1961, C. H. Mann (2 ♂) [CNCI]; **Montana.** Missoula, 24 Jul 1916 (1 ♀) [USNM]; **New Hampshire.** Mt. Washington, elev. 5,000 ft., 13 Aug 1951, G. S. Walley (2 ♂) [CNCI], [no date or elev.], W. F. F. (1 ♂, 1 ♀) [USNM]; New Hampshire, 23 Aug 1935, C. P. Alexander (1 ♂) [USNM]; **New York.** Mt. Marcy Summit, Essex Co., Alt. 5,344 ft., 20 Jul 1930, J. L. Buys (1 ♂) [USNM]; Mt. Mac Intyre Summit, Essex Co., Alt. 5,112 ft., 26 Jul 1930, J. L. Buys (3 ♂) [USNM]; **Vermont.** Mt. Mansfield, 4,000–4,500 ft., 21 Jul 1891 (1 ♂) [USNM].

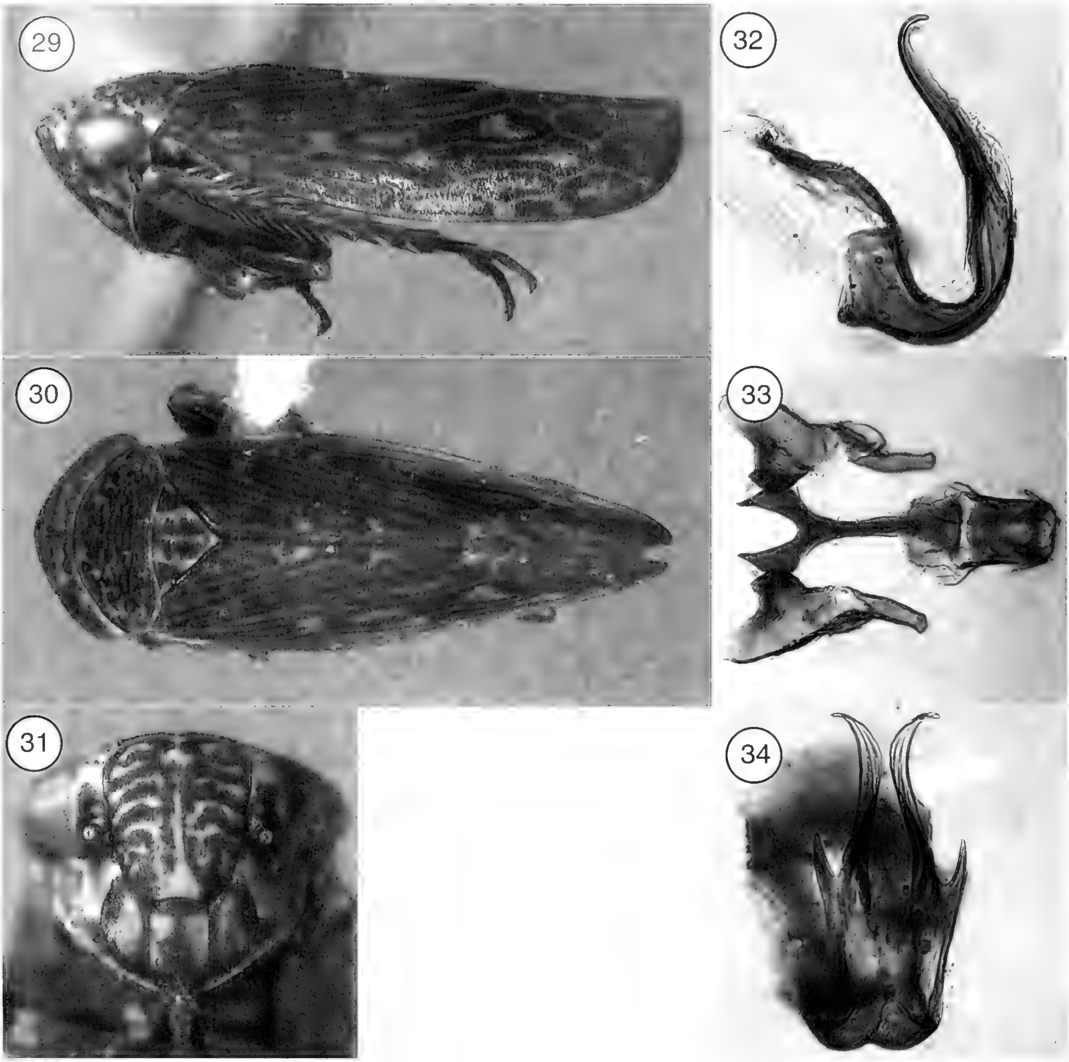
Remarks.—This species is one of a complex that share: characteristic forewing coloration (white veins and marginally infuscate cells) of subgenus; vertex subangulate (length at least 0.50× minimum width between eyes); aedeagal shaft with lateral margins subparallel and bearing one pair of long, basally broad, twisted and recurved apical processes. Other species in this group are *L.* (*S.*) *comptonianus, L.* (*S.*) *melastigmus, L.* (*S.*) *myralis, L.* (*S.*) *plutonius,* and *L.* (*S.*) *strictus.* These species principally differ from each other in basolateral angulation of style and in the proportions of the ventral connective, as specified in the diagnoses. The identity of the female lectotype is based on the aforementioned features and its association with two male specimens, both paralectotypes, collected at the same time and place.

Limotettix (*Scleroracus*) *balli* (Medler)
(Figs. 29–34)

Scleroracus balli Medler 1958a: 13 [n.sp.].
Limotettix (*Scleroracus*) *ball*: Hamilton 1994: 122 [n.comb.].

Diagnosis.—Vertex in dorsal view blunt, length 0.45–0.47× minimum width between eyes; aedeagal shaft bearing 2 pairs of apical processes, lateral pair directed dorsolaterally, mesal pair converging, almost touching preapically.

Measurements (mm). Length with forewings in repose, male 3.9–4.1; female 4.2–4.4. Width across eyes, male 1.3, female 1.5. *Head:* Vertex in dorsal view blunt, length 0.45–0.47× minimum width between eyes (Fig. 30). *Thorax:* Pronotum in lateral view depressed (Fig. 29). Forewing veins clearly demarcated (Fig. 29). Prothoracic tibia with row AV not distinctly bimodal, basal setae gradually increasing in size distally. *Abdomen:* Male. Pygofer with dorsal lobe posteriorly truncate, ventral lobe fused. Aedeagal atrium in lateral view moderately constricted before aedeagal shaft (Fig. 32); shaft in posterior view taller than broad, lateral margins weakly diverging distally, mesoapical processes approximately as long as shaft, distally attenuate and recurved, directed dorsoposterad and laterad, basolaterally with short acute processes directed dorsad (Fig. 34); dorsal connective emargination narrow, deep, sides parallel; ventral connective widest between robust, Y-shaped arms anteriorly, length



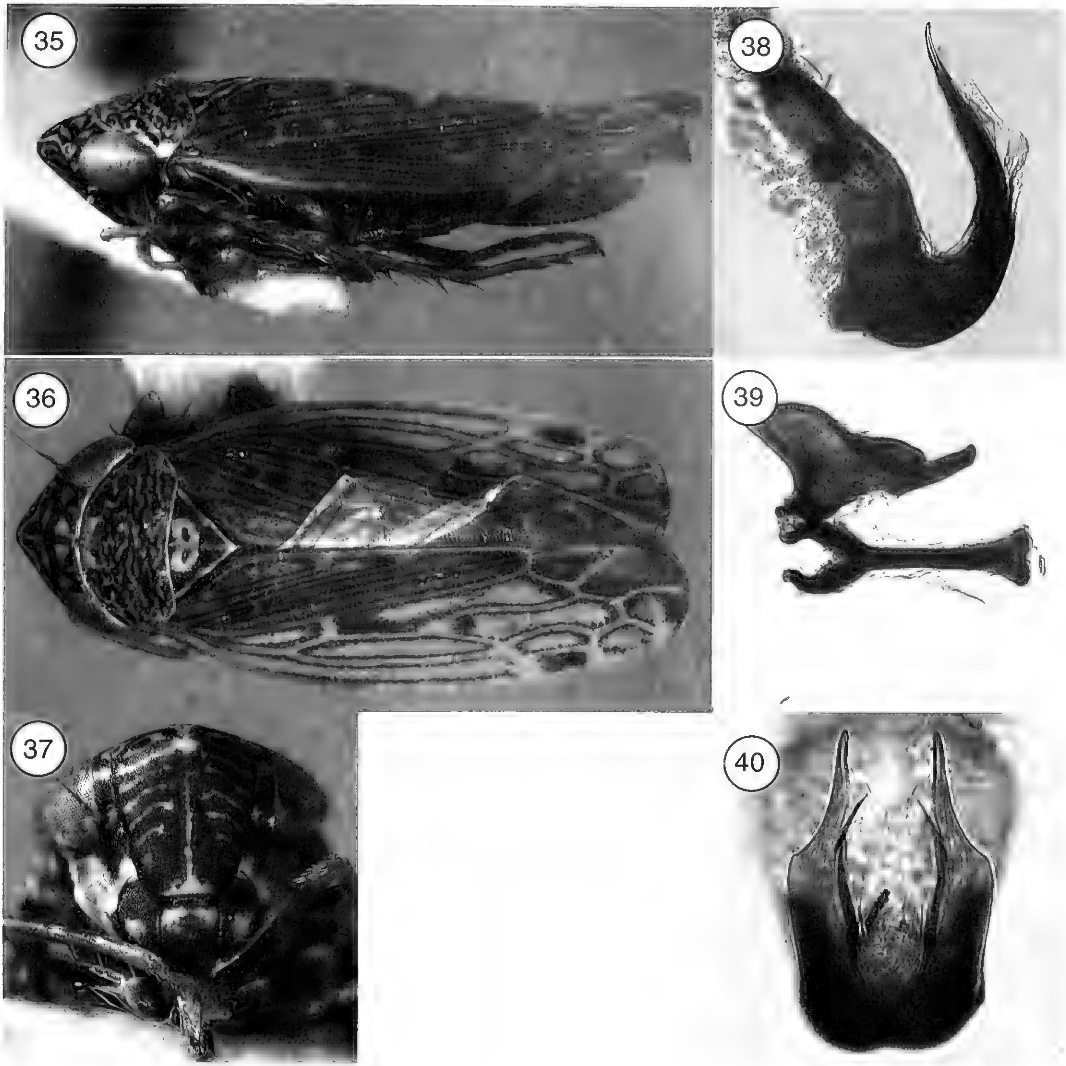
Figs. 29–34. *Limotettix* (*Scleroracus*) *balli*, paratypes. 29–31, Habitus in lateral, dorsal, and ventroanterior aspects, respectively. 32–34, Aedeagus in lateral, dorsal (with connectives and styles), and dorsoposterior aspects, respectively.

2.6× width across anterior arms and 3.0× their longitudinal length (Fig. 33); style short and apically truncate or moderately long and distally slender, slightly curved laterad, with ventral, rounded preapical lobe not especially prominent.

Coloration: Pro- and mesothoracic legs not bicolored (not as in Fig. 1); otherwise as shown (Figs. 29–31).

Hosts.—Unknown.

Specimens examined.—Holotype ♂ labeled: "EstesPark | COL 7-1[8] | Oman 193[5]", "MEDLER | FIG. 29", "HOLOTYPE | Scleroracus | balli | Medler" [USNM]. Paratypes. **USA: Colorado.** Estes Park, 18 Jul 1935, Oman (6 ♂, 3 ♀) [USNM]. Non-type specimens. **CANADA: Ontario.** 10 km W. of Gore Bay, 2 Aug 1991, K. G. A. Hamilton (1 ♂) [CNCI]; 18 km. E. of Little Current, 21 Jul 1991, K. G. A. Hamilton (2 ♂, 2 ♀) [CNCI]; 10 km. E. of Dyers Bay, 25 Jul 1993, K. G. A. Ham-



Figs. 35–40. *Limotettix* (*Scleroracus*) *beameri*, paratypes. 35–37, Habitus in lateral, dorsal, and ventroanterior aspects, respectively. 38–40, Genitalia in lateral (aedeagus and dorsal connective), dorsal (ventral connective and right style), and dorsoposterior (aedeagus and dorsal connective) aspects, respectively.

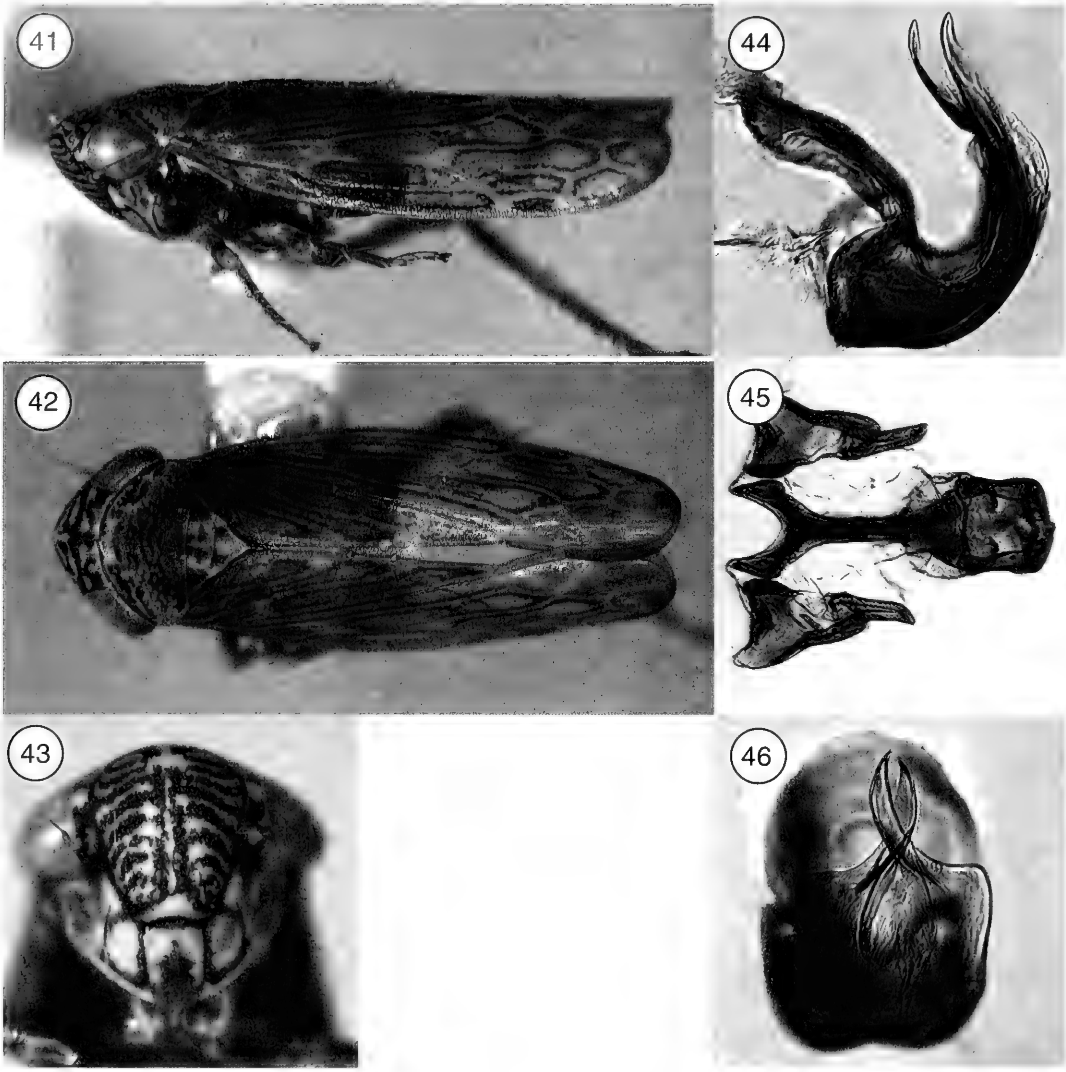
ilton (2 ♂, 1 nymph) [CNCI]. **USA: Colorado.** Pingree Park, 14 Jul 1951, E. W. Davis (1 ♀) [USNM]; Colorado, [no date], C. F. Baker (1 ♀) [USNM]; Estes Park, 7500 ft., 10 Aug 1961, J. R. Stainer (1 ♂) [CNCI]; **Michigan.** 10 km. NE Drummond, 27 Jul 1989, K. G. A. Hamilton (6 ♂, 6 ♀) [CNCI]; Tecumseh, 4 Jul 1994, K. G. A. Hamilton (8 ♂, 13 ♀, 3 nymphs) [CNCI]; Ortonville, 26 Jul 1991, K. G. A Hamilton (5 ♂, 4 ♀), 28 Jul 1991, K. G. A. Hamilton (4 ♀, 2 ♂) [CNCI].

Limotettix (*Scleroracus*) *beameri* (Medler) (Figs. 35–40)

Scleroracus beameri Medler 1958a: 16 [n.sp.].

Limotettix (*Scleroracus*) *beameri*: Hamilton 1994: 122 [n.comb.].

Diagnosis.—Vertex in dorsal view subangulate, length 0.55× minimum width between eyes; aedeagus with apical processes long, but shorter than shaft, gradu-



Figs. 41–46. *Limotettix (Scleroracus) brooksi,* holotype. 41–43, Habitus in lateral, dorsal, and ventroanterior aspects, respectively. 44–46, Aedeagus in lateral, dorsal (with connectives and styles), and dorsoposterior aspects, respectively.

ally narrowed, subparallel throughout their length, directed dorsad.

Measurements (mm). Length with forewings in repose, male 3.9; female 4.2–4.6. Width across eyes, male 1.2, female 1.3–1.4. *Head:* Vertex in dorsal view subangulate, length 0.55× minimum width between eyes (Fig. 36). *Thorax:* Pronotum in lateral view depressed (Fig. 35). Forewing veins clearly demarcated (Fig. 36). Prothoracic tibia with row AV bimodal, basal setae subequal to each other and distinctly shorter than distal macrosetae. *Abdomen:* Male Pygofer with dorsal lobe posteriorly acute, ventral lobe fused. Aedeagal atrium in lateral view strongly constricted before aedeagal shaft (Fig. 38); shaft in posterior view taller than broad, lateral margins subparallel, with apical processes long, basally broad, distally attenuate, subparallel, and directed dorsad (Fig. 40); dorsal connective emargination narrow, deep, sides parallel;

ventral connective widest between robust, Y-shaped arms anteriorly, length 3.3× width across anterior arms and 3.0× their longitudinal length (Fig. 39); style moderately long and distally slender, slightly curved laterad, with ventral, rounded preapical lobe not especially prominent.

Coloration. Pro- and mesothoracic legs not bicolored (not as in Fig. 1); otherwise as shown (Figs. 35–37).

Hosts.—Unknown.

Specimens examined.—Holotype ♂ labeled: "Hecita | Oregon 7-11-1935 | R. H. Beamer", "HOLOTYPE | Scleroracus | beameri | Medler" [SEMC]. Paratypes. **USA: Oregon.** Hecita, 11 Jul 1935, R. H. Beamer (1 ♀) [USNM]; **Washington.** Ft. Lewis, 5 Jul 1935, Oman (1 ♀) [USNM]. Non-type specimens. **CANADA: British Columbia.** Mission City, 20–30 Aug 1953, G. J. Spencer (1 ♂, 3 ♀) [CNCI]; MacGillivray Creek Game Reserve, nr Chilliwack, 14 Jul 1953 (2 ♂, 9 ♀) [CNCI]; Goldstream, 20 Jun 1924, W. Downes (1 ♂) [CNCI]; Saanich Dist., 18 Aug 1924, W. Downes (1 ♂) [CNCI].

Limotettix (*Scleroracus*) *brooksi* Hamilton
(Figs. 41–46)

Limotettix (*Scleroracus*) *brooksi* Hamilton 1994: 130 [n.sp.].

Diagnosis.—Aedeagal apical processes crossing each other.

Measurements (mm). Length with forewings in repose, male 3.8–3.9; female 3.9–4.7. Width across eyes, male 1.3, female 1.3–1.4. *Head:* Vertex in dorsal view subangulate, length 0.50× minimum width between eyes (Fig. 42). *Thorax:* Pronotum in lateral view depressed (Fig. 41). Forewing veins clearly demarcated (Fig. 41). Prothoracic tibia with row AV not distinctly bimodal, basal setae gradually increasing in size distally. *Abdomen:* Male. Pygofer with dorsal lobe posteriorly truncate, ventral lobe fused. Aedeagal atrium in lateral view strongly constricted before aedeagal shaft (Fig. 44); shaft in posterior view taller than broad, lateral margins parallel, apical processes moderately long, narrow, crossing each other mesially, apically acute and directed dorsad (Fig. 46); dorsal connective emargination broad basally, deep, sides parallel; ventral connective widest between robust, Y-shaped arms anteriorly, length 2.3× width across anterior arms and 3.3× their longitudinal length (Fig. 45); style moderately long and distally slender, slightly curved laterad, with ventral, rounded preapical lobe not especially prominent.

Coloration. Pro- and mesothoracic legs not bicolored (not as in Fig. 1); otherwise as shown (Figs. 41–43).

Hosts.—Unknown.

Specimens examined.—Holotype ♂ labeled: "Peace River | Alt.10 VII 1961 | A. R. Brooks", "HOLOTYPE | Limotettix | brooksi Hmlt. | CNC No.21387" [CNCI]. Paratypes. **CANADA: Alberta.** Peace River, 10 Jul 1961, A. R. Brooks (1 ♂, 4 ♀) [CNCI]; Black Foot Hills, 9 Aug 1940, A. R. Brooks (1 ♂) [CNCI].

Limotettix (*Scleroracus*) *bullatus* (Ball)
(Figs. 12, 47–52)

Thamnotettix bullata Ball 1902a: 17 [n. sp.].

Ballana bullata: DeLong & Caldwell 1937c: 49 [n.comb.].

Ophiola bullata: DeLong & Knull 1946a: 46 [n.comb.].

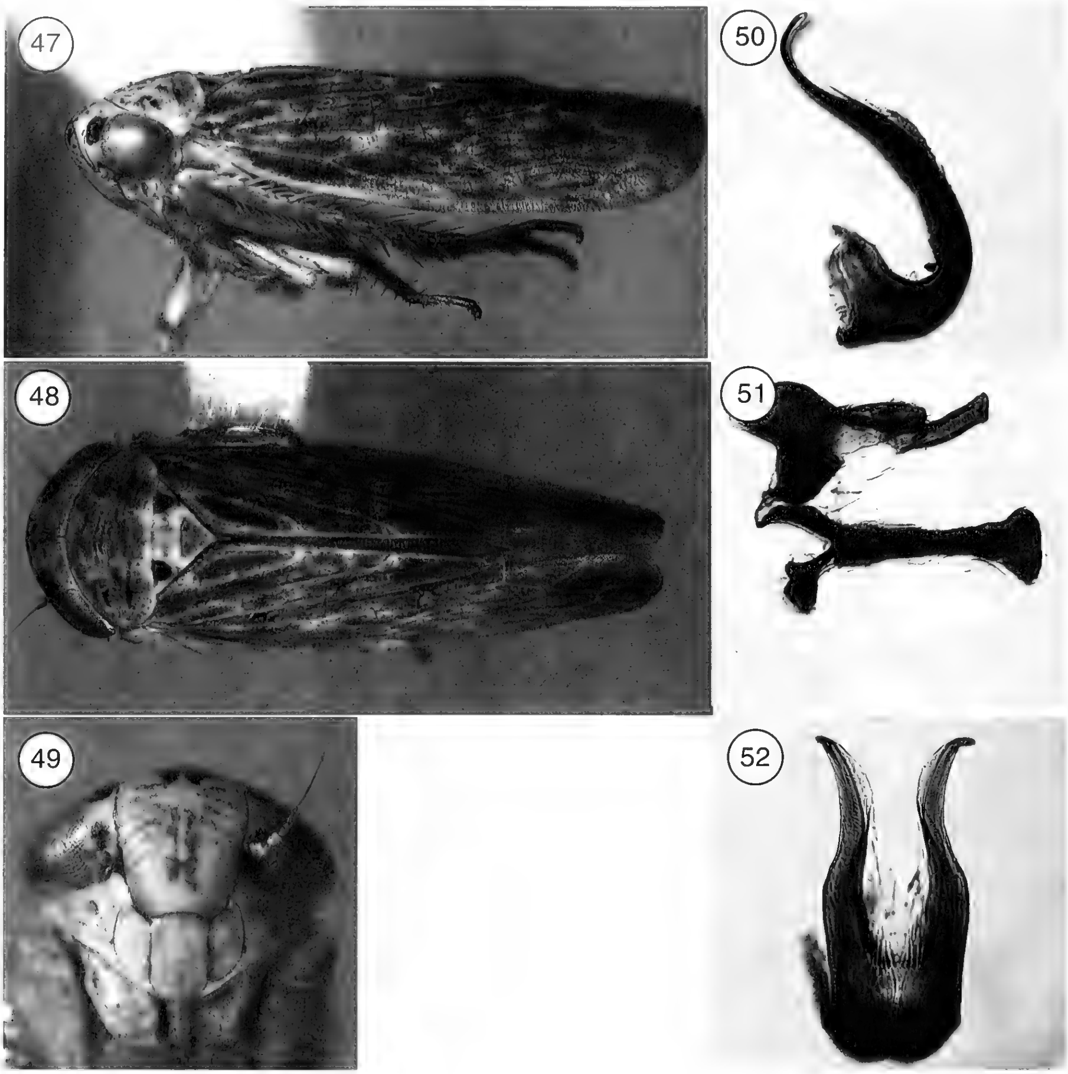
Frigartus obesus Knull 1954d: 37 [n. sp.]. Synonymy by Medler 1958b: 232.

Scleroracus bullatus: Oman 1947a: 205 [n.comb.].

Limotettix (*Scleroracus*) *bullatus*: Hamilton 1994: 122 [n.comb.].

Diagnosis.—Vertex in dorsal view blunt, length 0.40× minimum width between eyes, with space between ocelli and eye, and basal margins of scutellum, black.

Measurements (mm). Length with forewings in repose, male 3.8–4.2; female 4.9–5.0. Width across eyes, male 1.2–1.3, female 1.6. *Head:* Vertex in dorsal view blunt, length 0.40× minimum width be-



Figs. 47–52. *Limotettix* (*Scleroracus*) *bullatus*. 47–49, Habitus in lateral, dorsal, and ventroanterior aspects, respectively. 50–52, Genitalia in lateral (aedeagus), dorsal (ventral connective and right style), and dorsoposterior (aedeagus) aspects, respectively. Left arm of connective broken.

tween eyes (Fig. 48). *Thorax:* Pronotum in lateral view depressed (Fig. 47). Forewing veins clearly demarcated (Fig. 47). Prothoracic tibia with row AV not distinctly bimodal, basal setae gradually increasing in size distally. *Abdomen:* Male. Pygofer with dorsal lobe posteriorly truncate, ventral lobe fused. Aedeagal atrium in lateral view strongly constricted before aedeagal shaft (Fig. 50); shaft in posterior view taller than broad, lateral margins subparallel, apical processes approximately as long as shaft, distally attenuate and recurved, directed dorsoposterad and laterad (Fig. 52); dorsal connective emargination narrow, deep, sides parallel; ventral connective widest between robust, Y-shaped arms anteriorly, length 3.6× width across anterior arms and 3.1× their longitudinal length (Fig. 51); style long, distally slender, apically truncate, with ventral, rounded preapical lobe not especially prominent.

Coloration. Pro- and mesothoracic legs not bicolored (not as in Fig. 1); otherwise as shown (Figs. 47–49).

Hosts.—Label data: *Salix* spp. (willow; Salicaceae), *Solidago* spp. (goldenrod; Asteraceae).

Specimens examined.—Lectotype ♀ labeled: "LosAngeles | Co., Cal.", "Collection | Coquillett", "TYPE", "Cotype | No. 6089 | U.S.N.M.", "LECTOTYPE", "Thamnotettix | bullata | Ball" [USNM]. Paralectotype. **USA:** California. Los Angeles Co., [no date], Coquillett (1 ♀) [USNM]. Non-type specimens. **USA: California.** Hornbrook, 14 Jun 1959, Kelton and Madge (1 ♂, 2 ♀) [CNCI]; Yreka, 15 Jun 1959, swept from willow, Kelton and Madge (1 ♀), 15 Jun 1959, *Salix* sp., Kelton and Madge (2 ♀), 15 Jun 1959, on goldenrod, Kelton and Madge (1 ♀) [CNCI]; **Washington.** Franklin Co., Juniper Dunes Wilderness, ca 19 mi. SW Kahlotus, 31 May 1989, R. S. Zack (4 ♂) [CNCI].

Limotettix (*Scleroracus*) *cacheolus* (Ball)

(Figs. 2, 53–58)

Ophiola striatula cacheola Ball 1928c: 189 [n. subsp.].

Scleroracus cacheolus: Oman 1947a: 205 [n.comb.; elev. status]

Limotettix (*Scleroracus*) *cacheolus*: Hamilton 1994: 122 [n.comb.].

Diagnosis.—Vertex in dorsal view blunt; length 0.45× minimum width between eyes, forewing with most veins and cells entirely infuscate; aedeagus in posterior view with lateral margins parallel, apical processes long, broad and parallel for most of their length.

Measurements (mm). Length with forewings in repose, male 3.3–4.2; female 4.0–4.5. Width across eyes, male 1.1–1.2, female 1.4. *Head:* Vertex in dorsal view blunt, length 0.45× minimum width between eyes (Fig. 54). *Thorax:* Pronotum in lateral view depressed (Fig. 53). Forewing veins clearly demarcated (Fig. 53). Prothoracic tibia with row AV not distinctly bimodal, basal setae gradually increasing in size distally (Fig. 2). *Abdomen:* Male. Pygofer with dorsal lobe posteriorly truncate, ventral lobe fused. Aedeagal atrium in lateral view strongly constricted before aedeagal shaft (Fig. 56); shaft in posterior view taller than broad, lateral margins subparallel, apical processes approximately as long as shaft, distally attenuate and recurved, directed dorsoposterad and laterad (Fig. 58); dorsal connective emargination narrow, deep, sides parallel; ventral connective widest between robust, Y-shaped arms anteriorly, length 2.9× width across anterior arms and 2.9× their longitudinal length (Fig. 57); style moderately long and distally slender, slightly curved laterad, with ventral, rounded preapical lobe not especially prominent.

Coloration. Pro- and mesothoracic legs not bicolored (Fig. 2); otherwise as shown (Figs. 53–55).

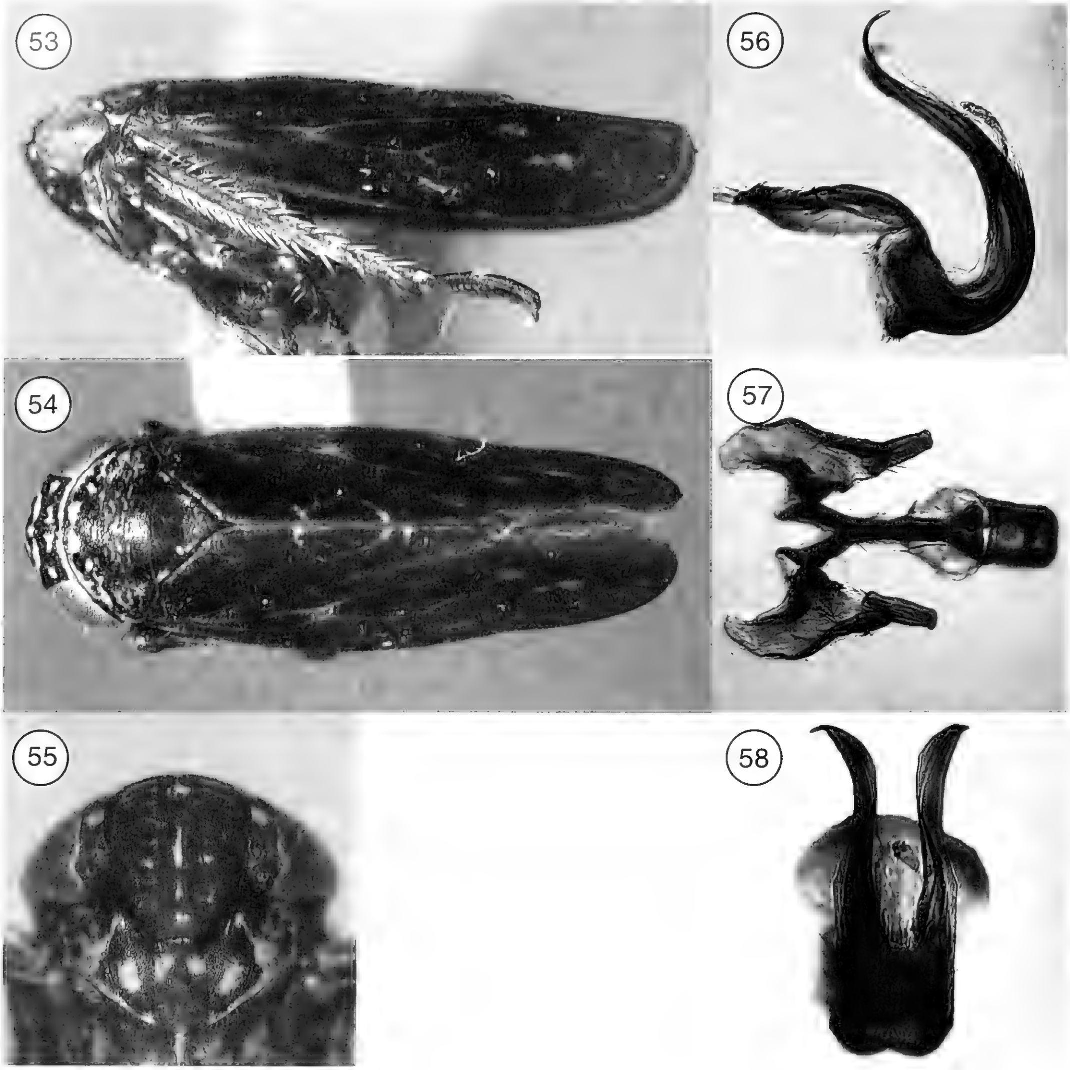
Hosts.—Unknown.

Specimens examined.—Holotype ♂ labeled: "Logan Ut | PK 7-9.1916", "HOLOTYPE | Ophiola | striatula | var. cacheola | E. D. Ball" [USNM]. Paratype. **USA: Utah.** Logan, 9 Jul 1916 (1 ♂) [USNM]. Non-type specimens. **USA: California.** 5 m. east Old Baldy, 9,000 ft. (1 ♂) [USNM]; **Colorado.** Little Beaver, 18 Jul 1898 (1 ♂) [USNM]; Trinidad, 13 Jul 1899 (1 ♀) [USNM]; Rockwood, 2 Jul 1933, P. W. Oman (17 ♂, 4 ♀) [USNM]; Colorado, [no date], C. F. Baker (13 ♂, 17 ♀) [USNM]; Estes Park, 18 Jul 1935, Oman (23 ♂, 4 ♀) [USNM]; **New Mexico.** Clouderft., 7 Jun 1933, P. W. Oman (3 ♂) [USNM]; **Utah.** Richfield, 23 Jul 1933, E. W. Davis (3 ♂, 2 ♀) [USNM]; **Washington.** Colton, collected on grazed grassland, 6 Jul 1948, K. L. Sturges (1 ♂, 1 ♀) [CNCI].

Limotettix (*Scleroracus*) *comptonianus* (Ball)

(Figs. 5, 59–64)

Ophiola comptoniana Ball 1928c: 186 [n. sp.].



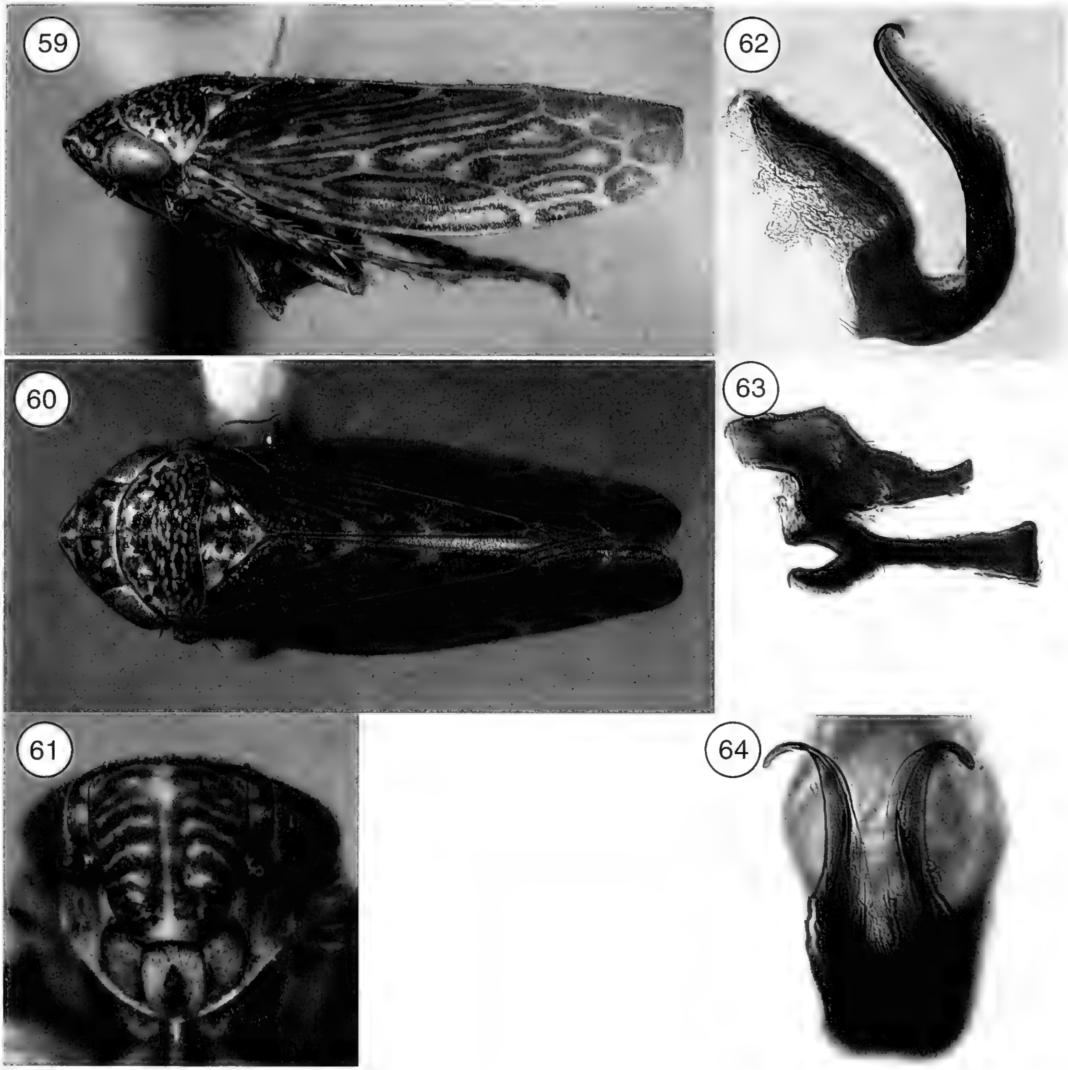
Figs. 53–58. *Limotettix* (*Scleroracus*) *cacheolus*. 53–55, Habitus of paratype in slightly ventrolateral, in dorsal, and in ventroanterior aspects, respectively. 56–58, Aedeagus in lateral, dorsal (with connectives and styles), and dorsoposterior aspects, respectively.

Scleroracus comptonianus: Oman 1947a: 205 [n.comb.].

Limotettix (*Scleroracus*) *comptonianus*: Hamilton 1994: 122 [n.comb.].

Diagnosis.—Vertex in dorsal view subangulate, length 0.55–0.57× minimum width between eyes; length with forewings in repose, male 3.8–3.9, female 4.4–4.6; genital style in dorsal view basolaterally angulate.

Measurements (mm). Length with forewings in repose, male 3.8–3.9; female 4.4–4.6. Width across eyes, male 1.1–1.2, female 1.3–1.4. *Head:* Vertex in dorsal view subangulate, length 0.55–0.57× minimum width between eyes (Fig. 60). *Thorax:* Pronotum in lateral view depressed (Fig. 59). Forewing veins clearly demarcated (Fig. 59). Prothoracic tibia with row AV not distinctly bimodal, basal setae gradually increasing in size distally. *Abdomen:* Male. Pygofer with dorsal lobe posteriorly trun-



Figs. 59–64. *Limotettix* (*Scleroracus*) *comptonianus*. 59–61, Habitus in slightly dorsolateral, in dorsal, and in ventroanterior aspects, respectively. 62–64, Genitalia in lateral (aedeagus and dorsal connective), dorsal (ventral connective and right style), and dorsoposterior (aedeagus and dorsal connective) aspects, respectively.

cate, ventral lobe fused (Fig. 5). Aedeagal atrium in lateral view strongly constricted before aedeagal shaft (Fig. 62); shaft in posterior view taller than broad, lateral margins weakly diverging distally, apical processes longer than shaft, distally attenuate and recurved, directed dorsoposterad and laterad, apex directed ventrad (Figs. 62, 64); dorsal connective emargination narrow, deep, sides parallel, ventral connective widest between robust, Y-shaped arms anteriorly, length 3.5× width across anterior arms and 1.6× their longitudinal length (Fig. 63); style moderately long, curving slightly laterad, apically truncate, with ventral, rounded preapical lobe not especially prominent.

Coloration. Pro- and mesothoracic legs not bicolored (not as in Fig. 1); otherwise as shown (Figs. 59–61).

Hosts.—Label data: *Comptonia* sp. (sweet fern; Myricaceae), *Comptonia pere-*

grina (L.) J. M. Coult (sweet fern; Myricaceae), *Pinus* sp. (pine; Pinaceae), *Solidago* spp. (goldenrod; Asteraceae).

Specimens examined.—Holotype ♀ labeled; "N.J. | 1786", "Collection | C. F. Baker", "HOLOTYPE | Ophiola | comptoniana | E. D. Ball" [USNM]. Non-type specimens. **CANADA: Ontario.** Toronto, 8 Aug 1924, E. D. Ball (1 ♂, 1 ♀) [USNM]; Madawaska, 25 Jun 1975, K. G. A. Hamilton (4 ♂, 1 ♀, 1 nymph) [CNCI]; Hastings Co., sweet fern, 12 Jul 1953, J. F. Brimley (1 ♀) [CNCI]; Deacon, 6 Aug 1975, K. G. A. Hamilton (1 ♂, 2 nymphs) [CNCI]; 5 mi. S. Barry's Bay, 6 Aug 1975, K. G. A. Hamilton (1 ♂, 1 ♀) [CNCI]; **Quebec.** Abitibi Co., Lac Berry, 22 Aug 1985, Larochelle, Lariviere (1 ♂, 1 ♀) [CNCI]; **New Brunswick.** Queens Co., Youngs Cove, 21 Aug 1973, K. G. A. Hamilton (1 ♂) [CNCI]; Kouchibouguac N.P., sweet fern, 23 Jul 1977, D. J. Brown (1 ♀) [CNCI]. **USA: Illinois.** Thornton, 20 Sep 1962, GL 173, Ross and Ross (1 ♀) [CNCI]; **Maine.** Alton, 4 Sep 1986, K. G. A. Hamilton (1 ♀) [CNCI]; **Massachusetts.** Natick, 21 Sep 1935, C. A. Frost (1 ♀) [USNM]; **Michigan.** Idlewild, *Comptonia peregrina,* 21 Jun 1989, K. G. A. Hamilton (12 ♂, 13 ♀, 8 nymphs) [CNCI]; **New Hampshire.** Durham, dry pasture, 18 Jul 1923 (1 ♀) [USNM]; Henniker, sweet fern, 30 Jun 1979, K. G. A. Hamilton (1 ♂, 3 ♀, 1 nymph) [CNCI]; **New Jersey.** Lakehurst, Aug 1925 (3 ♀) [USNM]; **New York.** Salem, Jun 1923, E. D. Ball (5 ♂, 3 ♀) [USNM]; Babylon, Long Island, 26 Jun 1934, goldenrod, F. S. Blanton (1 ♀), 9 Aug 1934, goldenrod, F. S. Blanton (2 ♀) [USNM]; **Ohio.** Whitehouse, 8 Aug 1992, K. G. A. Hamilton (4 ♂, 1 ♀, 1 nymph) [CNCI]; **Pennsylvania.** Pennsylvania, [no date], C. F. Baker (2 ♂, 2 ♀) [USNM]; **Wisconsin.** Camp Douglas, 1 Jul 1980, K. G. A. Hamilton (1 ♂, 3 ♀) [CNCI]; Hayward, 21 Aug 1980, K. G. A. Hamilton (1 ♂) [CNCI]; Sayner, 5 Jul 1969, Harris and Harris (1 ♂) [CNCI]; Trout Lake, 17 Sep 1917 (2 ♂) [USNM]; Tomah, 19 Aug 1917, E. D. Ball (1 ♂) [USNM].

Remarks.—See remarks under *L.* (*S.*) *arctostaphyli.*

Limotettix (*Scleroracus*) *dasidus* (Medler) (Figs. 65–70)

Scleroracus dasidus Medler 1955b: 212 [n.sp.].

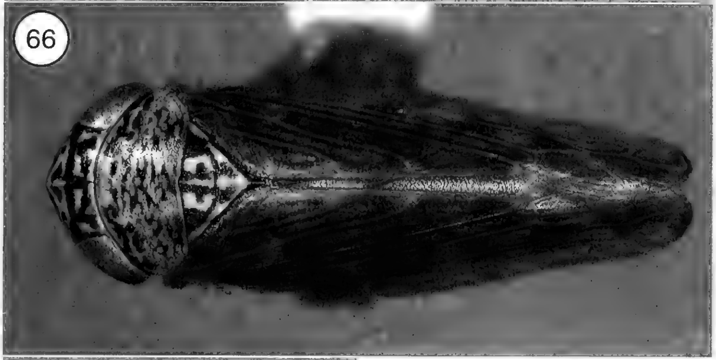
Ophiola dasida: Metcalf 1967: 188 [n. comb.].

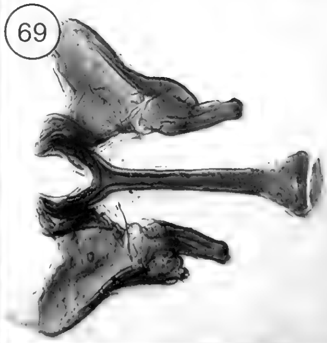
Limotettix (*Scleroracus*) *dasidus*: Hamilton 1994: 122 [n.comb.].

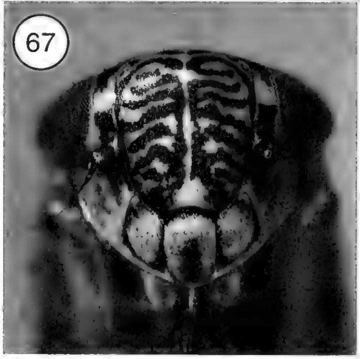
Diagnosis.—Aedeagus in posterior view taller than broad, dorsolaterally convex, apical processes short, atrium in lateral view not constricted before shaft.

Measurements (mm). Length with forewings in repose, male 3.6–3.7; female 4.2–4.3. Width across eyes, male 1.1, female 1.2–1.3. *Head:* Vertex in dorsal view subangulate, length 0.50–0.52× minimum width between eyes (Fig. 66). *Thorax:* Pronotum in lateral view depressed (Fig. 65). Forewing veins clearly demarcated (Fig. 65). Prothoracic tibia with row AV not distinctly bimodal, basal setae gradually increasing in size distally. *Abdomen:* Male. Pygofer with dorsal lobe posteriorly truncate, ventral lobe fused. Aedeagal atrium in lateral view not constricted before aedeagal shaft (Fig. 68); shaft in posterior view little taller than broad, lateral margins slightly diverging distally, apical processes short, acute, directed dorsad, and well separated from each other (Fig. 70); dorsal connective emargination slightly broader basally, attenuate distally, deep; ventral connective widest between robust, Y-shaped arms anteriorly, length vs. width across anterior arms and 3.6× their longitudinal length variable 3.0–3.4 (Fig. 69); style distally short and truncate, slightly curved laterad, with ventral, rounded preapical lobe not especially prominent.

Coloration. Pro- and mesothoracic legs not bicolored (not as in Fig. 1); otherwise as shown (Figs. 65–67).







Figs. 65–70. *Limotettix* (*Scleroracus*) *dasidus*, paratypes. 65–67, Habitus in lateral, dorsal, and ventroanterior aspects, respectively. 68–70, Genitalia in lateral (aedeagus and dorsal connective), dorsal (ventral connective and styles), and dorsoposterior (aedeagus and dorsal connective) aspects, respectively.

Hosts.—Label data: *Achillea millefolium* (L.) (yarrow; Asteraceae), *Salix* spp. (willow; Salicaceae).

Specimens examined.—Holotype ♂ labeled: "LOGAN UT | C[anyon] 7-26-1915", "MEDLER | F[smig[nm. 4", "HOLOTYPE | Scleroracus | dasidus | Medler" [USNM]. Paratypes. (1 ♀) ["Allotype"] with same data as holotype [USNM]. Other paratypes: **CANADA: British Columbia.** Kaslo, [no date], R. P. Currie (2 ♂, 1 ♀) [USNM]; **Manitoba.** Red Deer R., 3 Aug 1937, R. H. Beamer (1 ♂, 1 ♀) [CNCI]. **USA: Idaho.** Cataldo, 9 Jul 1935, Oman (1 ♂, 1 ♀) [USNM]; **Utah.** Logan Can., 24 Jul 1910 (1 ♀), 26 Jul 1973 (1 ♂, 1 ♀) [USNM]; Provo, 11 Jul 1908 (1 ♀) [USNM]; **Washington.** Buckley, 1935, Oman (5 ♂, 2 ♀) [USNM]; Pullman, 17 Jul 1911 (1 ♀) [USNM]. Non-type specimens. **CANADA: Alberta.** Beaverlodge, 1 Aug 1961, A. R. Brooks (2 ♂, 2 ♀) [CNCI];

British Columbia. Summit Lake, Mi 392 Alaska Highway, 4,200 ft., 19–21 Jul 1959, R. E. Leech (3 ♂, 2 ♀) [CNCI]; Terrace, 17 Jul 1960, W. R. Richards (1 ♂), 25 Jul 1960, W. R. Richards (2 ♂, 1 ♀) [CNCI]; Bowser, 20 Jun 1955, G. E. Shewell (2 ♂) [CNCI]; Keating, 12 Jul 1929, W. Downes (2 ♂) [CNCI]; St. Elias Mountains, Noisy Range, east Alsek River, elev. 140 m, flood plain 7.5 km N of Tatshenshini River, 59°32′ by 137°47′W, pitfall, herbs and shrubs, 24–29 Jul 1992, C. S. Guppy (2 ♂) [CNCI]; Glacier, 3,500 ft., *Salix* sp., 22 Aug 1978, K. G. A. Hamilton (1 ♂, 3 ♀) [CNCI]; **Saskatchewan.** Christopher Lake, 15 Jul 1959, A. and J. Brooks (1 ♂) [CNCI]; Candle Lake, 19 Aug 1959, A. and J. Brooks (1 ♂) [CNCI]; **Yukon.** Whitehorse, elev. 2,079 ft., 7 Aug 1951, H. C. Severin (1 ♂) [CNCI]; Rancheria, 11 Aug 1982, L. A. Kelton (2 ♂, 1 ♀) [CNCI]; Takhini Hot Springs, 2,400 ft., on yarrow, 16 Aug 1962, P. J. Skitsko (1 ♂, 1 ♀) [CNCI]. **USA: Alaska.** Matanuska, [no date or elev.], J. C. Chamberlin (1 ♀), elev. 300 ft., 1 Aug 1951, H. C. Severin (1 ♂, 1 ♀) [USNM], elev. 800 ft., 1 Aug 1951, H. C. Severin (2 ♂) [CNCI]; 25–50 mi. S. Pexton's Lodge, Richardson Hwy., car trap, temp. 63–65°F, 29 Jul 1944 (1 ♀) [USNM]; Christochina Lodge, 1 Aug 1968, Ross, Ross and Miller (2 ♂, 1 ♀) [CNCI]; McKinley Nat. Park, Elev. 1,750 ft., 30 Jul 1951, H. C. Severin, (1 ♂) [CNCI]; Fairbanks, elev. 488 ft., 4 Aug 1951, H. C. Severin (1 ♂) [CNCI]; Paxson, 23 Jul 1988, GL 1131, Ross, Ross and Miller (8 ♂, 3 ♀, 2 nymphs) [CNCI]; Alaska Highway mi. 1442, GL 1086, 16 Jul 1968, Ross, Ross and Miller (1 ♂) [CNCI]; Potter, 31 Jul 1968, GL 1127, Ross, Ross and Miller (2 ♂) [CNCI]; **California.** Quincy, 23 Jul 1912, E. D. Ball (1 ♀) [USNM]; **Colorado.** Ward, Aug 1899 (1 ♂) [USNM]; **Idaho.** Moscow, alt. 2,560 ft., 6 Jun 1931 (1 ♀) [USNM]; **Montana.** Condon, 9 Aug 1985, K. G. A. Hamilton (4 ♂, 3 ♀) [CNCI]; **Utah.** Salt Lake, 17 Jun 1934, E. W. Davis (1 ♀) [USNM]; **Washington.** Pullman, 17 Jul 1911 (1 ♀) [USNM]; 28 km. W Mazama, 5,400 ft., 16 Aug 1985, K. G. A. Hamilton (2 ♂, 16 ♀) [CNCI]; **Wisconsin.** Cranmoor, 21 Jun 1931 (1 ♂) [USNM]; **Wyoming.** 13 km SE Cooke City, MT, 6 Aug 1985, K. G. A. Hamilton (1 ♂, 1 ♀) [CNCI].

Limotettix (*Scleroracus*) *finitimus* (Van Duzee)

(Figs. 71–78)

Euscelis finitimus Van Duzee 1925b: 422 [n. sp.].

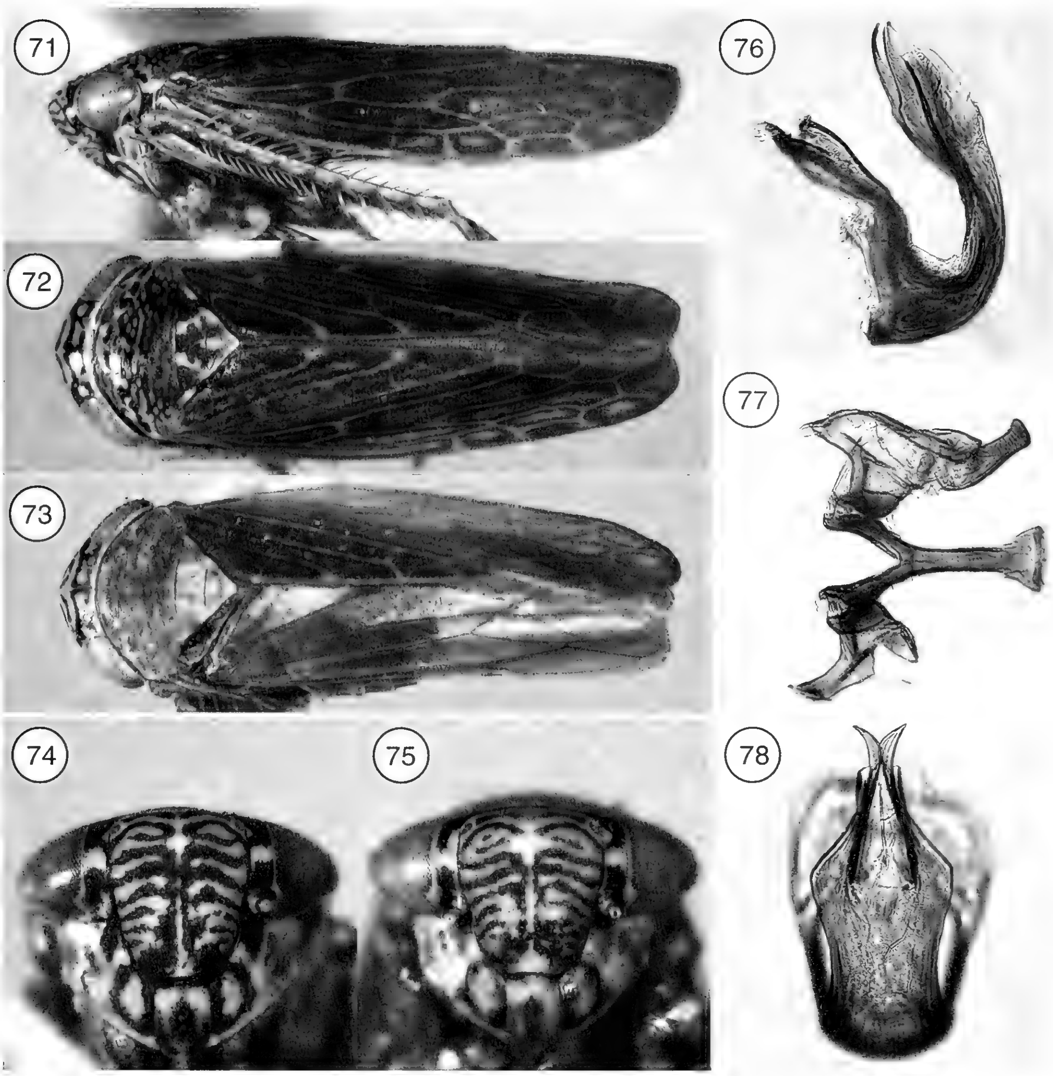
Ophiola gentilis finitima: Ball 1928c: 187 [n.comb.; reduced rank]

Scleroracus finitimus: Oman 1947a: 205 [n.comb.].

Limotettix (*Scleroracus*) *finitimus*: Hamilton 1994: 122 [n.comb.].

Diagnosis.—Male pygofer with dorsal lobe developed into an acute spine directed posterad, located dorsally, far removed the ventral lobe; aedeagus in posterior view with apical processes touching each other preapically.

Measurements (mm). Length with forewings in repose, male 4.4–4.5; female 4.7–5.1. Width across eyes, male 1.3–1.4, female 1.5–1.6. *Head:* Vertex in dorsal view blunt, length 0.43× minimum width between eyes (Fig. 72). *Thorax:* Pronotum in lateral view depressed (Fig. 71). Forewing veins clearly demarcated (Figs. 71–72). Prothoracic tibia with row AV not distinctly bimodal, basal setae gradually increasing in size distally. *Abdomen:* Male. Pygofer with dorsal lobe dorsoposteriorly developed into an acute process, ventral lobe fused. Aedeagal atrium in lateral view strongly constricted before aedegal shaft (Fig. 76); shaft in posterior view taller than broad, lateral margins weakly concave, apical processes basally broad, produced mesodorsad, long, touching each other or almost so preapically, distally attenuate and directed dorsolaterad (Fig. 78); dorsal connective emargination broad basally, deep, sides converging; ventral connective widest between ro-



Figs. 71–78. *Limotettix* (*Scleroracus*) *finitimus*. 71–75, Habitus in lateral, dorsal, and ventroanterior aspects, respectively (73, 75, color variant with left forewing missing). 76–78, Genitalia in lateral (aedeagus and dorsal connective), dorsal (ventral connective and styles), and dorsoposterior (aedeagus and dorsal connective) aspects, respectively. Distal portion of left style broken.

bust, Y-shaped arms anteriorly, length 2.4× width across anterior arms and 2.4× their longitudinal length (Fig. 77); style distally short and robust, slightly curved laterad, with ventral, preapical, rounded lobe prominent.

Coloration. Pro- and mesothoracic legs not bicolored (not as in Fig. 1); otherwise as shown (Figs. 71–75).

Hosts.—Label data: *Symphoricarpos albus* (L.) (snowberry, Caprifoliaceae) or *Festuca* spp. (fescue, Poaceae; probably erroneous), *Symphoricarpos racemosus* [?], *Symphoricarpos* spp. (waxberry, *Caprifoliaceae*).

Specimens examined.—Holotype ♀ labeled: "Colestin Jackson | Co. Oregon 7 13 18 | E. P. VanDuzee", "TYPE", "Euscelis | finitimus | VanD." [CASC]. Non-type specimens. **CANADA: British Columbia.**

Royal Oak, 6 Sep 1918, W. Downes (1 ♂, 1 ♀) [USNM]; Bear Ck., Okanagan Valley, weeds, 14 Jul 1970, K. G. A. Hamilton (1 ♂, 2 ♀) [CNCI]; Kelowna, 14 Jul 1950, B. P. Beirne (1 ♀) [CNCI]; Naramata, Site #6B 5B, 14 Aug 1974, J.E.H. (1 ♀) [CNCI]; Fairmont, 20 Aug 1978, K. G. A. Hamilton (3 ♀) [CNCI]. **USA: California.** Mt. Shasta, 29 Jun 1935, Oman (1 ♂) [USNM]; Quincy, 23 Jul 1912, E. D. Ball (1 ♀) [USNM]; S. Margarita, 23 Jun 1931, E. D. Ball (18 ♂, 16 ♀) [USNM]; **Idaho.** Elba, *Symphoricarpos racemosus,* 9 Aug 1931 (2 ♂, 4 ♀) [USNM]; **Montana.** Rexford, 14 Aug 1985, K. G. A. Hamilton (1 ♂, 2 ♀) [CNCI]; 33 km NE Lincoln, 8 Aug 1985, K. G. A. Hamilton (1 ♀) [CNCI]; 37 km NE Lincoln, 8 Aug 1985, K. G. A. Hamilton (1 ♀) [CNCI]; Montana, 27 Jul 1923 (1 ♂, 3 ♀) [USNM]; Drummond, 10 Jun 1935, Oman (2 ♂) [USNM]; **Oregon.** Corvallis, McDonald For., *Symphoricarpos albus* (L.), 21 Aug 1968, Oman (1 ♂, 2 ♀) [USNM]; La Grande, 29 Aug 1929 (3 ♀) [USNM]; **Utah.** Salt Lake, 25 Sep 1932, E. W. Davis (1 ♀) [USNM]; **Washington.** Tiger, 15 Aug 1985, K. G. A. Hamilton (1 ♀) [CNCI]; Mt. Rainier, Cottonwood flts., Oman, 1935 (1 ♂, 1 ♀) [USNM]; Pullman, [no date], W. M. Mann, 1 ♀), [no date], Piper (2 ♂) [USNM]; Colton, Virgin prairie survey, *Festuca* sp., *Symphoricarpos* sp., 16 Jul 1960, Wyatt W. Cone (1 ♂) [USNM]; Washington, [no date], C. F. Baker (1 ♂) [USNM].

Remarks.—Although the species was once treated as a subspecies of *gentilis* (Ball, 1928c), *finitimus* is a valid species and *gentilis* itself is a junior synonym of *L.* (*S.*) *shastus* (see below).

Limotettix (*Scleroracus*) *frigidus* (Ball), **new combination**

(Figs. 9, 79–84)

Athysanus frigidus Ball 1899c: 172 [n.sp.].
Frigartus frigidus: Oman 1949a: 150 [n.comb.].

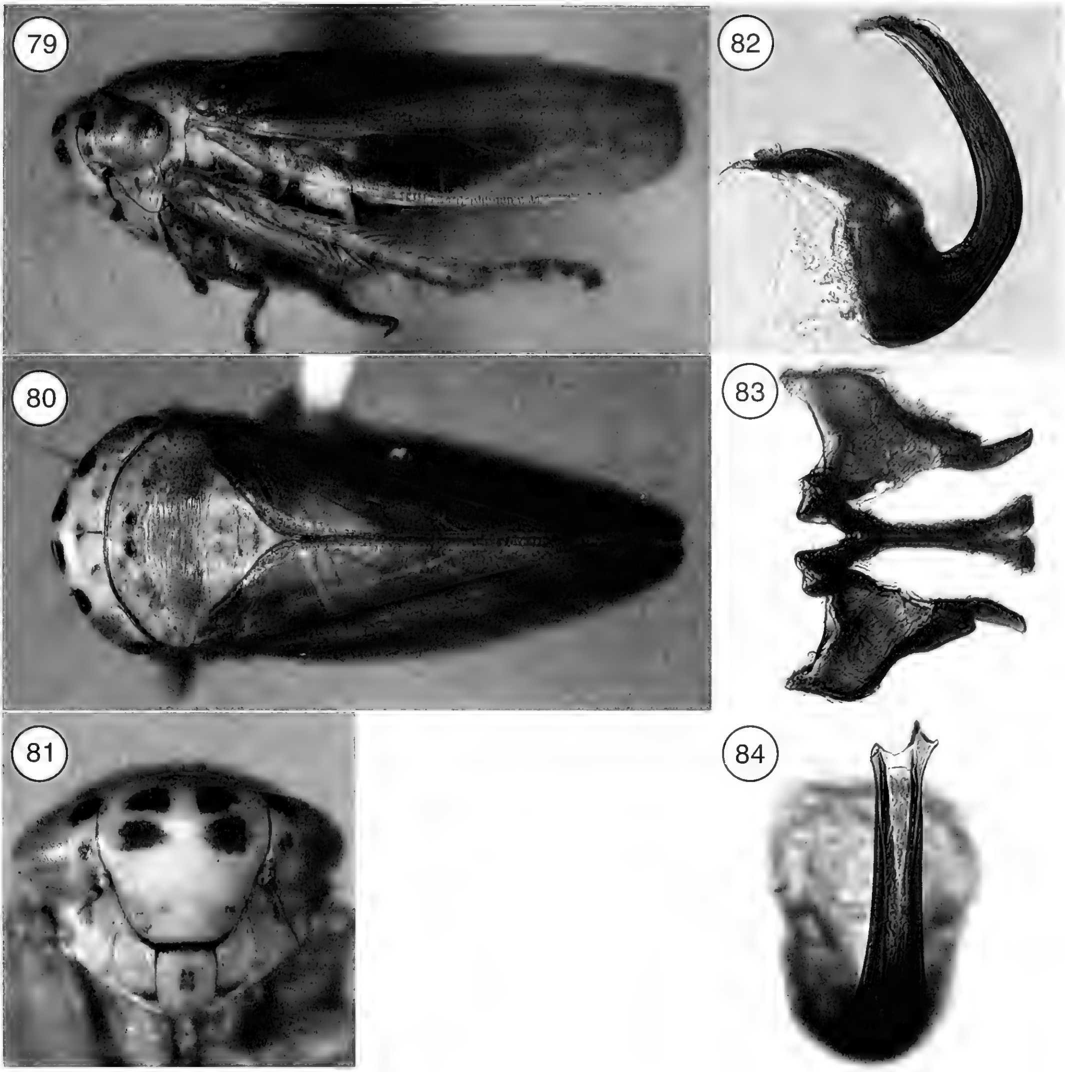
Diagnosis.—Vertex of head with transverse band of 4 spots, the 2 mesal maculae large; vertex in dorsal view blunt, length 0.40× minimum width between eyes.

Measurements (mm). Length with forewings in repose, male 3.5–3.6; female 3.6–4.6. Width across eyes, male 1.3–1.4, female 1.5–1.8. *Head:* Vertex in dorsal view blunt, length 0.40× minimum width between eyes (Fig. 80). *Thorax:* Pronotum in lateral view depressed (Fig. 79). Forewing veins clearly demarcated. Prothoracic tibia with row AV bimodal, basal setae subequal to each other and distinctly shorter than distal macrosetae. *Abdomen:* Male. Pygofer with dorsal lobe posteriorly truncate, ventral lobe fused. Aedeagal atrium in lateral view strongly constricted before aedeagal shaft (Fig. 82); shaft tubular, in posterior view much taller than broad, mesoapical processes short, acute, directed dorsad, basolaterally with minute acute process directed dorsolaterally (Fig. 84); dorsal connective emargination broad basally, shallow, sides subparallel; ventral connective widest between robust, Y-shaped arms anteriorly, length 2.2× width across anterior arms and 2.8× their longitudinal length (Fig. 83); style moderately long, slightly curved laterad, apex subacute (Fig. 83).

Coloration. Gray stramineus with four black maculae in a transverse row anteriorly on vertex. Forewing hyaline except posterior cubitus vein black in male (Fig. 80). Pro- and mesothoracic legs not bicolored (not as in Fig. 1); otherwise as shown (Figs. 79–81).

Hosts.—Label data: *Artemisia frigida* Willd. (fringed sagebrush; Asteraceae), *A. tridentata* Nutt. (basin sagebrush; Asteraceae), *Atriplex* spp. (saltbrush; Chenopodiaceae).

Specimens examined.—Lectotype, ♂, here designated to stablize the concept applied to the name *Athysanus frigidus,* labeled: "RistCanon | Col. 7 13 98", "TYPE", "Cotype No. | [no number] | U.S.N.M.", "LECTOTYPE | Athysanus | frigidus Ball | desig. McKamey 2000" [USNM]. Paralectotypes: (1 ♀, 2 ♂) with same data as lectotype; (2 ♀) (12 Oct 1898)



Figs. 79–84. *Limotettix* (*Scleroracus*) *frigidus*. 79–81, Habitus in lateral, dorsal, and ventroanterior aspects of male, respectively. 82–84, Genitalia in lateral (aedeagus and dorsal connective), dorsal (ventral connective and styles), and dorsoposterior (aedeagus and dorsal connective) aspects, respectively. Left aedeagal apical process broken.

(1 ♂) (8 Jul 1898) from Ft. Collins, Colorado; (1 ♀) (14 Aug 1898) from Pinewood, Colorado [all USNM]. Non-type specimens. **CANADA: Alberta.** 5 mi. E. Beiseker, 13 Aug 1981, K. G. A. Hamilton (1 ♀) [CNCI]; Castor, 7 Aug 1957, A. R. and J. E. Brooks (1 ♀) [CNCI]; Wainwright, 27 Jul 1957, A. R. and J. E. Brooks (1 ♀) [CNCI]; N. of Medicine Hat, CFB Suffield, Amiens area, 50°37.678′N, 110°18.371′W, pan trapping, 28 Jul 1994, D. A. Pollock (1 ♂) [CNCI]; Grand Prairie, 25 Jul 1961, A. R. Brooks (2 ♂, 1 ♀) [CNCI]; **British Columbia.** Bear Ck., Okanagan Valley, weeds, 14 Jul 1970, K. G. A. Hamilton (1 ♀) [CNCI]; 7 km W Douglas Lake, 5 Jun 1987, K. G. A. Hamilton (1 nymph) [CNCI]; **Manitoba.** Aweme, 29 Aug 1929, R. H. Handford (1 ♀) [CNCI]; **Saskatchewan.** Prince Albert, 23 Jul 1959, A. and J.

Brooks (1 ♀) [CNCI]; Rosetown, 27 Jul 1925, N. J. Atkinson (1 ♀) [CNCI]; Elbow, 12 Jul 1960, A. R. Brooks (9 ♂, 6 ♀) [CNCI]; Willow Bunch, 29 Jul 1955, A. R. Brooks (2 ♀) [CNCI]; Willow Bunch, 27 Jul 1955, A. R. Brooks (1 ♀) [CNCI]; 4 mi. NE Saskatoon, *Artemisia frigida,* 6 Aug 1981, K. G. A. Hamilton (1 ♀) [CNCI]; Saskatoon, all Kenneth M. King: 9 Jul 1929 (1 ♂), 23 Jul 1925 (2 ♀), 26 Jul 1930 (2 ♂), 29 Jul 1924 (1 ♀), 30 Jul 1929 (1 ♀), 4 Aug 1925 (1 ♂), 4 Aug 1927 (1 ♀) [CNCI]; Val Marie, 8 Aug 1955, A. R. Brooks (1 ♀), both A. R. Brooks: 9 Jul 1957 (1 ♀), 15 Jul 1957 (1 ♀), L. Konotopetz, 14 Sep 1949 (1 ♀) [CNCI]. **USA: Arizona.** Fredonia, 6 Aug 1930, Ball (1 ♀) [USNM]; **California.** Chilcoot, 22 Jul 1912, E. D. Ball (1 ♂) [USNM]; Pine Valley, 6 Jul 1931, E. D. Ball (1 ♀) [USNM]; **Colorado.** Poudre R. Canyon, 22 Aug 1931, J. Nottingham (1 ♀) [USNM]; Rifle, 25 Jul 1900 (1 ♂) [USNM]; Ft. Collins, 29 Jul 1898, E. D. Ball (1 ♀), 1 Aug 1902 (2 ♂), 30 Aug 1898, E. D. Ball (1 ♀) [USNM]; Dtch Geo., 13 Aug 1899 (1 ♂) [USNM]; Colorado, [no date] (1 ♀) [USNM]; Durango, 13 Aug 1933, E. D. Ball (2 ♀) [USNM]; ; Pinewood, 14 Aug 1898, E. D. Ball (1 ♀) [USNM]; Rist Canyon, 13 Jul 1898, E. D. Ball (2 ♀) [USNM]; **Idaho.** Naf, 13 Aug 1932, C. F. Knowlton and C. F. Smith (1 ♀) [USNM]; Amsterdam, wind vane trap, 19 Aug 1932 (1 ♀) [USNM]; Churchill, wind vane trap, 19 Aug 1932 (1 ♀) [USNM]; Hagerman, Blue Gulch, *A. tridentata,* 3–4 Sep 1932, David E. Fox (5 ♀) [USNM]; Burley, *A. tridentata,* 30 Aug 1932, David E. Fox (1 ♀) [USNM]; **Minnesota.** Battle Lake, 24 Jul 1935, Oman (4 ♂, 4 ♀) [USNM]; **Montana.** 13 km NW Monarch, 7 Aug 1985, K. G. A. Hamilton (1 ♂) [CNCI]; **Nebraska.** Kimball, 5 Aug 1899, E. D. Ball (1 ♀) [USNM]; **Nevada.** Wells, 20 Jul 1912, E. D. Ball (1 ♂) [USNM]; **South Dakota.** Sisseton, 23 Jul 1935, Oman (13 ♂, 10 ♀) [USNM]; **Utah.** Logan Canyon, 24 Jul 1910 (1 ♂, 1 ♀) [USNM]; Promontory, on *Atriplex* sp., 6 Aug 1930, G. F. Knowlton (1 ♀) [USNM]; Orderville, 7 Aug 1930, E. D. Ball (2 ♀) [USNM]; Soldier, 13 Aug 1906, E. D. Ball (2 ♀) [USNM]; Cove Fort, 6 Jul 1928, E. W. Davis (1 ♀) [USNM]; Wyoming. S. of Lusk, 21 Jul 1935 (1 ♀) [USNM]; Pintura, 19 Sep 1935, E. W. Davis (1 ♀) [USNM]; 1.5 mi. S. 5[?] W. Winnett, Petroleum Co., 26 Jul 1970, G. B. Hewitt (1 ♀) [USNM]; Provo, 9 Aug 1930 (8 ♀) [USNM]; Chad's, 23 Jul 1908, E. D. Ball (1 ♀) [USNM]; Spanish Fort, 24 Aug 1903, E. D. Ball (1 ♀) [USNM]; Mt. Emmonds, 17 Aug 1935, G. F. Knowlton (1 ♀) [USNM]; Leeds, 9 Aug 1936, C. F. Knowlton and C. F. Smith (1 ♀) [USNM]; **Washington.** Republic, 6 Aug 1931, R. H. Beamer (1 ♂) [USNM]; **Wyoming.** E. Laramie, GL 699, 5 Aug 1967, Ribble (1 ♀) [CNCI].

Remarks.—This species is referred to this subgenus because the male genitalia have the dorsal connective ventrally emarginate, a diagnostic feature of the subgenus. An unusual feature of this species is that its aedeagal shaft is tubular rather than platelike, as in most species of the subgenus. Also, in this study I found the ventral connective to be short, attaining but not exceeding the apex of the style (Fig. 83), rather than long, extending well beyond the apex of the style, as described by Oman (1949a).

Limotettix (*Scleroracus*) *glomerosus* (Ball)
(Figs. 85–90)

Thamnotettix glomerosa Ball 1910c: 308 [n. sp.].

Athysanus calvatus Ball 1916a: 173 [n. sp.]. Synonymy by Ball 1928c: 187.

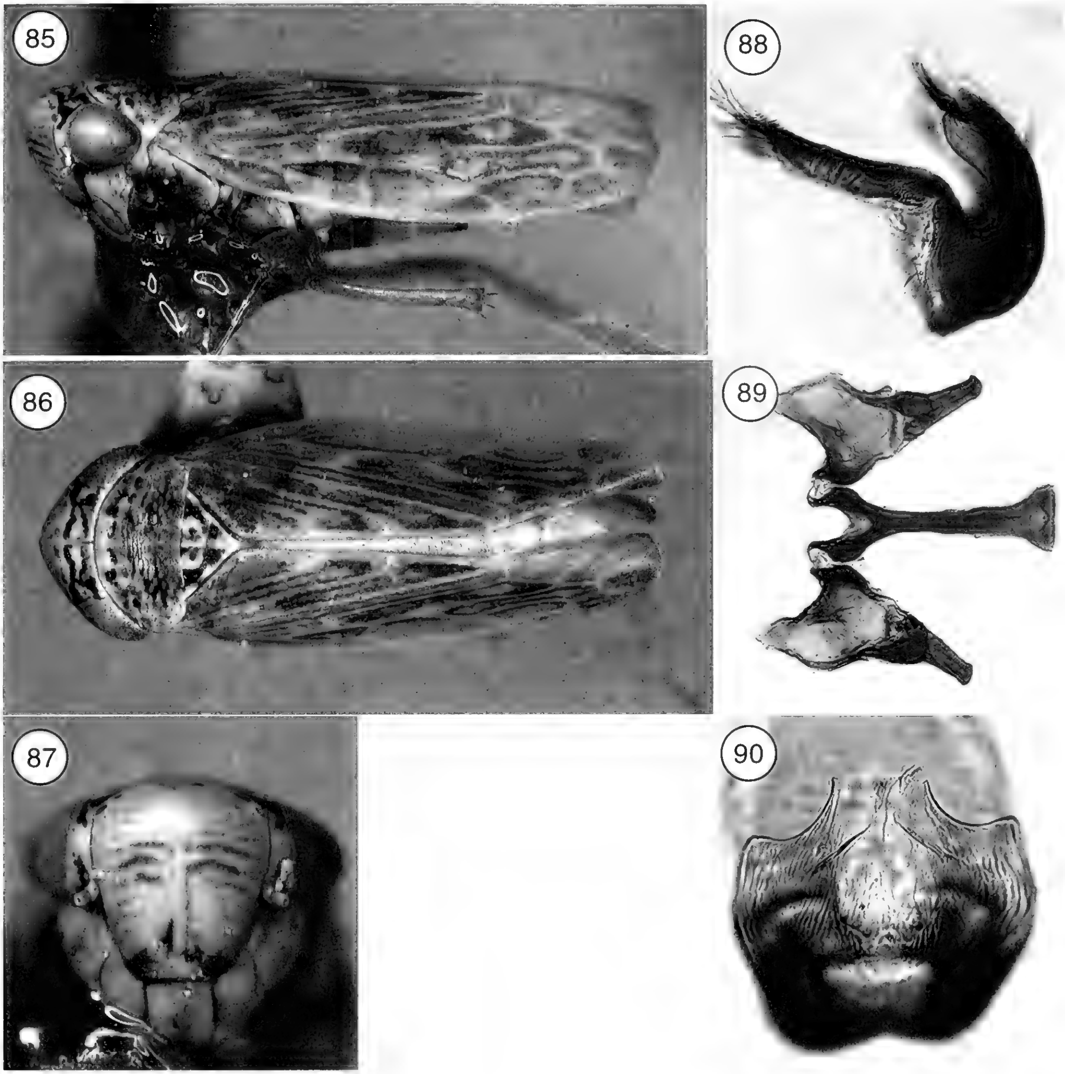
Euscelis calvatus: Van Duzee 1917b: 658 [n.comb.].

Ophiola glomerosa: Ball 1928c: 187.

Ophiola calvata: Sleesman 1930: 114 [n.comb.].

Ballana glomerosa: DeLong & Caldwell 1937c: 49 [n.comb.].

Scleroracus glomerosus: Oman 1947a: 205 [n.comb.].



Figs. 85–90. *Limotettix (Scleroracus) glomerosus*. 85–87, Habitus in lateral, dorsal, and ventroanterior aspects, respectively. 88–90, Genitalia in lateral (aedeagus and dorsal connective), dorsal (ventral connective and styles), and dorsoposterior (aedeagus and dorsal connective) aspects, respectively.

Limotettix (Scleroracus) glomerosus: Hamilton 1994: 122 [n.comb.].

Diagnosis.—Frontoclypeus weakly maculate; aedeagus in posterior view as broad as tall, dorsolaterally angulate, atrium in lateral view little constricted before shaft.

Measurements (mm). Length with forewings in repose, male 4.4–4.7; female 4.5–5.0. Width across eyes, male 1.3–1.5, female 1.3–1.6. *Head:* Vertex in dorsal view subangulate, length 0.50–0.55× minimum width between eyes (Fig. 86). *Thorax:* Pronotum in lateral view depressed (Fig. 85). Forewing veins clearly demarcated (Fig. 85). Prothoracic tibia with row AV bimodal, basal setae subequal to each other and distinctly shorter than distal macrosetae. *Abdomen:* Male. Pygofer with dorsal lobe posteriorly truncate, ventral lobe fused. Aedeagal atrium in lateral view little constricted before aedeagal shaft (Fig. 88); shaft in posterior view short and broad, lateral margins subparallel, apical processes long, abruptly produced from the middle, apically acute, and directed anterodorsad (Fig. 90); dorsal connective emargination narrow, deep, sides parallel; ventral connective widest between robust, Y-shaped arms anteriorly, length 3.3× width across anterior arms and 3.4× their longitudinal length (Fig. 89); style moderately long and distally robust, slightly curved laterad, with ventral, rounded preapical lobe not especially prominent.

Coloration. Pro- and mesothoracic legs not bicolored (not as in Fig. 1); otherwise as shown (Figs. 85–87).

Hosts.—Label data: *Sarcobatus vermiculatus* (Hook.) Torr. (greasewood; Chenopodiaceae), *Beta vulgaris* (L.) (beet; Chenopodiaceae).

Specimens examined.—*Thamnotettix glomerosa* lectotype ♀ labeled: "GndJune | Col. 12 8 00", "TYPE", "LECTOTYPE", "Thamnotettix glomerosa | Ball" [USNM]. *Athysanus calvatus* lectotype ♀ labeled: "Richfield | Ut 8-24-11", "TYPE", "LECTOTYPE", "Athysanus | calvatus | Ball" [USNM]. Non-type specimens. **USA: Colorado.** Delta, 7 Jul 1929, E. W. Davis (1 ♀) [USNM]; Grand Junction, 28 Jul 1900 (1 ♀) [USNM]; **Utah.** Richfield, 8 Jul 1960, E. W. Davis (1 ♂), 15 Jul 1929, Light trap (1 ♀) [CNCI], 15 Jul 1929, light trap, *Beta vulgaris,* H. E. Dorst (1 ♀), 8 Aug 1930 (3 ♂, 9 ♀), 8 Aug 1930, E. W. Davis (2 ♂, 5 ♀), light trap, 15 Aug 1929 (3 ♀), 24 Aug 1911 (4 ♀) [USNM]; Monroe, 25 Jul 1906 (3 ♀), 20 Jul 1911 (1 ♂) [USNM]; Oasis, 13 Sep 1915 (1 ♀) [USNM].

Remarks.—The idenity of the female lectotypes of *glomerosa* and its junior synonym, *calvatus,* were ascertained by their large size, moderately subangulate head, and the presence of pigmentation of the dorsum characteristic of the subgenus, but with only a weakly maculate frons.

Limotettix (*Scleroracus*) *humidus* (Osborn)
(Figs. 91–97)

Athysanus humidus Osborn 1915a: 131 [n. sp.].

Euscelis (*Euscelis*) *humidus*: Van Duzee 1916a: 72 [n.comb.].

Ophiola humida: Ball 1928c: 185 [n.comb.].

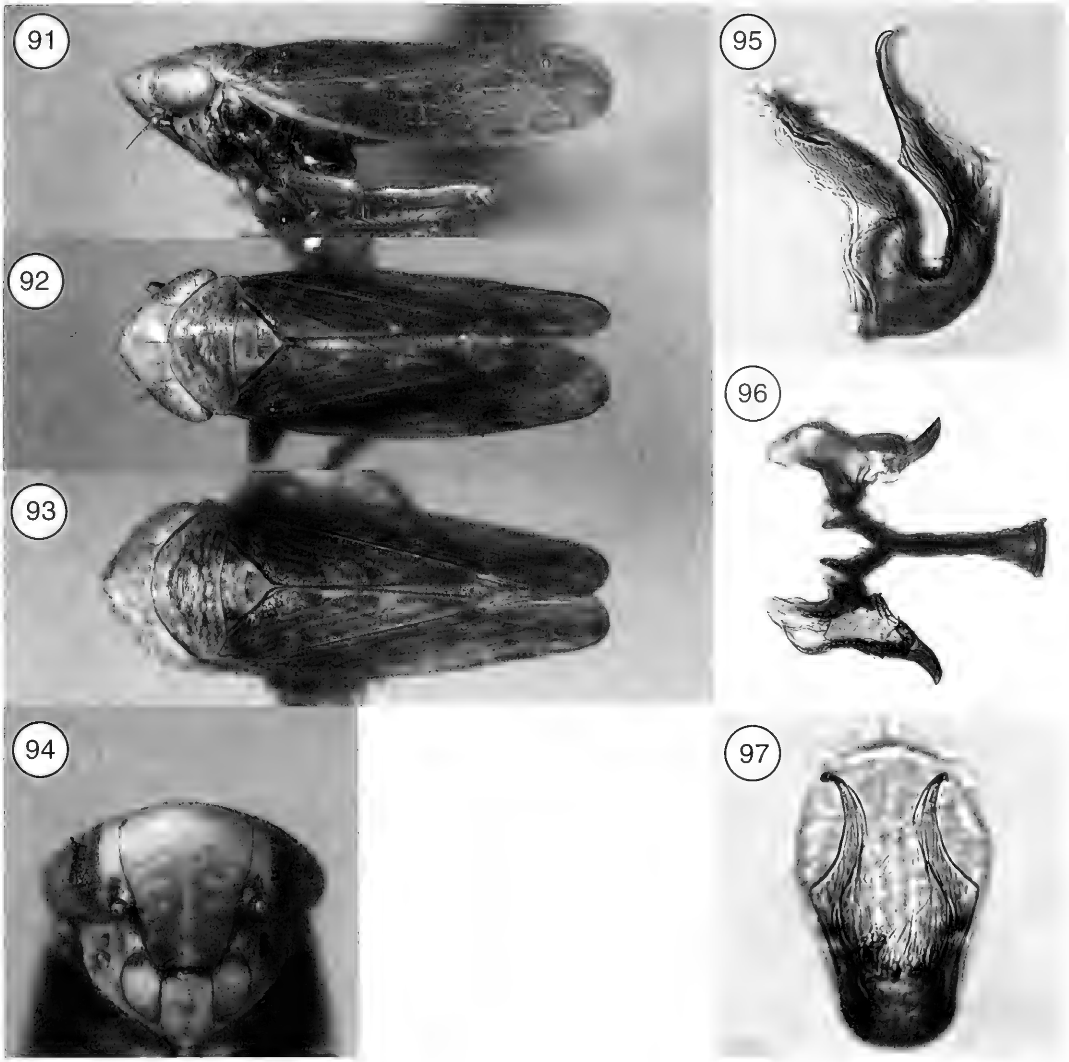
Scleroracus humidus: Oman 1947a: 205 [n.comb.].

Limotettix (*Scleroracus*) *humidus*: Hamilton & Langor 1987: 668 [n.comb.].

Diagnosis.—Vertex in dorsal view subangulate, length 0.65–0.71× minimum width between eyes, maculae faint or absent; aedeagus in posterior view taller than broad, dorsolaterally angulate, apical processes converging then diverging from each other, widely separated throughout.

Measurements (mm). Length with forewings in repose, male 3.1–3.4; female 3.6–3.7. Width across eyes, male 1.0–1.1, female 1.2. *Head:* Vertex in dorsal view subangulate, length 0.65–0.71× minimum width between eyes (Fig. 92, 93). *Thorax:* Pronotum in lateral view depressed (Fig. 91). Forewing veins clearly demarcated (Fig. 91). Prothoracic tibia with row AV not distinctly bimodal, basal setae gradually increasing in size distally. *Abdomen:* Male. Pygofer with dorsal lobe posteriorly truncate, ventral lobe fused. Aedeagal atrium in lateral view moderately constricted before aedeagal shaft (Fig. 95); shaft in posterior view taller than broad, lateral margins weakly diverging distally, apical processes long, distally attenuate and directed slightly dorsoposterad and laterad, separated from each other by more than their width at mid length (Fig. 97); dorsal connective emargination narrow, deep, sides parallel; ventral connective widest between robust, Y-shaped arms anteriorly, length 3.5× width across anterior arms and 3.4× their longitudinal length (Fig. 96); style distally short and apically subacute or moderately long and slightly curved laterad, with ventral, rounded preapical lobe not especially prominent.

Coloration. Pro- and mesothoracic legs not bicolored (not as in Fig. 1); otherwise as shown (Figs. 91–94).



Figs. 91–97. *Limotettix* (*Scleroracus*) *humidus*. 91–94, Habitus of paratype in lateral, dorsal (93, dark, non-type variant), and ventroanterior aspects, respectively. 95–97, Genitalia in lateral (aedeagus and dorsal connective), dorsal (ventral connective and styles), and dorsoposterior (aedeagus and dorsal connective) aspects, respectively.

Hosts.—Label data: *Carex exilis* [?] (sedge, Cyperaceae), *Chamaedaphne calyculata* (L.) Moench (leather-leaf, Ericaceae), *Arctostaphylos uva-ursi* (L.) Spreng. (bearberry, Ericaceae).

Specimens examined.—Holotype ♀ labeled: "Orono, Me. | 5 Aug. 13", "HOLOTYPE", "Athysanus | humidus | Osborn" [OSUC]. Paratypes. (2 ♂) with same data as holotype [USNM]. Non-type specimens. **CANADA: New Brunswick.** Prince of Wales, *Carex exilis,* 19 Aug 1984 (1 ♂, 1 ♀) [CNCI]; Rockwood Park, St. John, 7 Aug 1953, J. F. Brimley (1 ♂) [CNCI]; **Newfoundland.** 29 km N Milltown, 16 Aug 1984, K. G. A. Hamilton (7 ♂, 5 ♀) [CNCI]; Black Brook, 13 Aug 1984, K. G. A. Hamilton (25 ♂, 11 ♀) [CNCI]; 6 km SE Gallants, 9 Aug 1984, K. G. A. Hamilton (3 ♂, 2 ♀) [CNCI]; St. Veronica, 16 Aug 1984, K. G. A. Hamilton (6 ♂, 4 ♀) [CNCI]; 10 km W Valleyfield, 15 Aug

1984, K. G. A. Hamilton (5 ♂, 9 ♀) [CNCI]; Beachside, 12 Aug 1984, K. G. A. Hamilton (1 ♀) [CNCI]; Colinet, 8 Sep 1960, Ray F. Morris (1 ♂) [CNCI]; **Nova Scotia.** Benjie's Lake, CBHNP, 17 Aug 1983, K. G. A. Hamilton (2 ♂, 10 ♀) [CNCI]; Kempt, 21 Aug 1983, K. G. A. Hamilton (1 ♂) [CNCI]; North Mountain, CBHNP, 6 Aug 1984, K. G. A. Hamilton (20 ♂, 18 ♀) [CNCI]; Mackenzie Mt., CBHNR, 15 Aug 1983, J. E. H. and R. J. Martin (51 ♂, 1 ♀) [CNCI]; French Mtn., Cabot Trail, 14 Aug 1973, K. G. A. Hamilton (6 ♂, 2 ♀) [CNCI]; Paquet L., CBHNP, pan traps, 19–28 Aug 1983, M. Sharkey (9 ♂, 3 ♀) [CNCI]; Paquet L., CBHNP, pan traps, 5 Aug 1983, D. G. and J. E. Bright (43 ♂) [CNCI]; Cape Smokey, 7 Aug 1984, K. G. A. Hamilton (1 ♀) [CNCI]; **Ontario.** 7 km W Borup's Corner, 29 Aug 1985, K. G. A. Hamilton (1 ♂, 4 ♀) [CNCI]; 5 mi. NW Kemgami L., 13 Aug 1975, K. G. A. Hamilton (1 ♂, 2 ♀) [CNCI]; 10 km SW Ameson, 30 Aug 1985, K. G. A. Hamilton (1 ♂, 1 ♀) [CNCI]; Harris Hill, 4 Aug 1960, Kelton and Whitney (1 ♂) [CNCI]; Black Hawk, 3 Aug 1960, Kelton and Whitney (4 ♂, 1 ♀) [CNCI]; Mer Bleue, 9 Aug 1982, G. S. Walley (1 ♀), 6 Sep 1928, G. S. Walley (1 ♀) [CNCI]; Oliver Bog, 3 km. S. Galt, 3–9 Jul 1987 (1 ♂), 10–16 Jul 1987 (1 ♂), 17–23 Jul 1987, all D. Blades (2 ♂), 31 Jul–6 Aug 1987 (1 ♀), 4–11 Sep 1987 (1 ♀), 26 Sep–11 Nov 1987 (2 ♀) [CNCI]; 5 mi., NW Kemgami L., *Chamaedaphne calyculata,* 13 Aug 1975, K. G. A. Hamilton (1 ♂) [CNCI]; Black Stur. Lake, 1–15 Aug 1956, Lindberg (15 ♂, 1 ♀) [CNCI]; **Prince Edward Island.** 3 km N Caraross, 21 Aug 1999, K. G. A. Hamilton (1 ♂, 5 ♀) [CNCI]; West Point, *Arctostaphylos uva-ursi,* 20 Aug 1999, K. G. A. Hamilton (1 ♂, 8 ♀) [CNCI]; Albion Cross, 25 Aug 1999, K. G. A. Hamilton (2 ♀) [CNCI]; **Quebec.** Laverendrye Park, 25 km N. Dorval, 15 Jul 1982, K. G. A. Hamilton (1 ♂) [CNCI]; **Saskatchewan.** Elbow, 21 Jul 1957, A. R. Brooks (1 ♂) [CNCI]. USA: **Maine.** Orono, 5 Aug 1913 (1 ♀), 30 Aug 1913 (2 ♀) [USNM]; **Michigan.** Cheboygan Co., 10 Aug 1936, M. W. Sanderson (2 ♀) [USNM]; Wilson Mills, 4 Sep 1986, K. G. A. Hamilton (1 ♀) [CNCI]; **South Dakota.** Black Hills, Sheridan Lake, 17 Aug 1954, M. W. Sanders (1 ♀) [CNCI]; **West Virginia.** 12 km E Parsons, 13 Aug 1986, K. G. A. Hamilton (3 ♀) [CNCI]; **Wisconsin.** Sayner, 5 Jul 1969, Harris and Harris (3 ♂) [CNCI].

Remarks.—The narrow emargination of the dorsal connective, faintly visible in the middle of Fig. 97, disagrees with the observations reported by Hamilton (1994).

Limotettix (*Scleroracus*) *instabilis* (Van Duzee)

(Figs. 98–103)

Athysanus instabilis Van Duzee 1893a: 284 [n.sp.].

Athysanus elongatus Osborn 1915a: 129 [n.sp.].

Euscelis (*Euscelis*) *elongatus*: Van Duzee 1916a: 72 [n.comb.].

Euscelis (*Euscelis*) *instabilis*: Van Duzee 1916a: 72 [n.comb.].

Ophiola instabilis: DeLong & Caldwell 1937c: 38 [n.comb.].

[*Ophiola*] *elongatus*: DeLong & Caldwell 1937c: 38 To *Ophiola cornicula* Marshall [error].

Scleroracus instabilis: Oman 1947a: 205 [n.comb.].

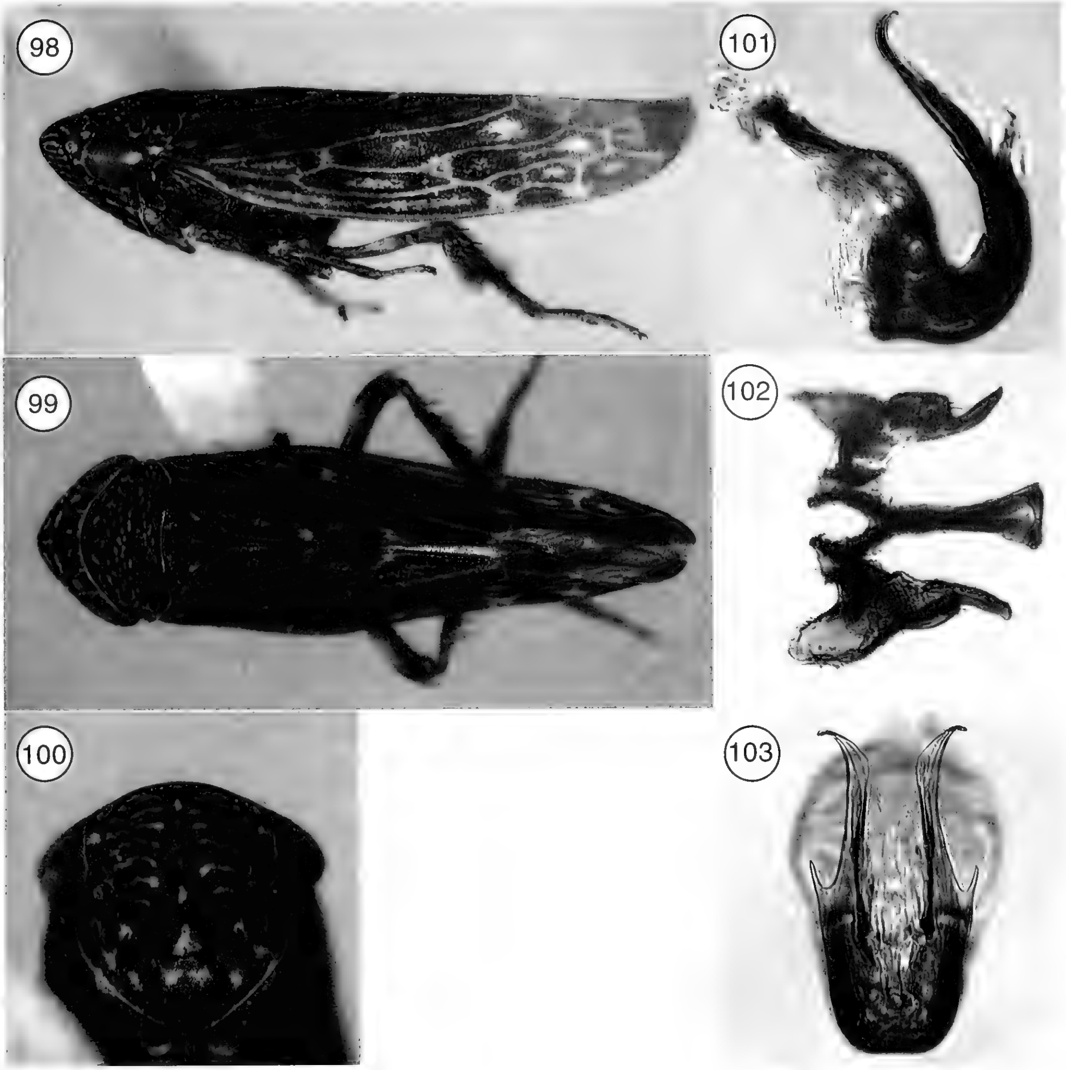
Scleroracus elongatus: Oman 1949a: 152 [n.comb.].

[*Limotettix* (*Scleroracus*)] *instabilis*: Ribaut 1952a: 157 To *Limotettix* (*Scleroracus*) *corniculus* Marshall [error].

[*Limotettix* (*Scleroracus*)] *elongatus*: Ribaut 1952a: 157 To *Limotettix* (*Scleroracus*) *corniculus* Marshall [error].

Ophiola elongata: Metcalf 1967: 189 [reinst.; n.comb.].

Limotettix (*Scleroracus*) *instabilis*: Hamilton 1994: 122 [reinst.; n.comb.]; 113 Equals *Athysanus elongatus* Osborn [n.syn.].



Figs. 98–103. *Limotettix* (*Scleroracus*) *instabilis.* 98–100, Habitus in lateral, dorsal, and ventroanterior aspects, respectively. 101–103, Genitalia in lateral (aedeagus and dorsal connective), dorsal (ventral connective and styles), and dorsoposterior (aedeagus and dorsal connective) aspects, respectively.

Diagnosis.—Aedeagal shaft bearing 2 pairs of apical processes, lateral pair directed dorsolaterally, mesal pair parallel and widely separated preapically; vertex in dorsal view subangulate but length 0.42× minimum width between eyes.

Measurements (mm). Length with forewings in repose, male 3.8–4.0; female 4.2–4.7. Width across eyes, male 1.0–1.1, female 1.2–1.3. *Head:* Vertex in dorsal view subangulate but length 0.42× minimum width between eyes (Fig. 99). *Thorax:* Pronotum in lateral view depressed (Fig. 98). Forewing veins clearly demarcated (Fig. 98). Prothoracic tibia with row AV bimodal, basal setae subequal to each other and distinctly shorter than distal macrosetae. *Abdomen:* Male. Pygofer with dorsal lobe posteriorly truncate, ventral lobe fused. Aedeagal atrium in lateral view strongly constricted before aedeagal shaft (Fig. 101); shaft in posterior view taller than broad, lateral margins weakly diverging distally, mesoapical processes approximately as long as shaft, distally attenuate and recurved, directed dorsoposterad and laterad, basolaterally with short acute processes produced dorsolaterad (Fig. 103); dorsal connective emargination narrow, deep, sides parallel; ventral connective widest between robust, Y-shaped arms anteriorly, length 3.2× width across anterior arms and 3.0× their longitudinal length (Fig. 102); style moderately long and distally slender, slightly curved laterad, with ventral, rounded preapical lobe not especially prominent.

Coloration. Pro- and mesothoracic legs not bicolored (not as in Fig. 1); otherwise as shown (Figs. 98–100).

Hosts.—Label data: *Prunus emarginata* (Hook.) Walp. (bitter cherry; Rosaceae), *Prunus virginiana L.* (chokecherry; Rosaceae), *Rhus glabra* L. (scarlet sumac; Anacardiaceae), *Salix discolor* Muhl. (pussy willow; Salicaceae), *Salix sepulcralis* [?] (weeping willow; Salicaceae), *Salix* sp. (willow, Salicaceae).

Specimens examined.—Lectotype ♂ labeled: "Ag.Coll.Mich., | 8-23 93.184", "Type" "♂", "COTYPE | (By E. P. Van Duzee) | Athysanus | instabilis | VanD.", "LECTOTYPE | Athysanus | instabilis | Van D. | Oman 1948" [USNM]. Non-type specimens. **CANADA: Alberta.** High Prairie, both A. R. Brooks, 17 Jul 1961 (1 ♂, 1 ♀), 26 Jul 1961 (1 ♂) [CNCI]; 3 Battle River Cross, 17 Jul 1940, C. L. Neilson (1 ♂, 1 ♀) [CNCI]; **British Columbia.** Quesnel, 11 Aug 1948, at light, H. R. MacCarthy (2 ♂) [CNCI], 14 Aug 1949, G. J. Spencer (1 ♀) [CNCI]; Salmon Arm, Sticky board, E3, on *Prunus emarginata,* 24–30 Jul 1971 (2 ♂) [CNCI]; Summit Lake, mi. 392 Alaska Hwy, 4,200 ft., 21 Jul 1959, R. E. Leech (1 ♂, 3 ♀) [CNCI]; W. B. Tests, Soda Creek, 16 Jul 1951, H. R. MacCarthy (1 ♂) [CNCI]; **Newfoundland.** 6 km SE Gallants, 9 Aug 1984, K. G. A. Hamilton (1 ♀) [CNCI]; **Prince Edward Island.** West Point, 20 Aug 1999, K. G. A. Hamilton (1 ♂) [CNCI]; **Quebec.** Lac Mondor, Ste. Flore, 8 Jul 1951, E. G. Munroe (5 ♂, 20 ♀) [CNCI]; Vallee-Junction, 14 Aug 1979, K. G. A. Hamilton (1 ♀) [CNCI]; St. Germain Co., Kam., 25 Jul 1973, K. G. A. Hamilton, *Salix discolor,* K. G. A. Hamilton (1 ♂) [CNCI]; Lacdela Vielle, LaVerendrye, 15 Jul 1982, K. G. A. Hamilton (5 ♂) [CNCI]; Berthierville, 19 Aug 1932, L. Daviault (1 ♀) [CNCI]; Kirks Ferry, in light trap, 10 Aug 1950, B. P. Beirne (1 ♂) [CNCI]; Bradore Bay, 24 Jul 1929, W. J. Brown (1 ♂) [CNCI]; Quelspel, 14 Aug 1949, G. J. Spencer (1 ♀) [CNCI]; **Manitoba.** 7 km E. St. Ambroise, 25 Jul 1991, K. G. A. Hamilton (1 ♀) [CNCI]; The Pas, 30 Aug 1959, A. and J. Brooks (2 ♀) [CNCI]; Aweme, 14 Jul 1930, R. M. White (1 ♀) [CNCI]; Emerson, 28 Jul 1991, K. G. A. Hamilton (1 ♂) [CNCI]; Winnipeg, all at lights, all K. G. A. Hamilton: 5–7 Aug 1966 (1 ♂), 20 Aug 1967 (1 ♀), 25 Aug 1967 (1 ♂), 26–28 Aug 1966 (1 ♀) [CNCI]; **Newfoundland.** 7 km E Gambo, 15 Aug 1984, K. G. A. Hamilton (2 ♂, 3 ♀) [CNCI]; Labrador, Goose Bay, 24–26 Sep 1981, M. Colbo (1 ♀) [CNCI]; **Ontario.** Prince Edward Co., 16 Aug 1945, Brimley (1 ♀) [CNCI]; 6 mi. E. Batchewana Bay P. Pk., *Rhus glabra,* 4 Jul 1975, K. G. A. Hamilton (1 ♀) [CNCI]; 7 km NE Evansville, 18 Aug 1988, K. G. A. Hamilton (1 ♂) [CNCI]; Ravenswood, *Prunus virginiana,* 12 Aug 1974, K. G. A. Hamilton (1 ♂) [CNCI]; Ottawa, *Salix sepulcralis,* 9 Aug 1979, K. G. A. Hamilton (1 ♂) [CNCI]; Trenton, 1 Aug 1908, Evans (1 ♀) [CNCI]; Trenton, 23 Jun 1911, Evans (1 ♂) [CNCI]; Trenton, 7 Aug 1904, Evans (1 ♂) [CNCI]; Ottawa, 23 Jul 1954, R. Hollinsworth (1 ♂) [CNCI]; Pays Plat., *Salix* sp., 2 Jul 1975, K. G. A. Hamilton (1 ♂) [CNCI]; Ottawa, 8 Aug 1923, C. H. Curran (1 ♂), 9 Aug 1979, *Salix sepulcralis,* K. G. A. Hamilton (1 ♀) [CNCI]; Ipperwash P. Pk., 15 Aug 1974, *Salix* sp., K. G. A. Hamilton (1 ♂) [CNCI]; 5 km Stobermory, 17 Aug 1988, K. G. A. Hamilton (1 ♂) [CNCI]; 20 mi. N. Red Lake Rd., 11 Aug 1960, Kelton and Whitney (1 ♂) [CNCI];

Saskatchewan. Tugaskie, 3 Aug 1981, K. G. A. Hamilton (1 ♂) [CNCI]; Change Island, 1–9 Aug 1981, D. Larson (1 ♂) [CNCI]; **Yukon.** Km 140.5, Dempster Hwy, 900 m, 27–29 Jul 1980, Wood and Lafontaine (1 ♂, 4 ♀) [CNCI]. **USA: Alaska.** Unalakleet, all R. Madge: 5 Aug 1961 (1 ♂) [CNCI]; Unalakleet, 8 Aug 1961 (3 ♂, 2 ♀), 10 Aug 1961 (2 ♂, 2 ♀), 13 Aug 1961 (1 ♀) [CNCI]; **Massachusetts.** Cambridge, 25 Jul 1951, Ross and Ross (1 ♂, 1 ♀) [CNCI]; **Michigan.** Tecumseh, 27 Jul 1993, K. G. A. Hamilton (1 ♂, 3 ♀) [CNCI]; **New Hampshire.** Mt. Washington, Lake of the Clouds, 5000 ft., 9 Aug 1954, Becker, Munroe and Mason (1 ♂) [CNCI]; **North Carolina.** Highlands, 22 Aug 1957, L. A. Kelton (1 ♀) [CNCI].

Remarks.—Medler (1958b) and Ribaut (1952a) treated *L.* (*S.*) *instabilis, L.* (*S.*) *elongata,* and *L.* (*S.*) *plutonius* as junior synonyms of *L.* (*S.*) *corniculus,* a Palearctic species. As mentioned above, Hamilton (1994) rejected this synonymy. Although *L.* (*S.*) *corniculus* has two apical processes on the aedeagus, as in *L.* (*S.*) *instabilis* and *L.* (*S.*) *elongatus* (but unlike *L.* (*S.*) *plutonius,* Fig. 161), the Palearctic species is smaller and has the mesoapical processes weakly recurved and the lateroapical processes aligned with the shaft in lateral view; this combination of features distinguishes it from the Nearctic species mentioned above. The species *L.* (*S.*) *corniculus* was adequately figured (under the genus *Ophiola*) by Ossiannilsson (1983).

Limotettix (*Scleroracus*) *kryptus* (Medler) (Figs. 104–111)

Scleroracus kryptus Medler 1955b: 213 [n.sp.].

Limotettix (*Scleroracus*) *kryptus*: Hamilton 1994: 122 [n.comb.].

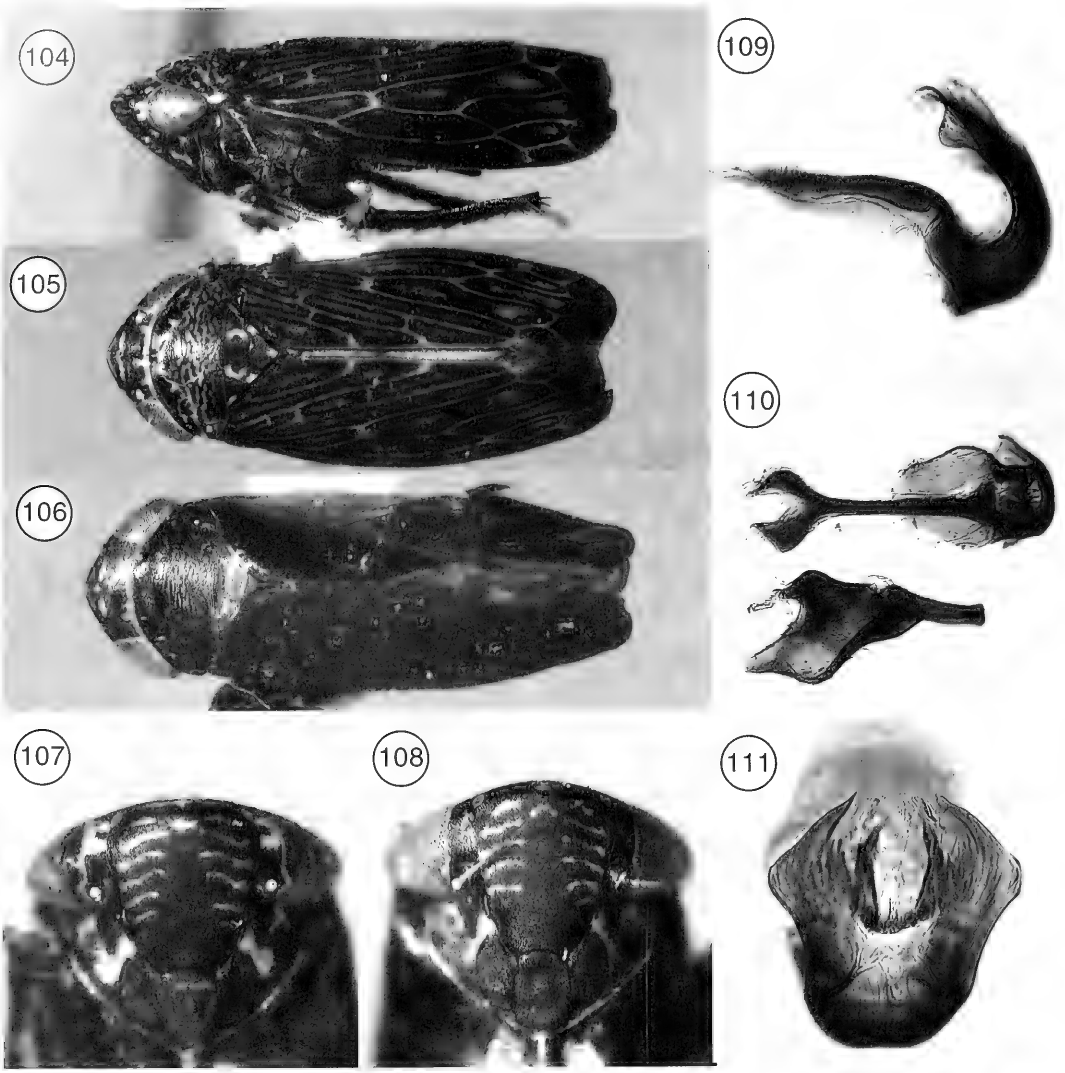
Diagnosis.—Prothoracic legs bicolored (as in Fig. 1); aedeagal shaft in posterior view short and broad, distally robust with apices converging but widely separated from each other.

Measurements (mm). Length with forewings in repose, male 3.8; female 4.4. Width across eyes, male 1.3, female 1.6. *Head:* Vertex in dorsal view subangulate, length 0.54× minimum width between eyes (Fig. 105). *Thorax:* Pronotum in lateral view slightly elevated (Fig. 104). Forewing sometimes with veins not clearly demarcated (Fig. 106), as in *L.* (*S.*) *anthracinus.* Prothoracic tibia with row AV not distinctly bimodal, basal setae gradually increasing in size distally. *Abdomen:* Male. Pygofer with dorsal lobe posteriorly truncate, ventral lobe articulated. Aedeagal atrium in lateral view weakly constricted before aedeagal shaft (Fig. 109); shaft in posterior view taller than broad, lateral margins initially diverging weakly, then more abruptly, apical processes basally broad, distally acute and directed dorsomesad, basolaterally produced anterolaterad, obtuse (Fig. 111); dorsal connective emargination narrow, deep, sides parallel; ventral connective widest between robust, Y-shaped arms anteriorly, length 3.1× width across anterior arms and 3.5× their longitudinal length (Fig. 110); style long and distally slender, straight, with ventral, rounded preapical lobe not especially prominent.

Coloration. Pro- and mesothoracic legs bicolored (as in Fig. 1); otherwise as shown (Figs. 104–108).

Hosts.—Label data: *Carya* sp. (hickory, Juglandaceae). Hamilton (1994) recorded composites (Asteraceae) as hosts.

Specimens examined.—Holotype ♂ labeled: "Muskego, Wisc | 7-21-39 PB | Lawson", "HOLOTYPE | Scleroracus | kryptus | Medler" [SEMC]. Paratypes. **CANADA: Manitoba.** Keld, 8 Aug 1937, R. H. Beamer (1 ♀) [CNCI]. Non-type specimens. **CANADA: Alberta.** Grande Prairie, 26 Jul 1961, A. R. Brooks (2 ♂, 1 ♀) [CNCI]; **Manitoba.** Keld, 8 Aug 1937, R. H. Beamer (1 ♀) [CNCI]; Boissevain, 29 Jul 1930, R. M. White (1 ♀) [CNCI]; **Nova Scotia.** Mapleton, 31 Jul 1973, K. G. A. Hamilton (1 ♀) [CNCI]; **Ontario.** Queenston, 8 Jul 1955, L. A. Kelton (1 ♀) [CNCI]; O. P. P.



Figs. 104–111. *Limotettix* (*Scleroracus*) *kryptus*, paratypes. 104–108, Habitus in lateral, dorsal, and ventroanterior aspects, respectively (106, 108, dark variant). 109–111, Aedeagus and dorsal connective in lateral, dorsal (with connectives and left style [detached]), and dorsoposterior aspects, respectively.

N. R., Windsor, 29 Aug 1988, K. G. A. Hamilton (1 ♀) [CNCI]; St. Lawrence Is. Nat. Park, Grenadier I. Centre, Malaise Trap, 8 Jul 1975, E. Sigler (2 ♂) [CNCI]; St. Lawrence Is. Nat. Park, Thwartway Is., 1 Jul 1975, Carter (1 ♀) [CNCI]; Rondeau Park, 18 Jul 1955, L. A. Kelton (1 ♀) [CNCI]; Ottawa, [no date] (1 ♀) [CNCI]; Carp, 19 Aug 1954, J. E. H. Martin (1 ♀) [CNCI]; Hamilton, 7 Jul 1955, L. A. Kelton (1 ♀) [CNCI]; Leamington, 10 Jun, 1929, G. S. Walley (1 nymph) [CNCI]; Prince Edward County, 6 Aug 1952, J. F. Brimley (1 ♀) [CNCI]; **Quebec.** Knowlton, 5 Jul 1927, W. J. Brown (1 ♀), Fabre, 12 Jul 1963, W. Gagne (2 ♂), 22 Jul 1929, L. J. Milne (1 ♀), 6 Aug 1929, G. S. Walley (1 ♀), 13 Aug 1929, G. S. Walley (1 ♀) [CNCI]; St. Antoine Abbe, 13 Aug 1979, K. G. A. Hamilton (5 ♀) [CNCI]; Contrecoeur, 22 Aug 1981, A. Larochelle (1 ♀) [CNCI]; Lac Mondor, Ste. Flore, 3 Aug 1951, E. G.

Monroe (2 ♂) [CNCI]; **Saskatchewan.** 8 km W. Kisbey, 23 Jun 1984, K. G. A. Hamilton (1 nymph) [CNCI]; Kenosee, 19 Jul 1958, A. and J. Brooks (2 ♀, 1 ♂) [CNCI]; Prince Albert, 2 Sep 1954, Brooks-Wallis (1 ♀) [CNCI]. **USA: Illinois.** 10 km E Morris, 13 Jun 1993, K. G. A. Hamilton (3 ♂, 1 ♀) [CNCI]; **Iowa.** Iowa. 26 Jun 1934, H. C. Knutson (1 ♂) [USNM]; **Michigan.** Berrien Springs, 28 Jul 1993, K. G. A. Hamilton (1 ♀) [CNCI]; Kinross, 28 Jul 1989, K. G. A. Hamilton (1 ♀) [CNCI]; Posen, 26 Aug 1988, K. G. A. Hamilton (1 ♀) [CNCI]; Tecumseh, 4 Jul 1994, K. G. A. Hamilton (1 ♀) [CNCI]; **Minnesota.** 8 km SW Rothsay, 10 Aug 1993, K. G. A. Hamilton (1 ♂, 6 ♀) [CNCI]; 11 km E Harold, 10 Aug 1993, K. G. A. Hamilton (2 ♀) [CNCI]; Grosse Isle, 22 Jul 1994, K. G. A. Hamilton (1 ♀) [CNCI]; 5 km S Slayton, 19 Jul 1994, K. G. A. Hamilton (1 ♀) [CNCI]; 8 km SW Rothsay, 8 Aug 1988, K. G. A. Hamilton (1 ♂) [CNCI]; **Montana.** 22 km S Havre, 21 Jun 1984, K. G. A. Hamilton (1 nymph) [CNCI]; **North Dakota.** 1A, 6 km ESE Langdon, 18 Jul 1994, K. G. A. Hamilton (1 ♀) [CNCI]; **Ohio.** Defiance, *Carya* sp., 24 Jun 1980, K. G. A. Hamilton (1 ♀) [CNCI]; **Tennessee.** Great Smoky Mountains, elev. 6,000 ft., 23 Aug 1950, G. S. Walley (1 ♀) [CNCI]; **West Virginia.** Pendleton Co, Spruce Knob, 4,700 ft., 22 Aug 1986, K. G. A. Hamilton (2 ♀) [CNCI]; **Wisconsin.** Berlin, 19 Jul 1996, K. G. A. Hamilton (1 ♀) [CNCI]; 4 kms Hubbleton, 19 Jul 1996, K. G. A. Hamilton (5 ♂, 6 ♀, 1 nymph) [CNCI]; Genesee, 6 Jul 1994, K. G. A. Hamilton, 2 ♂) [CNCI].

Limotettix (*Scleroracus*) *luteolus* (Sleesman)
(Figs. 112–117)

Ophiola luteola Sleesman 1930: 120 [n. sp.].

Scleroracus luteolus: Oman 1947a: 205 [n.comb.].

Limotettix (*Scleroracus*) *luteolus*: Hamilton 1994: 122 [n.comb.].

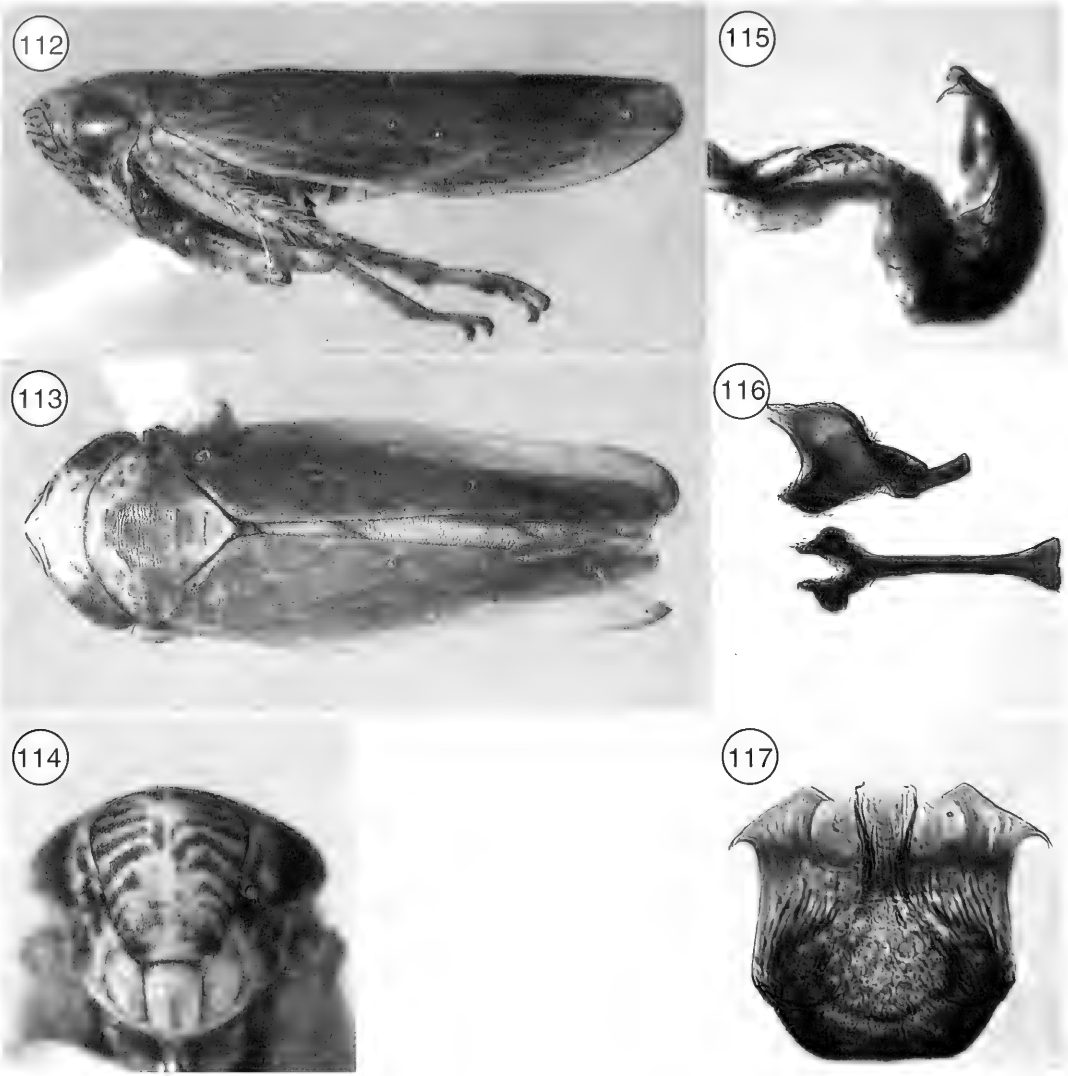
Diagnosis.—Aedeagus in posterior view short and broad with apical processes laterally produced into acute falcate processes directed ventrolaterad; body almost entirely pale; aedeagal apical processes falcate and directed mesad.

Measurements (mm). Length with forewings in repose, male 4.1; female 4.9. Width across eyes, male 1.3, female 1.5. *Head:* Vertex in dorsal view subangulate, length 0.55× minimum width between eyes (Fig. 113). *Thorax:* Pronotum in lateral view depressed (Fig. 112). Forewing veins clearly demarcated (Fig. 112). Prothoracic tibia with row AV not distinctly bimodal, basal setae gradually increasing in size distally. *Abdomen:* Male. Pygofer with dorsal lobe posteriorly truncate, ventral lobe articulated. Aedeagal atrium in lateral view not constricted before aedeagal shaft (Fig. 115); shaft in posterior view short and broad, lateral margins parallel, apical processes short, distally falcate and directed mesad, their basolateral angles produced lateroventrad and anterad, attenuate (Fig. 117); dorsal connective emargination broad basally, shallow, subtriangular; ventral connective widest between robust, Y-shaped arms anteriorly, length 3.2× width across anterior arms and 3.3× their longitudinal length (Fig. 116); style moderately long and distally slender, slightly curved laterad, with ventral, rounded preapical lobe not especially prominent.

Coloration. Pro- and mesothoracic legs not bicolored (not as in Fig. 1); otherwise as shown (Figs. 112–114).

Hosts.—Label data: None. Hamilton (1994) recorded bearberry (*Arctostaphylos uva-ursi,* Ericaceae) as a host.

Specimens examined.—Non-type specimens. **CANADA: New Brunswick.** 3 mi. S Cornhill, bearberry, 28 Jul 1973, K. G. A. Hamilton (1 ♂, 3 ♀) [CNCI]; **Nova Scotia.** Green Cove, Cabot Trail, 15 Aug 1973, K. G. A. Hamilton (1 ♀) [CNCI]; Broad Cove, CBHNP, 18 Aug 1983, K. G. A. Hamilton (1 ♀) [CNCI]; **USA: New York.**



Figs. 112–117. *Limotettix* (*Scleroracus*) *luteolus.* 112–114, Habitus in lateral, dorsal, and ventroanterior aspects, respectively. 115–117, Genitalia in lateral (aedeagus and dorsal connective), dorsal (ventral connective and right style [detached]), and dorsoposterior (aedeagus and dorsal connective) aspects, respectively.

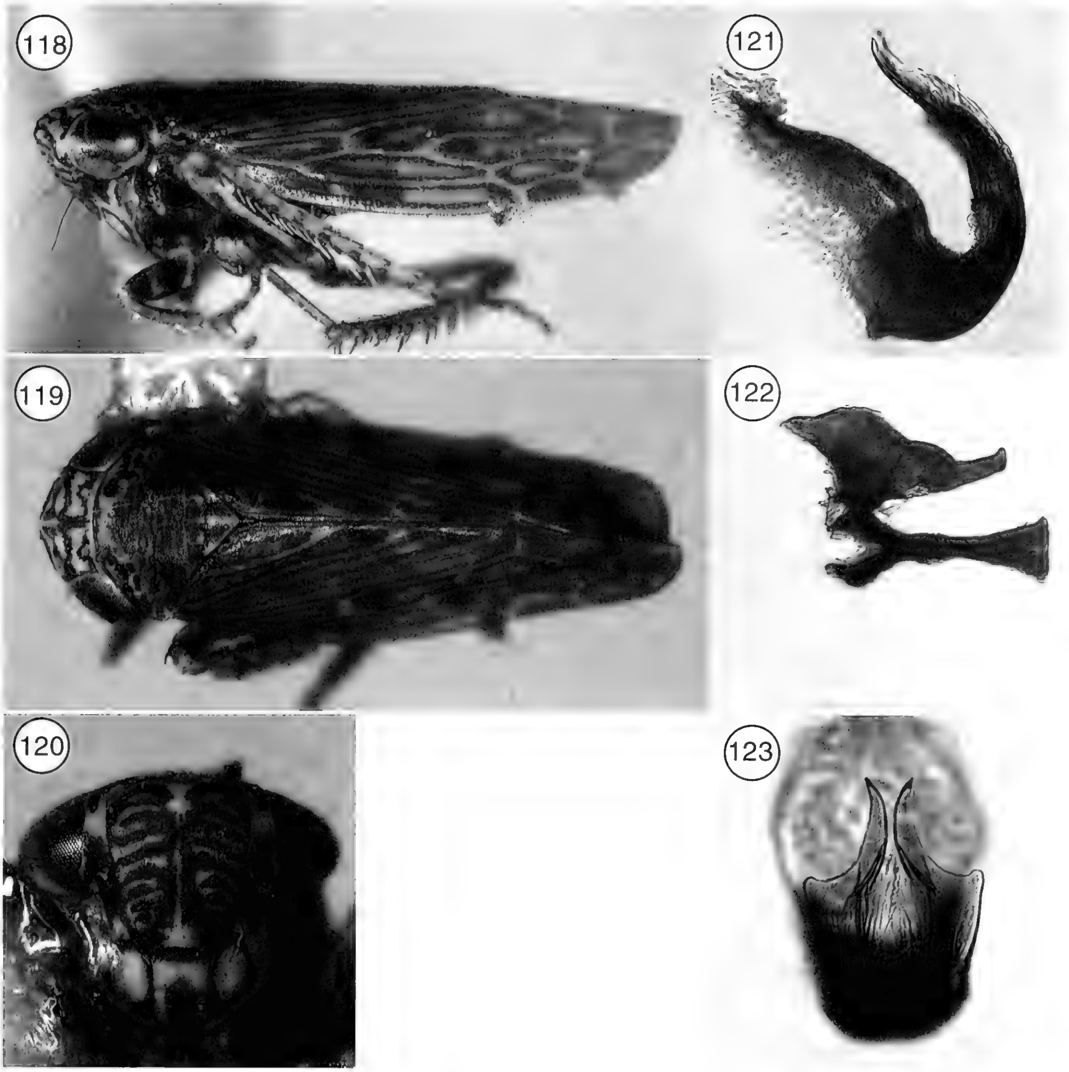
McLean Bogs, Tompkins Co., 21 Jul 1923, J. L. Buys (1 ♂) [USNM].

Remarks.—The holotype (♂) of *Ophiola luteola,* examined by Medler and apparently in OSUC, was not examined, but topotipic males (from McLean Bogs) in agreement with Medler's (1958b) description were examined (see above). For purposes of synonymy, it merits notice that the publication date of the original description is actually June 14, 1930.

Limotettix (*Scleroracus*) *medleri* Hamilton
(Figs. 118–123)

Limotettix (*Scleroracus*) *medleri* Hamilton 1994: 130 [n.sp.].

Diagnosis.—Aedeagus in posterior view taller than broad, dorsolaterally angulate, apical processes converging then diverging from each other, almost touching each other (separated by less than their width at mid length).



Figs. 118–123. *Limotettix* (*Scleroracus*) *medleri*, holotype. 118–120, Habitus in lateral, dorsal, and ventroanterior aspects, respectively. 121–123, Genitalia in lateral (aedeagus and dorsal connective), dorsal (ventral connective and right style), and dorsoposterior (aedeagus and dorsal connective) aspects, respectively.

Female unknown. Male. Measurements (mm). Length with forewings in repose 3.6. Width across eyes 1.2. *Head:* Vertex in dorsal view projecting but evenly convex, not subangulate, length 0.50× minimum width between eyes (Fig. 119). *Thorax:* Pronotum in lateral view depressed (Fig. 118). Forewing veins clearly demarcated (Fig. 118). Prothoracic tibia with row AV depressed in holotype, but apparently bimodal, basal setae subequal to each other and distinctly shorter than distal macrosetae. *Abdomen:* Pygofer with dorsal lobe posteriorly truncate, ventral lobe fused. Aedeagal atrium in lateral view strongly constricted before aedeagal shaft (Fig. 121); shaft in posterior view taller than broad, lateral margins evenly diverging distally, apical processes abruptly produced mesodorsad from middle, long, almost touching each other at mid length, distally acute and directed dorsad (Fig. 123); dorsal connective emargination broad basally, deep, sides parallel; ventral connective widest between robust, Y-shaped arms anteriorly, length 3.0× width across anterior arms and 3.0× their longitudinal length (Fig. 122); style moderately long and distally slender, slightly curved laterad, with ventral, rounded preapical lobe not especially prominent.

Coloration. Pro- and mesothoracic legs not bicolored (not as in Fig. 1); otherwise as shown (Figs. 118–120).

Hosts.—Unknown.

Specimens examined.—Holotype ♂ labeled: "Hudson Bay | Sask. 24-8 1954 | Brooks-Wallis", "HOLOTYPE | Limotettix | medleri Hmlt. | CNC No.21388" [CNCI].

Limotettix (*Scleroracus*) *melastigmus* (Medler)

(Figs. 8, 124–129)

Scleroracus melastigmus Medler 1955b: 214 [n.sp.].

Limotettix (*Scleroracus*) *melastigmus*: Hamilton 1994: 122 [n.comb.].

Diagnosis.—Forewings at rest barely exceeding abdominal apex; male pygofer with dorsal lobe developed into an acute spine directed posterad, adjacent to ventral lobe; aedeagus in posterior view distinctly taller than broad, apical processes long and directed dorsolaterally.

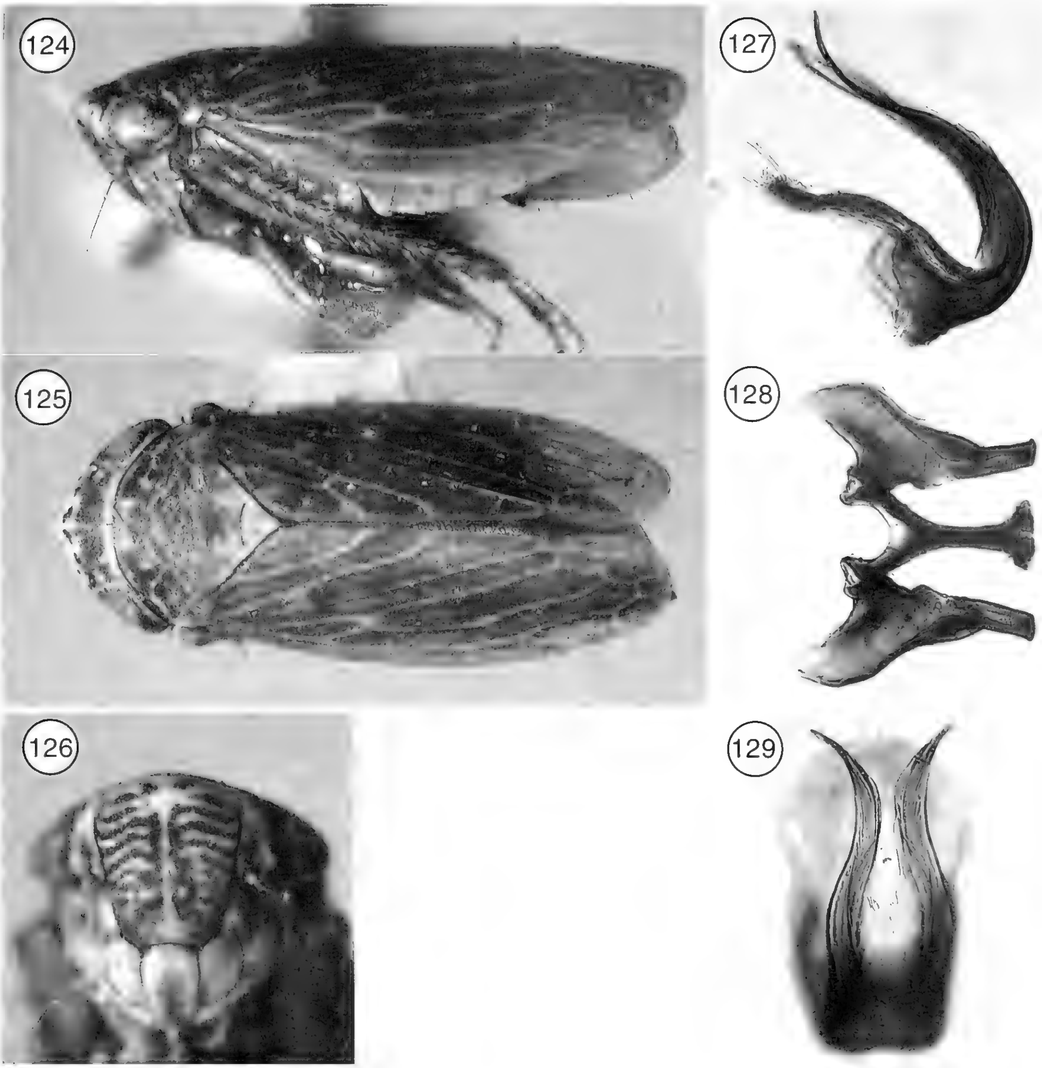
Measurements (mm). Length with forewings in repose, male 3.8–3.9; female 4.2–4.3. Width across eyes, male 1.3, female 1.5. *Head:* Vertex in dorsal view subangulate, length 0.50× minimum width between eyes (Fig. 125). *Thorax:* Pronotum in lateral view depressed (Fig. 124). Forewing veins clearly demarcated (Fig. 125). Prothoracic tibia with row AV bimodal, basal setae subequal to each other and distinctly shorter than distal macrosetae. *Abdomen:* Male. Pygofer with dorsal lobe posteriorly developed into an acute process, ventral lobe fused. Aedeagal atrium in lateral view strongly constricted before aedeagal shaft (Fig. 127); shaft in posterior view taller than broad, lateral margins subparallel, apical processes long, broad, at mid length separated by less than their width, distally acute and weakly recurved, directed dorsolaterad and weakly posterad (Fig. 129); dorsal connective emargination somewhat broad basally, deep, sides weakly convergant; ventral connective widest between robust, Y-shaped arms anteriorly, length 1.8× width across anterior arms and 2.1× their longitudinal length (Fig. 128); style moderately long and robust, distally slightly curved laterad, with dorsal, preapical, rounded lobe.

Coloration. Pro- and mesothoracic legs not bicolored (not as in Fig. 1); otherwise as shown (Figs. 124–126).

Hosts.—Label data: *Fragaria* spp. (strawberry; Rosaceae). Hamilton (1994) recorded snowberry (*Symphoricarpos* spp., Caprifoliaceae) as a host.

Specimens examined.—Holotype ♂ labeled: "Orono, Me. | 5 Aug. 13", "HOLOTYPE | Scleroracus | melastigmus | Medler" [SEMC]. Paratypes. **CANADA: Manitoba.** Keld, 8 Aug 1937, R. H. Beamer (1 ♂, 1 ♀) [USNM]; Keld, 8 Aug 1937, R. H. Beamer (1 ♂) [CNCI]. Nontype specimens. **CANADA: Alberta.** Beaverlodge, 1 Aug 1961, A. R. Brooks (2 ♂) [CNCI]; Grande Prairie, 26 Jul 1961, A. R. Brooks (1 ♂) [CNCI]; **Ontario.** Norway Point, Lake of Bays, 12 Jul 1922, J. McDunnough (1 ♀) [CNCI]; Black Sturgeon Lake, 15 Aug 1956, Lindberg (1 ♀) [CNCI]; Marmora, 2 Aug 1952, C. Boyle (1 ♂) [CNCI]; Madawaska, 7 Aug 1975, K. G. A. Hamilton (1 ♀) [CNCI]; Strathroy, 9 Jul 1925, H. F. Hudson (1 ♀) [CNCI]; **Quebec.** L'Assomption, strawberries, 20 Jul 1981 (2 ♂, 2 ♀) [CNCI]; 3 mi. SW Thetford Mines, 14 Aug 1979, K. G. A. Hamilton (1 ♂) [CNCI]. **USA: Montana.** Rexford, 14 Aug 1985, K. G. A. Hamilton (1 ♂) [CNCI]; **Washington.** 31 km W Kettle Falls, 15 Aug 1985, K. G. A. Hamilton (1 ♂, 1 ♀, 1 nymph) [CNCI].

Remarks.—See remarks under *L.* (*S.*) *arctostaphyli*.



Figs. 124–129. *Limotettix* (*Scleroracus*) *melastigmus,* paratypes. 124–126, Habitus in lateral, dorsal, and ventroanterior aspects, respectively. 127–129, Genitalia in lateral (aedeagus and dorsal connective), dorsal (ventral connective and styles), and dorsoposterior (aedeagus and dorsal connective) aspects, respectively.

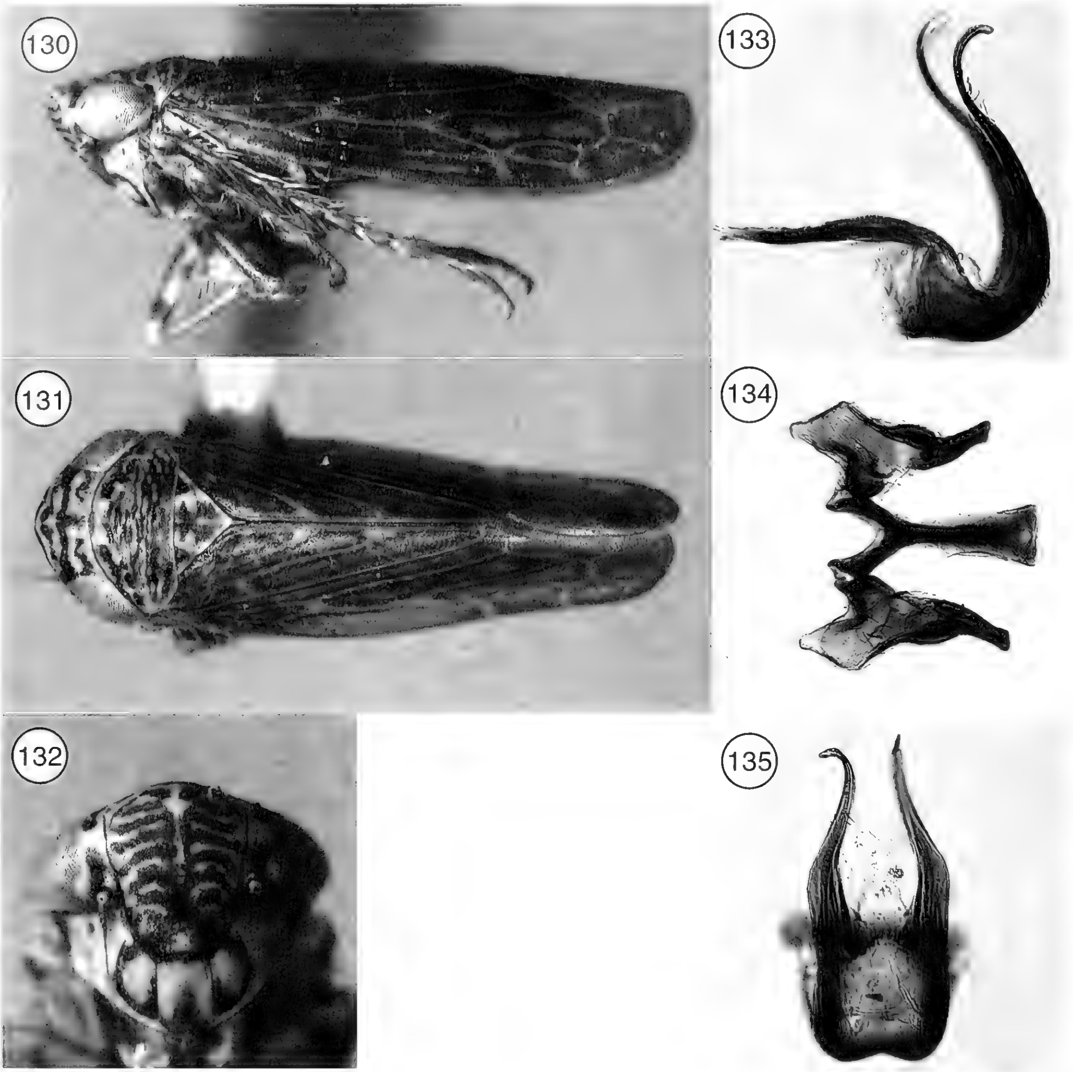
Limotettix (*Scleroracus*) *myralis* (Medler)
(Figs. 130–135)

Scleroracus myralis Medler 1958a: 14 [n.sp.].

Limotettix (*Scleroracus*) *myralis*: Hamilton 1994: 122 [n.comb.].

Diagnosis.—Vertex in dorsal view subangulate, length 0.51× minimum width between eyes; aedeagus in posterior view taller tha broad, apical processes long, gradually narrowed; style in dorsal view basolaterally angulate.

Measurements (mm). Length with forewings in repose, male 3.3–3.8; female 4.0–4.5. Width across eyes, male 1.1–1.2, female 1.3–1.4. *Head:* Vertex in dorsal view subangulate, length 0.51× minimum width between eyes (Fig. 131). *Thorax:* Pronotum in lateral view depressed (Fig. 130). Forewing veins clearly demarcated (Fig. 130). Prothoracic tibia with row AV not distinctly



Figs. 130–135. *Limotettix* (*Scleroracus*) *myralis*, paratypes. 130–132, Habitus in lateral, dorsal, and ventroanterior aspects, respectively. 133–135, Genitalia in lateral (aedeagus and dorsal connective), dorsal (ventral connective and styles), and dorsoposterior (aedeagus and dorsal connective) aspects, respectively.

bimodal, basal setae gradually increasing in size distally. *Abdomen:* Male. Pygofer with dorsal lobe posteriorly truncate, ventral lobe fused. Aedeagal atrium in lateral view strongly constricted before aedeagal shaft (Fig. 133); shaft in posterior view taller than broad, lateral margins subparallel, apical processes long, narrow, at mid length separated by much more than their width, distally attenuate and directed dorsoposterad and laterad (Fig. 135); dorsal connective emargination broad basally, deep, sides parallel; ventral connective widest between robust, Y-shaped arms anteriorly, length 2.4× width across anterior arms and 2.6× their longitudinal length (Fig. 134); style moderately long and distally slender, slightly curved laterad, with ventral, rounded preapical lobe not especially prominent.

Coloration. Pro- and mesothoracic legs not bicolored (not as in Fig. 1); otherwise as shown (Figs. 130–132).

Hosts.—Label data: *Symphoricarpos occidentalis* Hook. (western snowberry; Caprifoliaceae).

Specimens examined.—Holotype ♂ labeled: "Snyderville | UTAH 7-16 | Oman 1935", "MEDLER | FIG. 6", "HOLOTYPE | Scleroracus | myralis | Medler" and an allotype label for ♀ glued to same paper point as holotype [USNM]. Paratypes: (1 ♀) "Allotype" on same pin as holotype. Other paratypes: **USA: Colorado.** Colorado, [no date], C.F. Baker (3 ♂, 1 ♀) [USNM]; **Utah.** Altus, 30 Jul 1912 (1 ♀) [USNM]; Snyderville, 16 Jul 1935, Oman (1 ♀) [USNM]. Non-type specimens. **CANADA: Alberta.** Drumheller, *Symphoricarpos occidentalis,* 13 Aug 1981, K. G. A. Hamilton (1 ♂, 5 ♀) [CNCI]; **British Colombia.** Upper Carmanah Valley, UTM: 10U CK 803005, 10-29 Sep 1991, N. Winchester (1 ♂) [CNCI]; **Saskatchewan.** Saskatoon, 12 Jul 1926, Kenneth M. King (1 ♂) [CNCI]. **USA: Michigan.** 10 km NE Drummond, 27 Jul 1989, K. G. A. Hamilton (1 ♀) [CNCI]; **Montana.** 13 km NW Monarch, 7 Aug 1985, K. G. A. Hamilton (1 ♀) [CNCI].

Remarks.—The asymmetry in the distal orientation of the aedeagal apical processes is greater than in other species of the subgenus. Also see remarks under *L.* (*S.*) *arctostaphyli.*

Limotettix (*Scleroracus*) *obesura* Hamilton (Figs. 136–141)

Limotettix (*Scleroracus*) *obesura* Hamilton 1994: 130 [n.sp.].

Diagnosis.—Male pygofer with dorsal lobe developed into an acute spine directed posterad, adjacent to ventral lobe; aedeagus in posterior view as broad as tall, apical processes short, directed dorsomesad.

Measurements (mm). Length with forewings in repose, male 3.2–3.7; female 3.8–3.9. Width across eyes, male 1.2–1.3, female 1.4. *Head:* Vertex in dorsal view subangulate, length 0.55× minimum width between eyes (Fig. 137). *Thorax:* Pronotum in lateral view depressed (Fig. 136). Forewing veins clearly demarcated (Fig. 136). Prothoracic tibia with row AV bimodal, basal setae subequal to each other and distinctly shorter than distal macrosetae. *Abdomen:* Male. Pygofer with dorsal lobe posteriorly developed into an acute process, ventral lobe fused. Aedeagal atrium in lateral view weakly constricted before aedeagal shaft (Fig. 139); shaft in posterior view short and broad, lateral margins slightly diverging distally, apical processes basally broad, short, acute, directed dorsomesad, and widely separated from each other (Fig. 141); dorsal connective emargination narrow, deep, sides parallel; ventral connective widest between robust, Y-shaped arms anteriorly, length 3.3× width across anterior arms and 3.4× their longitudinal length (Fig. 140); style moderately long and distally slender, slightly curved laterad, with ventral, rounded preapical lobe not especially prominent.

Coloration. Pro- and mesothoracic legs not bicolored (not as in Fig. 1); otherwise as shown (Figs. 104–108).

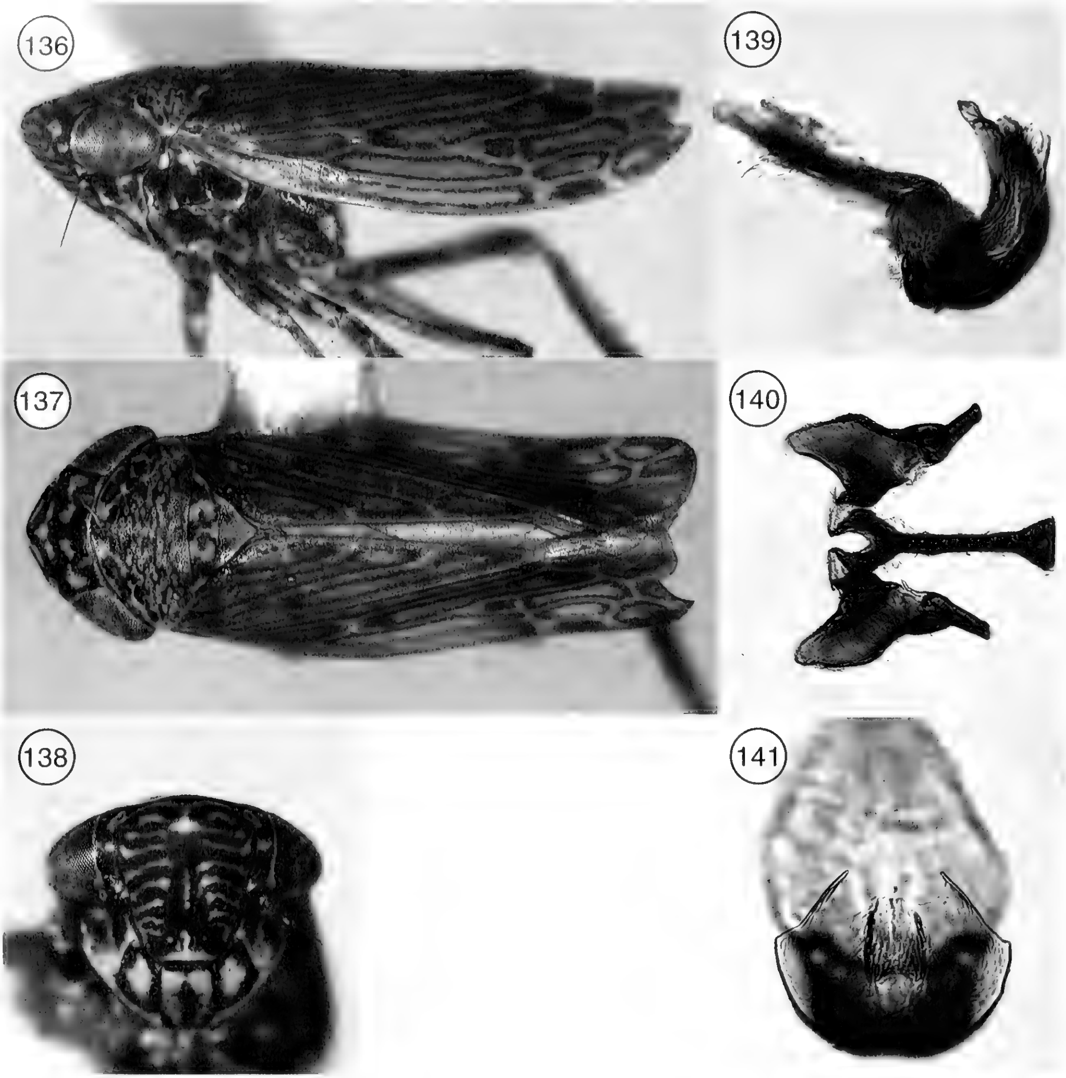
Hosts.—Label data: *Arctostaphylos uva-ursi* (L.) Spreng. (bearberry; Ericaceae).

Specimens examined.—Holotype ♂ labeled: "Ladysmith, B.C. | 12. VII.1959 | L. A. Kelton", "HOLOTYPE | Limotettix | obesura | Hamilton | CNC No.21389" [CNCI]. Paratypes. **CANADA: British Colombia.** Ladysmith, 12 Jul 1959, L. A. Kelton (5 ♂, 3 ♀) [CNCI]. Non-type specimens. **CANADA: British Colombia.** Alberni Summit, 4 mi. E Port Alberni, 375 m., *Arctostaphylos uva-ursi,* 27 Aug 1978, K. G. A. Hamilton (8 ♀) [CNCI]; 3 mi. W. Parksville, Van[couver] Is., *Arctostaphylos uva-ursi,* 27 Aug 1978, K. G. A. Hamilton (5 ♀, 1 nymph) [CNCI].

Limotettix (*Scleroracus*) *omani* (Medler) (Figs. 4, 14, 142–147)

Scleroracus omani Medler 1955b: 215 [n.sp.].

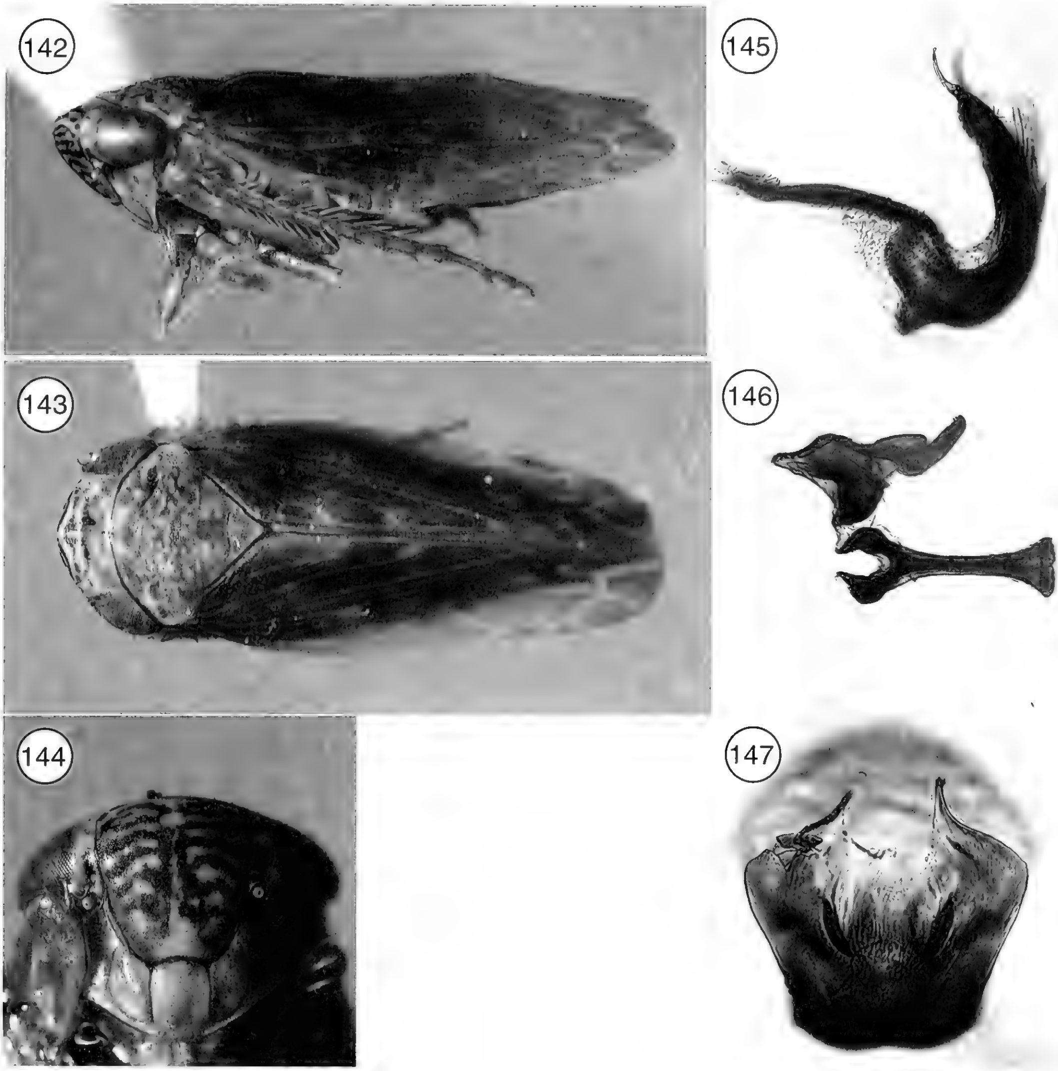
Limotettix (*Scleroracus*) *omani*: Hamilton 1994; 122 [n.comb.].



Figs. 136–141. *Limotettix* (*Scleroracus*) *obesura*, holotype. 136–138, Habitus in lateral, dorsal, and ventroanterior aspects, respectively. 139–141, Genitalia in lateral (aedeagus and dorsal connective), dorsal (ventral connective and styles), and dorsoposterior (aedeagus and dorsal connective) aspects, respectively.

Diagnosis.—Vertex in dorsal view somewhat blunt, length 0.45–0.47× minimum width between eyes; aedeagus in posterior view as broad as tall, lateral margins distally diverging, dorsolaterally evenly rounded, apical processes short and directed dorsad.

Measurements (mm). Length with forewings in repose, male 3.8–4.1; female 4.7–4.8. Width across eyes, male 1.2–1.4, female 1.5. *Head:* Vertex in dorsal view somewhat blunt, length 0.45–0.47× minimum width between eyes (Fig. 143). *Thorax:* Pronotum in lateral view depressed (Fig. 142). Forewing veins clearly demarcated (Fig. 142). Prothoracic tibia with row AV bimodal, basal setae subequal to each other and distinctly shorter than distal macrosetae (Fig. 4). *Abdomen:* Male. Pygofer with dorsal lobe posteriorly truncate, ventral lobe fused. Aedeagal atrium in lateral view moderately constricted before aedea-



Figs. 142–147. *Limotettix* (*Scleroracus*) *omani,* paratypes. 142–144, Habitus in lateral, dorsal, and ventroanterior aspects, respectively. 145–147, Genitalia in lateral (aedeagus and dorsal connective), dorsal (ventral connective and right style), and dorsoposterior (aedeagus and dorsal connective) aspects, respectively.

gal shaft (Fig. 145); shaft in posterior view short and broad, lateral margins divergant distally and evenly convex dorsolaterally, apical processes short, acute, produced from middle, distant from each other, directed dorsad (Fig. 147); dorsal connective broadly and deeply excavated (Fig. 14); ventral connective widest between robust, Y-shaped arms anteriorly, length 2.8× width across anterior arms and 3.5× their longitudinal length (Fig. 146); style distally long and slender, slightly curved laterad, with ventral, rounded preapical lobe not especially prominent.

Coloration. Pro- and mesothoracic legs not bicolored (not as in Fig. 1); otherwise as shown (Figs. 142–144).

Hosts.—Unknown.

Specimens examined.—Holotype ♂ labeled: "Park Rapids |MINN 2-24 | Oman 1935", MEDLER | FIG. 20", "HOLOTYPE | Scleroracus | omani | Medler"

[USNM]. Paratypes: (1 ♀) "Allotype" with same data as holotype [USNM]. Other paratypes: **USA: Minnesota.** Park Rapids, 24 Jul 1935, Oman (9 ♂, 5 ♀) [USNM]. Non-type specimens. **CANADA: Manitoba.** 6 km E. of Tolstoi, 23 Jul 1994, K. G. A. Hamilton (2 ♀, 1 ♂) [CNCI]; The Pas, 30 Aug 1959, A. and J. Brooks (1 ♀) [CNCI].

Limotettix (*Scleroracus*) *osborni* (Ball) (Figs. 148–155)

Ophiola osborni Ball 1928c: 190 [n. sp.].
Scleroracus osborni: Oman 1949a: 152 [n.comb.].
Limotettix (*Scleroracus*) *osborni:* Hamilton 1994: 122 [n.comb.].

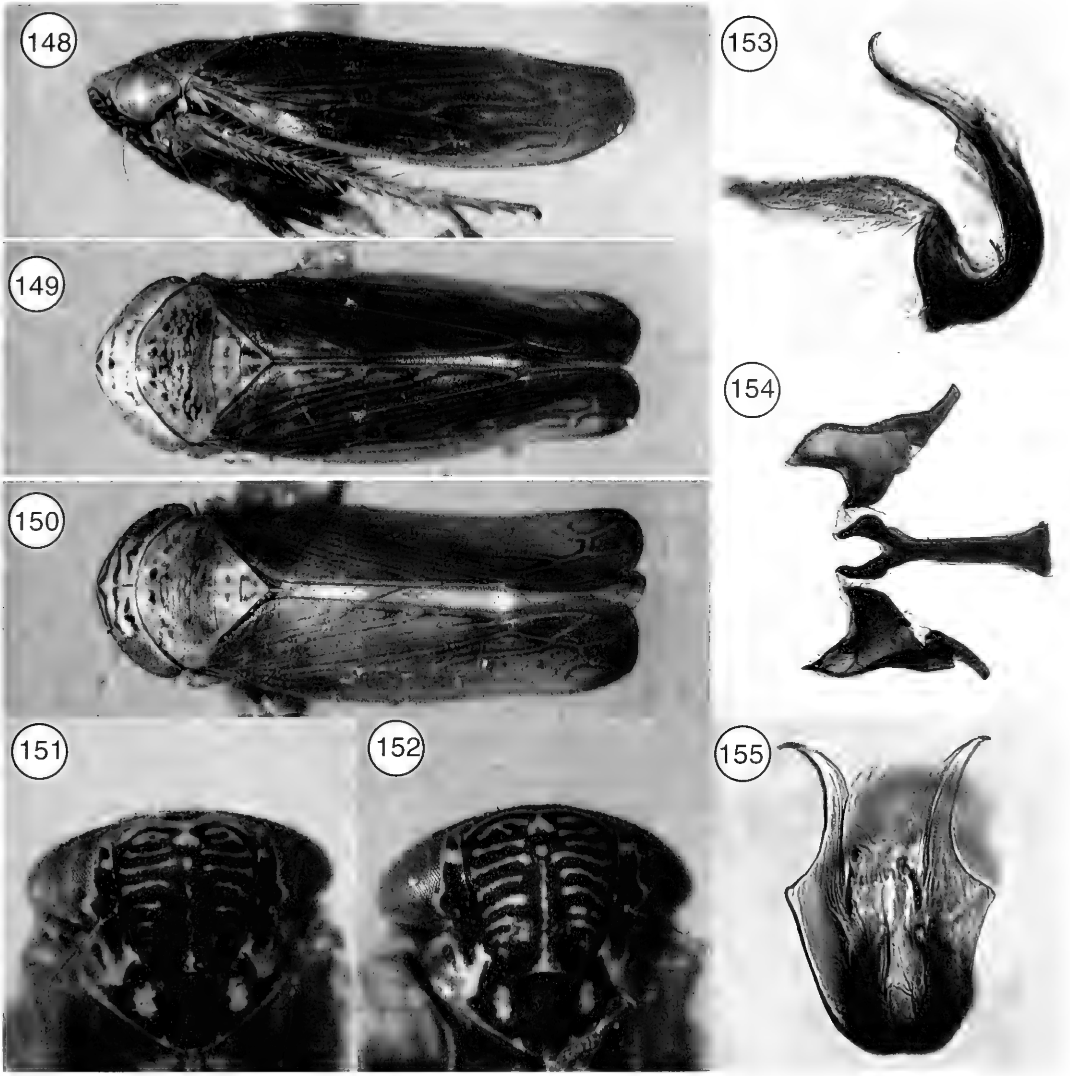
Diagnosis.—Prothoracic legs bicolored (as in Fig. 1); paler and, in dorsal aspect (Figs. 149, 150) more slender than other species with bicolored prothoracic legs (Figs. 17, 54, 105, 199).

Measurements (mm). Length with forewings in repose, male 3.3–4.0; female 3.9–4.5. Width across eyes, male 1.1–1.2, female 1.3–1.5. *Head:* Vertex in dorsal view subangulate, length 0.52× minimum width between eyes (Fig. 150). *Thorax:* Pronotum in lateral view depressed (Fig. 148). Forewing veins clearly demarcated (Fig. 148). Prothoracic tibia with row AV not distinctly bimodal, basal setae gradually increasing in size distally. *Abdomen:* Pygofer with dorsal lobe posteriorly truncate, ventral lobe fused. Aedeagal atrium in lateral view strongly constricted before aedeagal shaft (Fig. 153); shaft in posterior view little taller than broad, lateral margins evenly diverging distally, apical processes abruptly produced dorsolaterad from middle, approximately as long as shaft, at mid length separated from each other by much greater than their width, weakly recurved, distally attenuate, directed dorsoposterad and laterad, basolaterally produced anterolaterad (Figs. 153, 155); dorsal connective emargination very narrow, sides convergant; ventral connective widest between robust, Y-shaped arms anteriorly, length 3.1× width across anterior arms and 3.2× their longitudinal length (Fig. 154); style moderately long and distally slender, slightly curved laterad, with ventral, rounded preapical lobe not especially prominent.

Coloration. Pro- and mesothoracic legs bicolored (as in Fig. 1); otherwise as shown (Figs. 148–152).

Hosts.—Label data: *Arctostaphylos* spp. (bearberry; Ericaceae), *Solidago* spp. (goldenrod; Asteraceae), *Rubus* (*Eubatus*) spp. (blackberry; Rosaceae).

Specimens examined.—Holotype ♀ labeled: "E. D. Ball |8 19 | Ames, Ia.", "HOLOTYPE | Ophiola | osborni | E.D. Ball" [USNM]. Paratypes: (3 ♀) from same locality as holotype [USNM]. Non-type specimens. **CANADA: Alberta.** Stettler, 3 Aug 1957, A.R. and J.E. Brooks (1 ♂, 3 ♀) [CNCI]; Cowley, 13 Aug 1985, K. G. A. Hamilton (1 ♀) [CNCI]; Grand Prairie, 4 Jul 1940, C.L. Neilson (2 ♂) [CNCI]; Drumheller, 11 Aug 1957, A.R. and J.E. Brooks (1 ♀) [CNCI]; Castor, 7 Aug 1957, A.R. and J.E. Brooks (1 ♀) [CNCI]; **British Columbia.** Naramata. 16 Jul 1950, B.P. Beirne (1 ♀) [CNCI]; 7 km N Grasmere, 14 Aug 1985, K. G. A. Hamilton (1 ♀) [CNCI]; **Manitoba.** Melita, 25 Jul 1958, A. and J. Brooks (2 ♀) [CNCI]; 15 mi. N. Glenboro, 24 Jul 1958, J.G. Chillcott (1 ♀) [CNCI]; Russell, 14 Jul 1954, Brooks-Wallis (1 ♀) [CNCI]; Winnipeg, grass, 8 Jul 1966, K. A. Hamilton (1 ♂) [CNCI]; Shoal Lake, 31 Jul 1937, R.H. Beamer (24 ♀) [USNM]; **New Brunswick.** Atholville, 15 Aug 1979, K. G. A. Hamilton (1 ♀) [CNCI]; Madawaska, 7 Aug 1975, K. G. A. Hamilton (1 ♀) [CNCI]; **Nova Scotia.** McGrath Cove, 17 Aug 1963, W. and E. Mason (1 ♂) [CNCI]; Alma., 13 Aug 1973, K. G. A. Hamilton (1 ♀) [CNCI]; **Ontario.** Cape Croker, Bruce Pen., 25 Jul 1993, K. G. A. Hamilton (6 ♂, 14 ♀) [CNCI]; Wallacetown, 7 Sep 1977, K. G. A. Hamilton (1 ♀) [CNCI]; Elgin, 7 Aug 1974, K. G. A. Hamilton (1 ♀) [CNCI]; Norway Point, Lake of Bays, 10 Jul 1922, J. McDunnough (4 ♀) [CNCI]; Fisher Glen, 16 Jun 1931 (1



Figs. 148–155. *Limotettix* (*Scleroracus*) *osborni*. 148–152, Habitus of paratype in lateral, dorsal, and ventroanterior aspects, respectively (150, 152, pale, non-type variant). 153–155, Genitalia in lateral (aedeagus and dorsal connective), dorsal (ventral connective and styles), and dorsoposterior (aedeagus and dorsal connective) aspects, respectively.

♂) [CNCI]; G. S. Walley (1 ♂) [CNCI]; Southampton, 19 Aug 1928, G. S. Walley (1 ♀) [CNCI]; Belleville, 24 Jun 1989, K. G. A. Hamilton (1 nymph) [CNCI]; Camden E., 24 Jun 1989, K. G. A. Hamilton (1 nymph) [CNCI]; Lake Dalrymple, 17 Jun 1989, K. G. A. Hamilton (1 nymph) [CNCI]; 3 mi. S Spencerville, 4 Jul 1979, K. G. A. Hamilton (1 ♂) [CNCI]; Toronto, 8 Aug 1924, E.D. Ball (1 ♀) [USNM]; **Newfoundland.** Red Bay, 1 Sep 1988, K. G. A. Hamilton (1 ♀) [CNCI]; **Saskatchewan.** Esterhazy, 14 Aug 1954, Brooks-Wallis (1 ♀) [CNCI]; Kenosee, 19 Jul 1958, A. and J. Brooks (1 ♀) [CNCI]; Hudson Bay, 24 Aug 1954, Brooks-Wallis (1 ♀) [CNCI]; Elbow, all A.R. Brooks: Elbow, 12 Jul 1960 (1 ♀), 14 Jul 1960 (1 ♂, 3 ♀), 21 Jul 1957 (1 ♀) [CNCI]; Christopher Lake, 11 Jul 1959, A. and J. Brooks (1 ♀)

[CNCI]; Prince Albert, 23 Jul 1969, A. and J. Brooks (3 ♂, 2 ♀) [CNCI]; Saskatoon, 12 Jun 1949 (1 ♀), 9 Jul 1951 (1 ♀), 3 Aug 1929, Kenneth M. King (1 ♀), 9 Aug 1929, Kenneth M. King (1 ♂), 23 Aug 1929, *Arctostaphylos* sp., Kenneth M. King (1 ♀), Saskatoon, 6 Jul 1927, A.R. Brooks (1 ♀), Saskatoon, 4 Aug 1949, L. Konotopetz (1 ♀) [CNCI]; Willow Bunch, 10 Jul 1955, C. D. Miller (1 ♂), 27 Jul 1955, A. R. Brooks (8 ♀) [CNCI]; Rutland, both A. R. Brooks: 26 Jul 1940 (1 ♀), 2 Aug 1940 (1 ♀) [CNCI]; Val Marie, 6 Sep 1955, A. R. Brooks (1 ♀) [CNCI]; Neilburg, 24 Jul 1957, A. R. and J. E. Brooks (1 ♀) [CNCI]; **Quebec.** 15 km S Louvicourt, 15 Jul 1982, K. G. A. Hamilton (1 ♂) [CNCI]; Knowlton, 24 Jul 1929, L. J. Milne (4 ♀) [CNCI]; Berthierville, 15 Jul 1930, L. Daviault (1 ♀) [CNCI]; Wolf L., 7 Aug 1931, G. S. Walley (1 ♀) [CNCI]; 15 km S Louvicourt, 15 Jul 1982, K. G. A. Hamilton (1 ♂) [CNCI]; Knowlton, 5 Jul 1927, G. S. Walley (2 ♂), 24 Jul 1929, L. J. Milne (2 ♂, 1 ♀) [CNCI]. **USA: Arkansas.** Hoxie GL, 18 May 1959, Ross and Stannard (1 nymph) [CNCI]; **Arizona.** Oak Creek Canyon, 18 Aug 1933, E. D. Ball (1 ♂, 2 ♀) [USNM]; Williams, 13 Jul 1929, E. D. Ball (2 ♀), 15 Aug 1929, E. D. Ball (2 ♂, 3 ♀) [USNM]; Long Valley, 5 Aug 1929, E. D. Ball (3 ♂, 10 ♀) [USNM]; Flagstaff, 7 Aug 1929, E. D. Ball (4 ♀) [USNM]; Grand Canyon, 1 Aug 1930, E. D. Ball (1 ♀) [USNM]; Kaibab, both E. D. Ball: 5 Aug 1930, E. D. Ball (1 ♀), 9 Aug 1935 (2 ♀) [USNM]; **Colorado.** Fort Collins, 6 Jun 1902 (1 ♂), 12 Jun 1902 (1 ♂), 16 Jun 1898 (1 ♀), 22 Jun 1898 (1 ♀) [USNM]; Ridgway, 31 Jul 1900 (1 ♀) [USNM]; Colorado, [no date], C. F. Baker (1 ♂, 3 ♀) [USNM]; **District of Columbia.** 5 Jul 1920 (1 ♂, 1 ♀) [USNM]; **Illinois.** Zion, 27 Jul 1966, GL 734, Ross et al. (1 ♀) [CNCI]; **Iowa.** 5 mi. S. Stanhope, 5 Aug 1927, G. O. Hendrickson (1 ♀), 9 Aug 1928, G. O. Hendrickson (1 ♀) [USNM]; 3.5 mi. N. Ledyard, 7 Aug 1928, G. O. Hendrickson (1 ♀) [USNM]; Ames, 7 Jun 1898, Ames Exp. Station (1 ♀), 21 Jun 1928, H. H. Knight (2 ♂), 24 Jun 1928, H. H. Knight (1 ♂), 24 Jun 1897, Ames, Exp. Station (4 ♂), 1 Jul 1895, E. D. Ball (2 ♀), 6 Jul 1925, H. H. Knight (1 ♀), 18 Jul 1897, Ames Exp. Station (1 ♂), 1 Aug 1895, E. D. Ball (1 ♀), 4 Aug 1896, Ames Exp. Station (1 ♀), 15 Aug 1895, E. D. Ball (1 ♀) [USNM]; Little Rock, Exp. Station, 2 Jul 1897 (1 ♂, 3 ♀) [USNM]; Sergeant Bluff, 26 Jul 1928, G. O. Hendrickson (1 ♀) [USNM]; **Indiana.** Tremont, blackberry association, 21 Jun 1934, H. E. Brown (1 ♀) [USNM]; **Kansas.** Onaga, [no date] (2 ♀) [USNM]; **Maine.** Naples, 20 Aug 1934, R. H. Beamer (3 ♀) [USNM]; **Maryland.** College Park, [no date] (1 ♂) [USNM]; Ashton, 13 Aug 1938, Oman (2 ♀) [USNM]; South River, 4 mi. so. Annapolis, all P. W. Oman: 2 Jun 1932 (7 ♂, 8 ♀), 10 Jul 1934 (12 ♂), 24 Jul 1932 (5 ♀), 24 Jul 1937 (1 ♂) [USNM]; **Michigan.** 4 mi. S Garnet, 19 Aug 1980, K. G. A. Hamilton (1 ♀) [CNCI]; Menominee, 6 Sep 1904, E. S. G. Titus (1 ♀) [USNM]; **Minnesota.** Park Rapids, 24 Jul 1935, Oman, 22 ♀) [USNM]; Jackson, 26 Jul 1935, Oman, 10 ♀) [USNM]; **Montana.** W. of Manhattan, 11 Jul 1935, Oman (1 ♂, 4 ♀) [USNM]; Garrison, 10 Jul 1935, Oman (11 ♂, 4 ♀) [USNM]; Montana, 27 Jul 1923 (3 ♀) [USNM]; **Nebraska.** Kimball, 5 Aug 1899 (2 ♀) [USNM]; Nebraska, [no date], C. V. Riley (3 ♂, 4 ♀) [USNM]; Lincoln, 10 Jul 1929 (2 ♀) [USNM]; Lincoln, 9 Aug 1925 (1 ♀) [USNM]; **New Hampshire.** Bretton Woods, 31 Aug 1934, R. H. Beamer (7 ♀) [USNM]; Willey House, 20 Aug 1934, Oman (2 ♀) [USNM]; Crawford Ntch., 21 Aug 1934, Oman (2 ♀) [USNM]; **New Mexico.** Mayhill, 7 Jun 1933, P. W. Oman (1 ♂) [USNM]; Taos, 18 Jun 1937, E. D. Ball (1 ♀) [USNM]; Clouderft., 7 Jun 1933, P. W. Oman (1 ♂) [USNM]; **North Dakota.** 5 km SE Batta, 3 Aug 1985, K. G. A. Hamilton (1 ♀) [CNCI]; Medora, 25 Jul 1924, E. D. Ball (4 ♂, 10 ♀) [USNM]; **New York.** Canton, 8 Jul 1927, Lay's Falls Road, J. Buys (1 ♀), 9 Jul 1929, J. Buys (1 ♀), 19 Jul 1927, Lay's Falls Road, J. L.

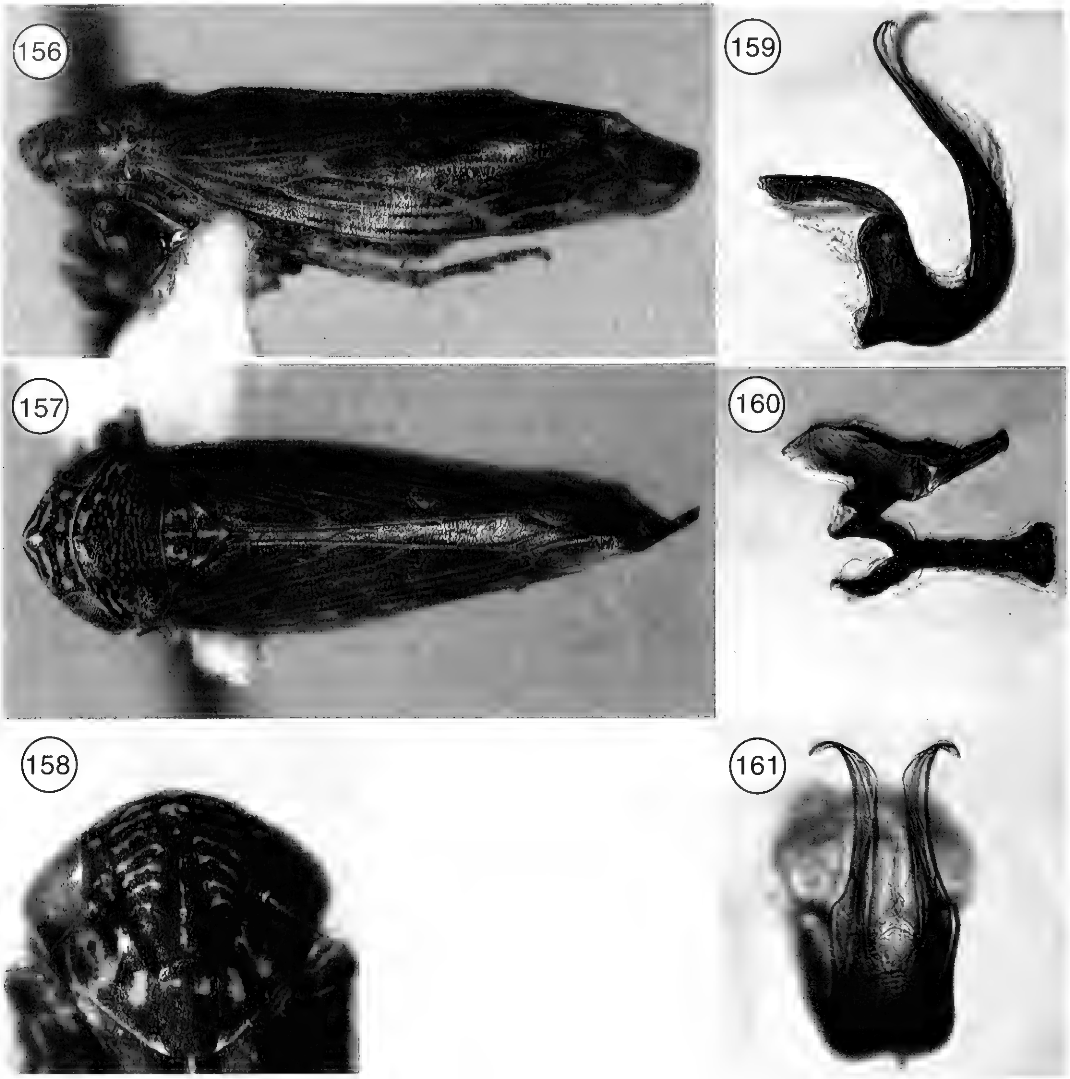
Buys (1 ♀), 21 Jul 1929, J. Buys (2 ♀), 31 Jul 1926, J. Buys (1 ♀), 11 Aug 1927, J. L. Buys (1 ♀) [USNM]; Slaterville, Wild Flower Preserve, 16 Aug 1928, J. L. Buys (1 ♀) [USNM]; Canton, McLean bogs, Tompkins Co., swept from bog plants, 21 Jul 1923, J. L. Buys (5 ♂) [USNM]; McLean Res., bog A, 11 Aug 1924, J. L. Buys (1 ♂) [USNM]; McLean, 14 Jul 1919, J. L. Buys (1 ♀) [USNM]; Buttermilk, Ithaca, 18 Jul 1933 (1 ♀) [USNM]; McLean, 14 Jul 1919 (1 ♀) [USNM]; Whiteface Mt., 22 Aug 1918, H. H. Knight (1 ♀) [USNM]; Salem, Jun 1926, E. D. Ball (1 ♂, 2 ♀), 27 Jul 1924, E. D. Ball (1 ♀), 28 Jul 1924, E. D. Ball (5 ♀) [USNM]; Babylon, Long Island, goldenrod, 26 Jun 1934, F. S. Blanton (5 ♂, 8 ♀), 9 Aug 1934, F. S. Blanton (2 ♀) [USNM]; **Ohio.** Smithfield, 1 Sep 1925, Paul Musgrave (1 ♀) [USNM]; **Pennsylvania.** Laceyville, 27 Aug 1934, R. H. Beamer (2 ♀) [USNM]; Larabee, 28 Aug 1934, R. H. Beamer (1 ♀) [USNM]; La Plume, 9 Aug 1921, J. L. Buys (1 ♀) [USNM]; **South Dakota.** Sisseton, 23 Jul 1935, Oman (1 ♀) [USNM]; Spearfish, 28 Jun 1947, H. C. Severin (1 ♂, 1 ♀) [USNM]; **Dakota** (North or South, as "Dac."). [no date], P. R. Uhler (2 ♀) [USNM]; **Utah.** Blacksmith Fork, 15 Jul 1914 (1 ♂, 1 ♀) [USNM]; Salt Lake City, 13 Jul 1935, Oman (2 ♀) [USNM]; Wellsville, 29 Jul 1903 (2 ♀) [USNM]; Provo, 10 Aug 1930 (4 ♀) [USNM]; Atlus, 30 Jul 1912 (1 ♀) [USNM]; **Vermont.** Manchester, 27 Jul 1924, E. D. Ball (4 ♀) [USNM]; **Virginia.** Shenandoah National Park, Alt. 1,800 ft., weeds, flowers, 20 Jun 1945, J. E. Graf (2 ♂, 1 ♀) [USNM]; Shenandoah National Park, Alt. 3000 ft., weeds, flowers, 20 Jun 1945, J. E. Graf (1 ♀) [USNM]; Vienna, 20 Aug 1931, P. W. Oman (1 ♀) [USNM]; **Wisconsin.** Sandhill "Game, afg." [?], 7 Jul 1969, Harris and Harris (1 ♀) [CNCI]; Florence, 19 Aug 1937, R. H. Beamer (7 ♀) [USNM]; Tomah, 10 Aug 1917, E. D. Ball (2 ♀) [USNM]; Warren, 10 Aug 1918, E. D. Ball (1 ♀) [USNM]; Rhinelander, 15 Jul 1917 (1 ♂) [USNM]; Trout Lake, 17 Jul 1917 (1 ♂) [USNM].

Limotettix (*Scleroracus*) *plutonius* (Uhler)
(Figs. 156–161)

Jassus plutonius Uhler 1877a: 470 [n. sp.].
Athysanus plutonius: Provancher 1889a: 282 [n.comb.].
[*Euscelis* (*Euscelis*)] *plutonius*: Van Duzee 1916a: 72 To *Euscelis* (*Euscelis*) *striatulus* (Fallén) [error]
Ophiola plutonia: Ball 1928c: 187 [reinst.; n.comb.].
Scleroracus plutonius: Oman 1949a: 152 [n.comb.].
[*Limotettix* (*Scleroracus*)] *plutonius*: Ribaut 1952a: 157 To *Limotettix* (*Scleroracus*) *corniculus* Marshall [error]
Limotettix (*Scleroracus*) *plutonius*: Hamilton 1994: 113, 122 [reinst.; n.comb.].

Diagnosis.—Vertex in dorsal view with length 0.48–0.50× minimum width between eyes; pronotum more dark than pale; forewing in repose far exceeding abdominal apex; aedeagus in posterior view taller than broad, with apical processes as long as shaft, equally broad for most of their length; style in dorsal view basolaterally convex.

Measurements (mm). Length with forewings in repose, male 3.6–4.5; female 3.6–5.1. Width across eyes, male 1.1–1.3, female 1.1–1.4. *Head:* Vertex in dorsal view with length 0.48–0.50× minimum width between eyes (Fig. 157). *Thorax:* Pronotum in lateral view depressed (Fig. 156). Forewing veins clearly demarcated (Fig. 156). Prothoracic tibia with row AV not distinctly bimodal, basal setae gradually increasing in size distally. *Abdomen:* Male. Pygofer with dorsal lobe posteriorly truncate and thickened, ventral lobe fused. Aedeagal atrium in lateral view strongly constricted before aedeagal shaft (Fig. 159); shaft in posterior view taller than broad, lateral margins subparallel, apical processes approximately as long as shaft, at mid length separated from each other by little more than their width,



Figs. 156–161. *Limotettix* (*Scleroracus*) *plutonius*. 156–158, Habitus in lateral, dorsal, and ventroanterior aspects, respectively. 159–161, Genitalia in lateral (aedeagus and dorsal connective), dorsal (ventral connective and right style), and dorsoposterior (aedeagus and dorsal connective) aspects, respectively.

distally attenuate and recurved, directed dorsoposterad and laterad (Figs. 159, 161), dorsal connective emargination broad basally, deep, sides parallel; ventral connective widest between robust, Y-shaped arms anteriorly, length 2.6× width across anterior arms and 2.4× their longitudinal length (Fig. 160); style moderately long and slightly curved laterad, with ventral, rounded preapical lobe not especially prominent.

Coloration. Pro- and mesothoracic legs not bicolored (not as in Fig. 1); otherwise as shown (Figs. 156–158).

Hosts.—Label data: *Prunus ilicifolia* (Nutt.) Walp. (wild cherry; Rosaceae), *Solanum* spp. (potato; Solanaceae).

Specimens examined.—Holotype ♀ labeled: "Jassus | Plutonius | Uhler | Clear | cr. Canon.", "Athysanus | plutonius | Uhl." [USNM]. Non-type specimens. **CANADA: Alberta.** 3 Battle River Cross, 17 Jul 1940, C. L. Neilson (1 ♂) [CNCI];

Peace River, 10 Jul 1961, A. R. Brooks (1 ♂) [CNCI]; Elkwater L., 21 Jul 1956, O. Peck (2 ♂) [CNCI]; **British Columbia.** Bear Lake, Jul 1920, Kaslo, R. P. Currie (1 ♂, 1 ♀) [USNM]; Kaslo, wild cherry, Sep 1949, D. B. Waddell (1 ♂) [CNCI]; Kersley, on potato, 12 Aug 1949, R. Stace-Smith (2 ♀) [CNCI]; Quesnel, 7 Aug 1948, in meadow, G. J. Spencer (2 ♂), 14 Jul 1948, in meadow, G. J. Spencer (2 ♂, 2 ♀), 21 Jul 1948, H. R. MacCarthy (2 ♂), 21 Jul 1948, H. R. MacCarthy (2 ♂), 27 Jul 1949, R. Stace-Smith, on potato (1 ♂); 14 Aug 1949, G. J. Spencer (2 ♂, 1 ♀) [CNCI]; Soda Creek, on potato, 10 Jul 1950, G. J. Spencer (1 ♂), 7 Aug 1951, W. B. Tests, H. R. MacCarthy (1 ♂, 1 ♀), 31 Aug 1951, W. B. Tests, H. R. MacCarthy (1 ♂) [CNCI]; Burnaby, 18 Aug 1923 (1 ♂, 2 ♀) [CNCI]; Prince George, 3 Aug 1948, H. R. MacCarthy (1 ♂) [CNCI]; LeFrance Cr., on willow, 17 Sep 1949, D. B. Waddell (1 ♂) [CNCI]; **Manitoba.** Camper, 22 Jun 1990, K. G. A. Hamilton (10 ♂, 7 ♀, 1 nymph) [CNCI]; Carberry, Jun 15 1953, Brooks-Kelton (1 ♂) [CNCI]; **Saskatchewan.** Big River, 5 Jul 1959, A. and J. Brooks (1 ♂) [CNCI]; Prince Albert, 23 Jul 1959, A. and J. Brooks (1 ♂) [CNCI]; Christopher Lake, 15 Jul 1959, A. and J. Brooks (2 ♂) [CNCI]; **Yukon.** Eagle Plains, km 371 Dempster Hwy, 66°23′N 136°43′W, 22 Jul 1982, G. G. E. Scudder (1 ♂) [CNCI]; Soda Creek, 12 Aug 1950, G. J. Spencer (1 ♂) [CNCI]. **USA: Alaska.** Palmer, 30 Aug 1956 (1 ♂) [USNM]; Fairbanks, elev. 448 ft., 4 Aug 1951, H. C. Severin (1 ♂, 1 ♀) [USNM]; Nome River, 8 mi. N. Nome, both Lindroth: 11 Aug 1958 (1 ♂), 13 Aug 1958 (2 ♂) [USNM]; Matanuska, on potato, 27 Aug 1943, J. C. Chamberlin (1 ♀), 28 Jul 1944, rotary traps, J. C. Chamberlin (2 ♂) [USNM]; 33 mi. W. Gulkana, Glenn Hwy., car trap, temperature 68–69 °F, 29, Jul 1944 (1 ♀) [USNM]; Valdez, Alaska Ins. Project, 5 Jul 1948, R. I. Sailer (1 ♂) [USNM]; **Colorado.** W. Chicago Creek, Clear Crk. Co., 9,800 ft., 11 Aug 1961, B. Poole (1 ♂) [CNCI]; Colorado, [no date], C. F. Baker (5 ♂, 4 ♀) [USNM]; Lizard hd., 1 Aug 1900 (1 ♂) [USNM]; Little Beaver, 8 Jul 1898 (1 ♂) [USNM]; **New York.** Cold Spring Harbor, Long Island, 31 Jul 1900 (1 ♀) [USNM]; **Oregon.** Schirupff [?] Bog, Allendale, 18 Jul 1925 (1 ♂) [USNM]; **Utah.** Richfield, Kimberley Mt., 20 Jul 1930 (1 ♂) [USNM]; Richfield, 15 Jul 1930 (1 ♂) [USNM]; **Washington.** 28 km W Mazama, 5400 ft., 16 Aug 1985, K. G. A. Hamilton (1 ♂) [CNCI]; **Wyoming.** 13 km SE Cooke City, MT, 6 Aug 1985, K. G. A. Hamilton (1 ♂) [CNCI].

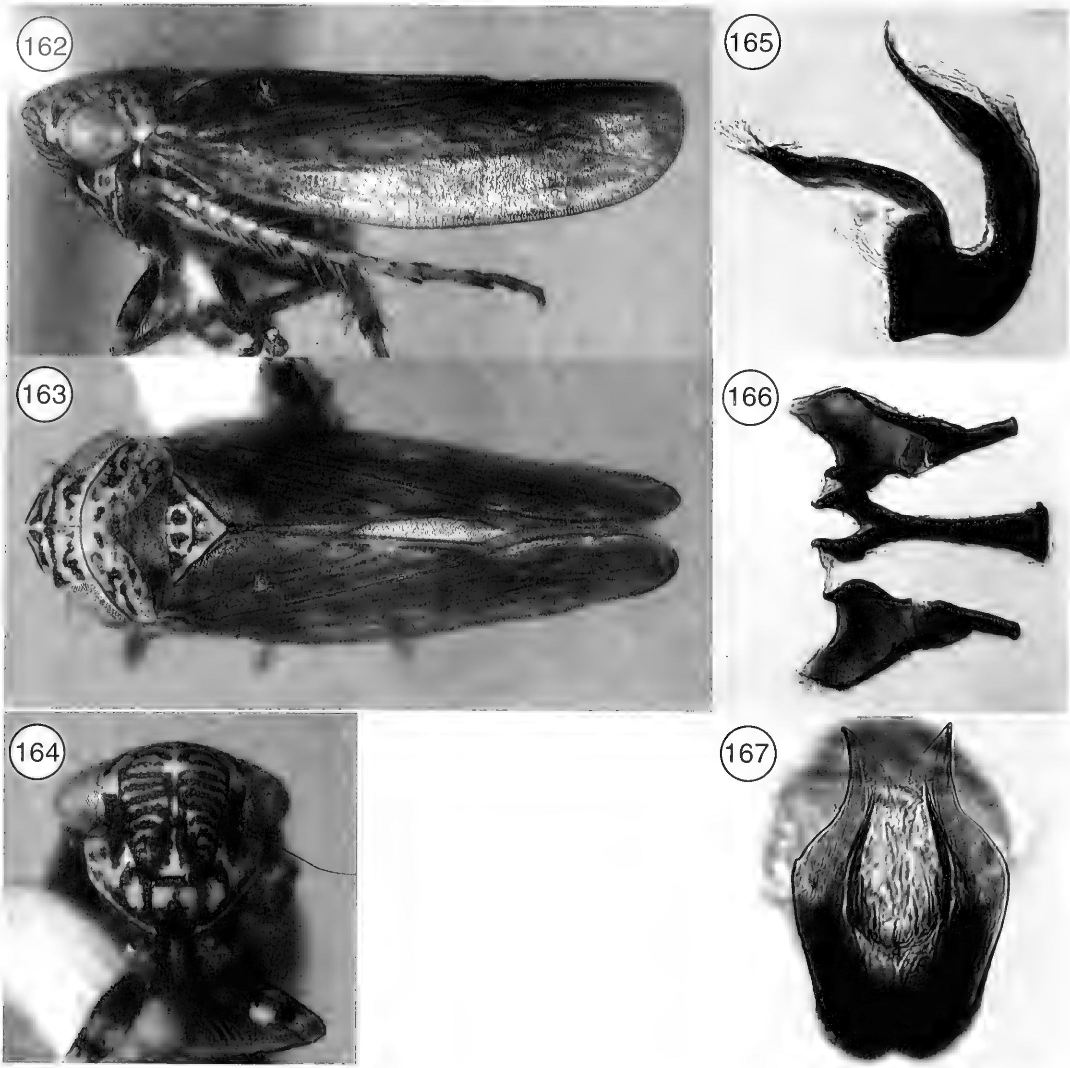
Remarks.—The identity of the female holotype was determined because females of this species have the scutellum, pronotum, and vertex with more dark areas than pale areas and have a moderately subangulate head (Fig. 157). In these respects it only resembles *instabilis*, which is even darker (Fig. 99). Also see remarks under *L.* (*S.*) *arctostaphyli.*

Limotettix (*Scleroracus*) *scudderi* Hamilton
(Figs. 10, 162–167)

Limotettix (*Scleroracus*) *scudderi* Hamilton 1994: 130 [n.sp.].

Diagnosis.—Aedaegus in lateral view with atrium weakly constricted before shaft, in posterior view vasiform, apical processes stout, shorter than shaft, acute.

Female unknown. Male. Measurements (mm). Length with forewings in repose 3.5. Width across eyes 1.1. *Head:* Vertex in dorsal view subangulate, length 0.55× minimum width between eyes (Fig. 163). *Thorax:* Pronotum in lateral view depressed (Fig. 162). Forewing veins clearly demarcated (Fig. 163). Prothoracic tibia with row AV not distinctly bimodal, basal setae gradually increasing in size distally. *Abdomen:* Pygofer with dorsal lobe posteriorly thickened and runcate, ventral lobe fused. Aedeagal atrium in lateral view weakly constricted before aedeagal



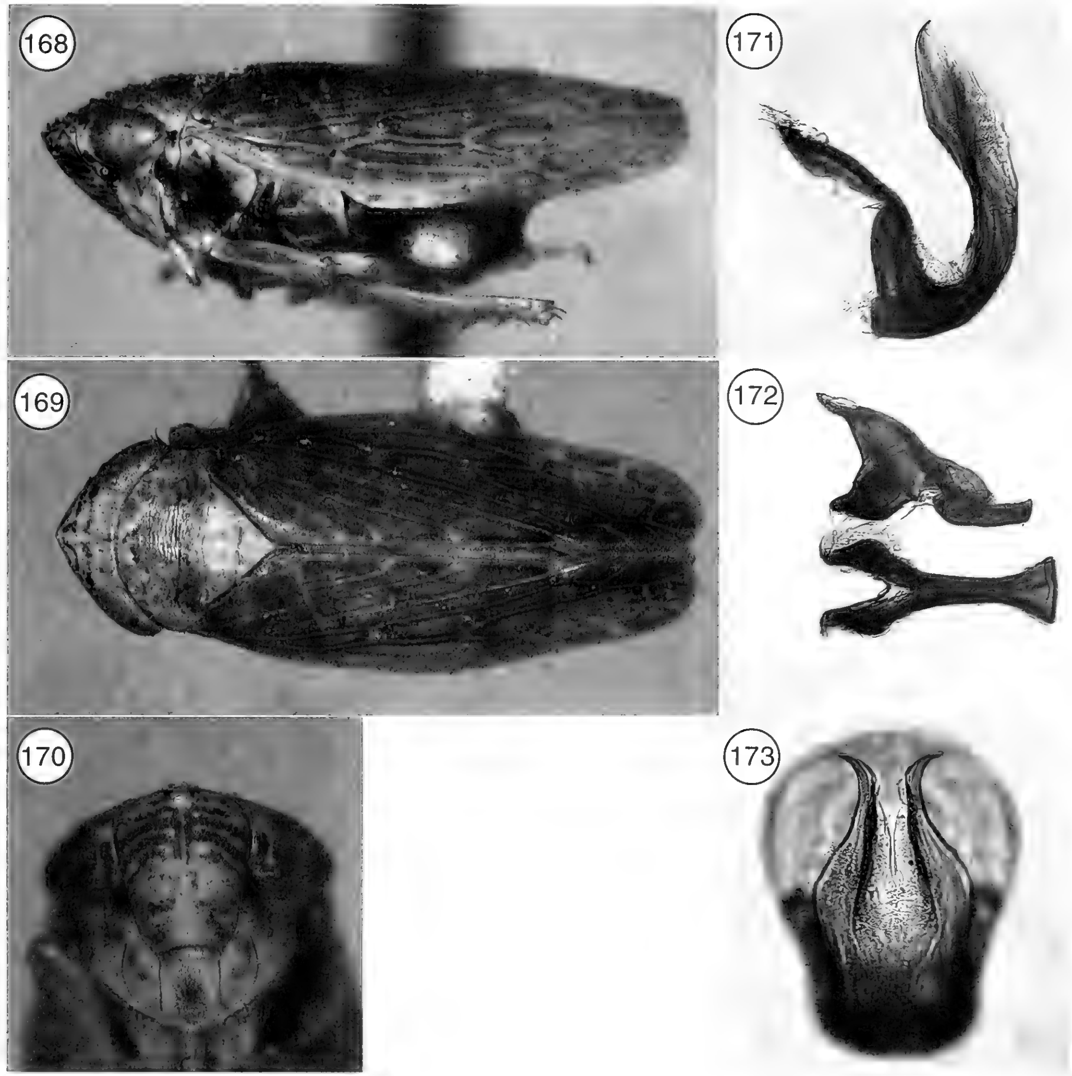
Figs. 162–167. *Limotettix* (*Scleroracus*) *scudderi*, holotype. 162–164, Habitus in lateral, dorsal, and ventroanterior aspects, respectively. 165–167, Genitalia in lateral (aedeagus and dorsal connective), dorsal (ventral connective and styles), and dorsoposterior (aedeagus and dorsal connective) aspects, respectively.

shaft (Fig. 165); shaft in posterior view taller than broad, vasiform, apical processes robust, apically acute, directed dorsad and weakly laterad, separated from each other by more than their width at mid length (Fig. 167); dorsal connective emargination broad, deep, parallel-sided; ventral connective widest between robust, Y-shaped arms anteriorly, length 3.2× width across anterior arms and 2.7× their longitudinal length (Fig. 166); style distally long and slender, slightly curved laterad, with ventral, rounded preapical lobe not especially prominent.

Coloration. Pro- and mesothoracic legs not bicolored (not as in Fig. 1); otherwise as shown (Figs. 162–164).

Hosts.—Unknown.

Specimens examined.—Holotype ♂ labeled: "YT [Yukon Territory, Canada], Campbell Hwy. | Lapie Canyon | 19.vii.1988 | G. G. E. Scudder", "HOLO-



Figs. 168–173. *Limotettix (Scleroracus) shastus.* 168–170, Habitus in lateral, dorsal, and ventroanterior aspects, respectively. 171–173, Genitalia in lateral (aedeagus and dorsal connective), dorsal (ventral connective and right style), and dorsoposterior (aedeagus and dorsal connective) aspects, respectively.

TYPE | Limotettix | scudderi Hmlt. | CNC No.21390" [CNCI].

Limotettix (*Scleroracus*) *shastus* (Ball) (Figs. 6, 15, 168–173)

Athysanus shastus Ball 1916a: 174 [n. sp.].
Euscelis shastus: Van Duzee 1917b: 657 [n.comb.].
Euscelis gentilis Van Duzee 1925b: 420 [n. sp.]. Synonymy by Medler 1958b: 234.
Ophiola shasta: Ball 1928c: 185 [n.comb.].
Ophiola gentilis: Ball 1928c: 187 [n.comb.].
Scleroracus shastus: Oman 1947a: 205 [n.comb.].
Limotettix (*Scleroracus*) *shastus*: Hamilton 1994: 122 [n.comb.].

Diagnosis.—Male pygofer with dorsal lobe developed into an acute spine directed posterad, located dorsally, far removed the ventral lobe; aedeagus in posterior view with apical processes separated from each other by approximately twice their width at mid length.

Measurements (mm). Length with forewings in repose, male 4.3–4.4; female 4.8–5.0. Width across eyes, male 1.3–1.4, female 1.3–1.6. *Head:* Vertex in dorsal view subangulate, length 0.60× minimum width between eyes (Fig. 169). *Thorax:* Pronotum in lateral view depressed (Fig. 168). Forewing veins clearly demarcated (Fig. 168). Prothoracic tibia with row AV not distinctly bimodal, basal setae gradually increasing in size distally. *Abdomen:* Male. Pygofer with dorsal lobe dorsoposteriorly developed into an acute process, ventral lobe fused (Fig. 6). Aedeagal atrium in lateral view strongly constricted before aedeagal shaft (Fig. 171); shaft in posterior view taller than broad, vasiform, apical processes long and basally robust, distally attenuate, directed dorsolaterad and weakly posterad, at mid length separated from each other by approximately twice their width (Fig. 173); gonopore membrane laterally sclerotized; dorsal connective emargination broadly and deeply excavated; ventral connective widest between robust, Y-shaped arms anteriorly, length 2.5× width across anterior arms and 2.4× their longitudinal length (Fig. 172); style dmoderately long and distally robust, slightly curved laterad, with ventral, preapical, rounded lobe prominent.

Coloration. Pro- and mesothoracic legs not bicolored (not as in Fig. 1); otherwise as shown (Figs. 168–170).

Hosts.—Label data: *Prunus emarginata* (Hook.) Walp. (bitter cherry, Rosaceae).

Specimens examined.—*Athysanus shastus* lectotype ♀ labeled: "Dunsmuir Cal | 13Aug12 | E. D. Ball", "TYPE", "LECTOTYPE", "Athysanus | shastus | Ball" [USNM]. *Euscelis gentilis* holotype ♀ labeled. "Cazadero, Cal | Sept. 2, 1918", "TYPE", "Euscelis | gentilis | VanD." [CASC]. Paralectotype: (1 ♂) with same data as holotype [USNM]. Non-type specimens. **CANADA: Alberta.** Wainwright, 27 Jul 1957, A. R. and J. E. Brooks (1 ♀) [CNCI]; **British Columbia.** Vancouver Island, Jul 1911 (1 ♀) [USNM]; Elko, 14 Aug 1985, K. G. A. Hamilton (1 ♂, 5 ♀) [CNCI]; Okanagan Valley, Ewings landing, sticky boards on *Prunus emarginata,* 19 Jul–12 Aug 1971, K. G. A. Hamilton (3 ♂) [CNCI]; Creston, Jul 1950, W. H. Wilde (1 ♀) [CNCI]; Naramata, Site # 6B 5B, 14 Aug 1974, J. E. H. (1 ♂) [CNCI]; Goldstream, 15 Jul 1923 (1 ♂) [CNCI]; **Prince Edward Island.** Albion, 25a, [no date], K. G. A. Hamilton (4 ♂) [CNCI]; **Saskatchewan.** Christopher Lake, 15 Jul 1959, A. and J. Brooks (1 ♀) [CNCI]. **USA: California.** Dunsmuir, 13 Aug 1912, E. D. Ball (2 ♀) [USNM]; Castella, May 1907, E. G. Titus (1 ♂, 1 ♀) [USNM]; Chici, 11 Aug 1912, E, D. Ball (1 ♂) [USNM]; **Oregon.** Oregon, [no date], C. F. Baker (1 ♀) [USNM].

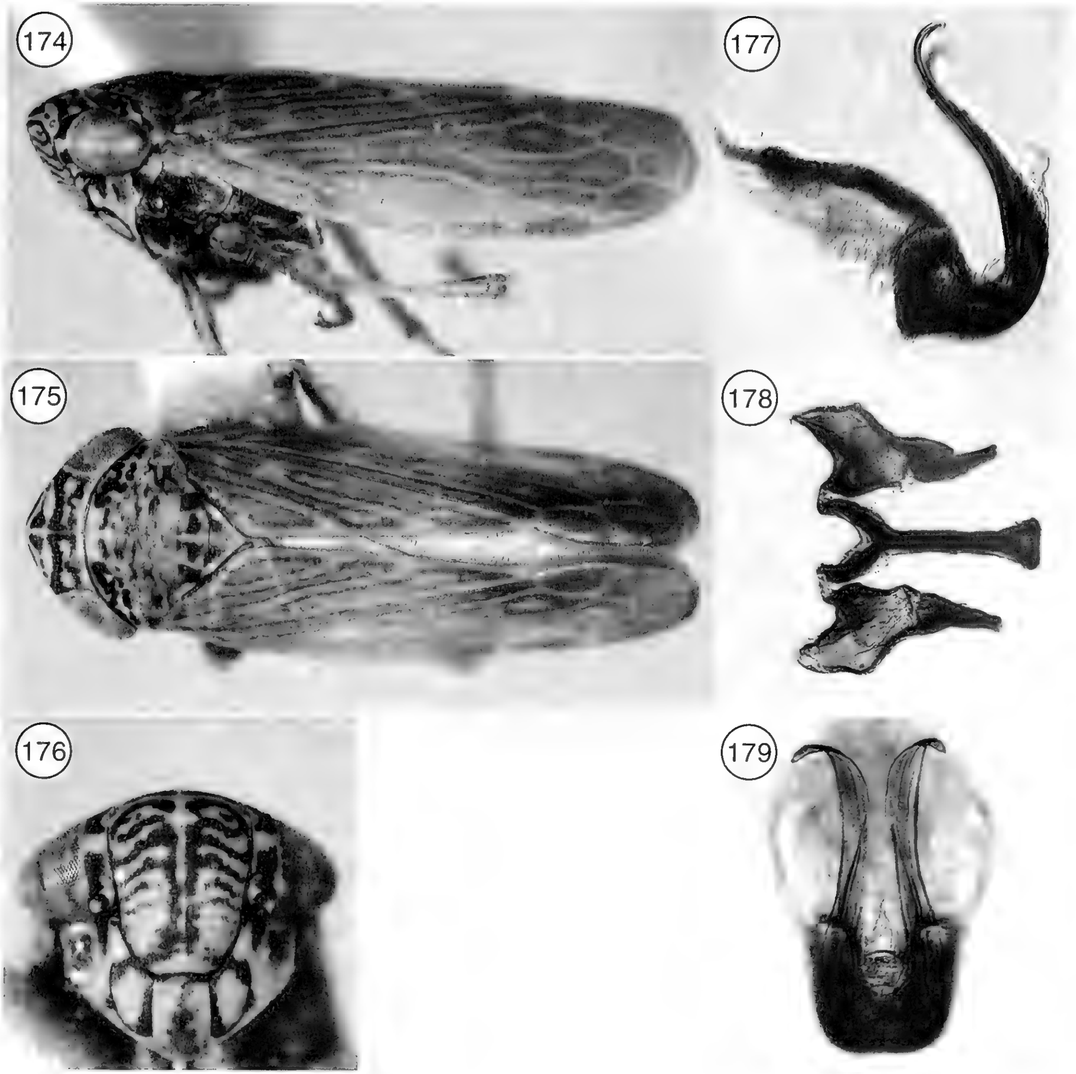
Remarks.—Establishing the idenities of the female lectotype of *shastus* and the female holotype of its junior synonym, *gentilis,* was possible because females of this species have the dorsum weakly pigmented and subangulate head, reducing the other possibilities to *uhleri* (some variants), which is broader, *humidus,* which is 1 mm smaller and has an immaculate frons, and *luteolus,* which differs in having uniformly pale forewing cells, as opposed to the white veins and marginally infuscate cells characteristic of many species, including *shastus.*

Limotettix (*Scleroracus*) *strictus* Hamilton (Figs. 174–179)

Limotettix (*Scleroracus*) *strictus* Hamilton 1994: 131 [n.sp.].

Diagnosis.—Body length with forewings in repose, male 3.4–3.5, female 3.6–3.9; aedeagus in posterior view taller than broad, apical processes longer han shaft, equally broad for most of their length; styles in dorsal view basolaterally angulate.

Measurements (mm). Length with forewings in repose, male 3.4–3.5; female 3.6–3.9. Width across eyes, male 1.2, female



Figs. 174–179. *Limotettix* (*Scleroracus*) *strictus*, holotype. 174–176, Habitus in lateral, dorsal, and ventroanterior aspects, respectively. 177–179, Genitalia in lateral (aedeagus and dorsal connective), dorsal (ventral connective and styles), and dorsoposterior (aedeagus and dorsal connective) aspects, respectively.

1.3–1.4. *Head:* Vertex in dorsal view produced but not subangulate, length 0.50× minimum width between eyes (Fig. 175). *Thorax:* Pronotum in lateral view depressed (Fig. 174). Forewing veins clearly demarcated (Fig. 175). Prothoracic tibia with row AV bimodal, basal setae subequal to each other and distinctly shorter than distal macrosetae. *Abdomen:* Male. Pygofer with dorsal lobe posteriorly truncate, ventral lobe fused. Aedeagal atrium in lateral view strongly constricted before aedeagal shaft (Fig. 177); shaft in posterior view taller than broad, lateral margins parallel, apical processes broad, as long as shaft, at mid length separated from each other by less than their width, distally attenuate, and weakly recurved, directed dorsolaterad and posterad (Figs. 177, 179); dorsal connective emargination narrow, deep, sides parallel; ventral connective widest between robust, Y-shaped arms anteriorly, length 2.8×

width across anterior arms and 3.3× their longitudinal length (Fig. 178); style moderately long and distally slender, slightly curved laterad, with ventral, rounded preapical lobe not especially prominent.

Coloration. Pro- and mesothoracic legs not bicolored (not as in Fig. 1); otherwise as shown (Figs. 174–176).

Hosts.—Unknown.

Specimens examined.—Holotype ♂ labeled: "LaPlatta, San Juan N. F. | Colo. 19-21.VII.68 | L. A. Kelton 8,500′", "HOLOTYPE | Limotettix | strictus Hmlt. | CNC No.21391" [CNCI]. Paratypes. **USA: Colorado.** LaPlatta, San Juan N. P., 8,500 ft., 19-21 Jul 1968, L. A. Kelton [CNCI]; (1 ♂, 2 ♀) [CNCI].

Remarks.—See remarks under *L.* (*S.*) *arctostaphyli.*

Limotettix (*Scleroracus*) *symphoricarpae* (Ball)
(Figs. 13, 180–185)

Athysanus symphoricarpae Ball 1901a: 5 [n. sp.].
Euscelis (*Euscelis*) *symphoricarpae*: Van Duzee 1916a: 72 [n.comb.].
Ophiola symphoricarpae: Ball, 1928c: 186 [n.comb.].
Scleroracus symphoricarpae: Oman 1947a: 205 [n.comb.].
Limotettix (*Scleroracus*) *symphoricarpae*: Hamilton 1994: 122 [n.comb.].

Diagnosis.—Aedeagus distally tubular, flanked by two small digitate processes.

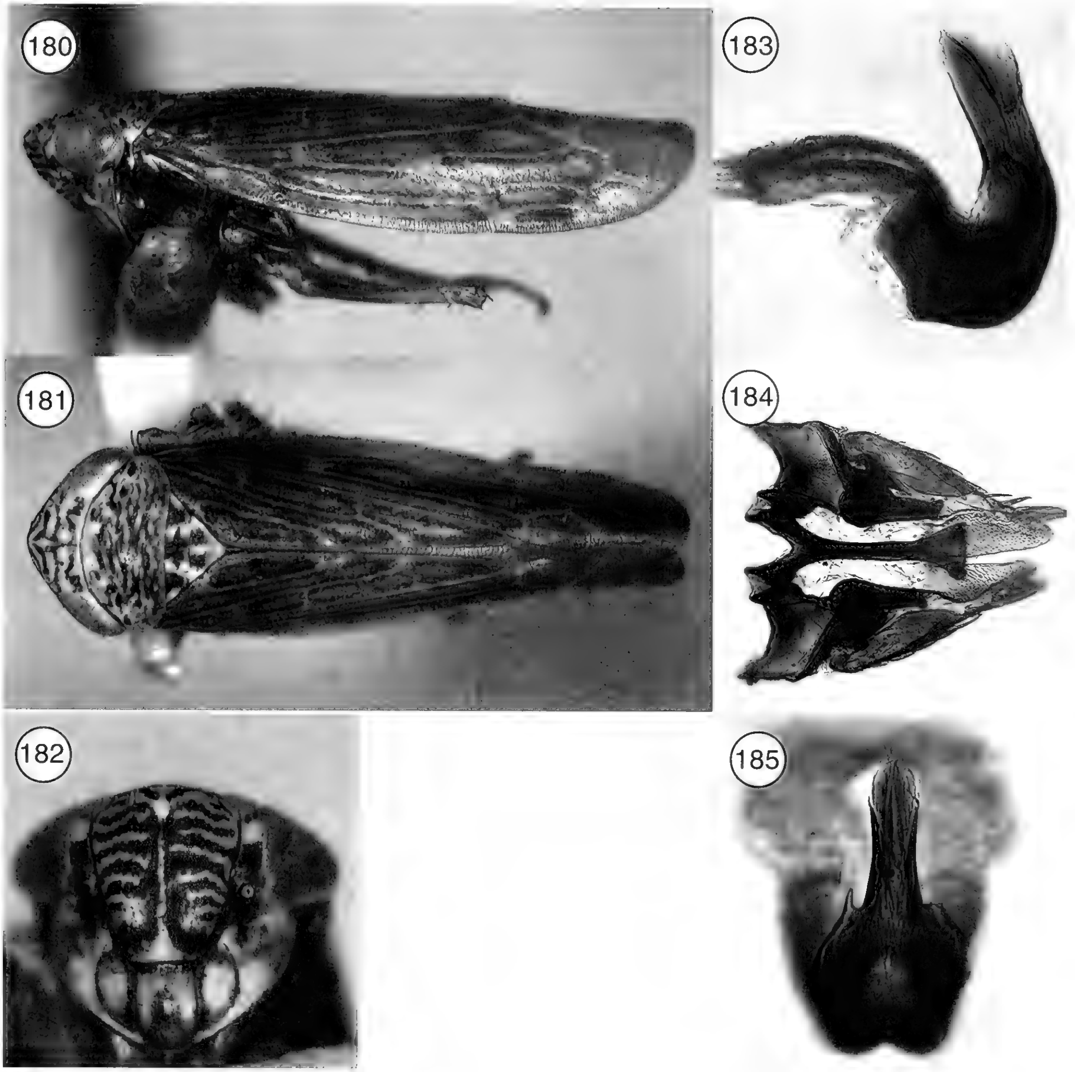
Measurements (mm). Length with forewings in repose, male 4.4–5.0; female 4.5–5.0. Width across eyes, male 1.3–1.4, female 1.4–1.5. *Head:* Vertex in dorsal view subangulate, length 0.52–0.55× minimum width between eyes (Fig. 181). *Thorax:* Pronotum in lateral view depressed (Fig. 180). Forewing veins clearly demarcated (Fig. 180). Prothoracic tibia with row AV bimodal, basal setae subequal to each other and distinctly shorter than distal macrosetae. *Abdomen:* Male. Pygofer with dorsal lobe dorsoposteriorly developed into an acute process, ventral lobe fused. Aedeagal atrium in lateral view weakly constricted before aedeagal shaft (Fig. 183); shaft in posterior view little taller than broad, lateral margins subparallel, mesially produced into a tubular projection, posterolaterally sclerotized gonopore membrane, mesal projection flanked by pair of short acute process, produced dorsad (Fig. 185); dorsal connective emargination narrow, deep, sides parallel; ventral connective widest between robust, Y-shaped arms anteriorly, length 2.7× width across anterior arms and 3.6× their longitudinal length (Fig. 184); style long and robust, distally slightly curved laterad, with ventral, preapical, rounded lobe prominent.

Coloration. Pro- and mesothoracic legs not bicolored (not as in Fig. 1); otherwise as shown (Figs. 180–182).

Hosts.—Label data: none. Hamilton (1994) recorded snowberry (*Symphoricarpos* spp., Caprifoliaceae) as a host.

Specimens examined.—Lectotype ♀ labeled: "Ridgeway | [C]ol. 73100", "TYPE", "LECTOTYPE", "Athysanus | symphoricarpae | Ball" [USNM]. Non-type specimens. **CANADA: Alberta.** 7 Jul 1936, G. F. Mason (1 ♀) [CNCI]; **Manitoba.** Winnipeg, at light, 24 Jul 1967, K. A. Hamilton (1 ♂, 1 ♀) [CNCI]; **Ontario.** Mer Bleue, 11 Jul 1935, F. A. Urquhart (2 ♀) [CNCI]. **USA: Wyoming.** Jackson Hole, 15 Aug 1971, H. H. Ross (1 ♂, 2 ♀) [CNCI]; **Utah.** Soldier, 13 Aug 1936 (4 ♂, 7 ♀) [USNM]; Soldier Summit, 13 Aug 1936, R. H. Beamer (1 ♂, 1 ♀) [USNM]; Logan Canyon, 13 Aug 1914, Craig (1 ♀) [USNM]; Altus, 30 Jul 1911 (1 ♂, 1 ♀) [USNM].

Remarks.—The distally tubular aedeagus of *L.* (*S.*) *symphoricarpae* resembles that of *L.* (*S.*) *frigidus,* and the gonopore membrane is laterally sclerotized, as in *L.* (*S.*) *finitimus* (Fig. 76) and *L.* (*S.*) *shastus* (Fig. 171). The female lectotype of *symphoricarpae* is a pale variant but with the faint pigmentation pattern on the forewing characteristic of the usual form of the spe-



Figs. 180–185. *Limotettix* (*Scleroracus*) *symphoricarpae*. 180–182, Habitus in lateral, dorsal, and ventroanterior aspects, respectively. 183–185, Genitalia in lateral (aedeagus and dorsal connective), dorsal (subgenital plates, ventral connective, and styles), and dorsoposterior (aedeagus and dorsal connective) aspects, respectively.

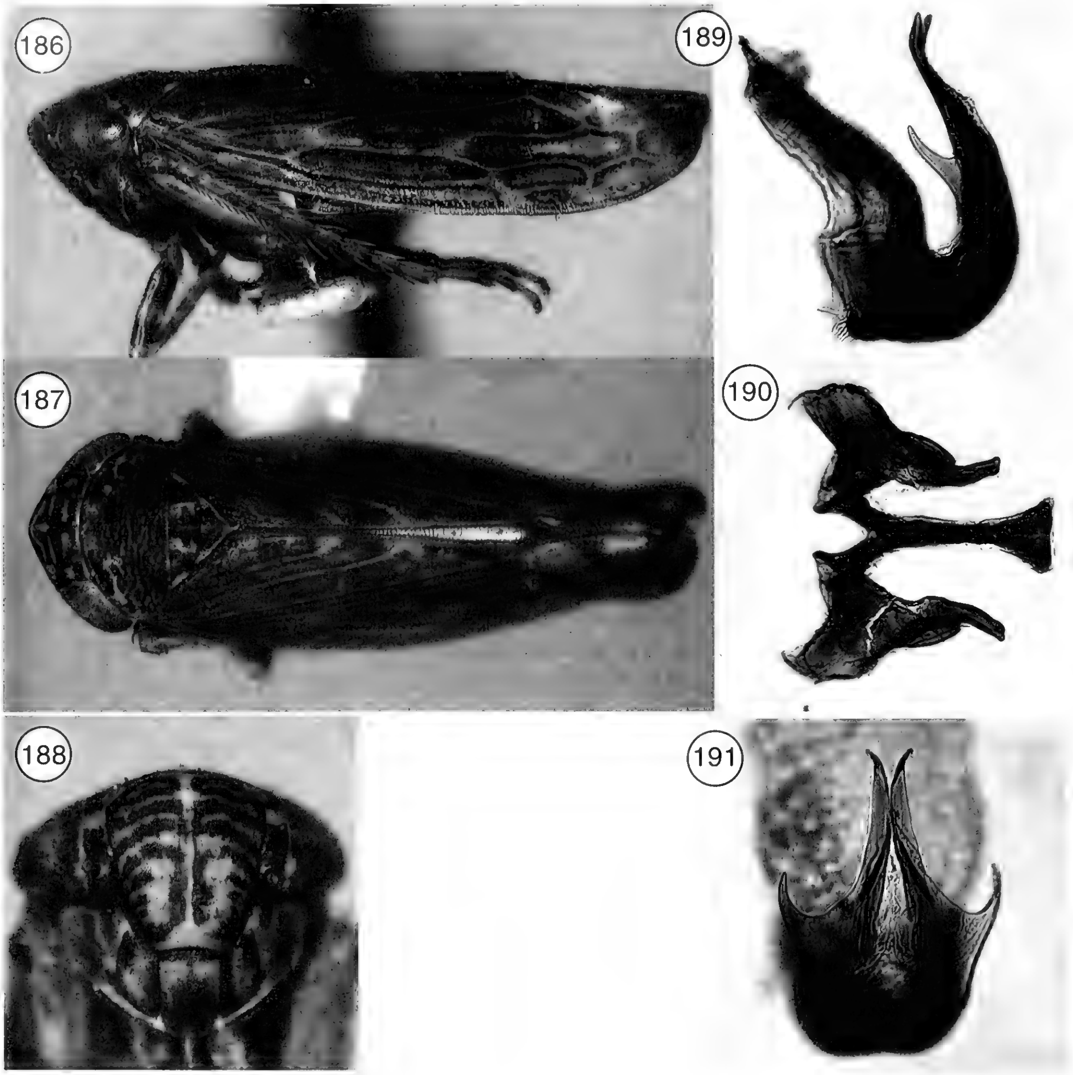
cies (Fig. 181) as well as others in the subgenus. Among the species lacking such maculation, the *symphoricarpae* holotype most resembles female *luteolus*, which differ in having no trace of forewing cell maculation, and *zacki*, which is known only from Northwest Canada rather than the more southernly distribution of *symphoricarpae* in Canada and the United States.

Limotettix (*Scleroracus*) *taramus* (Medler) (Figs. 186–191)

Scleroracus taramus Medler 1958a: 15 [n.sp.].

Limotettix (*Scleroracus*) *taramus*: Hamilton 1994: 122 [n.comb.].

Diagnosis.—Aedeagal shaft bearing 2 pairs of apical processes, lateral pair di-



Figs. 186–191. *Limotettix* (*Scleroracus*) *taramus*, paratypes. 186–188, Habitus in lateral, dorsal, and ventroanterior aspects, respectively. 189–191, Genitalia in lateral (aedeagus and dorsal connective), dorsal (ventral connective and styles), and dorsoposterior (aedeagus and dorsal connective) aspects, respectively. Left style broken.

rected dorsolaterally and curving anteriorly, mesal pair touching each other preapically.

Measurements (mm). Length with forewings in repose, male 4.4–5.0; female 4.9–5.0. Width across eyes, male 1.3–1.4, female 1.5. *Head:* Vertex in dorsal view subangulate, length 0.50 × minimum width between eyes (Fig. 187). *Thorax:* Pronotum in lateral view depressed (Fig. 186). Forewing veins clearly demarcated (Fig. 186). Prothoracic tibia with row AV not distinctly bimodal, basal setae gradually increasing in size distally. *Abdomen:* Male. Pygofer with dorsal lobe posteriorly truncate, ventral lobe fused. Aedeagal atrium in lateral view weakly constricted before aedeagal shaft (Fig. 189); shaft in posterior view taller than broad, lateral margins weakly diverging distally, mesoapical processes approximately as long as shaft, distally attenuate and recurved, directed dorsad and slightly posterad, touching each other preapically or almost so, basolaterally with short acute processes produced dorsolaterad and anterad (Figs. 189, 191); dorsal connective emargination narrow, deep, sides parallel; ventral connective widest between robust, Y-shaped arms anteriorly, length 2.7× width across anterior arms and 3.2× their longitudinal length (Fig. 190); style moderately long and robust, distally slender and slightly curved laterad, with ventral, rounded preapical lobe not especially prominent.

Coloration. Pro- and mesothoracic legs not bicolored (not as in Fig. 1); otherwise as shown (Figs. 186–188).

Hosts.—Unknown.

Specimens examined.—Holotype ♂ labeled: "Richfield, Ut | July 15, 1930 | Light Trap", "MEDLER | FIG. 14", "HOLOTYPE | Scleroracus | taramus | Medler" [USNM]. Paratypes. (1 ♀) "Allotype" with same data as holotype [USNM]. Other paratypes: **USA: Colorado.** Dolores, 2 Aug 1900 (1 ♀) [USNM]; **Utah.** Richfield, light trap, 15 Jul 1930 (1 ♀) [USNM].

Limotettix (*Scleroracus*) *uhleri* (Ball)
(Figs. 1, 7, 192–197)

Athysanus (*Conosanus*) *uhleri* Ball 1911a: 200 [n. sp.].

Euscelis (*Euscelis*) *uhleri*: Van Duzee 1916a: 72 [n.comb.].

Ophiola uhleri: Ball 1928c: 187 [n.comb.].

Ophiola uhleri speculata Ball 1928c: 187 [n.subsp.]. **NEW SYNONYMY.**

Scleroracus uhleri: Oman 1949a: 152 [n.comb.].

Scleroracus uhleri speculatus: Oman 1949a: 152 [n.comb.].

Limotettix (*Scleroracus*) *uhleri*: Hamilton 1994: 122 [n.comb.].

Diagnosis.—Prothoracic legs bicolored (Fig. 1); aedeagal shaft in posterior view slender with apices touching each other or almost so; male pygofer with ventral lobe articulated.

Measurements (mm). Length with forewings in repose, male 4.0; female 4.5–4.7. Width across eyes, male 1.3, female 1.5–1.6. *Head:* Vertex in dorsal view subangulate, length 0.58–0.60× minimum width between eyes (Fig. 193). *Thorax:* Pronotum in lateral view slightly elevated (Fig. 192). Forewing veins sometimes not clearly demarcated, as in *L.* (*S.*) *anthracinus*. Prothoracic tibia with row AV not distinctly bimodal, basal setae gradually increasing in size distally. *Abdomen:* Male. Pygofer with dorsal lobe posteriorly truncate or gradually declivous (Fig. 7), ventral lobe articulated. Aedeagal atrium in lateral view strongly constricted before aedeagal shaft (Fig. 195); shaft in posterior view more than 2× taller than broad, lateral margins parallel, apical processes short, apically acute, and directed dorsomesad, touching each other (Fig. 197); gonopore membrane laterally sclerotized adjacent to shaft; dorsal connective emargination narrow, deep, sides parallel; ventral connective widest between robust, Y-shaped arms anteriorly, length 3.6 × width across anterior arms and 3.3× their longitudinal length (Fig. 196); style moderately long and distally slender, slightly curved laterad, with ventral, rounded preapical lobe not especially prominent.

Coloration. Pro- and mesothoracic legs bicolored (Fig. 1); otherwise as shown (Figs. 192–194) except forewings fuscous throughout.

Hosts.—Label data: None. Hamilton (1994) recorded composites (Asteraceae) as hosts.

Specimens examined.—*Athysanus* (*Conosanus*) *uhleri* lectotype ♀ labeled: "E. D. Ball | 6 29 96 | Ames, Ia.", "LECTOTYPE", "Athy-Conos | uhleri | Ball" [USNM]; *Ophiola uhleri speculata* holotype ♀ labeled: "Speculator, N. Y. | 6 Aug, 1912 | N. Y. S. Coll.", "D. B. Young | Collector", "1940 EDBall | Collection", "HOLOTYPE | Ophiola uhleri | var. speculata" [USNM]. Non-type specimens. **CANADA: Alberta.** Elkwater Park, 29 Jul 1952, A. R. Brooks (2 ♀) [CNCI]; **Ontario.** Thwartway Island, St. Lawrence National Park, mafaise

Figs. 192–197. *Limotettix* (*Scleroracus*) *uhleri*. 192–194, Habitus in lateral, dorsal, and ventroanterior aspects, respectively. 195–197, Genitalia in lateral (aedeagus and dorsal connective), dorsal (ventral connective and left style), and dorsoposterior (aedeagus and dorsal connective) aspects, respectively.

trap, 1 Jul 1976, A. Carter (1 ♂) [CNCI]; Leamington, both G. S. Walley, 10 Jun 1929 (1 ♂), 26 Jun 1931, G. S. Walley (1 ♂) [CNCI]; Pt. Pelee, 13 Sep 1961, G. Brumpton (1 ♀) [CNCI]; New Glasgow, 27 Jun 1961, Kelton and Brumpton (1 ♂) [CNCI]; Leamington, 27 Jun 1931, G. S. Walley (1 ♀) [CNCI]; Finland, 11 Jul 1960, S. M. Clark (1 ♂) [CNCI]; **Quebec.** Gatineau Pk., Harrington, on grass, 2 Jul 1981, D. J. E. Brown (1 ♀) [CNCI]; Kingsmere, 23 Jul 1919, R. N. Chrystal (1 ♀) [CNCI]; L. a la Tortue, Laviolette Co., 28 Jun 1951, E. G. Munroe (1 ♂) [CNCI]; Province of Quebec, 31 Jul 1924, E. D. Ball (1 ♀) [USNM]; Quebec, [no date] (1 ♂) [USNM]. **USA: District of Columbia.** 4 Jul 1924, E. D. Ball (1 ♀) [USNM]; **Iowa.** Ames, E. D. Ball, [no date] (1 ♀) [USNM]; **New Hampshire.** Glen, 20 Aug 1934, P. W. Oman (1 ♀) [USNM]; **New Jersey.** Roselle, 23 Jun 1924, E. D. Ball (2 ♀)

[USNM]; **New York.** Hamburg [?], 10 Jul 1891, C. F. Baker (1 ♀) [USNM]; Ithaca, 27 Jun 1890, C. F. Baker (1 ♀) [USNM]; Kissina Park, Long Island, 11 Jul 1911, C. E. Olsen (1 ♀) [USNM]; Flatbush, Long Island, J. L. Zabriskie, 6 Jul 1893 (1 ♀) [USNM]; **Pennsylvania.** Conewago, 1 Jul 1917, J. G. Sanders (1 ♀) [USNM]; **South Dakota.** Seechee Hollow, 17 Jun 1955, H. C. Severin (1 ♂, 1 ♀) [USNM]; **Wisconsin.** Spg. Green, 1 Aug 1917, E. D. Ball (1 ♀) [USNM].

Remarks.—Metcalf (1967) attributed the synonymy of subspecies *speculata* to Oman (1949a), but Oman listed it as a subspecies. Medler (1958b) noted that he could not distinguish this pale form from usual *uhleri* based on the male genitalia, but nevertheless also treated the subspecies as valid. In this study, the synonymy of *speculata* is confirmed. Externally the features of the lectotype of *uhleri* closely resemble those of *kryptus,* with which it shares a broadly overlapping geographic distribution. Nevertheless, females of *uhleri* (including the lectotype of *uhleri* and the holotype of *uhleri speculata*) have a more angulate head and are a little larger than *kryptus* females.

Limotettix (*Scleroracus*) *vaccinii* (Van Duzee)

(Figs. 3, 198–203)

Athysanus vaccinii Van Duzee 1890h: 135 [n. sp.].

Euscelis (*Euscelis*) *vaccinii*: Van Duzee 1916a: 72 [n.comb.].

Ophiola vaccinii: Medler 1943a: 86 [n.comb.].

Scleroracus vaccinii: Oman 1947a: 206 [n.comb.].

Limotettix (*Scleroracus*) *vaccinii*: Hamilton & Langor 1987: 668 [n.comb.].

Diagnosis.—Aedeagus in posterior view as braod as tall, apical processes short, falcate, directed mesad; prothoracic femora banded fuscous (Fig. 3), not bicolored (not as in Fig. 1).

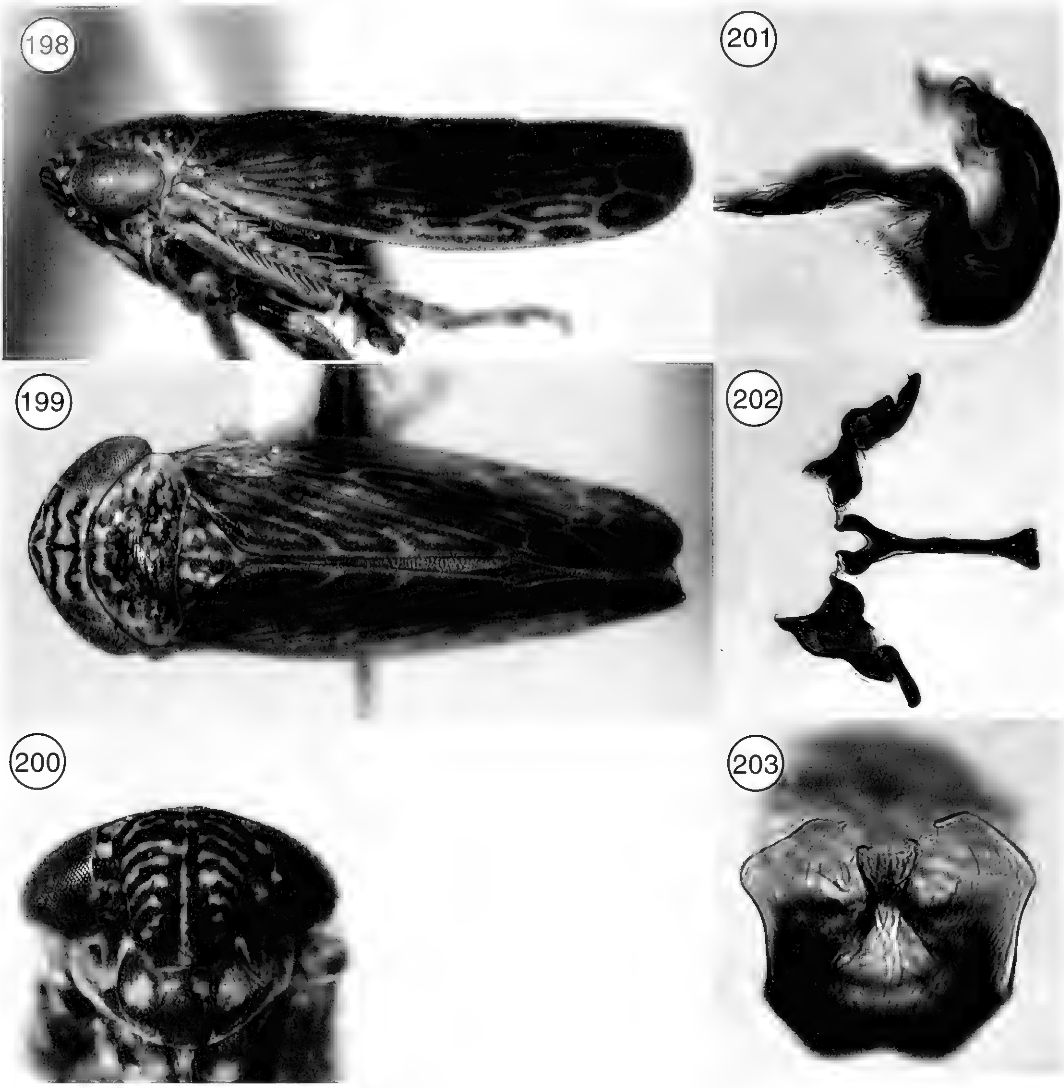
Measurements (mm). Length with forewings in repose, male 3.4–3.7; female 4.0–4.5. Width across eyes, male 1.1–1.2, female 1.3–1.4. *Head:* Vertex in dorsal view subangulate, length 0.52× minimum width between eyes (Fig. 199). *Thorax:* Pronotum in lateral view depressed (Fig. 198). Forewing veins clearly demarcated (Fig. 198). Prothoracic tibia with row AV not distinctly bimodal, basal setae gradually increasing in size distally (Fig. 3). *Abdomen:* Male. Pygofer with dorsal lobe posteriorly truncate, ventral lobe articulated. Aedeagal atrium in lateral view weakly constricted before aedeagal shaft (Fig. 201); shaft in dorsoposterior view short and broad, strongly curved dorsoanteriorly, lateral margins parallel, mesially with 2 short, divergant processes (the weakly sclerotized base of gonopore membrane), lateroapical processes sort, distally falcate and directed mesad, their basolateral angles produced anterolaterad, obtuse (Figs. 201, 203); dorsal connective emargination very narrow, shallow, V-shaped narrow; ventral connective widest between robust, Y-shaped arms anteriorly, length 3.4× width across anterior arms and 3.7× their longitudinal length (Fig. 202); style moderately long and distally slender, slightly curved laterad, with ventral, rounded preapical lobe not especially prominent.

Coloration. Pro- and mesothoracic legs not bicolored (not as in Fig. 1); otherwise as shown (Figs. 198–200).

Hosts.—Label data: *Chamaedaphne calyculata* (L.) Moench (leather-leaf, Ericaceae), *Gaylussacia* ssp. (dwarf huckleberry, Ericaceae), *Ledum groenlandicum* Oeder (Labrador tea, Ericaceae), *Ledum* spp. (Labrador tea, Ericaceae), *Salix purpurea* L. (purple-stem willow, Salicaeae), *Vaccinium* spp. (cranberry, Ericaceae).

Economic importance.—Important vector of false blossom disease of cranberry (*Vaccinium,* Ericaceae).

Specimens examined.—Lectotype ♂ labeled: "N. Jersey | J. B. Smith", "♂", "LECTOTYPE | Athysanus | vaccinii | VanD. | Oman 1946", "Athysanus | striatulus | ? Fall. [a misidentification]"



Figs. 198–203. *Limotettix* (*Scleroracus*) *vaccinii*. 198–200, Habitus in lateral, dorsal, and ventroanterior aspects, respectively. 201–203, Genitalia in lateral (aedeagus and dorsal connective), dorsal (ventral connective and styles), and dorsal (aedeagus and dorsal connective) aspects, respectively. Styles in unnatural position.

[USNM]. Paralectotypes: (1 ♂, 1 ♀) with same data as lectotype [USNM]. Non-type specimens. **CANADA: New Brunswick.** Kouchibouguac N. P., 16 Jul 1977, S. J. Miller (1 ♂), 26 Jul 1977, D. J. Brown (4 ♂), 30 Jul 1977, S. J. Miller (1 ♂) [CNCI]; Rockwood, St. John, both J. F. Brimley: 7 Aug 1953 (2 ♂), 12 Aug 1953 (2 ♂) [CNCI]; St. Andrews, 2 Aug 1957, G. E. Shewell (1 ♂) [CNCI]; **Newfoundland.** 10 km W Valleyfield, 15 Aug 1984, K. G. A. Hamilton (1 ♂) [CNCI]; **Nova Scotia.** Kings Co., Greenwood, 12 Aug 1973, K. G. A. Hamilton (1 ♂) [CNCI]; 3 mi. E Bible Hill, 13 Aug 1973, K. G. A. Hamilton (1 ♂) [CNCI]; Benjie's Lake, CBHNP, 17 Aug 1983 (1 ♂) [CNCI]; **Ontario.** Shawanaga, *Ledum* sp., 26 Aug 1962, L. A. Kelton (1 ♂) [CNCI]; 6 mi. SE English R., purple-stem willow, 3 Jul 1975, K. G. A. Hamilton (1 ♂) [CNCI]; 15 mi. SE Upsala, *Ledum groenlandicum,* 3 Jul 1975, K. G.

A. Hamilton (1 ♀) [CNCI]; Almonte, 16 Sep 1988, K. G. A. Hamilton (1 ♀) [CNCI]; 5 mi. NW Kemgami L., *Chamaedaphne calyculata,* 13 Aug 1975, K. G. A. Hamilton (1 ♀) [CNCI]; Mer Bleue, 3 Sep 1929, W. J. Brown, (11 ♂), 3 Sep 1929, L. J. Milne (4 ♂), 6 Sep 1928, W. J. Brown (1 ♂), 9 Aug 1932, G. S. Walley (7 ♂) [CNCI]; **Quebec.** Laniel, 29 Jun 1963, W. Gagne (2 ♂) [CNCI]; 3 mi. SW Thetford Mines, 14 Aug 1979, K. G. A. Hamilton (1 ♀) [CNCI]; Black Hawk, 3 Aug 1960, Kelton and Whitney (2 ♂) [CNCI]; 5 mi. W. Willard Lk., 10 Aug 1960, Kelton and Whitney (2 ♂) [CNCI]. **USA: Illinois.** Elgin, 7 Aug 1965, GL 537, Ross (1 ♀) [CNCI]; **Maine.** Bar Harbor, 23 Aug 1934, A. E. Brower (2 ♂, 8 ♀) [USNM]; Bar Harbor, 12 Sep 1934, A. E. Brower (1 ♀) [USNM]; Grand Lake, 15 Aug 1913 (1 ♀) [USNM]; Orono, 5 Aug 1913 (1 ♂, 1 ♀) [USNM]; **Massachusetts.** Wareham, dwarf huckleberry, 19 Jul 1948, H. J. Franklin (1 ♀) [USNM]; Sherborn, 1 Aug 1936, C. A. Frost (1 ♀) [USNM]; Woods Hole, both E. D. Ball: 4 Jul 1925 (2 ♂, 1 ♀), 7 Jul 1925 (9 ♂), 9 Jul 1925, E. D. Ball (2 ♂, 3 ♀) [USNM]; **New Hampshire.** Fabyan, 15 Jul 1979, K. G. A. Hamilton (1 ♂) [CNCI]; **New Jersey.** Lakehurst, 26 Jul [? Year] (1 ♂, 1 ♀) [USNM]; Lakehurst, 20 Aug [? Year] (1 ♀), 25 Aug 1914 (1 ♀) [USNM]; Whitesbog, 13 Jul 1914, H. B. Scammell (1 ♀) [USNM]; New Jersey, [no date], Smith (1 ♂) [USNM]; New Jersey, [no date] (5 ♂, 2 ♀) [USNM]; Woodland, ex. cranberry, 18 Jun 1946, W. E. Tomlinson (39 ♂, 19 ♀) [USNM]; Pemberton,]; Pemberton, Jun 1946, W. E. Tomlinson, *Chamaedaphne* sp. (50 ♂), 26 Jun 1914, on cranberry, H. B. Scammell (4 ♂), 30 Jul 1946, *Chamaedaphne* sp., W. E. Tomlinson (16 ♂, 89 ♀) [USNM]; Tom's River, 3 Jul 1929, Dobroscky (3 ♂), 6 Jul 1929, Dobroscky (1 ♂), 14 Aug 1929, Dobroscky (9 ♂, 1 ♀) [USNM]; Jamesbgh., cranberry bogs, 8 Aug [no year] (1 ♂, 1 ♀) [USNM]; **New York.** Whiteface Mt., 4,000 ft., 19 Jul 1962, J. R. Vockeroth (1 ♂) [CNCI]; Wanakena, 1-7 Aug 1917, C. J. Drake (1 ♂) [USNM]; Bay Shore, Long Island, 24 Jul 1910, C. E. Olsen (1 ♀) [USNM]; Oswego, 17 Jul 1896 (2 ♀) [USNM]; **Pennsylvania.** Pennsylvania, [no date], C. F. Baker (1 ♂) [USNM]; **Wisconsin.** Wisconsin Rapids, Biron Bog, 24 Jul 1930 (12 ♂) [USNM]; Wisconsin Rapids, 17 Jul 1931 (1 ♂) [USNM]; Merrillan, 27 Aug 1918, E. D. Ball (1 ♀) [USNM]; Cranmoor, 15 Jul 1931 (1 ♂), 20 Jul 1931 (1 ♀) [USNM].

Limotettix (*Scleroracus*) *varus* (Ball)

(Figs. 204–209)

Athysanus varus Ball 1901a: 5 [n. sp.].

Euscelis (*Euscelis*) *varus*: Van Duzee 1916a: 72 [n.comb.].

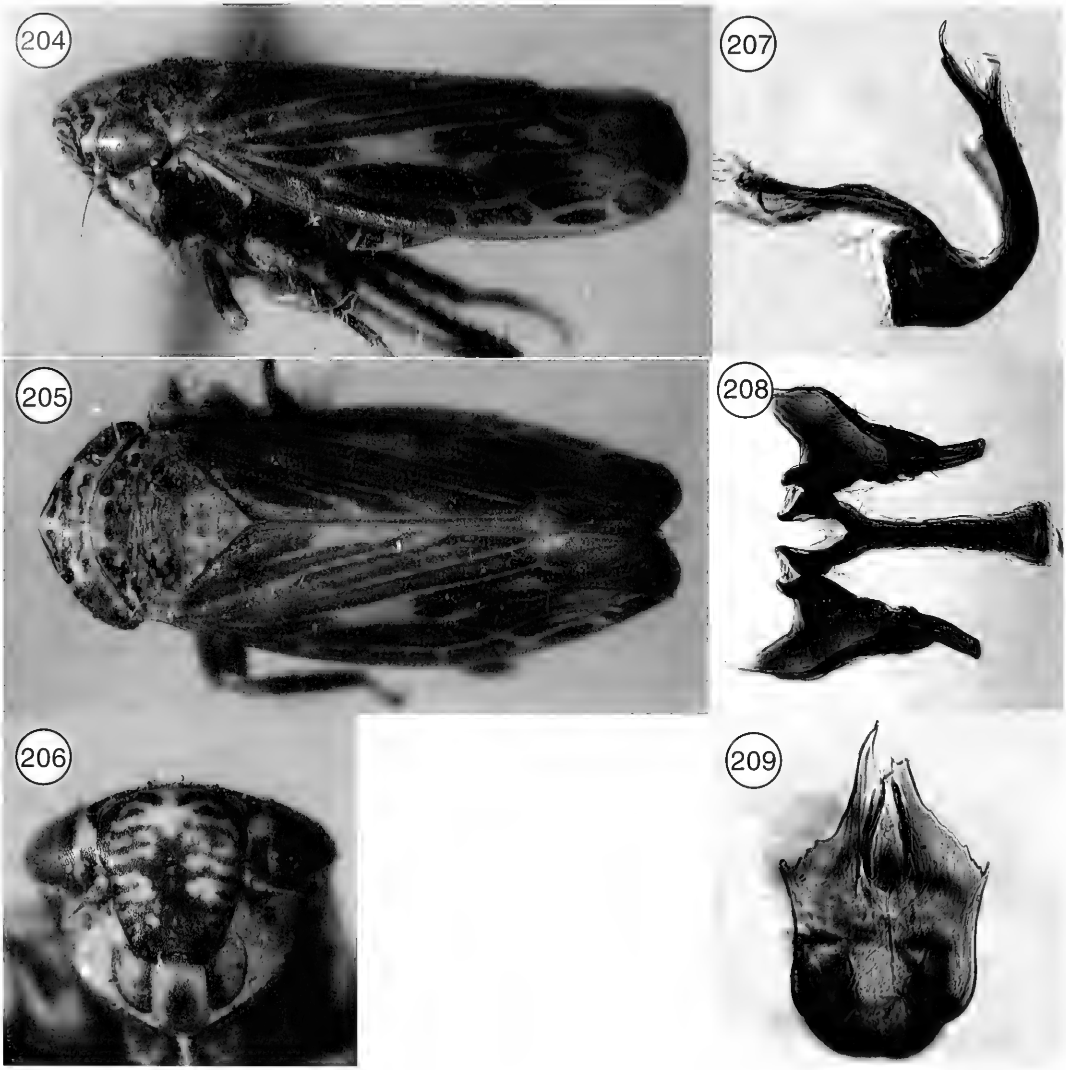
Ophiola vara: Sleesman 1930: 118 [n.comb.].

Scleroracus varus: Oman 1947a: 205 [n.comb.].

Limotettix (*Scleroracus*) *varus*: Hamilton 1994: 122 [n.comb.].

Diagnosis.—Forewing with large pale mark around first m-cu crossvein; female vertex in dorsal view blunt, length 0.40× minimum width between eyes; male pygofer with ventral lobe articulated.

Measurements (mm). Length with forewings in repose, male 4.4–4.9; female 4.1–5.4. Width across eyes, male 1.31.4, female 1.3–1.6. *Head:* Vertex in dorsal view blunt in female, more angulate in male, length 0.40 (females) or 0.47 (males) × minimum width between eyes (Fig. 205). *Thorax:* Pronotum in lateral view weakly elevated (Fig. 204). Forewing veins clearly demarcated (Fig. 204). Prothoracic tibia with row AV bimodal, basal setae subequal to each other and distinctly shorter than distal macrosetae. *Abdomen:* Male. Pygofer with dorsal lobe posteriorly developed into short truncate process, ventral lobe articulated. Aedeagal atrium in lateral view strongly constricted before aedeagal shaft (Fig. 207); shaft in posterior view taller than broad, lateral margins subparallel, dorsolaterally with short spine then irregularly serrate dor-



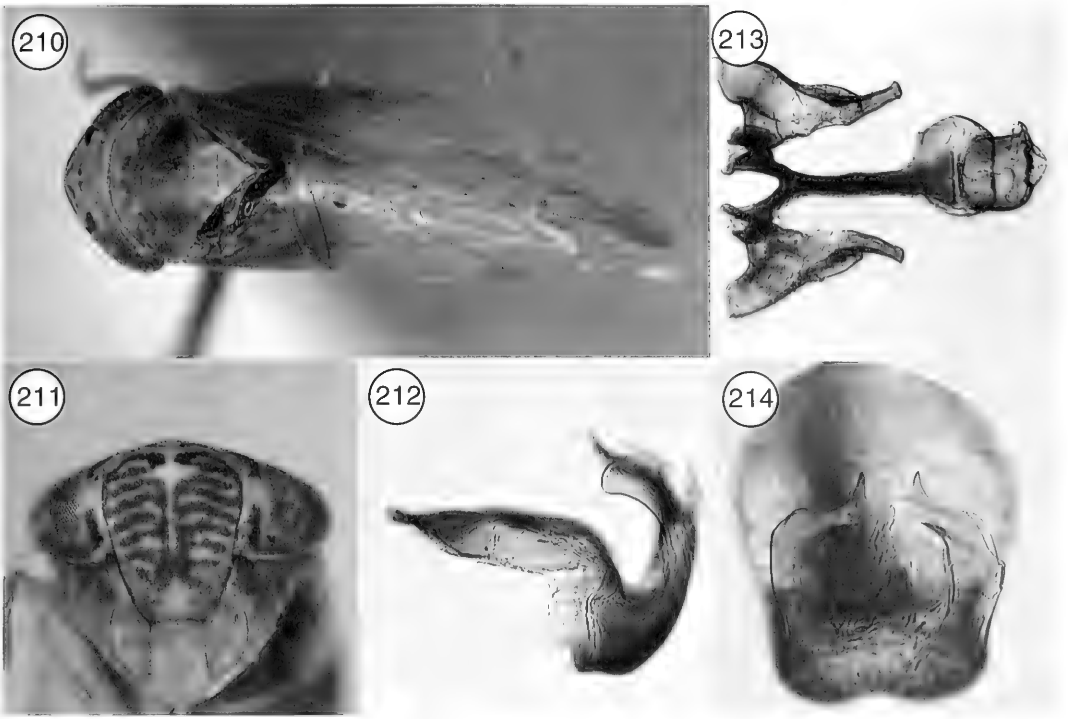
Figs. 204–209. *Limotettix* (*Scleroracus*) *varus*. 204–206, Habitus in slightly dorsolateral, in dorsal, and in ventroanterior aspects, respectively. 207–209, Genitalia in lateral (aedeagus and dorsal connective), dorsal (ventral connective and styles), and dorsoposterior (aedeagus and dorsal connective) aspects, respectively. Apex of right aedeagal apical process broken.

somesially to attenuate process directed dorsoposterad (Fig. 209); gonopore membrane weakly sclerotized ventrally; dorsal connective emargination broad basally, deep, sides convergant; ventral connective widest between robust, Y-shaped arms anteriorly, length 3.0× width across anterior arms and 3.0× their longitudinal length (Fig. 208); style moderately long and distally slender, slightly curved laterad, with ventral, rounded preapical lobe not especially prominent.

Coloration. Pro- and mesothoracic legs not bicolored (not as in Fig. 1); otherwise as shown (Figs. 204–206), forewing with large pale mark around first m-cu crossvein.

Hosts.—Label data: None. Hamilton (1994) recorded composites (Asteraceae) as hosts.

Specimens examined.—Lectotype ♀ la-



Figs. 210–214. *Limotettix* (*Scleroracus*) *zacki*, holotype. 210, 211, Habitus in dorsal and ventroanterior aspects, respectively. 212–214, Aedeagus in lateral, dorsal (with connectives and styles), and dorsoposterior aspects, respectively.

beled: "Ft. Collins | Col. 98", "TYPE", "LECTOTYPE", "Athysanus | varus | Ball" [USNM]. Non-type specimens. **USA: Colorado.** Colorado, [no date], C. F. Baker (1 ♀) [USNM]; Ft. Collins, [no date] (2 ♀) [USNM]; Ft. Collins, 26 Jun 1901, E. D. Ball (1 ♂, 2 ♀) [USNM]; Ft. Collins, 6 Jul 1901, E. D. Ball (1 ♂) [USNM]; **Indiana.** DeKalb Co., 10 Jul 1935, G. A. Ficht (1 ♀) [USNM]; **Minnesota.** Park Rapids, 24 Jul 1935, Oman (1 ♀) [USNM]; **Montana.** Bozeman, 14 Jul 1927 (1 ♀) [USNM]; **Nebraska.** Lincoln, collected at electric light, Jun [no year], E. D. Ball (1 ♂) [USNM]; **Washington.** Cliffdell, 7 Jul 1935, Oman (1 ♂) [USNM].

Limotettix (*Scleroracus*) *zacki* Hamilton
(Figs. 210–214)

Limotettix (*Scleroracus*) *zacki* Hamilton 1994: 131 [n.sp.].

Diagnosis.—Aedeagus in posterior view as broad as tall, lateral margins subparallel, dorsolaterally evenly convex, apical processes short, acute, directed dorsad.

Female unknown. Male. Measurements (mm). Length with forewings in repose 3.9. Width across eyes 1.2. *Head:* Vertex in dorsal view blunt, length 0.45 × minimum width between eyes (Fig. 210). *Thorax:* Pronotum in lateral view depressed. Forewing veins clearly demarcated. Prothoracic tibia with row AV depressed in holotype, probably not distinctly bimodal, basal setae gradually increasing in size distally. *Abdomen:* Pygofer with dorsal lobe posteriorly developed into short acute process, ventral lobe articulated. Aedeagal atrium in lateral view weakly constricted before aedeagal shaft (Fig. 212); shaft in posterior view short and broad, lateral margins subparallel, shaft produced medially, apical processes short, acute, directed dorsad from middle, and well separated from each other (Fig. 214); dorsal connective emargination shallow and V-shaped; ventral connective widest between robust, Y-shaped arms anteriorly, length 2.9× width across anterior arms and 3.4× their longitudinal length (Fig. 213); style moderately long and distally slender, slightly curved laterad, with ventral, rounded preapical lobe not especially prominent.

Coloration. Pro- and mesothoracic legs not bicolored (not as in Fig. 1); otherwise as shown (Figs. 210–211).

Hosts.—Unknown.

Specimens examined.—Holotype ♂ labeled: "Badger MtRoses | S. Waterville Wn | 6-4-18ACBurrill", "HOLOTYPE | Limotettix | zacki Hmlt. | CNC No. [no number]" [CNCI]. Hamilton (1994) reported that the holotype is CNC No. 21392.

Remarks.—The aedeagus of *L.* (*S.*) *zacki* strongly resembles that of *L.* (*S.*) *glomerosus,* differing principally in the degree of atrium constriction and in the dorsolateral form of the aedeagal shaft. The frons of *L.* (*S.*) *zacki* is much narrower than that of *L.* (*S.*) *glomerosu* (Fig. 87).

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DISCOVERY OF *CENOPALPUS PULCHER* (C. & F.) (ACARI: TENUIPALPIDAE) IN THE NEW WORLD

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Abstract.—A new exotic mite species, *Cenopalpus pulcher* (Camestrini and Fanzago), the flat scarlet mite, is reported in Benton and Linn counties, Oregon, USA infesting both apples and pears. This is the first published record of the genus *Cenopalpus* in the New World. *Cenopalpus pulcher* is a pest of pome and stone fruits in the Old World. Based on a 1990 collection and current surveys, it now appears that it is well established in the indicated area. *Cenopalpus pulcher* is an invasive species capable of spreading into new areas by its own means or as a passive contaminant of plant materials transported across geographical regions.

Key Words: Acari, acarology, *Cenopalpus pulcher,* flat scarlet mite, invasive species, Tenuipalpidae

Members of the false spider mite genus *Cenopalpus* Pritchard and Baker (*Brevipalpus spinosus* Donnadieu species group of Meyer 1979) feed on a variety of plant hosts in Europe, Asia, and Africa, but have never been recorded from the New World.[1] Recently, we collected a tenuipalpid mite species from pear and apple foliage and bark in Benton and Linn counties, Oregon, USA. GWK identified it as the flat scarlet mite, *Cenopalpus pulcher* (C. & F.), a recognized pest of pome and stone fruits in the Old World. The identification was confirmed by the Systematic Entomology Laboratory, USDA, Beltsville, Maryland, based on low temperature scanning microscope (LT-SEM) photographic analysis as described by Wergin et al. (2000). The voucher specimens are preserved in the Oregon State Arthropod Collection, Corvallis. Based on 1990–1994 collections taken from apple leaves in Corvallis by the senior author, it now appears that *C. pulcher* has been established in the Willamette Valley of western Oregon for at least 10 years.

A brief account of the morphology, biology, and ecology of *C. pulcher* is presented by Jeppson et al. (1975). *Cenopalpus pulcher* is small, broadly rounded, and scarlet in color (Fig. 1). Females are about 320 μm long and 160 μm wide. The male is shorter and paler than the female. The eggs are bright red, oval, and about 70 μm by 110 μm. The propodosoma of *C. pulcher* is evenly reticulate dorsomedially (Fig. 2), and the hysterosoma possesses 6 pairs of dorsolateral setae and a pair of dorsosublateral setae. The dorsal body setae are tapering and setiform, and the rostrum is short and does not reach the end of femur

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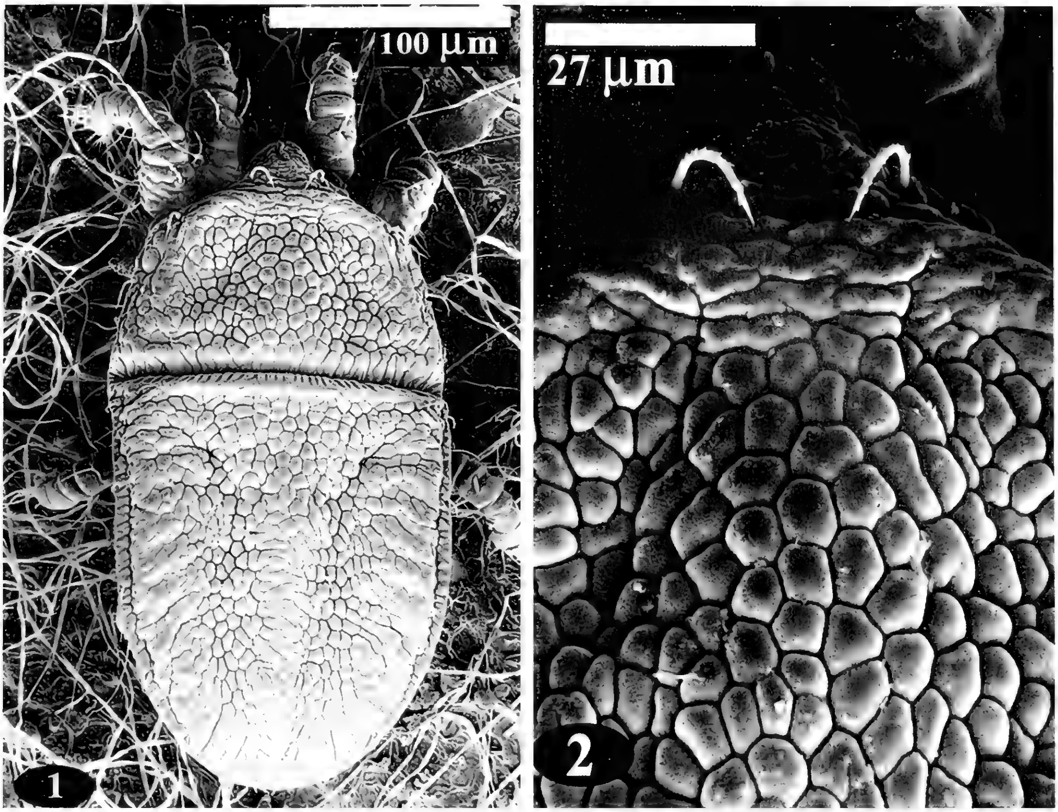
[1] However, Dr. Ronald Ochoa, USDA, ARS, Beltsville, MD, reports that two females of *C. pulcher* were collected from apple in Rio Negro-Cinco Saltos, Argentina, in February 1982, and that immature specimens were identified from the same site two months later.



Figs. 1–2. *Cenopalpus pulcher,* scanning electron micrographs of adult female. 1, Dorsal view; on an apple leaf. 2, Detail of diagnostic reticulations on propodosoma.

I. The mite feeds on the leaves, soft twigs, and fruit of apple, pear, peach, apricot, quince, plum, and cherry, and is also found on rose, walnut, cotoneaster, dogwood, and willow. Depending on climatic conditions, *C. pulcher* may go through 1–3 generations/year. The adult fertilized females overwinter in bark crevices and under bud scales of their host plants, usually in groups of 3–9 individuals. According to Sepasgosarian (1970), overwintering females can survive temperatures as low as −30°C. The first eggs are produced in early spring on the tree bark, but later generations place their eggs on the leaf undersurface near the midrib. Mating occurs late in the summer.

Cenopalpus pulcher is widely distributed in Europe, the Middle East, Central Asia, and North Africa (Pritchard and Baker 1958, Jeppson et al. 1975, Lattin and Oman 1983, El-Halawany et al. 1990), where populations may be regulated by natural enemies including the predatory phytoseiid mites *Amblyseius gossipi* Elbadry, *Phytoseius finitimus* Ribaga, and *Typhlodromus negevi* (Swirski and Amitai), and by the stigmaeid mite *Agistemus exsertus* Gonzalez (El-Tawab et al. 1971; El-Laithy and Fouly 1998; Rasmy et al. 1991a, 1991b). None of these predators is known to occur in Oregon, or in the USA. Co-occurrence of *C. pulcher* with predatory mite species found in pome and stone fruit trees in Oregon is discussed by Bajwa (1996), who found the phytoseiids *Typhlodromus pyri* Scheuten, *Amblyseius andersoni* Chant, *Kampimodromus abberans* (Oudemans), and the stigmaeid *Zetzellia mali* (Ewing) associated with *C. pulcher* colonies. However, predation was not observed.

The fact that *C. pulcher* appears to be well established in the Corvallis area suggests that the mite is sufficiently mobile and invasive to spread within and between orchards. In addition, the quiescent, sequestered overwintering females are ideally adapted for long range passive dispersal in shipments of vegetative plant material. Thus, the distribution of *C. pulcher* may well include other locales in the state of Oregon and beyond. Results of our preliminary surveys show that *C. pulcher* is a predominant faunal component in various pear varieties under study by the senior author in Corvallis. It is possible that *C. pulcher* was introduced into the Corvallis area via infested plants or plant material (e.g., scion wood) received by a nursery, a grower, or a research institution from an Old World site where the mite is already established.

Our recent studies showed that *C. pulcher* populations on three pear varieties (Anjou, Bartlett, and Nijisseiki) reached their peaks from early August to early September, and remained high until mid-October. Pear trees with high mite populations (1.23–2.88 mites/leaf, 7.25–10.41 overwintering females/twig) were found to have lower incidences of active and overwintering tetranychid mites than trees with lower populations of *C. pulcher* (0–0.05/leaf, 0–0.1 overwintering females/twig), suggesting the possibility of antagonism between *C. pulcher* and its co-occurring established tetranychid neighbors.

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VARIATION AND HOMOLOGY IN ELYTRAL MACULATION IN THE *ANOPLOPHORA MALASIACA/MACULARIA* SPECIES COMPLEX (COLEOPTERA: CERAMBYCIDAE) OF JAPAN AND TAIWAN

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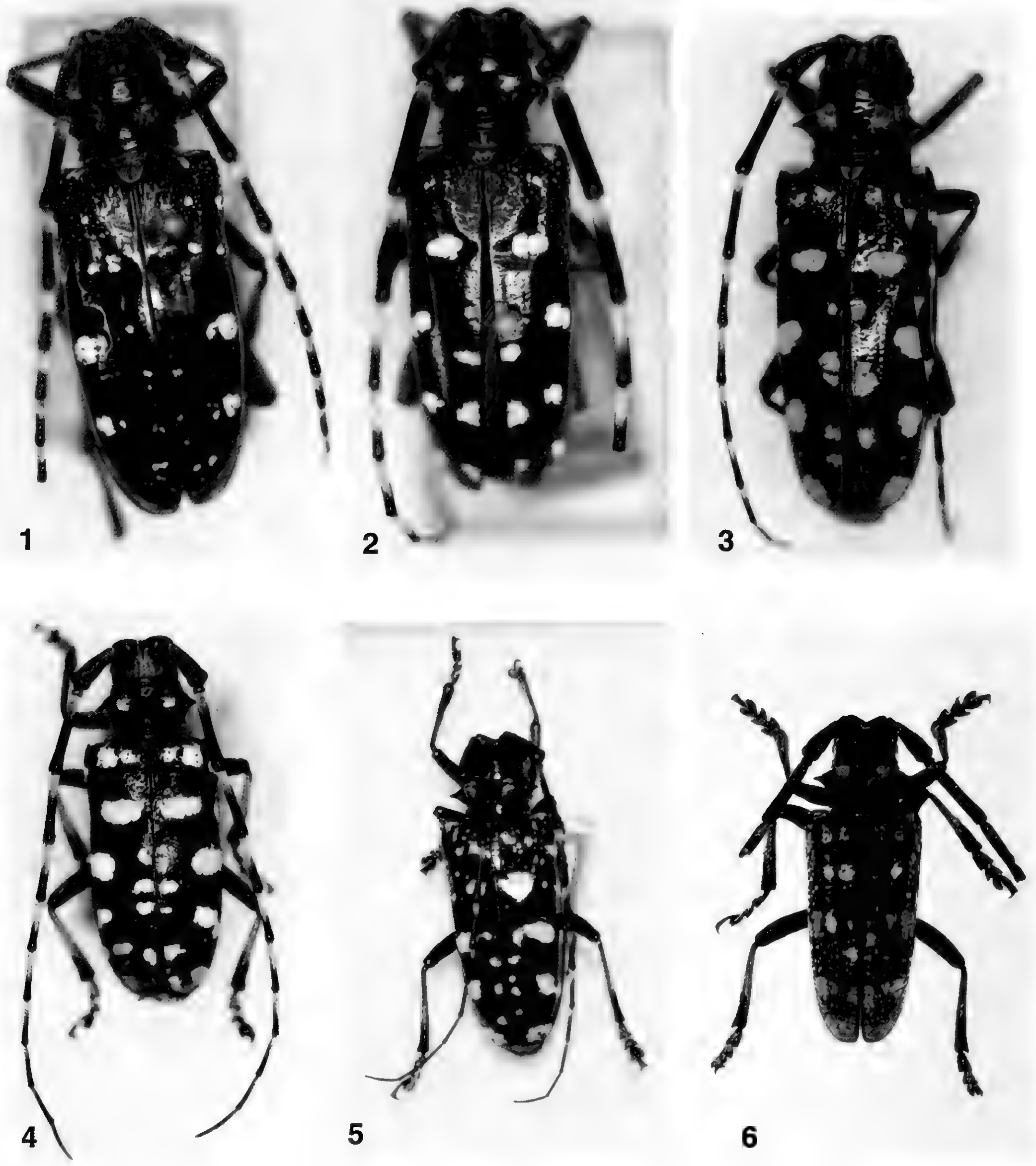
Abstract.—A description and assessment of elytral maculation and variation is provided for the following *Anoplophora* taxa in Japan and Taiwan: *Anoplophora malasiaca* (Thomson, 1865), *A. malasiaca tokunoshimana* Samuelson (1965), *A. macularia* (Thomson, 1865), *A. oshimana* (Fairmaire, 1895), *A. oshimana ryukyensis* Breuning and K. Ohbayashi (1964), and *A. ogasawaraensis* Makihara (1976). Elytral maculae are homologized and compared based on their position to each other and to other elytral features. Because considerable overlap in patterns of maculation occurs among members of the *A. malasiaca/macularia* complex, we conclude that elytral maculation alone should not be used to define these taxa.

Key Words: Asian Longhorned Beetle, *Anoplophora,* Cerambycidae, Lamiinae, Lamiini, woodborer, white-spotted citrus longhorn, Japan, Taiwan, systematics, morphoclinal variation

Our goal is to qualitatively define and assess variation of elytral maculation across individuals and species in the *Anoplophora malasiaca/macularia* complex of Japan and Taiwan. We extensively demonstrate the geographic variability in elytral maculation to assess the value of this character in *Anoplophora* taxonomy. These maculae are regions of very dense, fine, appressed white or yellow setae, arising from a field of minute punctures. Without magnification, they appear as white or yellow spots on the integument. These maculae have been used as a primary character system to distinguish species in *Anoplophora,* however no previous comparative analysis of their variation within species or homology among species has been made. These data, when combined with other morphological information in a forthcoming revision of *Anoplophora* Hope (Lingafelter and Hoebeke in prep.), will facilitate decision-making to stabilize the systematics of this group of longhorned beetles.

Approximately 40 valid species of *Anoplophora* have been described from the Oriental and eastern Palearctic regions; about 10 species and subspecies occur in Japan and Taiwan (Nakamura et al. 1982, Ohbayashi et al. 1992). This paper focuses on the *A. malasiaca/macularia* complex which includes species characterized by a black integument with white and/or flavous spots of pubescence on the elytra and pronotum, a distinct field of coarse granulae at the base of the elytra, and black and white annulated antennae. Larvae in this complex are most frequently associated with *Citrus* and have



Figs. 1–6. Taxa in *Anoplophora malasiaca macularia* complex. 1, Type of *A. malasiaca* (Thomson) (probably from Honshu, Japan). 2, Type of *A. macularia* (Thomson) (probably from Taiwan). 3, Syntype of *A. oshimana* (Fairmaire) (from Amami-Oshima, Japan). 4, Paratype of *A. oshimana ryukyensis* Breuning and K. Ohbayashi (from Yonaguni, Japan). 5, Holotype of *Anoplophora malasiaca tokunoshimana* Samuelson (from Tokunoshima, Japan). 6, Holotype of *A. ogasawaraensis* Makihara (from Ogasawara Islands, Japan).

been listed among the major insect pests in Japan (Anonymous 1981, Adachi 1988, Clausen 1931, Chang 1975, Ho et al. 1995). As generalist feeders, however, the larvae frequently develop in other tree genera including *Platanus, Acer, Zelkova, Salix,* and *Robinia* (Ohga et al. 1995). The following names have been proposed to date in the *A. malasiaca/macularia* complex: *Anoplophora malasiaca* (Thomson 1865), *A. malasiaca tokunoshimana* Samuelson (1965), *A. macularia* (Thomson, 1865), *A. oshimana*

7

Fig. 7. Homology and designation of elytral maculations for *A. malasiaca/macularia* complex of species, based on *A. malasiaca* (Thomson) from Honshu, Japan.

(Fairmaire 1895), *A. oshimana ryukyensis* Breuning and K. Ohbayashi (1964), and *A. ogasawaraensis* Makihara (1976). We have been unable to locate the holotypes of *A. wusheana* Chang (1960) and *A. flavomaculata* (Gressitt 1934) and their affinities are unclear based on the original descriptions. Because they both have non-annulated antennae (according to the original descriptions), they probably do not belong in the *A. malasiaca/macularia* group. A brief taxonomic history and description of the aforementioned taxa follows.

Anoplophora malasiaca and *A. macularia* were described by Thomson (1865). The type of *A. malasiaca* (Fig. 1) was stated to be from "Malasia", but no additional records of other specimens from Malaysia have been found. The label on the type specimen simply states, "Malas" and could refer to the collector's name, and not a locality (N. Ohbayashi personal communication). It most closely resembles specimens common on Honshu Island, Japan. The type locality of *A. macularia* (Fig. 2) is given as "China bor.[ealis]" and resembles specimens common to southern Japan (Ryukyu Islands including Yonaguni, Ishigaki, and sometimes Tokunoshima and Amami-Oshima) and Taiwan. *Anoplophora malasiaca tokunoshimana* (Fig. 5) from Tokunoshima in the Ryukyu Islands, was described by Samuelson (1965) and said to differ from the nominate form by the presence of larger maculations and to differ from *A. oshimana* by the white (rather than pale flavous) maculations. *Anoplophora oshimana* (Fig. 3), described by Fairmaire (1895) from the island of Amami-Oshima, has larger and more flavous maculations than *A. malasiaca* (Thomson). *Anoplophora oshimana ryukyensis* Breuning and K. Ohbayashi (1964) (Fig. 4), from the island of Yonaguni in the southern Ryukyu Islands, was described to be similar to the typical form but with fine, much more distinct elytral punctures and purely white maculations. It was elevated to species status in Ohbayashi et al. (1992). *Anoplophora ogasawaraensis* (Fig. 6) was described by Makihara (1976) from the Ogasawara Islands, about 1,100 km east of the Ryukyu Islands. This species is the most geographically isolated taxon of the complex and is distinctive because of its numerous yellow and white, large and small maculations, and the apices of the elytra are more completely suffused with white. Makihara (1976) noted that it differs from *A. macularia* of Taiwan and *A. malasiaca* and *A. oshimana* of the Ryukyus by having more numerous small elytral maculations, pale (not white) pubescence on the venter, and subtle differences in the hind wing color.

METHODS

Over 300 specimens of *Anoplophora* were examined for this study from the following institutions (acronyms from Arnett et al. 1993): Entomological Laboratory, College of Agriculture, Ehime University, Matsuyama, Shikoku, Japan (EUMJ); Entomological Laboratory, Faculty of Agriculture, Kyushu University, Fukuoka, Kyushu, Japan (KUEC); Bernice P. Bishop Museum, Honolulu, Hawaii, United States (BPBM); National Museum of Natural History, Smithsonian Institution, Washington, D. C., United States (USNM); Museum National d'Histoire Naturelle, Paris, France (MNHN); and The Natural History Museum, London, England (BMNH).

Representatives of each taxon in the *A. malasiaca/macularia* complex from Taiwan and most of the Japanese islands were examined and photographed. Drawings of elytra were made from scans of the slides using Adobe Photoshop™ and Adobe Illustrator™ on a Macintosh™ computer. The illustrated elytron for each island represents the median or the most common representation of maculation position for specimens of each sex (when both sexes were available) for each island based on all the material seen for a given island (see Material Examined). We have standardized elytral shape and size so that information of relative size and position of the maculations is most easily interpreted. Using an elytron of a representative specimen of *A. malasiaca* from Honshu, Japan as a template, primary elytral maculations were homologized based on their locations (Fig. 7). These maculations are lettered in order, starting at the base of the elytron, continuing around the outside lateral margin to the apex, and then continuing on the disk from base to apex and left to right in cases where maculations are paired or closely associated. The lettering then continues along the suture from base to apex. The maculations are referred to by these letters in the following descriptions. In most cases, maculations are easily homologized to this template based on their locations relative to one another, and to the costae, humerus, and apex of the elytron. The loss of sutural maculations (S1 to S4) and fusion of apical maculations (G, K, F) in some specimens can complicate interpretations. Rarely have we seen specimens with no maculations, and these are clearly genetic aberrants. The elytral maculations of each taxon in the *A. malasiaca/macularia* complex and representatives from most of the Japanese islands are illustrated (Figs. 9–12) and discussed in relation to the homology template (Fig. 7) and geography (Fig. 8).

RESULTS AND DISCUSSION

General trends in maculations.—There are several morphological clines evident (Fig. 8). As one moves farther south through the Japanese Islands, and particularly into the Ryukyu Islands, H3 and H4 generally become much larger. They are fused together in most specimens from Amami-Oshima, Ishigaki, Yonaguni, and Taiwan. The sutural maculations (S1–4) increase in size in most specimens from this southern region as well. The fused H3-H4 and large S1–4 maculations are characteristic of the type of *A. macularia* (Fig. 2), most of the syntypic series of *A. oshimana* (Fig. 3), and *A. oshimana ryukyensis* (Fig. 4). *Anoplophora malasiaca tokunoshimana* (Fig. 5) is similar, but there are small secondary maculations scattered around the basal half of the elytra and the sutural maculations are not noticeably larger than the typical *A. malasiaca* from Honshu.

Maculations are predominately white except for most specimens from the northern and middle Ryukyu Islands (Yakushima, Amami-Oshima, and Okinawa), where the maculations vary from off-white to flavous to orange. Some specimens from Tsushima in southwest Japan (but north of the Ryukyu Islands) also have flavous maculations. Aside from these minor clines, the pattern of maculations does seem to vary slightly from one locality to another. The specific patterns for each taxon and locality are discussed below.

Specific descriptions of maculations.—The holotype of *A. malasiaca,* like most *A. malasiaca* specimens from Honshu, has the characteristic pattern of maculations shown in Fig. 7. Specimens from Honshu (Figs. 9C, D) have the maculations most commonly white, but occasionally off-white to flavous. Maculations H1–4 are small and separate, I1–2 are partially fused, the apical maculations are small, usually with distinct F, G, and K maculae, S1–4 are small but distinct (occasional secondary maculae in this region) and S1 is always posterior of the middle of the elytron. Specimens of *A. malasiaca* from Kyushu (Figs. 10E, F) are most similar to Honshu specimens, but differ by having I1 and I2 fused and much smaller. Specimens from Hachijo (Figs. 9E, F), to the east of Honshu, differ from the typical form by having smaller maculations, I1 and I2 divided, the apical maculation enlarged with fusion of F, G, and K, and two sutural maculae, probably S1 and S4, lost. Specimens from Shikoku (Figs. 10C, D) differ from the typical form by having separate I1 and I2, a loss of a sutural macula, probably S1 or S4, the presence of a few small, secondary maculae, a more clear separation of the apical maculae F, G, and K, and off-white to flavous representatives are more common in the populations. Specimens from Tsushima (Figs. 10A, B) are quite similar to the typical form but have the maculations bolder and more commonly with flavous representatives. The apical maculae (F, G, and K) are partially fused. Hokkaido specimens (Figs. 9A, B) have very large fused patches of I1-I2 and J is typically quite large. The apical patches of F, G, and K are fused. Two sutural maculae (unable to make specific determination) are lost. In the northern and middle Ryukyu Islands, off-white to flavous maculated specimens of *A. malasiaca* occur in greater proportions in the populations. On Yakushima, specimens have bold white to off-white maculations (Figs. 11A, B). In particular H3-H4 and some of the sutural maculae are quite bold; otherwise, Yakushima specimens are similar to Honshu specimens.

Anoplophora oshimana (Figs. 3, 11C, D) from Amami-Oshima have the greatest proportion of flavous-maculated individuals of any region. They are also characterized by the large sutural maculae and fusion of H3 to H4 and I1 to I2. Tokunoshima specimens, described by Samuelson (1965) as *A. malasiaca tokunoshimana* (Fig. 5), vary from most *A. oshimana* by having white maculations and more numerous small, secondary maculae along the basal half and suture of the elytra. Specimens of *A. oshimana* from Okinawa (Fig. 11E, F) and Miyako (Fig. 12A) in the southern Ryukyu Islands typically have H3-H4 separate, and the sutural and apical maculae are much smaller than in specimens from other Ryukyu localities. Yonaguni specimens, described as *A. oshimana ryukyensis* by Breuning and K. Ohbayashi (1964) and treated as a species in Ohbayashi et al. (1992) (Figs. 4; 12C, D), have very large, bright white maculae. H1 is nearly fused with H2; H3 and H4 are fused into a broad macula; I1, I2, and D are all fused into a large patch; J is large and fused with E in many individuals. Specimens from Taiwan and Ishigaki, generally referrable to *A. macularia* (Figs. 2; 12B, E, F) are similar to *A. o. ryukyensis,* but with less fusion of J to E and I to D.

The most extreme variant within the *A. malasiaca/macularia* complex is *A. ogasawaraensis* (Fig. 6) but its maculations can be easily homologized with the typical form. The color of the maculations is unique among members of the *A. malasiaca/macularia* complex. The maculae are flavous around the outside of the elytra, while the discal maculae are mostly white. Color aside, it is most similar to specimens from the southern Ryukyus, in particular Miyako and Okinawa, by having separate H3 and H4 maculae, but very large and nearly fused I2-D and J-E maculae. The apex is fully maculate with F, G, and K

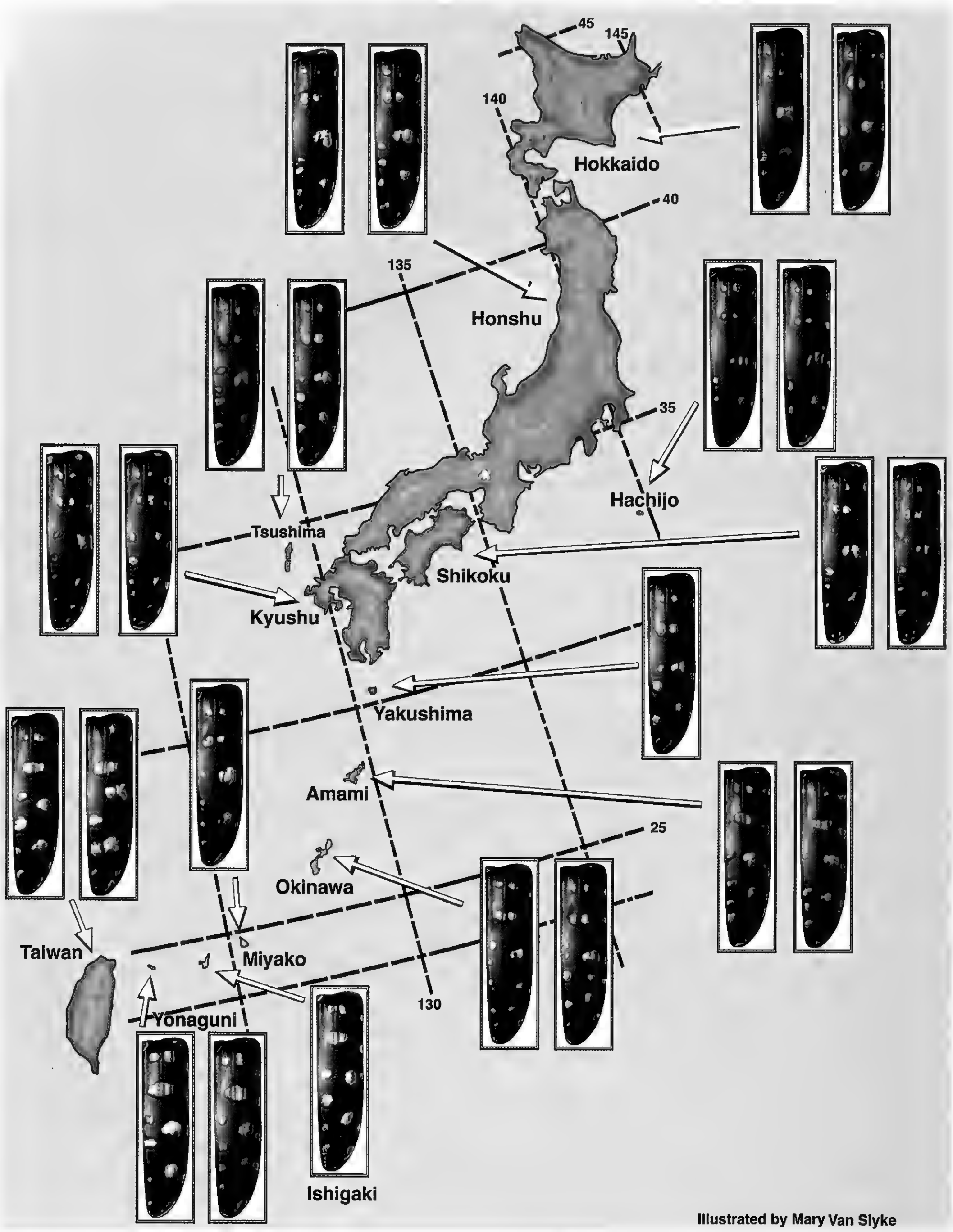


Fig. 8. Map of Japan and Taiwan showing geographical clinal variation in elytral maculation for all members of *A. malasiaca/macularia* complex of species. Thumbnail elytra are more fully illustrated in Figs. 9–12.

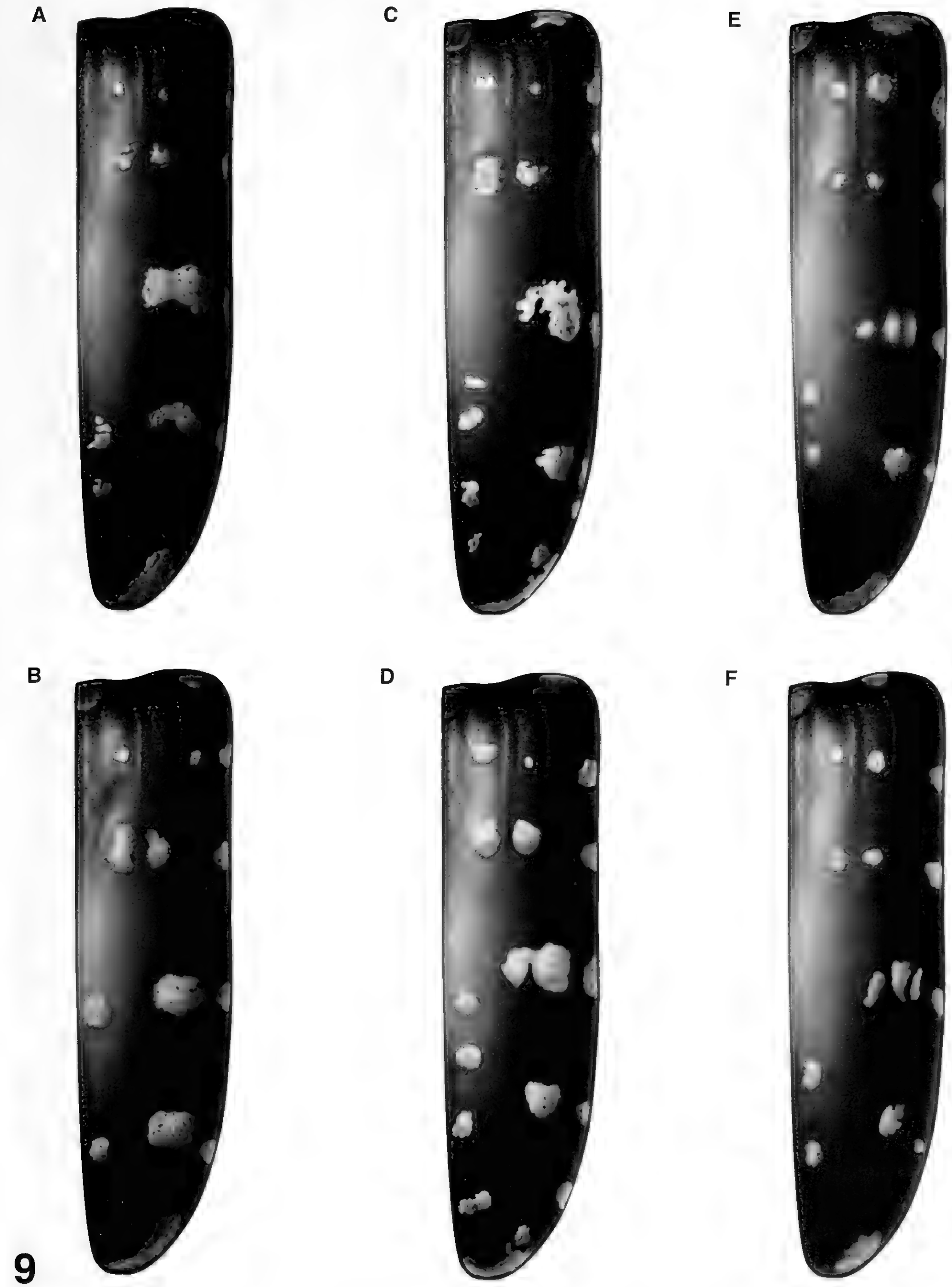


Fig. 9. Representative elytra of *A. malasiaca* (Thomson) from various Japan Islands. A, Hokkaido (female). B, Hokkaido (male). C, Honshu (female). D, Honshu (male). E, Hachijo (female). F, Hachijo (male).

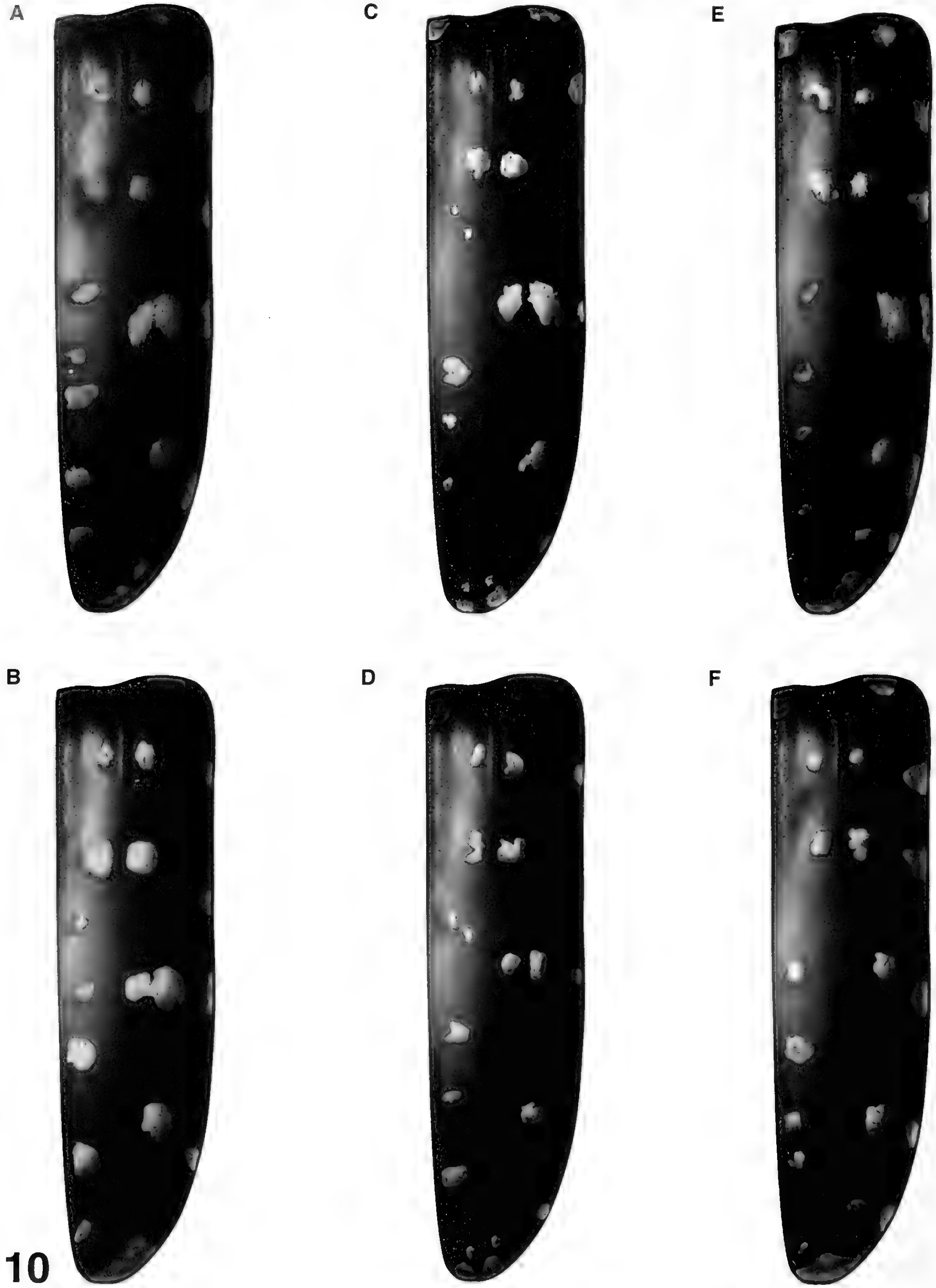


Fig. 10. Representative elytra of *A. malasiaca* (Thomson) from various Japan Islands. A, Tsushima (female). B, Tsushima (male). C, Shikoku (female). D, Shikoku (male). E, Kyushu (female). F, Kyushu (male).

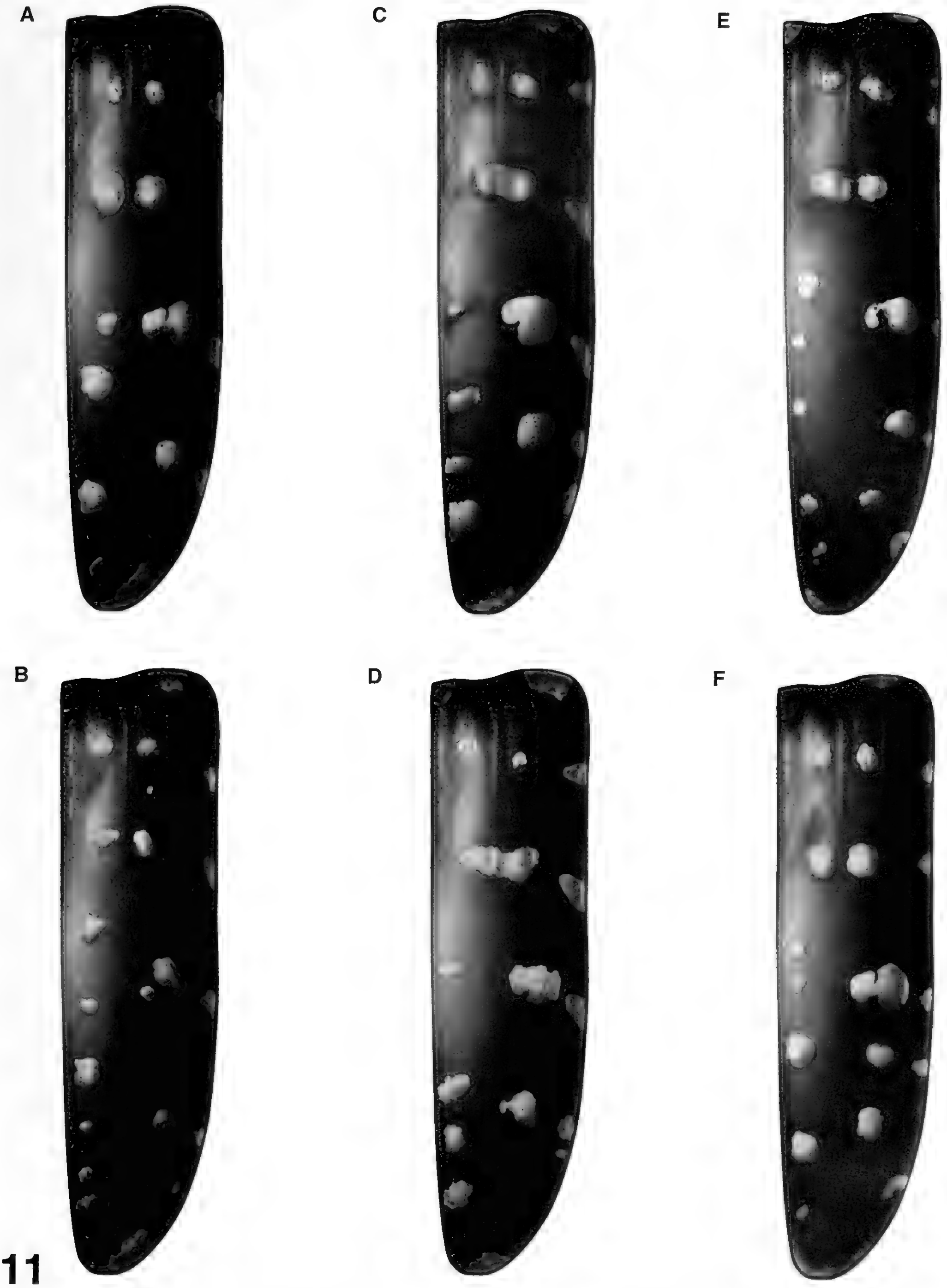


Fig. 11. Representative elytra of *A. malasiaca* (Thomson) from: A, Yakushima (male); B, Yakushima (male). Representative elytra of *A. oshimana* (Fairmaire) from: C, Amami-Oshima (female); D, Amami-Oshima (male); E, Okinawa (female); F, Okinawa (male).

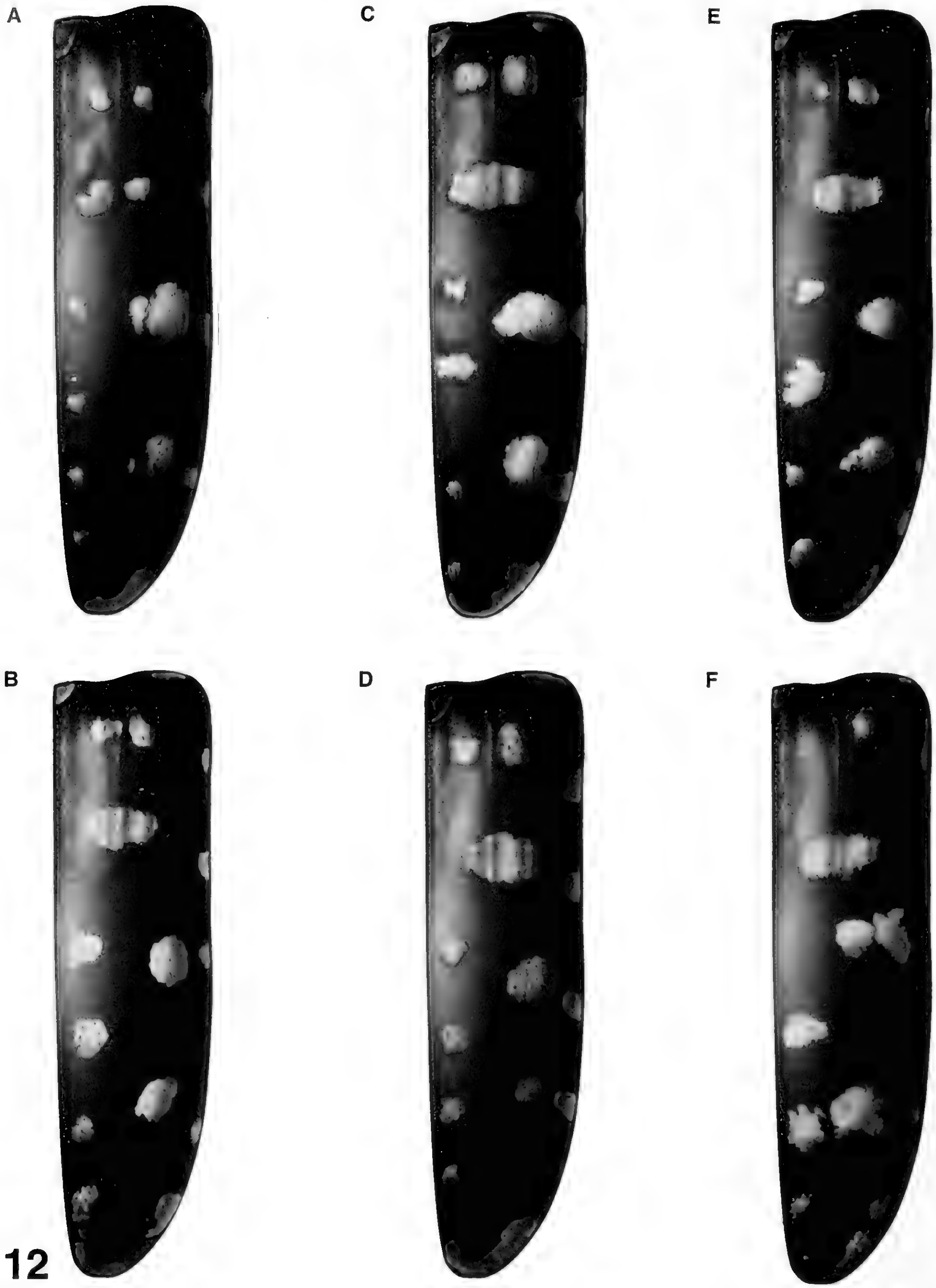


Fig. 12. Representative elytron of *A. oshimana* from: A, Miyako (female). Representative elytra of *A. oshimana ryukyensis* Breuning and K. Ohbayashi from: C, Yonaguni (female); D, Yonaguni (male). Representative elytra of *A. macularia* (Thomson) from: B, Ishigaki (male); E, Taiwan (female); F, Taiwan (male).

fused. It differs from most other forms by having numerous small secondary maculae, and by the characters of the ventral pubescence and slight curvature of the tegmen as originally described by Makihara (1976).

CONCLUSIONS

Our comparative study demonstrates that there are some geographical trends in some features of the elytral maculae, but there are also seemingly random variant patterns, with no apparent relationship to geography. Based on our careful consideration of this variability, we assert that elytral maculations alone cannot be used to define taxa, and further, their use should not be made without acknowledgment of their variability.

MATERIAL EXAMINED

***Anoplophora malasiaca* (Thomson)**: Malaysia?, "Malas" [MNHN, type]; Japan, Hayama, [BPBM, 1]; Japan, Kobe, [BPBM, 1]; Japan, Mimasaka, July, [BPBM, 1]; Tokyo; Gensan, [MNHN, 40]; Japan, Yokohama, [BPBM, 1]; Japan, Kagoshima, Chiran, July, [BPBM, 1]; Japan,Kyoto, [BPBM, 2]; Japan, Nagano-ken, July, [BPBM, 1]; Japan, Shikoku, Ehime, Matsuyama, July [EUMJ, 1]; Japan, Honshu, Tiamuji, Bushicity, August, [EUMJ, 1]; Japan, Shikoku, Cape Ashizuri, July 24, [EUMJ, 1]; Japan, Ninomiya, Kanagawa, July 18, [EUMJ, 1]; Japan, Mt. Yatsu, August 13, [EUMJ, 1]; Japan, Seki, Gifu, June 24, [EUMJ, 1]; Japan, Idani, Gifu, August 9, [EUMJ, 1]; Japan, Nagoya, June 25, [EUMJ, 1]; Japan, Seki, Gifu, June 29, [EUMJ, 1]; Japan, Ninomiya, Kanagawa, July 7, [EUMJ, 1]; Japan, Miura Peninsula, Kanagawa, July, [EUMJ, 1]; Japan, Mt. Tyotokusan, Okayama, June 22, [EUMJ, 1]; Japan, Shikoku, Tanimachi, Matsuyama, June/July, [EUMJ, 2]; Japan, Shikoku, Odamiyama, July 21, [EUMJ, 5]; Japan, Shikoku, Tarumi, Matsuyama, [EUMJ, 1]; Japan, Tsushima, Sasuna, 25–30 July, [EUMJ, 1]; Japan, Tsushima, Mt. Ohtoshiyama, 28 June, [EUMJ, 1]; Japan, Tsushima, Mt. Tatena, October 10, [EUMJ, 1]; Japan, Tsushima, Nagasaki, July 23, [EUMJ, 1]; Japan, Hokkaido, Kiyobe, Matsumae, July 5, [EUMJ, 1]; Japan, Kyushu, Kanose, Kuma vil., Kumamoto, June 6, [EUMJ, 1]; Japan, Kyushu, Chikugo, July 17, [EUMJ, 1]; Japan, Ishigaki, Mt. Banna, April 22, [EUMJ, 1]; Japan, Miyako, Hirara, 21 June, [EUMJ, 1]; Japan, Hachijo, Sueyoshi, July 8–15, [EUMJ, 6]; Japan, Hachijo, Kashidata, July 4, [EUMJ, 6]; Japan, Yakushima, Anbou, Kagoshima, July 6, July 24, [EUMJ, 2]; Japan, Okinawa, May 15, [EUMJ, 1]; Japan, Okinawa, Sueyoshi, Naha, 28 June, April 30, [EUMJ, 2]; Japan, Ryukyo, Shuri, May 27, [EUMJ, 1]; Japan, Nago, May–July, [EUMJ, 3]; Japan, Takari, Kunigami, June 29, [EUMJ, 2]; Japan, Okinawa Island, Shuri, Naha-city, 20-VI-1975, Tsutsumi [EUMJ, 1F]; Japan, Okinawa Island, Shuri, Naha-city, 1-V-1977, T. Nakamoto [EUMJ, 1M]; Japan, Okinawa Island, Shuri, Naha-city, 27-V-1975, Y. Notsu [EUMJ, 1M]; Japan, Okinawa Island, Sueyoshi, Naha-city, 16-VI-1976, M. Kinjo [EUMJ, 1M]; Japan, Okinawa Island, Ooyama, Ginowan-city, 17-V-1970, K. Miyagi [EUMJ, 1M]; Japan, Okinawa Island, Gogayama, Nakijin-son, 9-VI-1979, M. Kinjo [EUMJ, 1M]; Japan, Okinawa Island, Nago-city, 13-V-1980, N. Ooba [EUMJ, 1M]; Japan, Okinawa Island, Gushikawa, Gushikawa-city, 1-VII-1995, T. Matsumura [EUMJ, 1F]; Japan, Okinawa Island, Uehara, Oogimi-son, 22-VI-1999, S. Inada, Citrus spp. [EUMJ, 3–1M, 2F]; Japan, Okinawa Island, Takasato, Oogimi-son, 29-VI-1993, N. Ohbayashi [EUMJ, 1M]; Japan, Okinawa Island, Nejime, Oogimi-son, 2-VI-1995, T. Matsumura, Citrus spp. [EUMJ, 7–3M, 4F]; Japan, Okinawa Island, Nejime, Oogimi-son, 18-VI-1995, T. Matsumura, Citrus spp. [EUMJ, 4–1M, 3F]; Japan, Okinawa Island, Mt. Nekumachiji, Oogimi-son, 24-VII-1995, T. Sasaki [EUMJ, 1F]; Japan, Okinawa Island, Mt. Nekumachiji, Oogimi-son, 8-VIII-1995, T. Sasaki [EUMJ, 1F]; Japan, Okinawa Island, Mt. Nekumachiji, Oogimi-son, 14-VII-1996, T. Sasaki [EUMJ, 1F]; Japan, Okinawa Island, Kakazu, Ginowan-city, 30-IV-1995, T. Matsumura [EUMJ, 1F]; Japan, Okinawa Island, Kakazu, Ginowan-city, 11-V-1971, Tukasa Kohama [EUMJ, 1F]; Japan, Okinawa Island, Syoshi, Nakijin-son, 18-VI-1995, T. Matsumura [EUMJ, 1F]; Japan, Okinawa Island, Yona, Kunigami-son, 18-VII-1999, Teruya [EUMJ, 1M].

A. oshimana **(Fairmaire, 1895)**: Japan, Liao-Kiou Archipelago, I'le de Shima, Amami Island, June, July [BMNH, part of syntype series, 21]; Japan, Liou-Kiou Archipelago (I'le de Oshima), Ferrie coll., [MNHN, part of syntype series, 200]; Japan, Liao-Kiou Archipelago, I'le de Shima, Amami Island, [USNM, 2]; Japan, Amami, Hatsuno, July 3, [EUMJ, 1]; Japan, Amami Isl., Mt. Ogami, June 30, [EUMJ, 1]; Japan, Amami, Yakkachi, June2, [EUMJ, 1]; Japan, Amami-Oshimana, July, [EUMJ, 1]; Japan, Amami, Shimura, June 12, [EUMJ, 1]; Japan, Amami, Koshuku, June 5, [EUMJ, 1]; Japan, Amami, Sakibaru, June 18, [EUMJ, 1]; Japan, Amami, Higashinakame, July 17, [EUMJ, 1]; Japan, Hatsuno, Amami-Oshimana, July 27, [EUMJ, 1]; Japan, Shimura, July 19, [EUMJ, 1]; Japan, Amami, Hatsuno, July 3, [EUMJ, 1]; Japan, Naze, Amami, June 13, [EUMJ, 1]; Japan, Okinawa Island, Yamada, Onna-son, 6-VII-1999, M. Kimura, ex. Schima liukiuensis [EUMJ, 4–3M, 1F]; Japan, Okinawa Island, Yofuke, Nago-city, 3-VI-1999, S. Inada [EUMJ, 1F]; Japan, Okinawa Island, Isagawa, Nago-city, 27-V-1999, Sakashita [EUMJ, 1F].

A. oshimana ryukyensis **Breuning and K. Ohbayashi (1964)**: Japan, Is. Yonakuni, Tabaru-gawa, May 15, 1963, Y. Arita coll. [EUMJ, holotype]; Japan, Yonakuni, Sonai and Mt. Urabe, May 16, July 6, July 8, July 11 [EUMJ, 10 paratypes].

A. macularia **(Thomson, 1865)**: China bor., (no specific data), [MNHN, type]; Formosa (Taiwan), Sengpei, May 5, [EUMJ, 1]; Formosa (Taiwan), Mt. Yangminshan, June 3, [EUMJ, 1]; Formosa (Taiwan), Kenfing Park, Pingtung, May 3, June 5, [EUMJ, 2]; Taiwan, Jieyuehtan, Nantou, June 2, [EUMJ, 1]; Taiwan, Lu-Shan, May 23, [EUMJ, 1]; Taiwan, Nanshanchi, June 23, [EUMJ, 1]; Taiwan, Rozan, 1200m, July 29–30, [EUMJ, 1]; Taiwan, Peipo Hsinchu Hsien, June 7, [EUMJ, 1]; Taiwan, Chihpen Spa, Taitung Hsien, June 11, [EUMJ, 1]; Taiwan, Wulei, July 3, [EUMJ, 1]; Japan, Okinawa Island, Furushima, Naha-city, 29-VI-1999, Teruya [EUMJ, 1F]; Japan, Okinawa Island, Tomari, Naha-city, 3-VII-1999, M. Kimura [EUMJ, 2-M, F]; Japan, Okinawa Island, Tomari, Naha-city, 27-VII-1999, M. Kimura, Melia azedarach var. subtripinnata [EUMJ, 2-M, F]; Japan, Okinawa Island, Sueyoshi, Naha-city, 28-VI-1993, N. Ohbayashi [EUMJ, 4M]; Japan, Okinawa Island, Sueyoshi, Naha-city, 30-VII-1999, M. Kimura [EUMJ, 2F]; Japan, Okinawa Island, Maejima, Naha-city, VI-1999, H. Nakachi, Melia azedarach var. subtripinnata [EUMJ, 3–2M, 1F]; Japan, Okinawa Island, Ikehara, Okinawa-city, 30-VI-1999, S. Inada, Melia azedarach var. subtripinnata [EUMJ, 8–6M, 2F]; Japan, Okinawa Island, Goya, Okinawa-city, 29-VI-1999, S. Inada [EUMJ, 2-M, F]; Japan, Okinawa Island, Goya, Okinawa-city, 29-VI-1999, M. Kimura [EUMJ, 1F]; Japan, Okinawa Island, Yogi, Okinawa-city, 30-VI-1999, M. Kimura, Melia azedarach var. subtripinnata [EUMJ, 2M]; Japan, Okinawa Island, Yogi, Okinawa-city, 2-VII-1999, S. Inada [EUMJ, 3–2M, 1F]; Japan, Okinawa Island, Nishihara, Nakagami-gun, 1-VII-1999, T. Sasaki [EUMJ, 1F]; Japan, Okinawa Island, Nishihara, Nakagami-gun, 27-VII-1999, Teruya [EUMJ, 1F]; Japan, Okinawa Island, Kadena, Nakagami-gun, 9-VII-1999, N. Kawauchi [EUMJ, 1M]; Japan, Okinawa Island, Nakahusuku, Nakagami-gun, 27-VII-1999, T. Sasaki [EUMJ, 14M]; Japan, Okinawa Island, Kanekodan, Gushikawa-city, 30-VI-1999, S. Inada, Melia azedarach var. subtripinnata [EUMJ, 6–5M, F]; Japan, Okinawa Island, Kojya, Okinawa-city, 3-VII-1999, S. Inada, Melia azedarach var. subtripinnata [EUMJ, 5–3M, 2F]; Japan, Okinawa Island, Miyasato, Gushikawa-city, 15-V-1995, T. Matsumura

[EUMJ, 1M]; Japan, Okinawa Island, Nashiro, Itoman-city, 30-VII-1999, S. Inada [EUMJ, 1M]; Japan, Okinawa Island, Tamagusuku, Shimajiri-gun, 26-VII-1999, T. Sasaki [EUMJ, 1F]; Japan, Okinawa Island, Okubi, Kunigami-gun, 21-VII-1999, Teruya [EUMJ, 1M].

A. malasiaca tokunoshimana **Samuelson (1965)**: Japan, Amami Group, Tokunoshima, Mikyo, 200m, July 27, 1963, J. L. Gressitt, Coll. [BPBM, holotype].

A. ogasawaraensis **Makihara (1976)**: Japan, Ogasawara Isls., 2, VI, 1915, M. Suzuki, leg., [KUEC, holotype].

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BOOK REVIEWS

Ground Beetles and Wrinkled Bark Beetles of South Carolina (Coleoptera: Geadephaga: Carabidae and Rhysodidae). By J. C. Ciegler. 2000. Biota of South Carolina Vol. 1. Clemson University, Clemson, S. C. vi + 149 pp. ISBN 0-615-11426-1. Price: $20.00, to be ordered from: Public Service Bulletin Room, 82 Poole Agricultural Center, Clemson University, Clemson, S. C. 29634-0311; OR, on the Worldwide Web, http://cufan.clemson.edu/olos/

This volume, with attractive, bicolored green, soft covers, is 8.5 × 11 in., with the easily read text in two columns. On the front cover is a color photograph of a living individual of the large *Galerita bicolor* Drury, one of the more elegant carabid residents of eastern United States.

The purpose of this publication is to provide the means of identifying the species of Geadephaga known to live in South Carolina. Treated are 479 species arranged in 103 genera, 38 tribes, and two families. The sequence of tribes and genera is taxonomic, based on the catalogue of Bousquet and Larochelle (1993). Within each genus, species are arranged alphabetically, by specific epithet.

The contained information is easily accessible. A table of contents to supraspecific taxa, an index to all taxa, and names of taxa as titles in boldface, facilitate locating information. Methods employed in preparation of text and illustrations, and sources of previously published information are set out clearly in the Introduction, and a Literature Cited section of 98 references is useful in finding additional publications relevant to identification of Carabidae and Rhysodidae. A three page Glossary defines 184 morphological terms used in keys and taxonomic descriptions. Appendix A lists alphabetically all localities referred to in the text, and provides for each locality the county and physiographic region in which it occurs; maps are provided of the physiographic regions and counties. Appendix B lists alphabetically by genus and species the new state records reported. Numerous accurately labelled figures illustrate structural features referred to in keys and descriptions. The vitally important key to carabid genera (the best available in North American treatments of this family), is based on profusely illustrated features easily observed with a good microscope.

A key to suborders of Coleoptera and to families of Adephaga makes it possible for the user to ensure that an adult beetle in hand, collected in the southeast, is, or is not, a geadephagan. In addition to the keys to genera of Carabidae and Rhysodidae, keys to species are provided for each genus represented in South Carolina by more than one species. The source of each key is specified with the phrase "adapted from," followed by a bibliographical citation.

The text is modelled after those of Blatchley (1910) and Downie and Arnett (1996). For each tribe a common name is given along with a brief description. Each genus is characterized both morphologically and ecologically, and, where needed, synonyms are noted. Each species treatment includes: citation of original description; a short, non-comparative description with range of overall length (in mm.); and a few salient external character states contributing to ease of recognition; distribution records; and months of collection of specimens.

Although this publication is excellent overall, some shortcomings are evident. Because of the way it is bound, the book does not lie flat, and is kept open at a desired page only with the aid of a fairly heavy weight. Many illustrations do not give an accurate impression of the habitus of the beetle species to which the figures refer. The number of species and subspecies of Carabidae known from South Carolina is given as 479 (p. 20). But this number includes the four species of rhysodids; thus, the correct number of carabid taxa is 475. The descriptions, though comparable to one another in the information provided, are not comparative, so one might be confused more readily than otherwise about the identity of markedly similar species. It is especially important to make such comparisons when the species treatments are arranged alphabetically by specific epithet, rather than taxonomically or phylogenetically. The latter systems place in juxtaposition those species which are most similar to one another, thus facilitating their comparison. No reference is made to genitalic features, which have proven so useful in distinguishing among species that are markedly similar to one another in external features. But mitigating this reservation is the fact that, based on adults, most carabid species can be identified using only external features. The value of this volume to ecologists and evolutionary biologists, and thus potential sales, could have been increased with even an elementary analysis of species distributions in terms of physiographic region, habitat, and wing dimorphism.

Although its focus is on the geadephagans of one state in southeastern United States, this publication may be used successfully to identify most such species in adjacent states. Thus, it is a valuable addition to the web of faunal works treating North American geadephagans, including Bell (1970), Downie and Arnett (1996), Hatch (1953), Kavanaugh (1992), Lindroth (1961–1969), and a string of regional treatments of tiger beetles, such as Knisley and Schultz (1997) and Leonard and Bell (1999). Important gaps in the map are absence of faunal treatments of the geadephagans of the southwestern United States, especially of California with its strikingly precinctive and varied species assemblage. Jan Ciegler's work would be an excellent model for anyone interested in filling these gaps.

Because of its overarching clarity, this volume may be used to good advantage by both beginning and highly experienced coleopterists, as well as by others who need to be able to identify southeastern geadephagans. Because it is the first of a planned "Biota of South Carolina", we may assume that similar treatments of other insect taxa will follow. If, as seems likely, publications of this type and quality have the potential to stimulate interest in particular taxa, we can expect to see a crop of young insect taxonomists and taxon-oriented ecologists emerging from the southeast.

The reviewer extends his congratulations and appreciation to author and editors for their efforts and care in development and production of this exemplary "*Ground Beetles and Wrinkled Bark Beetles of South Carolina.*"

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Dragonflies of North America. Revised Edition. James G. Needham, Minter J. Westfall, Jr., and Michael L. May. 2000. Scientific Publishers, Gainesville, FL. xvi + 940 pp., 561 figs., 24 color plates (7 × 10 in). $125.00/cloth. ISBN 0-945417-94-2.

Dragonflies (Order: Odonata, suborder: Anisoptera) are arguably one of the most popular of North American insects. Their large size and fascinating habits have earned them the appellation birdwatcher's insects. Members of this order are also considered indicator organisms of healthy aquatic ecosystems. Thus, there has been a need for an authoritative manual from which to identify our dragonflies. This need was fulfilled somewhat when J. G. Needham and H. B. Heywood's *A handbook of the dragonflies of North America* appeared in 1929. That work was considered imperfect on many counts and was out of print when the first of an anticipated two-volume work appeared in 1955, *The Dragonflies of North America* by J. G. Needham and M. J. Westfall. The "manual," as it was often called, earned a place on every entomologist's bookshelf and was for over 40 years the only work with which to identify North American Anisoptera. The second volume covering the damselflies (*Damselflies of North America* by Minter J. Westfall, Jr., and Michael L. May) was not published until 1996. The 1955 manual was reprinted at least two times but finally went out of print just before the Zygoptera manual appeared.

Weighing in at about 4½ pounds, the new manual is a worthy successor to the 1955 volume. It will not disappoint. The two latter authors (J. Needham died in 1957) have stated that the new volume is not a revision but an update of the original edition. For those who believe that all of our Anisoptera have been described, consider that 54 species, including many newly described ones, have been added to the North American list since 1955. That's an addition of just over one species per year.

The organization of the new volume follows that of the old. Part one introduces dragonflies in general. This section contains morphological and ecological notes on the suborder. The text is generally that of the older version with up-to-date changes. Westfall and May mention in a footnote (p. 17) that the pretracheation hypothesis, so stubbornly advocated by Needham, is rejected by most odonatists. Disappointingly, the authors continue to use the old Comstock-Needham venation system, although they mention the newer versions currently available. I understand the difficulty of changing the vein terminology throughout the text to reflect a more modern nomenclature. But this book will, I fear, continue to introduce newcomers to a system that is not much in use by odonatists today. I would have preferred a table showing the homologies of various wing terminologies.

An updated version of preservation techniques, largely reprinted from the earlier 1996 Zygoptera volume, includes current methods of preparation including steeping specimens in acetone. It includes addresses and websites for suppliers of specialized 3″ × 5″ Odonata envelopes. With ever-increasing urbanization and habitat destruction, some naturalists are concerned about collecting activities. A short section on conservation and concerns addressing the collection of specimens might have been a worthy addition.

Part one includes a checklist of all 350 species from the United States, the Greater Antilles, and the border states of northern Mexico. Common names appear in the checklist, in each species account, and in a separate common name index. This will allow persons who prefer to use common names to identify and associate their specimens with scientific names. Usage follows the recent checklist by Paulson and Dunkle (1999 [not 1996 as cited] *A checklist of North American Odonata including English name terminology, type locality, and distribution.* Slater Museum of Natural History, University of Puget Sound Occasional Paper 56: 1–86). A map showing the biotic provinces of Dice (1943) is repeated at the end of the book on page 842.

The original 1955 manual had only two colored illustrations as a frontispiece. These were reprints from Needham's 1951 article (*Dragonflies—rainbows on the wing.* National Geographic Magazine 100(2): 215–229). The present volume has 24 colored plates between parts 1 and 2. The first 14 are painted illustrations by Dr. Larry Zettler of the bodies (mostly lateral view) of many members of the Aeshnidae, Gomphidae, Cordulegastridae, and Corduliidae. Each plate consists of about a dozen species. The renditions are generally excellent including coloration of the compound eyes in life. They should allow the user to see subtle differences among members of these groups, whose body coloration generally tends to be similar. However, reproductions of some of the illustrations are too purple, as can be seen in *Aeshna multicolor,* which has light blue eyes in life, and *Progomphus borealis,* whose thorax is gray.

Plates 15–24 are photos of live specimens. Each plate has about eight photos. Reproduction is generally good, though, as in the 1996 volume on Zygoptera, I found the photos to be a little washed out compared to their originals. The color plate section is a real plus, showing the diversity of perching habits of several families. Inclusion of the page number for each species account after each species legend would have allowed users to more easily flip from illustration to description.

Part two is the real meat of the book. The descriptions of the 350 species enable users to determine their material. All keys to adults and larvae have been rewritten and supporting illustrations for every species are provided. The first edition of the manual contained illustrations of the wing venation of a typical member of each genus (generally a species with hyaline wings), photographs of the all-important caudal appendages (expertly done by M. Westfall), and a photograph or drawing of the larva. The same photographs have reproduced well in this edition. In order to make this edition more up-to-date, many illustrations of important characters have been added. Most new shaded illustrations of corporal characters are by Elyse O'Grady. The renderings are excellent but the apparent size reduction of some (e.g., Figs. 236, 489, 542) make interpretation of some characters difficult. Illustrations of wing venation of two genera, *Gomphus* and *Cordulegaster,* have been added under respective generic accounts. The authors have borrowed illustrations from other sources for those species not illustrated in the original edition. There are no larval diagnoses at the species level other than in the keys.

Readers will find that the greatest changes in this volume are in the keys. Many have been extensively rewritten and include many new illustrations. Greatest changes occur in the keys to the family Gomphidae, and the genera *Erpetogomphus, Dythemis,* *Macrothemis,* and *Sympetrum.* Some large genera (≥ 10 species) include separate keys to each sex (e.g., *Aeshna, Erpetogomphus, Gomphus* (*Gomphus*), *Somatochlora*) but not for others (e.g., *Arigomphus, Gomphus* (*Gomphurus*), *Ophiogomphus, Stylurus, Erythrodiplax, Libellula, Sympetrum*). Key characters are usually supported by diagnostic illustrations, allowing easier identification of adults and larvae than the previous edition. The character tables for genera and species from the original edition have not been included here because they "contain . . . so many inaccuracies that bringing them up to date would have required a major additional revision". One might add that they take up too much space, although some users will miss them.

Each species treatment contains the common name (at the right margin), a brief synonymy, range of statistics on size, description, and distribution by states and dates. Though almost all species are illustrated and the keys refer to many figures, the species treatments do not refer to any figures or illustrations except the colored plates.

The sequence of families follows phylogeny, with Aeshnidae preceding Gomphidae, followed by Cordulegastridae. In each family, genera and species are arranged alphabetically. The authors have taken a generally conservative approach to taxonomy. They acknowledge contentious groups and provide references for those wishing to explore controversies. For example, *Cordulegaster* is used for our eight species instead of the six genera recognized by Lohmann; and *Epicordulia* and *Tetragoneuria* are used instead of *Epitheca.* Subgenera are always a thorny issue and their use here is no exception. Except in the large genus *Gomphus* (with subgenera *Gomphurus, Gomphus,* and *Hylogomphus*), subgenera are not used. Mention is made of proposed subgenera for *Ophiogomphus, Cordulegaster, Neurocordulia,* and *Sympetrum,* but not for *Aeshna* or *Erpetogomphus.*

In a book such as this, it is probably better to follow latest published opinion concerning questionable taxa at the species level and to state where some authorities disagree. The authors acknowledge some problematic taxa (e.g., *Macromia wabashensis, Sympetrum janae*), but I question whether this volume is the place to describe a new species (*Erythrodiplax bromeliicola* Westfall) especially because it is diagnosed only in the key to species. The elevation of the southwestern species formally known as *Erythrodiplax connata* to a separate species (*E. basifusca*), though possibly correct, has not been formally published. It might have been better to continue using *E. connata,* stating that some authors believe it is a distinct species.

The use of subspecies is conjectural amongst odonatists. Several are included in this book, but treatment is inconsistent. A brief diagnosis is made of some (*Aeshna interrupta interna, A. i. lineata, Ophiogomphus incurvatus alleghaniensis, O. severus montanus, Cordulegaster dorsalis deserticola, C. obliqua fasciata, Macromia illinoiensis georgina, Perithemis tenera seminole, Sympetrum occidentale californicum, S. o. fasciatum*). But others (*Gomphus* (*Gomphurus*) *fraternus manitobanus, Ophiogomphus mainensis fastigiatus, Erythrodiplax berenice naeva*) are simply listed under the species heading with no comment.

One serious error carried over from the 1955 Manual will result in not allowing for the correct placement of larvae of *Pantala.* On page 768, *Pantala* are placed with those genera which have no dorsal hooks. They have very definite dorsal hooks on abdominal segments 2–4, but these are often undetected because they are hidden by the wing pads. *Pantala* will not key correctly in the Libellulinae generic key (page 606, couplet 7) if the user notices the dorsal hooks.

The volume ends with a regional area map of North America with delimiting faunal regions. A regional species list for all 350 species is followed by a glossary. One of the greatest merits of this book is the inclusion of a detailed bibliography covering 28 pages. No bibliography was provided in the original 1955 edition. A detailed index listing names in boldface indicating valid taxa concludes the work. Any particular species will be found alphabetically not only under the species epithet, but also alphabetically under its genus. All page numbers are also listed with the page number in bold face referencing the main entry. This was a thoughtful consideration, allowing the user to easily go to the species description rather than having to wade through sequential series of page numbers.

In summary, the present volume represents a most worthy successor to the old 1955 edition. It is obvious that Westfall and May spent much time and care updating the 1955 version, and entomologists worldwide are the lucky recipients. The book is well edited, the binding excellent, and pages lie flat when opened. It will be of interest not only to odonatists and entomologists in general, but to aquatic ecologists, biologists, and ecological consultants interested in this fascinating group of aquatic insects.

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Diversity and Distribution of the Mayflies (Ephemeroptera) of Illinois, Indiana, Kentucky, Michigan, Ohio, and Wisconsin, by R. Patrick Randolph and W. Patrick McCafferty. 1998. Ohio Biological Survey Bulletin New Series, Volume 13, Number 1. vii + 188 pp. Softbound, 8.5 × 11 in. ISBN 0-86727-131-0. $30.00 + $3.00 shipping. Available from the Ohio Biological Survey, 1315 Kinnear Road, Columbus, Ohio 43212-1157 U.S.A. Phone (614) 292-9645, email fate.1@osu.edu.

The ability to identify and describe the distribution of species, the most basic of biological skills (Pimm and Lawton 1998), is greatly hampered by a shortage of taxonomists, facilities and funding (Wilson 2000). A lamentable situation, given the dispatch with which we are losing species.

Mayflies (Ephemeroptera) have been studied in the United States for nearly 200 years, yet simple, basic information on the diversity and distribution of species is sorely lacking. Efforts to provide this type of information have usually taken a political approach, with studies conducted on a state-by-state basis, such as Burian and Gibbs (1991) for Maine, Burks (1953) for Illinois, and Berner and Pescador (1988) for Florida. While mayflies do not respect political boundaries, state funding agencies do. Also, given the aforementioned limitations by Wilson (2000), it is often a more practical approach.

Rather than focus on the diversity and distribution of mayflies in just one state, Randolph and McCafferty examined six midwestern states: Illinois, Indiana, Kentucky, Michigan, Ohio and Wisconsin. This region includes six major physiographic provinces and three primary North American drainages. They accomplished this feat by making extensive use of published literature and studying recent collections.

The authors had two goals: the first, and obvious one, was to explain the diversity and distribution patterns of mayflies in this six state area.

The "Species Accounts" section, which takes up the bulk of the publication, provides detailed information about each of the 214 species (21 families) in this region. It is organized alphabetically by family, genus and species. For each species, previous records (county and stream) are indicated, drainage distribution identified, and a remarks section provided. New state and county records are also indicated. For new state records (n = 179), full collecting records are provided. Less information is listed for new county records (n = 2,529). Depositories are identified for specimens representing new records. Errors in published records are also indicated.

A map of the six state region, with counties identified, is provided. This map (less the county names) is provided near each species account, and the counties where a species has been collected are clearly marked. This format makes it much easier to appreciate the pattern of distribution for each species.

Randolph and McCafferty also analyzed this distributional data for patterns. They conclude that water temperature regimes, stream gradient, and glacial history have shaped the distribution of mayflies in this region. Much of the data leading to this conclusion is summarized in a table for the 214 species. Also, twenty distributional patterns, based on physiographic processes, are identified.

A comparison of the similarity (Sorenson's coefficient) of the mayfly fauna among forty drainages was also made. The appendices contain a species list for each state and for each of the 40 drainage basins.

All of this is the good news. The bad news is that 18 species have questionable survivorship status within the study region and four species (*Acanthametropus pecatonica, Ephemerella argo, Serratella frisoni,* and *Anepeorus simplex*) are probably threatened nationally. Randolph and McCafferty report that one species from the study region, *Pentagenia robusta* McDunnough, is extinct.

The authors' second goal was to produce a database that could be used as a prototype for future studies. Researchers who plan to do similar studies would do well to emulate Randolph and McCafferty's design. A similar report format is being used at the "Mayflies of the United States" web site (Kondratieff 2000).

This publication will be valuable to anyone who has an interest in the biodiversity or biogeography of mayflies, particularly in this region. The species accounts will make it easy to determine whether new collections represent new county or state records. The authors make the latter more likely by suggesting interesting areas to explore. In fact, they even provide a map identifying counties in this region for which no mayfly records are reported.

One might want to check with the Ohio Biological Survey before ordering a copy—the copy I reviewed had a sewn binding, but I have seen this publication with a spiral binding, too.

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DESCRIPTION, BIOLOGY, AND KARYOTYPE OF A NEW *PSILOCHALCIS* KIEFFER (HYMENOPTERA: CHALCIDIDAE) FROM INDIANMEAL MOTH PUPAE (LEPIDOPTERA: PYRALIDAE) ASSOCIATED WITH CULLED FIGS

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Abstract.—***Psilochalcis brevialata*** **Grissell and Johnson, new species**, is described and illustrated based on specimens from a laboratory culture reared on *Plodia interpunctella* (Hübner) pupae. This species, isolated from laboratory-reared *P. interpunctella* placed at a culled fig warehouse in central California, is the first *Psilochalcis* associated with stored product pyralids. In the laboratory, *P. brevialata* also sucessfully parasitized *Cadra figulilella* (Gregson), *C. cautella* (Walker), *Ephestia elutella* (Hübner) and *Amyelois transitella* (Walker). The karyotype of *P. brevialata* showed a haploid chromosome number (n) of 6, the highest n value known for the family Chalcididae. Female *P. brevialata* had relatively long reproductive lives of 39.3 days, producing an average of 3.3 progeny/day for a total of 128.7 progeny per female.

Key Words: Hymenoptera, Chalcididae, *Psilochalcis brevialata,* new species, Pyralidae, pupae

A review of the hymenopterous parasites of stored product insects (Gordh and Hartman 1991) included only two chalcidid species: *Antrocephalus aethiopicus* Masi and *A. mahensis* Masi, both parasitoids of *Corcyra cephalonica* (Stainton) (Lepidoptera: Pyralidae). No *Psilochalcis* species has previously been recovered from stored product pyralids, and few host records are known for the genus (Bouček 1992). Grissell and Schauff (1981) summarized the then known hosts, which consisted of two pyralid species in the Old World and a pyralid and gelechiid species in the New World. Narendran (1989) reported as a host a species of the family Oecophoridae from India. No biological observations have been made on any species, but in the few reared instances, adult wasps emerged from the pupal stage of its host moth.

Psilochalcis (as *Invreia*), originally considered an Old World genus, was first reported in the New World based upon three species described from Oklahoma and Texas (Grissell and Schauff 1981). A fourth species from Arizona and Hawaii was added later (Bouček 1984). Bouček (1992) reported that less than 20 species of *Psilochalcis* were known from the western hemisphere. Bouček and Halstead (1997) recently stated that at least 10 undescribed species occurred in the Nearctic Region.

As part of a project to integrate natural enemies into non-chemical control programs for postharvest dried fruits and nuts, a survey was made of the insects present at a culled fig warehouse in Fresno, California (Johnson et al. 2000). Because culled, substandard figs are judged unsuitable for human consumption, little or no attempt is made to control pests within the warehouse. Consequently, large pyralid populations develop in these figs, which in turn support various parasitoid populations. During the course of the survey, we discovered an undescribed species of *Psilochalcis* (Hymenoptera: Chalcididae) parasitizing pupae of the Indianmeal moth, *Plodia interpunctella* (Hübner) (Lepidoptera: Pyralidae). In this paper, we describe the new species *Psilochalcis brevialata* Grissell and Johnson and include observations on its culture, biology and karyotype.

METHODS AND MATERIALS

Maintenance of laboratory culture.—We began a laboratory culture of *Psilochalcis* using material reared from traps baited with host pupae placed at the culled fig warehouse in November 1994 and June 1995 (Johnson et al. 2000). Host pupae were from a laboratory culture of Indianmeal moth reared in glass jars (4l) with about 350 g of wheat bran diet (Tebbets et al. 1978). Corrugated cardboard strips (2.5 cm × 2 m) were placed on the diet surface, coiled along the inner wall of the jar, to serve as pupation sites for Indianmeal moth larvae. Strips with 1–3 day old pupae were transferred to clean jars, along with a handful of diet containing mature larvae. About 1 g of honey was smeared along the inside wall of the jar before adding 50–100 adult *Psilochalcis.*

Psilochalcis rearing jars were kept in environmental chambers at 27°C, 60% RH, and a photoperiod of 14:10 (L:D) h. Moths from unparasitized hosts were removed as quickly as possible, but not before some were able to lay eggs. Because these eggs produced larvae capable of feeding on parasitized host pupae, 1 week after the addition of adult *Psilochalcis,* pupae were removed from the pupation strips and examined for evidence of parasitization (melanized spots). Parasitized pupae were placed in plastic Petri dishes (90 × 15 mm) lined with filter paper. A small amount of honey was smeared on the underside of the lid. Dishes were held under rearing conditions until emergence of adult *Psilochalcis.* These adults, along with any remaining in the jars, were used to continue the culture. Specimens from several generations of the laboratory colony were killed in 70% ETOH and sent to E. Grissell for taxonomic study.

Karyotype.—Parasitized hosts from the laboratory culture were sent to V. Gokhman for karyotype determination. Chromosome preparations were obtained from cerebral ganglia of prepupae according to the technique of Imai et al. (1988). Chromosomes of three males and three females of *P. brevialata* were studied. For making chromosome measurements, ten haploid metaphase plates were scanned directly from the preparations using an optic microscope fitted with a static TV camera connected to a personal computer equipped with the image analysis program ImageExpert® version 1.0. Scanned images were measured using Adobe Photoshop® version 3.0.5. Statistical analysis was performed with the help of STATISTICA® version 4.3.

Life history.—We obtained adult *Psilochalcis* of known age by placing individual parasitized host pupae in glass culture tubes (12 × 75 mm) closed with foam plugs. Within 24 hours of emergence, adult parasitoids were removed from the culture tubes and sexed. Single pairs of male and female wasps were placed in plastic Petri dishes (90 × 15 mm) lined with filter paper. A small amount of honey was smeared on the underside of each lid. Only pairs that were observed *in copulo* were used in the study. A total of 15 pairs were used. Ten 1- to 4-day old Indianmeal moth pupae in cocoons were added to each dish. After 24 hrs, pupae were removed, placed in plastic sample cups (30 ml), and held at 27°C, 60% RH, and a photoperiod of 14:10 (L:D) h for emergence of either moths or *Psilochalcis.* Host pupae were provided each day to each *Psilochalcis* pair until the death of the female. A similar test with 10 virgin females also was done.

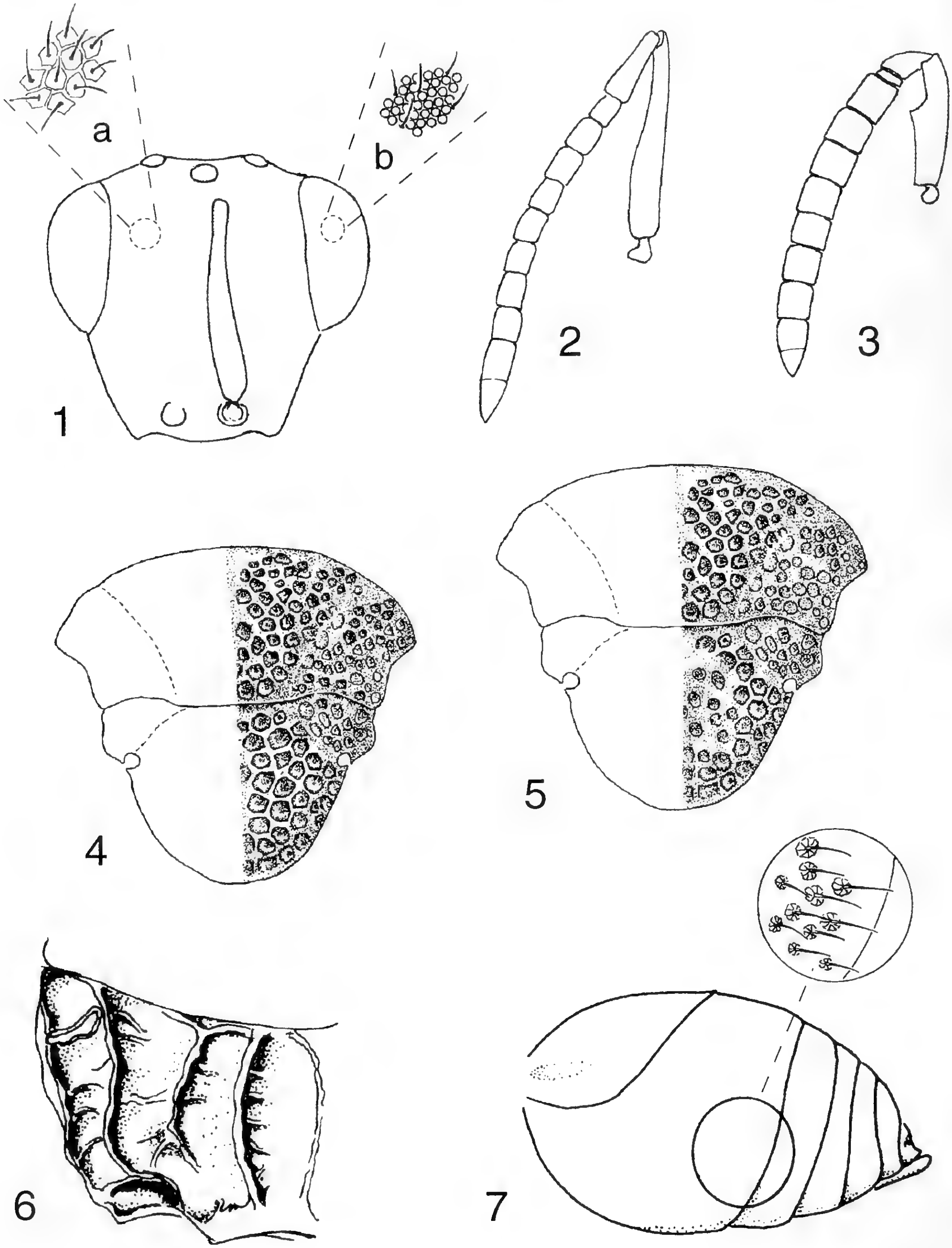
Potential host range.—Pupae from laboratory cultures of various postharvest Lepidoptera other than *P. interpunctella* were offered to recently emerged and mated *Psilochalcis* females held in plastic sample cups. After 24–72 hours, the pupae were removed and held at rearing conditions for emergence of either moths or *Psilochalcis*. A total of five pyralid species (Lepidoptera: Pyralidae) were tested: *Cadra figulilella* (Gregson), *C. cautella* (Walker), *Ephestia elutella* (Hübner), *Amyelois transitella* (Walker) and *Galleria mellonella* (Linnaeus). We also tested pupae of the codling moth, *Cydia pomonella* (Linnaeus) (Lepidoptera: Tortricidae).

RESULTS AND DISCUSSION

Psilochalcis brevialata Grissell and Johnson, new species

(Figs. 1–7)

Description.—Female length 3.0 to 4.0 mm (holotype 3.5 mm). Ratio head : mesosoma : metasoma : forewing ca. 1.5:5:5:6 (holotype 7:23:25:29). Black except the following yellow to dark reddish brown: tegula, tarsi, tibiae (except sometimes pro- and mesotibiae basally brown to black), metafemur at apex and base, metatrochanter, scape and flagellum (basal half of scape and apex of pedicel may be yellow). *Head:* Face (Fig. 1) wider than high (holotype 5:4), eye (Fig. lb) with sparse erect setae ca. 2 to 3 ommatidia in length, 1 to 1.5× own length apart; eye height less than least interocular distance (at vertex) (holotype 5:6), ratio lateral ocellus : ocellocular length : postocellar length ca. 1:1:4 (holotype 7:5:20), malar distance shorter than intermalar distance (holotype 7:8); upper face with contiguous punctures each with recurved silvery seta (Fig. 1 a); lower face laterad of scrobes rugose and covered with appressed dense silvery pubescence; scrobe nearly reaching venter of median ocellus, separated from it dorsally by about one ocellus diameter (an area covered with effaced sculpture); flagellum (Fig. 2) filiform, scape widest in basal ⅓, pedicel 2 to 3× longer than any funicular segment, slightly shorter than clava, which appears to be one-segmented (ratio in holotype beginning with scape 55:18:7:8:9:9:9:9:9:9:21); scape ca. 1.3× as long as eye height; pedicel 3× longer than greatest width (apical). *Mesosoma:* Ratio pronotum : mesoscutum : scutellum : propodeum ca. 3:4:4:3 (holotype same); pronotum, scutum, and scutellum with evenly spaced, nearly contiguous setigerous punctures except punctures on median area of scutellum vary from nearly contiguous (as for male, Fig. 4) to 1 to 2 diameters apart (Fig. 5), seta length 1 to 2× puncture diameters; interspaces reticulate-aciculate; midlobe of mesoscutum with punctures ca. ½ own diameter apart (especially posteriorly); scutellum medially with punctures less than own diameter apart (as in Fig. 5); mesepisternum with forecoxal depression not prolonged into flange ventrally; propodeum (Fig. 6) with complete well-developed submedian carina, prespiracular sulcus carinate laterally, an irregular diagonal carina joined from anterior of sublateral carina to inner posterior carina of prespiracular sulcus, with many transverse carinae between main longitudinal carinae; midfemur distally swollen, rounded ventrally, 3× wider distally than proximally; forewing 2–3× as long as wide (holotype 8:3), hyaline, ratio submarginal: marginal: stigmal veins ca. 9:1.5:1 (holotype 27:5:3), barely reaching apex of tergum 3 when folded flat. *Metasoma:* Elliptical in side view; tergum I reaching ca. 0.4× length of metasoma, epipygidium and ovipositor barely visible from above; tergum I anterolaterally with longitudinal elliptical depression which is mostly bare except for a dorsal line of several long overlapping setae with bases much closer together than length of seta, area ventrad of depression with numerous, short setae, tergum laterally polished, dorsally finely punctate to reticulate except posterior ⅕ of margin smooth and polished;



Figs. 1–7. *Psilochalcis brevialata.* 1, Face, female, insets show sculpture on upper frons (a) and eye setation (b). 2–3, Antenna (lateral view). 2, Female. 3, Male. 4–5, Mesonotum (dorsal view, setae not shown). 4, Male. 5, Female. 6. Propodeum (dorsal view), female. 7, Metasoma (lateral view), female, inset shows sculpture.

tergum II laterally covered with appressed silver setae each in minute, shallow depression, surrounded by small depressions ("petallike" arrangement, Fig. 7), entirely finely aciculate except semicircular dorsomedian area smooth; tergum III–VI with posterior margins rimmed with fine reticulation and 1 or 2 rows of silver setae.

Male length 2.3 to 3.5 mm. Color as for female except some orange areas on scape, tegula, and femora replaced with black. Scape (Fig. 3) subapically incised, with upward projecting denticle on outer margin; antennal ratio beginning with scape 32:10:2:10:9:9:9:9:9:9:18 (clava counted as one); scape subequal to eye height, pedicel ca. 1.5× longer than wide; funiculars evenly covered with short appressed silver setae arranged in 4 or 5 rows; sculpture and setae of mesosoma and metasoma same as for female except median area varies less, with punctures less than own diameter apart (Fig. 4).

Type material.—Holotype ♀, USA, California, Fresno County, Horticulture Crops Research Lab, 10-I-2000, J. Johnson, reared from culture of *Plodia interpunctella,* deposited in the National Museum of Natural History, Smithsonian Institution, Washington, DC. Paratype data same as holotype except as follows: 15 ♀ 29-XI-1999; 14 ♀, 8 ♂ 10-I-2000; 10 ♀ 12-IV-2000; 4 ♀, 7 ♂ XI-1999; 5 ♀, 5 ♂ V-1999, Johnson/Gill, from culled fig warehouse. Paratypes are deposited in the National Museum of Natural History, Smithsonian Institution, Washington, DC, the California Department of Food and Agriculture, Sacramento, the Canadian National Collection, Ottawa, Canada, and The Natural History Museum, London, U.K.

Etymology.—From *brevis* (short) and *alata* (wing), in reference to the shortened wing.

Variation.—Most variation in females is found in the coloration of the tegula, scape (basally), and pro- and mesolegs. These areas vary from dark red brown to bright orange yellow. The degree of sculpture on the median area of the scutellum also varies as described above. The males are fairly consistent in coloration and sculpture.

Host.—Originally reared from laboratory-reared *Plodia interpunctella* pupae. Natural hosts at the culled fig warehouse are believed to be *P. interpunctella* and *Cadra figulilella.*

Discussion.—Representatives of all described Nearctic species (including types) have been examined as a basis for recognizing *P. brevialata.* The species cannot be confused with *P. hespenheidei* Bouček, which forms its own distinct species group (species *sola*) as discussed by Bouček (1984). In the key to Nearctic species of *Psilochalcis* (as *Invreia*) by Grissell and Schauff (1981), females of *P. brevialata* would run to *P. usta* (Grissell and Schauff) and males to *P. deceptor* (Grissell and Schauff). The difficulty of defining *Psilochalcis brevialata* is that it has several unique character states as well a unique combination of character states that overlap the other Nearctic *Psilochalcis* species. For this reason we first discuss the defining characters of *P. brevialata* and then compare characters with the three species with which it might be confused.

The unique characters that distinguish *P. brevialata* from *P. usta, P.* deceptor, and *P. threa* (all Grissell and Schauff, 1981) are as follows. In *P. brevialata* the eye has erect setae that are 2 to 3 ommatidia diameters in length and are separated at the base by 1 to 1.5 times their own length. In *P. deceptor, P. threa,* and *P. usta* the eyes have setae scarcely 1 ommatidium in length and are separated by 2 to 3 times their own length. In *P. brevialata* the upper face has contiguous pits separated by carinate walls. *Psilochalcis deceptor* and *P. usta* have punctures with flat spaces between them which may be 0.5 to 1 times the width of a puncture; *P. threa* has area covered with rugulose sculpture. Similar sculpturing is also found on the mesoscutum and scutellum as well, though it is more defined in these areas and the interspaces tend to be

Fig. 8. Male (a) and female (b) karyotype of *Psilochalcis brevialata*. (scale bar indicates 10 μm).

slightly wider than on the face. In *P. deceptor* these areas are covered with evenly spaced punctures with polished flat spaces between them; *P. threa* is similar to *P. deceptor* but has reticulate spaces between punctures; *P. usta* has irregularly placed punctures with polished areas between them and the median area of the scutellum is highly polished without punctures. In females of *P. brevialata* the wings when folded flat over the metasoma (i.e., the normal condition) barely reach the apex of tergum 3. In *P. deceptor, P. threa,* and *P. usta* the wings reach or exceed the apex of the metasoma.

Additional diagnostic characters that help to distinguish *P. brevialata* from the other known species are as follows: in both sexes, *P. brevialata* has tergum 1 sculptured dorsally and polished laterally as in *P. usta*. In *P. deceptor* tergum 1 is polished entirely; *P. threa* is sculptured entirely. In *P. brevialata* the propodeum has well defined submedian, sublateral, and postspiracular carinae, with distinct glossy pits formed by transverse carinae as in *P. deceptor* and *P. usta*. In *P. threa* there are no transverse carinae and the entire propodeum is covered with granulate sculpture. Females of *P. brevialata* have the pedicel 3× longer than wide as in *threa* (5× in *P. deceptor*, 4× in *P. usta*). In males of *P. brevialata* the scape has a weakly developed denticle projecting slightly upward as in *P. deceptor*. In *P. threa* and *P. usta* it is well developed but points outward.

There is no indication that distributions of Old and New World species of *Psilochalcis* overlap. Although we have not examined every Old World species in the genus, we have checked Old World keys and discussions of taxa, and have found no reference to species of *Psilochalcis* (or its present synonyms) with shortened wings as found in *P. brevialata*. Included in our examination were the key to species known up to 1960 (Nikol'skaya 1960) and subsequent descriptions and transfers of species by Steffan (1962, 1976), Habu (1970), and Narendran (1989).

Karyotype (Figs. 8–9).—The haploid chromosome number (n) in this species is six, its karyotype containing four metacentric (M) and two submetacentric (SM) chromosomes (Fig. 8a). The arm number (NF^n) therefore equals 12. Similarly, for the diploid karyotype 2n = 12 (8M + 4SM) and NF = 24 (Fig. 8b).

In the karyotype of *P. brevialata* two long metacentrics are followed by a smaller chromosome of the same type, sometimes appearing as submetacentric due to a large segment of pericentromeric heterochromatin. Other chromosomes are obviously

Table 1. Relative length and centromeric index of chromosomes in *Psilochalcis brevialata*.

Chromosome	Relative Length	Centromeric Index
1	21.39 ± 0.88	47.22 ± 2.18
2	20.64 ± 0.86	44.79 ± 3.37
3	18.56 ± 1.27	42.48 ± 3.25
4	15.18 ± 0.73	46.47 ± 2.10
5	12.82 ± 1.05	28.49 ± 3.17
6	11.41 ± 0.45	26.38 ± 2.56

shorter than the preceding ones. They are represented by a medium-sized metacentric and two small submetacentric (sometimes close to subtelocentric) chromosomes. Relative lengths and centromeric indices of the chromosomes are given in Table 1, and the haploid ideogram is shown in Fig. 9.

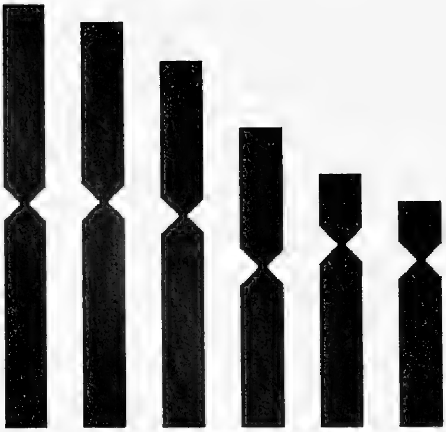


Fig. 9. Haploid ideogram of *Psilochalcis brevialata.*

Karyotypes of four members of the family Chalcididae are known (Gokhman & Quicke 1995), but none of them has the haploid chromosome number of 6 found in *P. brevialata* (Table 2). However, two smaller submetacentrics in this species have very short arms, which may indicate that its n value was probably derived from the most usual number in the family, n = 5, by chromosomal fission.

Description of original habitat.—The culled fig warehouse was located in Fresno, California, in an area of light industry and residences. The facility consisted of an enclosed, unheated warehouse and a covered, open-sided, raised dock. Figs were stored in wooden bins in the warehouse or on the dock until they could be dumped onto a large pile in the center of the dock. Culled figs were brought in from throughout the fig-producing region of central California beginning in August and continuing through October. Sale and distribution of the figs as cattle feed began soon after receipt and continued throughout the year. During summer months, water was often added to the fig mass in order to maintain a suitable moisture content. No insect controls were used, other than occasional insecticide applications along the perimeter of the warehouse for ant control. Common Lepidoptera found at the warehouse include several pyralids, particularly Indianmeal moth, raisin moth (*C. figulilella*), and navel orangeworm (*Amyelois transitella*). Although all three of these pyralids were brought into the warehouse in new figs, only Indianmeal moth actually reproduced within the warehouse environment. Other pyralid parasitoids commonly found at the warehouse included *Habrobracon hebetor* (Say) (Hymenoptera: Braconidae) and species of *Goniozus* Förster (Hymenoptera:

Table 2. Chromosome numbers of Chalcididae.

Species	n	2n	References
Brachymeria intermedia (Nees)	3	6	Hung 1986
B. lasus (Walker)	5	10	Hung 1986
B. ovata (Say)	5	10	Hung 1986
Dirhinus himalayanus Westwood	5	10	Amalin et al. 1988
Psilochalcis brevialata Grissell and Johnson	6	12	present paper

Bethylidae), both external larval parasites, *Venturia canescens* (Gravenhorst) (Hymenoptera: Ichneumonidae) an internal larval parasite, and *Mesostenus gracilis* (Cresson) (Hymenoptera: Ichneumonidae), an external prepupal and pupal parasite.

Behavioral observations.—Large numbers of *Psilochalcis* adults were recovered from yellow sticky traps hung about 1 m off the ground at the culled fig warehouse in late summer and early fall (Johnson et al. 2000). Adult *Psilochalcis* were also seen flying at the culled fig warehouse in warm weather. Although they were capable of flight, *Psilochalcis* reared in the laboratory did not readily do so. Adults flew most often when warmed in direct sunlight. When disturbed, adults would often drop to the substrate, legs tucked in close to the body, and remain motionless.

Adult female *Psilochalcis* used their antennae to examine empty host cocoons and host pupae. Females used their mandibles to tear through cocoons to reach host pupae, and were rarely seen to sting their hosts through cocoons. Females showed no obvious preference for any location on the host, and seemed to sting whichever portion of the host was accessible. Dark, sclerotized spots on host pupae were evident within 24 h of stinging. We found evidence of as many as 20 stings on an individual host.

The ovipositional behavior of 40 females was observed. Females normally examined hosts for several seconds or even minutes before beginning to sting. A female in the process of stinging a host could be identified by a characteristic, vigorous twisting of the head. This head twist was also often noticed as the female withdrew her ovipositor. The length of time for a female to sting a host varied considerably, from 3–32 minutes, averaging about 13 minutes. Females appeared to host feed at the exudates from recent stings. Females were likely to sting the same host several times in succession, even when other host pupae were available. Single parasite eggs were normally found in dissected hosts, even those that had been stung several times. Several eggs (2–5) were found in single hosts exposed to one female in less than 1% of those dissected.

In spite of evidence of single hosts receiving multiple stings, no more than one wasp was seen to emerge from a single host. Developing parasites did not entirely consume their host; about 50–70% of the host's body mass remained after parasite emergence. Adult *Psilochalcis* normally emerged from the anterior half of the host, but the exact location varied considerably.

Host preference.—The laboratory culture of *Psilochalcis brevialata* was established from laboratory-reared Indianmeal moth pupae that had been placed at the culled fig warehouse and parasitized. Shortly after establishment of the culture on laboratory-reared Indianmeal moth, *P. brevialata* females successfully parasitized pupae from laboratory cultures of *Cadra figulilella, C. cautella, Ephestia elutella,* and *Amyelois transitella,* all pyralids. Females did not successfully parasitize pupae of laboratory-reared *Galleria mellonella* or *Cydia pomonella.* After *P. brevialata* had been in culture on Indianmeal moth for about one year, females still readily parasitized *C. figulilella* and *E. elutella,* but rejected *A. transitella.*

During weekly sampling over a two-year period, 4,824 *P. brevialata* were recovered from yellow, sticky flight traps at the culled fig warehouse (Johnson et al. 2000). Large numbers of postharvest pyralids were also recovered from pheromone traps at the warehouse. Indianmeal moth was the most prevalent of these, and commonly infested new figs as well as reproduced within the warehouse environment. New figs also were heavily infested with *C. figulilella,* a common field pest of drying fruits such as raisins and figs. Although *P. brevialata* was never reared from field-collected hosts, we believe that the recovery of *P. brevialata* from laboratory-reared Indianmeal moth, and the ease with which it is reared on Indianmeal moth, *Cadra,* and *Ephestia* species indicate that these are its natural hosts, at least within the culled fig warehouse.

Table 3. Life history parameters for 15 mated pairs and 10 unmated females of *Psilochalcis brevialata.*

Parameter	Mean ± SE	Max	Min
	Mated Pairs		
Female lifespan (days)	43.3 ± 3.38	67	20
Male lifespan (days)	35.4 ± 3.19	64	19
Female reproductive lifespan (days)	39.3 ± 2.39	53	23
Total progeny	128.7 ± 11.70	201	32
Female progeny	69.0 ± 6.00	109	25
Male progeny	59.7 ± 7.30	109	7
Sex ratio (female/male)	1.4 ± 0.20	3.57	0.53
Progeny development period (days)	24.5 ± 0.31	26	22
Female development period (days)	25.8 ± 0.42	29	24
Male development period (days)	24.3 ± 0.54	29	21
	Unmated Females		
Female lifespan (days)	37.3 ± 6.77	84	13
Female reproductive lifespan (days)	26.4 ± 4.76	40	5
Progeny (all male)	39.2 ± 7.02	64	6

It is uncertain how *P. brevialata* became established at the culled fig warehouse. Most likely, it was brought in with parasitized hosts in new figs. As such, it could have originally been from any of the orchards contributing figs to the warehouse, in either Indianmeal moth, *C. figulilella,* or *A. transitella* pupae. An alternate explanation is that *P. brevialata* was present in existing stored product pyralid populations. Several other food-processing plants and residences, both known sources for Indianmeal moths, are in the same area as the culled fig warehouse.

Life history.—Results of the life history studies are summarized in Table 3. On average, mated females lived nearly a week longer (43.3 days) than unmated females (37.3 days), although the longest lived female in the study (84 days) was unmated. Males lived about 2 days less (35.4 days) than unmated females. The reproductive lifespan for mated females (39.3 days) was nearly 2 weeks longer than for unmated females (26.4 days). Mated females produced an average of 128.7 progeny, more than 3 times the number of progeny produced by unmated females (39.2). The sex ratio for progeny from mated females was slightly skewed (1.4) towards females. Unmated females produced only male progeny. Overall, mean development time at 27°C for progeny of mated females averaged 24.5 days, with females (25.8 days) taking 1–2 days longer to develop than males (24.3 days). Developmental period was not measured for progeny of unmated females.

The average number of progeny produced per day for mated females is shown in Fig. 10. Very few host pupae were successfully parasitized the first day after adult emergence, but the number rose sharply to a peak 4–11 days after emergence. After about 11 days, the number of progeny produced each day slowly declined, with females producing no progeny the last 2–4 days of their lives. Females were never able to parasitize all 10 available hosts in a single day. Although the rate of parasitization per day seems low, the relatively long reproductive life of the females allows production of more than 120 offspring per female.

The highest number of *P. brevialata* was recovered from flight traps at the culled fig warehouse during the warm summer months, when other pyralid parasitoids such as *H. hebetor, V. canescens, M. gracilis,* or *Goniozus* spp. were far less active (Johnson et al. 2000). Other laboratory observations indicate that *P. brevialata* is relatively heat tolerant. *Psilochalcis brevialata* may there-

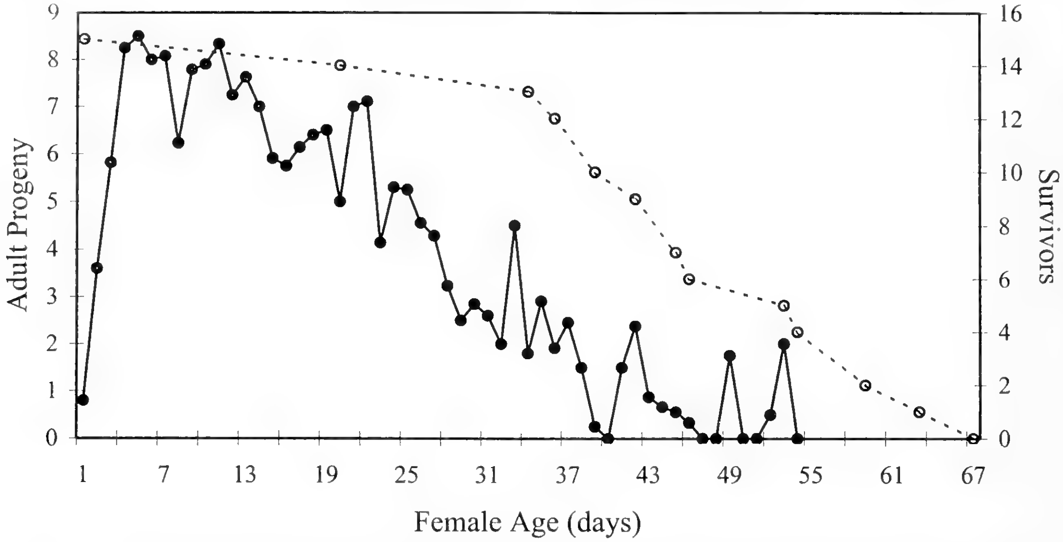


Fig. 10. Age specific fecundity (average adult progeny production per day of female life) of *Psilochalcis brevialata.*

fore prove to be a useful component of a biologically based control program for postharvest dried fruits and nuts.

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REVISED STATUS OF *ROLANDYLIS* GIBEAUX (LEPIDOPTERA: TORTRICIDAE: COCHYLINI), WITH DESCRIPTIONS OF TWO NEW SPECIES FROM NORTH AMERICA

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Abstract.—The genus *Rolandylis* Gibeaux is considered a valid genus (**revised status**) with three species based on the following autapomorphies: 1) maxillary palpus absent, 2) valve broad at base with an erect proximal costal process with spiculations, and 3) base of aedoeagus with winglike lateral projections. Two new species of *Rolandylis* from eastern United States are described, ***R. fusca*** and ***R. virilia*.** The type species of *Rolandylis, R. catalonica* Gibeaux, is a **new synonym** of *R. maiana* (Kearfott). The head and wing venation are illustrated, as well as the habitus and genitalia of all species. The genus is known from the United States, (Michigan, Illinois, Indiana, Missouri, Mississippi, Pennsylvania, New Hampshire, and Maine), Canada (Nova Scotia), and France. The phylogenetic relationships of *Rolandylis* within Nearctic Cochylini are discussed.

Key Words: revision, North America, goldenrod, *Solidago,* Asteraceae

The Nearctic Cochylini fauna is poorly known, and the generic placements of many species are suspect. Early generic classifications of the tribe were based on wing venation and some genitalic characters (Busck 1939). Busck's generic concepts were such that most species of Cochylini were assigned to the genus *Phalonia* Hübner. Razowski (1970, 1977) synonymized *Phalonia* with *Aethes* Billberg based on the examination of the type species of *Phalonia, Aethes tesserana* (Schiffermüller and Denis). Powell (1983) removed all species that had been placed in *Phalonia,* treating them as *incertae sedis.* I recently came across the genus *Rolandylis* Gibeaux, described for the single French species *R. catalonica* Gibeaux (Gibeaux 1985), which is synonymous with *Phalonia maiana* Kearfott, 1907 (considered *incertae sedis* by Powell (1983)). Razowski (1996) synonymized the genus *Rolandylis* with *Cochylis* Treitschke, thereby treating the type species, *R. catalonica,* as *Cochylis catalonica.* In his treatment of the Cochylini fauna of Canada, Razowski (1997) did not recognize *maiana* as conspecific with *R. catalonica,* nor did he place *maiana* in the genus *Cochylis,* but left it as *Phalonia maiana.* Much work is being done on the Cochylini fauna of the upper midwestern United States, and, to facilitate descriptions of new species from this area, this taxonomic problem is resolved and two new species are described.

A phylogeny of the genera of Nearctic Cochylini was presented by Pogue and Mickevich (1990, fig. 55). Eight trees were produced with the genus *Rolandylis* as *Clothoa* being a sister taxon to "*Nycthia*" (undescribed genus) in 4 trees, and as a sister taxon to "*Nycthia*" and *Cochylidia* Obraztsov, 1956 in a second set of 4 trees. Currently, *Rolandylis* contains 3 species, two species described here and *R. maiana* (Kearfott). The genus is known from the U.S. in Mississippi, in the midwest from Illinois, Indiana, Ohio, Missouri, and Texas, and in the east from Pennsylvania, New Jersey, and New Hampshire. *Rolandylis maiana* has also been recorded from Nova Scotia, Canada (Razowski 1997) and France (Gibeaux 1985).

Measurements within the descriptions are defined as follows. The supraocular index equals height of the head capsule above the compound eye divided by total height of head capsule (from top of epicranium to tip of subgenal process). Leg indices are a ratio between the femur and tibia, basitarsus, and tarsus. Legs were removed and descaled from the thorax. Measurements were made along the greatest length of these structures. Wing lengths and widths were measured to the nearest 0.1 mm using an ocular micrometer in a stereo dissecting microscope at 25×. Wing length is defined as the straight line distance from point of thoracic wing attachment to wing apex, including the fringe. Wing width is the distance from the costa to the posterior margin along the outer margin of the discal cell. Wing shape is expressed as a ratio of length to width.

Genitalia were prepared as outlined in Clarke (1941). A double stain was found most suitable for bringing out structural detail. The first stain was an aqueous solution of Chlorazol Black E, in which the specimen was left until the desired color was achieved. After thorough rinsing in water, the abdomen and attached genitalia were placed in a 2% aqueous solution of mercurochrome for 15 minutes. Chlorazol Black E stains membranous structures and mercurochrome stains sclerotized structures resulting in a useful contrast.

The following acronyms of institutions and private collections where material is housed were used: BMC—Bryant Mather collection, Jackson, Mississippi; JRH—J. R. Heitzman, Independence, Missouri; USNM—National Museum of Natural History, Smithsonian Institution, Washington, DC; UMSP—University of Minnesota, St. Paul, Minnesota.

Rolandylis Gibeaux, **revised status**

Rolandylis Gibeaux 1985: 348.

Type species: *Rolandylis catalonica* Gibeaux (= *R. maiana* (Kearfott)). By monotypy.

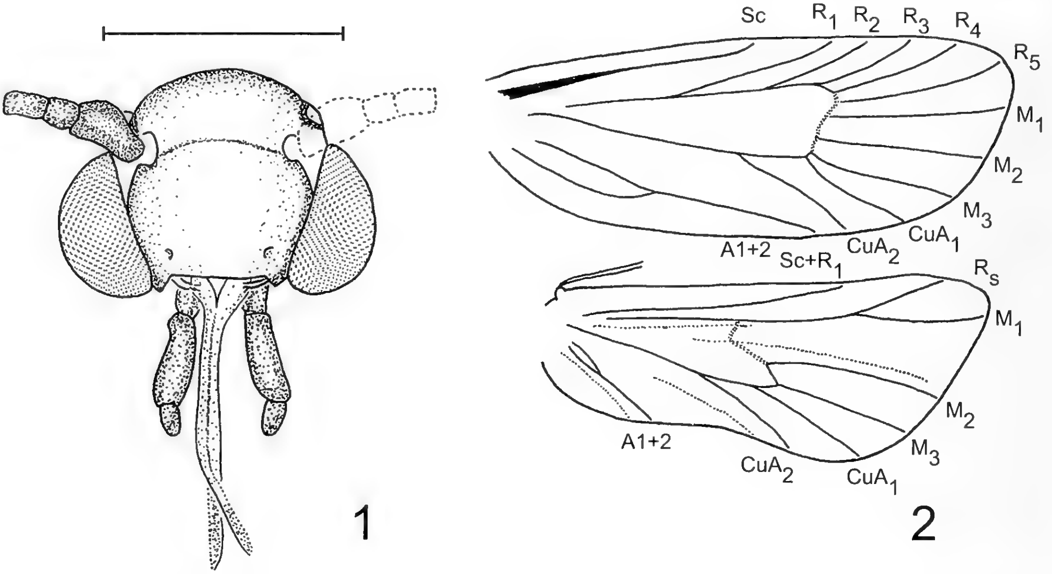
Clothoa Pogue 1990: 322 (in Pogue and Mickevich 1990) ***nomen nudum***.

Cochylis Treitschke; Razowski 1996: 134 (in part).

Diagnosis.—The most useful characters for separating Cochylini genera are structures of the male genitalia, especially in smaller non-descript species such as *Rolandylis*. Species of *Rolandylis* are superficially similar to other small species of *Lorita* Busck, *Cochylis,* and *Thyraylia* Walsingham. Genital dissections must be made for accurate identification. Autapomorphies defining *Rolandylis* are: 1) maxillary palpus absent, 2) valve broad at base with an erect proximal costal process with spiculations, and 3) base of aedoeagus with winglike lateral projections.

Description.—*Head:* Vestiture rough. Compound eye well developed. Supraocular index 0.39. Ocellus present. Antenna filiform, scaled dorsad, setose ventrad; 29–33 segments. Labial palpus porrect; scales of median segment with dorsal expansion greater than ventral; median segment equal to vertical eye diameter; apical segment exposed; apical segment 0.6× basal segment; median segment 2.1× basal segment, equal to vertical eye diameter, and length 3.1× width. Maxillary palpus absent.

Thorax: Posterior crest absent. Lateral scale tufts of metanotum flat and uniform with those of scutellum. Prothoracic leg with epiphysis 0.5 length of tibia. Mesothoracic tibia with a single pair of unequal sized apical spurs, longest 0.67 length of tibia. Metathoracic tibia with 2 pairs of unequal sized spurs, basal pair originating at 0.6 from tibial base, longest spur 0.33



Figs. 1–2. *Rolandylis fusca.* 1, Head, frontal. (Scale = 0.5 mm). 2, Wing venation.

length of tibia; apical pair at subapex, longest spur 0.33 length of tibia. All spurs with basal fenestra. Leg indices [femur : tibia : (basitarsus) tarsus] for prothoracic leg 1: 0.7:(0.6) 1.4; mesothoracic leg 1:0.9:(0.6) 1.1; metathoracic leg 1:1.6: (0.7) 1.4.

Forewing: Male length 3.4–4.5 mm; length 2.6–2.9× width, moderately broad. Female length 3.8–4.9 mm; length 2.7–2.9× width, moderately broad. Costa straight; apex round; termen straight. Sc less than 0.5 wing length. R_1 originating beyond middle of discal cell; R_2 nearer R_3 than R_1; R_5 ending at costa. M_3 and CuA_1 separate. CuA_2 originating at 0.67 length of discal cell. CuP absent. A1+2 stalked at 0.5 total length.

Hindwing: Male length 2.9–3.7 mm; length 2.6–3.0× maximum width, moderately broad. Female length 3.1–4.3 mm; length 2.8–3.1× maximum width, moderately broad to elongate. Costa straight; apex rounded; termen straight. Male costal fold 0.6 wing length; $Sc+R_1$ 0.67 length of M_1. Rs and M_1 stalked.

Male genitalia: Uncus absent; socii triangulate; gnathos with well developed median process; valve broad at base with an erect proximal costal process with spiculations; apex produced and curved toward costa; sacculus well developed; base of aedoeagus with winglike lateral projections.

Female genitalia: Papillae analis an elongate pad, setose; sterigma large, well developed; ductus bursae short, barely differentiated from corpus bursae; corpus bursae ovate, covered with minute spicules; signum absent.

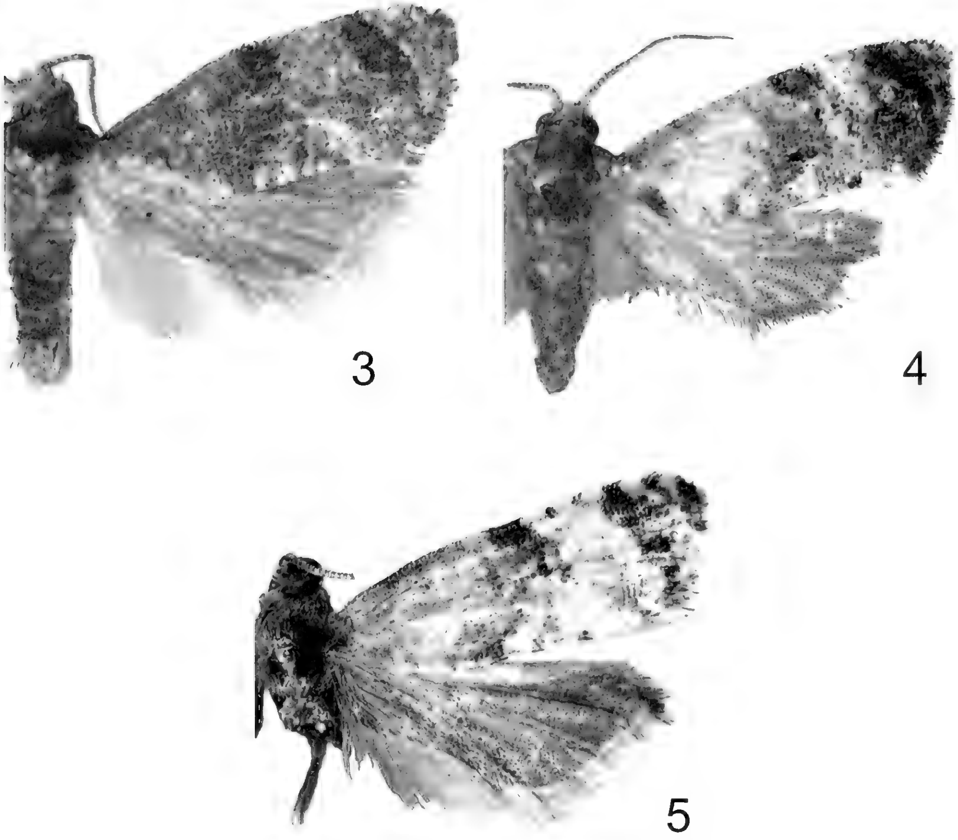
KEY TO SPECIES OF *ROLANDYLIS*

1. Forewing ground color fuscous (Fig. 3), male genitalia with dorso-proximal projection of valve perpendicular to costa (Fig. 6) . . . . . *fusca*
– Forewing ground color cream; male genitalia with dorso-proximal projection of valve parallel to costa 2
2. Forewing with apex tawny, with some fuscous scales (Fig. 4); male genitalia with apex of sacculus not extending beyond margin of valve (Fig. 8) . . . . *maiana*
– Forewing with apex fuscous (Fig. 5); male genitalia with apex of sacculus an elongate projection in distal 0.5 of valve, spiculate, extending beyond margin of valve (Fig. 10) . . . . *virilia*

Rolandylis maiana (Kearfott), **new combination**

(Figs. 4, 8, 9)

Phalonia maiana Kearfott 1907:82; Barnes and McDunnough 1917:179; Mc-



Figs. 3–5. *Rolandylis* species, adults. 3, *R. fusca*. 4, *R. maiana*. 5, *R. virilia*.

Dunnough 1939:6; Klots 1942: 417; Razowski 1997:137.
Rolandylis catalonica Gibeaux 1985: 350. **New synonym.**
Phtheochroa maiana: Poole and Gentili 1996:876.

Diagnosis.—This species and *R. virilia* have the forewing ground color cream as compared to fuscous as in *R. fusca*. The apex of the forewing in *R. maiana* is tawny with some fuscous scales; in *R. virilia* the apex is cream with a line of scales just below apex and a small fuscous spot at apex. In the male genitalia the dorso-proximal projection of the valve is longer in *R. maiana* than in *R. virilia,* extending beyond middle of costal margin.

Description.—*Male: Head:* Labial palpus cream sprinkled with fuscous externally, white internally. Scales of front and vertex cream. Scape and antenna cream.

Thorax: Mesonotum and tegula cream to pale gray; lateral scale tufts of metanotum and scales of scutellum cream. Underside shining white; pro- and mesothoracic legs cream sprinkled with fuscous, apical tarsal rings cream; metathoracic leg cream.

Forewing: Length 3.3–4.6 mm; length 2.8–3.1× width, moderately broad. Ground color cream, basal band pale fuscous with scattered pale tawny scales; median band fuscous with mostly tawny scales covering discal cell; subapical band black extending from costa to tornus, expanded medially toward apex, scattered with tawny scales; apex tawny with some fuscous scales; fringe mixed tawny and fuscous. Underside pale fuscous; fringe concolorous.

Hindwing: Length 3.0–4.0 mm; length 2.7–3.0 width, moderately broad. Entirely pale fuscous; fringe concolorous. Underside white with scattered pale brown marks from middle to termen.

Abdomen: Pale fuscous to cream; genital tuft white.

Genitalia: Dorso-proximal projection of valve wider at base than apex, parallel to costa, not extending above socii; sacculus sclerotized in basal half of valve, apex not extending beyond margin of valve.

Female: Sterigma with a central shield-shaped plate; ductus bursae short, immediately giving rise to corpus bursae; corpus bursae widest in middle and tapering to a round apex. Illustraed in Gibeaux (1985, fig. 6).

Type material.—Lectotype ♂ of *P. maiana* in USNM, designated by Klots (1942), with the following labels: 1) Essex Co., N.J., G. N. [Great Notch], V. [May] 10, W.D. Kearfott; 2) TYPE Collection of W.D. Kearfott [red label]; 3) *Phalonia maiana* Cotype Kearf [hand written] Named by Kearfott [printed]; 4) ♂ genitallia on slide, Feb. 2, 1941, J.F.G.C. #3442; 5) Lectotype designated by Klots 1942, J.F.G.C. 1952; 6) Genitalia Slide, by J.F.G.C ♂, USNM 23819. Right forewing missing. Two ♂ paralectotypes with same data as lectotype; Genitalia Slide USNM 23919.

Rolandylis catalonica Holotype ♂, in R. Robineau collection, France, Pyrénées-Orientales, Alénya, étang de Saint-Nazaire, 17-V-1983 (R. Robineau); ♀ paratype with same data as holotype, in C. Gibeaux collection.

Material examined.—NEW HAMPSHIRE: Hampton, June 3, 1908, S.A. Shaw, 2 ♂, Genitalia Slide USNM 23124. PENNSYLVANIA: 1 ♂, Genitalia Slide USNM 23745.

Distribution.—Eastern North America from Nova Scotia (Razowski 1997) south to New Hampshire, Pennsylvania, and New Jersey. Also recorded from southern France (Gibeaux 1985).

Discussion.—Poole and Gentili (1996) included *R. maiana* in the genus *Phtheochroa* without explanation. This is odd because Razowski (1991) described new species of *Phtheochroa* from Mexico and did not include *R. maiana* in a world list of what he interpreted as *Phtheochroa* species. No other literature has been found placing *R. maiana* in *Phtheochroa.* In an unpbulished list of Tortricinae, Powell does not refer *R. maiana* to any genus, leaving it unassigned as in Razowski (1997).

Several species of Cochylini have Holarctic distributions. Razowski (1997) reported six Holarctic species from Canada. Most of these are widespread species that occur across Europe and Asia to Japan, ranging into Alaska, British Columbia, Alberta, and Ontario. A few range through the western United States across the northern latitudes to Pennsylvania, New Hampshire, and Maine. All species of *Rolandylis* are uncommon in collections, and the record from France is possibly an introduction, or the genus has been overlooked elsewhere in the Palaearctic.

Rolandylis fusca Pogue, new species

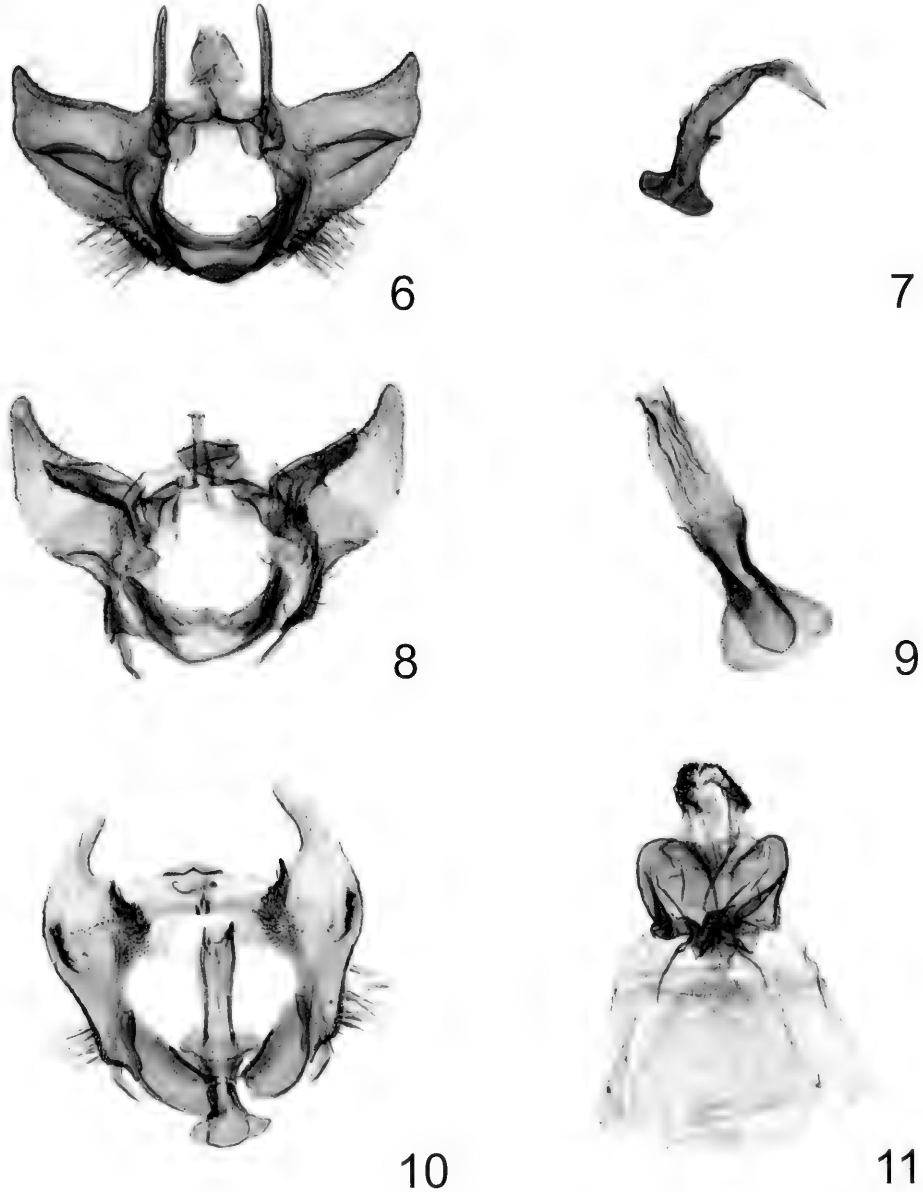
(Figs. 1–3, 6–7, 11)

Diagnosis.—This species is easily separated from *R. maiana* and *R. virilia* by its dark fuscous coloration of the forewing. In the male genitalia, the dorso-proximal projection of the valve is perpendicular to the costa in *R. fusca* and this structure is parallel to the costa and more heavily covered with spicules in *R. maiana* and *R. virilia.*

Description.—*Male: Head:* Labial palpus light fuscous externally, white internally; median segment equal to vertical eye diameter. Scales of front and vertex gray. Scape and antenna gray.

Thorax: Mesonotum and tegula fuscous mixed with tawny to gray; lateral scale tufts of metanotum and scales of scutellum gray. Underside shining white; pro- and mesothoracic legs fuscous, apical tarsal rings cream; metathoracic leg cream, tarsus gray with cream apical ring.

Forewing: Length 3.4–4.7 mm; length



Figs. 6–11. *Rolandylis* species, genitalia. 6, *R. fusca*, male genitalia. 7, *R. fusca*, aedoeagus. 8, *R. maiana*, male genitalia. 9, *R. maiana*, aedoeagus. 10, *R. virilia*, male genitalia and aedoeagus. 11, *R. fusca*, female genitalia.

2.6–2.9× width, moderately broad. Ground color fuscous, basal band black with scattered tawny scales; indistinct black median band scattered with tawny scales; subapical band black extending from costa to tornus, expanded medially toward apex, with scattered tawny scales; apex black with a few tawny scales; fringe with black basal band, scales mixed fuscous and tawny. Underside brown; fringe concolorous.

Hindwing: Length 3.0–4.0 mm; length 2.7–3.0 width, moderately broad. Entirely fuscous; fringe pale fuscous. Underside concolorous with upperside.

Abdomen: Gray; genital tuft white.

Genitalia: Dorso-proximal projection of valve elongate, of uniform width, perpendicular to costa, extending above socii; dorsal edge of sacculus produced into a vertical plate that is joined at apex with a second vertical plate arising from the middle of the valve.

Female: As described for male except forewing length 3.8–4.4 mm; length 2.6–2.9× width, moderately broad to elongate.

Genitalia: Papillae analis elongate, setose; sterigma a complicated well sclerotized structure with curved projections that curve outward then continue around dorsally, apex round, a central plate surrounding ostium with a median projection; ductus bursae short; corpus bursae ovate, covered with minute spicules.

Type material.—Holotype ♂, in USNM with the following labels: Illinois: Putnam Co., June 10, 1962, M.O. Glenn.

Eight male and five female paratypes: ILLINOIS: Putnam Co., July 26, 1950, M.O. Glenn, 1 ♂, genitalia in vial; June 18, 1951, 1 ♂, Wing Slide USNM 30302, complete dissection in genitalia vial; June 9, 1965, 1 ♂, Genitalia Slide USNM 23123; July 23, 1965, 1 ♂; Aug. 15, 1965, 1 ♂; July 30, 1950, 1 ♀, genitalia in vial; June 19, 1957, Reared ex-larva, unfolded leaves of goldenrod, 1 ♀, genitalia in vial; July 17, 1959, 1 ♀, Genitalia Slide USNM 23122 (USNM). MISSOURI: Jackson County, Independence, 19 July 1967, Taken at U V Light, Leg. J.R. Heitzman, 1 ♂, genitalia on slide MGP 607; 3 June 1968, at black light, Leg. J.R. Heitzman, 1 ♂, (JRH). PENNSYLVANIA: Allegheny Co., Oak Station, May 5, 1911, Fred Marloff, 1 ♂, Genitalia Slide USNM 23121, Wing Slide USNM 23121; May 2, 1913, 2 ♀, Genitalia Slide USNM 23215, Wing Slide USNM 30290 (USNM).

The following specimen data (not paratypes) were sent to me by Michael Sabourin: ILLINOIS: Mason Co., Sand Ridge State Forest, 17 June 1995, at UV light, T. Harrison, (UMSP). INDIANA: St. Joseph Co., 6 May 1999, 1 ♂, 27 July 1999, 1 ♂, 5 Aug. 1998, 1 ♂, At light, J. Vargo (UMSP). MICHIGAN: Berrien Co., 11 June 1999, J. Vargo, 1 ♀ (UMSP). MISSISSIPI: Hinds Co., Jackson, 30 May 1963, Mather collection, 1 ♀ (BMC). The following specimen data (not paratypes) were sent to me by Eric Metzler: OHIO: Greene Co., Bath Township, Wright-Patterson Air Force Base: Huffman Prairie, site B-2, Tall grass prairie, 39°48.4′N x 84°3.5′W, 14 July 1995, 1 ♂, 11 August 1995, 2 ♂, 13 August 1993, 1 ♂, 17 September 1993, 1 ♂, Eric H. Metzler. Erie Co., Margaretta Township, Resthaven Wildlife Area: Tallgrass Prairie, site R-5: 41°24.4′N x 82°49.1′W, 26 June 1999, 1 ♂, 19 July 1998, 2 ♂, 19 August 1996, 1 ♀, Eric Metzler.

Larval host plant.—Larvae reared on leaves of goldenrod (*Solidago* sp.) (Asteraceae).

Distribution.—Known from Mississippi, Illinois, Indiana, Missouri, Ohio, and Pennsylvania (Fig. 12).

Discussion.—*Rolandylis fusca* has a flight period from early May to September throughout its range. Possibly overwinters as a last instar larva or as a pupa that emerges in late spring. From the collections in Ohio, *R. fusca* may be a tall grass prairie specialist, especially considering its larval host plant.

Etymology.—The species epithet means dark in color, which pertains to the overall appearance of the moth.

***Rolandylis virilia* Pogue, new species**
(Figs. 5, 9, 10)

Diagnosis.—The length of the valve, from proximal end of sacculus to apex, is substantially larger in *R. virilia* (0.74 mm) than in *R. maiana* (0.54–0.60 mm). Apex of the sacculus is an elongate projection covered with spicules that projects beyond the margin of the valve; in *R. maiana* the apex does not extend beyond margin of valve.

Description.—*Male: Head:* Labial palpus cream externally, white internally; me-

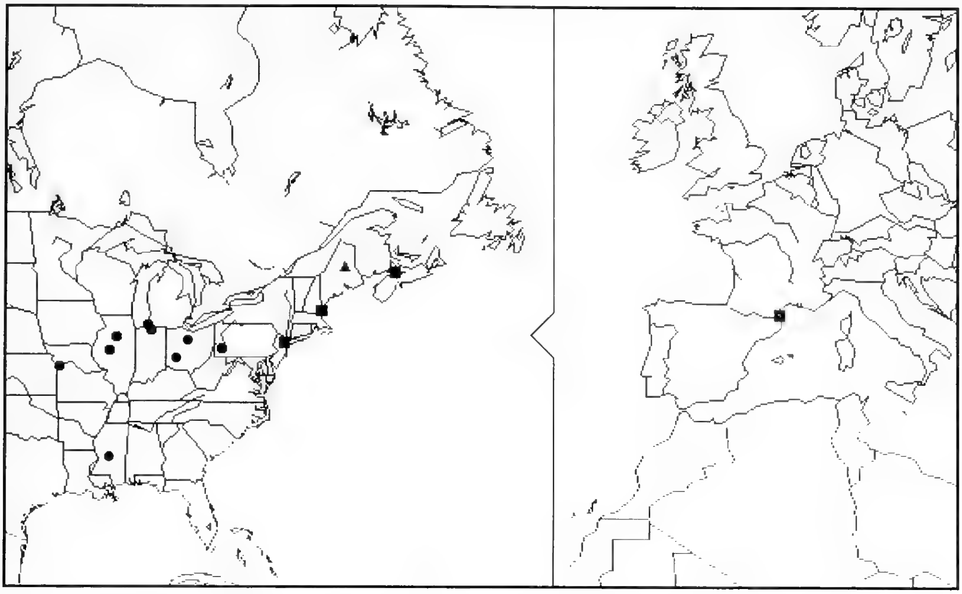


Fig. 12. Distribution of *Rolandylis* species, ■ = *R. maiana,* ● = *R. fusca,* ▲ = *R. virilia.*

dian segment equal to vertical eye diameter. Scales of front and vertex cream. Scape and antenna cream.

Thorax: Mesonotum and tegula cream; lateral scale tufts of metanotum and scales of scutellum cream. Underside shining white; pro- and mesothoracic legs pale fuscous; metathoracic leg cream.

Forewing: Length 4.5 mm; length 3.1× width, moderately broad. Ground color cream; basal band cream with a few pale fuscous scales; median band pale fuscous; subapical band pale fuscous extending from costa to tornus; apex fuscous; fringe mixed cream and pale fuscous. Underside pale fuscous; fringe concolorous.

Hindwing: Length 3.6 mm; length 2.4× width, broad. Entirely pale fuscous; fringe concolorous. Underside white with scattered pale brown marks from middle to termen.

Abdomen: Dark dorsally, light ventrally.

Genitalia: Dorso-proximal projection of valve wider at base than apex; parallel to costa; not extending above socii; apex of sacculus an elongate projection in distal 0.5 of valve, spiculate; area of valve between dorso-proximal projection to sacculus spiculate.

Female: Unknown.

Type material.—Holotype ♂, in USNM with the following labels: 1) Millinocket, Maine, July 18; 2) Genitalia Slide USNM 24341.

Distribution.—Known only from type locality.

Discussion.—The only specimen known is the holotype, which is in poor condition. Most of the scales are missing from the head. The specimen has been glued to the pin and one labial palp and one antenna are embedded in the glue. The forewings are rubbed. *Rolandylis virilia* is most closely related to *R. maiana* on the basis of the male genitalia.

Etymology.—The name refers to the larger size of the male genitalia as compared to its most closely related species, *R. maiana.*

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THE GENUS *LEPTOPTERNA* FIEBER (HETEROPTERA: MIRIDAE: STENODEMINI) IN NORTH AMERICA

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Abstract.—The genus *Leptopterna* Fieber and its three North American species are redescribed. A lectotype is designated for *L. amoena* Uhler. It is **restored from synonymy** with *L. ferrugata* (Fallén), and occurs throughout most of North America. *Leptopterna silacea* Bliven is proposed as a **new junior synonym** of *L. amoena.* In the Nearctic Region *L. ferrugata* is confined to Alaska, the Yukon and the western part of the Northwest Territory.

Key Words: Heteroptera, Miridae, Stenodemini, *Leptopterna,* grass-feeding plant bugs, North America, introduced species, redescription, lectotype, synonym, distribution, host, key

The stenodemine genus *Leptopterna* Fieber is currently represented in North America by two species (Kelton 1980). *Leptopterna dolabrata* (Linnaeus) is an adventive species (Wheeler and Henry 1992), absent from Alaska, Yukon, Northwest Territories, Nunavut, Alberta, and Saskatchewan (Maw et al. 2000). On the other hand, *L. ferrugata* (Fallén) is more widely distributed and is generally regarded as being naturally Holarctic (Wheeler and Henry 1992). Although a third species, *L. silacea* Bliven is listed by Henry and Wheeler (1988), this is regarded as a *nomen dubium* (Schwartz 1987).

In a study of the Yukon fauna, Scudder (1997) examined specimens of *L. ferrugata* from Alaska and the Yukon and found them to be identical to Palearctic material collected in England and Sweden. *Leptopterna ferrugata* was thus recorded from the Yukon, and the species was considered to have a circumboreal distribution. However, in our study of material from British Columbia, and elsewhere in North America, we have found that *L. ferrugata* is not widely distributed in the Nearctic. We propose that there are two species under this name in material from the New World. The true *L. ferrugata* is confined to Alaska, Yukon, and the western part of the Northwest Territory. Specimens from elsewhere in Canada and the continental United States are distinct, and evidently represent the species *L. amoena,* described originally from Idaho and "Dakota" by Uhler (1872) and previously was considered a junior synonym of *L. ferrugata,* following Carvalho (1959).

In this paper, we present a diagnosis of the genus *Leptopterna,* designate a lectotype for *L. amoena* and restore it from synonymy, and present a key and detailed redescriptions for the three species now recognized in North America. The mean and range for selected measurements of ten male and female individuals are reported.

Wheeler and Henry (1992) provided an excellent summary of the host plants and habits for *L. dolabrata,* and in their account of *L. ferrugata,* they reported this species in the Palearctic. The biological records from Wyoming (Kumar et al. 1976, Stephens 1982), Utah (Knowlton 1947), Oregon (Kamm 1979), New Hampshire and Maine (Wheeler and Henry 1992), should be referred to *L. amoena.*

Genus *Leptopterna* Fieber

Leptopterna Fieber 1858: 302.
Lopomorphus Douglas and Scott 1865: 293 (synonymized by Reuter 1910: 167).

Diagnosis.—*General habitus:* Elongate, male macropterous, female usually brachypterous; impunctate; dull, pale yellow and black, male sometimes tinged with orange or pink, vestiture moderately pilose with erect, mostly pale simple setae; male genitalia with tubercles dorsal to both paramere insertions on genital segment; vesica with two elongate, narrow spiculae; female genitalia with large, extensively developed anterior portion of ventral labiate plate, and with large well-sclerotized and convoluted inter-ramal sclerotization. *Head:* Oblique, diamond-shaped; broader than long; frons smooth, rounded, tumid; vertex without basal carina, with shallow mesal depression, without medial sulcus; postocular region of head moderately developed; maxillary plate, mandibular plate slightly produced, gena wide; gular region wide; buccal cavity circular, buccula short; eye small, bulging, eye height one-third head height; postocular portion of head remote from anterior margin of collar; antennal insertion removed anterior margin of eye with ventral margin situated even with ventral margin of eye; antenna cylindrical, first segment long, extending greatly beyond apex of clypeus; with densely or moderately distributed, reclining, coarse or fine black setae, sometimes with a few slightly longer, more erect setae; second segment with stiff, erect, black setae; third and fourth segments thinner than first and second with pale, short, simple setae; first antennal segment thick, thicker in female than in male; second segment tapering from base to apex; rostrum reaching from apex of middle coxa to base of hind coxa. *Pronotum:* Triangular, surface dull; lateral margin carinate; proepisternum extending lateral to pronotal margin; posterior margin broader than length; collar flattened; calli convex, separate, with very faint anterior and posterior sulci; pronotal disc broad, convex; coxal cleft deep; propleuron impunctate; mesoscutum broadly exposed, convex; scutellum convex. *Hemelytra:* Densely to sparsely pubescent; males macropterous, females macropterous or brachypterous; embolium narrow and extending to coxal cleft, incisure deep, interior cell small, triangular, much shorter than cuneus; outer cell large, longer than cuneus, not deflected; membrane slightly fuscate, veins pale. *Venter:* Dull, pale with dark vittae, pilose. *Legs:* with long, densely distributed, erect or reclining, dark simple setae; pale yellow with many spots or more uniformly darkened; hind femur slightly tapered distally, just longer than abdomen, and shorter than distally expanded hind tibia; hind tarsus with first segment subequal to combined length of second and third segments. *Male genitalia:* Genital segment with large tubercle dorsal to left and right paramere insertions and posteroventral portion flange-like in lateral view; left paramere: with small sensory lobe and shaft; right paramere with bulbous distal portion; vesica with two long, basally connected, basal processes, sometimes with plate-like sclerotization basally; front of membrane with variable size spinose field; membrane small situated basally, sometimes with narrow, elongate lobes. *Female genitalia:* Sclerotized rings large, round; dorsal labiate plate with deeply concave pocket-like sclerite anteriorly; ventral labiate plate large, extending anteriorly; posterior wall with inter-ramal sclerite large and wide; dorsal structure large, sac-like; inter-ramal lobes narrow, one-half width of sclerite.

Remarks.—Three species occur in North America, one Holarctic, one Nearctic, and one adventive from the Palearctic.

KEY TO NORTH AMERICAN SPECIES OF *LEPTOPTERNA*

1. Stiff black setae on first antennal segment with at least some longer and more erect than rest; first antennal segment about as long as width of head (Fig. 2); female with second antennal segment much thinner than front tibia . . . . *L. dolabrata* (Linnaeus)

– Stiff or fine black setae on first antennal segment all of same length and reclining, none erect; first antennal segment slightly to much longer than width of head (Figs. 1, 3); female with second antennal segment almost as thick as front tibia 2

2. Length of first antennal segment more than 1.25 mm, setae densely distributed and fine (Fig. 1); length of second antennal segment longer: male 3.35–3.80 mm, female 3.70–4.40; spinose field on membrane adjacent to ductus seminis small or absent (Figs. 5–7); sclerotized rings separated (Fig. 13) . . . . . *L. amoena* Uhler

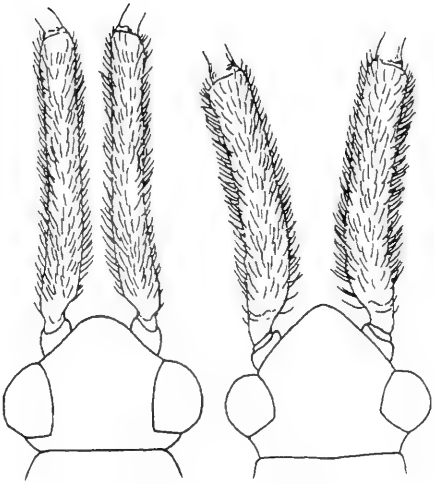
– Length of first antennal segment less than 1.25 mm, setae moderately distributed and coarse (Fig. 3); length of second antennal segment shorter: male 2.33–3.30 mm, female 2.90–3.73; spinose field on membrane adjacent to ductus seminis large (Fig. 4); sclerotized rings contiguous medially (Fig. 14) . . . . *L. ferrugata* (Fallén)

Leptopterna amoena Uhler, **restored status**
(Figs. 1, 5–7, 9–10, 13, 15)

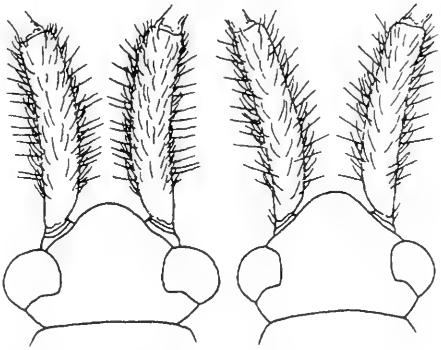
Leptopterna amoena Uhler 1872 ("1871"): 409.

Leptopterna silacea Bliven 1973: 136. **New synonym.**

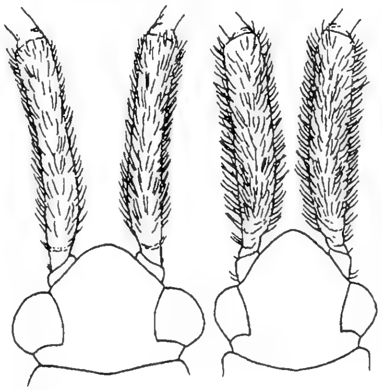
Diagnosis.—Distinguished by length of first antennal segment being much greater than head width, with length greater than 1.25 mm, and densely distributed, fine, reclining, black setae all of same length (Fig. 1); female with second antennal segment almost as thick as front tibia; length of second antennal segment long; vesical membrane with subquadrate sclerotized region on posterior surface and with small or absent spinose field on membrane adjacent to ductus seminis (Figs. 5–7); distal portion of



1 ♂ *Leptopterna amoena* ♀

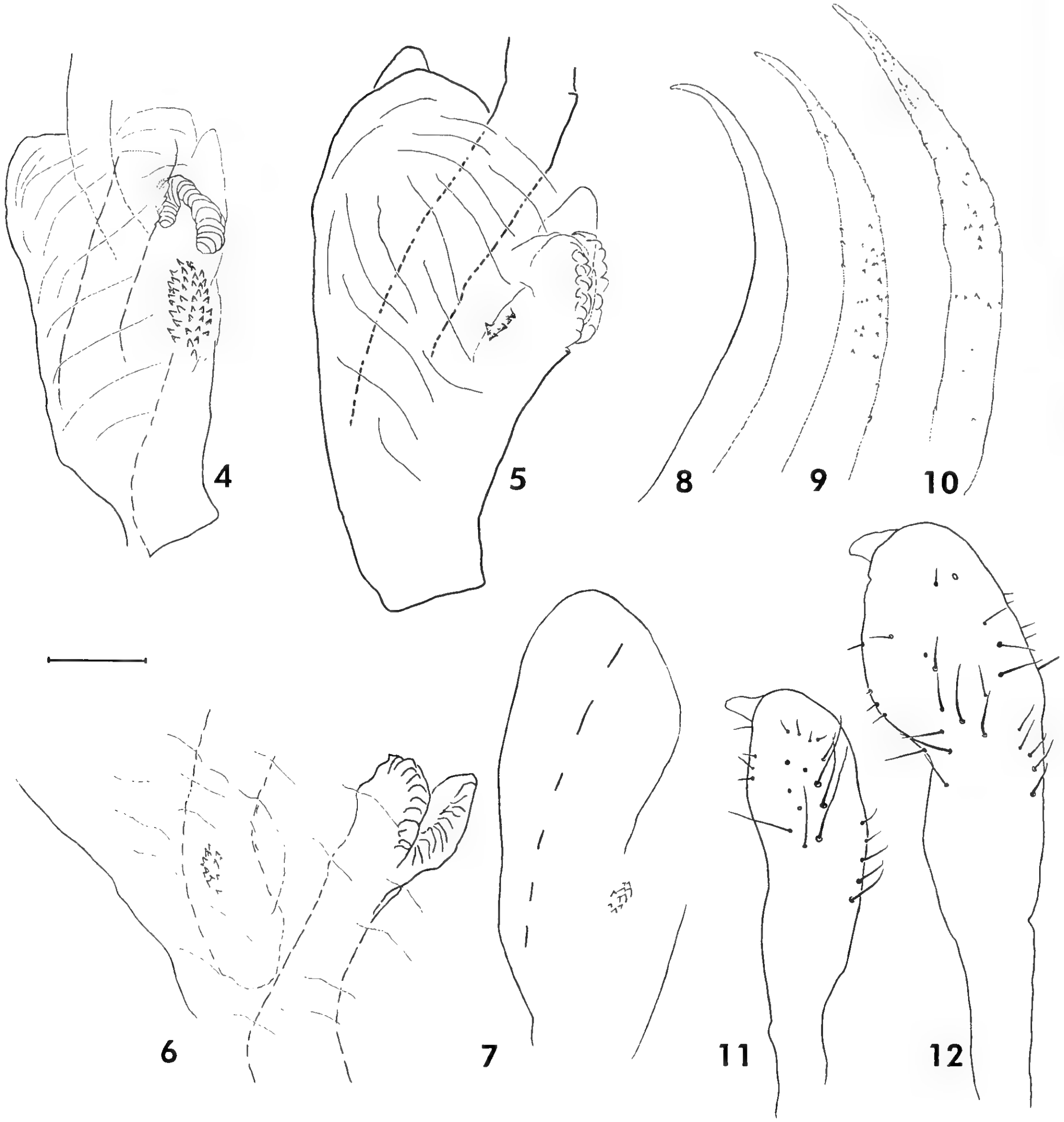


2 ♂ *Leptopterna dolobrata* ♀



3 ♂ *Leptopterna ferrugata* ♀

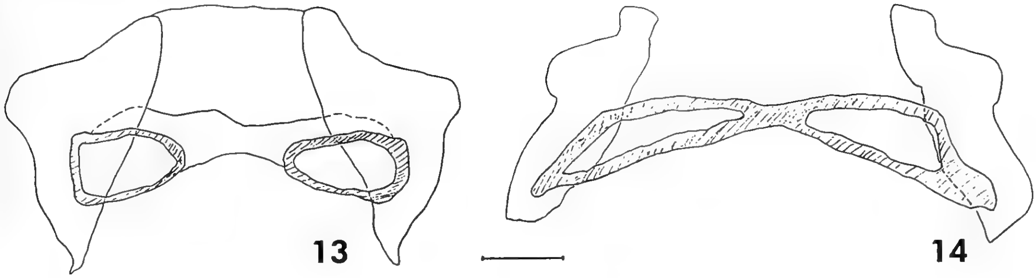
Figs. 1–3. Head and first antennal segment of *Leptopterna* spp., dorsal view (left, male; right, female). 1, *L. amoena*. 2, *L. dolabrata*. 3, *L. ferrugata*.



Figs. 4–12. Male genitalia of *Leptopterna* spp. 4–7, Lateral view of vesica, spinose field denoted by arrow. 4, *L. ferrugata* (UK: Bald Hill). 5–7, *L. amoena* (5, BC: 9 mi E of Grand Forks. 6, AB: Onefour. 7, CO: La Platta). 8–10, Distal portion of left vesical spiculum. 8, *L. ferrugata* (UK: Bald Hill). 9–10, *L. amoena* (9, AB: Cypress Hills Prov. Pk. 10, AB: Onefour). 11–12, Lateral view of left paramere. 11, *L. ferrugata* (UK: Bald Hill). 12, *L. amoena* (CO: LaPlatta). Scale = 0.10 mm.

left spiculum with numerous minute spines (Figs. 9–10); right paramere large with strong medial constriction (Fig. 12); and sclerotized rings separated (Fig. 13).

Description.—Pale yellow with black areas on head, pronotum and scutellum, diffuse brown on endocorium; dorsum with moderately distributed, moderate length, erect pale simple setae. *Head:* Dark brown to black with pale yellow to brownish yellow markings; pale on vertex and frons broadly adjacent to eye; variable streak on frons medially; bilaterally areas on collum, sometimes merging with pale on vertex; female pale except for dark Y-shaped mark on frons that extends to collum and mark



Figs. 13–14. Female genitalia of *Leptopterna* spp., dorsal view, sclerotized rings and dorsal labiate plate. 13, *L. amoena* (AB: Kananaskis). 14, *L. ferrugata* (UK: Braunton Burrows). Scale = 0.10 mm.

posterior to eye; mandibular plate and maxillary plate pale; gena pale below antennal tubercle and eye, female with ventral aspect of head pale except for gula and on sutures; head width male 1.15 (1.05–1.20) mm, female 1.19 (1.13–1.20) mm; vertex width male 0.51 (0.45–0.55) mm, female 0.62 (0.57–0.67) mm; antenna brown to dark brown; first segment with dark irregular fields; sometimes with black basally, distally and rarely on lateral surface; first segment in female pale yellowish brown, with diffuse darkening; first segment one-quarter to one-fifth longer than head width, with densely distributed, equal length, fine black setae; female with second segment at base equal to diameter of front tibia; antennal measurements male 1.40 (1.27–1.50): 3.62 (3.35–3.80): 1.93 (1.60–2.20): 0.83 (0.70–0.93) mm, female 1.51 (1.43–1.57): 4.37 (3.70–4.40): 2.07 (2.00–2.30): 0.84 (0.77–0.93) mm; rostrum pale brown to brown, first segment pale; rostral extending to apex of middle coxa; length male 2.67 (2.47–

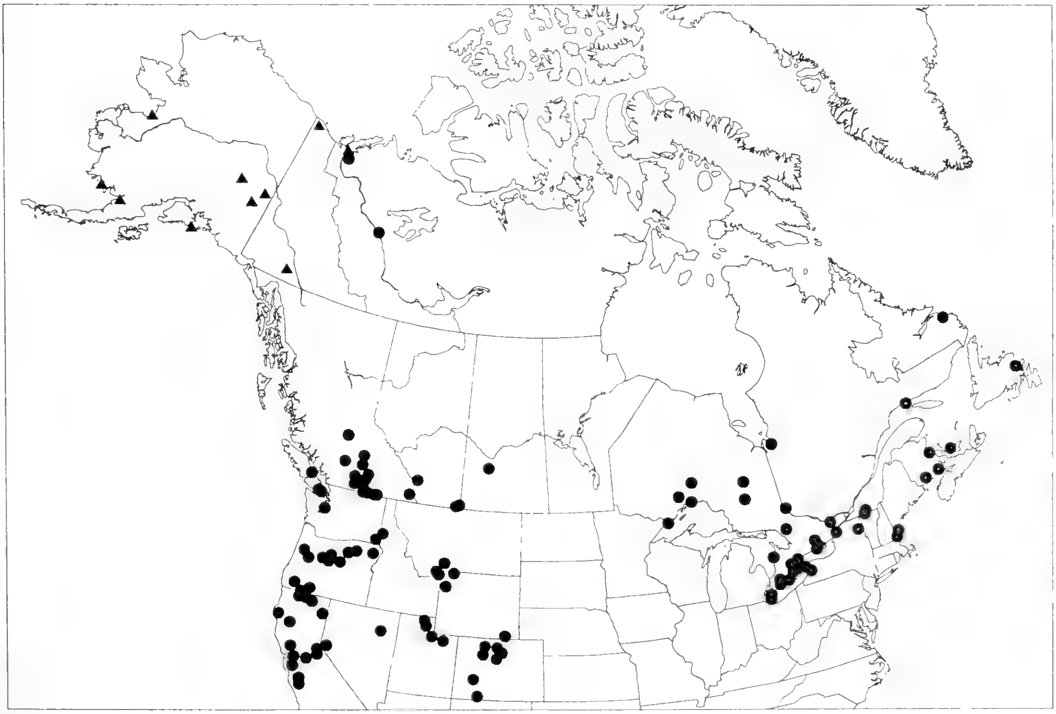


Fig. 15. Distribution of *Leptopterna amoena* (●) and *L. ferrugata* (▲) in North America.

2.90) mm, female 3.05 (3.03–3.07) mm. *Pronotum:* Yellowish brown; with broad, black, bilateral, longitudinal bands, extending from anterior to posterior margin and passing through calli; sometimes female with only calli diffusely darkened; pronotal width male 1.65 (1.53–1.77) mm, brachypterous female 1.54 (1.43–1.67) mm, macropterous female 1.62 (1.57–1.67) mm. Scutellum entirely pale with lateral margin black to black with medial pale streak; mesoscutum black with broad, pale yellow mesial streak; female pale with extreme basal angles dark. *Hemelytra:* Yellowish brown to brownish yellow on endocorium; exocorium dull yellow; membrane pale brown, veins yellow; female macropterous or brachypterous with hemelytra reaching onto tergum V. *Legs:* Pale yellow to yellowish brown with brown spots; tibiae with reclining black erect setae, shorter than diameter of tibia; tarsi dark brown. *Venter:* Pale yellow to yellowish brown, pleura sometimes marked with black; abdomen ventrally with lateral longitudinal fuscous vittae; male genital segment diffusely darkened. *Total length:* Male 8.2 (7.4–8.0) mm, brachypterous female 7.7 (6.8–8.3) mm, macropterous female 8.2 (8.1–8.4) mm.

Biology.—Breeds on grasses; collected on wheat, march grass, *Heracleum,* and timothy also adventive on *Erigeron, Juniperus,* and *Potentilla.* Host records, exclusive of the Palearctic, Alaska, and the Yukon, reported in Wheeler and Henry (1992) and Scudder (1997) refer to this species.

Distribution (Fig. 15).—Southern Northwest Territory and British Columbia, east to Newfoundland, south to New Hampshire and southern Ontario and in the western United States from Colorado to California. Wheeler and Henry (1992) documented the distribution to include twelve states and two provinces.

Type designation.—Uhler (1872) stated in his original description that the syntypes of this species were female and from the vicinities of "Snake River, Idaho" and "Dakota." Two specimens were located in the National Museum of Natural History, Washington, DC, collection by T. J. Henry. The exact label data for each is as follows: the macropterous female (with abdomen missing) from Snake River, Idaho–label 1 (handwritten), "Snake Riv[.] Idaho"; 2 (handwritten), "Leptopterna amoena Uhler[,] Idaho"; 3 (red), "Type No. 1118 U. S. N. M." and the brachypterous female from Dakota–1, "Dak."; 2, "PR Uhler Collection"; 3 (handwritten), "Leptopterna amonena Uhler[,] Dak."; 3 (handwritten), "Leptopterna amoena Uhler[,] Dak[,] Det Uhler [Det Uhler is printed]"; 4 (handwritten), "Miris amoenus (Uhler)." We here designate and have labeled the more intact Dakota specimen as the lectotype to ensure the proper and consistent application of the name.

Discussion.—Bliven (1973) described *L. silacea,* based on specimens from Humboldt Co., California, without noting how his new species differed from congeners. Examination of the holotype, paratypes, or any *Leptopterna* specimens collected by Bliven was not possible because all specimens documented in his 1973 paper are presumed lost (see Schwartz 1989: 33). The original description of *L. silacea* stated that the first antennal segment was "clothed with long, black, antrose, simple hairs," the length of the first and second antennal segments (male/female) were 1.60/1.67 mm and 3.84/4.16 mm, and the head width of the male was 1.16 mm. If these observations of Bliven's were accurate, then the first antennal segment of *L. silacea* does not have some setae which are longer and more erect than the others, the length of the first antennal segment is much greater than the width of the head and longer than 1.25 mm, and the length of the second antennal segment of either sex is longer than 3.80 mm. We propose that *L. silacea* is a junior synonym of *L. amoena* because these measurements only match our observations of the latter North American species and the fact that currently *L. amoena* is the only *Lep-*

topterna species known from northern California (Fig. 15).

Leptopterna dolabrata (Linnaeus)
(Figs. 2, 16)

Cimex dolabratus Linnaeus 1758: 449.
Miris belangeri Provancher 1872: 78 (synonymized by Provancher 1886: 104).

Diagnosis.—Distinguished by first antennal segment about equal to head width and with stiff black setae, at least some longer and more erect than the rest (Fig. 2); female with second antennal segment much thinner than front tibia; male genitalia without subquadrate sclerotized region on posterior surface of vesical membrane; sclerotized rings separated.

Description.—Black with pale yellow areas and orange-brown on endocorium; dorsum with densely distributed, long, erect, pale simple setae. *Head:* Black with pale yellow markings; pale on vertex adjacent to eye; short streak on frons medially; two spots on collum; female with more extensive and coalescing pale areas; mandibular plate and maxillary plate pale or pale mesially; gena distinctly pale below antennal tubercle and near eye, female with ventral aspect of head almost totally pale; head width male 1.29 (1.25–1.35) mm, female 1.37 (1.30–1.40) mm; vertex width male 0.61 (0.58–0.63) mm, female 0.72 (0.69–0.80) mm; antenna black; sometimes male with first segment pale along inner surface with black spots, or yellow with black spots throughout; spots tending to coalesce; first segment in female yellow, with base and apex narrowly fuscous; male with base of second segment rarely paler; basal two-thirds of second segment in female pale; first segment as long as head width, with stiff black setae, at least some longer and more erect than the rest; second segment at base thinner than front tibia; antennal measurements male 1.32 (1.25–1.50): 3.93 (3.75–4.15): 2.08 (1.90–2.30): 1.06 (0.90–1.18) mm, female 1.36 (1.30–1.40): 4.07 (3.85–4.33): 2.04 (1.90–2.25): 1.08 (1.00–1.15) mm; rostrum brown, first segment pale; rostral extending to base of hind coxa; length male 3.08 (2.95–3.20) mm, female 3.46 (3.15–3.65) mm. *Pronotum:* Yellowish brown, in male grading to pale orange posteriorly; with broad, black, bilateral, longitudinal bands, extending from anterior to posterior margin and passing through calli; pronotal width male 1.95 (1.80–2.10) mm, female macropterous 2.04 (1.98–2.10) mm, brachypterous 1.81 (1.70–1.88) mm. Scutellum and mesoscutum with broad, pale yellow mesial streak, black laterally; female with pale areas at extreme basal angles. *Hemelytra:* Pale yellow to bright orange in male, with embolium pale; membrane brown, veins yellow to orange in male; brachypterous female with hemelytra reaching onto tergum VI. *Legs:* Basally pale yellow; front coxa black, pale posteriorly; middle and hind coxae black with apex and dorsal surface pale; trochanters pale, black at joints; femora in male black dorsally, pale ventrally with black blotches tending to merge, or like female being spotted with black throughout; tibiae with base and apex tending to fuscous; tibiae with erect, black setae, longer than diameter of tibia; tarsi dark brown. *Venter:* Generally pale yellow to reddish brown, pleura marked with black; abdomen ventrally with lateral longitudinal fuscous vittae, these broken up in female; male genital segment fuscous basally and mid-ventrally. *Total length:* Male 8.9 (8.5–9.8) mm, female macropterous 9.0 (8.5–9.5) mm, brachypterous male 8.6 (8.3–9.8) mm.

Biology.—Hosts are grasses. Known from *Phleum pratense* L., *Bromus commutatus* Schrad., *Festuca ovina* var *glauca* (Lam.) C. D. J. Koch and *F. rubra* L. Recorded as causing economic injury to grasses and cereals (Wheeler and Henry 1992).

Distribution (Fig. 16).—Palearctic, introduced to eastern and western North America (Wheeler and Henry 1992). In North American found from British Columbia to Newfoundland (except for Saskatchewan), and south to Oregon and Tennessee.

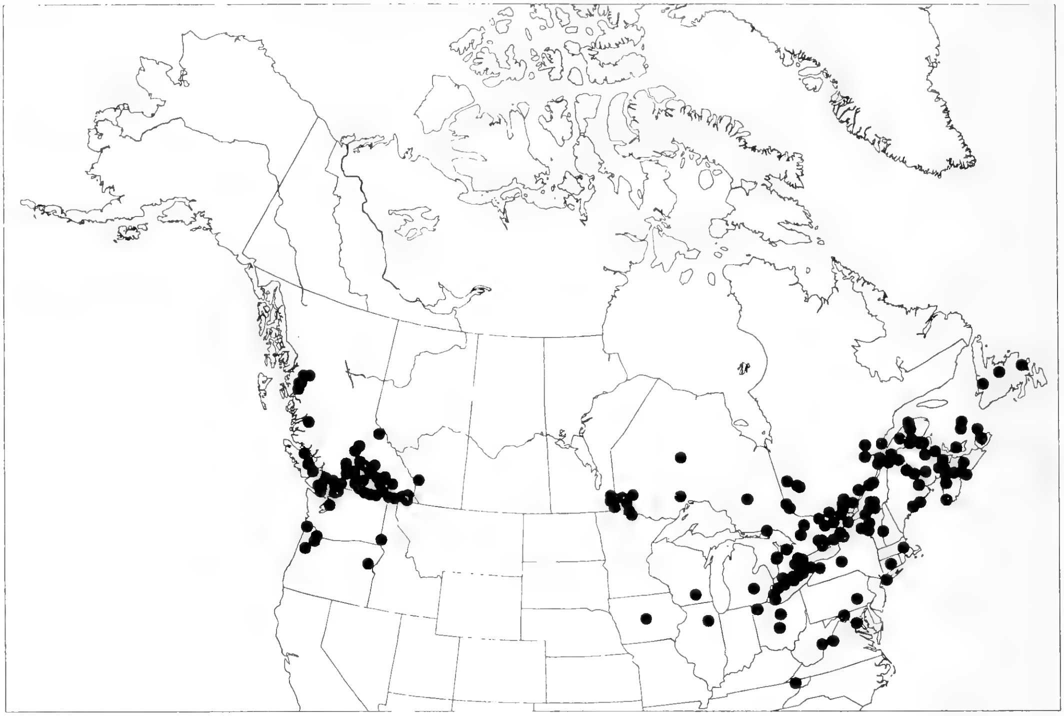


Fig. 16. Distribution of *Leptopterna dolabrata* in North America.

Leptopterna ferrugata (Fallén)
(Figs. 3, 4, 11, 14, 15)

Miris ferrugatus Fallén 1807: 107.
Lopus discors Costa 1853: 33 (synonymized by Puton 1875: 33).

Diagnosis.—Distinguished by first antennal segment subequal to slightly greater than head width, with length less than 1.25 mm, and moderately distributed, coarse, reclining black setae all of same length (Fig. 3); female with second antennal segment almost as thick as front tibia; length of second antennal segment short; vesical membrane with subquadrate sclerotized region on posterior surface and with relatively large spinose field on membrane adjacent to ductus seminis (Fig. 4); distal portion of left spiculum smooth without spines (Fig. 8); right paramere small with slight medial constriction (Fig. 11); and sclerotized rings contiguous medially (Fig. 14).

Description.—Pale yellow with dark brown on head, pronotum and scutellum, suffused with brown on endocorium; dorsum with moderately to sparsely distributed, moderate length, erect, pale simple setae. *Head:* Dark brown to black with pale yellow to brownish yellow markings, sometimes head almost completely darkened; pale on vertex and frons broadly adjacent to eye; frons usually dark, sometimes with short streak medially; bilaterally areas on collum usually confluent with pale on vertex; female pale except for irregular and faint darkening on frons mesially, which extends to collum and broad mark posterior to eye; mandibular plate and maxillary plate pale, except for anterior margin of maxillary plate; gena variably pale below antennal tubercle and eye, female with ventral aspect of head pale except for gula and ventral margin of maxillary plate; head width male 1.07 (1.00–1.12) mm, female 1.09 (1.03–1.15) mm; vertex width male 0.50 (0.47–0.53) mm, female 0.58 (0.53–0.60) mm; antenna brown to dark brown; first segment sometimes broadly pale on inner margin; first segment subequal to just longer than head width, with moderately distributed, equal length, coarse black setae; female with second segment at base equal to diameter of front tibia; antennal measurements male 1.01 (0.90–1.13): 2.82 (2.33–3.30): 1.80 (1.40–2.10): 0.81 (0.57–0.90) mm, female 1.13 (1.00–1.23): 3.32 (2.90–3.73): 1.79 (1.48–2.00): 0.77 (0.67–0.83) mm; rostrum pale brown to brown, first segment pale; rostral extending to apex of middle coxa; length male 2.47 (2.33–2.60) mm, female 2.73 (2.57–3.00) mm. *Pronotum:* Yellowish brown; with broad, black, bilateral, longitudinal bands, extending from anterior to posterior margin and passing through calli; sometimes entire disk black, except for pale base medially and lateral margin or dark bands obscure on posterior lobe of pronotal disk; pronotal width male 1.64 (1.50–1.82) mm, brachypterous female 1.57 (1.50–1.63) mm, macropterous female 1.56 (1.48–1.74) mm. Scutellum and mesoscutum usually black with narrow, pale medial streak; sometimes broadly pale with lateral margins dark; female pale with extreme basal angles dark. *Hemelytra:* Yellowish brown to brownish yellow on endocorium; exocorium dull yellow; membrane pale brown, veins yellow; female macropterous or brachypterous with hemelytra reaching onto tergum IV or V. *Legs:* Pale yellow to yellowish brown with brown spots; tibiae with reclining black erect setae, shorter than diameter of tibia; tarsi dark brown. *Venter:* Pale yellow to yellowish brown, pleura sometimes marked with black; abdomen ventrally with lateral longitudinal fuscous vittae; male genital segment diffusely darkened apically. *Total length:* Male 7.5 (7.0–7.8) mm, brachypterous female 7.1 (6.7–7.7) mm, macropterous female 6.9 (6.2–7.9) mm.

Biology.—Breeds on grasses. Collected from *Calamagrostis* in Alaska. The Palearctic grass hosts are listed in Wheeler and Henry (1992) and Scudder (1997).

Distribution (Fig. 15).—Holarctic species from Europe and southern Russia, naturally occurring in Alaska, Yukon, and extreme western Northwest Territories.

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LIFE HISTORY AND DESCRIPTIONS OF ADULTS AND IMMATURE STAGES OF *TEPHRITIS TEERINKI*, NEW SPECIES (DIPTERA: TEPHRITIDAE) ON *HULSEA VISTITA* A. GRAY (ASTERACEAE) IN SOUTHERN CALIFORNIA

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Abstract.—***Tephritis teerinki*** **Goeden, n. sp.**, is a fruit fly (Diptera: Tephritidae) producing a single, annual generation in the flower heads of *Hulsea vestita* A. Gray (Asteraceae) belonging to the subtribe Chaenactidinae of the tribe Helenieae in southern California. It also has been reared from mature flower heads of *Hulsea californica* Torrey and A. Gray. The egg, first-, second- and third-instar larvae, puparium, and adults are described and figured, and these stages are compared with those of other southern California *Tephritis*. The adults are distinguished by a combination of characters involving wing pattern, wing length, and leg color. The egg is covered by a smooth, membraneous sheath of unknown function. The description of the first instar of *T. teerinki* is the first for this instar in the genus *Tephritis*. Noteworthy for the first instar is the fusion of its integumental petal with the stomal sense organ. Similarly, the description of the second instar is only the second for the genus *Tephritis*. The third instar has the fewest number of integumental petals among third instars of three other described species and apparently has bidentate, not tridentate, mouthhooks like the other three congeners. The life cycle is of the aggregative type and overwintering occurs as long-lived, sexually immature adults.

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

To date, the life histories and immature stages of three species of *Tephritis* from southern California have been described in detail: *T. arizonaensis* Quisenberry (Goeden et al. 1993), *T. baccharis* (Coquillett) (Goeden and Headrick 1991), and *T. joanae* Goeden (Goeden 1993, 2001b). The immature stages of a fourth species, *T. stigmatica* (Coquillett), await description, and soon will be described by me, although its biology is well known (Tauber and Toschi 1965; Goeden 1988a, 1993). This paper describes the life history and immature stages of a fifth and new species, *T. teerinki* Goeden.

MATERIALS AND METHODS

The present study was based in large part on dissections of samples of flower heads of *Hulsea vestita* A. Gray (Asteraceae) collected at five locations during 1993 to 1997: (1) Osa Meadow at 2,610-m elevation, Sequoia National Forest (north section), Tulare Co., 15.vii.1993, 21.vi.1994; (2) northwest of Rodeo Flat at 2,290 m, Sequoia National Forest (north section), Tulare Co., 15.ix.1993; (3) east of Poison Meadow at 2,180 m, Sequoia National Forest (north section), Tulare Co., 12.vi.1994; and (4) northeast of Magic Mountain at 1,330 m, Angeles National Forest, Los Angeles Co.,27.v.1996; and (5) east of Mt. Gleason at 1,750 m, Angeles National Forest., Los Angeles Co., 22.v.1996, 30.iv.1997, 14.v.1997, 28.v.1997. 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. Twenty-one eggs, eight first-, 19 second-, and 34 third-instar larvae, and seven puparia dissected from flower heads were preserved in 70% EtOH for scanning electron microscopy (SEM). Additional 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, and 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. Thirteen 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) contained one each, virgin, initially 19 to 30 days-old, male and a female 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), and the terminology in Foote et al. (1993). Terminology and telegraphic format used to describe the immature stages follow Goeden (2001a, b), Goeden et al. (1993), Goeden and Headrick (1991), Goeden and Teerink (1999), Teerink and Goeden (1999), and our earlier works cited therein. The holotype, allotype, and 106 reared paratypes of each sex of this new species have been deposited in the National Museum of Natural History, Smithsonian Institution, Washington, DC (USNM). The holotype, allotype, and 22 paratypes used for measurements to describe *T. teerinki* originated from one collection on 28.v.1997 at the Mt. Gleason site. All remaining paratypes and voucher specimens not designated as paratypes, voucher specimens of immature stages, and reared parasitoids of this tephritid 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

Adult.—The new species from *Hulsea vestita* described below is most similar in its biology to *T. araneosa* and *T. ovatipennis* (unpublished data). However, adults of these two species and all other described North American congeners can be distinguished by the combinations of characters described below. Accordingly, the following key couplets modifying couplet 6 and replacing couplet 17 in the key of Foote et al. (1993), and as previously modified in Goeden (1993), enables one to distinguish

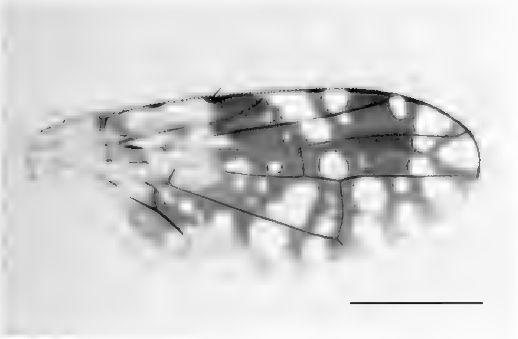

Fig. 1. Right wing of *Tephritis teerinki, female.* Line = 1 mm.

this new species. The three-digit, figure numbers in couplets 6, 17, and 17a refer to Foote et al. (1993), not to the present publication.

6. Preapical brown area of wing interrupted by numerous round subhyaline spots (fig. 428, c); 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); Y-shaped mark in wing apex rarely broken as above 10
17. Wing length usually under 3.5 mm, wing pattern as in fig. 437 . . . *araneosa* (Coquillett)
– Wing length usually exceeding 3.5 mm . . 17a
17a. Femora, especially of hind leg, dark tomentose; frons reddish brown-tomentose; wing pattern as in fig. 438 . . . . . . *ovatipennis* Foote
b. Femora mostly yellow; frons mostly white to yellow tomentose; wing pattern as in Fig. 1 . . . . *teerinki* Goeden, n. sp.

Tephritis teerinki Goeden, new species
(Figs. 1, 8H, I)

Female (holotype).—*Head:* In profile, 1.1 to 1.2 times as high as long, face distinctly protruding below antennae, face and frons meeting at an angle of about 120°, gena below eye 0.13 to 0.21 times eye height, genal bristle and most genal setulae light brown, some fading to white anteriorly; occiput swollen; frons yellow, with white dorsal and lateral margins, and sometimes sparsely mottled with light or reddish brown, 0.6 to 0.7 mm wide at vertex, narrowing to 0.5 to 0.6 mm at antennal bases, 0.4 to 0.5 mm long; the two frontal setae shining black; posterior orbital seta white, 0.5 to 0.7 times as long as anterior orbital seta; inner vertical seta dark brown, 0.54 to 0.71 times as long as head height, outer vertical bristle white, 0.22 to 0.30 times as long as head height; face, including antennal foveae, white; palpi light yellow, with 4–9 prominent, dark brown to black setulae apically; antenna 0.8 to 0.9 as long as face midline, yellow, sometimes reddish, arista dark brown except base ocherous.

Thorax: Scutum, scutellum, and pleural sclerites yellowish-gray pollinose over shiny black ground-color, short, white setulae invest entire scutum; scutellum slightly darker centrally and apically than marginally, where yellowish; complement of thoracic bristles usual for the genus, all dark brown or black except posterior notopleural, white; subscutellum and mediotergite gray pollinose; scutellar setulae shorter and inserted closer to each other than are scutal setulae; scutellum bare centrally, setulae present only laterally; halters yellow, ocherous basally. Legs mostly entirely light to ocherous yellow, sometimes hind femur with light brown, ventrolateral longitudinal streak; hind tibia with parallel rows of yellow to dark brown or black setulae and distinct anterodorsal row of dark brown to black setae on basal ⅔, the longest seta about as long as width of tibia; hind femur with black setulae on dorsum. Wing pattern as in Fig. 1, with a prominent hyaline area immediately distad of pterostigma extended from costal margin posterior to and touching vein R_{4+5}, but only rarely extending to vein M; instead, usually oval, sometimes elliptical to bell-shaped, hyaline spot in basal end of cell r_{4+5} arising on and always touching vein M, usually extending more than ⅔ across cell r_{4+5}, and occasionally reaching vein R_{4+5}; dark area in pterostigma extended posteriorly to vein R_{2+3}, usually with one, sometimes none or two, hyaline, tiny to prominent spots each in cells r_1 and r_{2+3}, thence to vein R_{4+5} with a few 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 may cross vein CuA_1 and extend anteriorly nearly across cell dm, or anteriorly divide into hyaline spots (Fig. 1); anal lobe light brown posteriorly to spurious vein or just beyond, then sometimes faint brown to posterior wing margin between large hyaline spots.

Abdomen: All tergites gray pollinose except T_6, which has shiny, dark brown to black spot medially, 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; six, long, dark brown to black setae along posterior margin and one or two setae laterally on last abdominal tergite; oviscape flat, dark brown or black, with setulae on basal half similar to those on abdominal tergites, apical half with extremely fine, short black setae; oviscape in dorsal view 2.5 to 3.2 times as long as last abdominal tergite and 0.9 to 1.3 as wide at base as long.

Male (allotype).—*Thorax:* Like ♀, but more ♂ than ♀ with light brown, ventrolateral streak on hind femur.

Variation.—Examination of reared *T. teerinki* with intact setation confirmed that the holotype, allotype, and most adults had two pairs of black frontal setae; however, five (3.7%) of 136 ♀ paratypes had three pairs of frontal setae, of which the third pair was weak and black and inserted between or ventral to the other two pairs. Another 14 (10.3%) of the 136 ♀ paratypes had five frontal setae, one of which was weak and black, but with all five setae similar in size in two other ♀ paratypes. Six (3.4%) of 147 ♂ paratypes had three pairs of frontal setae, in all but one of which, the third pair was weaker than the other pair and was inserted between or ventral to the other two pairs. Thus, a single ♂ had three pairs of black, frontal setae of similar size. Another 13 (8.8%) of the 147 ♂ paratypes had five frontal setae, one of which was weak and black in 11 ♂ paratypes, weak and white in one ♂ paratype, and with all five similar in size in another ♂ paratype. Foote et al. (1993) noted that *Tephritis baccharis* sometimes has one or two additional pairs of weak setae, variation of the type also now reported in *T. teerinki.*

Twenty-six (13.1%) of the 136 ♀ paratypes had one hylaline spot in cell r_1 in the dark area extending posteriorly from the stigma in both wings. In another 40 (29.4%) of the 136 ♀ paratypes, one hyaline spot occurred in cell r_1 in only one wing; whereas, the other wing in three of these paratypes had two spots or lacked spots in the other 37 ♀ paratypes. The holotype and 69 (51.4%) of the 136 ♀ paratypes lacked spots in cell r_1 in the dark area extending posteriorly from the stigma in both wings. Fifty-eight (42.6%) of the 136 ♀ paratypes had one hyaline spot in cell r_{2+3} in the dark area extending posteriorly from the stigma in both wings. In another 29 (21.3%) of the 136 ♀ paratypes, one hyaline spot occurred in cell r_{2+3} in only one wing; whereas, the other wing in 11 of these paratypes had two spots or lacked spots in the other 18 ♀ paratypes. Six (4.4%) of the 136 ♀ paratypes had two hylaline spots in cell r_{2+3} in the dark area extending posteriorly from the stigma in both wings. The holotype and 43 (32.4%) of the 136 ♀ paratypes lacked spots in cell r_{2+3} in the dark area extending posteriorly from the stigma in both wings.

Forty (27.2%) of the 147 ♂ paratypes had one hylaline spot in cell r_1 in the dark area extending posteriorly from the stigma in both wings. In another 36 (24.5%) of the 147 ♂ paratypes, one hyaline spot occurred in cell r_1 in only one wing; whereas, the other wing in all 36 of these paratypes lacked spots. The allotype and 71 (48.9%) of the 147 ♂ paratypes lacked spots in cell r_1 in the dark area extending posteriorly from the stigma in both wings. The allotype and 61 (41.5%) of the 147 ♂ paratypes had one hyaline spot in cell r_{2+3} in the dark area extending posteriorly from the stigma in both wings. In 39 (26.5%) of the 147 ♂ paratypes, one hyaline spot occurred in cell r_{2+3} in only one wing; whereas, the other wing in 19 of these paratypes had two spots or lacked spots in the other 20 ♂ paratypes. Eight (5.4%) of the 147 ♂ paratypes had two hylaline spots in cell r_{2+3} in the dark area extending posteriorly from the stigma in both wings. Thirty-eight (25.8%) of the 147 ♂ paratypes lacked spots in cell r_{2+3} in the dark area extending posteriorly from the stigma in both wings.

In 18 (13%) of the 136 ♀ paratypes, the hyaline spot crossed cell r_{4+5} anteriorly in both wings and reached vein R_{4+5}, but still remained oval, elliptical, or bell-shaped; however, in two of these 18 ♀ paratypes, this spot broadly joined vein R_{4+5}. Five more (3.7%) ♀ paratypes had this hyaline spot crossing cell r_{4+5} anteriorly and just touching vein R_{4+5} in one wing. In seven (4.8%) of the 147 ♂ paratypes, the hyaline spot crossed cell r_{4+5} anteriorly in both wings and reached vein R_{4+5}, but usually still remained oval, elliptical, or bell-shaped. Five more (3.4%) ♂ paratypes had this hyaline spot crossing cell r_{4+5} anteriorly and just touching vein R_{4+5} in one wing.

Sixty-six (48.5%) of the 136 ♀ paratypes had a light brown, ventrolateral longitudinal streak on hind femur; whereas, the allotype and 127 (86.3%) of the 147 ♂ paratypes had such a marking, which also was smaller in the females. The holotype and the remaining paratypes lack such brown markings on their hind femora.

Fourteen (10.3%) of the 136 ♀ paratypes had a third hyaline spot in cell r_1 near the apex in both wings, of which three pairs were tiny and at least one spot was small and faint in two more ♀. In 18 additional ♀ (13.2%), only one wing had such a mark, of which seven were small and faint. Six (4.0%) of the 147 ♂ paratypes had such spots in both wings, but two of these pairs were small and faint. Another 15 (10.2%) of the 147 ♂ paratypes had a third spot in only one wing, of which eight spots were small and faint.

Thirty four (26.4%) of the 136 ♀ paratypes had cell a_2 light brown, noticeably pigmented posteriorly to spurious vein, but faint brown between large hyaline spots to posterior wing margin. Fifty one (34.7%) of the 147 ♂ paratypes showed this same pigmentation. The holotype, allotype, and remaining paratypes had anal lobes with unpigmented margins.

Diagnosis.—The main morphological character distinguishing the adults of *T. teerinki* from most other North American species north Mexico is the dark band in the wing extending obliquely from the pterostigma to cover vein r-m (Fig. 1). A wing length usually exceeding 3.5 mm then distinguishes. *T. teerinki* from *T. araneosa* (Coquillett). The oval, sometimes elliptical to bell-shaped, hyaline spot in the basal end of cell r_{4+5} also distinguishes *T. teerinki* from *T. araneosa* as well as *T. joanae* (Goeden 1993), in which this spot broadly connects veins R_{4+5} and M. The lack of pigmentation posteriorly much beyond the spurious vein (A_2) in the anal lobe also distinguishes most specimens of *T. teerinki* from *T. joanae* in which the anal lobe is pigmented to the wing margin (Goeden 1993). Foote et al. (1993) provided the main character for distinguishing *T. teerinki* from *T. ovatipennis* Foote, this being the dark tomentose color of the femora, especially those of the hind legs in *T. ovatipennis,* compared with the yellow femora, only sometimes marked with a light brown ventrolateral longitudinal streak on the hind femora in *T. teerinki.* The dark brown wing pattern of *Tephritis signatipennis* Foote distinctly extends to the posterior margin along the entire wing, but usually only extends posteriorly just beyond the spurious vein (A_2) in the anal lobe, or occasionally very faintly to the margin of the anal lobe, in *T. teerinki* (Fig. 1). *Tephritis teerinki* usually lacks the third hyaline spot near the apex of cell r_1 noted by Foote et al. (1993)

to be present in most specimens of *T. signatipennis.* Also, hyaline markings occupy most of cell m and extend posteriorly to posterior margin, as do large hyaline markings in cell cua_1 in *T. teerinki* (Fig. 1), as distinguished from *T. signatipennis* with its much darker wing (Foote et al. 1993).

The host relations of *T. teerinki, T. ovatipennis,* and *T. signatipennis* 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 (*candidipennis, ovatipennis, signatipennis*) to distinguish those larger species with longer oviscapes, and Blanc (Foote and Blanc 1979) described another, *leavittensis,* on the basis of additional characters." Goeden (1993) described *T. joanae,* another of those species with longer oviscapes, which now also includes *T. teerinki.* Other segregates will be described in my next paper.

Types.—Holotype, ♀; E(ast) of M(oun)t Gleason on USFS (U.S. Forest Service) R(oa)d 3N17 at 1,747 m (5,730 ft); Angeles Nat(ional) Forest, Los Angeles Co(unty), CA; T(ownship)3N(orth), R(ange)12W(est), S(ection)4; 28.v.1997, R. D. Goeden, coll. (hereafter RDG, coll.)/J. A. Teerink, coll. (hereafter JAT, coll.); reared from flower head of *Hulsea vestita;* allotype, ♂, same data as holotype (USNM). Paratypes: CALIFORNIA: 48 ♂ and 34 ♀; same data as holotype (23 ♂ and 23 ♀ to USNM). 12 ♂ and 5 ♀; same data as holotype, except 22.v.1996; RDG/JAT, coll. (2 ♂ and 2 ♀ to USNM). Unless otherwise indicated the following specimens also were reared from flower head of *Hulsea vestita.* 15 ♂ and 17 ♀; Deadman Creek, Inyo Nat. Forest, Mono Co.; T3S, R27E, S5; 9.ix.1986; RDG, coll. (3 ♂ and 3 ♀ to USNM). 7 ♂ and 7 ♀; Deadman Creek, Inyo Nat. Forest, Mono Co.; T3S, R27E, S5; 21.vii.1987; RDG, coll. (2 ♂ and 2 ♀ to USNM). 2 ♂ and 4 ♀; Trail to Fish Creek M(eado)w, S(an) Bernardino Nat. Forest, San Bernardino Co.; TIN, R2E, S33; 14.viii.1987; RDG, coll. (1 ♂ and 1 ♀ to USNM). 3 ♂ and 5 ♀; Thomas Mountain, San Bernardino Nat. Forest, Riverside Co.; 28.vi.1998; RDG, coll. (1 ♂ and 1 ♀ to USNM). 1 ♂ and 2 ♀; Osa Meadow, Sequoia Nat. Forest, Tulare Co.; 8550 ft (2606 m), T20S, R34E, S16; 15.vii.1993; RDG/JAT, coll. (1 ♀ to USNM). 4 ♂; E of Poison Meadow, Sequoia Nat. Forest, Tulare Co.; 7170 ft (2185 m), T22S, R33E, S27; 22.vi.1994; RDG/JAT, coll. (1 ♂ to USNM). 6 ♂ and 9 ♀; NW of Magic Mountain on USFS Rd 3N17, Angeles Nat. Forest, Los Angeles Co.; 4,370 ft (1,332 m), 22.v.1996; RDG/JAT, coll. (2 ♂ and 2 ♀ to USNM). 3 ♂ and 2 ♀; Mill Creek Summit on USFS Rd. 3N17, Angeles Nat. Forest, Los Angeles Co.; 5,020 ft (1530 m), T4N, R12W, S25; 14.v.1997; RDG/JAT, coll. (1 ♂ and 1 ♀ to USNM). 18 ♂ and 18 ♀; SE of Mission Springs, San Bernardino Nat. Forest, San Bernardino Co.; 8130 ft (2,478 m), T1S, R2E, S2; 17.vii.1997; RDG/JAT, coll. (5 ♂ and 5 ♀ to USNM). 31 ♂ and 31 ♀ (mounted of 171 ♂ and 164 ♀ reared); Liebre Mountain, Angeles Nat. Forest, Los Angeles Co.; T7N, R17W, S12; 14.vii.1982; RDG, coll.; reared from flower heads of *Hulsea californica* Torrey and A. Gray; (12 ♂ and 12 ♀ to USNM).

Etymology.—This tephritid is named for my coworker, Jeffrey A. Teerink, who aided me in studying this tephritid as *Tephritis ovatipennis,* and many other tephritids for 8 years, during one of the more satisfying periods in my career.

Immature stages.—The egg, first-, second-, and third-instar larvae, and puparium are described below.

Egg: Fifty-five eggs measured *in situ* in field-collected, preblossom flower heads were white, opaque, smooth, elongate-ellipsoidal, 0.80 ± 0.006 (range, 0.76–0.82) mm long, 0.21 ± 0.003 (range, 0.20–0.24) mm wide, smoothly rounded at tapered basal end (Fig. 2A); pedicel button-like, 0.02 mm long, circumscribed apically by different-sized, semicircular, oval, or elliptical, some-

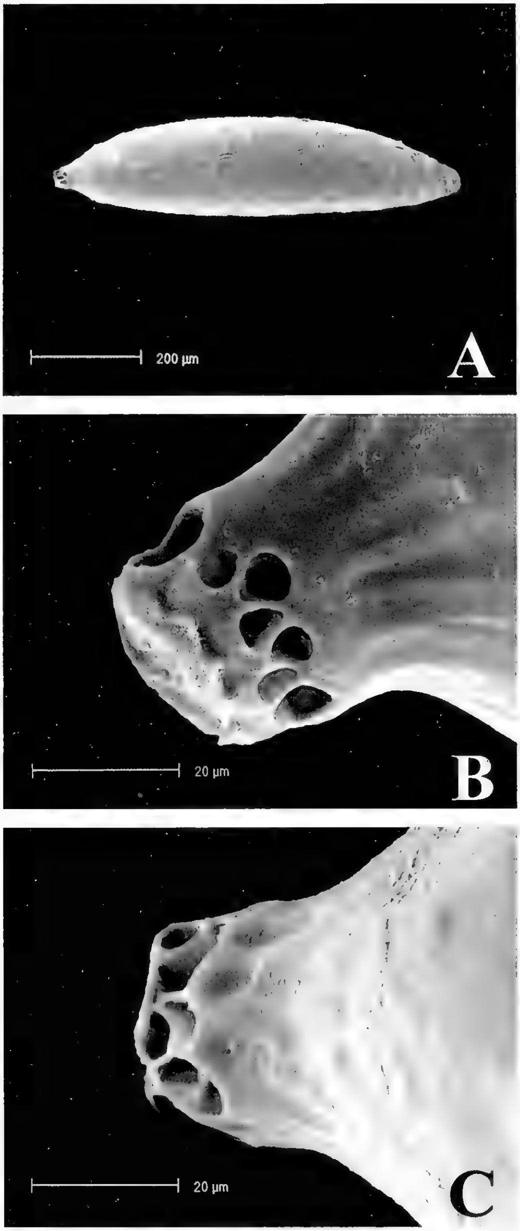

Fig. 2. Egg of *Tephritis teerinki*: (A) habitus, anterior end to left; (B) pedicel showing pattern and shapes of aeropyles; (C) pedicel of another egg showing different shapes of aeropyles.

times partitioned, aeropyles arranged in a single row perpendicular to the long axis of the egg (Figs. 2B, C).

The egg of *T. teerinki,* like that of *joanae* (Goeden 2001b), 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. Except for the pedicel (Fig. 2B), the eggs of *T. teerinki* and *T. joanae* are covered by a smooth, membranous sheath (Fig. 2A, Goeden 2001b), which remains intact and is not partly shed and peeled back during oviposition as in the other two species. In *T. arizonaensis* (Goeden et al. 1993), this membranous sheath also is prominently, longitudinally striated. The function of this membranous 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 four species of *Tephritis.*

First instar: White, cylindrical, body segments well-defined (Fig. 3A); gnathocephalon conical (Fig. 3B); dorsal sensory organ well-defined, round, flattened (Figs. 3B-1, C-1, D-1); anterior sensory lobe (Figs. 3B-2, C-2, D-2) with terminal sensory organ (Fig. 3C-3), lateral sensory organ (Fig. 3C-4), supralateral sensory organ (Fig. 3C-5), and pit sensory organ (Fig. 3C-6); stomal sense organ (Figs. 3B-7, C-8, D-5) ventrolaterad of anterior sensory lobe and fused with flattened, protrudent, "lateral" integumental petal (Figs. 3B-3, C-7, D-3) dorsad of each mouth hook; two more, rounded, protrudent, "median" integumental petals, one above the other, between anterior sensory lobes (Figs. 3C-9, D-4); mouthhook bidentate (Figs. 3B-4, D-6); median oral lobe laterally compressed, apically rounded, ventrally flattened (Figs. 3B-5, D-7), basally attached to labial lobe (Figs. 3B-6, D-8) bearing two, prominent apical pores; three verruciform sensilla (Figs. 3B-9, D-9) dorsolaterally, laterally, and ventrolaterally circumscribe gnathocephalon; prothorax circumscribed anteroventrally by posteriorly directed, teethlike, minute acanthae (Fig. 3B-8); mesothorax laterally bears six verruciform sensilla, five in vertical row, plus a sixth sensillum close

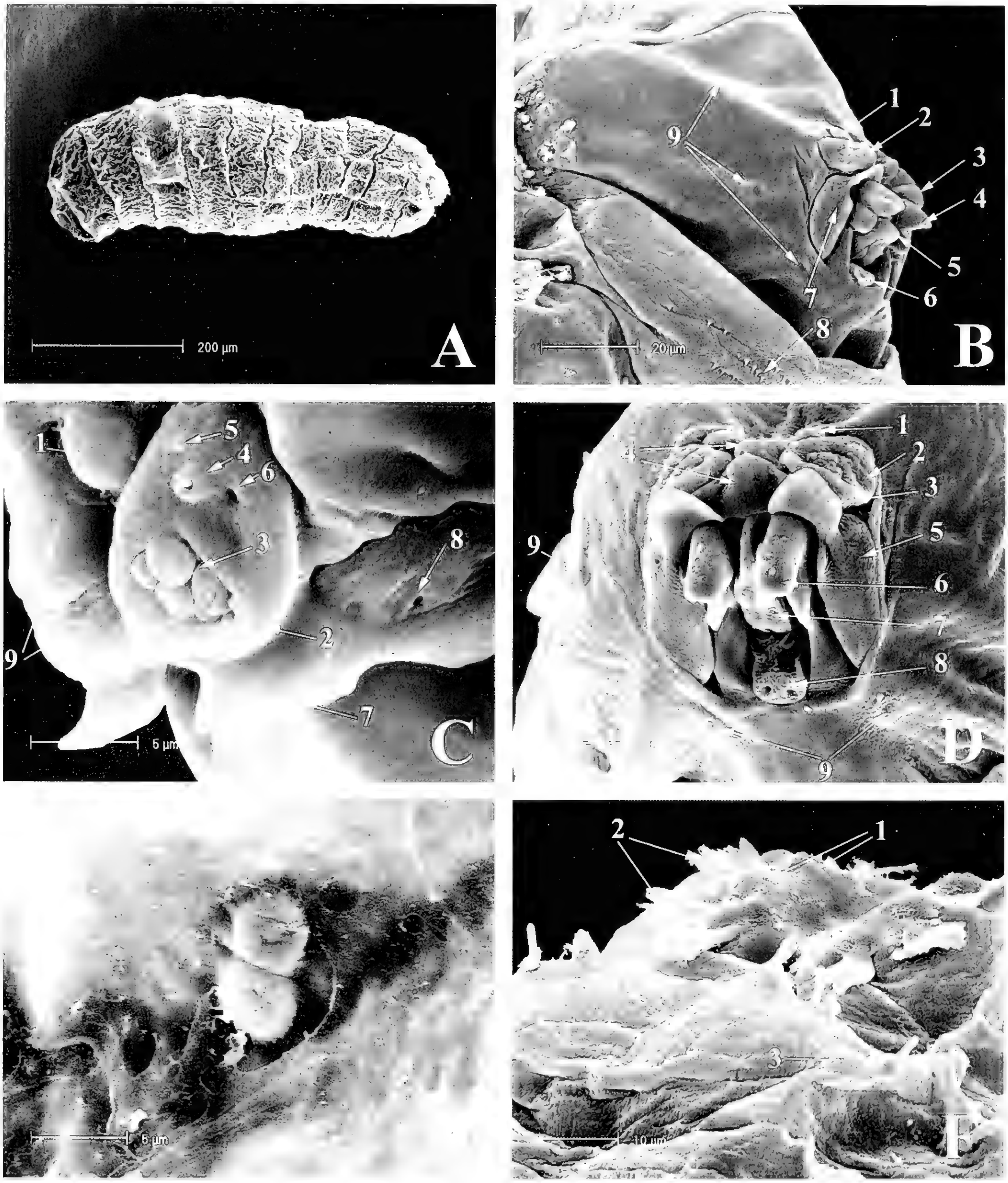

Fig. 3. First instar of *Tephritis teerinki*: (A) habitus, anterior end to left; (B) gnathocephalon, ventrolateral view, 1—dorsal sensory organ, 2—anterior sensory lobe, 3—integumental petal, 4—mouthhook, 5—median oral lobe, 6—labial lobe, 7—stomal sense organ, 8—minute acanthae, 9—verruciform sensilla; (C) 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 petal, 8—stomal sense organ, 9—"median" integumental petals; (D) oral cavity, ventral view, 1—dorsal sensory organ, 2—anterior sensory lobe, 3—"lateral" integumental petal, 4—"median" integumental petals, 5—stomal sense organ, 6—mouthhook, 7—median oral lobe, 8—labial lobe, 9—verruciform sensilla; (E) "doubled," (close-set), lateral verruciform sensilla on mesothorax; (F) posterior spiracular plate, 1—rimae, 2—interspiracular processes, 3—ventrolateral stelex sensillum, 4—intermediate sensory complexes.

to second-most dorsal sensillum (Fig. 3E) or slightly separated therefrom (not shown); anterior tenth of meso- and metathorax circumscribed by minute acanthae, as are anterior fourth of first abdominal segment (A-I), anterior third of A-II, and anterior halves of A-III to A-VIII (not shown), posterior spiracular plate bears three ovoid rimae (Fig. 3F-1), ca. 0.01 mm long, and four interspiracular processes (Fig. 3F-2), each with two to four, foliose branches with one to three, apical teeth, longest branch measuring 0.01 mm; stelex sensillum dorsolaterad and ventrolaterad (Fig. 2F-3) of posterior spiracular plate; intermediate sensory complexes (Fig. 3F-4) each with a stelex sensillum and a medusoid sensillum.

This description of the first instar of *T. teerinki* is the first for this instar in the genus *Tephritis*; hence, there is no basis for comparison with other congeneric species. However, it is worth noting that an integumental petal fused with the stomal sense organ also distinguishes the first instars from subsequent instars of at least five species of *Neaspilota* (Goeden 2001a), and as first reported for the first instar of *Trupanea vicina* (Wulp) (Goeden and Teerink 1999). Also, the two stelex sensilla dorso- and ventrolaterad of each posterior spiracular plate as well as the two ventral intermediate sensory complexes, agree with the type, number, and arrangement of these sensilla reported for four species of *Neaspilota* (Goeden 2001a) and at least three species of *Trupanea* (Goeden and Teerink 1999, Teerink and Goeden 1999). Other intergeneric comparisons, like intrageneric comparisons, are deferred until the first instars of additional species of *Tephritis* are described.

Second instar: White, cylindrical, rounded anteriorly, truncated posteriorly, body segments well-defined (Fig. 4A); gnathocephalon conical, anteriorly flattened, and medially halved by vertical suture (Fig. 4B); dorsal sensory organ well-defined, flattened (Figs. 4B-1, C-1), with two pits dorsolaterad of its base (Fig. 4C-2); anterior sensory lobe (Figs. 4B-2, C-3) with terminal sensory organ (Fig. 4C-4), lateral sensory organ (Fig. 4C-5), supralateral sensory organ (Fig. 4C-6), and pit sensory organ (Fig. 4C-7); stomal sense organ (Figs. 4B-4, C-9, D-2) ventrolaterad of anterior sensory lobe; mouthhook bidentate (Figs. 4B-5, D-4); median oral lobe, clavate, laterally compressed, apically rounded (Figs. 4B-6, D-5); about four, flattened, foliose, integumental petals dorsad of each mouthhook (Figs. 4B-3, C-8, D-1); at least five, complete, oral ridges (Figs. 4B-7, C-10) laterad of anterior sensory lobe, and at least two incomplete oral ridges dorsad of the aforementioned oral ridges (Fig. 4B); prothorax circumscribed anteriorly by at least two rows of minute acanthae (Fig. 4B-8); anterior thoracic spiracle with four, doliform papillae (not shown); lateral spiracular complexes not seen; posterior spiracular plate bears three ovoid rimae (Fig. 4E-1), ca. 0.02 mm long, and four interspiracular processes (Fig. 4E-2), each with two to three, foliose branches with one to three, apical teeth, longest branch measuring 0.02 mm; stelex sensillum ventrolaterad (Fig. 4F-1) of posterior spiracular plate, other sensilla, either at lateral or dorsolateral positions not seen; intermediate sensory complexes (Fig. 4F-2) each with a stelex sensillum (Fig. 4F-3) and a medusoid sensillum (Fig. 4F-4).

The habitus of the second instar of *T. teerinki* (Fig. 4A) approximates those of *T. baccharis* (Goeden and Headrick 1991), *T. arizonaensis* (Goeden et al. 1993) and *T. joanae* (Goeden 2001b). The dorsal sensory organ is well-defined in the second instar of *T. teerinki* (Figs. 4B-1, C-1), *T. baccharis* (Goeden and Headrick 1991), *T. arizonaensis* (Goeden et al. 1993), and *T. joanae* (Goeden 2001b). Only the second instars of *T. teerinki* and *T. joanae* (Goeden 2001b) were described in sufficient detail to date to allow comparison of additional characters. Accordingly, the integumental petals of *T. teerinki* (Figs. 4B-3, C-8, D-1) at four are fewer in number, foliose not papilliform, and reduced dorsomedially to a single, papilliform pair, not three or four pairs in a

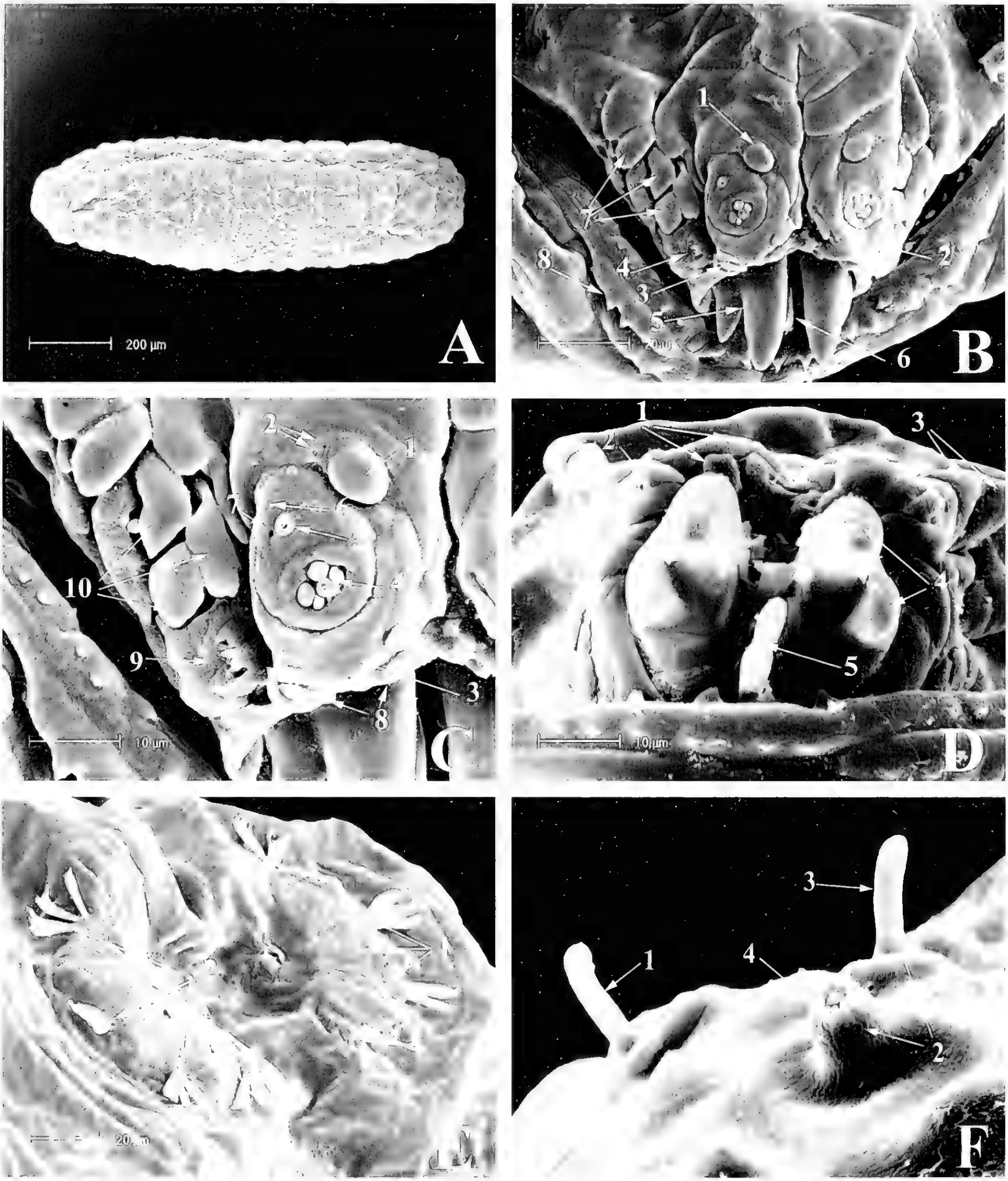

Fig. 4. Second instar of *Tephritis teerinki*: (A) habitus, anterior end to left; (B) gnathocephalon, frontal view, 1—dorsal sensory organ, 2—anterior sensory lobe, 3—integumenal petal, 4—stomal sense organ, 5—mouthhook, 6—median oral lobe, 7—oral ridges, 8—minute acanthae; (C) 1—dorsal sensory organ, 2—pair of pits, 3—anterior sensory lobe, 4—terminal sensory organ, 5—lateral sensory organ, 6—supralateral sensory organ, 7—pit sensory organ, 8—integumental petals, 9—stomal sense organ, 10—oral ridges (complete); (D) oral cavity, ventral view, 1—integumental petals, 2—stomal sense organ, 3—oral ridges, 4—mouthhook, 5—median oral lobe; (E) posterior spiracular plate, 1—rimae, 2—interspiracular processes, (F) 1—ventrolateral stelex sensillum, 2—intermediate sensory complex, with 3—stelex sensillum and 4—medusoid sensillum.

vertical series between the anterior sensory lobes as in *T. joanae* (Goeden 2001b). The oral ridges of the second instars of both *T. teerinki* (Figs. 4B-7, C-10) and *T. joanae* (Goeden 2001b) lie laterad of each terminal sensory organ. The anterior spiracle of *T. teerinki* bears four, not five, doliform papillae like that of *T. joanae* (Goeden 2001b). The lateral spiracular complexes of the metathorax and the first abdominal segment remain described only for *T. joanae* (Goeden 2001b). Only minor differences in the number of branches on the interspiracular processes, i.e., two to three for *T. teerinki* (Fig. 4E-2) versus two to four for *T. joanae* (Goeden 2001b), were noted.

Third instar: White, ovoidal, distinctly segmented, tapered anteriorly, truncated posteriorly (Fig. 5A); gnathocephalon conical, anteriorly flattened, and medially cleaved by a vertical suture; posteriorly directed, spinose, minute acanthae incompletely circumscribe prothorax anteriorly (Fig. 5B-1); dorsal sensory organ well-defined, hemispherical (Figs. 5B-2, C-1); anterior sensory lobe (Figs. 5B-3, C-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 spatulate, integumental petals in two rows above each mouthhook (Fig. 5C-7), the lower petal continuing laterally around oral cavity, separate from stomal sense organ (Figs. 5B-4, C-8) ventrolaterad of anterior sensory lobe; three complete oral ridges (Figs. 5B-5, C-10) laterad of each anterior sensory lobe; mouthhook (Figs. 5B-6, C-9) apparently bidentate; median oral lobe not seen; verruciform sensilla dorsolaterad (Fig. 5B-7) and laterad (Fig. 5C-11) of oral ridges; anterior thoracic spiracle (Figs. 5D, E-1) on posterior margin of prothorax bears five, doliform papillae (Fig. 5D); mesothoracic and metathoracic lateral spiracular complexes with five (Fig. 5E-3) and six verruciform sensilla (Fig. 5E-5), respectively, aligned vertically (Figs. 5E-3, -5), mesothoracic spiracle (Fig. 5E-2) and metathoracic spiracle (Figs. 5E-4, F-1) greatly reduced; mesothoracic spiracle (Fig. 5E-2) anterior to dorsal-most verruciform sensillum (Fig. 5E-3); metathoracic spiracle (Figs. 5E-4, F-1) anterior to second-most-dorsal verruciform sensillum (Figs. 5E-5, F-2); posteriorly directed, tooth- or claw-like, minute acanthae (Fig. 6A) incompletely circumscribe anterolateral ⅛th of mesothorax, anterolateral ⅓rd of metathorax (Fig. 6A), anterolateral half of 1st abdominal segment (A-1), and all or most of A-II through A-VIII (Fig. 6B); each posterior spiracular plate surrounded by a pair of dorsolateral stelex sensilla (Fig. 6B-1) and ventrolateral pair of stelex sensilla (Fig. 6B-2); each posterior spiracular plate bears three ovoid rimae (Fig. 6B-3), ca. 0.01 mm in length, and four, two- to four-branched, single-, bi- or trifurcately-tipped, interspiracular processes, each ca. 0.025 mm long (Figs. 6B-4, C); intermediate sensory complex (Figs. 6B-5, D-1) with a stelex sensillum (Fig. 6D-2) and a medusoid sensillum (Fig. 6D-3).

The habitus of the third instar of *T. teerinki* (Fig. 5A) more closely resembles that of *T. joanae* (Goeden 2001b) in shape than the cylindrical shape described for *T. baccharis* (Goeden and Headrick 1991) and *T. arizonaensis* (Goeden et al. 1993). This correlates with the obligatory florivorous habit of the former pair of species, compared to the gallicolous or branch-mining development of one generation of each of the bivoltine latter pair. The gnathocephalon, or at least the anterior sensory lobes of all four species are separated by a vertical medial suture (Goeden and Headrick 1991; Goeden et al. 1993; Goeden 2001b; Fig. 6B). More minute acanthae anteriorly circumscribe the thoracic and abdominal segments of the third instar of *T. teerinki* (Figs. 6A, B) than those of *T. baccharis* (Goeden and Headrick 1991), *T. arizonaensis* (Goeden et al. 1993), and *T. joanae* (Goeden 2001b).

The integumental petals in the third instars of all three congeners examined to date are arranged in a double row above each mouthhook, but here again, those of *T. teerinki* (Fig. 5A) are fewer in number

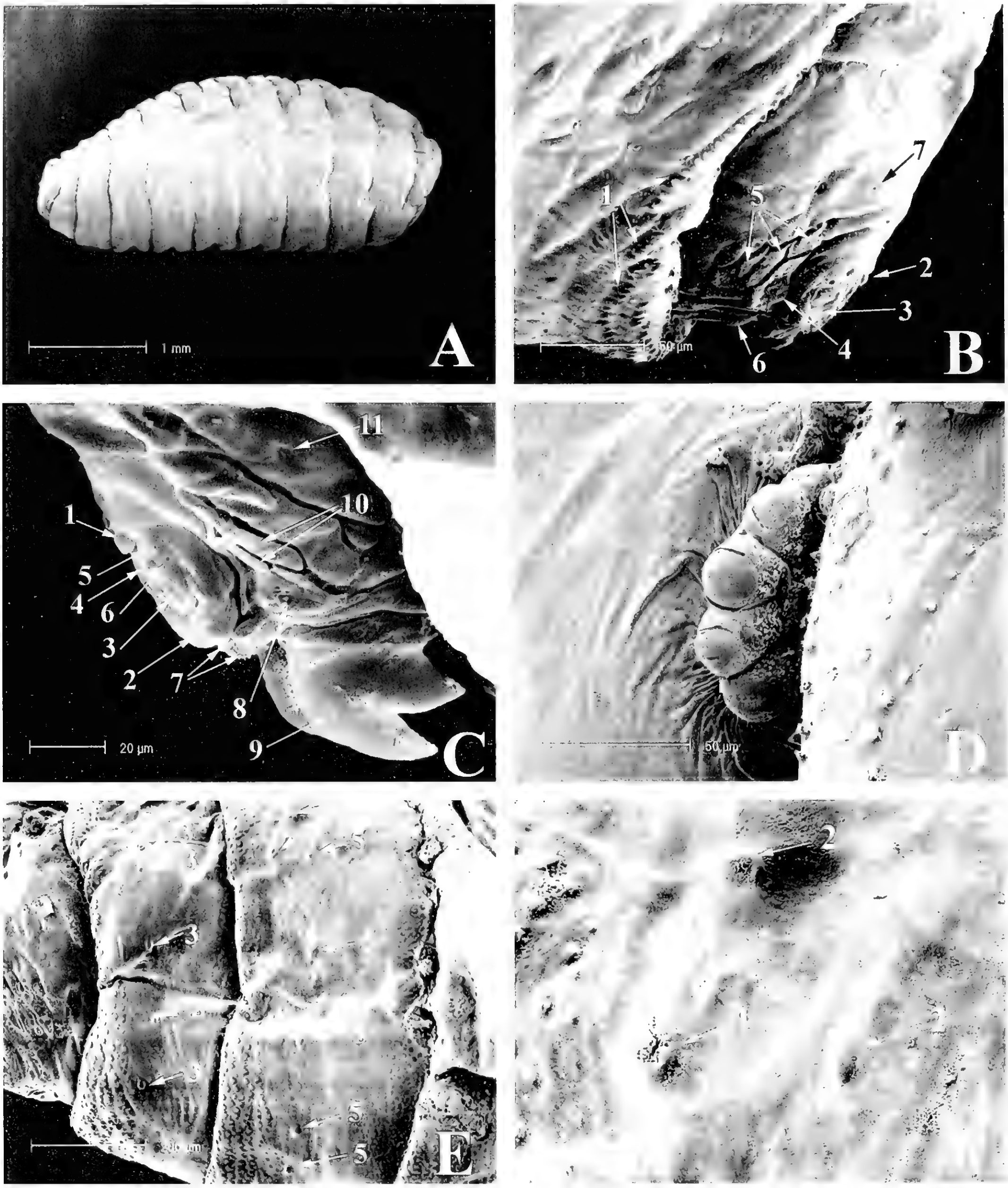

Fig. 5. Third instar of *Tephritis teerinki*: (A) habitus, anterior to left; (B) gnathocephalon and prothorax, lateral view, 1—minute acanthae, 2—dorsal sensory organ, 3—anterior sensory lobe, 4—stomal sense organ, 5—oral ridges, 6—mouthhook; (C) gnathocephalon, lateral view, 1—dorsal sensory organ, 2—anterior sensory lobe, 3—terminal sensory organ, 4—lateral sensory organ, 5—supralateral sensory organ, 6—pit sensory organ, 7—integumental petals, 8—stomal sense organ, 9—mouthhook, 10—oral ridges, 11—verruciform sensillum; (D) anterior spiracle; (E) mesothoracic and metathoracic, lateral spiracular complexes, 1—anterior spiracle on prothorax, 2—mesothoracic spiracle, 3—verruciform sensilla of mesothorax, 4—metathoracic spiracles, 5—verruciform sensilla of metathorax; (F) 1—metathoracic spiracle, 2—verruciform sensilla.

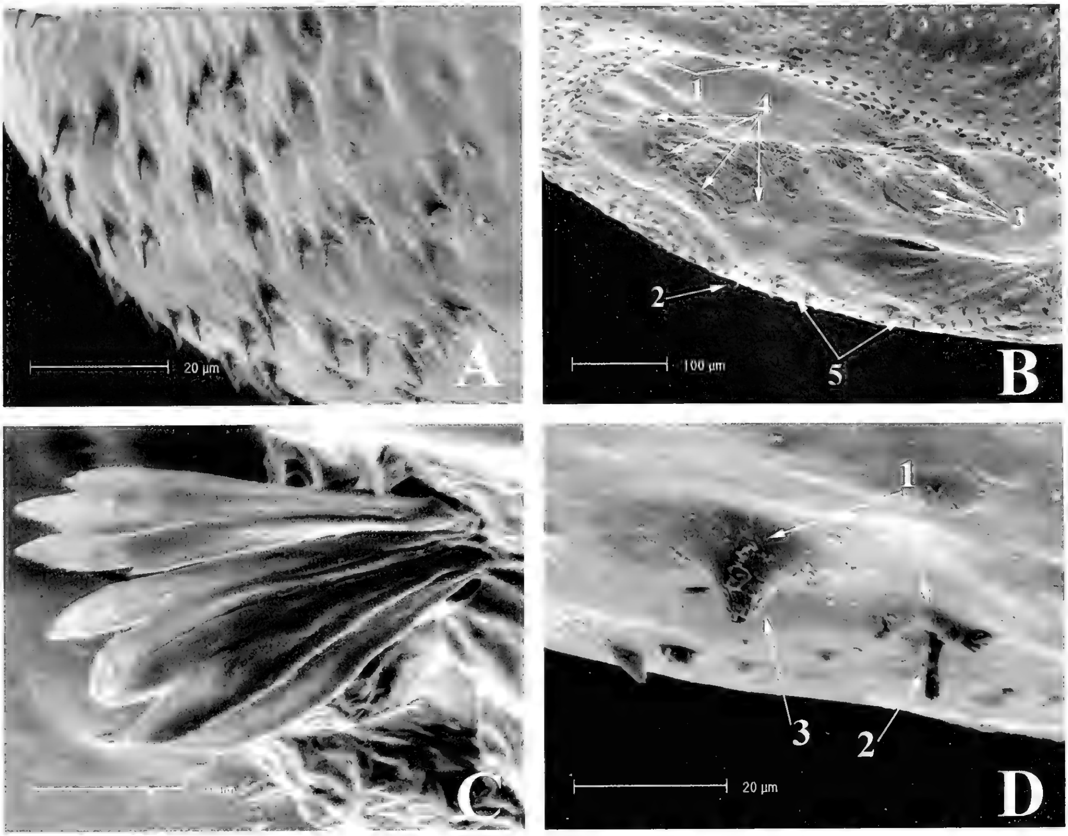

Fig. 6. Third instar of *Tephritis teerinki,* continued: (A) minute acanthae on metathoracic venter; (B) caudal segment, 1—dorsolateral stelex sensilla, 2—ventrolateral stelex sensillum, 3—rimae, 4—interspiracular processes, 5—intermediate sensory complex; (C) interspiracular process; (D) 1—intermediate sensory complex, 2—stelex sensillum, 3—medusoid sensillum.

than those of *T. baccharis* (Goeden and Headrick 1991), *T. arizonaensis* (Goeden et al. 1993), and *T. joanae* (Goeden 2001b), and *T. teerinki* also apparently lacks 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. 5B-2; Goeden and Headrick 1991; Goeden et al. 1993; Goeden 2001b). The integumental petals increase in number between the last two instars of both *T. teerinki* (Figs. 4B-3, C-8, D-1, 5A) and *T. joanae* (Goeden 2001b).

The ventral oral ridges of the third instars of *T. teerinki* (Figs. 5B-5, C-10), *T. baccharis* (Goeden and Headrick 1991), and *T. arizonaensis* (Goeden et al. 1993) lack the bluntly toothed ventral margin found in the third instar of *T. joanae* (Goeden 2001b).

The mouthhooks of the third instars of *T. teerinki* (Figs. 5B-6, C-9) 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 34 specimens of third instar *T. teerinki* examined by SEM had their mouthparts hidden, which precluded examination of the oral cavity in ventral view by scanning electron microscopy, as was possible with the first and second instars (Figs. 3D, 4D).

The anterior spiracle of the third instar of *T. teerinki* (Fig. 5D) bore five papillae, one more than the second instar, but not three in the second instar and three or four in the third instar, as shown by *T. joanae* (Goeden 2001b), i.e., five to three or four papillae, and in most other Tephritinae examined to date. The lateral spiracular complex of the mesothorax of the third instar of *T. teerinki* (Fig. 5E-5) contained one more verruciform sensillum than that of *T. joanae* (Goeden 2001b).

The number of stelex sensilla surrounding the posterior spiracular plates of the third instars apparently differ among the three *Tephritis* species examined to date. Ten stelex sensilla reportedly surround the margin of the caudal segment of *T. arizonaensis* (Goeden et al. 1993) in a four-dorsal, six-ventral arrangement, not including the two intermediate sensory complexes ventrad of the spiracular plates. The medusoid sensilla in the intermediate sensory complex was described as tuberculate, being topped by what appear to be only two, short papillae. On the other hand, the caudal segment of the third instar of *T. baccharis* is ringed by three pairs of stelex sensilla, one pair each at dorsal, medial, and ventral positions, and a pair of medusoid sensilla inaccurately reported by Goeden and Headrick (1991) as associated with the dorsal pair of stelex sensilla. This should have read ". . . ventrally each closely paired with a separate stelex sensillum . . ." to constitute the intermediate sensory complex as pictured in Goeden and Headrick (1991). Here, the medusoid sensillum was described as a dome with a raised crown bearing several open pores, and thus, either having extremely short apical papillae, or lacking same. In contrast, the caudal segment of the third instar of *T. teerinki* (Fig. 6B), like that of *T. joanae* (Goeden 2001b), apparently is surrounded by only a dorsolateral and ventrolateral pair of stelex sensilla as well as a ventral pair of intermediate spiracular complexes (Fig. 6B), the medusoid sensilla of which each bears short apical papillae (Fig. 6D-3) more typical of this type of chemosensillum (Goeden 2001a, b; Goeden and Teerink 1999, and references therein).

Further interspecific, intraspecific, and intergeneric comparisons of larval taxonomy are deferred until the next two papers on *T. araneosa* and *T. stigmatica.*

Puparium: Dull black, a few mostly unpigmented and darkened only anteriorly and posteriorly, ellipsoidal, and smoothly rounded at both ends (Fig. 7A); anterior end bears the invagination scar (Fig. 7B-1) and anterior thoracic spiracles (Fig. 7B-2); posterior spiracular plate bears three broadly elliptical rimae (Fig. 7C-1), and four, two- to four-branched, single, bi- or trifurcately-tipped, interspiracular processes (Fig. 7C-2). Seventy-two puparia averaged 3.86 ± 0.023 (range, 3.19–4.35) mm in length; 1.82 ± 0.013 (range, 1.43–2.02) mm in width.

Distribution and Hosts

To date, *Tephritis teerinki* is only known from California and from flower heads of *Hulsea californica* and *H. vestita*; however, it has been reported elsewhere by me (Goeden 1993), and possibly by others, as *T. ovatipennis,* and this should be corrected. Accordingly, *T. teerinki,* possibly may be a nearly monophagous species on *Hulsea* spp. in the subtribe Chaenactidinae of the Tribe Helenieae (Bremer 1994). I also have reared a series of small-sized specimens, i.e., with wing lengths less than 3.5 mm (Foote et al. 1993), morphologically also near *T. ovatipennis,* but from another host plant in a different tribe. I also have some larger specimens near *T. araneosa* that probably also represent a separate species, but my coworkers and I have not studied its life history and immature stages like *T. baccharis* (Goeden and Headrick 1991), *T. arizonaensis* (Goeden et al. 1993), and *T. joanae* (Goeden 2001b), and now, *T. teerinki.* As I have noted elsewhere, locating a good sized, readily reached, field population is requisite for intensive studies of the type needed to sort out the *araneosa* complex. Two specimens in my collection key to *araneosa* based on the small size of their wing, i.e., less than 3.5 mm, but which oth-

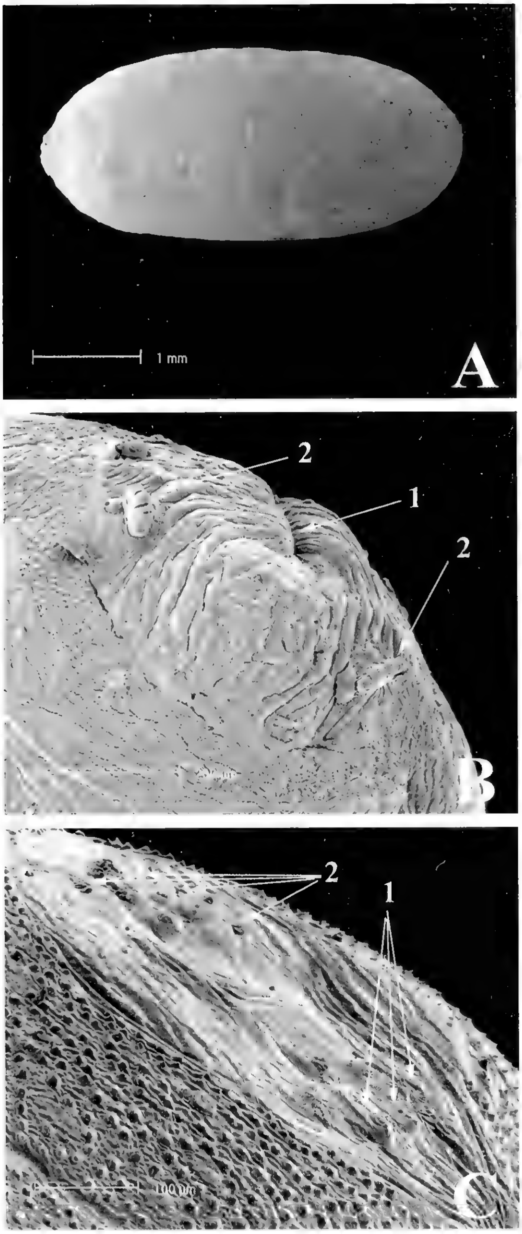

Fig. 7. Puparium of *Tephritis teerinki*: (A) habitus, anterior to left; (B) anterior end, 1—invagination scar, 2—anterior thoracic spiracle; (C) posterior spiracular plates, 1—rimae, 2—interspiracular processes.

erwise fit the newly described *T. teerinki.* Each of these ♂ specimens was reared from different hosts, *Achillea millefolium* L., which belongs to the subtribe Achilleae of the tribe Anthemidae, or *Artemisia tridentata* Nuttall, which belongs to the subtribe Artemisiinae of the tribe Anthemideae (Bremer 1994) and both earlier were reported and identified by me as *T. ovatipennis* (Goeden 1993). Since then, I have had access to the immeasurely helpful handbook of Foote et al. (1993), and the keys therein, and have learned to be less trustful of my identifications of single reared specimens. *Tephritis araneosa* is a small species associated with *Artemisia* spp. (Goeden, unpublished data); therefore, these specimens could well be variants of *T. araneosa,* or perhaps another undescribed species in this complex, but at the least should not have been identified as *T. ovatipennis* by Goeden (1993), nor now as *T. teerinki.*

BIOLOGY

Egg.—In each of 22, closed, preblossom, immature flower heads of *Hulsea vestita* an average of 3.3 ± 0.5 (range, 1–10) eggs of *T. teerinki* was inserted pedicel-last through the phyllaries into or among peripheral or inner florets or ovules (Fig. 8A). Thus, the aculeus penetrated one or more phyllaries during oviposition. Forty-six eggs (72%) of 63 eggs recorded rested with their long axes parallel to the receptacles of the flower heads. The remaining eggs rested at an angle of 45° or perpendicular to the surface of the receptacle (Fig. 8A), and an average of 1.8 ± 0.4 (range, 1–9) florets/ovules were damaged per flower head by oviposition. Thus, about 2.4% (range, 1.3–6.2%) of an average total of 75 (range, 12–182) ovules/soft achenes counted in 143 infested and uninfested, preblossom, blossom, and postblossom flower heads were damaged by oviposition. The receptacles of preblossom heads that contained eggs averaged 4.34 ± 0.15 (range, 3.42–6.27) mm in diameter.

Larva.—Upon eclosion, an average of 1.2 ± 0.12 (range, 1–3) first instars found feeding in 19 closed, preblossom flower heads tunneled immediately into a floret or ovule and then continued to feed parallel to the receptacle on one or more ovules (Fig. 8B). The receptacles averaged 1.94 ± 0.32

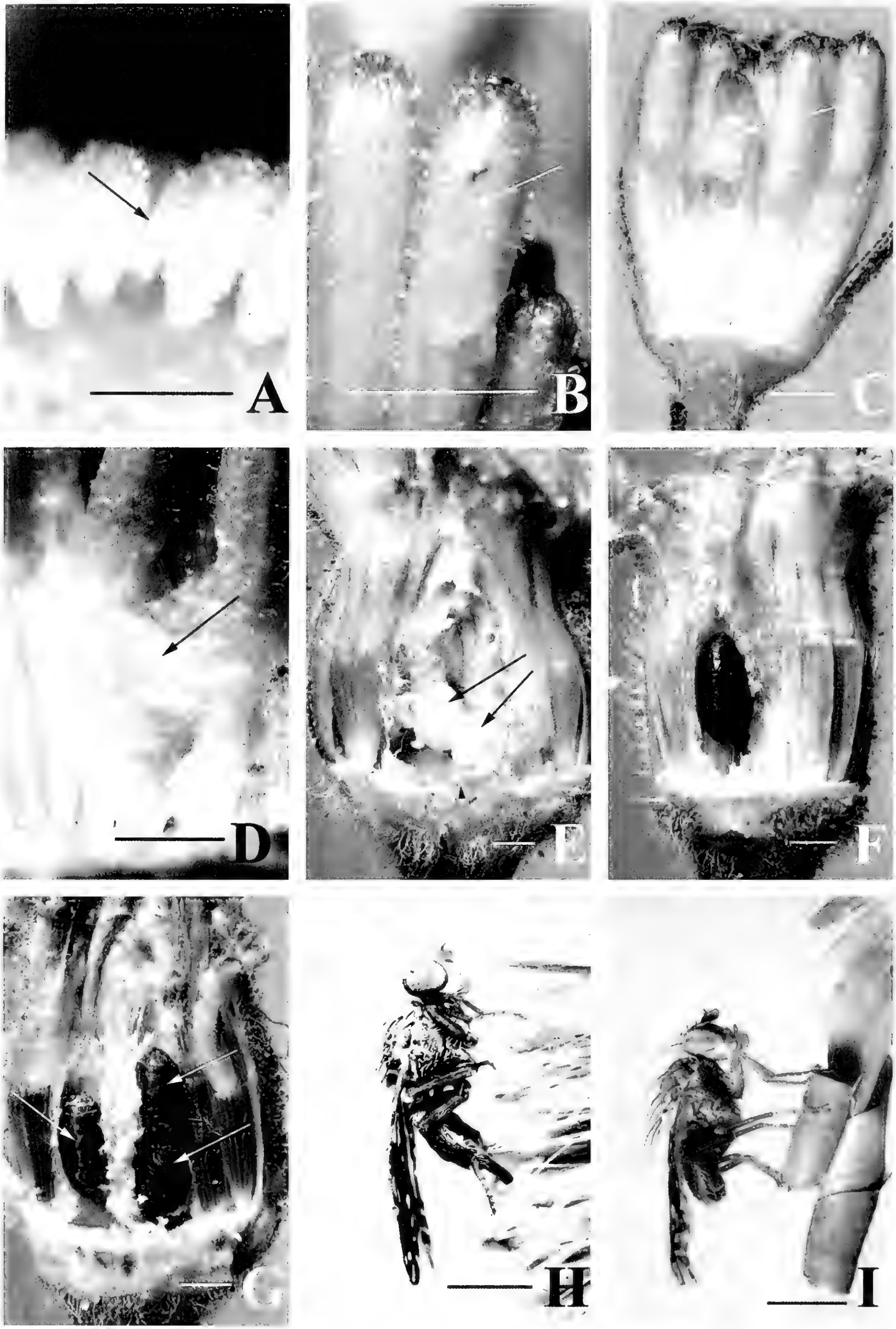

Fig. 8. Life stages of *Tephritis teerinki* in flower heads of *Hulsea vestita:* (A) egg (arrow) in closed, preblossom flower head between two florets; (B) first instar (arrow) feeding within floret in preblossom flower head; (C) first instar (arrow) feeding in adjacent florets in preblossom flower head; (D) second instar (arrow) feeding on florets and ovules in closed, preblossom flower head; (E) third instars (arrows) feeding gregariously on soft achenes and receptacle; (F) single puparium in center of flower head surrounded by damaged achenes; (G) three puparia (arrows) in damaged flower head; (H) adult female; (I) adult male. Lines = 1 mm.

(range, 1.14–4.84) mm in diameter and an average of 3.0 ± 0.45 (range, 0–7) ovules was damaged in these 19 flower heads. No receptacle was abraded or pitted by larval feeding. Thus, about 4% (range, 0–9%) of an average total of 75 ovules/soft achenes counted for the above-mentioned, 143 flower heads were damaged by the first instars.

Second instars continued feeding on ovules in closed, preblossom flower heads, or in a few cases on soft achenes in open flower heads. They fed with their bodies parallel or perpendicular to the receptacles, but always well above the receptacles (Fig. 8C). Receptacles of 25 flower heads containing second instars averaged 4.30 ± 0.22 (range, 2.28–6.84) mm in diameter. These 25 flower heads each contained an average of 2.1 ± 0.3 (range, 1–6) larvae that had damaged an average of 9.9 ± 1.9 (range, 1–29) ovules/soft achenes, or about 13.2% (range, 1.3–38.7%) of the average total of 75 ovules/soft achenes per flower head counted within the above-mentioned, 143 flower heads.

Third instars (Fig. 8D) initially continued to feed mainly on ovules and soft achenes in preblossom, blossom, or postblossom flower heads. Fifty-eight flower heads that averaged 5.50 ± 0.19 (range, 1.99–7.13) mm in diameter contained an average of 2.1 ± 0.2 (range, 1–7) third instars. An average of 23.6 ± 2.1 (range, 3–80) of the ovules or soft achenes therein were damaged, or about 31% (range, 4–100%) of the average total of 75 ovules/soft achenes per flower head.

Third instars in flower heads fed with their long axes oriented perpendicular to the receptacles, and with their mouthparts commonly directed towards, or less commonly, away from the receptacles (Fig. 8E). The receptacles were abraded or pitted in 37 of 58 (64%) flower heads containing third instars, and the central feeding areas were moist, suggesting that sap constituted at least part of the diet of third instars of *T. teerinki*. 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 of *T. teerinki* oriented with their anterior ends away from the receptacles, retracted their mouthparts, and formed puparia.

Pupa.—The receptacles of 35 flower heads which contained an average of 2.0 ± 0.19 (range, 1–5) puparia (Figs. 8F, G) averaged 6.12 ± 0.15 (range, 4.56–8.40) mm in diameter. The receptacles were abraded or pitted in 34 of 35 (97%) flower heads containing puparia, further confirming that sap constituted part of the diet of the third instars. An average of 29.4 ± 1.9 (range, 10–47) of the ovules or soft achenes within these flower heads were damaged, or 39% (range, 13–63%) of the average total of 75 ovules/soft achenes per flower head.

Adult.—Adults (Figs. 8H, I) are long-lived and apparently constitute the only overwintering stage in southern California. Under insectary conditions, 31 unmated males (Fig. 8I) lived an average of 52 ± 5 (range, 8–95) days, and 15 virgin females (Fig. 8H) averaged 45 ± 6 (range, 28–104) days. Such 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. teerinki* 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. teerinki* were tracking and side-stepping by males and females (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).

Asynchronous supination, like that reported for *T. arizonaensis* (Goeden et al. 1993), was either irregular, i.e., one wing was extended more than once, and often held extended for several seconds; or regular, i.e., each wing was extended in turn without pause. Agonistic behavior by males involved facing other males while synchronously supinating both wings. Males did not exhibit any of the common tephritid courtship displays, including regular, abdominal pleural distension. Only a single pair was observed to mate once at mid-day 30 days after their emergence. This mating lasted 5.5 h (330 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).

Seasonal history.—The life cycle of *T. teerinki* on *Hulsea* spp. in southern California follows an aggregative pattern (Headrick and Goeden 1994, 1998) in which the adult is the principal overwintering stage. Consequently, come spring (April), 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 summer (June–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 a second generation is produced on one or more, as yet unknown, high-elevation, alternate hosts.

Natural enemies.—Many *Pteromalus* sp. (Hymenoptera: Pteromalidae) were individually reared from isolated puparia of *T. teerinki* or from caged samples of *T. teerinki*-infested, *H. vestita* flowerheads as solitary, larval-pupal endoparasitoids.

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PHAEDON DESOTONIS BALSBAUGH (COLEOPTERA: CHRYSOMELIDAE): NEW DISTRIBUTION RECORDS, FIRST HOST-PLANT ASSOCIATIONS, AND SEASONALITY OF A SELDOM-COLLECTED BEETLE OF ROCK-OUTCROP COMMUNITIES

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Abstract.—The only previous record of the Nearctic chrysomelid *Phaedon desotonis* Balsbaugh is an adult male (holotype) collected in northeastern Alabama in May 1963. New state records for *P. desotonis* are Georgia, South Carolina, and Tennessee; additional Alabama records are provided, and the known distribution is mapped. The adult is redescribed, the male genitalia are described and illustrated, and the female spermatheca is illustrated. *Phaedon desotonis* occurs on *Coreopsis grandiflora* (Asteraceae) in specialized communities (granitic and sandstone outcrops and a cedar glade), as well as in ornamental plantings of *Coreopsis.* The larvae skeletonize host foliage and are patchily distributed on their hosts in rock outcrops. It is a univoltine species. Adults overwinter and emerge in early spring; larvae are present as early as late March or early April. Adults of the new generation emerge by early May and are present on *Coreopsis* only for three or four weeks before aestivating and recolonizing their hosts the following spring.

Key Words: Insecta, Chrysomelidae, insect distribution, seasonal history, *Coreopsis grandiflora,* rock outcrops

Phaedon desotonis Balsbaugh was described from a single male collected on 18 May 1963 in De Soto State Park, DeKalb County, Alabama (Balsbaugh 1983). No specific collection site (the park is ca. 64 km long) or host plant were given in the original description. Prior to its recognition as undescribed, *P. desotonis* was listed in the Chrysomelidae of Alabama (Balsbaugh and Hays 1972) as *P. purpurea* Linell, a western U.S. species. No additional specimens have been reported, the beetle remaining known only from the holotype.

In 1991, this chrysomelid was rediscovered on a granitic dome (monadnock) in South Carolina. Additional fieldwork in other rock-outcrop communities in the southeastern United States (by AGW) allows us to provide the first host-plant associations for *P. desotonis* and notes on its seasonal history. The adult is also redescribed, the male genitalia are described and illustrated, and the female spermatheca is illustrated (by ERH).

Methods and Sample Sites

Information on the seasonal history of *P. desotonis* was obtained during periodic observations at Glassy Mountain Heritage Preserve near Pickens, S.C. *Coreopsis grandiflora* Hogg ex Sweet (Asteraceae), scattered at the edge of granitic outcrops near the fire tower, was examined for the beetle's characteristic feeding injury (see

Distribution below for collection dates). Plants also were tapped over a white enamel pan to detect larvae or adults. On each sample date, at least 20 plants were examined or sampled, notes were made on feeding injury, and representative stages of *P. desotonis* were collected. Additional attempts to collect the beetle at Glassy Mountain were made in all months during studies of other insect species (Wheeler 1994; AGW, unpublished data). Voucher specimens of larvae and adults are deposited in the Cornell University Insect Collection, Ithaca, N.Y.

To obtain additional information on distribution and host relationships of this chrysomelid, *Coreopsis* species and other potential herbaceous host plants, particularly composites, were sampled in other rock-outcrop and specialized communities. At all supplemental sites where *P. desotonis* was found, at least one repeat visit was made to sample *Coreopsis* colonies.

TAXONOMY

The genus *Phaedon* belongs to the subfamily Chrysomelinae, a group characterized by rather convex beetles possessing widely separated antennal insertions, pronotum with distinct lateral margins, front coxae transverse and widely separated, and the head inserted into the pronotum to the eyes. From other closely related genera in North America (i.e., *Chrysomela, Gastrophysa,* and *Plagiodera*), adults of *Phaedon* can be recognized by the following combination of characters: body oval, convex, shining, and metallic blue, green, or bronze black; head and pronotum with punctures of mixed sizes; elytra with scutellar and 9 discal series of punctures of varying sizes; tarsomere 3 distinctly emarginate, bilobed; and the apical segments of the maxillary palpi cylindrical, attenuate apically. There are 8 named species of *Phaedon* currently recognized in North America (Balsbaugh 1983).

In describing *P. desotonis,* Balsbaugh (1983) elected not to dissect the unique male holotype. As a result, his generic revision did not include an illustration of the male genitalia. Herein, we illustrate for the first time the male aedeagus and the female spermatheca to complement the illustrations of genitalic features of other species treated in Balsbaugh's revision.

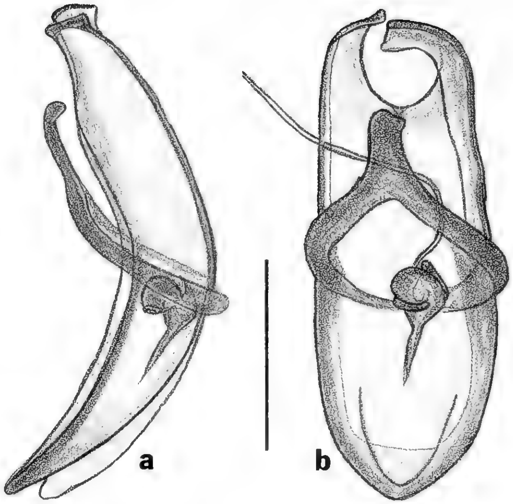

Fig. 1. Male genitalia (a, left lateral aspect; b, dorsal view) of *P. desotonis* (South Carolina). Scale line = 0.25 mm.

Diagnosis.—From all other North American species of the genus, *P. desotonis* can be distinguished (and in particular from *P. purpurea* to which it appears most similar, *sensu* Balsbaugh, 1983) by the fronto-clypeal suture being distinct medially; by the blackish elytra and contrasting greenish, distinctly alutaceous pronotum; and by the distinctive male and female genitalia, as illustrated in Figs. 1 and 2.

Redescription (adapted, in part, from Balsbaugh 1983).—Winged. Body elongate-ovate. Head black, coarsely but sparsely punctate between eyes, finely alutaceous; clypeus densely, coarsely punctate, recessed lower than frons; fronto-clypeal suture distinct, including median portion. Antennae piceous; first antennomere (scape) dark testaceous; apical 5 antennomeres increasingly clavate, setose. Pronotum metallic green, dull, distinctly alutaceous, finely, moderate-

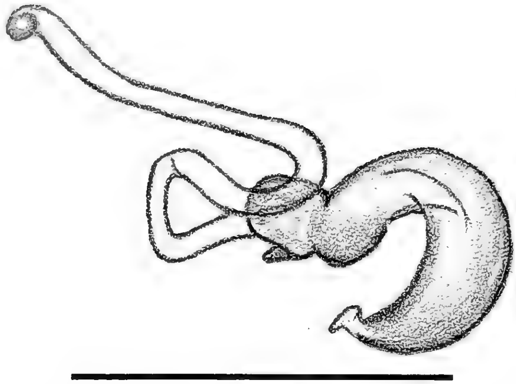

Fig. 2. Female genitalia (spermatheca) of *P. desotonis* (Tennessee). Scale line = 0.25 mm.

ly sparsely punctate on middle of disk, more coarsely, densely punctate toward lateral margins. Scutellum black, broadly ovate, alutaceous, impunctate. Elytra black, elongate, slightly convex, gradually tapering caudad; surface finely, transversely coriaceous; nine complete strial rows of punctures, plus short juxtascutellar row; striae weakly impressed, finely punctate throughout; interstriae impunctate. Venter black, with metallic luster, shining, finely microreticulate, sparsely, coarsely punctate; apical margin of last visible (5th) segment testaceous. Legs and tarsi piceous. Length: 3.54–4.44 mm; mean 3.91 mm (n = 32). Habitus photomicrograph of adult (holotype) provided by Balsbaugh (1983: 58, fig. 8).

Male genitalia (Fig. 1): Aedeagus moderately broad, length 2.8 times width. In lateral view, moderately curved or deflexed at middle. Apical margin of aedeagus broad, slightly projecting at middle. Dorsal plate of ostium broad, acutely rounded apically, nearly reaching apex of aedeagus. Apical portion of ejaculatory duct heavily sclerotized and swollen. Tegmen Y-shaped, forming nearly a complete ring around aedeagus; manubrium much shorter than tegmen arms; apex of manubrium, in lateral view, recurved toward base of aedeagus.

Female genitalia: Spermatheca as in Fig. 2.

DISTRIBUTION

In the following list of new records for *P. desotonis* (see also Fig. 3), the numbers of adults collected are given in parentheses; records without a parenthetical number refer to larvae only. All collections were made by the first author.

ALABAMA: Chambers Co., 2.9 km NNW of Penton (33°01.9′N, 85°29.2′W), 9 Apr. 1997 (2) and 8 Apr. 2000, ex *Coreopsis grandiflora*; Etowah Co., Noccalula Falls, Gadsden (34°02.5′N, 86°01.8′W), 9–10 Apr. 1997 (3), 10 May 1998 (1), and 3 May 2000, ex *Coreopsis grandiflora*; Jackson Co., Rt. 71, Flatrock (34°46.1′N, 85°42.2′W), 3 May 2000, ex *Coreopsis grandiflora*; Randolph Co., 0.4 km SW of Almond (4.8 km NW of Wadley) (33°08.7′N, 85°37.5′W), 9 Apr. 1997 (7) and 8 Apr. 2000, ex *Coreopsis grandiflora.* GEORGIA: Columbia Co., jct. Rt. 28 and Evans-to-Lock Rd., Martinez (33°33.0′N, 82°05.4′W), 26 Apr. 1997 (9) and 4 Apr. 1998, ex *Coreopsis grandiflora.* SOUTH CAROLINA: Pickens Co., Glassy Mountain Heritage Preserve, 4.2 km NE of Pickens (34°54.1′N, 82°39.6′W), 4 May 1991 (4); 30 May 1993 (5); 14 May 1995; 13 Apr. (1) and 10 May 1997; 5, 12 Apr. and 5, 12 May 1998 (2); 26 Mar. and 18 May 2000 (1), ex *Coreopsis grandiflora*; South Carolina Botanical Garden, Clemson University, Clemson (34°40.2′N, 82°49.7′W), 26 Mar., 7 May (6), and 12 May 2000 (19), ex *Coreopsis* sp. TENNESSEE: Davidson Co., Mt. View Rd. Cedar Glade, 6 km NW of La Vergne (36°04.2′N, 86°35.5′W), 12 June 1997 (2), ex *Coreopsis grandiflora.*

BIONOMICS

Habitats and host plants.—*Phaedon desotonis* was found on *C. grandiflora* in several specialized communities. Collections in Alabama from Chambers and Randolph counties and in South Carolina from Glassy Mountain were from granitic outcrops (a monadnock and several flatrocks), whereas those in Alabama from Etowah and Jackson

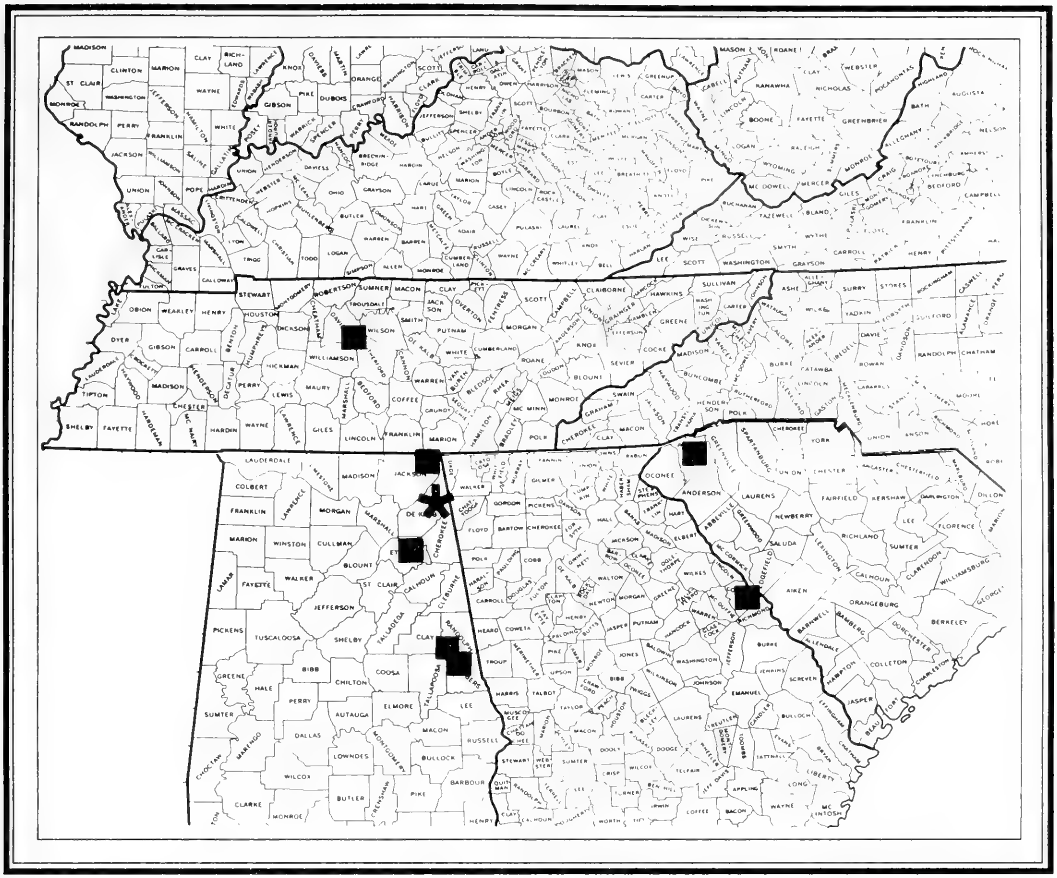

Fig. 3. Known distribution of *P. desotonis.* Asterisk denotes original collection site (type locality); solid squares represent new locality records reported herein.

counties were from sandstone outcrops. In Tennessee, this chrysomelid was collected in a cedar glade.

Ornamental plantings of *Coreopsis* also can be colonized by *P. desotonis.* The Georgia collection was from a small roadside colony of *C. grandiflora* that might have been planted. In the South Carolina Botanical Garden, larvae defoliated two specimen plants of *Coreopsis* sp. in a small garden outside Clemson University's Geology Museum.

Seasonal history and habits.—Adults overwinter, presumably in protected places near *C. grandiflora.* They emerge in early spring to feed on their hosts, the injury consisting of small holes in the foliage or notches at leaf edges. Adults are difficult to detect on the basal rosettes of *Coreopsis* (leaves 5–12 cm high). Overwintered adults were found mainly during the first two weeks of April and only in small numbers (typically 1 or 2 and never >10).

Eggs were not found, but early-instar larvae were present on an ornamental *Coreopsis* sp. as early as late March in the garden at Clemson, S.C., and on *C. grandiflora* in early April in granitic and sandstone outcrops in Alabama and South Carolina. Larvae skeletonized the foliage of their host plants, the injury patchily distributed on *Coreopsis* plants in rock outcrops. Severely damaged plants were scattered among numerous undamaged and slightly damaged plants. When larvae were concentrated on two specimen plants in the botanical garden in South Carolina, they defoliated their hosts and apparently fed on the stems; only a few bare stalks (5–20 cm high) were left at the base of each plant.

Adults of the new generation emerged from late April to mid-May. In contrast to the well-dispersed overwintered adults, the new adults were often concentrated on a few plants. At Glassy Mountain, for example, 20–25 adults were congregated on the stem (ca. 15 cm high) of one plant on 10 May. At Glassy Mountain and Alabama's Noccalula Falls, and in the botanical garden at Clemson, S.C., late instars overlapped with newly emerged adults, the presence of larval stragglers suggesting that oviposition in early spring is spread over several weeks.

The latest collection of adults (12 June) was in the Tennessee cedar glade. At Glassy Mountain, where *C. grandiflora* was monitored periodically throughout the year, neither adults nor larvae were found after late May. *Phaedon desotonis* appears to be a univoltine chrysomelid, the new adults feeding briefly and sparingly on host foliage before aestivating in the litter layer during the summer, overwintering, and eventually reemerging to colonize their hosts the following spring.

DISCUSSION

Phaedon desotonis is an apparent *Coreopsis* specialist and a characteristic insect of granitic and sandstone outcrops. The principal host plant is *C. grandiflora,* the only species on which we observed the beetle in rock outcrops and in a cedar glade. This composite is found on granitic outcrops in Alabama, Georgia, and South Carolina (e.g., Shelton 1968 [as *C. saxicola* Alexander], Murdy and Carter 2000) but is not nearly as abundant in outcrops as indicated by McVaugh (1943) (see Burbanck and Platt 1964). Although *C. grandiflora* has not been recorded from Tennessee (Chester et al. 1997), it, rather than the morphologically similar *C. lanceolata* L., was the host of *P. desotonis* in the Davidson County, Tenn., cedar glade. A recent analysis of phylogenetic relationships in *Coreopsis,* based on molecular data, suggests that *C. grandiflora* and *C. lanceolata* are sister taxa (Kim et al. 1999).

The occurrence of *P. desotonis* in specialized communities such as rock outcrops and cedar glades might be partly responsible for this chrysomelid's previous obscurity. Insects in most specialized communities have received relatively scant attention from entomologists (e.g., Wheeler 1991, 1995; Anderson et al. 1999). The beetle's patchy distribution within *Coreopsis* colonies that themselves are often widely scattered at the periphery of outcrops also might explain the lack of prior collections of *P. desotonis.* Moreover, adults of this early-season species are present on their host plants only a short time relative to that spent aestivating or overwintering in the litter layer, and they tend to drop from their hosts when infested plants are disturbed.

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FIVE NEW SPECIES AND A NEW SUBGENUS OF FLEAS (SIPHONAPTERA: CHIMAEROPSYLLIDAE, CTENOPHTHALMIDAE) FROM AFRICA

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Abstract.—Five new species of fleas and one new subgenus of fleas are described from Africa. They include ***Chiastopsylla* (*Ctenomacropsylla*) *petroma*, n. subgen., n. sp.** (Chimaeropsyllidae) from Cape Province, South Africa, ***Hypsophthalmus baxteri*, n. sp.** (Chimaeropsyllidae) from Natal, South Africa, ***Ctenophthalmus* (*Ethioctenophthalmus*) *hottentotus*, n. sp.** (Ctenophthalmidae) from Transvaal, South Africa, ***Ctenophthalmus* (*Ethioctenophthalmus*) *nigeriensis*, n. sp.** (Ctenophthalmidae) from Nigeria, and ***Ctenophthalmus* (*Ethioctenophthalmus*) *truncatus*, n. sp.** (Ctenophthalmidae) from Transvaal, South Africa and Manicaland, Zimbabwe. A key is provided for the species of *Hypsophthalmus.*

Key Words: *Chiastopsylla, Ctenophthalmus, Hypsophthalmus, Ctenomacropsylla,* Africa, fleas

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I recently identified over 15,000 fleas from the National Museum of Natural History (NMNH), Smithsonian Institution, Washington, DC. The fleas were collected in many different African countries during the 1960s as part of a large mammal study conducted by a team of mammalogists under the direction of the late Henry W. Setzer. Among the material were four new species and a new subgenus. These specimens from South Africa and Zimbabwe are described herein. A fifth new species from Nigeria identified as new to science by the late Robert Traub but never described is also included in this paper. The most recent and comprehensive treatise on fleas of Africa is that of Segerman (1995).

MATERIALS AND METHODS

Voucher study skins of mammalian hosts collected by the Setzer team are deposited in the NMNH and have assigned USNM Host numbers. These associated numbers are listed with respective specimen data under type material.

Reference to numbers of setae per side on thoracic or abdominal segments are counted from anterior to posterior. Female characters may be assumed to be the same as males unless otherwise specified within the respective descriptions. Illustrations were prepared with the aide of a camera lucida mounted on a Carl Zeiss® compound microscope. Terminology follows that of Rothschild and Traub (1971).

RESULTS

Hastriter (1998) described *Chiastopsylla tetratricha* and a new subgenus (*Megatarsopsylla*) from four male specimens from Garies, Cape Province. The acquisition of a new taxon of a single female from near Springbok, Cape Province, a distance of less than 100 km from the type locality of

C. tetratricha, was initially thought to be the undescribed female of *C. tetratricha.* However, it represents a different species and possibly a new genus. It is inadvisable to describe a new genus from a single specimen; however, the opportunity for collection of additional specimens in this remote locality is unlikely in the immediate future. It therefore seems prudent to erect a new subgenus for this flea, which remarkably shares characteristics with all members of the Chiastopsyllinae (*Chiastopsylla* Rothschild 1910, *Cryptopsylla* DeMeillon 1949, and *Praopsylla* Ingram 1927), but is allied most closely with *Chiastopsylla.* Characters that are common with *Chiastopsylla* (not present among *Praopsylla* and *Cryptopsylla*) include a sclerotized interantennal suture, pronotal comb, conical frons, marginal spinelets present on metanota and some abdominal segments, and two rows of abdominal setae. The first three characters are only found in some *Chiastopsylla* spp., whereas the latter two are found in all species of *Chiastopsylla.*

CHIMAEROPSYLLIDAE

Chiastopsylla (*Ctenomacropsylla*) Hastriter, new subgenus

(Figs. 1–5)

Diagnosis.—Distinguished immediately from females of the subgenus *Chiastopsylla* by the number of spines in the pronotal comb. *Ctenomacropsylla* has 14 spines, while females of the subgenus *Chiastopsylla* have 12 or fewer. The relative length of the pronotum to the length of the more dorsal spines is 1:1 or less among taxa of the subgenus *Chiastopsylla* and 1:2 in *Ctenomacropsylla* (Fig. 1). The number of pronotal spines of all males belonging to the 17 species within the subgenus *Chiastopsylla* is equal to or greater than that of females. This generic trend would suggest that females of *Megatarsopsylla* (currently unknown) are unlikely to possess more spines than the male of the type species, which has only 10 spines that are equal in length to the pronotum. This trend may be substantiated or refuted only with future collection of females of *Megatarsopsylla.* The dorsal margins of all three pairs of tibiae (Fig. 3) possess false combs (similar to the genus *Cryptopsylla*). These are absent in species of the subgenera *Megatarsopsylla* and *Chiastopsylla.* The general shape of the spermatheca is unique compared to that of other species of *Chiastopsylla* and the duct of the spermatheca enters the bulga at the apex in *Ctenomacropsylla,* while it is ventral in all taxa of other subgenera (Fig. 5).

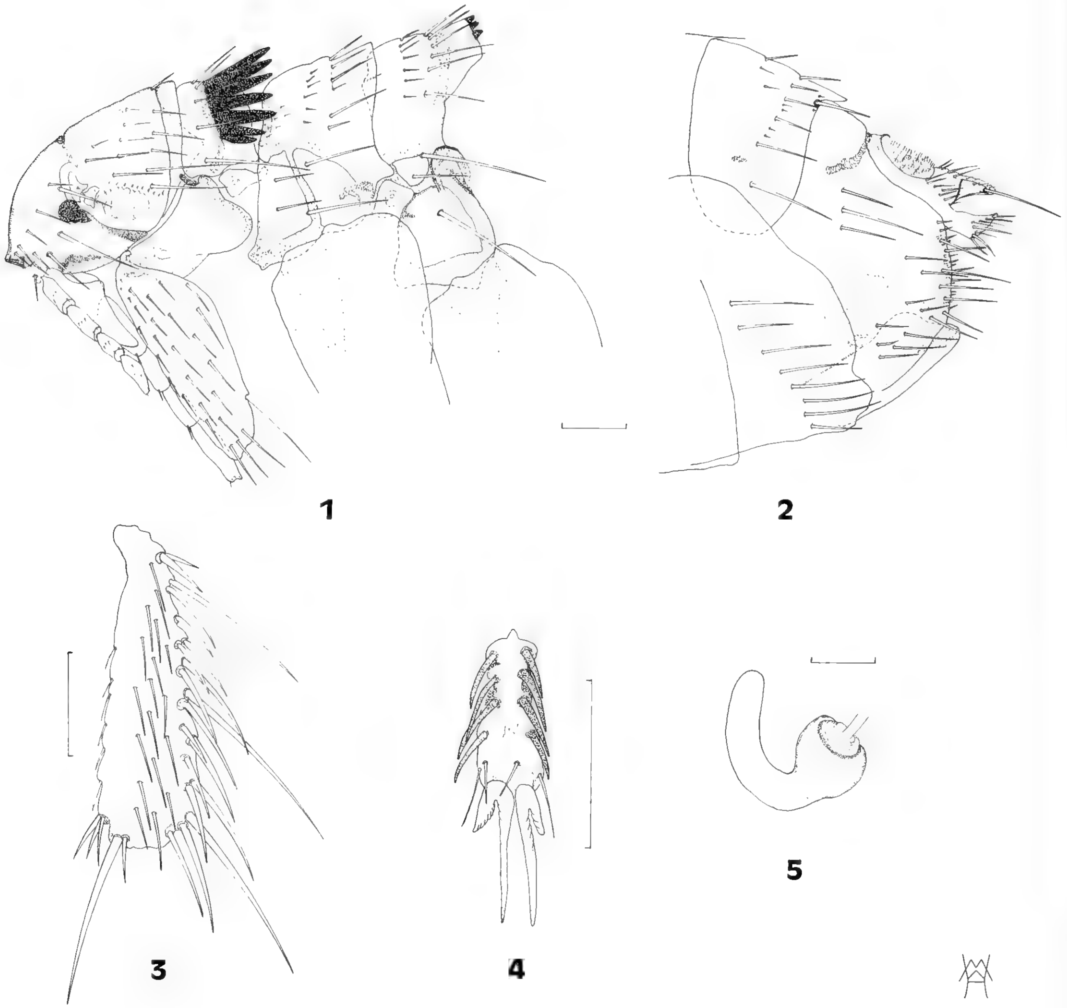
Chiastopsylla (*Ctenomacropsylla*) *petroma* Hastriter, new species

(Figs. 1–5)

Type material.—Holotype ♀, USNM Host no. 343961, ex *Petromus typicus* Smith, 1831 (Rodentia: Petromuridae), 4 mi ESE Springbok Aerodrome, Cape Province, South Africa, 12 December 1963, R.E. Cole. Deposited in the NMNH.

Diagnosis.—Separable from all other members of the subfamily Chiastopsyllinae by characteristics discussed in diagnosis of the subgenus.

Description (holotype female).—*Head* (Fig. 1): Frons forms a distinct conical angle near oral angle. Eye round and pigmented. Genal process acutely pointed without ctenidia. Ocular row of 3 setae, 2 below and 1 above level of eye. Seven setae somewhat parallel and anterior to ocular row. Two placoid pits along obliquely rounded frons (dorsal to sharp oral angle). Three rows of occipital setae (per side: 2, 5 and 6–7). Row of 10 minute setae along antennal fossa. Preantennal and occipital area divided by interantennal suture. Scape with single lateral seta, pedicel with fringe row of 6–7 setae, none of which reach first segment of clavus, and clavus asymetrical with 9 segments extending only to posterior margin of antennal fossa. Maxillary palpus of 4 segments, extending to ½ length of fore coxa. Labial palpus of 4 segments, apical segment longest and extending to near apex of trochanter. *Thorax* (Fig. 1): Pronotal



Figs. 1–5. *Chiastopsylla (Ctenomacropsylla) petroma,* female. 1, Head and thorax. 2, Modified abdominal segments. 3, Hind tibia (note false comb). 4, Fifth segment of hind tarsus. 5, Spermatheca. Scale = 100 μ.

comb of 14 long spines, longest 2.5 times width of dorsal margin of pronotum. Height of pronotum 2.5 times its width with single row of 6 setae per side with intercalaries. Lowest seta of row extends far beyond longest pronotal spine. Prosternum broadest basally. Mesonotum with 3 rows of setae (per side: 2, 8 and 7), main row with intercalaries. Antero-ventral margin has patch of 11–12 small setae (under pronotal spines). Mesonotal collar with 2 pseudosetae per side. Mesepisternum and mesepimeron with 6 setae. 1st and 2nd thoracic link-plates well developed. Metanotum with 2 rows of setae (per side: 8 and 6), main row with intercalaries. Marginal spinelets 3 per side. Lateral metanotal area with 2 setae (1 long, 1 short). Pleural ridge heavy and pleural arch extremely developed. Metepisternum with single long seta, metasternum vestigial. Metepimeron with 8 setae, 1 dorsal to spiracle. *Legs* (Figs. 3–4): Fore coxa with 26–27 setae, excluding marginals. Two large femorotibial bristles on all femora, lateral largest on fore femur and lateral shortest on mid and hind femora. Setae of mid coxa restricted to antero-ventral marginals and 5 apical setae. Outer internal ridge incomplete ventrally. Oblique breakline only indicated on postero-ventral margin. Numerous setae along antero-apical half of hind coxa; oblique line of 12–13 spiniform setae on mesal surface. Outer internal ridge complete and sturdy. Lateral aspects of mid and hind femora devoid of setae, limited to dorsal marginal setae and 2 strong setae at postero-ventral margin of each. False combs formed along dorsal margin of mid and hind tibia by several large bristles adjacent to bristles occupying dorsal notches. Numerous scattered setae adorn the lateral surface of both mid and hind femora. Orientation of fore femora precludes observation of chaetotaxy. Fifth tarsal segments all bearing 4 pairs of lateral plantar bristles, 2 preapical plantar bristles (fore tarsi with 2 on one side and 3 on the other), and 2 preapical plantar hairs. *Unmodified abdominal segments:* Apical spinelets on t. I–III, 1 per side. Each tergite with 2 rows of setae, main row with intercalaries. One seta of main row below level of spiracles on all segments. Tergum VII with 3 antesensilial bristles (2 minute); lobe extends caudally between antesensilial bristles. Sternites II–VI, each with single row of setae (per side: 1, 5, 5, 6 and 6). *Modified abdominal segments* (Fig. 2): Dorsal margin of t. VIII heavily sclerotized anterior to vermiform spiracular fossa. Vertical line of 3 lateral setae; patch of 10–11 submarginal setae, and fringe of numerous marginal setae along broadly truncate caudal lobe. Sensilium appears to have 14 sensilial pits per side. Sides of anal stylet strongly angled from base to apex; width of base nearly equal to length of stylet. Single long apical bristle and 3 minute setae, 2 dorsal and 1 ventral. Ventral anal lobe uniquely angulate ventrally with many slender setae and 2 spiniform bristles at ventral angle. Caudal margin of st. VII with broad lobe subtended by shallow sinus; latter slightly sclerotized, and oblique main row of 7 setae. Sides of st. VIII parallel, obliquely truncate at apex and without setae. Ventral ⅓ of st. VIII with parallel layers of rugulose wrinkles. Duct of spermatheca enters bulga terminally. Bulga small and globular and hilla long and narrow (Fig. 5). Bursa copulatrix delicately membranous and unsclerotized. Ventral floor of oviduct sclerotized anterior to bursa copulatrix.

Remarks.—Additional collecting of the rarely collected host species (*P. typicus*) is needed to discover the male and elucidate the distribution and true host affinities of this interesting flea.

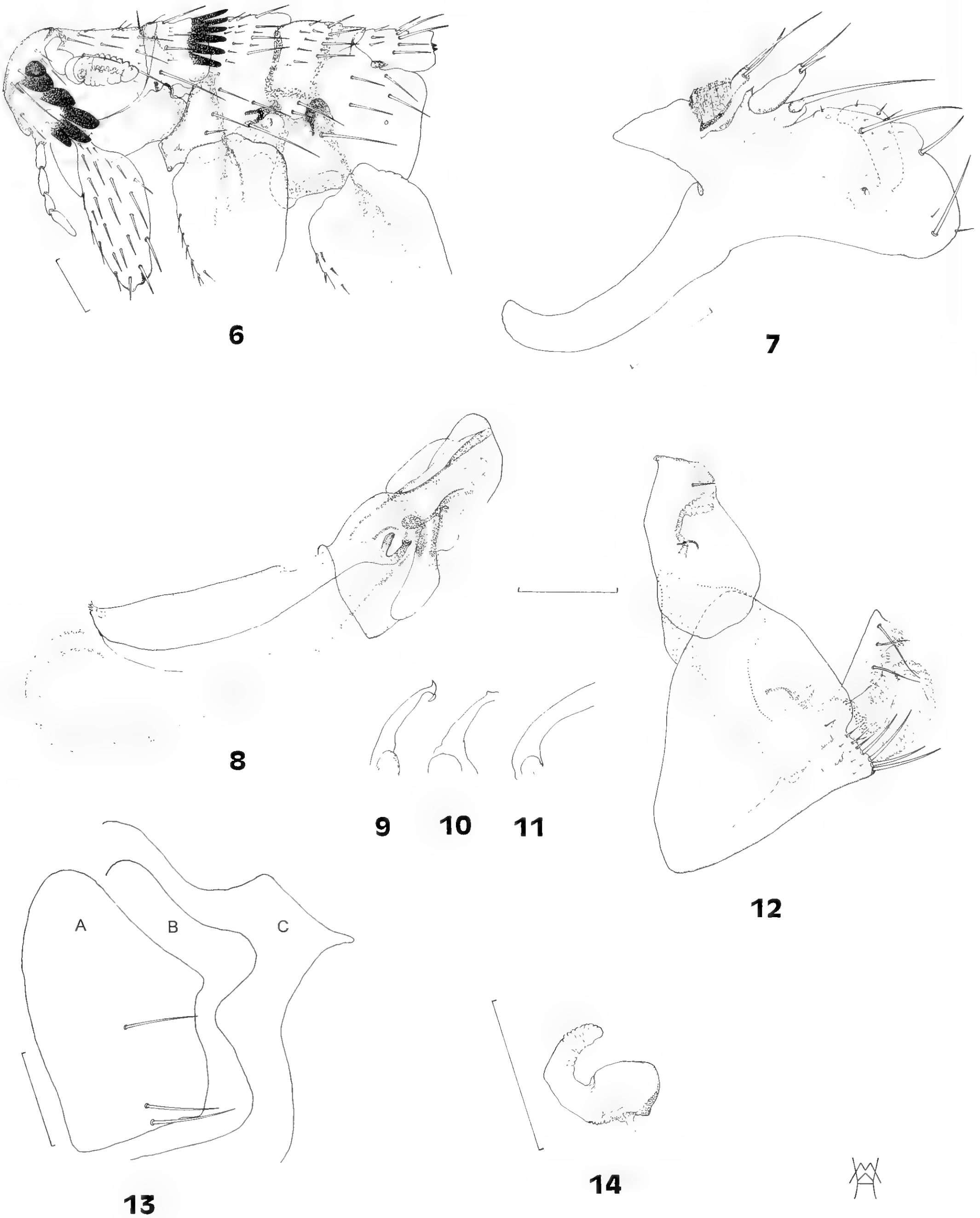
Etymology.—The ctenidia of the pronotal comb are more numerous and longer than those of other taxa of the subfamily Chiastopsyllinae (pronotal comb absent in some species), thus a compounding of the Greek roots "ktenos" = comb, "makros" = long, and "psylla" = flea for the subgeneric epithet *Ctenomacropsylla*. The specific name is derived from its apparent host genus *Petromus*.

***Hypsophthalmus baxteri* Hastriter, new species**

(Figs. 6–14)

Type material.—Holotype ♂, USNM Host No. 380510, ex: *Myosorex varius* (Smuts 1832)(Insectivora: Soricidae), collected "Sani Pass, (29°36′S, 29°18′E), 2,866 m, Basutoland/Natal border, near rock," Natal, South Africa, 9 January 1966, T.N. Liversedge; allotype ♀ and paratypes, 3 ♂, 2 ♀, same data as holotype. Paratypes, 2 ♂, 1 ♀, ex: *M. varius,* southern slopes of Gaika's Kop (32°31′S, 26°55′E), 1,700 m, Hogsback District, Eastern Cape, South Africa, (host was field collected 14–17 September 1999, fleas collected from captive laboratory host in October 1999), R. Baxter. Holotype, allotype and 5 paratypes (3 ♂, 2 ♀) deposited in the NMNH, and 3 paratypes (2 ♂, 1 ♀) deposited in the author's collection.

Diagnosis.—Immediately separable from *Hypsophthalmus montivagens* De Meillon and Hardy 1954 by the blunt genal spines. *Hypsophthalmus campestris* Jordan and



Figs. 6–14. 6–9, *Hypsophthalmus baxteri*. 6, Male head and thorax. 7, Basimere and telomere. 8, Aedeagus. 9, Sclerotized inner tube. 10, *H. temporis,* sclerotized inner tube. 11, *H. campestris,* sclerotized inner tube. 12–13a, H. baxteri. 12, Male eighth tergum, eighth and ninth sternites (note membranous extension of eighth sternum). 13a, Female seventh sternum. 13b, *H. campestris,* female seventh sternum. 13c, *H. temporis,* female seventh sternum. 14, *H. baxteri,* spermatheca. Scale = 100 μ.

Rothschild 1913 and *Hypsophthalmus temporis* De Meillon 1940 are more closely allied but easily distinguished in both sexes by the 4th genal spine (beginning count from oral angle), which is much broader than the first three spines (Fig. 6). The genal spines are each about equal in width in *H. campestris* and *H. temporis.* The male is further distinguished from those of *H. campestris* and *H. temporis* by the absence of a ventral lobe on the basimere and the telomere obviously wider apically than basally and never extending beyond the dorso-apical margin of the basimere. They also differ in details of the st. IX and aedeagus (Figs. 8–12). The female is separable by the presence of a dorso-caudal bluntly triangular lobe on st. VII with little indication of subtending sinus (Figs. 13A–C), and by the shape of the spermatheca (Fig. 14). The bulga of the spermatheca is globose and similar to that of *H. campestris,* but the hilla is more robust and longer than the bulga; the bulga of *H. temporis* is not globose but barrel shaped.

Description.—*Head* (Fig. 6): Preantennal region divided dorsally and ventrally by an internal incrassation of frons. Vertical genal comb of 5 spatulate spines, first spine reduced and fifth spine as wide as long, mostly confluent with large heavily pigmented eye. Dorsal margin of frons slightly longer from antennal sulcus to frontal angle than from frontal angle to oral angle (latter heavily sclerotized). Two placoid pits along upper frons. Definite demarcation of marginal sclerotization and pale submarginal band. Four setae along line of demarcation, large ocular seta anterior to eye and smaller seta posterior to eye. Ventral preantennal area with 2 marginal setae, 1 large submarginal seta, a single seta between oral angle and base of maxillary palpus, and 7 minute scattered setae. Dorsal margin of occiput concave (convex in female), three rows of setae (per side: 3, 4, and 5), posterior row with intercalaries. Nine or 10 setae along dorsal margin of antennal fossa. Pedicel of antenna with small setae hardly reaching first segment of clavus, latter not extending onto propleuron. Maxillary and labial palpi about equal length, each with 4 segments, extending ⅗ length of fore coxa. *Thorax* (Fig. 6): Pronotal comb of 12 blunt spines and single row of 5 setae with intercalaries. Propleuron without setae. Mesonotum longer than high with 3 distinct rows of setae (per side: 3–4, 6–7, and 5), main row with intercalaries. Numerous additional minute setae line the anterior edge of mesonotum. Mesonotal collar with a single pseudoseta per side. Mesepisternum with 3 setae, ventral margin with hyper developed 2nd thoracic link plate (appearing as a C-shaped sclerite). Mesosternum divided into 2 sclerites by narrow ridge of sclerotization. Mesepimeron with 2 setae. Metanotum with 3 rows of setae (per side: 2, 5, and 5), main row with intercalaries. Posterior lateral margin of metanotum membranous and indiscernible. Lateral metanotal area with 2 setae (upper long, lower short). Pleural arch well developed with stout pleural rod. Metepisternum bearing 1 seta; squamulum present. Metasternum with single minute seta. Metepimeron with 5 setae below level of pointed spiracle. *Legs:* Fore coxa with 5 anterior marginal setae, 16–17 dorso-apical setae and 22 lateral setae. Femora with single minute mesal seta, medial lateral row of 3 setae, and 2 dorsal marginal rows. Two femorotibial bristles, outer bristle larger. Tibia with 6 dorsal tibial notches (notches with 2 bristles each) and 11 lateral setae. Outer internal rod of mid coxa incomplete, inner internal rod obscure apically; oblique break complete. Two pre-apical ventral setae and spiculate setae along dorsal margin of mid femur; single seta on mesal surface. Oblique row of 5–6 spiniform setae on mesal surface of hind coxa. Patch of setae along anterior apical ⅔ of hind coxa; 4 minute marginal setae along dorso-posterior margin and 2 stout setae at apical posterior margin. Hind femur with spiculate setae along dorsal margin, 2 apical ventral setae, and 3 proximal ventral setae. Lateral surface with longitudinal course sculpture; mesal surface with wide perpendicular sculpturing, proximal pattern tuberculate. Mid and hind tibiae with 16–17 lateral setae and 8 notches on dorsal margin, each bearing 2 bristles except for the third and sixth, which have 1 each. Lateral femoro-tibial bristle of mid and hind femora smaller of two bristles. Segment V of tarsi with 4 pairs of lateral plantar bristles, tarsal claws well developed. *Unmodified abdominal segments:* Tergites I–VI with apical spinelets (per side: 2, 2, 2, 2, 1, and 1). Two rows of setae on t. I–VI, main rows with intercalaries; a single seta in each main row placed below level of spiracle. Three antesensilial bristles present, medial and lateral greatly reduced. Sternites II–VII each with a single row of setae; per side, st. II with single seta and others each with 2 setae. *Modified abdominal segments* (holotype male) (Figs. 7, 12): Tergum VIII reduced. Tergum IX highly modified; P^1 of basimere widens apically bearing 4 large marginal setae (2dorsal, 2 apical), telomere curved cephalad, broadening towards apex. P^2 associated with base of basimere bears 2 long apical setae. A modified seta projects caudally just posterior to base of P^2. Manubrium larger than median lamina of aedeagus, apodeme of t. IX reduced. Sensilium with 14 sensilial pits, paired projections positioned between the paired P^2, each bearing 2 apical setae. The projections appear to extend from sensilial plate. Sternum VIII adorned with 7–8 dorsally curved setae per side on posterior margin; a membrane with minute spiculate surface protrudes outward beyond apex of st. VIII. Proximal arm of st. IX massive, distal arm club-like, bearing 2 large lateral setae and a small seta between. A membranous tongue-like flap projects up from base of proximal arm to near its apex; a second membranous intersegmental fold projects from mesal surface of apical club of st. IX. *Aedeagus* (Fig. 8): Median dorsal lobe hooked cephalad and covered with membrane that envelopes end chamber. Lateral lobes delicate. Aedeagus lacking dorsal or ventral armature, Ford's sclerites, or crochets. Ventral lobe on aedeagal pouch sclerotized along margin. Aedeagal pouch protruding ventrad beyond ventral lobe. Penis rods extend just beyond apex of median lamina. Sclerotized inner tube with both a dorsal and ventral hook at apex. Crescent sclerite covering about ⅓ of tectum appearing straight in lateral view. A dorsal expansion of aedeagus occurs dorsal to crescent sclerite. *Modified abdominal segments* (allotype female) (Figs. 13A, 14): Tergum IX with 2–3 small setae anterior to eighth spiracle. Margin of t. VIII with 6–7 setae accompanied by an irregular patch of 3–6 setae. Anal stylet 3 times as long as wide, bearing 2 minute setae at base of a single terminal long seta. Ventral lobe evenly rounded along ventral margin, adorned with 6–7 setae, distal seta being very long and single middle seta somewhat spiniform. Sternum VII with 3 lateral setae per side, dorsal seta widely separated from ventral pair. Dorso-posterior margin of st. VII with triangular lobe; margin below lobe entire and rather straight (Fig. 13A). Bulga of spermatheca nearly globular, hilla longer than length of bulga (Fig. 14).

Remarks.—Two separate collections of this new species from *M. varius* separated by 400 km would suggest that this shrew is the preferred host. This host is found among rocky habitats along streams in montane situations from NW Cape Province to Transvaal and Natal. The three flea specimens collected by R.M. Baxter were taken from *M. varius,* field collected (southern slopes of Gaika's Kop) in early September, kept in laboratory enclosures at 22°C, and removed when hosts were examined in late October. This indicates that the fleas survived nearly eight weeks on captive animals under laboratory conditions.

Etymology.—This new species is named in honor of Dr. Rodney M. Baxter, Senior Lecturer, Department of Zoology, University of Fort Hare, Alice, South Africa. The author is most grateful to Dr. Baxter for kindly contributing these specimens for study.

KEY TO SPECIES OF *HYPSOPHTHALMUS*

1. Genal teeth each tapering to a sharp point (female unknown) . . . . *montivagans*
– Genal teeth all apically rounded (Fig. 6) 2
2. Male 3
– Female 5
3. Apex of sclerotized inner tube with dorsal and ventral hooks (Fig. 9); apico-ventral margin of basimere (ventral to articulation of telomere) without a broad lobe (Fig. 7) . . . . *baxteri*, n. sp.
– Apex of sclerotized inner tube without hooks (Figs. 10–11); basimere with a broad lobe below telomere 4
4. Second genal tooth (counting from ventral to dorsal) distinctly longer than third genal tooth, base of second genal tooth above level of apex of genal lobe . . . . *campestris*
– Second and third genal teeth subequal, base of second genal tooth even with or below level of apex of genal lobe . . . . *temporis*
5. Caudal margin of st. VII with a square lobe directed dorso-caudally, bearing an acute process on ventral portion of lobe (Fig. 13c). . . . . *temporis*
– Lobe of st. VII rounded and not directed upward (Figs. 13a–b) 6
6. Sternum VII with row of 3 setae per side, lobe on caudal margin of st. VII small, with at most a shallow concavity below (Fig. 13a); second genal tooth (counting from ventral to dorsal) subequal in length to third tooth (Fig. 6) . . . . *baxteri*, n. sp.
– Sternum VII with row of 4 setae per side, lobe on caudal margin of st. VII well developed forming a subtending sinus (Fig. 13b); second genal tooth distinctly longer than third . . . . *campestris*

CTENOPHTHALMIDAE

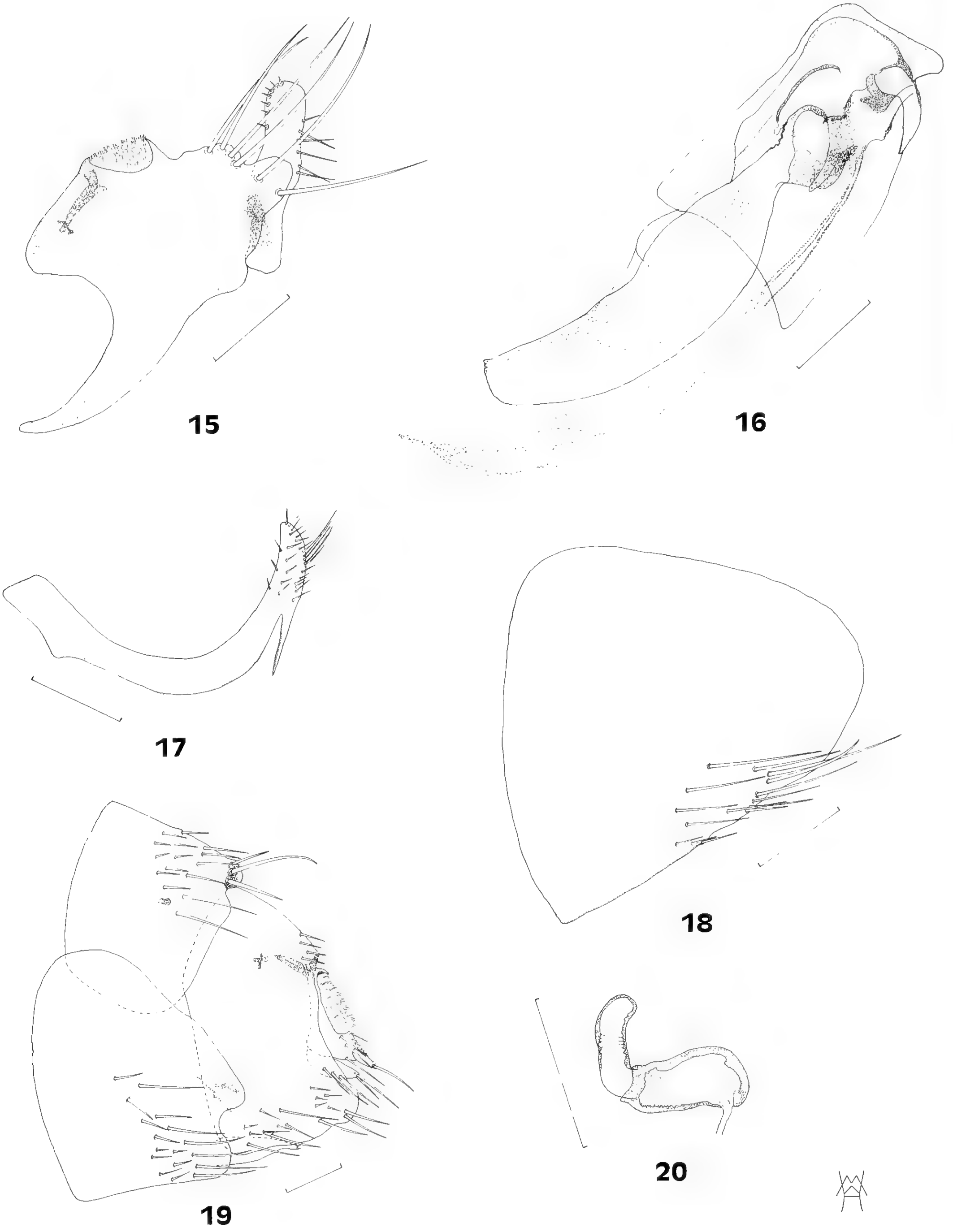
Ctenophthalmus (*Ethioctenophthalmus*) *hottentotus* Hastriter, new species

(Figs. 15–20)

Type material.—Holotype ♂, USNM Host no. 384688, ex: *Cryptomys hottentotus* (Lesson 1826) (Rodentia: Bathyergidae), 2 mi E Houtbosdorp, South Africa 27 January 1967, A.R. Silberstein. Allotype ♀ and paratypes, 1 ♀, USNM Host no. 382445, 3 ♂, 1 ♀, USNM Host no. 382443, 1 ♂, 1 ♀, USNM Host no. 382447, all same data as holotype except 25 October 1966; 1♀, USNM Host no. 381965, ex: *Aethomys chrysophilus* (de Winton 1897) (Rodentia: Muridae), 2 mi SW Barberton (25°49′S, 31°01′E), Transvaal, South Africa, 16 November 1966, A.R. Silberstein, and 1 ♂, USNM Host no. 381561, ex: *Rhinolophus clivosus* Cretzschmar 1828 (Chiroptera: Rhinolophidae), 2 mi SW Barberton, Transvaal, South Africa, 16 November 1966, I.L. Rautenbach. Holotype, allotype, and 7 paratypes (4 ♂, 3 ♀) deposited in the NMNH, and 2 paratypes (1 ♂, 1 ♀) deposited in the author's collection.

Diagnosis.—Using the key by Hopkins and Rothschild (1966), males key to subspecies of *Ctenophthalmus cophurus* but differ in details of the aedeagus (Fig. 16) and the telomere is much narrower and strap-like (compare Fig. 15 with figs. 450–451, 453, Hopkins and Rothschild 1966). The female keys to *Ctenophthalmus singularis* Jordan 1936 but can be distinguished by a broad oblique lobe along the caudal margin of st. VII subtended by a deep sinus (Fig. 19) vs. two sinuses divided by a triangular lobe as in *C. singularis* (fig. 461, Hopkins and Rothschild 1966). Sternum VIII of the new species is also strongly tapered, not bluntly rounded as *C. singularis*.

Description.—*Head:* Frons evenly rounded with triangular tubercle at frontal angle. Preantennal area with anterior row of 6 setae, ventral most small and placed at oral angle. Ocular row of 3 larger setae. Eye vestigial, arch of tentorium clearly visible. Three placoid pits distributed along margin of frons. Occipital area with 3 rows of setae (per side: 3, 4, and 5), intercalaries on marginal row. Three placoid pits on occipital area. Eleven sharp setae along dorsal margin of antennal fossa. Setae along margin of pedicel not reaching first segment of clavus. Genal comb of 3 spines, middle rather blunt. Four segmented maxillary palpus reaching ⅓ length of fore coxa. Labial palpus with 5 segments, extending ⅔ length of



Figs. 15–20. *Ctenophthalmus hottentotus.* 15, Basimere and telomere. 16, Aedeagus. 17, Male ninth sternum. 18, Male eighth sternum. 19, Female, modified abdominal segments. 20, Spermatheca. Scale = 100 μ.

fore coxa. *Thorax:* Pronotal comb of 14 (16 in other specimens) spines, each longer than length of pronotum; single row of 5 setae per side with intercalaries. Propleuron without setae, proximal ventral apodeme protruding well into mesepisternum. Mesonotum with basal row of fine setae (beneath pronotal comb), 2 rows of setae (per side: 6 and 5), main row with intercalaries. Mesonotal collar with a single pseudoseta per side. Mesepisternum and mesepimeron with 7 setae. Metanotum with 3 rows of setae (per side: 2, 7, and 5), main row with intercalaries. Lateral metanotal area with 2 setae. Metepisternum with 1 seta, squamulum and moderately developed pleural arch. Metasternum with 2 minute setae dorso-anteriorly. Metepimeron with pointed spiracle, subtended by 2 vertical rows of 3 setae each. *Legs:* Fore coxa bearing more than 50 setae excluding marginal setae; arranged unevenly but somewhat in 5 oblique rows. Fore femur with a single seta on mesal surface. Femora with two stout ventrally directed setae near articulation of trochanters, both positioned to protect a non-sclerotized pit-like structure. Femorotibial bristles number 1, 2, and 2 on each tibia, mid and hind tibiae with lateral bristle much shorter than medial. Each tibia with a single lateral row of setae and dorsal notches of 6, 7, and 7, respectively. Segment V of all tarsi with 5 lateral plantar bristles, first proximal pair shifted onto plantar surface between second pair. Each tarsal segment with numerous minute setae scattered on plantar surface, 2 spiniform preapical plantar bristles, and pair of preapical plantar hairs. *Unmodified abdominal segments:* Apical spinelets on t. I–IV (per side: 1, 2, 1, and 1). Each tergite with 2 rows of setae, intercalaries in main row. One setae below level of each spiracle. Antesensilial bristles 3, medail ⅓ and lateral ½ length of long middle bristle. Sternum II with a single seta per side, st. II–VII each with 2 rows (per side: 2 in anterior row, 4 in main row for each segment). *Modified abdominal segments* (holotype male) (Figs. 15, 17–18): Tergum VIII reduced with row of 6 setae cephalad to eighth spiracle. Eighth spiracular fossa boot-shaped. Apodeme of t. IX wide along dorsal margin; manubrium sharp and curved up at apex. Dorsal lobe of basimere with 3 apical setae hidden behind a lateral marginal row of 6 large setae. Dorsal and ventral lobes separated by a shallow sinus. Posterior margin of ventral lobe with single acetabular bristle. Telomere 3.5 times as long as wide; its ventral portion extending well below fovea and apex nearly half its length above ventral lobe of basimere. Tetrad bristles all above level of acetabular bristle. Sternum VIII with expansive lobe extending posteriorly beyond st. IX; 14–15 setae per side on mid-ventral surface. Sternum IX thumb-like with numerous small setae on its apico-ventral ⅓. Apodeme of st. IX absent. *Aedeagus* (Fig. 16): Median dorsal lobe fused at dorso-apical margin and expanding ventrally as paired lateral lobes. Ford's sclerite parallels margin of medial dorsal lobe and lateral lobes. Crochet hooked downward into sharp point. Sclerotized inner tube with heavily sclerotized dorsal process; tube as short as its widest basal width. Crescent sclerite (and tectum) extending well into end chamber at same level as sclerotized inner tube. Penis rods short. Median lamina exceedingly sclerotized, thick, and blunt apically. Small sail cephalad to girdle. *Modified abdominal segments* (allotype female) (Figs. 19–20): Tergum VII with 3 rows of setae (per side: 3, 5, and 5), main row with intercalaries; 3 antesensilial bristles, medial ½ and lateral ⅓ length of long middle bristle. Tergum VIII with 3–4 setae anterior to spiracle; apical margin forming triangular lobe, patch of 5 setae above and patch of 14 scattered setae below level of apex of lobe. Paired unciform sclerotization on anterior margin of t. VIII. Tergum IX and st. IX clearly fused at their ventral and dorsal margins, respectively; st. IX bearing 2 minute lateral setae. Antero-ventral angle of dorsal anal lobe forming right angle, anal stylet with single apical bristle and 2 minute setae. Ventral margin of ventral lobe adorned with slender setae. Sternum II with 1 ventral and 1 lateral setae per side. Sternites III-VI each with anterior patch of setae and posterior main row (per side: patch of 5 and row of 5, 4 and 4, 4 and 4, and 3–6 and 5). Sternum VII with broad oblique caudal lobe subtended by a deep ventral sinus; patch of 10–13 irregularly arranged setae anterior to main row of 7–8 large setae per side. Sternum VIII narrow, tapering to a blunt point with a few minute setae at apex (Fig. 19). Hilla of spermatheca sclerotized on apical half and sclerotization of bulga extending onto base of hilla; duct of spermatheca joining cribriform area on ventral surface of bulga (Fig. 20). Bursa copulatrix delicately sclerotized; perula expanded slightly and transluscent.

Remarks.—The single male collected from a bat, *R. clivosus,* is an accidental association and the preferred host appears to be *Cryptomys hottentotus.*

Etymology.—The species is named for the specific name of its preferred host, *Cryptomys hottentotus,* as a noun in apposition.

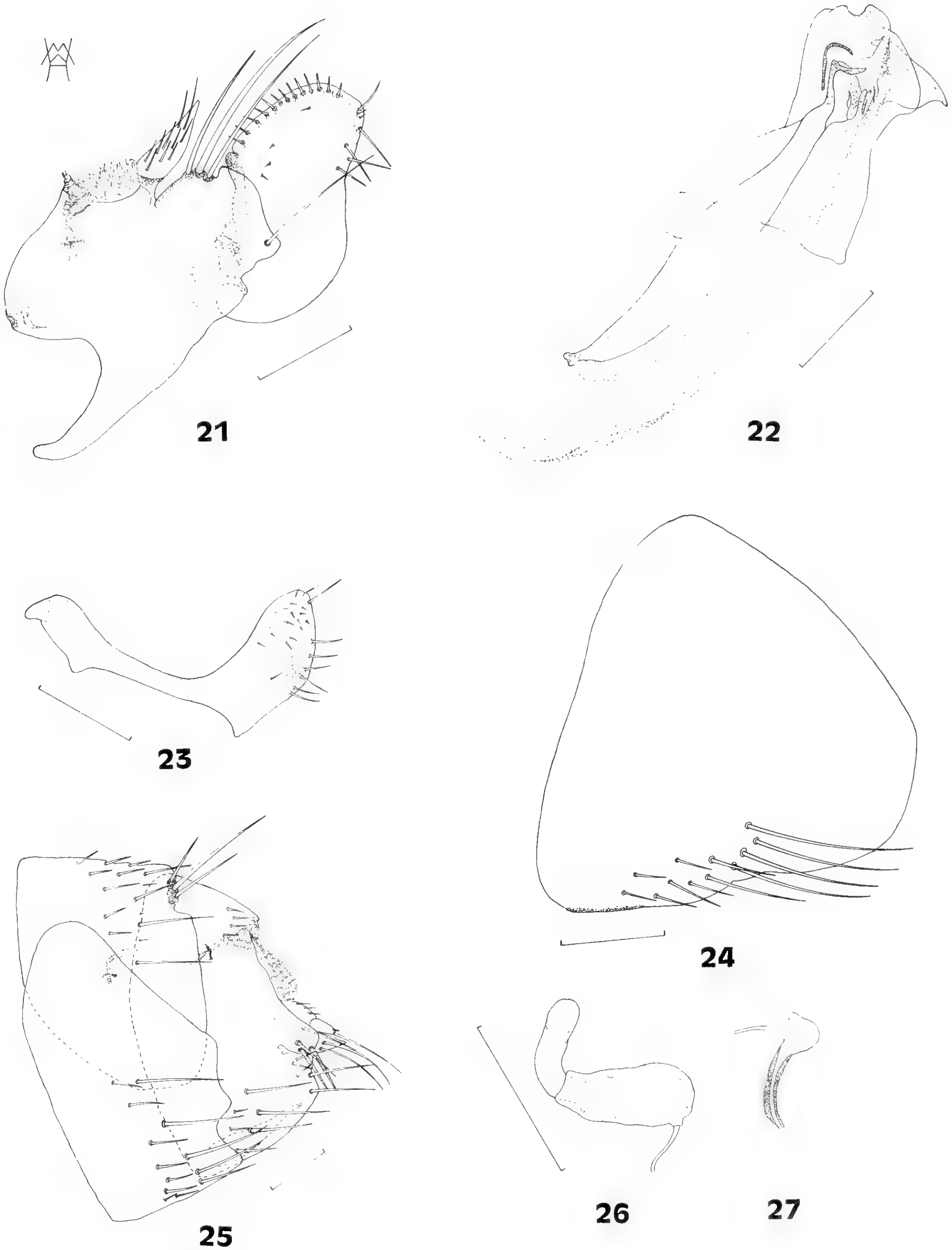
Ctenophthalmus (*Ethioctenophthalmus*) *nigeriensis* Hastriter, new species

(Figs. 21–27)

Type material.—Holotype ♂, B-93613, ex: *Lemniscomys striatus* (Linn. 1758)(Rodentia: Muridae), bush along river, Eastern Nigeria, 20 December 1977. Allotype ♀, B-93597, ex: *Crocidura* sp. (Insectivora: Soricidae), bush, Eastern Nigeria, 18 December 1977. Paratypes, 1 ♀, B-93598, ex: *L. striatus,* bush, Eastern Nigeria, 18 December 1977; 2 ♂, 3 ♀, B-93599-601, B-93611-612, ex: *Mastomys hildebrandtii* (Peters 1878) (Rodentia: Muridae), bush, Eastern Nigeria, 19–20 December 1977; 1♂, B-92580, ex: *M. hildebrandtii,* bush along stream, Zonkwa (9°50′N), Nigeria, 1 ♀, B-93592, ex: *Praomys tullbergi* (Thomas 1894) (Rodentia: Muridae), house, Eastern Nigeria, 16 December 1977; 1 ♂, 1 ♀, B-93652, ex: *Taterillus gracilis* (Thomas 1892) (Rodentia: Muridae), bush along river, Eastern Nigeria, 16 December 1977; 1 ♂, B-94327, ex: *Mastomys erythroleucus* (Temminck 1853) (Rodentia: Muridae), house, Pankshin, Nigeria, 20 September 1978; 1 ♀, B-94363, ex: *M. hildebrandtii,* cultivated land, Pankshin, Nigeria, 27 September 1978; 2 ♂, 4 ♀ B-94677, ex: *L. striatus,* bush, Eastern Nigeria, 11 February 1979; and 1 ♂, 3 ♀, B-94678, ex: *Uranomys ruddi* Dollman 1909 (Rodentia: Muridae), bush, Eastern Nigeria, 11 February 1979. Holotype, allotype, and 15 paratypes (5 ♂, 10 ♀) deposited in the Carnegie Museum of Natural History, Pittsburgh, PA, 3 paratypes (1 ♂, 2 ♀) in the NMNH, and 4 paratypes (2 ♂, 2 ♀) in the author's collection.

Diagnosis.—*Ctenophthalmus. nigeriensis* resembles the western African *moratus* group (Smit 1963) in having the lowest bristle of the frontal row situated in a notch (the notch is particularly distinct in the male and less so in the female), but has more affinities with the *atomus* group (Smit 1963). The tetrad bristles are dorsal to the L^2 of basimere as in the *atomus* group, but shorter than the width of the telomere at their level of insertion. Anatomically, *C. nigeriensis* is most like *Ctenophthalmus atomus* Jordan and Rothschild 1914 (Angola and Congo) and *Ctenophthalmus machadoi* Ribeiro 1974 (Angola). The male is distinguished from each by tetrad bristles that are shorter than width of telomere at level of their insertion, presence of a sinus between the L^1 and L^2 of basimere, presence of a sinus on the apical margin of the dorsal median lobe, and an acutely pointed crochet (Figs. 21–22). The posterior margin of the spermatheca of the female is wholly convex in *C. nigeriensis* (Fig. 26) whereas a concavity exists in *C. atomus* and *C. machadoi* (Figs. 20, 33). The modified abdominal segments of the female are very similar in the three species. To separate females for certainty, associated males and locality must be considered.

Description.—Chaetotaxy and morphology are similar to *C. hottentotus* and only



Figs. 21–27. *Ctenophthalmus nigeriensis.* 21, Basimere and telomere. 22, Aedeagus. 23, Male ninth sternum. 24, Male eighth sternum. 25, Female, modified abdominal segments. 26, Spermatheca. 27, Bursa copulatrix and perula. Scale = 100 μ.

differences are noted. *Head:* Eye well developed and pigmented sufficiently to obscure most of tentorium. Preantennal area with scattered patch of 8–12 minute setae between anterior row and ocular row. Row of 13–14 setae along dorsal margin of antennal fossa. Three genal spines distincly grooved longitudinally, middle tooth basally broad, overlapping posterior tooth. Posterior tooth convex along dorsal margin and noticeably longer than others, extending beyond apex of genal lobe. Maxillary and labial palpi about equal length, extending only to middle of fore coxa. Maxillae sharply pointed. *Thorax:* Pronotal comb of 16 spines and single row of 6 setae per side, with intercalaries. Propleuron without setation. Mesonotum with 4 pseudosetae per side (3 dorsal and 1 ventral) under mesonotal flange, 7 setae per side in main row with intercalaries, anterior row of 6 setae per side, and scattered minute setae along anterior third. Four setae on mesepimeron and 2 on mesepisternum. Metanotum without apical spinlets, main row of 5–6 setae per side, with intercalaries, anterior row of numerous small setae and several scattered setae anteriorly. Lateral metanotal area with 2 setae, pleural arch moderately developed. Metepisternum with single large seta, squamulum, and metasternum ventrally lobed with 2 minute setae dorso-anteriorly. Spiracle of metepimeron large and pointed posteriorly, 6 setae all ventral to spiracle. *Legs:* Fore coxa with 38–40 lateral setae (excluding marginals) arranged more or less in 5 oblique rows. Single bristle guarding femorotibial joint very long, extending to middle of tibia. *Unmodified abdominal segments:* One apical spinelet per side on t. I–V. Sternum II with single seta per side, st. II–VII each with 2 rows (per side: 2 in anterior row, 3 in main row for each segment). Setae more numerous in st. II–VI of female (3 rows per segment, anterior row varying from 1–3 per side, middle row 3–5, and main row 3–4). *Modified abdominal segments* (holotype male) (Figs. 21, 23–24): Tergum VIII with patch of 4–5 small setae per side just anterior to boot-shaped spiracle. Apodeme of t. IX broadly rounded anteriorly, manubrium tapering to an upcurved blunt point. Basimere adorned with 3 long setae subtended by an elevated squared lobe. Single acetabular bristle. Telomere broadly rounded, broader basally than apically, with 13 subspiniform setae along dorso-anterior margin. Anterior margin slightly expanded with blunt denticle at margin of ventral lobe. Tetrad bristles well above acetabular bristle. Sternum VIII large, covering st. IX and most of t. IX, adorned with oblique line of setae and anterior patch of 8–9 smaller setae. Distal portion of st. IX with zone of transparency from which haemocoeles lead to a number of slender setae along its caudal margin. Tendon absent on st. IX (Fig. 23). *Aedeagus* (Fig. 22): Prominent sail along dorsal portion of aedeagus. Penis rods extend just beyond apex of median lamina. Crescent sclerite conspicuosly L-shaped, membranous portion of tectum also lightly sclerotized. Median dorsal lobe with an obvious sinus at apex. Sclerotized inner tube heavily sclerotized on dorsal margin. Crochet strongly sclerotized dorsally, extending beyond the lateral lobe, and acutely pointed. In lateral view, crochet resembles profile of a pelican's beak. *Modified abdominal segments* (allotype female) (Figs. 25–27): Sternum VII with main row of 5 setae per side, anterior row 7 smaller setae per side. Caudal margin of st. VII with broadly squared lobe (slightly concave) subtended by a broad sinus and small ventral lobe. Sternum VIII more darkly sclerotized than surrounding chitin, tapering to a narrow blunt point, tufted with several minute setae (Fig. 25). Three antesensilial bristles configured as in male. Tergum VIII with row of 4 setae per side anterior to boot-shaped spiracle, apical margin angulate with several marginal setae, lateral main row of 4 setae and several smaller scattered setae. Anal stylet with 1 minute seta as base of single long apical seta. Ventral anal lobe with 1 large lateral seta and 2 spiniform setae on ventral margin. Bulga of spermatheca with thick walls extending onto hilla ~ ¼ its length, duct entering bulga ventrally (Fig. 26). Bulga not constricted or incised on proximal end. Bursa copulatrix sclerotized, perula delicately hooded (Fig. 27).

Remarks.—This species displays little host specificity, although specimens were collected most frequently on species of *Mastomys* and *Lemniscomys.* It is remarkable that the species had not been collected and described previously, since such a large series was collected from a broad variety of hosts (six different genera of hosts comprising seven different species). This undoubtedly reflects the dearth of collecting in Nigeria and future work might yield more undescribed species.

Etymology.—The new species bears the name of the country from which it was collected.

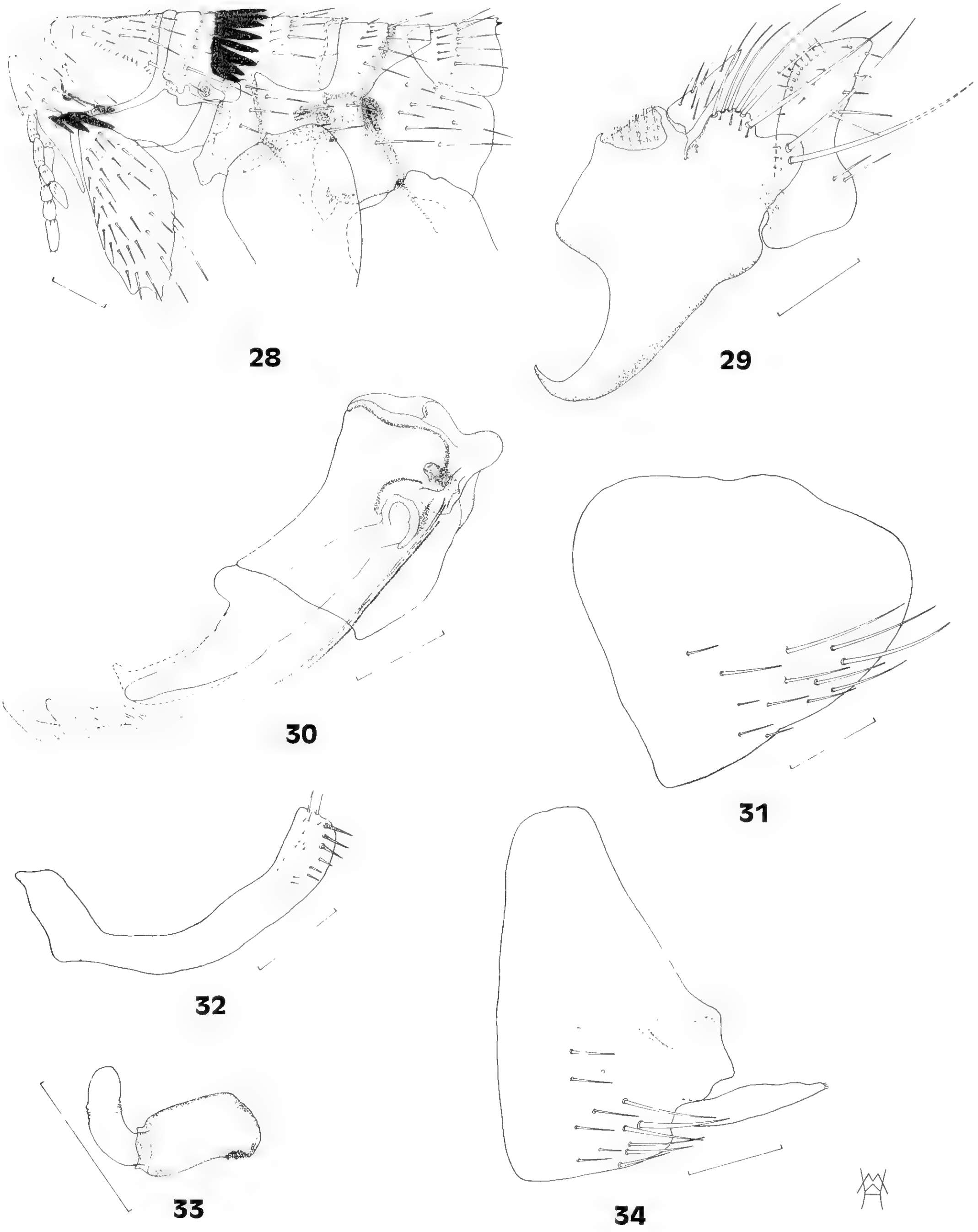
Ctenophthalmus (*Ethioctenophthalmus*) *truncatus* Hastriter, new species

(Figs. 28–34)

Type material.—Holotype ♂, USNM Host no. 381517, ex: *Myosorex cafer* (Sundevall 1846) (Insectivora: Soricidae), 2 mi E Haenertsburg (23°56′S, 29°57′E), Transvaal, South Africa, 17 October 1966, A.R. Silberstein; allotype ♀, USNM Host no. 381510-1, (same data as holotype except 13 October 1966). Paratypes, 1 ♀, USNM Host no. 425234-8, ex: *M. cafer,* South of Banti Reserve (19°10′S, 32°25′E), Manicaland, Zimbabwe, 9 November 1967, S.W. Goussard; 1 ♂, USNM Host no. 382156, ex: *Mastomys* sp. (Rodentia: Muridae), 2 mi SW Barberton (25°49′S, 31°01′E), Transvaal, South Africa, 17 November 1966, I.L. Rautenbach; and 1 ♂, USNM Host no. 428101-115, ex: *Mastomys* sp., Chirinda Forest (19°14′S, 32°14′E), Manicaland, Zimbabwe, 1 October 1967, H.W. Setzer. Types deposited in the NMNH.

Diagnosis.—This species can not be adapted to the key to the species of (*Ethioctenophthalmus*) in Hopkins and Rothschild (1966). The lowest bristle of the frontal row is located in a notch near the frontal angle of the male but is unlike any members of the *moratus* group of Smit (1963). The female does not possess a seta born in a notch near the frontal angle. The st. IX of the male, which bears a line of spiniform setae along the apico-posterior margin (Fig. 32) is distinct from all other species within the subgenus except *Ctenophthalmus acanthurus* Jordan and Rothschild 1913. It is immediately distinguished from *C. acanthurus* by details of the telomere which is broadly rounded in the latter and tapered to an acute point in *C. truncatus* (Fig. 29). The female is similar to that of *C. acanthurus* but differs in possession of delicate unciform sclerotizations on the anterior portion of t. VIII (residual lapping under st. VII in Fig. 34), a broad sinus on caudal margin of t. VIII, and the broad lobe along the caudal margin of st. VII (Fig. 34) is more squared with a deeper subtending sinus than those of *C. acanthurus.*

Description.—The general morphology and chaetotaxy of *C. truncatus* are sufficiently similar to *C. hottentotus* that only differences will be pointed out. *Head* (Fig. 28): Middle spine of genal comb acutely pointed. Setae along dorsal margin of antennal fossa number 13–14. Lowest setae of frontal row situated in a notch in male but not in female. *Thorax* (Fig. 28): Pronotal comb with 16 spines. Second row of meso- and metathorax with 4 and 6 setae per side, respectively. *Legs:* Fore coxa with 30 setae excluding marginals. *Unmodified abdominal segments:* Tergites I–V each with 1 apical spinelet per side. Sternum II with 1 seta per side, st. III–IV each with 3 rows (per side: 2, 3, and 4; 1, 2, and 3, respectively) and st. V–VII each with 2 rows (per side: 2, 3; 2, 3; and 2, and 4, respectively). *Modified abdominal segments* (holotype male) (Figs. 29, 31–32): Three setae on t. VIII anterior to spiracle VIII. Manubrium hooklike with sharply turned up apex. Apex of basimere divided into dorsal and ventral lobes, each separated by shallow sinus. Dorsal lobe with 6 long marginal setae and



Figs. 28–34. *Ctenophthalmus truncatus*. 28, Male, head and thorax. 29, Basimere and telomere. 30, Aedeagus. 31, Male eighth sternum. 32, Male ninth sternum. 33, Spermatheca. 34, Female seventh and eighth sternites. Scale = 100 μ.

5 shorter setae (not included in illustration) mesal to them. Ventral lobe with 2 acetabular bristles. Approximately ½ length of telomere extends beyond ventral lobe, lobe opposite fovea with 2 marginal setae (Fig. 29). Dorsal portion of telomere ⅔ width of dorsal and ventral lobes and fringed along anterior margin with 9–10 non-pigmented spiniform setae. Sternum VIII with broad apical lobe, lateral patch of 12 setae per side (6 large, 6 small) below lobe. Sternum IX truncate apically, bearing 3 spiniform setae along apico-caudal margin (Fig. 32). Distal arm with numerous minute setae and transluscent zone looping up middle of distal arm. *Aedeagus* (Fig. 30): Median dorsal lobe dorsally expanded. Ford's sclerite undulating from dorsum to sclerotized inner tube. Apex of end chamber with medial and ventral lobes. Sclerotized inner tube short with heavily sclerotized dorsal armature fused with Ford's sclerite. Crescent sclerite thickened on anterior portion. Crochet sharp and ventrally hooked within end chamber. Girdle of end chamber extending nearly ½ length of median lamina. Sail extending ¾ length of median lamina. Penis rods extending just beyond apex of median lamina. *Modified abdominal segments* (allotype female) (Figs. 33–34): Tergum VII with 2 rows of setae (per side: 4 and 4), main row with intercalaries. Three antesensilial bristles, lateral ⅔ and medial ⅓ length of long medial bristle. Tergum VIII with 2 setae anterior to spiracle VIII, caudal margin with dorsal lobe subtended by patch of 14–16 variable sized setae. Dorsal anal lobe with long seta at base of anal stylet. Latter 4 times as long as wide with single long apical seta and 2 minute setae. Ventral anal lobe smoothly convex ventrally. Sternum VII bearing a truncate lobe on dorso-caudal margin subtended by 2 sinuses; 9 setae per side (Fig. 34). Apical ⅓ of hilla pigmented, bulga extending onto base of hilla. Duct of spermatheca enters cribriform area on ventral surface (Fig. 33). Bursa copulatrix lightly sclerotized and perula indistinct.

Remarks.—Collections of this new species are from two geographically isolated mountain ranges, separated by 600 km of the lowland drainage basins of the Limpopo and Save Rivers. Within the southern mountain range, two disjunct collections are separated by more than 225 km. It is most unusual that so few specimens of such a distinct taxon could be collected from such a broad geographical area (across 825 km). This flea is an inhabitant of montane regions and was found on *M. cafer* and an unknown species of *Mastomys* in both mountain ranges indicating one or both are likely its preferred host.

Etymology.—The specific name is derived from the truncate nature of the apex of the st. IX of the male, which is quite unlike all other taxa of *Ctenophthalmus* (except *C. acanthurus*).

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MORPHOLOGY OF THE CHORION OF *DIAPHEROMERA FEMORATA* (SAY) (PHASMIDA: HETERONEMIIDAE)

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Abstract.—The ovoid and globular egg of *Diapheromera femorata* (Say) has a prominent capitulum on the anterior operculum and a distinct, dorsal micropylar plate. Capitular struts are irregularly shaped and enclose a sheet-like material which has large, circular holes. Ridges and indentations are situated at the junction of the operculum and egg capsule and provide an attachment mechanism for the operculum. The size, form, and spacing of these ridges differ among genera and may have some taxonomic importance. The internal micropylar stalk has a thick wall that surrounds a spongy material.

Key Words: capitular strut, chorionic extensions, micropylar stalk, opercular ridges

The taxonomic importance of egg morphology is increasingly significant in a wide variety of insect orders, such as Ephemeroptera (Gaino et al. 1989), Orthoptera (Rampini and Saltini 1994), Plecoptera (Stark and Szczytko 1982, Stark and Lentz 1988) and Diptera (Lounibos et al. 1997). The morphological characteristics of stick insect eggs are very useful in the systematics of Phasmida and Kaup (1871) made use of such characteristics. In the last two decades, a standardized set of descriptive morphological terms for stick insect eggs has been used in the classification at the subfamilial and generic levels (Clark 1976a, b, 1979; Sellick (Clark) 1988, 1994, 1997).

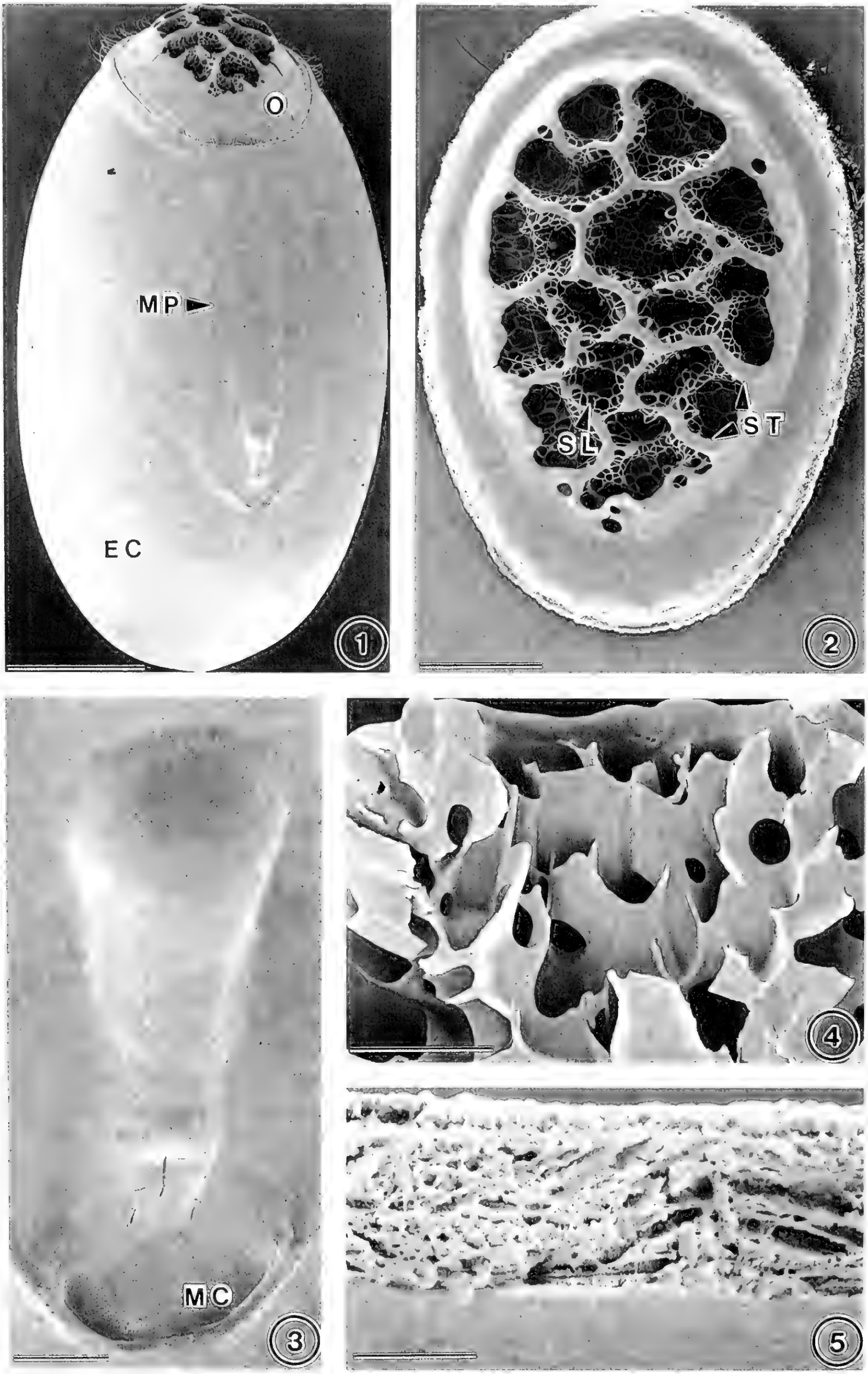
Séverin (1910) and Clark (1976a) published descriptions of *Diapheromera femorata* (Say) eggs using light microscopy. The purpose of the present morphological study is to give a detailed description of the egg of *D. femorata,* using scanning electron microscopy (SEM) in order to provide more detailed data for heteronemiine eggs, for which there is a scarcity of information.

MATERIALS AND METHODS

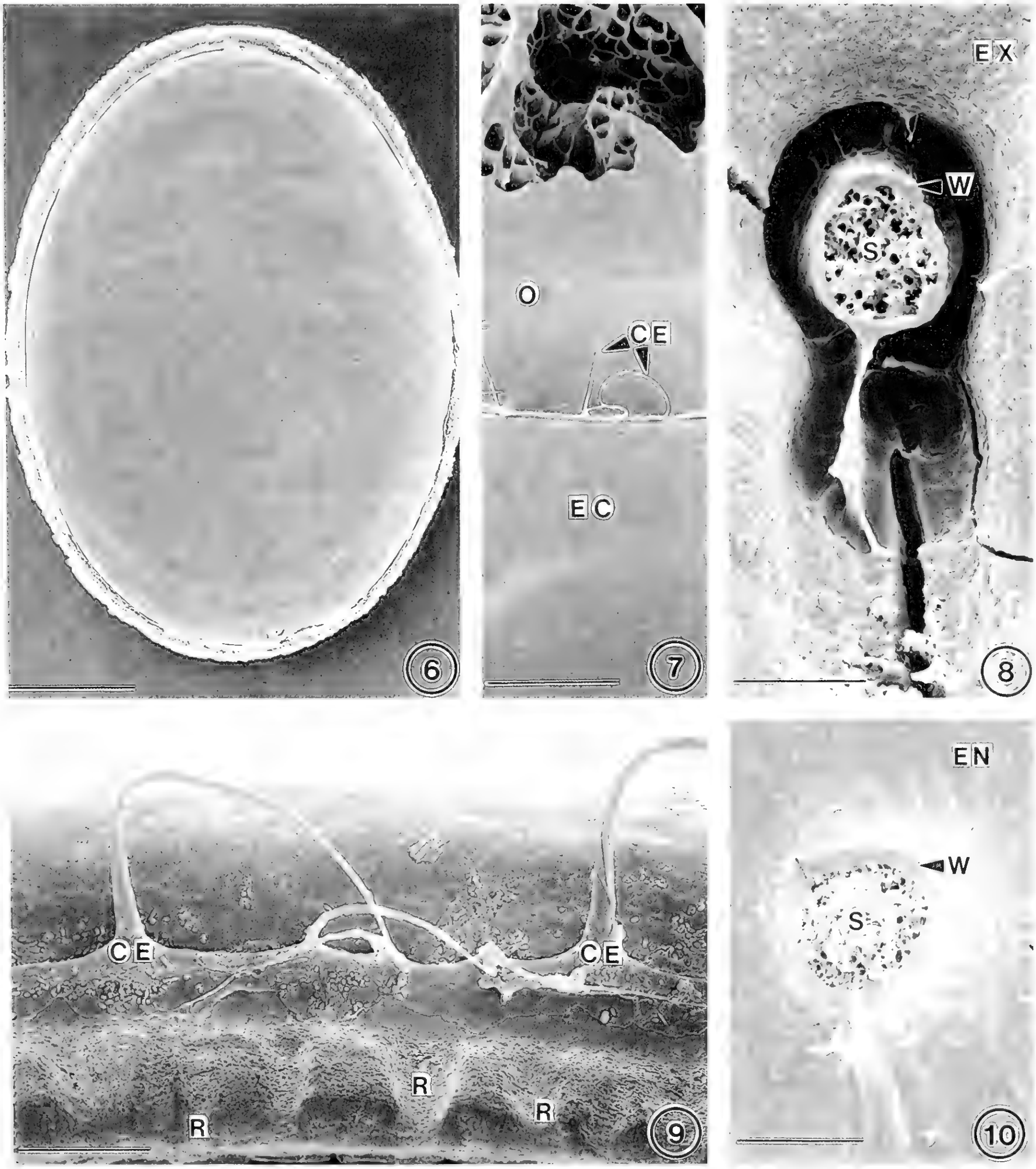
Oviposited eggs were obtained from two field collected females and were immersed in 3% glutaraldehyde and 3% paraformaldehyde in 0.1 M Na-cacodylate buffer, pH 7.1, for 12 h at 4°C. The specimens were rinsed in buffer and post-fixed for 4 h in 2% $0s0_4$ using the same buffer. The eggs were dehydrated in a graded series of ethanol and then either critical point dried or air dried from hexamethyldisilazane. After the eggs were mounted on aluminum stubs, they were coated with gold-palladium. The eggs were examined with a LEO 360s scanning electron microscope at 15kV. Six eggs were placed on slides and measured with a dissecting microscope. The measurements are given as a mean plus the range, and the structures measured for this study are defined by Sellick (Clark) (1997).

RESULTS

Dimensions of the *Diapheromera femorata* egg are as follows: capsule length 2.35 mm (2.10–2.85), capsule width 1.38 mm



Figs. 1–5. *Diapheromera femorata* egg. 1, Habitus of the egg with the apical operculum (O) and the dorsal micropylar plate (MP) on the egg capsule (EC). Scale bar = 500 μm. 2, Irregularly shaped struts (ST) on the capitulum and the sheet-like (SL) material in the spaces between the struts. Scale bar = 200μm. 3, Higher magnification of the posterior end of the micropylar plate in Fig. 1 showing the micropylar cup (MC). Scale bar = 50 μm. 4, Sheet-like material among the struts. Scale bar = 50 μm. 5, Broken edge of the egg capsule. Scale bar = 10 μm.



Figs. 6–10. *Diapheromera femorata* egg. 6, Aporous underside of the operculum. Scale bar = 200 μm. 7, Chorionic extensions (CE) encircle the egg at the junction of the operculum (O) and egg capsule (EC). Scale bar = 100 μm. 8, Internal view of posterior end of micropylar plate showing exochorion surface (EX) and the wall (W) and spongy (S) material of the micropylar stalk. Scale bar = 20 μm. 9, Chorionic extensions (CE) of the operculum and the ribbing or ridges (R) on the edge of the operculum. Scale bar = 20 μm. 10, Endochorionic surface (EN) showing the wall (W) and spongy (S) material of the micropylar stalk. Scale bar = 20 μm.

(1.25–1.52), capsule height 1.70 mm (1.65–1.74), h/l% = 72, w/h% = 81, w/l% = 59 (Fig. 1), operculum length 0.95 mm (0.88–1.05), operculum width 0.67mm (0.64–0.70) (Fig. 2); micropylar plate length 1.35 mm (1.31–1.38), mircopylar plate width 0.36 mm (0.33–0.40) (Fig. 3). The eggs are dark grey to black with light grey patches around the micropylar plate. The egg has a relatively smooth surface at low magnification and has a rough appearance at higher magnifications. The exochorion of the egg capsule is 12.5 μm (11.0–13.5) thick and is composed of irregular layers of material that give a porous appearance (Fig. 5).

The capitulum, which is an integral part of the operculum, consists of a distinct elliptical ridge that has narrow, irregularly shaped struts radiating toward the capitular center (Fig. 2). It is 0.77 mm (0.74–0.79) long and 0.55 mm (0.52–0.57) wide. Circular holes are also found in this ridge (Fig. 2). A sheet-like material is situated in the enclosures that are created by the struts and gives a spongy appearance to the capitulum (Fig. 2). This sheet-like material is an extension of the strut and has very distinct round holes in its surface (Figs. 2, 4).

When the operculum is removed from the egg, the anterior end has a truncate appearance and the underside of the operculum is non-porous and smooth (Fig. 6). A fringe of long, chorionic extensions is found at the junction of the operculum and egg capsule (Figs. 1, 7, 9). At the junction of the egg capsule and the operculum, the surface of these two structures is distinctly ridged (Fig. 9). The ridges vary in shape and width, are similar in length, and are spaced irregularly.

The micropylar plate is long, parallel sided, round ended and raised from the surface of the egg capsule (Fig. 1). An U-shaped and distinctly raised micropylar cup is situated at the posterior end of the micropylar plate (Figs. 1, 3), and this is where the micropyles are located. Internally, the exochorion and endochorion are connected by the micropylar stalk which is about 50 μm wide and consists of a distinct wall that surrounds a spongy substance (Figs. 8, 10).

DISCUSSION

The morphometric ratios of h/l% and w/h% proposed by Sellick (Clark) (1997) for phasmid eggs indicate that the egg of *Diapheromera femorata* (h/l% = 72; w/h% = 81) is rounded and not flattened. In previous descriptions of the *D. femorata* egg by Séverin (1910) and Clark (1976a, b), the sheet-like material among the capitular struts and the distinct circular holes in this material are not mentioned. The aforementioned material is not found among the capitular struts of *Megaphasma dentricus* (Stål) (Heteronemiidae), which is a closely related species (Stark and Lentz 1986), and the struts of *D. femorata* make a very irregular pattern as compared to the anastomosing struts of *M. dentricus* (Stark and Lentz 1986). Another distinct difference between these two heteronemiid species is the surface texture. The egg surface of *M. dentricus* is covered throughout with micro-tubercular projections, and the egg surface of *D. femorata* is basically smooth.

Indentations and ridges that are found on the surface of the egg capsule and operculum at the junction of these two structures also may have some taxonomic significance. The form, size and the spacing of the ridges are very distinct among the species where it has been observed. In *Bacillus rossius* (Rossi), ridges are regularly shaped, evenly and closely spaced, of different lengths, but similar widths (Mazzini and Scali 1977); in *Carausius morosus* (Brunner), ridges are triangularly shaped, of equal spacing and length, but vary in width (Larink 1978); in *Anchiale maculata* (Olivier), ridges are similar in shape (tubular) and length, closely spaced, and vary in width (Viscuso and Longo 1983); and in *D. femorata*, ridges vary in shape and width, are irregularly spaced, but of similar length.

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A NEW, OCELLATE SPECIES IN THE GENUS *LOJUS* McDONALD (HETEROPTERA: PENTATOMIDAE)

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Abstract.—A **new species**, ***Lojus ocellatus***, from Ecuador is described. It is the first known species of *Lojus* with hind wings and ocelli, though both are reduced in size compared to pentatomid species capable of flight.

Key Words: stink bug, brachyptery, ocelli, Ecuador

Pentatomids in the New World genus *Lojus* (McDonald 1982) are rarely encountered insects. They are remarkable because they are flightless, an unusual adaptation among stink bugs. Their dark color and cryptic outline, along with their rarity in collections, suggests that their natural habitat is some dark, hidden place, out of sight of the general collector. The recorded distribution of the four described species is from Costa Rica to Ecuador. The described species lack hind wings and the ocelli are absent or rudimentary. The loss of ocelli in the Heteroptera is generally correlated with a loss of flight (Schuh and Slater 1995). Thus, the discovery of an alate member of the genus is notable, and in accordance with expectations, the ocelli are also present. In this new species, the hind wings are present in both sexes, though reduced in size, being roughly coextensive with the hemelytral corium. In the female specimen the hemelytral membranes are distinctly less developed than in the males, reaching only to the penultimate abdominal segment, whereas the tips of the wing membranes surpass the abdominal apex in the males (Fig. 1). In a typical stink bug the hind wings are roughly equal in length to the hemelytra. The ocelli in the new species are also much smaller than is typical for members of the family. Thus, one might characterize the capacity for flight in this species as vestigial, rather than absent. Intraspecific dimorphism in wing development is not uncommon in brachypterous insects, and, when more specimens are known, it may prove to be the case in this species as well.

Inasmuch as the definition of the genus (Thomas 1997) included the absence of hind wings and ocelli, a revised diagnosis must emphasize the unusual metathoracic scent gland orifice, which lacks the auricle or ruga found in other stink bugs with the exception of some Strachiini (e.g., *Murgantia* Hahn). In *Lojus* the orifice is a simple slit arising from the side of a small elevation located at the base of the evaporatorium. Also, the venation of the hemelytral membrane is reticulate, which, in combination with the character of the scent gland orifice, separates *Lojus* from all other pentatomine genera.

Lojus ocellatus Thomas, new species
(Figs. 1–4)

Description.—Body dorsoventrally depressed with angular outline (Fig. 1). Surface coarsely rugose, punctate throughout, dark, dusky brown. Length of male 7.0 mm,

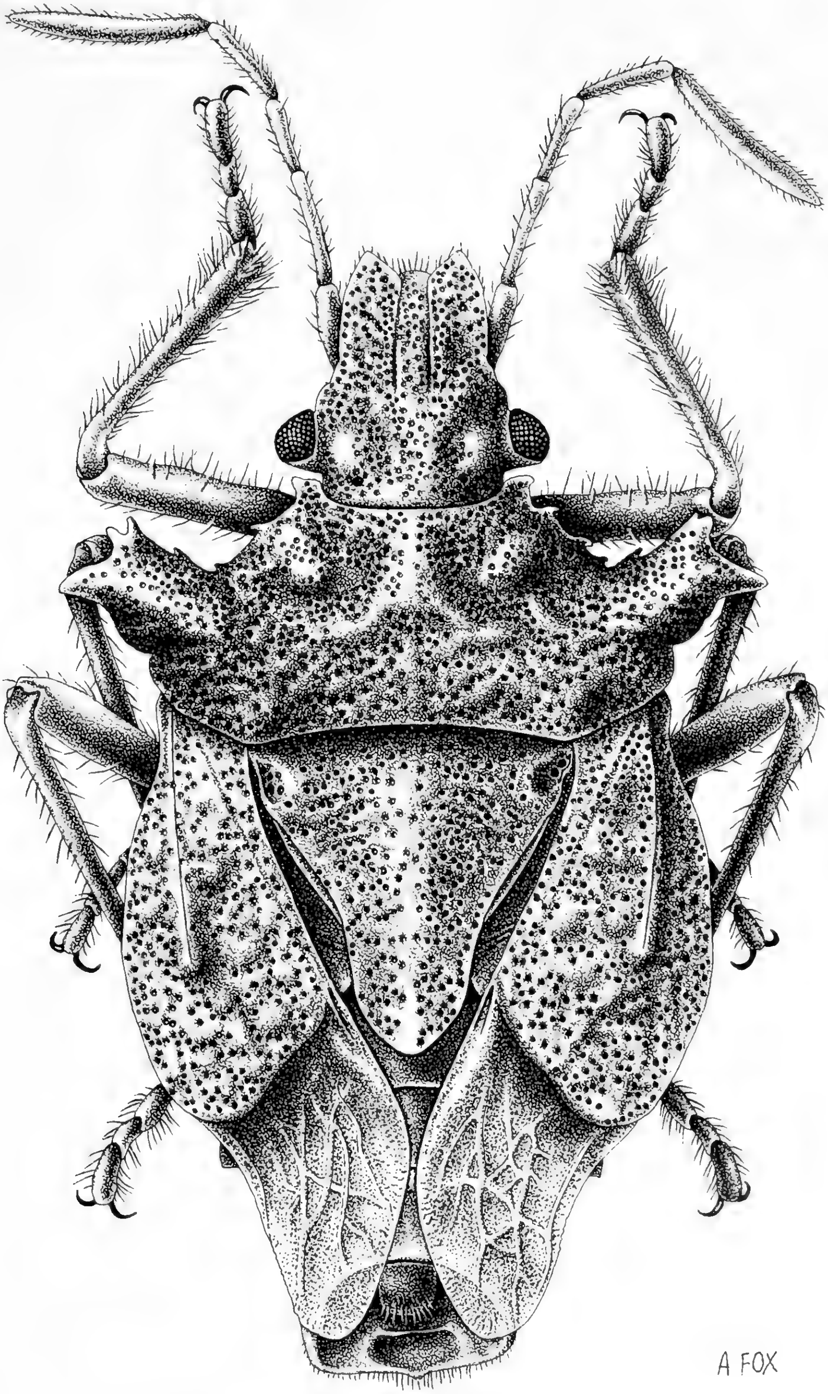


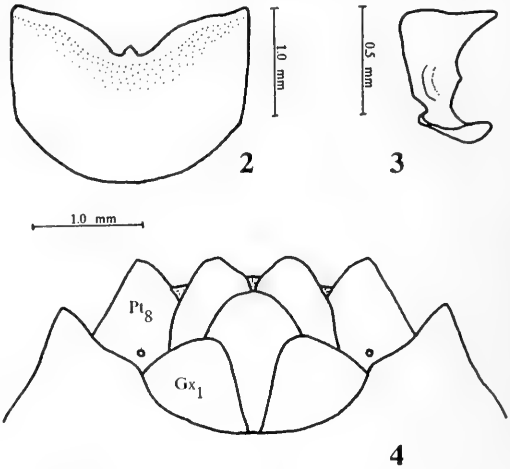
Fig. 1. *Lojus ocellatus,* dorsal habitus.

pronotal width 4.5 mm; female length 9.0 mm, width 5.3 mm.

Head: Anteocular length from tip of jugum to anterior margin of eyes subequal to width between eyes. Anteocular width of head 1.2 mm. Length of head from ocelli to tip of juga, 1.5 mm. Eyes subpedunculate, proximal to but not touching anterior pronotal angle. Jugal width twice width of tylus at base. Lateral margins of juga sinuate in dorsal view. Apex of tylus obtuse; apices of juga angulate. Buccula low except anteriorly developed into carina with a pronounced angular cusp. Antennal segments tan; V longest, about twice as long as III; I shortest, slightly shorter than III; II and IV subequal and longer than III. Apex of rostrum in repose attaining 3rd visible abdominal sternite; segment III longest, slightly longer than II which is slightly longer than IV.

Thorax: Humeral angles strongly quadrately produced, dorso-ventrally depressed, apex emarginate, angles acute. Anterior pronotal angle with outwardly directed cusp. Anterolateral pronotal margins concave in dorsal view bearing 3–4 irregular teeth. Cicatrices and midline of pronotal dorsum tumid. Length of pronotum at midline 1.4 mm. Length of scutellum 2.0 mm. Each basal angle of scutellum with shallow fovea. Apex of scutellum with narrow, elongate, sordidly pale, vitta. Apex of hemelytral corium broadly rounded, extending posteriorly to middle of penultimate tergite. Hemelytral membrane falcate, surpassing abdominal apex in male, not reaching apex in female; venation reticulate. Hind wings present, about equal in length with corium. Venter of thorax dark brown except for coxae, distal half of femora, and mesopleuron, yellow. Metapleural scent gland orifice small, slit-like, located on side of small, transverse elevation, unattended by auricle, sulcus or ruga. Evaporatorium occupying about one-third of metapleural surface. Femora unarmed. Metatibia feebly sulcate on planar surface.

Abdomen: Laterotergites of connexivum broadly exposed, apices obtusely produced. Venter dark brown except margin of each sternite with yellow blotch at middle. Greatest width of abdomen 3.6 mm.



Figs. 2–4. *Lojus ocellatus,* genitalia. 2, Pygophore, ventral view. 3, Left paramere, ental view. 4, Female terminalia, ventral view. Pt_8 = eighth paratergite; Gx_1 = first gonoxoxite.

Genitalia: Posterior margin of male pygophore shallowly emarginate in caudal view with small tooth at middle of emargination (Fig. 2). Reniform excavation present between posterior margin and inferior ridge. Paramere flattened with entally directed, acute lateral projection near apex (Fig. 3). Eighth and ninth paratergites of female with angular apices projecting posteriorad beyond margin of tenth tergite. Spiracles present on eighth paratergite. Mesial margins of first gonocoxites separate and divergent (Fig. 4).

Types.—Holotype ♂, verbatim label data: "ECUADOR: Napo Prov. Sierrazul, 2,200 m SW of Baeza. 0°40′S 77°55′W 22–30 Jan. 1996, T. J. Henry" (deposited in the National Museum of Natural History, Smithsonian Institution, Washington D.C). Allotype ♀, same label data as holotype (deposited in author's collection). Paratype ♂: "ECUADOR: Napo Prov. Caba as San Isidro 2 Km NW Cosanga, 0°33′S 77°55′W, VII-20-23-1998, 2,150 m, premontane rain forest, Ratcliffe, Jameson, Smith, Villatoro" (deposited in the University of Nebraska State Museum, Lincoln).

Remarks.—*Lojus ocellatus* is represented by three specimens from two locations in Ecuador, a country from which two of the other species are also known. The primary characters which differentiate species of Pentatomidae are found in the male genitalia, and this appears to hold for *Lojus* as well. Fortunately, the one female specimen of *L. ocellatus* was associated with a male. One of the described Ecuadorian species, *L. ateuchus* Thomas, is known from but a single female. The anterolateral pronotal margin is toothless in the latter species, differentiating it from all other species. In the key to species by Thomas (1997), *L. ocellatus* will go to *L. bordoni* (Brailovsky and Rolston 1986). In the latter species the posterior margin of the male pygophore is deeply emarginate in caudal view and the parameres are digitoid. In *L. ocellatus* the pygophoral margin is shallowly emarginate with a tooth at the middle (Fig. 2) and the parameres are foliate with a lateral, apical, projection (Fig. 3).

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ZYTHYNNUS, A NEW GENUS OF THYNNINAE (HYMENOPTERA: TIPHIIDAE) FROM QUEENSLAND

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Abstract.—The new genus ***Zythynnus*** is described from Queensland, Australia, based on the **new species *Zythynnus vespoides*** and ***Zythynnus flavipes.***

Key Words: *Zythynnus,* Australia, Queensland, Tiphiidae, Thynninae

Superficially this genus resembles *Agriomyia* Guérin-Méneville, and preliminary phylogenetic analyses indicate that the two are sister groups. Both share the following apomorphic male features: face flattened with widely separated antennal sockets and antennal lobes obsolescent, stipes flat, polished and bladelike, stipal fringe obsolescent and hypopygium with ventral surface shallowly indented medially.

Zythynnus species also bear an uncanny resemblance to *Rhopalidia* Guérin-Méneville species (Vespidae) found in the same region. The biology of *Zythynnus* is unknown, and females are only known for *Z. vespoides,* making generalizations about female generic characteristics impossible.

Specimens were obtained from the Australian National Insect Collection, CSIRO, Canberra, ACT, and both holotypes will be deposited in that collection. Paratypes will be placed in the Australian National Insect Collection and in the Bohart Museum of Entomology, University of California, Davis, USA.

Zythynnus Kimsey, new genus

Male.—*Head* (as in Figs. 2–4): Clypeus narrowly truncate apicomedially, truncation apically rounded and narrower than distance between antennal sockets; antennal sockets broadly separated and weakly elevated laterally; subantennal sclerite as broad or broader than clypeal apex; frons without medial groove extending nearly to midocellus; labrum slender basally, apically narrowly bilobate; vertex without red spot between eye and ocelli; palpi unmodified; hypostomal plate obsolescent, and punctate; occipital and hypostomal carinae convergent medially, weakly defined laterally along hypostomal plate; prementum polished, without discrete long setae or brushes; stipes polished with scattered setae, without discrete brushes or long setae; flagellomeres I–XI less than twice as long as broad; flagellomeres V–XI with tyloids. *Thorax:* Pronotal disk anterior margin with sharp, ridge-like transverse carina; mesopleuron with scrobal sulcus well-developed; propodeum bulging dorsally adjacent to metanotum, flattened posteriorly and sloping obliquely from metanotum to petiolar socket, without petiolar grooves adjacent to socket; propleuron convex; forecoxa globular; legs unmodified. *Metasoma:* Tergum I about as broad as long or broader, posteriorly narrowed adjacent to tergum II giving appearance of a petiolar segment (as in Fig. 14); sternum I convex, strongly declivous posteriorly; terga I–VI covered with short, dense, velvety pubescence; tergum III with abbreviated subspiracular sulcus; terga and sterna without subapical transverse sulcus; epipygium with broad impunctate, polished medial zone merging with broad impunctate rim (as in Fig. 12); hypopygium rounded laterally, with short medial tooth apically, inner surface with arcuate transverse subapical carina (as in Fig. 8). *Genital capsule* (as in Figs. 5–7, 9–11): Gonocoxa enlarged dorsally and dorsoapically bilobate, narrowly attached to gonobase in profile; paramere curved ventrally with bluntly tapered apex, sparsely setose apically, strongly bulging ventrally above gonobase; aedeagus with robust, medially bulging basal column and short apical strap or loop; volsella large, with angulate apex, apex bending posteriorly in rounded lobe; penis valves digitate, bending toward aedeagus. *Color:* Black, with yellow, red and orange markings.

Female.—*Thorax:* Pronotum with strongly elevated medial disc; scutum obscured dorsally; scutellum more than half as long as pronotum; propodeum with broad dorsal surface. *Metasoma:* Tergum I with broadly W-shaped transverse sulcus; tergum II with five transverse ridges; tergum VI with broadly ovoid medial plate delimited by two sublateral longitudinal carinae, innermost carina subtended by dense brush of setae arising from inner margin of outer carina (as in Fig. 13); sternum V with dense elongate brush of setae adjacent to tergum VI; sternum VI broadly hoof-like. *Color:* Brown.

Type species.—*Zythynnus vespoides* Kimsey, new species.

Etymology.—The name, *Zythynnus,* is a nonsense combination of letters combined with "*thynnus*" a common generic suffix in the Thynninae; gender, masculine.

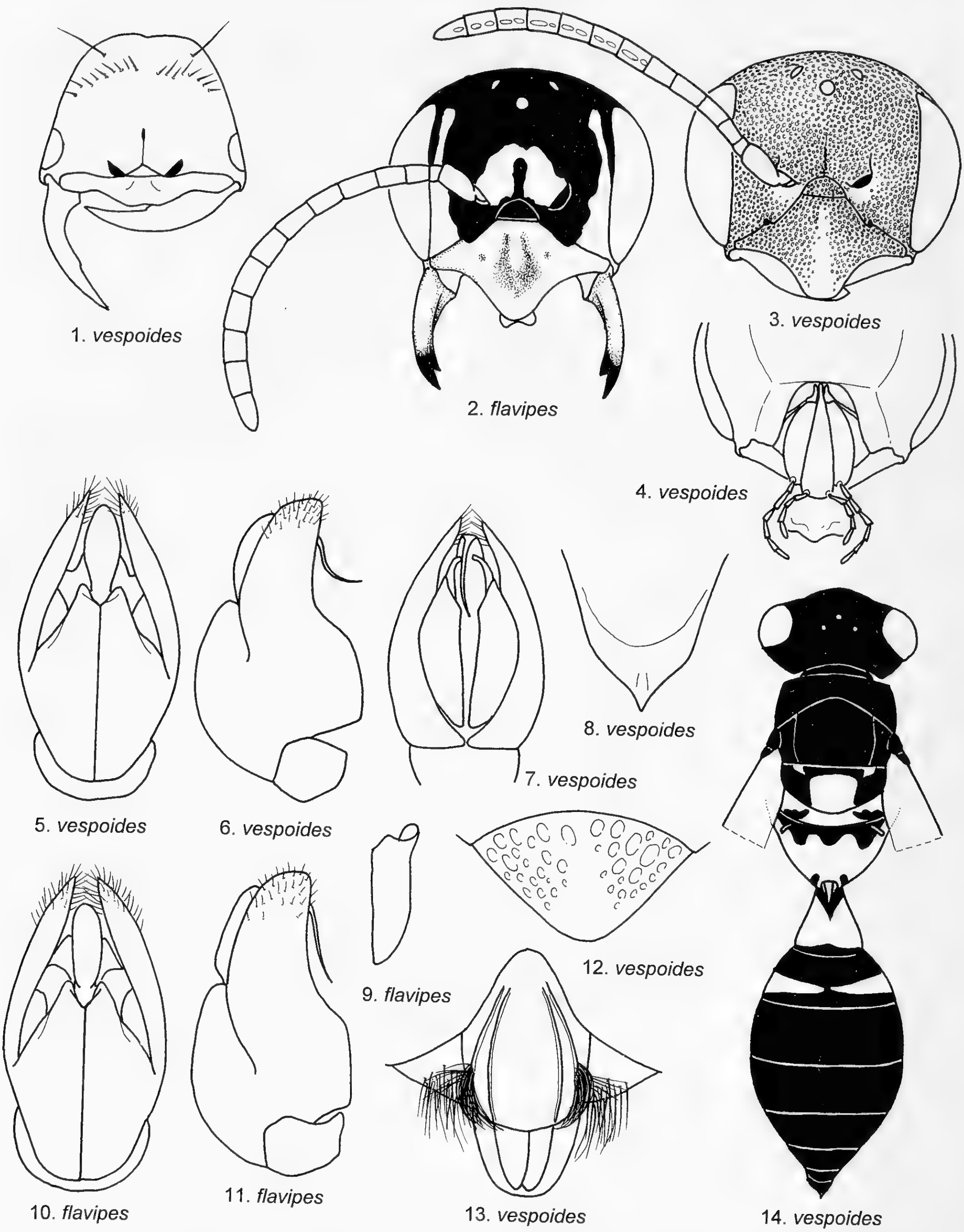
Included species.—*Zythynnus vespoides,* new species and *Zythynnus flavipes,* new species.

Distribution.—Northeastern Queensland.

Discussion.—*Zythynnus* can be distinguished from *Agriomyia* by a number of apomorphies in the male, including the obsolescent hypostomal plate, flagellomeres less than twice as long as broad, metasomal segment I petiolate and segments III–VII covered with dense, short, velvet-like pubescence, oblique subspiracular sulcus restricted to metasomal terga I and II, with a short remnant on III, and lateral petiolar socket grooves absent on the propodeum. *Agriomyia* species are characterized by having tyloids on the apical flagellomeres, metasomal sternum I with a long medial prong (in most species), and forefemur basally indented.

Zythynnus flavipes **Kimsey, new species**
(Figs. 9–11)

Male.—Body length 8 mm; punctation and sculpturing as in *vespoides. Head:* Clypeal apex 0.8× greatest width of clypeus; clypeus greatest width 1.8× as length; face 1.5× as long as greatest width above antennal sockets; midocellus 6 midocellus diameters from nearest eye margin; flagellomere I 1.1× as long as broad; flagellomere II 1.4× as long as broad; flagellomere III 1.8× as long as broad; flagellomere VIII 1.5× as long as broad. *Thorax:* Propleuron convex; forecoxa globular; pronotal punctures contiguous, small and transverse striatiform anterior face polished and nearly impunctate, transverse anterior carina thin and sharp-edged; scutal and mesopleural punctures dense small and contiguous, appearing granular; scutellar punctures 0.5–1.0 puncture diameters apart; metanotum nearly impunctate; propodeal anterior margin bulging dorsally, posterior surface nearly flat from metanotum to petiolar socket, punctures dense and nearly contiguous dorsally and laterally, nearly impunctate above petiole. *Metasoma:* Tergum I highly polished, with scattered punctures, remaining terga and sterna appearing granular with dense fine shagreening obscuring punctures, punctures large, 1–2 puncture diameters apart; tergum II–VI covered with dense short velvety pubescence; sternum I abruptly declivous posteriorly. *Genital capsule* (Figs. 9–11): Paramere tapering to apex from apical fourth or beyond. *Color:* Body black, with yellow to orange markings. Face with yellow band



1. *vespoides*
2. *flavipes*
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9. *flavipes*
10. *flavipes*
11. *flavipes*
12. *vespoides*
13. *vespoides*
14. *vespoides*

Figs. 1–14. Illustrations of *Zythynnus* species. 1, Front view of female face, antennae removed. 2–3, Front view of male face, right antenna removed. 4, Ventral view of male head. 5, 10, Dorsal view of genital capsule. 6, 11, Lateral view of genital capsule. 7, Ventral view of genital capsule. 8, Dorsal view of hypopygium. 9, Ventral view of volsella. 12, Dorsal view of epipygium. 13, Posterior view of female metasomal apex. 14, Dorsal view of male with legs, antennae and wings removed. White areas in Figs. 2 and 14 indicate yellow coloration, stippled areas in Fig. 2 indicate orange coloration.

along inner eye margin and two large barely separated yellow spots above antennal sockets; clypeus yellow, with lateral small round black spot, irregular brown medial band, and central yellowish spot; mandible basomedially yellow; gena with small yellow spot above mandible and one near upper eye margin; pronotum with transverse yellow anterior band broken medially and laterally; scutum entirely black; mesopleuron with subalar yellow spot; scutellum and metanotum with large yellow medial spot and small anterolateral one; propodeum with sublateral longitudinal yellow band and heart-shaped medial one; tegula and parategula yellow; legs: coxae, femora and trochanters dark brown, becoming redder toward femoral apices, tibiae and tarsi orange; wing veins brown, membrane yellow-tinted.

Female.—Unknown.

Type material.—Holotype ♂: Bundaberg, Sept. 1972, H. Frauca (CANBERRA).

Etymology.—The species name refers to the yellow-tinted wings.

Discussion.—This species is smaller-bodied, 8 mm long as opposed to 9–12 mm in *vespoides,* and more brightly marked than *vespoides,* with more extensive yellow and orange markings and the yellow-tinted wing membrane. Additional distinguishing features include the broader clypeal apex, 0.8× the greatest clypeal width versus 0.2×, and shorter distance between the eye and hindocellus, 6 in *flavipes* versus 7–8 midocellus diameters in *vespoides.*

Zythynnus vespoides Kimsey, new species

(Figs. 1, 3–8, 12–14)

Male.—Body length 9–12 mm. *Head* (Fig. 3): Facial punctures dense and contiguous except for impunctate longitudinal medial band on clypeus, and along lower half of antennal socket; clypeal apex 0.2× greatest width of clypeus; clypeus greatest width 1.7× as length; face 1.1× as long as greatest width above antennal sockets; midocellus 7.7 midocellus diameter from nearest eye margin; flagellomere I 1.4× as long as broad; flagellomere II 1.6× as long as broad; flagellomere III 1.8× as long as broad; flagellomere VIII 1.5× as long as broad. *Thorax:* Pronotal disc punctures contiguous, small and transversely striatiform, anterior pronotal face polished and nearly impunctate, transverse anterior carina thin and sharp-edged; scutal and mesopleural punctures dense small and contiguous, appearing granular; scutellar punctures 0.5–1.0 puncture diameter apart; metanotum nearly impunctate; propodeal anterior margin bulging dorsally, posterior surface nearly flat from metanotum to petiolar socket, punctures dense and nearly contiguous dorsally and laterally, except integument nearly impunctate above petiole. *Metasoma:* Tergum I highly polished, with scattered punctures, remaining terga and sterna appearing granular with dense fine shagreening obscuring punctures, punctures large, 1–2 puncture diameters apart; tergum II–VI covered with dense short velvety pubescence; sternum I abruptly declivous posteriorly. *Genital capsule* (Figs. 5–7): Paramere tapering toward apex from medial bend. *Color* (Fig. 14): Head entirely black to black with dark orange between antennal sockets along margins, across clypeal apex and on mandibles; antenna bright orange; prothorax and mesothorax black to black shading to orange on mesopleuron and anterior and ventral pronotal margins; scutellum black, with large medial and smaller anterolateral yellow spots; metanotum yellow, with sublateral fovea blackish; propodeum yellow becoming orange to black laterally, with trilobate black band across anterior margin; tegula black to dark brown; coxae and trochanters blackish; legs with dark red femora becoming red or orange on tarsomeres; metasomal sterna blackish; tergum I mostly yellow, with dark brown to red anteromedial triangular spot, posterior margin may be blackish; tergum II blackish, with complete or incomplete broad transverse yellow band; remaining terga blackish becoming reddish toward metasomal apex;

wing veins reddish brown, membrane untinted, except marginal cell brown-tinted.

Female.—Body length 8–9 mm; integument finely shagreened except on densely punctate scutellum and propodeal dorsum. *Head* (Fig. 1): Sides converging toward vertex; frons bulging in profile, with row of long hairs and one long hair on either side of vertex; underside of head longitudinally grooved on either side of occipital foramen and oral fossa. *Thorax:* Pronotum with strongly elevated medial disc, disc anteromedially emarginate, pronotum laterally with short tooth-like ridge separated from medial disc by convexity; scutellum one-third as long as pronotum, covered with dense erect setae; propodeum with broad rounded dorsal surface, covered with dense long, erect setae, setae longer than scutellum, becoming shorter toward petiole, propodeum broadly ovoid in posterior view. *Metasoma:* Tergum II with five transverse ridges. *Color:* Dark reddish brown.

Type material.—Holotype ♂: 8–15 km e Mareeba, 9 May 1987, H. E. and M. A. Evans (CANBERRA). Paratypes: 1 ♂, 1 ♀: same data as holotype; 2♂: Luster Crk., 8 km w by n Mt. Molloy, 21–22 May 1980, I. D. Naumann & J. C. Cardale; 1♂: Edgehill, Cairns, 26 Dec. 1969, R. E. Parrott; 1 ♂, 1 ♀: 9 km from Black Mnt., road toward Mareeba, 30 Mar. 1984, Weir & Calder (CANBERRA, DAVIS).

Etymology.—The species name refers to the distinctively vespid-like appearance of this species.

Discussion.—*Zythynnus vespoides* males can be distinguished from those of *flavipes* by their larger size, dark-colored tegula, the blackish propodeum, with transverse yellow band (versus the yellow lateral band and heart-shaped medial spot of *flavipes*), black face, and longer distance between the midocellus and closest eye margin, as discussed under *flavipes.*

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NEW CRANE FLIES (DIPTERA: TIPULIDAE, LIMONIIDAE) FROM DOMINICAN AND MEXICAN AMBER

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Abstract.—Four new species of crane flies (Diptera, Limoniidae) are described from Dominican amber: ***Geranomyia euchara, Elephantomyia grata, Epiphragma aurora,*** and ***Styringomyia optiva***. Additionally two Limoniidae belonging to the genera *Epiphragma* Osten Sacken 1859 and *Toxorhina* Loew 1851 and one Tipulidae of the genus *Brachypremna* Osten Sacken 1886, still unknown from Dominican amber, are characterized. Two new species are described from Mexican amber (Oligocene/Miocene): ***Trentepohlia mexicana*** and ***Trentepohlia immemorata***.

Key Words: Dominican amber, Mexican amber, Tipulidae, Limoniidae, fossil crane-flies

Fossil crane flies from Dominican amber have been investigated little and from Mexican amber are unknown (Evenhuis 1994; Krzeminski 1992, 1996; Podenas and Poinar 1999). In the present study, seven species of crane flies (Diptera: Tipulidae, Limoniidae) are characterized from Dominican amber. Four of these are described as new species in the genera *Geranomyia* Haliday 1833, *Elephantomyia* Osten Sacken 1859, *Epiphragma* Osten Sacken 1859, and *Styringomyia* Loew 1845, and three are assigned to the genera *Brachypremna* Osten Sacken 1886, *Epiphragma* Osten Sacken 1859, and *Toxorhina* Loew 1851. Specimens of the latter three genera, which were previously unknown in Dominican amber, are discussed with many characters featured, but the absence of certain diagnostic characters prohibits a comparison with recent species. Two new species in the same piece of Mexican amber are described in the genus *Trentepohlia* Bigot 1854.

MATERIALS AND METHODS

The Dominican amber specimens are believed to have originated from mines in the Cordillera Septentrional of the Dominican Republic. These mines are in the El Mamey Formation (Upper Eocene), which is a shale-sandstone interspersed with a conglomerate of well-rounded pebbles (Eberle et al. 1980). The exact age of the amber is unknown, with estimates based on foraminifera indicating a range of 15–20 million years (Iturralde-Vincent and MacPhee 1996) and with coccoliths a range reaching 30–45 million years (Cepek 1990). The Mexican amber specimens originated from amber mines in the State of Chiapas in southern Mexico. The amber occurs in the Balumtun sandstone, Mazantic shale and La Quinta formations ranging from the Lower Miocene to the Upper Oligocene (22–26 mya) (Poinar 1992).

In the following descriptions, terminology of genitalia and wing venation follows that presented in the "Manual of Nearctic Diptera" (McAlpine 1981). All specimens originated from the Poinar amber collection maintained at Oregon State University, Corvallis, Oregon. Accession numbers pertaining to these specimens are presented under the section "material examined."

Abbreviations used in the drawings are: air=air bubble; arc=arculus; dm=discal cell; fl=flagellum; gon=gonocoxite; g=gonostylus; i g=inner gonostyle; in a=inner arm of gonostyle; int a -intermediate arm of gonostyle; m-cu=medial-cubital cross vein; og=outer gonostyle; p=penis; pm=paramere; ped=pedicel; R_1=first branch of radius vein; RS=radial sector; rst=rostrum; Sc_1=first subcostal vein; scp=scape; st 9=ninth sternite; tg 9=ninth tergite. We have used the r cross vein here to represent a cross vein connecting R_1 with R_2 or one of the other radial sector veins.

TIPULIDAE

Subfamily Dolichopezinae

Brachypremna Osten Sacken 1886

Species of this genus have long, slender legs with the tarsi almost as long as the femora and tibiae combined, and hind tibiae spurred but the fore and middle tibiae apparently spurless. They are characterized by the most developed neck of all crane flies (Savchenko 1983). The male genitalia are inverted, a rare situation among Tipulidae. The larvae are covered with dense pubescence (Rogers 1949). Recent species have a tropical distribution except for one species which occurs in the southern and eastern Nearctic (Alexander and Byers 1981). Other fossil *Brachypremna* are restricted to the study by Krzeminski (1996) since *B. eocenica* Meunier 1906 was transferred to the genus *Tipula* (Evenhuis 1994).

Brachypremna sp.

(Fig. 1)

A single poorly preserved female with the tip of the ovipositor missing. Body length approximately 11.5 mm. Wing length 12.5 mm. Head and dorsum of thorax covered with reddish oxidative dust from the fossilization process; antennae not visible. Haltere 1.8 mm long. Wing (Fig. 1) long and narrow, totally clear except for brownish stigma; veins light brown. Venation: Sc_1 long, extending almost to the tip of R_{1+2}; tip of R_{1+2} perpendicular to the remainder of the vein; Rs strongly arcuated at origin; deflection of R_{4+5} distinct; petiole of cell m_1 shorter than cell itself; r-m short but present; m-cu immediately beyond the fork of M; vein A_2 very short. Femur II: 11.3 mm, III: 10.7 mm long.

Examined material.—♀, D-7-39D, Dominican amber.

Discussion.—This specimen is probably undescribed, but the inability to see many characters makes a comparison with recent *Brachypremna* impossible. It is clearly different from the fossil species described by Krzeminski (1996) from the same deposits.

LIMONIIDAE

Subfamily Limoniinae

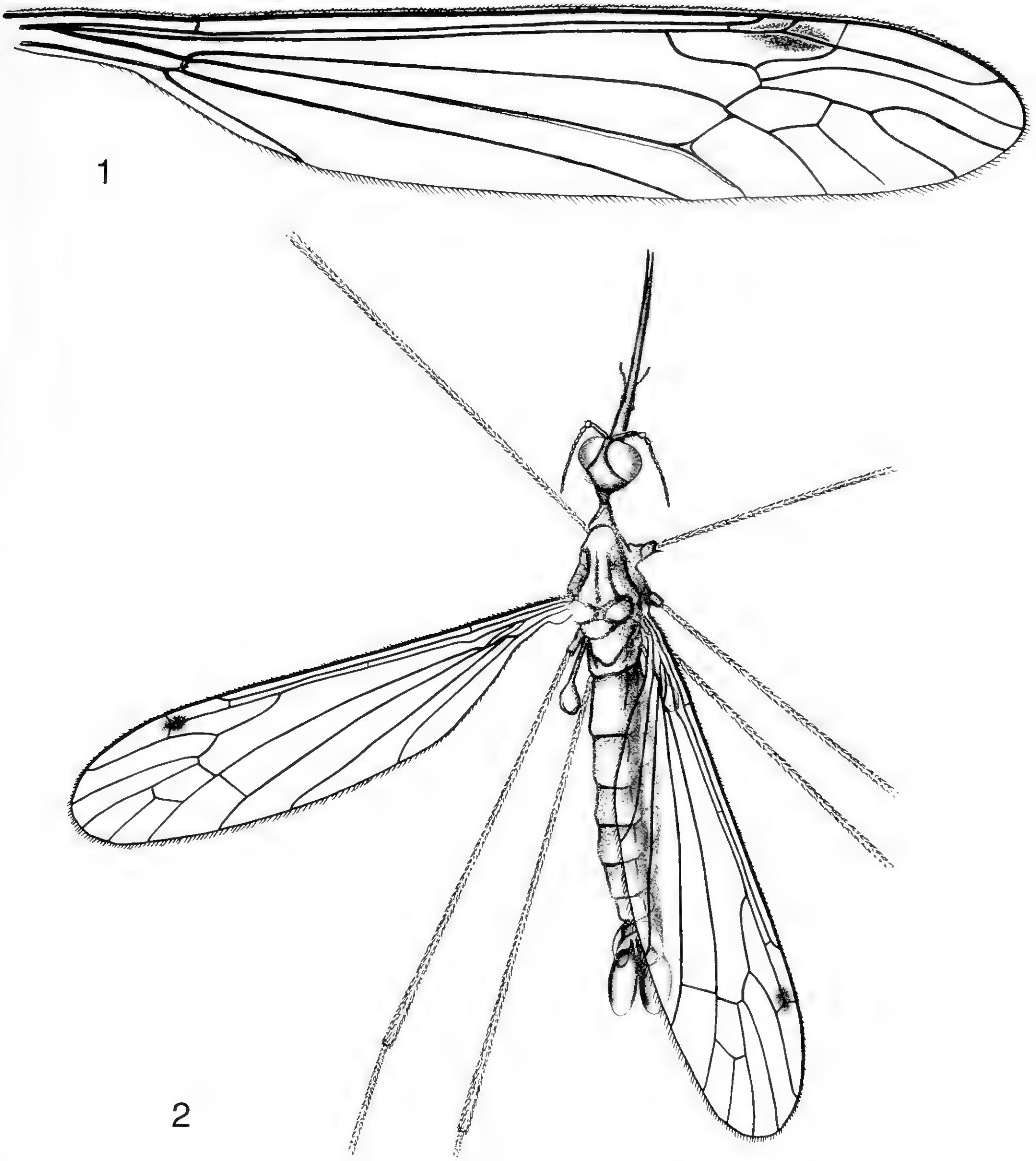
Geranomyia Haliday 1833

The very large and complex genus *Geranomyia* has its center of distribution in the Neotropical Region. Many species are widely distributed while others seem to be rather local (Alexander 1921). The snout (rostrum) in *Geranomyia* is very long, while the sucking mouthparts are drawn out still further. Adults feed on nectar of composite flowers (*Eupatorium, Solidago, Aster, Silphium, Rudbeckia, Verbesina, Cacalia,* etc.) (Knab 1910). The larvae live under water (even salt water), feeding on algae, diatoms, etc.; sometimes they make silken cases (Oldroyd 1966). No representatives have been described from any amber source (Evenhuis 1994).

***Geranomyia euchara* Podenas and Poinar, new species**

(Figs. 2–7)

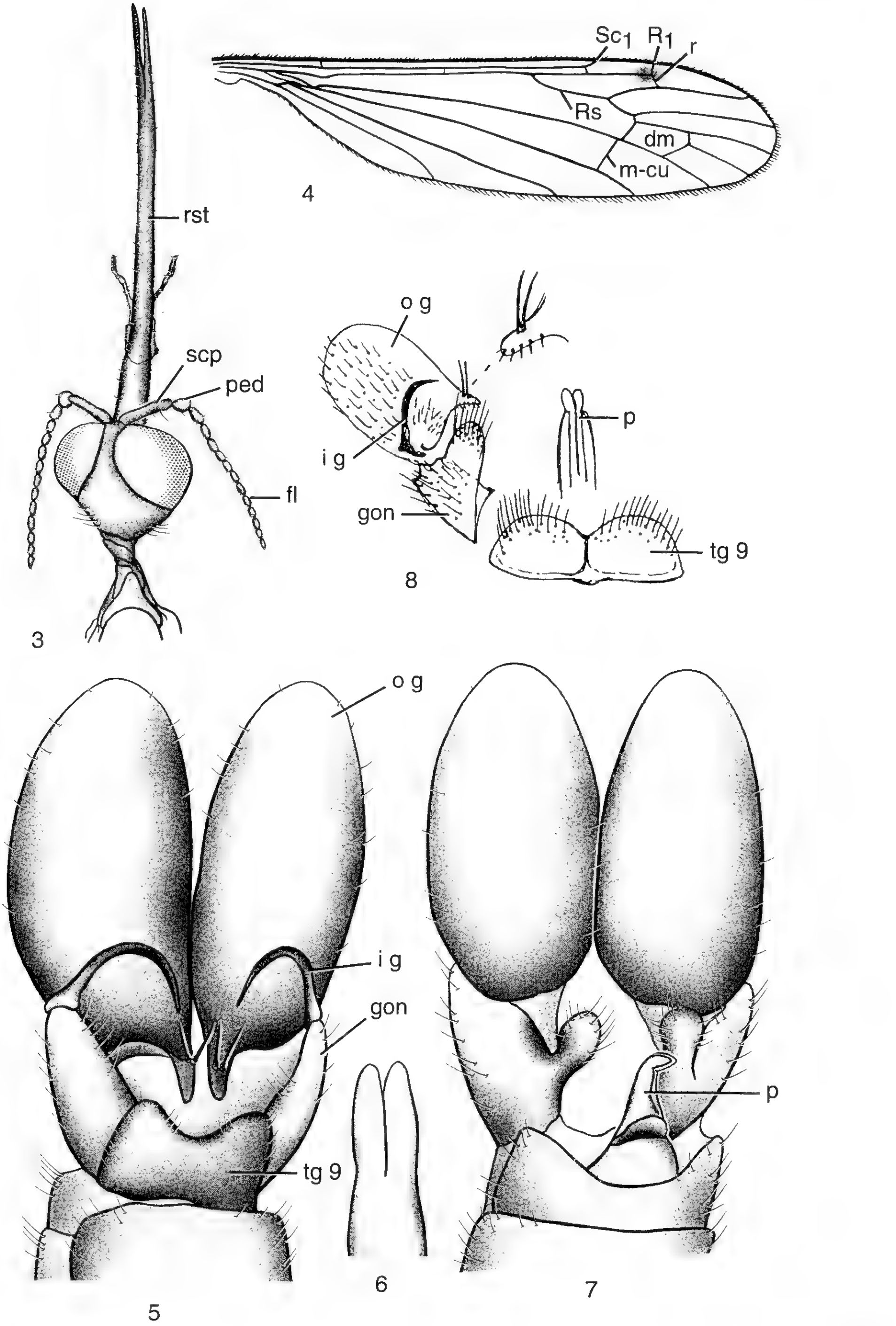
Diagnosis.—General coloration brown; body with only very sparse, short, brownish



Figs. 1–2. 1, *Brachypremna* sp., wing. 2, *Geranomyia euchara*, holotype, general view.

hairs, mostly on posterior margins of abdominal tergites and sternites. Wing completely clear, without dark spots except for small brownish stigma. Male terminalia with large, elongate-oval inner gonostylus bearing two rostral spines of the same length and a comparatively small, strongly hooked outer gonostylus; 9th tergite with shallow but broad posterior incision; apex of penis bilobed. Clearly differs from related species by structure of male genitalia.

Male.—Body length 5.3 mm (without rostrum), rostrum 1.9 mm long, wing length 5.1 mm. Vertex of head dark brown, with short brown hairs. Frons rusty dorsally to light brown ventrally. Eyes nearly meeting ventrally. Rostrum, mouthparts and palpi light brown. Palpi with short, sparse,



Figs. 3–8. 3–7, *Geranomyia euchara,* holotype. 3, Head. 4, Wing. 5, Male genitalia, dorsal view. 6, Tip of aedeagus. 7, Male genitalia, ventral view. 8, *G. subvirescens*, male genitalia, dorsal view (after Alexander 1970). (See Materials and Methods for abbreviations.)

brownish setae. Antenna short, 1.1 mm long, 14-segmented, brown, if bent backwards, barely reaching frontal margin of thorax. Scape cylindrical, three times as long as rounded pedicel (Fig. 3). Flagellomeres shortly oval. Verticils short, not exceeding length of respective segments.

Thorax light brown; prescutum with dark, narrow, median stripe extending onto scutellum. Wing (Fig. 4) without dark spots, except for small, brownish stigmal area. Veins brown. Venation: Sc_1 ends at middle of Rs; Sc_2 close to Sc_1; supernumerary cross-vein in cell sc far from Rs base; R_{1+2} and R_2 in nearly transverse alignment; R_3 and R_{4+5} parallel. Discal cell twice as long as wide; cross-vein m-cu slightly before fork of M. Halter light brown, 0.8 mm long. Coxae, trochanters and legs uniformly brown; femur I: 4.1 mm long, II: 4.8 mm, III: 5.0 mm, tibia II: 4.4 mm, III: 4.6 mm, tarsus II: 2.7 mm and III: 3.0 mm long.

Abdomen brown; short, sparse brownish hairs on posterior margins of tergites and sternites. Genitalia (Figs. 5–7) same color as rest of abdomen; posterior border of ninth tergite shallowly and broadly emarginate, lateral lobes with sparse setae; gonocoxite elongate, narrowing apically, with rounded ventro-mesal lobe; inner gonostyle comparatively large, elongate-oval, covered with sparse, short setae, rostral portion with two equal spines emerging from basal portion; spines divergent, situated slightly beyond base of rostrum, their tips acute; outer gonostyle hook-like, comparatively large, tip acute; tip of penis bilobed.

Female.—Unknown.

Material examined.—Holotype: ♂, D-7-39B, Dominican amber.

Etymology.—The species name is based on *eucharis,* which is Latin for gracious and charming.

Discussion.—The new species is closely related to *G. subvirescens* (Alexander 1930), which is known from Cuba (Trinidad Mountains—type locality), Dominica, Panama and Venezuela (Alexander 1970). Both species have unpatterned wings and similar male genitalia. However *G. euchara* differs from *G. subvirescens* (Fig. 8) in possessing a much longer inner gonostylus, a longer and more curved outer gonostylus, a smaller and rounded ventro-mesal lobe of the gonocoxite, the posterior border of the ninth tergite more emarginate and the apical lobes of the penis longer and strongly downturned. Wing venation of the new species has a distinct cross-vein r-m, which is very short to obliterated in *G. subvirescens.* This is the first species of the genus described from amber.

Elephantomyia Osten Sacken 1859

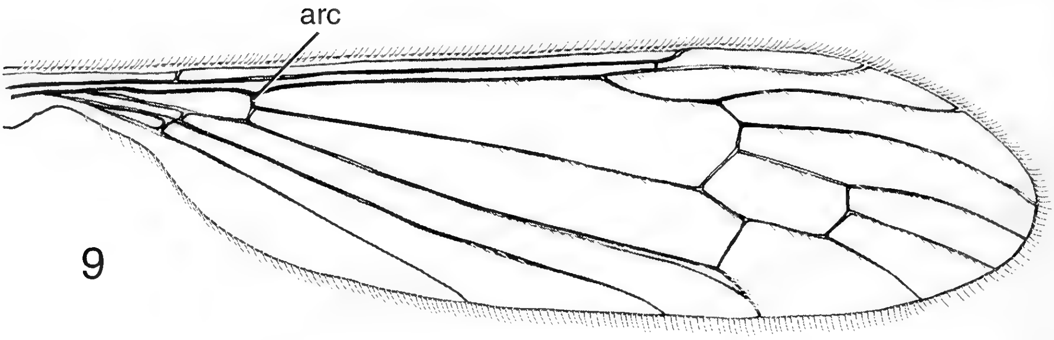
Medium sized flies, distinguished chiefly by the greatly lengthened rostrum, commonly as long as or longer than the entire body. The immature stages occur in wet, decaying wood of various hardwood trees (Alexander 1948). Adults feed from tubular flowers, mostly Compositae (Oldroyd 1966). The genus is widely distributed throughout the major regions of the world, with especially numerous species in the Neotropics and Ethiopian Regions. Four species are known from Baltic amber (Evenhuis 1994).

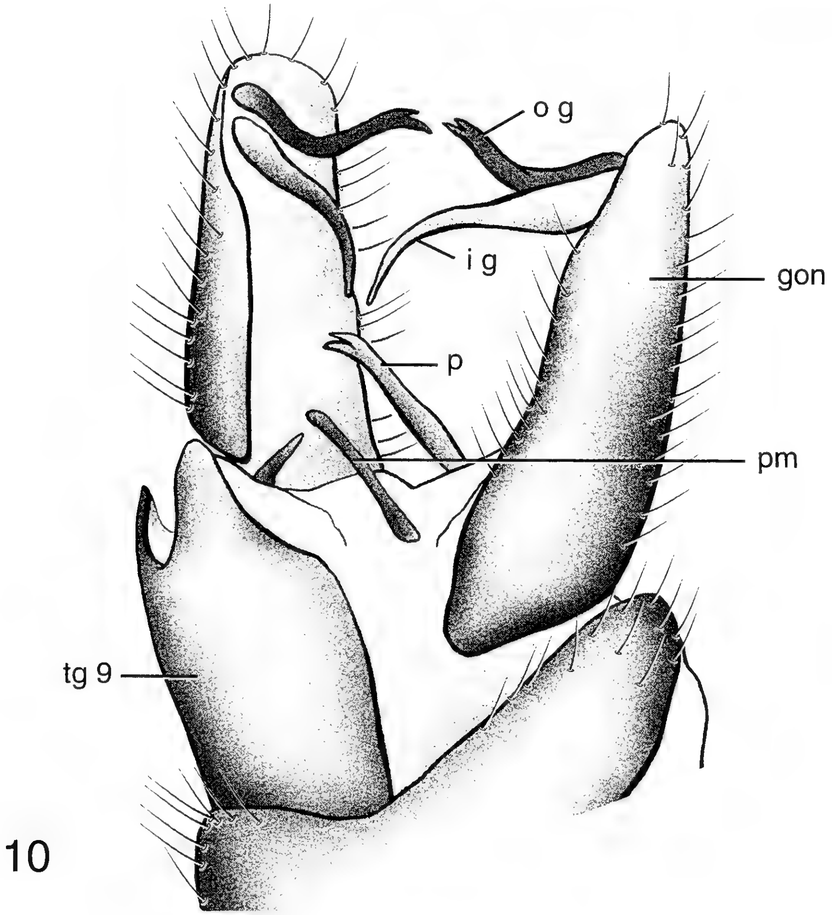
***Elephantomyia (Elephantomyia) grata* Podenas and Poinar, new species**

(Figs. 9–10)

Diagnosis.—General body coloration brown. Antennae 15-segmented. Wings totally clear without any dark spots. Male terminalia with the outer gonostylus slender, glabrous, curved, bifid at tip; inner gonostylus elongate with apical portion slender and turned inwards; 9th tergite deeply emarginate. Differs from related species in structure of male genitalia.

Male.—Body length 3.0 mm, rostrum 3.3 mm, wing length 3.5 mm. Head brown, covered with sparse,short, dark brown hairs. Eyes very large, anterior vertex correspondingly narrowed. Rostrum longer than entire body, brown, covered with dense, short setae; palpi reduced, at apex of rostrum. Antenna about 0.9 mm long,





Figs. 9–10. *Elephantomyia grata,* holotype. 9, Wing. 10, Male genitalia, latero-dorsal view. (See Materials and Methods for abbreviations.)

brown, 15-segmented; scape cylindrical, pedicel oval; both segments approximately equal in length, dark brown; basal two flagellar segments united into fusion-segment; succeeding segments cylindrical, with comparatively short verticils reaching 1.5 length of respective segment.

Dorsum of thorax brownish with dark brown median line, covered with sparse, brown hairs. Pleura with darker brown spots. Wing (Fig. 9) clear without dark spots. Veins light brown, with comparatively abundant setae. Venation: Sc_1 ends at level of two- thirds of Rs, Sc_2 near its tip, at level of about one-third length of Rs; Rs short; R_2 absent; R_4 and R_5 slightly diverging; r-m connecting with R_5; discal cell large, twice as long as wide; cross-vein m-cu clearly beyond the fork of M; anterior arculus preserved. Halter light brown, 0.7 mm long. Legs light brown; tibial spurs very small; both forelegs missing in holotype; femur II: 3.9 mm long, III: 4.0 mm; tibia II and III: 4.6 mm long, tarsus II: 4.6 mm long.

Abdomen with dark brown tergites and sternites, with light intersegmental membranes; hairs brownish. Male genitalia (Fig. 10) with gonocoxite elongated and simple; outer gonostylus slender, glabrous, curved, bifid at tip; outer tooth smaller than inner; inner gonostylus longer, its outer one-third narrowed and turned inward; ninth tergite comparatively large, deeply emarginate. Penis simple, comparatively short, rod-like, with bifid apex. Paramere rod-like.

Female.—Unknown.

Material examined.—Holotype: ♂, D-7-39C, Dominican amber.

Etymology.—The species name is based on *gratus,* which is Latin for pleasing.

Discussion.—The new species does not resemble any of the recent local species. It clearly differs from the latter by its very small size, long rostrum and specific structure of the male genitalia, somewhat resembling those of *E. krivosheinae* Savchenko 1976 of the Palaearctic Region (Savchenko et al. 1992). The new species clearly differs from this species by the ninth tergite, which has a deep posterior emargination, a rather unusual structure among all *Elephantomyia.*

Subfamily Hexatominae

Epiphragma Osten Sacken 1859

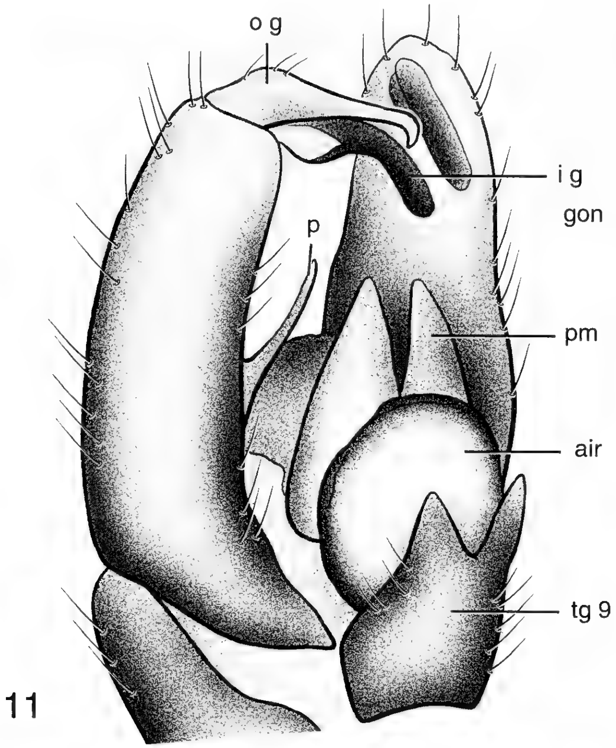
Species belonging to this genus have a yellowish-brown to brown body and darkly patterned wings. Additional characters are: costal cell with additional cross-vein, anterior arculus missing; *Rs* angulate at origin, discal cell closed, cell m_1 with short petiole; abdominal tergites with a pair of transverse impressions before midlength. Species of this genus occur in all zoogeographical regions except Ethiopian. The greatest diversity of species is observed in the Neotropics and Australia (Savchenko 1989). The immature stages usually occur in wet rotting wood; some species develop in comparatively hard decomposing wood (Krivosheina 1969). No species were previously known from amber (Evenhuis 1994).

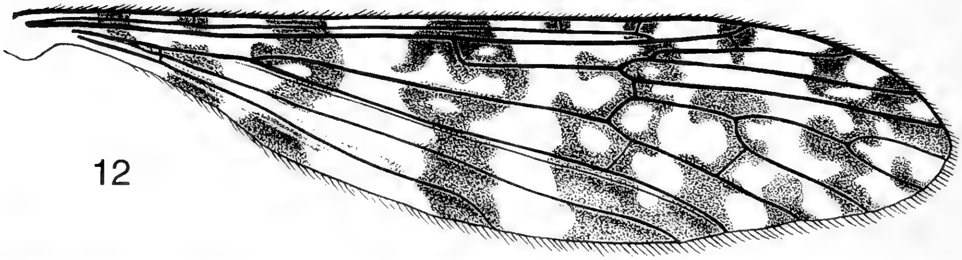
***Epiphragma aurora* Podenas and Poinar, new species**

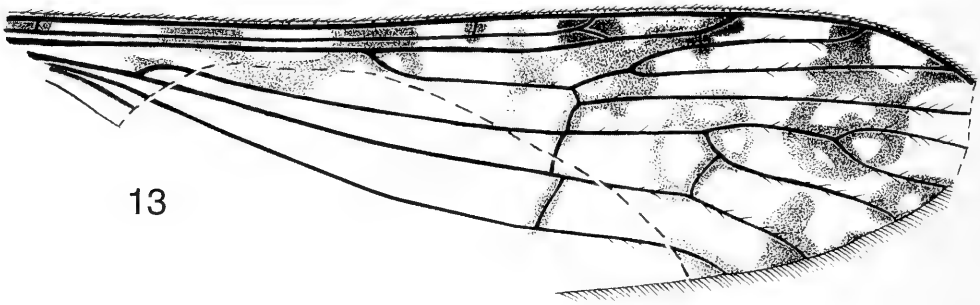
(Figs. 11–12)

Diagnosis.—General body coloration dark brown. Antennae 16-segmented, flagellum conspicuously bicolored, reddish basally, brown distally. Wings yellowish with a brown-spotted pattern. Femora with two blackish rings. Male hypopygium with elongate simple gonocoxite; outer gonostyle slender, flattened at base and with slender distal part, apex curved inwards, tip acute; inner gonostyle longer than outer, flattened at base, tip obtuse; ninth tergite with two posterior triangular lobes separated by V-shaped notch. Differs from related species by structure of male genitalia and wing pattern.

Male.—Body length 6.3 mm, wing length 6.4 mm. Head dark brown, covered with sparse black hairs. Eyes broadly separated. Rostrum blackish, palpi blackish with lightened apical segment. Antenna 1.6 mm long, 16-segmented. Basal segments blackish; scape cylindrical, pedicel pear-shaped, half as long as scape. Two basal flagellar segments united into an elongate oval fusion-segment, about same length as pedicel. Flagellar segments cylindrical, increasing in length distally. Fusion-segment reddish, rest of flagellum brownish. Ventral verticils about as long as respective segments, dorsal verticils on median segments reaching 1.5 times length of respective segments.







Figs. 11–13. 11–12, *Epiphragma aurora*, holotype. 11, Male genitalia, dorso-lateral view. 12, Wing. 13, *Epiphragma* sp., fragment of wing. (See Materials and Methods for abbreviations.)

Dorsum of thorax uniformly brown, covered with sparse brown hairs. Mediotergite with narrow, dark, median longitudinal line. Pleura with dark brown spots. Wing (Fig. 12) yellowish with an abundant brown-spotted pattern; ocellate pattern virtually lacking, represented only by one circle at origin of Rs and incomplete circle at arculus; other major areas brown along cord and outer end of discal cell, marginal spots at ends of all longitudinal veins, in costal and second anal cells. Spots uniformly brown, without darker margin; slightly darker in costal area. Veins light brown, darker in patterned areas, covered with sparse brownish setae. Venation: Sc_1 ends slightly before level of beginning of R_{2+3}, Sc_2 ends slightly beyond tip of Sc_1; additional cross-vein in costal cell beyond level of half Rs; Rs long, angulate at origin; R_3 and R_4 slightly diverging; R_4 and R_5 parallel; discal cell elongate, more than twice as long as wide; cell M_1 slightly shorter than it's petiole; cross-vein m-cu clearly beyond the fork of M; anterior arculus lacking. Stem of haltere with whitish base and brownish distal part; knob with brownish base and reddish apex. Halter 1.1 mm long. Coxae and trochanters brown; femora with two blackish rings in distal part, apices light brown; tibiae brown; femur I: 4.7 mm long, II: 4.0 mm long, III: 4.6 mm; tibia I: 4.3 mm long. Legs covered with dense dark brown hairs.

Abdomen with dark brown rings at bases of segments 2–7; posterior half of segments reddish-brown. Hairs covering tergites and sternites sparse, dark brown. Male genitalia (Fig. 11) with elongate, simple gonocoxite; outer gonostyle slender, flattened at base and with slender distal part, apex curved inwards, tip acute; inner gonostyle longer than outer, flattened at base, slightly bent inwards, tip obtuse; ninth tergite with two posterior triangular lobes, separated by V-shaped notch; parameres wide, triangular plates; penis simple, rod-like.

Female.—Unknown.

Material examined.—Holotype: ♂, D-7-39A, Dominican amber.

Etymology.—The species name is based on *aurora,* Latin for dawn.

Discussion.—The new species, the first representative of the genus from amber, is unique, resembling recent *Epiphragma* only in some details. The most characteristic structures are the comparatively broad parameres of the male genitalia, forming wide, triangular plates. The wing pattern is closest to that of *E. sappho* Alexander 1943 described from a single female from Peru. However, *E. aurora* differs from it by the absence of small wing dots.

Epiphragma sp.

Only one poorly preserved female was found. The head and tip of the ovipositor are missing, but body length is approximately 12.0 mm. The wing apex is also missing, but an approximate wing length is 9.3 mm. The posterior wing margin is strongly folded, but the costal and distal parts of the wing (Fig. 13) show a totally different wing pattern and venation from the previously described species (Fig. 12). The wing pattern is partially ocellate, with a complete circle having it's center on the base of cell m_1, another circle on the distal portion of the discal cell and a third, incomplete circle at the point of *Rs* branching. There is probably no circle on the base of *Rs.* Five dark spots, except on the stigma, occur in the costal cell. Femora with two broad dark brown circles in distal half.

Material examined.—♀, D-7-39I, Dominican amber.

Discussion.—This specimen is the second species of the genus from amber, but the absence of many characters prohibits us from comparing it with recent *Epiphragma.*

Subfamily Eriopterinae

Styringomyia Loew 1845

These flies have a rounded head with a short rostrum, 16-segmented antennae, characteristic wing venation (both veins Sc and R_1 very short, ending at or before mid-length of wing; R_2 and R_3 absent), abdominal segments two to seven twice as long as wide, male genitalia inverted 180 degrees-the tergite thus being ventral in position-the sternite dorsal, gonostyle a single complex structure, usually with a long slender outer arm and two or three usually flattened and variously ornamented inner arms. Immature stages develop in rotting material and adults sometimes form swarms (Alexander 1972). Of the 159 recent species, virtually all are Paleotropical with only a few Neotropical species. *S. dominicana* Podenas and Poinar (1999) is the only species previously described from Dominican amber; *S. gracilis* Loew 1850, is the only species known from Baltic amber.

Styringomyia optiva Podenas and Poinar, new species

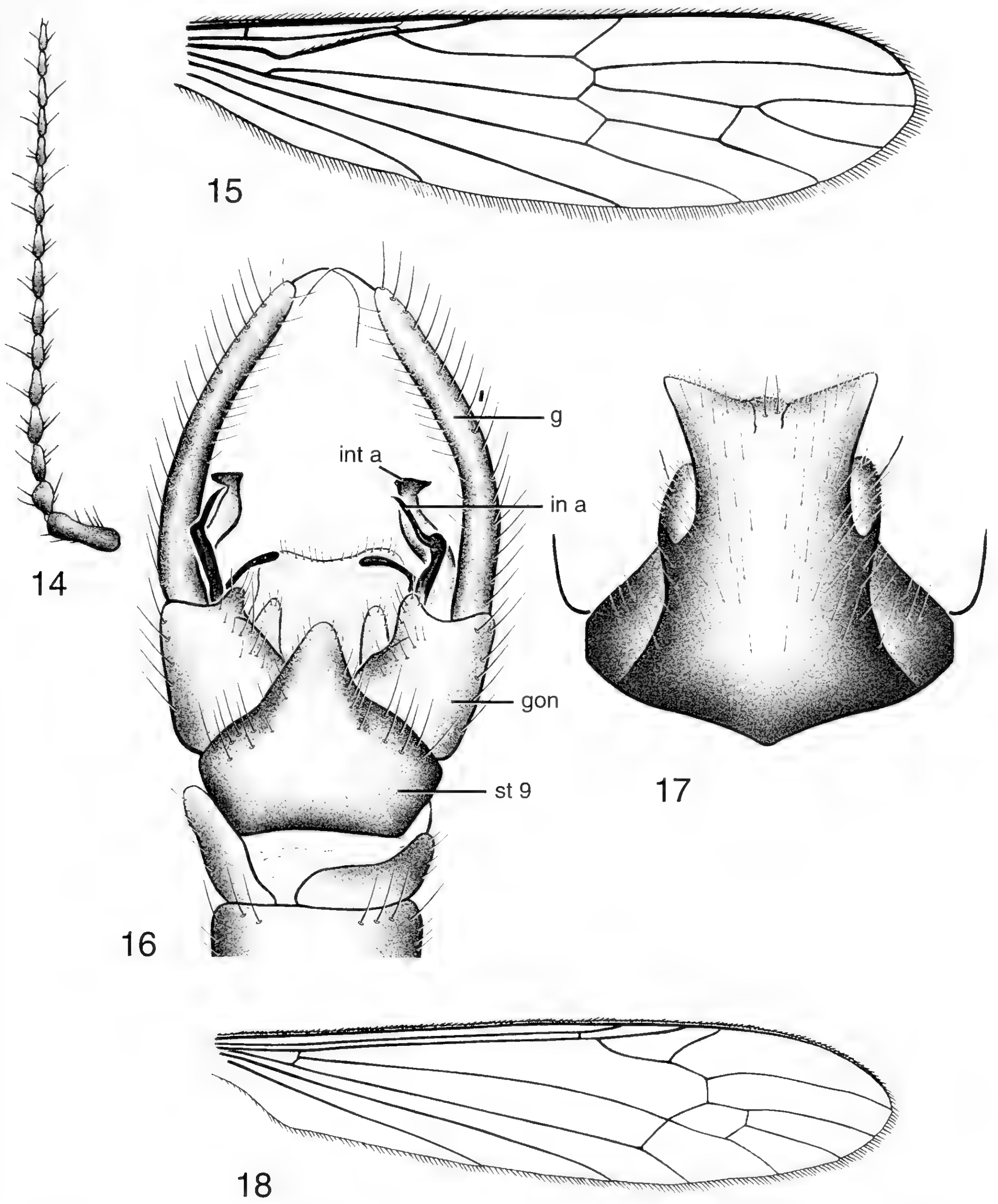
(Figs. 14–17)

Diagnosis.—General body coloration light brown. Antennae 16-segmented, also light brown. Wings totally clear. Abdomen elongate, longer than wings. Male hypopygium very characteristic: ninth tergite with apex shallowly emarginate, with elongate lobes on lateral margins; ninth sternite elongate posteriorly; gonocoxite short, with small apical tubercle on sternal side and blackened rod-like structure on tergal side; gonostyle single, outer apical lobe long and narrow, with long setae; inner armature of style consisting of two elongated structures; intermedite arm flattened with an outward-pointing tip forming right angle with longitudinal axis of style; inner arm with basal part broader than apical, slightly sinuous, apical part forming angle with basal part, tip acute; differs from related species by structure of male genitalia.

Male.—Body length 6.9 mm; wing length 4.0 mm; head grayish; rostrum short, light brown; palpi brown, covered with short (about half length of respective segment) brown setae. Antenna (Fig. 14) 16-segmented, 1.2 mm long; scape three times as long as wide; pedicel pear-shaped, half as long as scape; basal segments of both brownish; flagellar segments elongated, with slightly broader bases, apical segments nearly cylindrical; verticils about as long as the respective segments; apical segment nearly as long as preceding segment; flagellum whitish brown.

Dorsal part of thorax grayish brown, with indication of three darker longitudinal stripes; setae sparse, brownish; prothorax large; pleura light brown with longitudinal brown stripe. Coxae and trochanters grayish brown. Rest of all legs of holotype missing. Wing clear, without stigma. Venation typical for genus (Fig. 15): Sc short; Sc_1 ending just beyond Rs base, Sc_2 near tip of Sc_1; R very short, not reaching middle of wing; radial sector (Rs) with only two branches; discal cell long and narrow, cell m_1 shortly petiolated, cross-vein m-cu clearly beyond the base of discal cell, anal veins divergent. Halter grayish brown, 0.7 mm long.

Abdomen light brown; abdominal segments elongate; tergites with brown posterior margin and narrow, transverse, whitish sutures interrupted in central part, approximately in the middle of segment; sternites uniformly light brown; abdominal segments covered with short yellowish hairs, more dense on lateral margins of segments. Male hypopygium (Fig. 16) light brown; ninth tergite (Fig. 17) a depressed, flattened plate, posterior border broadly extended, apex very shallowly emarginate to produce angulated lobes, lateral margins with elongate hairy lobes; ninth sternite elongate posteriorly, bluntly pointed; gonocoxite short, having small apical tubercle on sternal side and blackened rod-like structure with slightly thickened apical part on tergal side (this appendage similar to same structure in *S. sabroskyi* Alexander 1972, interpreted by Alexander (1972) as part of gonocoxite or basistyle); gonostyle single, outer apical lobe long and narrow, with long setae, longest apical one curved inward; inner armature of style consisting of two elongated structures (sometimes interpreted as median and inner gonostyles (Alexander 1947a)), intermediate arm flattened with outward-pointing tip, forming a right angle with lon-



Figs. 14–18. 14–17, *Styringomyia optiva,* holotype. 14, Antenna. 15, Wing. 16, Male genitalia, ventral view. 17, 9th tergite of male genitalia. 18, *Toxorhina* sp., wing. (See Materials and Methods for abbreviations.)

gitudinal axis of style; inner arm with basal part broader than apical, slightly sinuous, apical part forming angle with basal part, slender, tip acute.

Female.—Unknown.

Material examined.—Holotype: ♂, D-7-39H, Dominican amber.

Etymology.—The species name is based on optivus, Latin for endeavor.

Discussion.—The new species clearly

differs from all recent species by its distinct male genitalia, especially the very elongate outer arm of the gonostyle. Somewhat similar structures occur in *S. sabroskyi* Alexander 1972 described from Micronesia, but that species has a totally different inner armature of the style, the outer arm of which is much shorter. *S. optiva* sp. n. is closest to *S. dominicana* Podenas and Poinar 1999, also described from Dominican amber. Both species can be separated by the structure of the inner armature of the style (which was interpreted as inner gonostyle in Podenas and Poinar 1999); the intermediate arm of the new species has the tip forming a right angle with the longitudinal axis of the style, while in *S. dominicana,* the tip is bilobed. Also the inner arm is angulated in the *S. optiva* but nearly straight in *S. dominicana.* Differences are also present in the structure of the ninth tergite (posterior margin rounded in *S. dominicana* and emarginate in the new species).

Toxorhina Loew, 1851

This genus is characterized not only by the elongate rostrum, bearing reduced mouthparts at the tip, which in many species exceeds in length the entire body or wing, but also by the greatly lengthened cervical region, with the anterior mesonotal prescutum jutting forward over the base of the neck. Male antennae 12-segmented, with several basal segments united into a truncate-conical fusion-segment, those of the female 14 or 15 segmented. Setae of legs deeply bifid. Wing venation very reduced. Gonostyle of male hypopygium single, of various shapes. Aedeagus deeply bifid. The immature stages have not been described (Alexander 1947b).

The subgenus *Ceratocheilus* contains few strictly tropical American species. There are relatively few species in the Ethiopian and Oriental Regions, but more in the Australian Region.

Toxorhina (Ceratocheilus) sp.

One specimen was found with missing genitalia and tip of rostrum. Body length (without rostrum) approximately, 7.3 mm, remnant of rostrum, 3.1 mm, wing length 5.5 mm. Head light brown with darker vertex; setae sparse, dark brown; rostrum dark brown; eyes shining green; antenna 12-segmented, 0.8 mm long; scape short, cylindrical; pedicel large, with wide apical portion, slightly longer than scape; fusion-segment oval, shorter than pedicel; remaining segments of flagellum short-oval, brownish, the outer four articles provided with elongate verticils, which nearly reach half the length of the whole flagellum.

Thorax light brown with three longitudinal brown stripes, median one marginated with dark brown; pleura with longitudinal brown stripe; wing clear, without darker spots, without stigma; veins light brown; wing venation (Fig. 18): Sc short, Sc_1 ending just beyond origin of Rs, Sc_2 a short distance from the tip of Sc_1, before the origin of Rs; anterior branch of Rs shorter than Rs; discal cell closed; m-cu at fork of M; anal veins divergent; anterior arculus preserved; halter light brown, 0.7 mm long; coxae, trochanters and legs brown; femur II: 4.9 mm long; abdominal tergites brown, each with light brown suture at mid-length; sternites light brown with darkened posterior margin.

Material examined.—Sex unknown- D-7-207, Dominican amber.

Discussion.—This specimen probably belongs to an unknown species, but the absence of many characters prohibit us from describing it as a new species. It is related to *T. americana* (Alexander 1913), which has the anterior branch of Rs a little longer than Rs and oblique in position, while in other Neotropical species the anterior branch of Rs is much longer than Rs and extends generally parallel to the posterior branch.

Trentepohlia Bigot, 1854

Wings with veins Cu_1 and 1st A fused for a distance. Crane flies of this genus are all tropical. One species, belonging to the typical subgenus, occurs in Baltic amber

(Alexander 1931), and another, belonging to the subgenus *Paramongoma,* was described from Dominican amber (Podenas and Poinar 1999).

Trentepohlia (Paramongoma) mexicana Podenas and Poinar, new species

(Figs. 19–21)

Diagnosis.—General body coloration dark brown. Antennae 16-segmented, dark brown. Wings clear except stigma. Ninth tergite of male genitalia with shallowly emarginate posterior margin; gonocoxite elongate, simple; gonostyle single, narrow, with apex turned inwards. Differs from related species by structure of male genitalia.

Male.—Body length 6.0 mm, wing length 4.8 mm. Head of holotype is seen only from ventral side; rostrum short, light brown; palpi brown; eyes large, meeting ventrally. Antenna (Fig. 20) 16-segmented, 1.3 mm long; scape three times as long as wide, dark brown; pedicel with slightly widened apical portion, only slightly shorter than scape, brown; flagellar segments cylindrical, decreasing in length toward apex; verticils shorter than respective segments; flagellum brown with darkened apex.

Dorsal part of thorax dark brown, with indication of three darker longitudinal stripes; pleura light brown with darker spots. Coxae, trochanters and legs brown; tips of femora, tibiae and tarsi starting from middle of third segment darkened. Femur II: 8.3 mm long, III: 7.4 mm; tibia III: 7.5 mm; tarsus III: 4.7 mm long. Wing narrow, clear, with small, brownish stigma. Veins brown. Venation as usual in genus (Fig. 19): Sc long, Sc_1 at level of middle of R_{2+3+4}, Sc_2 slightly before level of Rs branching; Rs very slightly curved, nearly straight; discal cell narrow, three times as long as wide; cross-vein m-cu proximal to base of discal cell; tip of CuA_2 not reaching tip of A_1. Halter dark brown with lightened base of stem, 0.6 mm long.

Abdominal tergites dark brown; basal sternites brown, sternites 6th to 9th dark brown; lateral margins of both tergites and sternites narrowly whitened; hairs on abdomen short, sparse, brown. Male hypopygium (Fig. 21) same color as preceeding segments; ninth tergite with shallowly emarginate posterior margin, thus forming two small rounded lateral lobes; gonocoxite elongate, simple, without additional lobes; gonostyle single, narrow, with apex turned inward.

Female.—Unknown.

Material examined.—Holotype: ♂ on angiosperm leaf (the following described *Trentepohlia* male in the same amber piece is adjacent to the leaf), D-7-212, Mexican amber.

Etymology.—The species name is based on the country of origin, Mexico.

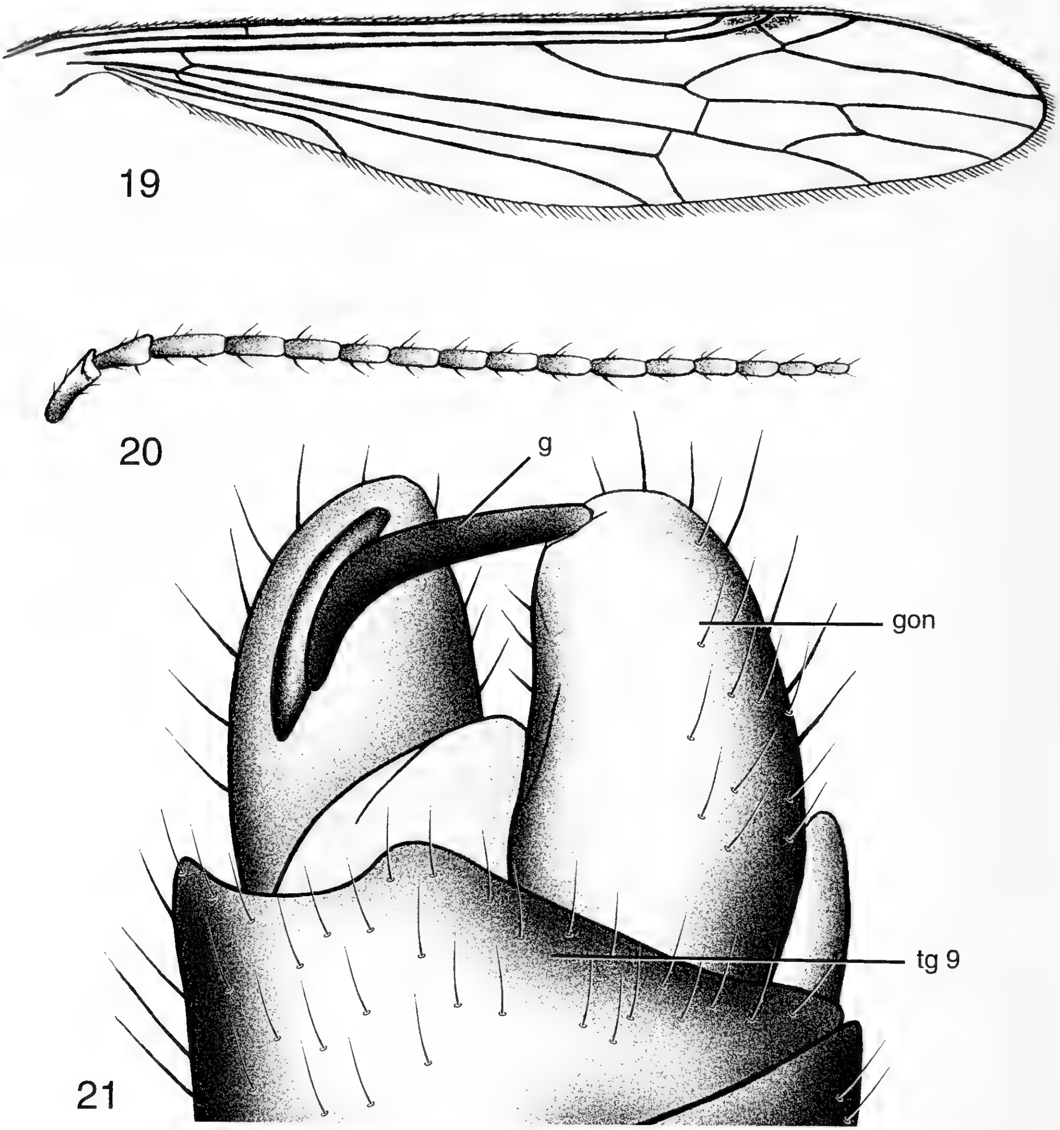
Trentepohlia (Paramongoma) immemorata Podenas and Poinar, new species

(Figs. 22–24)

Diagnosis.—General body coloration dark brown. Antennae 16-segmented, dark brown. Wings clear except stigma. Ninth tergite of male genitalia with widely emarginate posterior margin; gonocoxite elongate, oval; gonostyle single, narrow, with large, blunt tooth on basal half. Differs from related species by structure of male genitalia.

Male.—Body length 6.3 mm, wing length 5.6 mm. Head brown; rostrum short, brown; palpus brown; eyes large, meeting each other dorsally. Antenna (Fig. 23) 16-segmented; scape three times as long as wide, yellowish basally, brown distally; pedicel pear-shaped, brown, shorter than scape; flagellar segments oval, brown, decreasing in length apically; verticils shorter than respective segments.

Dorsal part of thorax castaneous brown, with indication of median longitudinal stripe; post-sutural parts of scutum and scutellum dark brown; pleura light brown with darker spots. Coxae and trochanters brown; femora dark brown, tibiae and tarsi brown. Femur II: 8.0 mm, tibia II: 7.3 mm long. Wing clear with small brownish stigma.



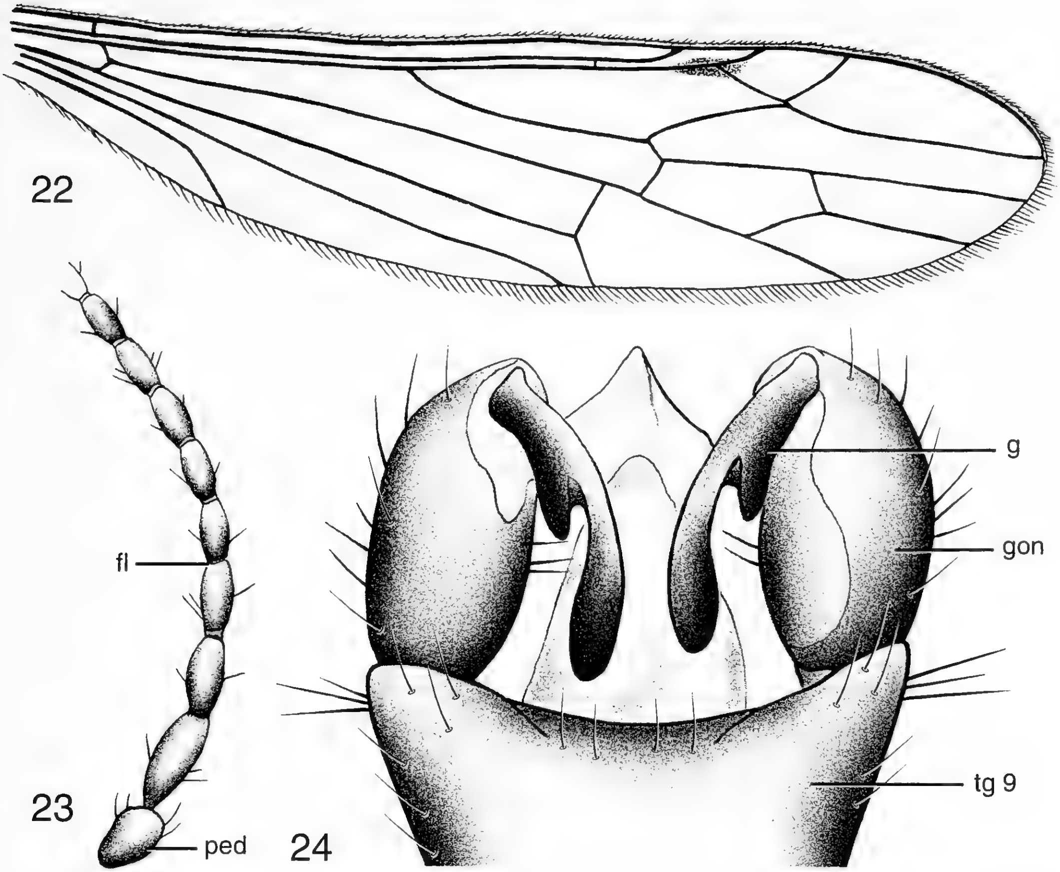
Figs. 19–21. *Trentepohlia mexicana,* holotype. 19, Wing. 20, Antenna. 21, Male genitalia, dorso-lateral view. (See Materials and Methods for abbreviations.)

Veins brown. Venation typical for genus (Fig. 22): Sc long, Sc_1 at level of one fifth of R_{2+3+4}, Sc_2 at the level of three-fourths of Rs length; Rs long, very slightly bent, nearly straight; discal cell widened, approximately three times as long as wide; crossvein m-cu before base of discal cell. Stem of halter whitish basally, brownish distally, knob dark brown; halter 0.7 mm long.

Abdominal tergites dark brown; hairs on abdomen short, sparse, brown. Male hypopygium (Fig. 24) same color as rest of abdomen; ninth tergite with widely emarginate posterior margin; gonocoxite oval, simple, without additional lobes; gonostyle single, narrow, with large blunt tooth on basal half.

Female.—Unknown.

Material examined.—Holotype: ♂ adjacent to angiosperm leaf (male of *Trente-*



Figs. 22–24. *Trentepohlia immemorata,* holotype. 22, Wing. 23, 2–10 antennal segments. 24, Male genitalia, dorsal view. (See Materials and Methods for abbreviations.)

pohlia mexicana sp. n. in the same amber piece is on the leaf), D-7–212, Mexican amber.

Etymology.—The species name is based on *immemoratus,* Latin for immemorial.

Discussion.—Both new species of *Trentepohlia* Bigot 1854 are closely related, differing mostly in the structure of male genitalia, wing venation and antennae. The major difference is seen in the male gonostyle: it is not toothed in *T. mexicana,* but has a large tooth on the basal half in *T. immemorata.* Also the flagellomeres of *T. mexicana* are cylindrical and the pedicel is elongate, while the flagellomeres of *T. immemorata* are oval and the pedicel short and pear-shaped; vein Rs is also shorter in *T. mexicana.* Closely related to both new species and especially to *T. immemorata* is *T. agri* Podenas and Poinar (1999), a comparatively abundant species in Dominican amber. The latter species differs from both Mexican amber species by a very short vein Rs, elongate-oval flagellomeres, longer gonocoxites and a smaller tooth on the basal half of the gonostyle.

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LIGHT TRAP CATCHES OF LEPIDOPTERA IN TWO CENTRAL APPALACHIAN FORESTS

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Abstract.—On 15 sampling dates from May through mid-August 1995 and 1996, 12-watt blacklight traps were operated simultaneously in 18, 200-ha plots, 9 plots each in the George Washington (GWNF) and Monongahela National Forests (MNF) in Virginia and West Virginia, respectively. A total of 438 species of Lepidoptera in 13 selected families was identified including 222 noctuids, 127 geometrids, 27 notodontids, 26 arctiids, 10 sphingids and 9 saturniids. For both years, 334 species were shared by both forests; 45 species were collected only in the GWNF and 59 species were collected only in the MNF. Moth collections totaled 135,271 specimens and varied by forest and year. Variation may have been related to differences in vegetational makeup between the forests and differences in rainfall and temperature between the two years. The GWNF is a warmer, more xeric oak/pine forest while the MNF is relatively more mesic, mixed hardwood forest at a higher elevation. For both forests combined, the most abundant light-trapped species were, in decreasing abundance, *Acronicta ovata* Grote (Noctuidae), *Idia rotundalis* (Walker) (Noctuidae), *Hypoprepia fucosa* Hübner (Arctiidae), *Idia aemula* Hübner (Noctuidae), *Polygrammate hebracicum* Hübner (Noctuidae), *Hydrelia inornata* Hulst (Noctuidae), *Itame pustularia* (Guenée) (Geometridae), *Spilosoma congrua* Walker (Arctiidae), *Lambdina fervidaria* (Hübner) (Geometridae), and *Halysidota tesselaris* (J. E. Smith) (Arctiidae).

Key Words: Lepidoptera, blacklight trap, West Virginia, Virginia

Communities of adult Lepidoptera have been the subject of numerous studies in recent years. Lepidoptera are considered to be of high conservation value (Magurran 1985) and frequently serve as "flagship taxa" in biodiversity studies (Lawton et al. 1998). Moths have been used as indicator organisms for monitoring changes in tropical (Holloway 1984) and temperate zones (Magurran 1985).

In North America, blacklight trapping of moths has been conducted in several locations for a number of purposes. For example, Rings et al. (1987) and Moulding and Madenjian (1979) conducted surveys in the same forests for several years to determine composition of the Lepidoptera community. Use of light traps in evaluation of sampling methods for biodiversity studies was conducted by Butler et al. (1999), Thomas (1996), and Thomas and Thomas (1994). Studies to determine Lepidoptera baseline composition before forest disturbance by outbreak defoliator species or application of insecticides for forest pest suppression have included those of Butler and Kondo (1991) and Grimble et al. (1992). Light trapping of moths has also served to evaluate nontarget impact of forest-applied insecticides (Butler and Kondo 1993, Butler et al. 1995, Sample et al. 1996).

In 1994, we began a study of the impact of the biological spray, *Bacillus thuringiensis* var. *kurstaki* (*Btk*), and defoliation by gypsy moth (*Lymantria dispar* L.) on nontarget arthropods in large plots in adjacent national forests in the central Appalachians. Because *Btk* targets caterpillars (Boberschmidt et al. 1989), an emphasis of this study has been Lepidoptera. Our study dealt with moths from 13 selected families: Drepanidae, Thyatiridae, Geometridae, Epiplemidae, Mimallonidae, Apatelodidae, Lasiocampidae, Saturniidae, Sphingidae, Notodontidae, Arctiidae, Lymantriidae, and Noctuidae. Pretreatment sampling of adult moths was conducted in 1995 and 1996. Comparisons were made of number of species and abundance between the two years and between the two forests. Here we present the results of the pretreatment portion of that study. Other papers in this series present results of larval sampling by foliage pruning and canvas bands. A final paper will present species diversity indices and accumulation curves for the lepidopteran community.

MATERIALS AND METHODS

In 1994, 18 200-ha study plots were designated and flagged in gypsy moth-susceptible, oak-dominated forests. Plots 1 through 9 are located primarily on the eastern slope of Great North Mountain in the Deerfield Ranger District of the George Washington National Forest (GWNF) in Augusta County, Virginia (centered at 38°07′30″N, 79°22′30″W. The GWNF plots are approximately 50 km east of the MNF plots. Maps of the study sites are given in Butler and Strazanac (2000 a,b). The GWNF plots represent a relatively xeric forest of mixed oak and pine with a range in elevation of 586 m to 781 m. Plots 10 through 18 are located in the Monongahela National Forest (MNF) in Pocahontas County, West Virginia (plots 10–15 centered at 38°22′30″N, 79°52′30″W, plots 16–18 centered at 38°15′N, 80°00′W). Plots 10 through 12 are in the southern Greenbrier Ranger District on Chestnut Ridge (Paddy Knob North); plots 13 through 18 are in the Marlinton Ranger District with plots 13 through 15 near Sugar Camp Run (Paddy Knob South); and plots 16 through 18 on Marlin Mountain. The MNF plots represent a relatively more mesic forest with a range of elevation of 860 m to 1,070 m.

Basal area of major tree species was measured at 28 randomly selected points within a central 30-ha core subplot within each of the 18 plots. Basal area was estimated using a 10 basal area factor (BAF) Cruz-all (Jim-Gem; Forestry Suppliers, Inc.; Jackson, MS).

On 20 June 1995, rain gauges and maximum/minimum thermometers were installed in all plots. Additional weather data were obtained from the N.O.A.A. weather stations closest to the plots.

A 12-watt blacklight trap (BioQuip Products, Gardena, CA) powered by a 12-volt battery was operated within the 30-ha core subplot in each of the 18 study plots on Monday night of each week from early May through mid-August (8 May through 14 August 1995; 6 May through 12 August, 1996) to give 15 samples per plot per year. Each trap was equipped with a photoelectric eye to facilitate automatic dusk to dawn operation. Insects were killed by Vapona™ insecticide strips placed in the light trap bucket. Each trap was suspended about 1.5 m above the ground between two trees, approximately 2 m apart. Care was taken in trap placement to select locations that appeared similar among plots with regard to vegetation density and composition (within the limitations of core plot differences), and to avoid sites where traps would be shielded by tree limbs.

Trapped insects were collected each Tuesday morning, placed in plastic cartons between layers of Kimwipes™, held in coolers, returned to the laboratory, and stored in a freezer. Moths were identified to species by Kondo and Butler and counts made by week for each species. Species are named after the checklist given by Hodges et al. (1983). Voucher specimens from the study are deposited in the WVU Arthropod Collection.

RESULTS

A total of 438 species of moths in 13 families was collected by blacklight trap in 1995 and 1996 (Table 1). Fifty-one percent of the species were Noctuidae (222 species), 29 percent were Geometridae (127 species), 6 percent each were Notodontidae (27 species) and Arctiidae (26 species), and 2 percent each were Sphingidae (10 species) and Saturniidae (9 species). These percentages of species per family are similar to those given in Hodges' (1983) checklist where these families represented 58 percent, 28 percent, 3 percent, 5 percent 2.5 percent, and 1.4 percent respectively. The remaining 7 families were represented by 5 or fewer species. Over both years, 379 and 393 species were collected from the GWNF and the MNF, respectively. Collections for 1995 totaled 339 and 334 species for the GWNF and the MNF, respectively, while 1996 numbers were 313 and 338 species. For both years, 334 species were shared by both forests; 45 species were represented only in the GWNF, and 59 species were collected only in the MNF (Table 1).

During both years of the study and in both forests, a total of 135,271 moths were collected and identified (Table 1). The highest abundance of moths was collected on the MNF in 1996 (39,069); followed by GWNF, 1995 (35,745); MNF, 1995 (35,593); and GWNF, 1996 (24,864). The family with the highest abundance for both forests and both years was Noctuidae with 65,115 individuals followed by Geometridae (37,744), Arctiidae (18,279), Notodontidae (9,839), Lasiocampidae (1,400), Saturniidae (1,286), Sphingidae (856), and Lymantriidae (474). All other families were represented by fewer than 100 individuals.

Over both years and both forests the most abundant species listed in order of decreasing abundance were *Acronicta ovata* Grote (Noctuidae), *Idia rotundalis* (Walker) (Noctuidae), *Hypoprepia fucosa* Hübner (Arctiidae), *Idia aemula* Hübner (Noctuidae), *Polygrammate hebraeicum* Hübner (Noctuidae), *Hydrelia inornata* Hulst (Geometridae), *Itame pustularia* (Guenée) (Geometridae), *Spilosoma congrua* Walker (Arctiidae), *Lambdina fervidaria* (Hübner) (Geometridae), *Halysidota tesselaris* (J.E. Smith) (Arctiidae), *Acronicta increta* Morrison (Noctuidae), *Acronicta haesitata* (Grote) (Noctuidae), *Clemensia albata* Packard (Arctiidae), *Probole alienaria* (Herrich-Schäffer) (Geometridae), *Hypagyrtis unipunctata* (Haworth) (Geometridae), *Nadata gibbosa* (J.E. Smith) (Noctuidae), *Peridea angulosa* (J.E. Smith) (Noctuidae), *Eupithecia matheri* Rindge (Geometridae), *Anorthodes tarda* Guenée (Noctuidae), and *Semiothisa bisignata* (Walker) (Geometridae) (Table 1).

Among the 20 more abundant species, 7 were notably more abundant in the MNF (*A. ovata, I. rotundalis, H. inornata, S. congrua, L. fervidaria, P. alienaria,* and *A. tarda*); 4 were notably more abundant in the GWNF (*I. aemula, P. hebraeicum, I. pustularia* and *S. bisignata*). The remaining 9 species were in similar abundance in both forests (Table 1). Among the 438 species identified during this study (Table 1), 35 were represented over both years by a single individual.

During 1995 and 1996 combined, 45 moth species were trapped only in the GWNF and 59 species were trapped only in the MNF. Of those 104 species, half (53 species) were represented by only one or two individuals (Table 1). Several species trapped only in the GWNF in some abundance were the geometrid, *Lytrosis permagnaria* (Pack); the saturniids, *Eacles imperialis* (Drury) and *Anisota stigma* (F.); the arctiids, *Crambidia cephalica* (Grote and Robinson); and the noctuids *Catocala flebilis* Grote and *C. similis* Edwards. Among species unique to the MNF were the geometrids *Itame evagaria* (Hulst), *Aethalura intertexta* (Walker), *Epirrhoe alternata* (Müller), and *Heterophleps refusaria*

Table 1. Species of Lepidoptera and their abundance collected by light traps on the George Washington (GWNF) and Monongahela (MNF) national forests, 1995 and 1996. Ranks and flight ranges are included.

Family Species	GWNF			MNF			Grand Total	Rank	Flight Period
	1995	1996	Total	1995	1996	Total			
Apatelodidae									
Apatelodes torrefacta (J.E. Smith)	1	5	6	1	0	1	7	199	10 Jun–17 Jul
Olceclostera angelica (Grote)	0	4	4	1	1	2	6	200	26 Jun–15 Jul
Arctiidae									
Apantesis anna (Grote)	13	21	34	1	2	3	37	171	29 May–26 Jun
Apantesis figurata (Drury)	4	0	4	0	0	0	4	202	22 May–29 May
Apantesis nais (Drury)	8	2	10	0	0	0	10	196	13 May–12 Jun
Apantesis virgo (L.)	0	0	0	1	0	1	1	205	17 Jul
Cisseps fulvicollis (Hübner)	1	0	1	0	0	0	1	205	31 Jul
Cisthene plumbea Stretch	43	14	57	3	3	6	63	149	5 Jun–14 Aug
Clemensia albata Packard	913	216	1,129	713	258	971	2,100	13	15 May–14 Aug
Crambidia cephalica (Grote & Robinson)	224	54	278	0	0	0	278	81	22 Jul–14 Aug
Crambidia pallida Packard	235	36	271	187	37	224	495	56	27 May–14 Aug
Cycnia tenera Hübner	2	2	4	0	0	0	4	202	1 Jul–7 Aug
Ecpantheria scribonia (Stoll)	0	2	2	0	0	0	2	204	24 Jun
Euchaetes egle (Drury)	2	0	2	1	2	3	5	201	24 Jun–3 Jul
Halysidota tessellaris (J.E. Smith)	681	1,068	1,749	454	935	1,389	3,138	10	22 May–14 Aug
Haploa clymene (Brown)	3	1	4	4	2	6	10	196	3 Jul–5 Aug
Haploa colona (Hübner)	3	1	4	2	6	8	12	194	26 Jun–8 Jul
Haploa contigua (Walker)	4	0	4	1	0	1	5	201	3 Jul
Haploa lecontei (Guérin-Méneville)	79	89	168	37	51	88	256	85	10 Jun–5 Aug
Holomelina aurantiaca (Hübner)	7	0	7	0	0	0	7	199	29 May–31 Jul
Holomelina opella (Grote)	157	116	273	9	28	37	310	77	22 May–7 Aug
Hyphantria cunea (Drury)	3	0	3	509	0	509	512	53	19 Jun–10 Jul
Hypoprepia fucosa Hübner	2,073	1,237	3,310	2,904	1,153	4,057	7,367	3	19 Jun–14 Aug
Hypoprepia miniata (W.F. Kirby)	56	31	87	6	6	12	99	128	8 Jul–5 Aug
Lophocampa caryae Harris	8	1	9	1	0	1	10	196	22 May–5 Jun
Pyrrharctia isabella (J.E. Smith)	1	3	4	0	9	9	13	193	3 Jun–5 Aug
Spilosoma congrua Walker	604	396	1,000	246	2,292	2,538	3,538	8	6 May–7 Aug
Spilosoma latipennis Stretch	0	1	1	0	1	1	2	204	3 Jun–24 Jun
Drepanidae									
Drepana arcuata Walker	4	4	8	24	24	48	56	154	6 May–14 Aug

Table 1. Continued.

Family Species	GWNF 1995	GWNF 1996	GWNF Total	MNF 1995	MNF 1996	MNF Total	Grand Total	Rank	Flight Period
Oreta rosea (Walker)	16	5	21	6	3	9	30	177	29 May–14 Aug
Epiplemidae									
Calledapteryx dryopterata Grote	26	35	61	2	0	2	63	149	29 May–14 Aug
Geometridae									
Aethalura intertexta (Walker)	0	0	0	23	7	30	30	177	6 May–10 Jul
Anacamptodes defectaria (Guenée)	9	97	106	0	98	98	204	96	3 Jun–12 Aug
Anacamptodes ephyraria (Walker)	0	41	41	0	82	82	123	119	24 Jun–5 Aug
Anagoga occiduaria (Walker)	4	1	5	7	17	24	29	178	6 May–12 Aug
Anavitrinelia pampinaria (Guenée)	191	19	210	213	17	230	440	61	6 May–14 Aug
Antepione thisoaria (Guenée)	5	35	40	0	2	2	42	166	6 May–5 Aug
Anticlea multiferata (Walker)	1	0	1	0	0	0	1	205	8 May
Anticlea vasiliata Guenée	0	1	1	0	1	1	2	204	6 May–20 May
Besma endropiaria (Grote & Robinson)	30	115	145	553	228	781	926	32	22 May–10 Jul
Besma quercivoraria (Guenée)	180	220	400	394	248	642	1,042	28	6 May–14 Aug
Biston betularia (L.)	101	94	195	89	105	194	389	68	6 May–14 Aug
Cabera erythemaria Guenée	16	16	32	94	112	206	238	90	6 May–3 Jul
Campaea perlata (Guenée)	188	102	290	299	169	468	758	41	22 May–5 Aug
Caripeta angustiorata Walker	0	0	0	3	0	3	3	203	24 Jul
Caripeta aretaria (Walker)	12	7	19	5	13	18	37	171	27 May–14 Aug
Caripeta divisata Walker	2	18	20	50	52	102	122	120	19 Jun–12 Aug
Cepphis armataria (Herrich-Schäffer)	2	2	4	2	4	6	10	196	19 Jun–29 Jul
Chlorochlamys chloroleucaria (Guenée)	1	3	4	0	1	1	5	201	20 May–10 Jun
Cladara anguilineata (Grote & Robinson)	1	9	10	1	6	7	17	189	6 May–15 May
Cladara atroliturata (Walker)	9	0	9	36	17	53	62	150	6 May–1 Jul
Cyclophora packardi (Prout)	12	23	35	12	25	37	72	142	6 May–12 Aug
Cyclophora pendulinaria (Guenée)	29	47	76	45	130	175	251	87	6 May–14 Aug
Dichorda iridaria (Guenée)	1	1	2	0	0	0	2	204	29 May–5 Aug
Dyspteris abortivaria (Herrich-Schäffer)	0	1	1	2	3	5	6	200	22 May–12 Aug
Dysstroma hersiliata (Guenée)	0	0	0	0	2	2	2	204	17 Jun–1 Jul
Dysstroma truncata (Hufnagel)	0	0	0	1	0	1	1	205	3 Jul
Ectropis crepuscularia (Denis & Schiffermüller)	4	40	44	1	48	49	93	132	6 May–29 Jul
Ennomos subsignaria (Hübner)	1	0	1	0	1	1	2	204	3 Jul–5 Aug
Epimecis hortaria (F.)	2	8	10	2	1	3	13	193	15 May–5 Aug

Table 1. Continued.

Family Species	GWNF			MNF			Grand Total	Rank	Flight Period
	1995	1996	Total	1995	1996	Total			
Epirrhoe alternata (Müller)	0	0	0	7	8	15	15	191	22 May–3 Jul
Erastria coloraria (F.)	1	1	2	0	0	0	2	204	17 Jun–26 Jun
Eubaphe mendica (Walker)	21	37	58	6	11	17	75	140	17 Jul
Euchlaena irraria (Barnes & McDunnough)	11	12	23	6	13	19	42	166	8 May–3 Jul
Euchlaena marginaria (Minot)	7	1	8	2	2	4	12	194	8 May–29 May
Euchlaena milnei McDunnough	9	0	9	3	0	3	12	194	26 Jun–3 Jul
Euchlaena obtusaria (Hübner)	7	7	14	4	6	10	24	182	22 May–14 Aug
Euchlaena pectinaria (Denis & Schiffermüller)	4	12	16	2	2	4	20	186	8 May–1 Jul
Euchlaena tigrinaria (Guenée)	7	2	9	19	18	37	46	162	29 May–15 Jul
Eufidonia notataria (Walker)	40	51	91	83	33	116	207	95	15 May–19 Jun
Eugonobapta nivosaria (Guenée)	15	7	22	12	7	19	41	167	19 Jun–5 Aug
Eulithis diversilineata (Hübner)	20	30	50	6	13	19	69	145	8 Jul–14 Aug
Eulithis explanata (Walker)	15	3	18	28	6	34	52	157	19 Jun–7 Aug
Euphyia unangulata (Haworth)	4	3	7	48	18	66	73	141	20 May–14 Aug
Eupithecia columbiata Dyar	1	6	7	0	15	15	22	184	6 May–5 Aug
Eupithecia matheri Rindge	530	296	826	376	318	694	1,520	18	6 May–14 Aug
Eusarca confusaria Hübner	4	2	6	1	3	4	10	196	3 Jun–7 Aug
Eutrapela clemataria (J.E. Smith)	2	20	22	11	14	25	47	161	6 May–5 Aug
Glena cribrataria (Guenée)	3	0	3	2	24	26	29	178	22 May–1 Jul
Glenoides texanaria (Hulst)	0	78	78	0	169	169	247	88	8 Jul–29 Jul
Heliomata cycladata Grote & Robinson	42	54	96	34	64	98	194	97	6 May–26 Jun
Hesperumia sulphuraria Packard	22	3	25	3	1	4	29	178	24 Jun–17 Jul
Heterophleps refusaria (Walker)	0	0	0	16	8	24	24	182	29 May–5 Aug
Heterophleps triguttaria Herrich-Schäffer	0	1	1	14	19	33	34	173	10 Jun–12 Aug
Hethemia pistasciaria (Guenée)	3	2	5	0	0	0	5	201	15 May–17 Jun
Homochlodes disconventa (Walker)	2	0	2	192	112	304	306	78	6 May–7 Aug
Hydrelia condensata (Walker)	0	11	11	1	6	7	18	188	27 May–29 Jul
Hydrelia inornata (Hulst)	163	20	183	2,232	1,928	4,160	4,343	6	6 May–14 Aug
Hydria prunivorata (Ferguson)	6	0	6	10	1	11	17	189	29 May–14 Aug
Hydriomena pluviata (Guenée)	79	41	120	217	23	240	360	71	6 May–3 Jul
Hydriomena transfigurata Swett	16	98	114	29	200	229	343	72	6 May–1 Jul
Hypagyrtis unipunctata (Haworth)	422	397	819	431	608	1,039	1,858	15	15 May–14 Aug
Hypomecis umbrosaria (Hübner)	10	20	30	0	1	1	31	176	15 May–12 Aug
Idaea furciferata (Packard)	10	0	10	2	0	2	12	194	10 Jul–14 Aug
Idaea obfusaria (Walker)	2	4	6	0	0	0	6	200	8 Jul–17 Jul

Table 1. Continued.

Family Species	GWNF			MNF			Grand Total	Rank	Flight Period
	1995	1996	Total	1995	1996	Total			
Iridopsis larvaria (Guenée)	107	108	215	179	218	397	612	47	6 May–14 Aug
Itame evagaria (Hulst)	0	0	0	4	9	13	13	193	24 Jun–10 Jul
Itame pustularia (Guenée)	1,968	768	2,736	1,150	344	1,494	4,230	7	17 Jun–14 Aug
Itame subcessaria (Walker)	1	0	1	2	2	4	5	201	3 Jul–31 Jul
Lambdina fervidaria (Hübner)	391	665	1,056	860	1,471	2,331	3,387	9	6 May–14 Aug
Lambdina pellucidaria (Grote & Robinson)	29	67	96	5	49	54	150	112	6 May–22 May
Lobophora nivigerata Walker	0	2	2	3	0	3	5	201	6 May–29 May
Lomographa glomeraria (Grote)	1	0	1	28	66	94	95	131	6 May–22 May
Lomographa semiclarata (Walker)	0	0	0	0	1	1	1	205	20 May
Lomographa vestaliata (Guenée)	30	66	96	384	491	875	971	30	6 May–22 Jul
Lytrosis permagnaria (Packard)	10	4	14	0	0	0	14	192	3 Jun–17 Jun
Lytrosis unitaria (Herrich-Schäffer)	235	299	534	125	141	266	800	38	10 Jun–24 Jul
Melanolophia canadaria (Guenée)	195	117	312	235	277	512	824	37	6 May–14 Aug
Melanolophia signataria (Walker)	0	0	0	2	6	8	8	198	6 May–8 May
Mesoleuca ruficillata (Guenée)	0	1	1	2	1	3	4	202	20 May–24 Jul
Metanema inatomaria (Guenée)	0	0	0	1	5	6	6	200	10 Jun–5 Aug
Metarranthis angularia (Barnes & McDunnough)	10	0	10	6	0	6	16	190	3 Jul–14 Aug
Metarranthis duaria (Guenée)	3	1	4	3	4	7	11	195	8 May–19 Jun
Metarranthis hypocharia (Herrich-Schäffer)	0	5	5	2	32	34	39	169	20 May–24 Jun
Metarranthis obfirmaria (Hübner)	7	0	7	15	0	15	22	184	8 May–26 Jun
Nacophora quernaria (J.E. Smith)	18	79	97	31	42	73	170	104	6 May–10 Jul
Nematocampa limbata (Haworth)	80	98	178	65	31	96	274	82	17 Jun–14 Aug
Nemoria bistriaria Hübner	31	114	145	31	77	108	253	86	6 May–14 Aug
Nemoria lixaria (Guenée)	0	38	38	1	25	26	64	148	6 May–7 Aug
Nemoria mimosaria (Guenée)	44	7	51	60	16	76	127	116	20 May–31 Jul
Nepytia semiclusaria (Walker)	121	112	233	17	6	23	256	85	10 Jul–14 Aug
Orthofidonia flaviventa (Hulst)	1	0	1	0	0	0	1	205	8 May
Orthonama centrostrigaria (Wollaston)	12	23	35	22	24	46	81	138	29 May–14 Aug
Orthonama obstipata (F.)	2	3	5	4	8	12	17	189	8 May–12 Aug
Patalene olyzonaria (Walker)	0	1	1	0	0	0	1	205	5 Aug
Perizoma basaliata (Walker)	0	0	0	2	0	2	2	204	10 Jul
Pero honestaria (Walker)	33	41	74	42	67	109	183	99	6 May–14 Aug
Pero morrisonaria (Henry Edwards)	0	0	0	2	1	3	3	203	20 May–12 Jun
Phigalia titea (Cramer)	0	0	0	2	0	2	2	204	15 May–22 May

Table 1. Continued.

Family Species	GWNF			MNF			Grand Total	Rank	Flight Period
	1995	1996	Total	1995	1996	Total			
Plagodis alcoolaria (Guenée)	241	308	549	145	226	371	920	33	6 May–14 Aug
Plagodis fervidaria (Herrich-Schäffer)	0	246	246	0	65	65	311	76	6 May–12 Aug
Plagodis kuetzingi (Grote)	0	2	2	1	2	3	5	201	20 May–5 Aug
Plagodis phlogosaria (Guenée)	265	49	314	125	125	250	564	51	6 May–12 Aug
Plagodis serinaria Herrich-Schäffer	21	34	55	284	457	741	796	39	15 May–26 Jun
Probole alienaria (Herrich-Schäffer)	230	84	314	793	912	1,705	2,019	14	6 May–17 Jul
Probole amicaria (Herrich-Schäffer)	11	44	55	84	30	114	169	105	22 May–12 Aug
Prochoerodes transversata (Drury)	21	29	50	13	38	51	101	127	3 Jul–14 Aug
Protoboarmia porcelaria (Guenée)	4	1	5	0	0	0	5	201	6 May–12 Jun
Scopula inductata (Guenée)	26	3	29	12	3	15	44	164	22 May–14 Aug
Scopula limboundata (Haworth)	64	127	191	71	169	240	431	63	29 May–14 Aug
Selenia kentaria (Grote & Robinson)	0	0	0	1	1	2	2	204	20 May–24 Jul
Semiothisa aemulataria (Walker)	44	82	126	39	114	153	279	80	6 May–14 Aug
Semiothisa bicolorata (F.)	58	0	58	39	0	39	97	129	22 May–14 Aug
Semiothisa bisignata (Walker)	356	604	960	193	220	413	1,373	20	6 May–12 Aug
Semiothisa distribuaria (Hübner)	11	28	39	1	0	1	40	168	15 May–14 Aug
Semiothisa fissinotata (Walker)	53	111	164	222	205	427	591	48	6 May–14 Aug
Semiothisa granitata (Guenée)	322	79	401	39	13	52	453	58	6 May–31 Jul
Semiothisa minorata (Packard)	254	488	742	93	172	265	1,007	29	6 May–14 Aug
Semiothisa ocellinata (Guenée)	50	77	127	85	161	246	373	70	6 May–14 Aug
Semiothisa ulsterata (Pearsall)	1	0	1	3	0	3	4	202	22 May–14 Aug
Sicya macularia (Harris)	7	5	12	4	3	7	19	187	17 Jun–10 Jul
Tetracis cachexiata Guenée	35	44	79	166	131	297	376	69	15 May–8 Jul
Tetracis crocallata Guenée	0	1	1	2	0	2	3	203	19 Jun–26 Jun
Trichodezia albovittata (Guenée)	0	0	0	2	0	2	2	204	31 Jul–7 Aug
Xanthorhoe ferrugata (Clerck)	0	0	0	0	1	1	1	205	20 May
Xanthorhoe labradorensis (Packard)	0	0	0	3	0	3	3	203	22 May–7 Aug
Xanthorhoe lacustrata (Guenée)	0	0	0	0	1	1	1	205	20 May
Xanthotype sospeta (Drury)	3	5	8	14	21	35	43	165	17 Jun–14 Aug
Lasiocampidae									
Malacosoma americanum (F.)	237	111	348	124	117	241	589	49	5 Jun–24 Jul
Malacosoma disstria Hübner	207	168	375	154	148	302	677	43	17 Jun–31 Jul
Phyllodesma americana (Harris)	6	64	70	9	23	32	102	126	6 May–15 Jul
Tolype notialis Franclemont	22	8	30	1	1	2	32	175	15 Jul–14 Aug

Table 1. Continued.

Family Species	GWNF			MNF			Grand Total	Rank	Flight Period
	1995	1996	Total	1995	1996	Total			
Lymantriidae									
Dasychira spp.	66	50	116	115	142	257	373	70	17 Jun–14 Aug
Lymantria dispar (L.)	39	6	45	24	16	40	85	136	26 Jun–12 Aug
Orgyia leucostigma (J.E. Smith)	5	5	10	2	4	6	16	190	24 Jun–14 Aug
Mimallonidae									
Cicinnus melsheimeri (Harris)	2	10	12	20	28	48	60	151	5 Jun–26 Jun
Lacosoma chiridota Grote	1	1	2	0	1	1	3	203	29 May–17 Jun
Noctuidae									
Abagrotis alternata (Grote)	15	5	20	15	3	18	38	170	26 Jun–14 Aug
Achatia distincta Hübner	27	6	33	20	32	52	85	136	6 May–29 May
Achatodes zeae (Harris)	0	0	0	0	1	1	1	205	22 Jul
Acronicta afflicta Grote	137	76	213	4	7	11	224	92	6 May–14 Aug
Acronicta americana (Harris)	25	16	41	28	18	46	87	134	6 May–5 Aug
Acronicta fragilis Guenée	1	0	1	45	13	58	59	152	22 May–5 Aug
Acronicta haesitata (Grote)	805	421	1,226	627	858	1,485	2,711	12	20 May–14 Aug
Acronicta hamamelis Guenée	2	14	16	2	4	6	22	184	20 May–5 Aug
Acronicta hasta Guenée	11	7	18	5	24	29	47	161	6 May–7 Aug
Acronicta impleta Walker	50	1	51	2	0	2	53	156	22 May–31 Jul
Acronicta increta Morrison	832	838	1,670	529	921	1,450	3,120	11	20 May–14 Aug
Acronicta innotata Guenée	0	2	2	80	65	145	147	113	8 May–12 Aug
Acronicta laetifica J.B. Smith	1	0	1	1	0	1	2	204	8 May–26 Jun
Acronicta lithospila Grote	12	6	18	0	1	1	19	187	8 May–12 Aug
Acronicta lobeliae Guenée	23	5	28	7	7	14	42	166	6 May–15 Jul
Acronicta modica Walker	272	113	385	214	182	396	781	40	15 May–7 Aug
Acronicta morula Grote & Robinson	5	10	15	26	41	67	82	137	20 May–14 Aug
Acronicta ovata Grote	2,187	1,955	4,142	2,386	7,481	9,867	14,009	1	20 May–14 Aug
Acronicta pruni Harris	2	7	9	3	3	6	15	191	6 May–12 Aug
Acronicta radcliffei (Harvey)	0	0	0	0	2	2	2	204	24 Jun–8 Jul
Acronicta retardata (Walker)	2	5	7	0	5	5	12	194	22 May–5 Aug
Acronicta spinigera Guenée	0	0	0	4	5	9	9	197	15 May–10 Jun
Acronicta superans Guenée	0	0	0	1	0	1	1	205	3 Jul
Acronicta tristis J.B. Smith	46	0	46	3	0	3	49	159	15 May–5 Jun
Acronicta tritona (Hübner)	0	2	2	0	0	0	2	204	20 May–12 Aug

Table 1. Continued.

Family Species	GWNF 1995	GWNF 1996	GWNF Total	MNF 1995	MNF 1996	MNF Total	Grand Total	Rank	Flight Period
Agriopodes fallax (Herrich-Schäffer)	2	7	9	0	1	1	10	196	20 May–31 Jul
Agriopodes teratophora (Herrich-Schäffer)	2	4	6	5	6	11	17	189	22 May–5 Aug
Agroperina dubitans (Walker)	0	0	0	3	0	3	3	203	31 Jul–14 Aug
Agrotis ipsilon (Hufnagel)	8	5	13	1	6	7	20	186	15 May–14 Aug
Allagrapha aerea (Hübner)	2	1	3	1	3	4	7	199	19 Jun–5 Aug
Allotria elonympha (Hübner)	156	174	330	2	4	6	336	73	6 May–14 Aug
Amphipoea americana (Speyer)	1	0	1	1	1	2	3	203	17 Jul–29 Jul
Amphipoea velata (Walker)	2	0	2	2	0	2	4	202	3 Jul–24 Jul
Amphipyra pyramidoides Guenée	3	0	3	3	5	8	11	195	31 Jul–12 Aug
Anagrapha falcifera (W.F. Kirby)	1	0	1	1	1	2	3	203	20 May–26 Jun
Anathix ralla (Grote & Robinson)	3	0	3	2	0	2	5	201	14 Aug
Anomogyna badicollis (Grote)	43	45	88	162	184	346	434	62	17 Jun–14 Aug
Anorthodes tarda (Guenée)	915	302	1,217	226	63	289	1,506	19	6 May–14 Aug
Apamea vulgaris (Grote & Robinson)	0	0	0	1	0	1	1	205	24 Jul
Autographa precationis (Guenée)	5	4	9	3	1	4	13	193	22 May–17 Jul
Baileya dormitans (Guenée)	27	15	42	34	33	67	109	124	6 May–14 Aug
Baileya levitans (J.B. Smith)	50	128	178	8	73	81	259	84	6 May–29 Jul
Baileya ophthalmica (Guenée)	93	59	152	163	182	345	497	55	6 May–5 Aug
Balsa labecula (Grote)	204	144	348	485	221	706	1,054	27	8 May–14 Aug
Balsa malana (Fitch)	0	16	16	0	4	4	20	186	6 May
Bleptina caradrinalis Guenée	152	171	323	71	26	97	420	64	29 May–12 Aug
Bomolocha abalienalis (Walker)	1	0	1	0	1	1	2	204	5 Jun–17 Jun
Bomolocha baltimoralis (Guenée)	49	38	87	178	191	369	456	57	6 May–14 Aug
Bomolocha deceptalis (Walker)	1	6	7	10	14	24	31	176	6 May–14 Aug
Bomolocha edictalis (Walker)	21	3	24	42	5	47	71	143	3 Jul–14 Aug
Bomolocha palparia (Walker)	0	21	21	2	22	24	45	163	20 May–12 Aug
Caenurgina erechtea (Cramer)	0	1	1	2	3	5	6	200	17 Jun–12 Aug
Callopistria cordata (Ljungh)	9	4	13	5	5	10	23	183	5 Jun–17 Jul
Callopistria mollissima (Guenée)	5	7	12	101	100	201	213	94	20 May–14 Aug
Catocala amica (Hübner)	357	74	431	14	2	16	447	60	10 Jul–14 Aug
Catocala andromedae Guenée	143	23	166	30	11	41	207	95	3 Jul–14 Aug
Catocala blandula Hulst	0	0	0	1	0	1	1	205	3 Jul
Catocala coccinata Grote	24	10	34	2	1	3	37	171	26 Jun–5 Aug
Catocala connubialis Guenée	8	0	8	0	1	1	9	197	3 Jul–15 Jul

Table 1. Continued.

Family Species	GWNF 1995	GWNF 1996	GWNF Total	MNF 1995	MNF 1996	MNF Total	Grand Total	Rank	Flight Period
Catocala dejecta Strecker	26	7	33	1	1	2	35	172	17 Jul–14 Aug
Catocala epione (Drury)	138	38	176	0	2	2	178	101	26 Jun–14 Aug
Catocala flebilis Grote	19	0	19	0	0	0	19	187	24 Jul–31 Jul
Catocala grynea (Cramer)	2	0	2	0	0	0	2	204	17 Jul–24 Jul
Catocala ilia (Cramer)	4	2	6	3	5	8	14	192	8 Jul–14 Aug
Catocala micronympha Guenée	379	149	528	73	50	123	651	45	26 Jun–14 Aug
Catocala palaeogama Guenée	8	1	9	2	1	3	12	194	17 Jul–14 Aug
Catocala similis W.H. Edwards	47	8	55	0	0	0	55	155	26 Jun–15 Jul
Catocala sordida Grote	153	89	242	19	6	25	267	83	24 Jun–14 Aug
Catocala ultronia (Hübner)	2	0	2	0	2	2	4	202	22 Jul–14 Aug
Cerastis tenebrifera (Walker)	0	0	0	1	4	5	5	201	6 May–8 May
Cerma cerintha (Treitschke)	14	12	26	9	17	26	52	157	10 Jun–5 Aug
Cerma cora Hübner	1	0	1	4	3	7	8	198	8 May–5 Jun
Charadra deridens (Guenée)	11	51	62	13	77	90	152	111	6 May–14 Aug
Chrysanympha formosa (Grote)	4	9	13	16	5	21	34	173	10 Jun–31 Jul
Chytolita morbidalis (Guenée)	110	55	165	768	385	1,153	1,318	22	20 May–10 Jul
Chytonix palliatricula (Guenée)	194	77	271	60	75	135	406	65	8 May–14 Aug
Cissusa spadix (Cramer)	1	6	7	30	20	50	57	153	6 May–29 May
Colocasia propinquilinea (Grote)	72	19	91	35	55	90	181	100	6 May–5 Aug
Copivaleria grotei (Morrison)	0	0	0	2	2	4	4	202	6 May–20 May
Cosmia calami (Harvey)	165	102	267	81	47	128	395	67	26 Jun–14 Aug
Crambodes talidiformis (Guenée)	1	1	2	0	1	1	3	203	20 May–3 Jul
Crocigrapha normani (Grote)	13	3	16	54	25	79	95	131	6 May–29 May
Diarsia jucunda (Walker)	0	0	0	4	3	7	7	199	10 Jul–29 Jul
Egira alternans (Walker)	6	9	15	0	5	5	20	186	6 May–20 May
Elaphria festivoides (Guenée)	609	218	827	205	227	432	1,259	24	6 May–14 Aug
Elaphria georgei (Moore & Rawson)	22	32	54	10	3	13	67	146	6 May–3 Jul
Elaphria grata Hübner	1	4	5	0	0	0	5	201	8 Jul–12 Aug
Elaphria versicolor (Grote)	15	25	40	27	37	64	104	125	8 May–14 Aug
Euagrotis illapsa (Walker)	0	1	1	1	1	2	3	203	17 Jun–5 Aug
Euclidia cuspidea (Hübner)	4	5	9	0	1	1	10	196	6 May–31 Jul
Eudryas grata (F.)	38	30	68	8	17	25	93	132	19 Jun–5 Aug
Eueretagrotis perattenta (Grote)	0	0	0	0	4	4	4	202	1 Jul–15 Jul
Euparthenos nubilis (Hübner)	39	17	56	72	59	131	187	98	8 May–12 Aug
Euplexia benesimilis McDunnough	5	9	14	17	31	48	62	150	20 May –14 Aug

Table 1. Continued.

Family Species	GWNF 1995	GWNF 1996	GWNF Total	MNF 1995	MNF 1996	MNF Total	Grand Total	Rank	Flight Period
Eutolype electilis (Morrison)	0	0	0	0	1	1	1	205	6 May
Feltia herilis (Grote)	4	0	4	0	1	1	5	201	29 Jul–14 Aug
Feralia comstocki (Grote)	0	1	1	6	13	19	20	186	6 May–19 Jun
Galgula partita (Guenée)	1	3	4	0	1	1	5	201	3 Jun–15 Jul
Heptagrotis phyllophora (Grote)	6	2	8	7	8	15	23	183	26 Jun—-24 Jul
Homohadena infixa (Walker)	1	2	3	0	1	1	4	202	17 Jun–22 Jul
Homorthodes furfurata (Grote)	227	50	277	27	18	45	322	75	6 May–14 Aug
Hypena humuli Harris	4	0	4	7	0	7	11	195	8 May–14 Aug
Hypenula cacuminalis (Walker)	1	0	1	0	0	0	1	205	22 May
Hyperstrotia pervertens (Barnes & McDunnough)	66	193	259	100	882	982	1,241	25	20 May–14 Aug
Hyperstrotia secta (Grote)	0	0	0	0	2	2	2	204	15 Jul
Hyppa xylinoides (Guenée)	0	0	0	2	4	6	6	200	10 Jun–14 Aug
Hypsoropha hormos Hübner	4	3	7	0	0	0	7	199	29 May–5 Aug
Idia aemula Hübner	2,900	1,232	4,132	850	598	1,448	5,580	4	20 May–14 Aug
Idia americalis (Guenée)	225	100	325	219	287	506	831	36	8 May–14 Aug
Idia diminuendis (Barnes & McDunnough)	62	13	75	45	1	46	121	121	19 Jun–14 Aug
Idia forbesi (French)	1	0	1	1	0	1	2	204	3 Jul–17 Jul
Idia lubricalis (Geyer)	8	4	12	19	21	40	52	157	26 Jun–14 Aug
Idia rotundalis (Walker)	2,096	1,023	3,119	2,757	2,588	5,345	8,464	2	10 Jun–14 Aug
Idia scobialis (Grote)	14	0	14	45	0	45	59	152	26 Jun–14 Aug
Lacanobia grandis (Guenée)	0	1	1	0	1	1	2	204	20 May–17 Jun
Lacanobia legitima (Grote)	0	0	0	6	0	6	6	200	19 Jun–14 Aug
Lacanobia lutra (Guenée)	5	7	12	0	4	4	16	190	20 May–5 Aug
Lacinipolia anguina (Grote)	41	18	59	14	3	17	76	139	6 May–3 Jun
Lacinipolia olivacea (Morrison)	0	0	0	23	2	25	25	181	24 Jul–14 Aug
Lacinipolia renigera (Stephens)	29	1	30	45	16	61	91	133	22 May–14 Aug
Leucania linda Franclemont	1	16	17	0	1	1	18	188	29 May–1 Jul
Leucania pseudargyria Guenée	0	1	1	0	5	5	6	200	24 Jun–22 Jul
Leucania ursula (W.T.M. Forbes)	1	0	1	1	0	1	2	204	15 May–14 Aug
Leuconycta diphteroides (Guenée)	3	1	4	5	8	13	17	189	29 May–5 Aug
Leuconycta lepidula (Grote)	2	0	2	0	0	0	2	204	5 Jun–31 Jul
Lithacodia carneola (Guenée)	33	32	65	35	32	67	132	115	20 May–14 Aug
Lithacodia concinnimacula (Guenée)	0	0	0	14	7	21	21	185	29 May–19 Jun
Lithacodia muscosula (Guenée)	2	9	11	73	200	273	284	79	20 May–14 Aug
Lithacodia synochitis (Grote & Robinson)	4	16	20	15	13	28	48	160	20 May–31 Jul

Table 1. Continued.

Family Species	GWNF			MNF			Grand Total	Rank	Flight Period
	1995	1996	Total	1995	1996	Total			
Lithophane antennata (Walker)	0	0	0	1	0	1	1	205	15 May
Lithophane hemina Grote	0	0	0	1	0	1	1	205	22 May
Lithophane innominata (J.B. Smith)	0	0	0	4	10	14	14	192	6 May–29 May
Meganola minuscula (Zeller)	251	130	381	212	310	522	903	34	6 May–14 Aug
Meganola spodia Franclemont	1	3	4	0	23	23	27	179	20 May–22 Jul
Melanchra adjuncta (Guenée)	2	3	5	1	0	1	6	200	29 May–5 Aug
Metalectra discalis (Grote)	3	0	3	0	2	2	5	201	5 Jun–31 Jul
Morrisonia confusa (Hübner)	58	91	149	252	101	353	502	54	6 May–5 Jun
Morrisonia evicta (Grote)	50	8	58	9	6	15	73	141	6 May–29 May
Nedra ramosula (Guenée)	1	0	1	1	0	1	2	204	31 Jul
Nola pustulata (Walker)	0	0	0	2	0	2	2	204	19 Jun
Nola triquetrana (Fitch)	11	0	11	23	5	28	39	169	6 May–8 May
Ochropleura plecta (L.)	0	2	2	0	3	3	5	201	20 May–5 Aug
Ogdoconta cinereola (Guenée)	0	3	3	0	1	1	4	202	5 Aug
Oligia bridghami (Grote & Robinson)	0	0	0	0	1	1	1	205	8 Jul
Oligia fractilinea (Grote)	1	0	1	0	0	0	1	205	14 Aug
Orthodes cynica (Guenée)	9	3	12	142	178	320	332	74	15 May–5 Aug
Orthosia revicta (Morrison)	1	0	1	1	0	1	2	204	8 May
Orthosia rubescens (Walker)	23	9	32	18	41	59	91	133	6 May–20 May
Oruza albocostaliata (Packard)	2	4	6	1	0	1	7	199	26 Jun–29 Jul
Paectes oculatrix (Guenée)	2	0	2	0	0	0	2	204	19 Jun–24 Jul
Paectes pygmaea Hübner	0	6	6	0	1	1	7	199	17 Jun–5 Aug
Palthis angulalis (Hübner)	25	23	48	28	10	38	86	135	20 May–14 Aug
Palthis asopialis (Guenée)	1	0	1	0	0	0	1	205	29 May
Pangrapta decoralis Hübner	201	46	247	95	57	152	399	66	6 May–14 Aug
Panopoda carneicosta Guenée	47	53	100	19	43	62	162	107	29 May–14 Aug
Panopoda rufimargo (Hübner)	67	77	144	39	57	96	240	89	5 Jun–14 Aug
Panthea acronyctoides (Walker)	2	5	7	10	24	34	41	167	3 Jul–5 Aug
Panthea furcilla (Packard)	25	14	39	3	8	11	50	158	6 May–14 Aug
Parallelia bistriaris Hübner	21	7	28	106	38	144	172	103	8 May–14 Aug
Peridroma saucia (Hübner)	0	0	0	1	0	1	1	205	10 Jul
Perigea xanthioides Guenée	1	0	1	0	1	1	2	204	22 May–22 Jul
Phalaenophana pyramusalis (Walker)	0	1	1	0	1	1	2	204	20 May–10 Jun
Phalaenostola larentioides Grote	1	0	1	0	2	2	3	203	17 Jun–19 Jun
Phlogophora iris Guenée	0	0	0	7	7	14	14	192	3 Jun–3 Jul

Table 1. Continued.

Family Species	GWNF			MNF			Grand Total	Rank	Flight Period
	1995	1996	Total	1995	1996	Total			
Phoberia atomaris Hübner	1	3	4	7	85	92	96	130	6 May–20 May
Phosphila miselioides (Guenée)	6	13	19	1	2	3	22	184	20 May–14 Aug
Phosphila turbulenta Hübner	0	2	2	3	0	3	5	201	26 Jun–8 Jul
Phyprosopus callitrichoides Grote	0	1	1	0	0	0	1	205	5 Aug
Plathypena scabra (F.)	1	5	6	2	5	7	13	193	22 May–14 Aug
Platysenta vecors (Guenée)	10	26	36	24	39	63	99	128	6 May–12 Aug
Polia detracta (Walker)	259	288	547	192	229	421	968	31	20 May–5 Aug
Polia goodelli (Grote)	1	0	1	0	0	0	1	205	5 Jun
Polia imbrifera (Guenée)	0	0	0	7	0	7	7	199	3 Jul–10 Jul
Polia latex (Guenée)	52	117	169	137	150	287	456	57	15 May–5 Aug
Polia nimbosa (Guenée)	0	0	0	68	56	124	124	118	8 Jul–5 Aug
Polychrysia morigera (Henry Edwards)	0	0	0	0	1	1	1	205	5 Aug
Polygrammate hebraeicum Hübner	2,527	1,714	4,241	255	414	669	4,910	5	15 May–14 Aug
Protolampra brunneicollis (Grote)	6	24	30	1	8	9	39	169	17 Jun–14 Aug
Protorthodes oviduca (Guenée)	4	3	7	0	1	1	8	198	6 May–22 May
Psaphida resumens Walker	0	0	0	0	6	6	6	200	6 May
Pseudaletia unipuncta (Haworth)	11	9	20	8	7	15	35	172	20 May–14 Aug
Pseudorthodes vecors (Guenée)	0	0	0	0	19	19	19	187	15 Jul–5 Aug
Pyreferra hesperidago (Guenée)	0	1	1	4	6	10	11	195	6 May–15 May
Pyrrhia exprimens (Walker)	0	0	0	5	0	5	5	201	19 Jun–24 Jul
Raphia frater Grote	0	2	2	0	1	1	3	203	17 Jun–1 Jul
Renia discoloralis Guenée	15	14	29	17	13	30	59	152	1 Jul–14 Aug
Renia factiosalis (Walker)	0	13	13	2	18	20	33	174	20 May–14 Aug
Renia fraternalis J.B. Smith	1	0	1	0	0	0	1	205	24 Jul
Renia sobrialis (Walker)	3	0	3	41	0	41	44	164	7 Aug–14 Aug
Rhynchagrotis cupida (Grote)	0	0	0	2	1	3	3	203	10 Jul–5 Aug
Schinia rivulosa (Guenée)	2	0	2	0	0	0	2	204	14 Aug
Sideridis congermana (Morrison)	1	0	1	0	0	0	1	205	22 May
Spaelotis clandestina (Harris)	59	25	84	68	22	90	174	102	29 May–14 Aug
Spodoptera ornithogalli (Guenée)	2	0	2	0	0	0	2	204	29 May–24 Jul
Synedoida grandirena (Haworth)	3	2	5	3	2	5	10	196	22 May–22 Jul
Syngrapha rectangula (W.F. Kirby)	3	0	3	0	0	0	3	203	31 Jul–7 Aug
Tarachidia candefacta (Hübner)	0	1	1	0	0	0	1	205	8 Jul
Tarachidia erastrioides (Guenée)	1	1	2	1	0	1	3	203	29 May–29 Jul
Thioptera nigrofimbria (Guenée)	13	11	24	1	7	8	32	175	5 Jun–14 Aug

Table 1. Continued.

Family Species	GWNF 1995	GWNF 1996	GWNF Total	MNF 1995	MNF 1996	MNF Total	Grand Total	Rank	Flight Period
Tricholita signata (Walker)	0	2	2	6	2	8	10	196	17 Jun–14 Aug
Ulolonche culea (Guenée)	59	46	105	42	10	52	157	110	6 May–19 Jun
Xestia badinodis (Grote)	0	0	0	2	1	3	3	203	31 Jul–14 Aug
Xestia dolosa Franclemont	17	18	35	25	39	64	99	128	8 May–14 Aug
Xestia normaniana (Grote)	0	0	0	2	0	2	2	204	7 Aug–14 Aug
Zale bethunei (J.B. Smith)	2	2	4	0	0	0	4	202	8 May–8 Jul
Zale duplicata (Bethune)	6	4	10	6	5	11	21	185	6 May–17 Jul
Zale helata (J.B. Smith)	63	129	192	5	26	31	223	93	6 May–14 Aug
Zale lunifera (Hübner)	2	8	10	0	6	6	16	190	6 May–8 May
Zale minerea (Guenée)	162	67	229	208	133	341	570	50	6 May–5 Aug
Zale obliqua (Guenée)	8	0	8	0	1	1	9	197	8 May–8 Jul
Zale phaeocapna Franclemont	0	1	1	1	11	12	13	193	6 May–3 Jun
Zale squamularis (Drury)	1	0	1	0	0	0	1	205	8 May
Zale submediana (Strand)	2	0	2	1	0	1	3	203	15 May–22 May
Zale undularis (Drury)	1	1	2	2	0	2	4	202	29 May–22 Jul
Zale unilineata (Grote)	62	43	105	162	55	217	322	75	6 May–19 Jun
Zanclognatha cruralis (Guenée)	28	6	34	56	25	81	115	123	12 Jun–31 Jul
Zanclognatha inconspicualis (Grote)	0	0	0	0	7	7	7	199	29 Jul–5 Aug
Zanclognatha jacchusalis (Walker)	25	10	35	56	2	58	93	132	3 Jun–31 Jul
Zanclognatha laevigata (Grote)	218	17	235	634	207	841	1,076	26	3 Jul–14 Aug
Zanclognatha lituralis (Hübner)	1	11	12	46	41	87	99	128	3 Jun–5 Aug
Zanclognatha martha Barnes	26	31	57	4	9	13	70	144	24 Jun–5 Aug
Zanclognatha ochreipennis (Grote)	114	94	208	207	216	423	631	46	3 Jul–14 Aug
Notodontidae									
Clostera albosigma Fitch	0	0	0	1	0	1	1	205	24 Jul
Dasylophia anguina (J.E. Smith)	5	12	17	3	7	10	27	179	22 May–5 Aug
Datana angusii Grote & Robinson	6	15	21	1	8	9	30	177	3 Jun–31 Jul
Datana ministra (Drury)	36	102	138	7	16	23	161	108	22 May–7 Aug
Ellida caniplaga (Walker)	1	5	6	9	11	20	26	180	6 May–5 Aug
Furcula borealis (Guérin-Méneville)	0	0	0	2	1	3	3	203	20 May–24 Jul
Gluphisia septentrionis Walker	0	1	1	0	1	1	2	204	10 Jun–5 Aug
Heterocampa biundata Walker	13	4	17	68	83	151	168	106	22 May–14 Aug
Heterocampa guttivitta (Walker)	296	342	638	336	324	660	1,298	23	6 May–5 Aug
Heterocampa obliqua Packard	92	110	202	33	49	82	284	79	19 Jun–12 Aug

Table 1. Continued.

Family Species	GWNF 1995	GWNF 1996	GWNF Total	MNF 1995	MNF 1996	MNF Total	Grand Total	Rank	Flight Period
Heterocampa umbrata Walker	321	104	425	15	80	95	520	52	8 May–29 Jul
Hyparpax aurora (J.E. Smith)	0	1	1	0	0	0	1	205	22 Jul
Hyperaeschra georgica (Herrich-Schäffer)	242	187	429	157	87	244	673	44	6 May–7 Aug
Lochmaeus manteo Doubleday	21	4	25	24	37	61	86	135	20 May–12 Aug
Macrurocampa marthesia (Cramer)	226	58	284	310	119	429	713	42	19 Jun–14 Aug
Nadata gibbosa (J.E. Smith)	677	299	976	517	298	815	1,791	16	6 May–14 Aug
Nerice bidentata Walker	0	0	0	1	0	1	1	205	29 May
Oligocentria lignicolor (Walker)	23	0	23	92	3	95	118	122	19 Jun–14 Aug
Oligocentria semirufescens (Walker)	12	3	15	83	34	117	132	115	19 Jun–12 Aug
Peridea angulosa (J.E. Smith)	434	255	689	623	305	928	1,617	17	17 Jun–14 Aug
Peridea basitriens (Walker)	9	3	12	104	42	146	158	109	22 May–7 Aug
Peridea ferruginea (Packard)	0	0	0	12	3	15	15	191	19 Jun–5 Aug
Schizura ipomoeae Doubleday	8	4	12	29	35	64	76	139	19 Jun–14 Aug
Schizura leptinoides (Grote)	19	22	41	73	80	153	194	97	22 May–14 Aug
Schizura unicornis (J.E. Smith)	0	0	0	1	0	1	1	205	14 Aug
Symmerista canicosta Franclemont	36	8	44	795	528	1,323	1,367	21	27 May–7 Aug
Symmerista leucitys Franclemont	26	72	98	160	118	278	376	69	29 May–12 Aug
Saturniidae									
Actias luna (L.)	52	42	94	25	15	40	134	114	6 May–7 Aug
Anisota stigma (F.)	17	55	72	0	0	0	72	142	24 Jun–31 Jul
Anisota virginiensis (Drury)	2	1	3	0	0	0	3	203	24 Jun–10 Jul
Antheraea polyphemus (Cramer)	91	6	97	23	5	28	125	117	15 May–5 Aug
Automeris io (F.)	4	4	8	1	2	3	11	195	29 May–8 Jul
Callosamia angulifera (Walker)	4	3	7	0	0	0	7	199	15 May–8 Jul
Callosamia promethea (Drury)	1	0	1	0	0	0	1	205	8 May
Dryocampa rubicunda (F.)	161	166	327	261	280	541	868	35	15 May–5 Aug
Eacles imperialis (Drury)	43	22	65	0	0	0	65	147	3 Jul–31 Jul
Sphingidae									
Ceratomia undulosa (Walker)	2	0	2	11	5	16	18	188	20 May–14 Aug
Darapsa myron (Cramer)	5	3	8	1	1	2	10	196	10 Jun–31 Jul
Darapsa pholus (Cramer)	10	10	20	0	1	1	21	185	6 May–7 Aug
Deidamia inscripta (Harris)	21	15	36	2	1	3	39	169	6 May–29 May
Eumorpha pandorus (Hübner)	1	0	1	0	0	0	1	205	31 Jul

Table 1. Continued.

Family Species	GWNF 1995	GWNF 1996	GWNF Total	MNF 1995	MNF 1996	MNF Total	Grand Total	Rank	Flight Period
Laothoe juglandis (J.E. Smith)	9	12	21	16	6	22	43	165	20 May–5 Aug
Lapara coniferarum (J.E. Smith)	143	205	348	42	62	104	452	59	20 May–12 Aug
Paonias excaecatus (J.E. Smith)	46	38	84	113	35	148	232	91	29 May–12 Aug
Paonias myops (J.E. Smith)	2	2	4	26	8	34	38	170	22 May–12 Aug
Sphinx gordius Cramer	2	0	2	0	0	0	2	204	8 May–22 May
Thyatiridae									
Euthyatira pudens (Guenée)	13	1	14	12	1	13	27	179	6 May–29 May
Habrosyne scripta (Gosse)	0	0	0	1	0	1	1	205	19 Jun
Pseudothyatira cymatophoroides (Guenée)	2	1	3	9	11	20	23	183	29 May–12 Aug
Totals	35,745	24,864	60,609	35,593	39,069	74,662	135,271		

Table 2. Temperature and rainfall measurements from May through August, 1995 and 1996 for the GWNF and the MNF.

Year	Forest	Temperature (°C) Av. Low	Temperature (°C) Av. High	Rainfall (cm)
1995	GWNF	16.8	28.5	21.8
	MNF	13.9	23.8	16.8
1996	GWNF	12.0	27.1	39.1
	MNF	10.0	24.4	49.3

(Walker); the notodontid *Peridea ferruginea* (Packard); and the noctuids *Lithacodia concinnimacula* (Guenée), *Phlogophora iris* Guenée, *Lithophane innominata* (Smith), *Polia nimbosa* Guenée, *Lacinipolia olivacea* (Morrison), and *Pseudoorthodes vecors* (Guenée).

Temperature and rainfall recorded over a 30-year period (1961–1990) at NOAA stations near our plots indicate annual maximum temperatures are higher in the GWNF (17.8°C) than the MNF (16.4°C) and median annual rainfall is lower in the GWNF (96.8 cm) than the MNF (125.5 cm) (Owenby and Ezell 1992). During our current study, average low and high temperatures were higher in the GWNF than the MNF for both years (Table 2). In 1995, total rainfall recorded in our plots from May through August was higher in the GWNF than the MNF. Most of that rain fell during one large storm event in the GWNF in early June 1995. The 1996 rainfall was higher in the MNF than the GWNF, thus being more typical of the 30-year trend.

No clear trend in lepidopteran abundance was seen between the two years of the study. Higher overall abundance was collected in 1995 (71,336), the warmer, drier year (Table 1). The difference between years for the GWNF was considerable with 51% higher abundance of moths trapped in 1995. For the MNF, the reverse occurred with the abundance in 1996 being 9% higher than in 1995. Several of the more abundant species showed a notable shift in abundance between the two years.

The mean basal area contributed by dom-

Table 3. Abundance of major tree groups as indicated by mean basal areas for the GWNF and the MNF. Range and standard error are given.

Tree	GWNF			MNF		
	Mean	Range	SE	Mean	Range	SE
Acer spp.	0.52	0.08–0.90	0.21	2.70	0.55–8.16	0.56
Carya spp.	1.13	0.74–2.05	0.47	2.48	0.66–6.31	0.63
Pinus spp.	4.98	0.90–10.16	0.99	2.77	0.0–8.44	0.56
Q. alba	0.78	0.0–1.64	0.28	3.41	0.33–7.95	0.61
Q. prinus	6.45	2.46–10.25	1.00	3.85	0.74–7.29	0.87
Q. (*Erythrobalanus*)	6.37	5.33–8.44	0.94	4.45	1.97–8.44	0.81
Other	1.08	0.25–1.97	0.42	2.78	0.74–5.49	0.76

inant tree species including the host species emphasized in our study is given in Table 3. Basal areas of hickories, maples, white oak, and other species, were higher in the MNF while basal areas of chestnut oak, red oaks (subgenus *Erythrobalanus* spp.), and pines were higher in the GWNF. The higher composition of red oak/pine in the GWNF is indicative of more xeric conditions. The mean basal area represented by "other species" on our plots was 61% higher in the MNF than the GWNF, indicating an overall greater diversity in species composition of woody vegetation. Included in the "other" category in the MNF were black (*Betula lenta* L.) and yellow birch (*B. alleghaniensis* Britt.), black cherry (*Prunus serotina* Ehrh.), choke cherry (*P. virginiana* L.), blackgum (*Nyssa sylvatica* Marsh.), black locust (*Robinia pseudo-acacia* L.), serviceberry (*Amelanchier* spp.), white ash (*Fraxinus americana* L.), and mountain laurel (*Kalmia latifolia* L.). With the exception of blackgum and mountain laurel, these species were not abundant in the GWNF plots.

The abundance of moth species within our two study forests depends on many factors, among them, the availability of larval host plants. Many of the species of moths reflect differences in basal area of host trees in the two forests. For example, the basal area of pine is 44% greater in the GWNF plots in comparison with the MNF plots (Table 3). Among moth species requiring pine as a larval host, we typically see a higher abundance on the GWNF: the geometrids, *Semiothisa minorata* (Packard) and *Nepytia semiclusaria* (Walker); the sphingid, *Lapara coniferarum* (J.E. Smith); and the noctuid *Zale helata* (J.B. Smith). Species with larval hosts of *Prunus* spp. (*Lomographa* spp., *Probole alienaria, Paonias* spp.); *Robinia* (*Zale unilineata* (Grote), *Euparthenos nubilis* (Hübner); or *Betula* spp. (*Drepana arcuata* Walker, *Acronicta fragilis* Guenée) were typically more abundant in the MNF where the greater vegetational diversity included these tree species in greater abundance. Species with larval hosts of blackgum (*Allotria elonympha* (Hübner), *Polygrammate hebraeicum*) were more abundant in the GWNF where blackgum was 84% more abundant in the core plots.

Abundance of selected moth species (Table 4) was highly variable among the 18 plots, and did not relate clearly to abundance of the preferred larval host plant on the plots. For example, while *Semiothisa minorata* was generally more abundant in the GWNF with the highest basal area of pine (Table 3), the highest abundance was not on plot 9 with the highest basal area of pine (10.16) in the core plot. Instead, the highest abundance was trapped on plot 3, with only half the pine basal area. *Hypoprepia fucosa,* larvae of which are lichen feeders, was relatively evenly distributed among the plots. The *Idia* spp. whose larvae of which are litter feeders were abundant on all plots with the exception of plot 10. Plot 10 showed a relatively low abundance of most of the selected species (Table

4) except *Hydrelia inornata,* a maple feeder, and *Hypoprepia fucosa,* the lichen feeder. Plot 10 had a higher basal area of maple than any other tree species emphasized in our study. Much of plot 10 is covered with boulders and rock rubble that is frequently covered with lichens. While the highest count of black cherry in the understory of the core plots occurred on plot 12, the highest catch of the cherry-feeder, *Lomographa vestaliata,* occurred in plot 11. Highest numbers of black locust trees were in core plot 12, corresponding with the highest catch of *Euparthenos nubilis* and relatively high catch of *Zale unilineata,* larvae of which are locust specialists.

Examination of the flight period for the 438 lepidopteran species in this study indicates that some species have broad seasonal ranges while others are more restricted (Table 1). True seasonal ranges are best assessed for those species that were caught in relative abundance. Broad flight periods occur for some univoltine species with unsynchronized eclosion periods such as the notodontid *Heterocampa guttivitta* (Walker), the arctiids *Hypoprepia fucosa* and *Spilosoma congrua,* and the noctuids *Polia detracta* (Walker) and *Polia latex* (Guenée). Broad flight periods may reflect bivoltine or multivoltine life cycles as, for example, the geometrids *Melanolophia canadaria* (Guenée), *Hypagyrtis unipunctata, Lomographa vestaliata* (Guenée), and the *Lambdina* spp.; the saturniid, *Dryocampa rubicunda* (F.); the notodontid, *Heterocampa umbrata* Walker; the arctiids, *Clemensia albata,* and *Halysidota tesselaris*; and the noctuids *Idia aemula, I. rotundalis,* and *Zale minerea* (Guenée). Examples of species with narrow flight periods include the univoltine lasiocampids *Malacosoma* spp. and the arctiid, *Hyphantria cunea* (Drury).

Considerable fluctuation occurred over the 15-week period of each season regarding species numbers and abundance (Figs. 1–2). Generally, the number of species was higher in the GWNF in the spring and higher in the MNF in the summer sampling periods. No defined peak was noted in species numbers; about 125 species per week were trapped from late May to August. Weekly abundance was generally lowest in the spring sampling periods and highest in July and early August. The highest abundance over the two year period was taken in the MNF on 9 July 1996. Lowest richness and abundance occurred in both forests on the nights of 13 June 1995 and 14 May 1996. While minimum temperatures were not unseasonably low on 13 June (13°C), it was the night of the full moon with 0.999 percent illumination. On 14 May 1996, moonphase was not a factor (3.2 days before the new moon), but minimum temperature was near 0°C for both forests.

DISCUSSION

During our two-year study, we collected 438 species of moths, 379 species in the GWNF and 393 species in the MNF. In each forest, blacklight traps were operated at 9 different locations. The numbers of species we collected in this study are consistent with species numbers in hardwood forests in some other studies. Moulding and Madenjian (1979) trapped 410 species of macromoths in a virgin oak forest in New Jersey over a five-year period. Rings et al. (1987) recorded 426 species of macromoths over 9 years in Stark County, Ohio. Work et al. (1998) identified 256 species in 8 red-oak dominant stands in Northern Michigan. Butler and Kondo (1991) trapped 400 species of macromoths with a single 15 watt blacklight trap at one site at Coopers Rock State Forest, WV over a three year period. Butler et al. (1995) trapped 376 species on four small adjacent watersheds at Fernow Experimental Forest, Tucker County, WV over a 5-year period.

Many species were trapped in the current study that were not recorded in the Coopers Rock or Fernow Studies. Several explanations are possible. The vegetation makeup of the current study included significant stands of pine, spruce, or hemlock not present at the earlier study locations. Species

Table 4. Lepidopteran abundance by plot for 1995 and 1996, combined. Host associations of larvae are indicated.

	Plot					
Species	1	2	3	4	5	6
Semiothisa minorata (Packard)[1]	72	67	124	61	66	106
Lomographa vestaliata (Guenée)[2]	21	22	14	15	0	5
Hydrelia inornata (Hulst)[3]	21	20	20	25	8	29
Lapara coniferarum (J.E. Smith)[1]	27	33	20	75	43	68
Hypoprepia fucosa Hübner[4]	475	288	225	277	386	450
Idia aemula Hübner[5]	312	135	128	360	628	435
Idia rotundalis (Walker)[5]	454	300	240	248	466	381
Zale helata (J.B. Smith)[1]	9	14	12	72	19	31
Zale unilineata (Grote)[6]	10	24	12	7	6	6
Euparthenos nubilis (Hübner)[6]	15	2	3	3	4	1
Allotria elonympha (Hübner)[7]	58	28	69	27	41	30
Acronicta ovata Grote[8]	562	334	262	452	735	575
Polygrammate hebraeicum Hübner[7]	498	303	222	932	384	786
Total	2,534	1,570	1,351	2,554	2,786	2,903

Host Associations
[1] Pine.
[2] Black Cherry.
[3] Maple.
[4] Lichen.
[5] Litter.
[6] Black Locust.
[7] Black Gum.
[8] Oak.

in the current study associated with these conifers include the geometrids, *Caripeta angustiorata* Walker, *C. aretaria* (Walker), *Patalene olyzonaria* (Walker), the sphingid, *Lapara coniferarum,* and the noctuids, *Zale squamularis* (Drury), *Z. submediana* (Strand), *Z. duplicata* (Bethune), *Z. helata, Z. bethunei* (J.B. Smith), *Panthea acronyctoides* (Walker), and *P. furcilla* (Packard) (Covell 1984; Forbes 1948, 1954). Several species in the current study are considered to be uncommon: the geometrids, *Orthofidonia flaviventa* (Hulst), *Lytrosis permagnaria* (Packard), *Caripeta aretaria,* the notodontid *Hyparpax aurora* (J.E. Smith), and the noctuids, *Zanclognatha martha* Barnes, *Zale squamularis, Z. submediana, Z. bethunei, Catocala connubialis,* Guenée, *Cerma cora* Hübner, *Acronicta tritona* (Hübner), *A. spinigera* Guenée, *Oligia bridghami* (Grote and Robinson), *Homohadena infixa* (Walker), and *Sideridis congermana* (Morrison) (Covell 1984; Forbes 1948, 1954; Rings et al. 1992).

Because our light trapping period extended only for a 15-week period in May, June, July, and August, moth species that fly before or after that time were not collected. Species in this category that have been collected as larvae in our plots (Butler and Strazanac 2000a,b) include the geometrids *Alsophila pometaria* (Harris), *Phigalia denticulata* Hulst, *P. strigataria* (Minot), *Erannis tiliaria* (Harris), *Lambdina fiscellaria* (Guenée), and the noctuids, *Cosmia calami* (Harvey), *Lithophane quequera* Grote, *L. grotei* Riley, *Eupsilia* n. sp., *E. morrisoni* (Grote), *Xystopeplus rufago* (Hübner), *Eutolype rolandi* Grote, *Copipanolis styracis* (Guenée), *Orthosia hibisci* (Guenée), and *Himella intractata* (Morrison).

Several groups were not fully identified. It is likely that additional species of *Eupithecia* (Geometridae) are present in our

Table 4. Extended.

Plot												Total
7	8	9	10	11	12	13	14	15	16	17	18	
114	68	64	4	1	0	58	48	7	30	24	93	1,007
7	7	5	17	245	189	50	18	30	129	53	144	971
30	14	16	550	537	1,552	226	223	391	250	234	197	4,343
10	38	34	0	2	0	12	16	2	5	12	55	452
318	537	354	390	555	521	609	558	346	610	219	249	7,367
269	1,301	564	91	217	230	154	177	191	222	50	116	5,580
404	368	258	42	357	238	1,455	689	759	401	699	705	8,464
12	12	11	0	0	9	2	2	1	5	0	12	223
5	29	6	14	51	35	13	45	31	18	1	9	322
3	18	7	9	20	27	11	18	18	14	9	5	187
20	30	27	0	1	0	1	2		1	0	1	336
117	620	485	38	207	347	1,865	3,574	230	1,442	500	1,664	14,009
166	360	590	1	13	2	86	70	9	328	96	64	4,910
1,475	3,402	2,421	1,156	2,206	3,150	4,542	5,440	2,015	3,455	1,897	3,314	48,171

samples. The arctiid *Holomelina opella* (Grote) included some *H. nigricans* Reakirt. The lymantriid *Dasychira* spp. includes *D. dorsipennata* (Barnes and McDunnough), *D. obliquata* Grote and Robinson, *D. basiflava* (Packard), and *D. plagiata* (Walker). *Dasychira* specimens in the light traps were frequently rubbed leaving the pattern difficult to distinguish. Most of these species are highly variable in wing pattern and lack distinctive genitalia (Ferguson 1978).

Among the moth species collected exclu-

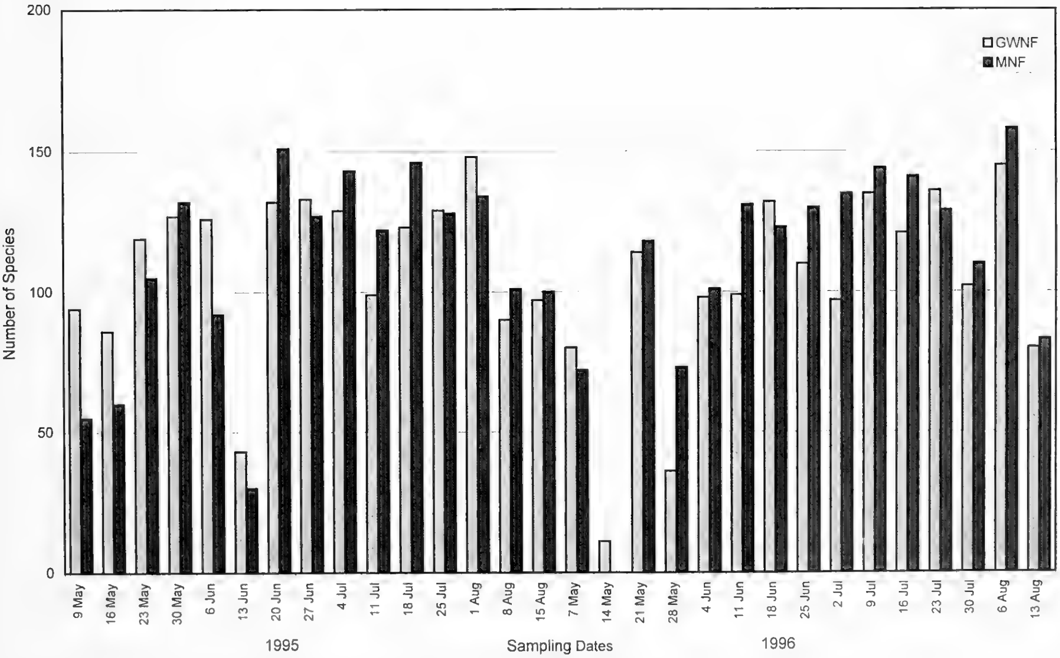

Fig. 1. Lepidopteran species numbers over 15 week sampling periods during 1995 and 1996 in the George Washington (GWNF) and (MNF) Monongahela national forests.

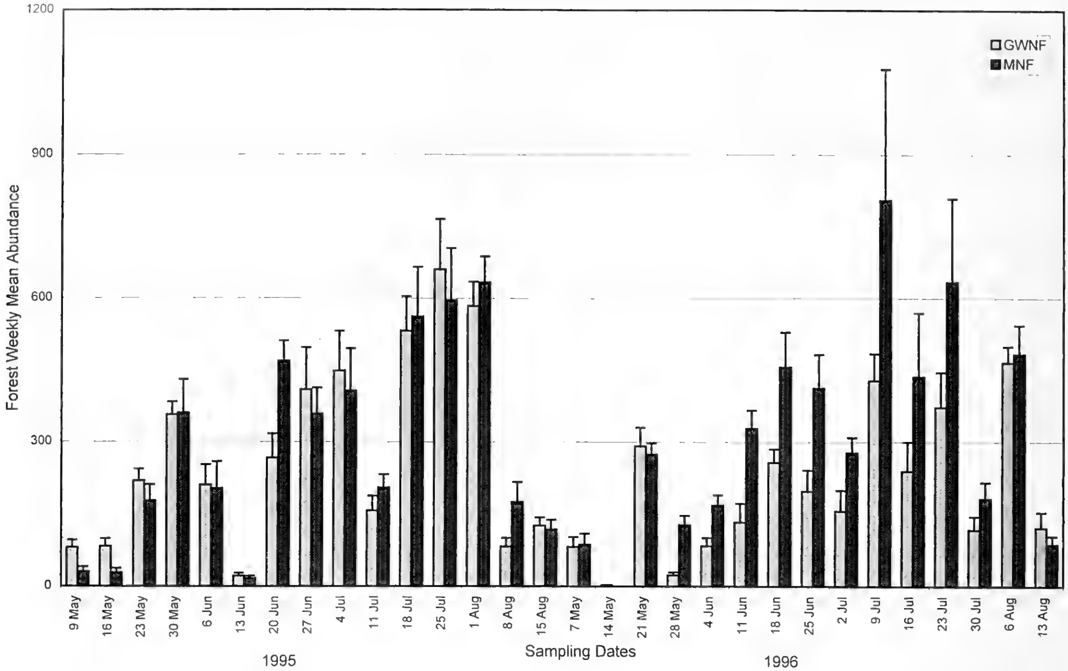

Fig. 2. Lepidopteran weekly mean abundance over 15 week sampling periods during 1995 and 1996 in the George Washington (GWNF) and (MNF) Monongahela national forests.

sively in the GWNF in numbers greater than one or two, we recorded *Lytrosis permagnaria,* likely a more southern species (Forbes 1948). Many of the moths trapped only in the MNF are more northern species that are found south only in the higher elevations. Some of these species probably have their southern range limit in WV. Species included in this category are the geometrids *Itame evagaria, Epirrhoe alternata,* and *Heterophleps refusaria;* and the noctuids *Lithacodia concinnimacula, Phlogophora iris, Lithophane innominata, Polia nimbosa, Lacinipolia olivacea,* and *Pseudorthodes vecors* (Covell 1984; Forbes 1948, 1954). The geometrid, *Aethalura intertexta* (Walker) is considered to be uncommon (Covell 1984), but we recorded 30 individuals in the MNF in two years.

Weather conditions differed between the two years with 1995 being warmer and drier and 1996 cooler and wetter. Numerous studies have shown direct and indirect effects of weather trends and atypical catastrophic temperature and rain events on insect populations (Martinat 1987). We saw no clear pattern of higher or lower numbers of moths between the two years.

We can comment on weather influence on nightly flight activity of moths. Weather effects on light trap catches of moths are well known. Influences include barometric pressure, humidity, nightly temperature, rainfall, and wind (Hardwick 1972, McGeachie 1989, Williams 1940). Light-trap catches are often at their lowest around the period of a full moon, and at their highest at periods of no moon or new moon (Williams 1936, Yela and Holyoak 1997, Butler et al. 1999). The night sky without a moon gives about 140 times less light radiation than one with a full moon (Kuiper 1938). Cloud cover reduces illumination and increases light-trap catches; radiation passing through vegetation is reduced in intensity (Bowden 1982). Light-trap catches are generally higher on warm, humid nights with no moonlight (McGeachie 1989). In sampling of noctuid moths by light trap in Spain, temperature was the dominant environmental factor influencing trapped moth numbers (Yela and Holyoak 1997). Average light trap catch varied 6- to 9-fold because of changes in temperature. Moonlight and cloud cover were second in influence and caused light trap catches to vary by 2-fold (Yela and Holyoak 1997). In our current study, nights of reduced sample size were influenced by full moon or unseasonably low temperatures (Butler et al. 1999).

During this study, sampling was restricted to a 15-week period, May through mid-August. While 438 species indicate relatively high diversity, increasing the length of the sampling season and sampling for additional years would produce records for many additional species. Other factors also limit species numbers as sampled by blacklight trap. All nocturnal lepidopterans do not respond equally well, or at all, to wavelengths emitted by blacklight traps; some species do not disperse far from the site of the larval host plants (Grimble et al. 1992).

In future publications from this study, we will evaluate the impact of two consecutive years of applications of *Bacillus thuringiensis kurstaki* on lepidopteran larvae as measured by richness and abundance of moths in light traps.

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THE STATUS OF *HEIKERTINGERELLA*, *MONOTALLA*, *PSEUDODIBOLIA*, AND *SPHAERODERMA* (COLEOPTERA: CHRYSOMELIDAE: ALTICINAE) IN THE NEW WORLD

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Abstract.—Based primarily on characters of the metatibia and head, justification of the validity and status of the genera *Heikertingerella, Monotalla, Pseudodibolia,* and *Sphaeroderma* in the New World is given. Two species of *Sphaeroderma* reported in the New World are transferred to other genera. ***Neosphaeroderma*** is described as a **new genus**. **New combinations** are *Pseudodibolia opima* (LeConte) and *Neosphaeroderma coerulea* (Jacoby). The genus *Monotalla* Bechyné previously placed as a synonym of *Pseudodibolia,* is considered valid. *Monotalla* has only 10 segmented antenna a rare character in the Alticinae.

Resumen.—Se provee una justificación de la validez de los géneros de Nuevo Mundo *Heikertingerella, Montalla, Pseudodibolia y Sphaeroderma* basada en carácteres de la metatibia y cabeza. Dos especies de *Sphaeroderma* registradas para el Nuevo Mundo son transferidas a otros géneros. Se describe ***Neosphaeroderma*** como un **género nuevo.** Se establecen dos **combinaciónes nuevas** *Pseudodibolia opima* (LeConte) y *Neosphaeroderma coerulea* (Jacoby). Se revalida el género *Monotalla* considerado anteriormente un sinónimo de *Pseudodibolia. Monotalla* posse un carácter muy raro en la Alticinae, sólo 10 segmentos en la antena.

Key Words: Neotropical, flea beetles, new combination, new genus, *Neosphaeroderma,* key

For some years, those interested in New World Chrysomelidae, specifically of the subfamily Alticinae, have questioned the correct status of the genera *Heikertingerella* Csiki, *Monotalla* Bechyné, *Pseudodibolia* Jacoby and *Sphaeroderma* Stephens, in particular the species placed in some of these genera.

The first question arose when Furth (1989) studied on the jumping apparatus (metafemoral spring) in 91 Neotropical Alticinae genera in which he arranged them into morphological groups already established from studies of the Palearctic and Nearctic genera (Furth 1985). Furth (1989) mentioned for the first time that there were morphological similarities among *Pseudodibolia, Heikertingerella* and "*Sphaeroderma,*" and indicated that "*Sphaeroderma opima*" LeConte is not congeneric with the Palearctic species of *Sphaeroderma.* He (Furth 1989) presented some figures demonstrating the similarity of the metatibia of *S. opima* and *Pseudodibolia.* Later Furth in Flowers et al. (1994), discussing the host plants of Florida Alticinae, mentioned that "*Sphaeroderma opima*" was not a true representative of the genus *Sphaeroderma* from the Old World. Furth (in Flowers et al. 1994) said that a narrow relationship may exist between that species and those of *Heikertingerella* and *Pseudodibolia*; however, at that point he considered *S. opima* to be nearer to *Heikertingerella* than to *Pseudodibolia.*

During recent studies of a variety of Neotropical Alticinae by the authors, we discovered that several genera with similar external morphological features caused some confusion in attempting to identify specimens. These characters are primarily a round to globose, very convex body shape (coccinelliform) and the pronotum with a bisinuate, lobed, projecting, posterior margin. There is no other particular apparent relationship of these genera and the primary purpose of this study is to clarify the nomenclatural status of these genera. Because of this confusion, we conducted studies that would help clarify the correct status of each taxon, concentrating primarily on the study of the external morphology of some representatives of the genera in question. For practical reasons (e.g., ease of identification purposes for general users), we have chosen here to only concentrate on external morphological characters. We have also found some more detailed internal characters, but these will be presented in a more comprehensive morphological study in the future (Savini in preparation).

MATERIALS AND METHODS

Specimen were examined from the following museums: (USNM): National Museum of Natural History, Smithsonian Institution, Washington, DC; (MIZA): Museo del Instituto de Zoología Agricola Francisco Fernández Yépez, Facultad de Agronomía, U.C.V., Maracay, Venezuela; (MCZC): Museum of Comparative Zoology, Harvard University, Cambridge, MA (F. C. Bowditch collection); (INBIO): Instituto Nacional de Biodiversidad, Costa Rica; (NHMB): Naturhistorisches Museum, Basel (Frey Collection), Switzerland; BMNH: The Natural History Museum, London, United Kingdom; (FAMU): Florida A. M. University, Tallahassee, FL; Hungarian Natural History Museum, Budapest, Hungary (HNHB).

We made many dissections of specimens of *Heikertingerella, Pseudodibolia,* and *Sphaeroderma.* The body parts were disarticulated to allow examination of the maximum number of possible external characters and to prepare them for the Scanning Electron Microscope photos; however, in the current study we use only external characters. For the genus *Monotalla,* dissections were not made, because the only specimens to be studied were the holotype and paratype of *Monotalla guadeloupensis* Bechyné; therefore, only external characters were examined, studied and illustrated by line drawings.

The terminology for external morphological characters generally follows Snodgrass (1935). However, in this study we have used some different terminology as follows. The frontoclypeus is the area between the clypeo-labral suture to and including the inter-antennal space. This area is defined as the frontoclypeus because when we made a detailed examination of the internal morphology of the head capsule, we were able to observe that the anterior tentorial arms are just underneath the inferior border of the antennal cavities. According to classical morphological theory, the tentorial pits define the division between the clypeal and frontal regions and the suture between these pits is called the epistomal suture. However, when the epistomal suture is absent, such as with the genera studied here, it is more appropriate to name this area the frontoclypeus. The term frontal sulcus is applied in this study to include the orbital sulcus plus the supracallinal sulcus (sensu Konstantinov and Vandenberg 1996).

Once dissected, the parts were submerged in 10% KOH for about 10 hours to eliminate the maximum amount of material that could obstruct visibility of the characters to be studied. Next, the parts were submerged in distilled water and then in ammonia for approximately one hour, in order to eliminate the fat tissue. Once this procedure was complete, the parts were dried and each dissected specimen was mounted onto a metal stub for metallic coating and photography using AMRAY 1810 Scanning Electron Microscope.

Also, we present a key for the identification of the genera and a diagnosis for each genus accompanied by some illustrations of the characters studied.

RESULTS

KEY TO THE GENERA *HEIKERTINGERELLA*, *MONOTALLA*, *NEOSPHAERODERMA*, *PSEUDODIBOLIA*, and *SPHAERODERMA*

All genera except *Sphaeroderma* (= *Neosphaeoderma*) can be identified using the key of Scherer (1962, 1983); however, *Pseudodibolia* and *Monotalla* are contained in the same couplet of that key to Neotropical genera because of the synonymy established by Scherer (1962).

1. Dorsal outer edge of metatibia serrate (Figs. 6–9, 17) 2
– Dorsal outer edge of metatibia not serrate (Figs. 10–12, 14–16) 3
2. Head without frontal sulcus (Fig. 5). Metatibia with a very long apical spur, almost half length of first metatarsomere (Figs. 16–17). Metasternum very short, approximately equal length of prosternum and mesosternum processes together . . . . *Monotalla*
– Head with frontal sulcus strongly impressed (Fig. 1). Metatibia with a very short apical spur (Fig. 7). Metasternum longer than prosternum and mesosternum processes together . . . . *Pseudodibolia*
3. Metatibia with preapical tooth on dorsal outer edge (Figs. 10–11) . . . . *Heikertingerella*
– Metatibia smooth, without tooth on dorsal outer edge (Figs. 12–15) 4
4. Head with horizontal frontal sulcus (Fig. 3). Anterior coxal cavities open . . . . *Sphaeroderma*
– Head with frontal sulcus obliquely angled and convergent towards antennal socket (Fig. 4). Anterior coxal cavities closed . . . . *Neosphaeroderma*, n. gen.

Heikertingerella Csiki 1940:350
(Figs. 2, 10–11)

Type species: *Homophyla adusta* Harold 1877:138 (Peru).

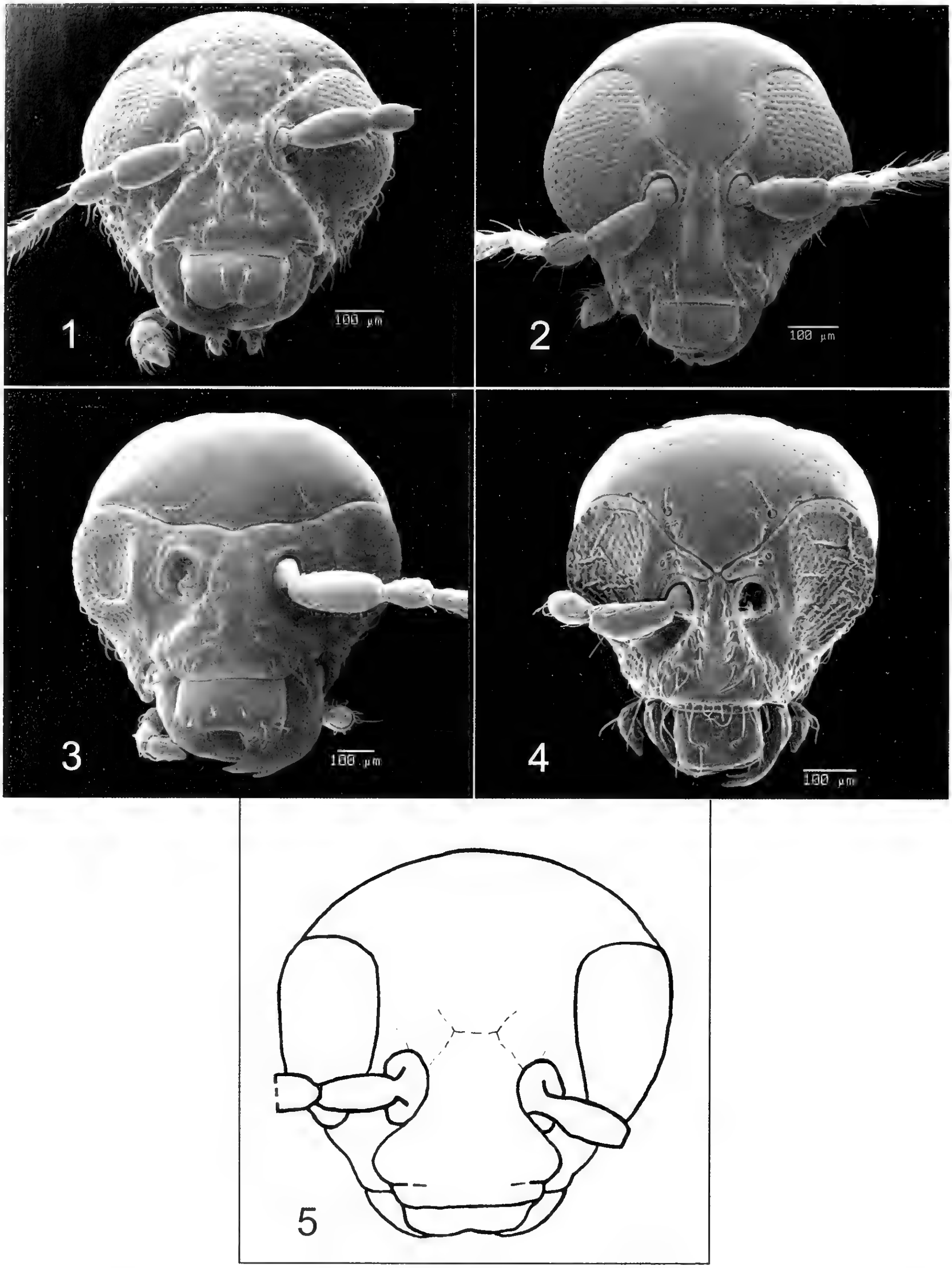
Heikertingerella Csiki 1940:350 (established as a replacement name due to homonymy).

Homophyla Harold 1877:138. Type species *H. adusta* Harold.

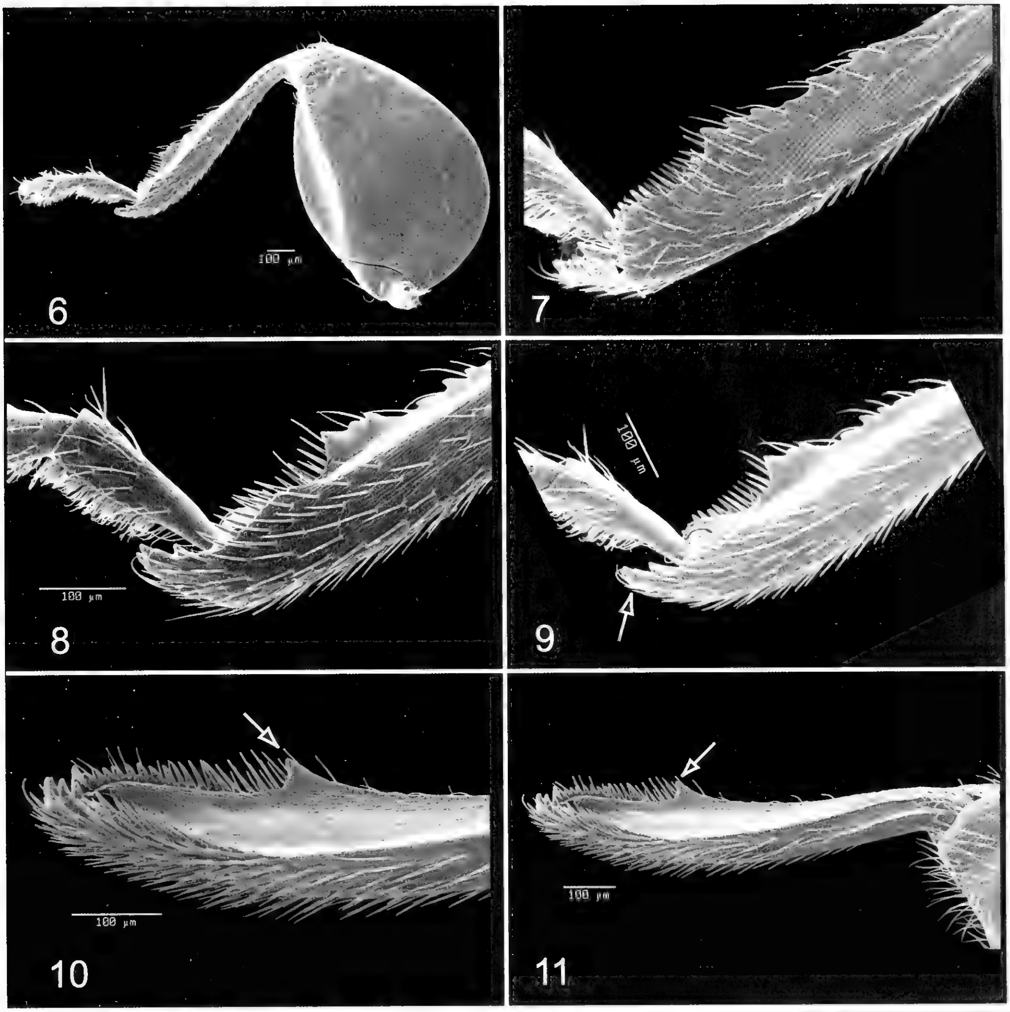
Euplectroscelis Jacoby 1885:392 (not Crotch 1873:57, 75), see also Remarks below.

Description.—Body oval short, broad, very convex, color not metallic. *Head:* Frontoclypeus with longitudinal carina always present; clypeal transverse carina present or evident only laterally. Frontal sulcus always present oblique and convergent towards antenal socket. Supraantennal calli absent or very narrow (Fig. 2). *Thorax:* Pronotum convex and without prebasal transverse impression; anterolateral angle beveled. Anterior coxal cavities open. Metasternum as long as or longer than length of prosternal and mesosternal processes together. *Legs:* Metafemur thickened but narrower than width of abdomen. Metatibia dorsally flattened in middle with raised edges from approximately apical half and with one preapical tooth; outer edge smooth; inner edge apically somewhat widely prolonged posteriorly (Figs. 10–11). First metatarsomere generally subcylindrical. Apical spur distinct but short. *Elytra:* Punctuation fine and confused, sometimes with tendency to form striae; epipleura slightly broadened, but somewhat wider towards anterior ¼, laterally visible and gradually tapered toward apex.

Remarks.—The genus *Heikertingerella*, currently includes 125 species and 3 subspecies (Savini 1999) most of these are recorded from South America and 19 from Central America (Furth and Savini 1996).



Figs. 1–5. Heads. 1, *Pseudodibolia opima*. 2, *Heikertingerella* sp. 3, *Sphaeroderma testaceum*. 4, *Neosphaeroderma coerulea*. 5, *Monotalla guadeloupensis*.



Figs. 6–11. Metatibiae. 6–9, *Pseudodibolia opima* (fig. 7, arrow = apical spur. fig. 9, arrow = apical spur). 10–11, *Heikertingerella* sp. (arrows = preapical tooth on outer edge).

Since 1940, no taxonomic work has been published indicating confusion with other related genera. *Heikertingerella* is actually very diverse; however, we predict, based on recent examination of material from various Neotropical countries (Savini and Furth, unpublished), that its recorded diversity will increase greatly and that possibly its distributional range will be greatly expanded in the New World. We examined many specimens of several species from Costa Rica (INBIO, FAMU). Baly (1877:319–322), mistakenly described 6 species of *Homophyla* as *Euplectroscelis* Crotch.

Monotalla Bechyné 1956:588, **revised status**

(Figs. 5, 16–17)

Type species: *Monotalla guadeloupensis* Bechyné 1956:588 (Guadeloupe) by monotypy.

Pseudodibolia Jacoby 1891 (Scherer 1962: 583 placed *Monotalla* in synonymy).

Description.—Micropterus insects. Body oval, very short and wide, strongly convex, color not metallic. *Head:* 10-segmented antenna, segments 1–2 elongate somewhat swollen, 3–5 tiny and thin, 6–10 larger, swollen, rounded and almost spherical. Without frontal carina. Frontoclypeus triangular, inflated; longitudinal and traverse carinae barely evident. Supraantennal calli faint (Fig. 5). *Thorax:* Pronotum convex and without prebasal transverse impression; anterior angles almost rounded, not beveled. Anterior coxal cavities open. Metasternum very short, approximately length of prosternal and mesosternal processes together. *Legs:* Metafemur greatly thickened, only slightly narrower than width of abdomen. Metatibia flattened laterally, consequently toward ventral area of tibia a carinae is present from near base until apex; dorsally metatibia flattened with raised edges from near base to the apex; inner edge serrate from approximately apical half (Fig. 17); outer edge smooth, but with distinct preapical excavation (Fig. 16). Apical spur very long, half length of first tarsal segment, clearly wider at base. (Figs. 16–17). First metatarsomere subcylindrical. *Elytra:* Punctures arranged in striae of 9 impressed longitudinal rows, but confused apically; epipleura totally visible in lateral view and ending abruptly at apex.

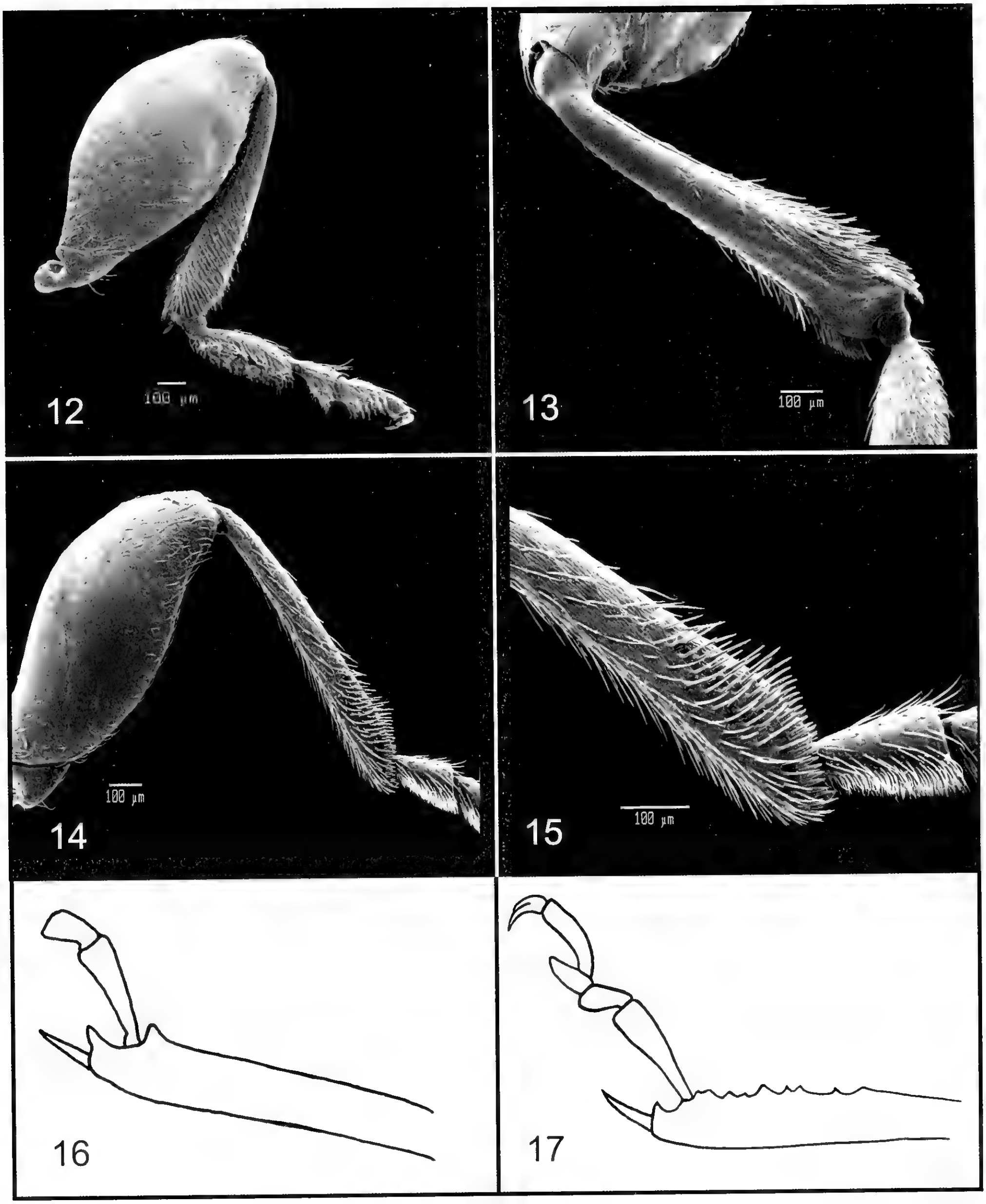
Remarks.—A very special discovery in the current study is that *Monotalla* has only 10-segmented antennae. This is only the third genus known in the Alticinae (with over 500 genera worldwide) with less than 11 segments in the antennae. The others are *Psylliodes* Latreille with 10 segments and *Nonarthra* Baly with 9 segments. Until now only two species were known in the genus *Monotalla: M. guadeloupensis* Bechyné (Guadeloupe) and *M. nigrita* (Jacoby) (Grenada). The male holotype (NHMB) and the female paratype (HNHM) specimens of *M. guadeloupensis* were examined. We have examined all known syntypes of *M. nigrita* (MCZC [2], BMNH [7]) and have determined that it is not con-generic with *M. guadeloupensis. Monotalla nigrita* was originally described in the genus *Glyptina* LeConte; however, we do not believe it belongs in that genus either. The placement of *M. nigrita* will need to be resolved at some time in the future. During the review of the status of *Monotalla* and specimens from many collections, we have been able to discover some new genera distributed in South and Central America with similar external morphology to *Monotalla* (Savini and Furth in preparation).

Pseudodibolia Jacoby 1891:291
(Figs. 1, 6–9)

Type species: *Pseudodibolia picea* Jacoby 1891:291 (Mexico) by monotypy.

Description.—Body oval, short, wide, convex, not metallic. *Head:* Frontoclypeus triangular; longitudinal and transverse carina faint. Frontal sulcus present, oblique and convergent towards antennal socket (Fig. 1). Supraantennal calli faint or absent. *Thorax:* Pronotum convex, without prebasal transverse impression; anterior angles beveled. Anterior coxal cavities open. Metasternun longer than prosternal and mesosternal processes together. *Legs:* Metafemur thickened but narrower than width of abdomen. Metatibia slightly flattened dorsally in apical half; outer and inner edges distinct only in approximately apical half (Figs. 6–7); inner edge serrate in apical half and excavated near apex; apex of inner edge of tibia prolonged posteriorly (Figs. 8–9). First metatarsomere generally subcylindrical. *Elytra:* Striate punctuation distributed in 9 longitudinal rows but not very regular. Epipleura as in *Heikertingerella.*

Remarks.—In contrast to *Heikertingerella,* the genus *Pseudodibolia,* originally described from Mexico, has been confused with the genus *Monotalla* Bechyné (1956). Scherer (1962, 1983) synonymized it with *Pseudodibolia.* However, based on the current study, these genera are different, as demonstrated by differences in certain morphological characters. *Monotalla* was originally described from the Guadeloupe Isle in the West Indies. We suppose that this synonymy was based only on the original description of *Pseudodibolia* (Jacoby 1891) and that Scherer (1962) made an erroneous



Figs. 12–17. Metatibiae. 12, 13, *Sphaeroderma testaceum*. 14, 15, *Neosphaeroderma coerulea* (outer view). 16, 17, *Monotalla guadeloupensis* (inner edge and outer edge, respectively).

interpretation of the characters described by Jacoby. This synonymy established by Scherer, resulted in *Pseudodibolia* appearing to have a wider distribution, because it included West Indian *Monotalla*. We have examined the syntypes of *P. picea* (BMNH [2], MCZC [4], USNM [2]) all from Teapea, Tabasco, Mexico. Also, *Sphaeroderma opima* LeConte has been placed in *Sphaeroderma* by many authors for a long time (see Introduction), but Furth (1989) and Flowers et al. (1994) began to question this. Based on external morphological characters, the current study has shown that *S. op-*

ima belongs in the genus *Pseudodibolia* (Figs. 1, 6–9) (**new combination**). This species is recorded from the northeastern(Ohio, Maryland), midatlantic (North Carolina), southeastern (Florida) and south central (Texas) states of the USA (Wilcox 1975, Flowers et al. 1994). We have examined *P. opima* specimens from Florida (USNM).

Sphaeroderma Stephens 1831:328 (Figs. 3, 12–13)

Type species: *Altica testacea* Fabricius 1775:114 (Europe) by subsequent designation of Maulik 1926:316.

Description.—Body spherical in shape, wide, very convex. *Head:* Frontoclypeus subtriangular; frontal sulcus horizontal from upper margin of compound eyes toward center of front (Fig. 3). Supraantennal calli present. *Thorax:* Pronotum convex, without prebasal transverse impression; anterior angles projected anteriorly, thickened, very blunt and not beveled. Anterior coxal cavities open. Metasternum longer than prosternal and mesosternal process together. *Legs:* Metafemur not greatly thickened, evidently narrower than width of abdomen. Metatibia dorsally rounded, without excavation on outer edge of tibia and without preapical tooth (Fig. 13). First metatarsomere triangularly enlarged and very thick. *Elytra:* Very fine and confused punctation, with tendency to form striae. Epipleura totally visible laterally, very wide in anterior half then gradually tapering apically almost reaching apex of elytron.

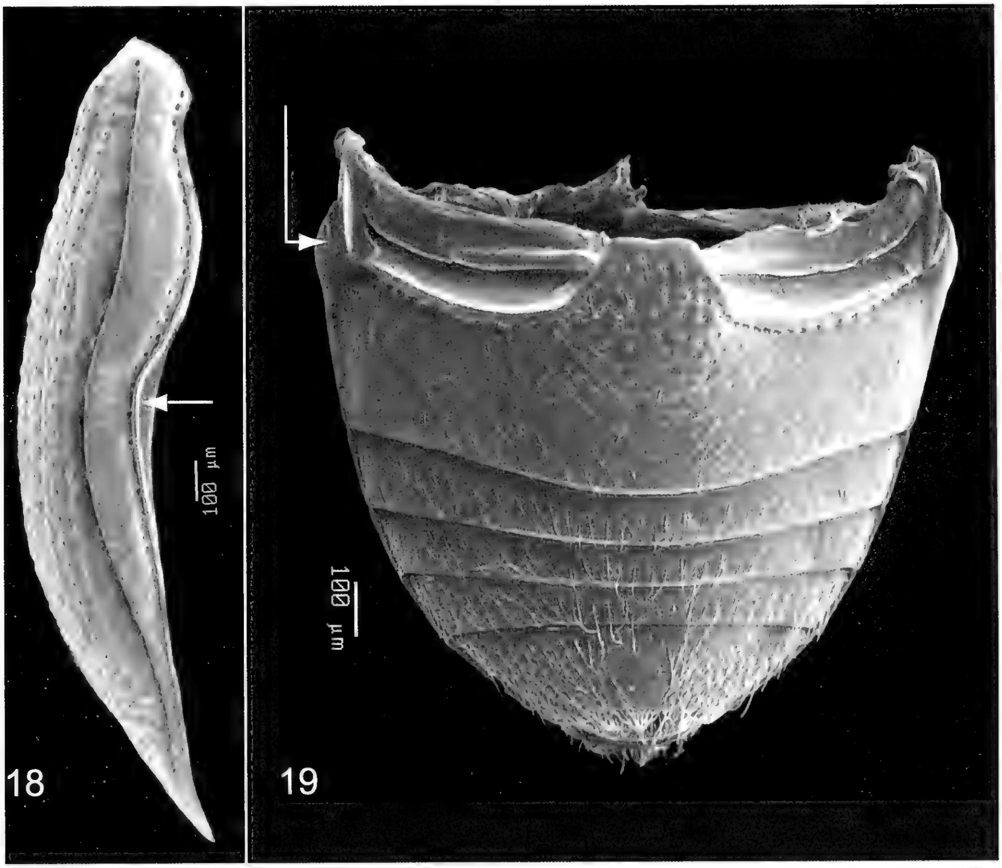
Remarks.—The current distribution of *Sphaeroderma* is composed of over 150 species in the Old World, mostly in the Oriental and Afrotropical regions (Konstantinov and Vandenberg 1996, Heikertinger and Csiki 1940, Furth 1989, Flowers et al. 1994); however, LeConte (1878) and Jacoby (1891) reported two species in the New World: *Sphaeroderma opima* LeConte (USA) and *Sphaeroderma coerulea* Jacoby (Panama), respectively (see also Furth and Savini 1996). The taxonomy and the status of these two species has not been previously reviewed; however, we now realize that both species should be placed in two different genera: *S. opima* should be placed in the genus *Pseudodibolia* and *S. coerulea* needs to be placed in a new genus (see Remarks sections for *Pseudodibolia* and *Neosphaeroderma,* respectively). We have examined specimens of *S. testaceum* F. from Europe (USNM) and *S. seminigrum* Jacoby from China (USNM).

***Neosphaeroderma* Savini and Furth, new genus** (Figs. 4, 14–15, 18–19)

Type species: *Sphaeroderma coerulea* Jacoby 1891:310 (Panama).

Neosphaeroderma coerulea (Jacoby), **new combination**.

Description.—Body oval, short, very convex, not metallic. *Head:* Frontoclypeus subtriangular and with abundant setae; coarse punctuation on dorsal half; longitudinal carina present, but not very inflated; transverse carina absent. Frontal sulcus present oblique and convergent towards antennal socket (Fig. 4). Supraantennal calli present. Antenna with 10 segments. *Thorax:* Pronotum convex, with only a slight impression near base, but laterally more evident; 1.6 times wider than long; anterior angles rounded and thickened, not projecting. Posterior angles not evident. Posterior border bisinuate and with well-developed central lobe. Anterior coxal cavity closed. Prosternal process wide, almost as long as wide, with coarse punctures on both sides and with many setae. Metasternum as wide or wider than length of prosternal and mesoternal processes together. *Legs:* Metafemur like *Sphaeroderma.* Metatibia dorsally rounded, without preapical tooth on outer edge (Figs. 14–15). First metatarsomere slightly subtriangular. *Elytra:* Punctuation striate in 9 longitudinal rows; epipleura not very wide, with an evident concavity where



Figs. 18–19. 18, Elytron and epipleuron: *Neosphaeroderma coerulea* (right lateral view). 19, Abdomen: *Neosphaeroderma coerulea.* (ventral view, arrow = lateral projection of first abdominal segment).

lateral projection from first abdominal segment fits (Figs. 18–19).

Remarks.—The last elytral character mentioned (epipleura concave, Fig. 18) was used by Bechyné to group the Crepidoderini and Chaetocnemini (Bechyné and Bechyné 1975). We have examined the syntypes of this species (MCZC [# 19385], BMNH [1]) both from Bugaba, Panama, as well as other specimens from Costa Rica (INBIO La Amistad, Sect. Altamira, Buenos Aires, Prov. Punta, 1,200 m, 21 Feb.–10 Mar. 1994, R. Delgado [7], Sector Cerro Cocori, Fca. De E. Rojas, 150 m, Prov. Limón, May 1993, E. Rojas [2]). Further details of external morphology can be found in the original description of *S. coerulea* Jacoby (1891:310, plate 42: fig. 22).

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TWO NEW SPECIES OF *NESODIPRION* ROHWER (HYMENOPTERA: DIPRIONIDAE) FROM JAPAN

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Abstract.—***Nesodiprion nigrum***, **n. sp.**, and ***Nesodiprion tsugae***, **n. sp.**, from Japan are described and illustrated. *Nesodiprion tsugae* was reared from *Tsuga diversifolia* Masters.

Key Words: Symphyta, Diprionidae, *Nesodiprion,* new species, food plant, *Tsuga diversifolia,* Japan

In 1998, I reported on the five species of the conifer sawfly genus *Nesodiprion* Rohwer from Japan. Recently, I received 20 specimens of this genus from Dr. A. Shinohara, the National Science Museum (Nat. Hist.), Tokyo, and Professor Emeritus Dr. T. Okutani, Kawagoe City, Kanagawa Prefecture. Among them, I discovered two undescribed species. These new species are very closely allied to *Nesodiprion shinoharai* Togashi and *N. nigerrimus* Togashi, but they are distinguished from the latter two by the shape of the 3rd antennal segment and by the shape of the pad-like area of the sawsheath. In this paper, I describe and illustrate these two new species.

Nesodiprion nigrum Togashi, new species
(Figs. 1–9, 14–16)

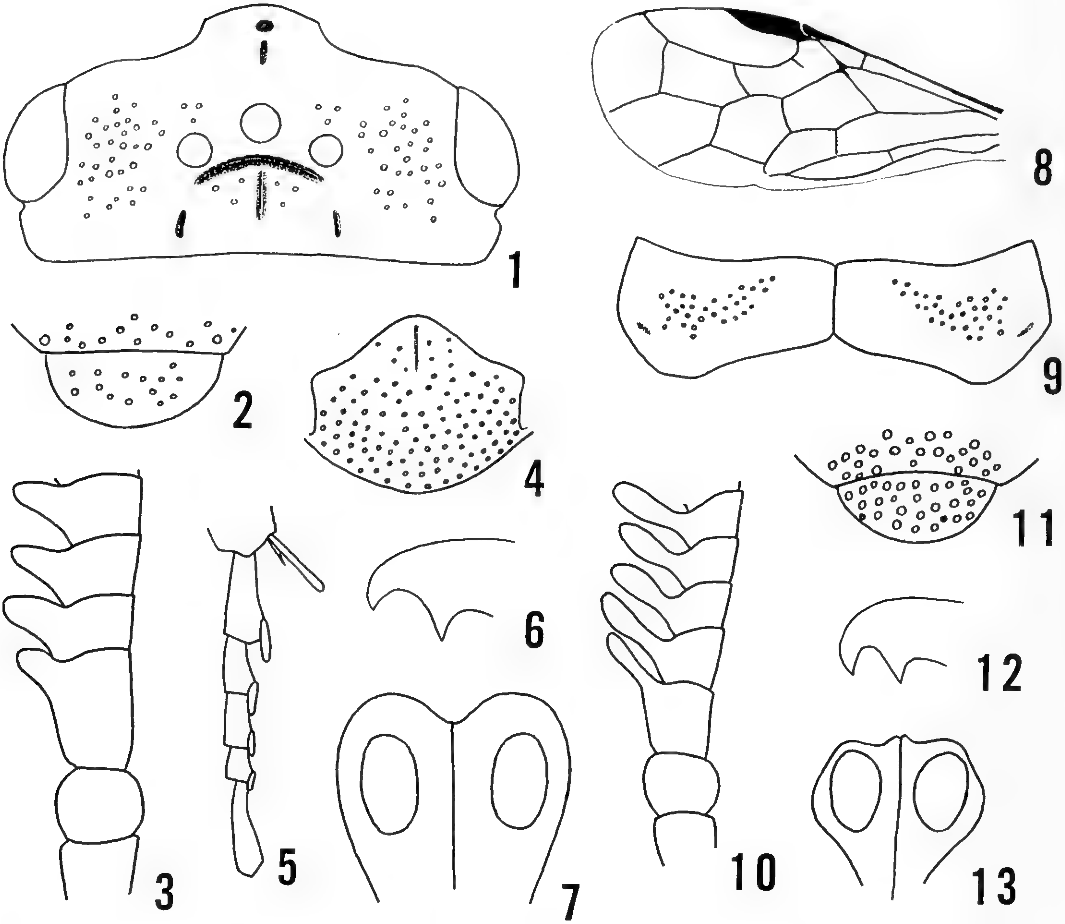
Female.—Length 8 mm. Head, antenna, and body entirely black. Wings hyaline; stigma and veins black. Legs black with following parts reddish brown to dark brown: knee of fore femur, fore tibia, fore tarsus, and mid and hind tarsi.

Head: Normal; postocellar area transverse and convex, with a longitudinal median furrow but posterior portion ill-defined (Fig. 1); circumocellar and interocellar furrows rather ill-defined; postocellar and lateral furrows distinct and deep; OOL:POL:OCL = 1.1:1.0:0.9; frontal area nearly flattened, anterior half of frontal area with distinct and deep medial furrow (Fig. 1), but not connected with median fovea (Fig. 1); median fovea distinct, rectangular shaped (Fig. 1); lateral fovea distinct, circular in outline; distance between antennal sockets shorter than antenno-ocular distance (ratio about 1.0:1.6); supraclypeal area slightly convex; anterior margin of clypeus nearly truncate (Fig. 2); malar space nearly as long as diameter of front ocellus; postorbital groove distinct.

Antenna 20-segmented; shorter than costa of forewing (ratio about 1.0:1.5); pedicel subquadrate; 3rd antennal segment with distinct but rather short projection (Fig. 3); rami of other segments rather short (Fig. 3).

Thorax: Normal; mesoscutellum nearly flattened, with rather distinct median longitudinal suture but absent in posterior ⅔ (Fig. 4). Cenchri broad, distance between cenchri shorter than the breadth of one. Wing venation of forewing as in Fig. 8. Legs: hind basitarsus shorter than following 2 segments combined (ratio about 1.0:1.3) (Fig. 5); claw as in Fig. 6.

Abdomen: Normal; pad-like area of saw-



Figs. 1–13. 1–9, *Nesodiprion nigrum,* holotype. 1, Head, dorsal view. 2, Clypeus and labrum, front view. 3, Antenna, lateral view. 4, Mesoscutellum. 5, Hind tarsus, lateral view. 6, Tarsal claw, lateral view. 7, Pad-like area of sawsheath. 8, Forewing venation. 9, 1st abdominal tergite. 10–13, *N. tsugae,* holotype. 10, Antenna, lateral view. 11, Clypeus and labrum, front view. 12, Tarsal claw, lateral view. 13, Pad-like area of sawsheath.

sheath rather circular in outline (Fig. 7); lancet with 11 annuli (Fig. 14); ventral margin straight.

Punctation: Head and thorax distinctly but sparsely and shallowly punctured (Fig. 1), interspaces practically impunctate, shining; clypeus sparsely punctured; labrum distinctly but sparsely and shallowly punctured, with interspaces practically impunctate, shining; outer side of cervical sclerites finely punctured, inner side practically impunctate, shining; basisternum practically impunctate, shining; first abdominal tergite distinctly but sparsely and shallowly punctured, interspaces and other portion practically impunctate, shining (Fig. 9); 2nd to 4th abdominal tergites finely punctured; lateral side of 6th abdominal tergite and 7th to last tergites distinctly but sparsely and shallowly punctured.

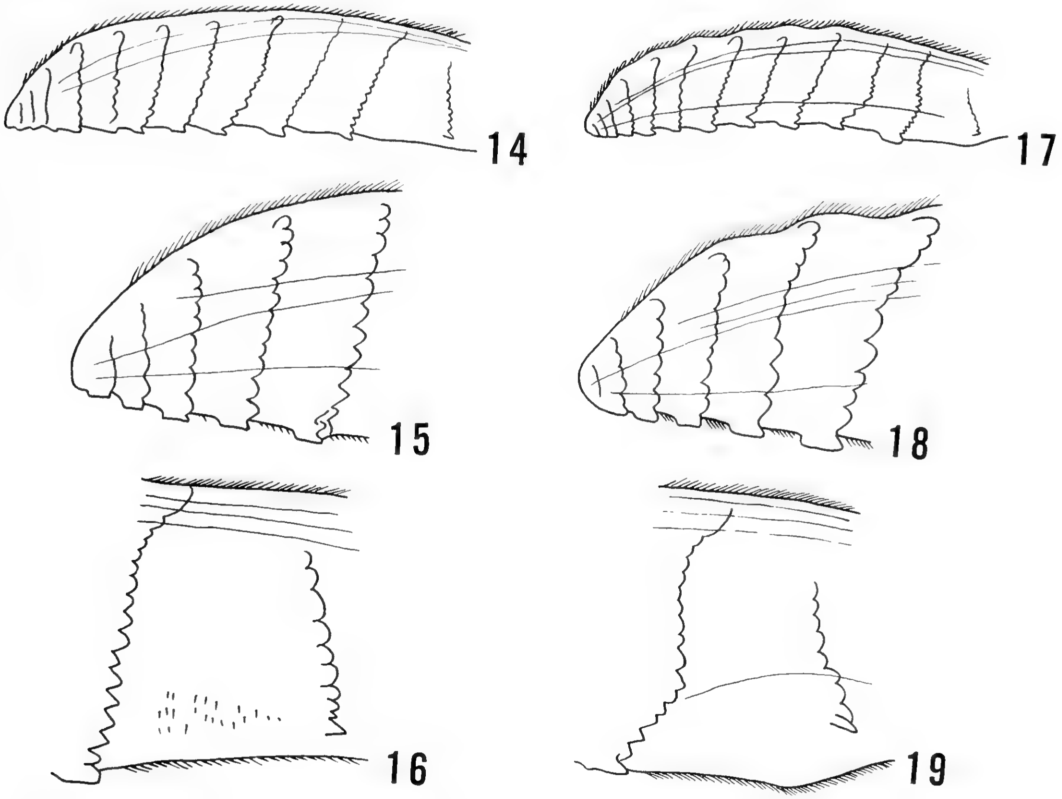
Male.—Unknown.

Distribution.—Japan (Honshu).

Food plant.—Unknown.

Holotype.—♀, 5–6.VII.1989, Tokusawa, Kamikochi, Nagano Prefecture, A. Shinohara leg., deposited in the collection of the National Science Museum (Nat. Hist.), Tokyo.

Remarks.—This new species is very closely allied to *N. shinoharai* but it is eas-



Figs. 14–19. 14–16, *Nesodiprion nigrum,* holotype. 14, Lancet. 15, Apical portion of lancet. 16, Basal 2 annuli of lancet. 17–19, *N. tsugae,* holotype. 17, Lancet. 18, Apical portion of lancet. 19, Basal 2 annuli of lancet.

ily separated from the latter by the distinct projection of the 3rd antennal segment (in *shinoharai,* the projection of the 3rd antennal segment is very small), by the circular pad-like area of the sawsheath (in *shinoharai,* the pad-like area of the sawsheath is rather ill-defined), by the dark brown tarsi (in *shinoharai,* the tarsi are dirty white), by the shallowly punctured 1st abdominal tergite (in *shinoharai,* the central portion of the 1st abdominal tergite is striate), and by the presence of punctures on the labrum (in *shinoharai,* the labrum has no punctures).

Nesodiprion tsugae Togashi, new species
(Figs. 10–13, 17–19)

Female.—Length 6 mm. Head and body black; mandible except for basal portion reddish brown; posterior margin of pronotum brown. Antenna black but basal 2 segments light brown, basal half of 3rd segment rather brown. Wings hyaline; stigma of forewing light brown but surrounding portion dark brown; other veins dark brown to black. Legs yellow with following parts dark brown to black: coxae but apical halves yellow, femora except for knees, apical ¼ of hind tibia.

Head: Postocellar area transverse (ratio between breadth and length about 1.0:0.4–0.5), convex; OOL:POL:OCL = 0.9:1.0:0.9; circumocellar furrow rather defined; interocellar furrow distinct and deep; postocellar and lateral furrows distinct; frontal area nearly flattened; median fovea distinct and rather elongate; lateral fovea distinct, circular in outline; antenno-ocular distance slightly longer than distance between antennal sockets (ratio about 1.0:0.7); supraclypeal area slightly convex; anterior margin of clypeus slightly emarginate (Fig. 10), malar space nearly as long as diameter of front ocellus.

Antenna 21-segmented; 3rd antennal segment with long projection, projection nearly as long as breadth of 3rd antennal segment (Fig. 10); pedicel rectangular (ratio between length and breadth about 1.0:1.4).

Thorax: Normal; mesoscutellum nearly flattened, without median suture; cenchrus broad, distance between them shorter than breadth of one (ratio about 1.0:1.8). Wing venation normal. Legs: hind basitarsus slightly shorter than following 2 segments combined (ratio about 1.0:1.3). Claw as in Fig. 12.

Abdomen: Normal; pad-like area of sawsheath rather circular in outline (Fig. 13); lancet with 12 annuli, ventral margin of lancet slightly concave (Fig. 17).

Punctation: Head and thorax covered with moderate, sparse, and shallow punctures; punctures on postocellar area sparser than those on vertex; lower half of inner orbits, supraclypeal area, lower half of genae, and malar space distinctly and rather reticulately punctured; clypeus and labrum moderately and rather deeply punctured; central area of 1st abdominal tergite with some shallow punctures; 2nd to last tergites practically impunctate, shining.

Male.—Unknown.

Distribution.—Japan (Honshu).

Food plant.—*Tsuga diversifolia* Masters.

Holotype.—♀, 6. V. 1985, reared from larva feeding on *Tsuga diversifolia,* Togakushi, Nagano Prefecture, M. Kojima leg., deposited in the collection of the National Science Museum (Nat. Hist.), Tokyo.

Remarks.—This new species is very closely allied to *Nesodiprion nigerrimus,* but it is easily distinguished from the latter by the light brown basal 2 segments of the antenna (in *nigerrimus,* the antenna is entirely black), by the 21-segmented antenna (in *nigerrimus,* the antenna consists of 24 segments), by the absence of the median longitudinal furrow on the mesoscutellum (in *nigerrimus,* the mesoscutellum has median longitudinal furrow), by the circular pad-like area of the sawsheath (in *nigerrimus,* the shape of the pad-like area of the sawsheath is elongate), and by the 12 annuli of the lancet (in *nigerrimus,* the lancet has 10 annuli).

Okutani (1967), Smith (1974), and Xiao et al. (1994) reported that the larvae of the genus *Nesodiprion* feed pine (*Pinus* spp.). The larvae of *N. tsugae* feed on the foliage of *Tsuga.* This is the first host record other than pine for a species of *Nesodiprion.*

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A NEW GENUS AND A NEW SPECIES OF LEPTOSCELIDINI (HETEROPTERA: COREIDAE: COREINAE) FROM BRAZIL

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Abstract.—***Leptopelios ventus*** **new genus** and **new species** from Brazil are described, illustrated, and included in the tribe Leptoscelidini (Coreidae).

Key Words: Insecta, Heteroptera, Coreidae, Leptoscelidini, new genus, new species, Brazil

The Leptoscelidini is a New World tribe with is greatest diversity in the tropics. Some species exhibit an attractive green or blue iridescence, although coloration throughout the tribe varies widely. It is abundant and diverse not only in the number and variety of taxa present, but in the abundance of many individuals of some species.

The tribe previous to this contribution contains 11 genera and 45 species (Brailovsky 1996, 1997) and can be recognized by the porrect head, produced forward between bases of antennae; the blunt tylus, slightly exceeding the juga; the femora usually armed; the tibiae simple, cylindrical, sulcate, and lacking foliaceous dilations; and the body usually medium sized and elongate (Packauskas 1994, Brailovsky 1997).

In this paper, I add one new genus and one new species collected in Brazil. A striking feature of this new genus is its strongly produced humeral angles, directed obliquely upward and ending as a long acute spine.

All measurements are given in millimeters.

Leptopelios Brailovsky, new genus

Diagnosis.—Like *Malvana* Stål, this genus has each humeral angle projected as a long and acute spine (Figs. 2–3), and the body lacks metallic iridescens. *Malvana* species are longer and more robust (19.50 mm to 23.50 mm), the tylus smooth without a tubercle, the mesopleura, metapleura and abdominal sterna III to VII each with a black discoidal spot, the abdominal spiracle closer to the anterior border of each segment, and the hind tibiae armed with one row of inner spines. In *Leptopelios,* the body is short than 16.00 mm, the tylus has a well developed tubercle, the mesopleura, metapleura and abdominal sterna III to VII lack black discoidal spots, the abdominal spiracle is closer to the posterior border, and the hind tibiae are unarmed.

Leptopelios, as well as *Phthia* Stål, has the abdominal spiracle closer to the posterior border of each segment, the scutellum longer than wide, and antennal segment I longer than the head and shorter than antennal segment II. In *Leptopelios* the head is porrect and the humeral angles strongly produced, directed upward and ending on a long and acute spine (Fig. 3). In *Phthia* the head is declivent and the humeral angles obtuse (Fig. 4) or with a small subacute projection (Fig. 5).

Generic description.—Nearly parallel sided. *Head:* longer than wide, shorter than length of pronotum, elongate, porrect, apically subacute and produced anteriorly to antenniferous tubercle; tylus blunt, slightly exceeding juga, with small subapical tubercle dorsally; juga unarmed, thickened; antenniferous tubercle moderately divergent, widely separated, unarmed; posttylar depression deep, without longitudinal ridge medially, forming single sulcus; antennal segment I longer than head, thicker than succeeding segments, and slightly curving; segments II–III cylindrical, segment IV stout fusiform; segment IV longest, III shortest, and II longer than I; preocellar pit small, nearly circular; ocellar tubercles slightly raised; eyes hemispherical and prominent; bucculae short, not extending beyond antenniferous tubercle, entire, without spine-like anterior projection; rostrum reaching posterior margin of metasternum; rostral segment I longest, III shortest, and II longer than IV; rostral segment I not extending beyond base of head; neck short.

Thorax: Pronotum wider than long, trapeziform, gradually declivent; collar wide; anterolateral border obliquely straight, with few extremely small tubercles; humeral angles strongly produced, directed obliquely upward and ending as a long, slender and acute spine; posterolateral border straight, smooth; posterior border concave across base of scutellum, smooth; disc without tubercles or spines; calli uniformly elevated, raised area between calli with two small circular pits; disc posteriorly with low median longitudinal carina; posterior margin with low transverse carina. Prosternum with deep excavation; mesosternum with shallow longitudinal groove; metasternum entire; anterior lobe of metathoracic peritreme elevated, and reniform and posterior lobe small, acute.

Legs: Fore and middle femora with one row of two subdistal ventral spines; hind femur not strongly incrassate, ventrally armed with two rows of long and robust spines, the outer row with five, and the inner row with one spine; tibiae sulcate, not angled.

Scutellum: Longer than wide, triangular, flat, with apex subacute.

Hemelytra: Macropterous, extending beyond apex of last abdominal segment; costal margin emarginate; apical margin slightly sinuate, extending beyond middle third of membrane.

Abdomen: Connexival segments higher than margin of hemelytron at rest; posterior angle of each connexival segment entire, not extending on a short spine; abdominal spiracle closer to posterior border.

Integument: Body surface dull; posterior lobe of pronotum, clavus and corium strongly punctate; acetabulae and posterior margin of prothorax, mesothorax, and metathorax scarcely punctate; scutellum transversely striate and punctate; head, calli, connexival segments, propleuron, mesopleuron and metapleuron, prosternum, mesosternum and metasternum, abdominal sterna and genital plates smooth; body surface clothed with short decumbent to semidecumbent erect setae; abdominal sterna, femora, tibiae and tarsi densely clothed with large erect bristle-like setae; antennal segments I to III with erect medium sized bristle-like setae, not densely adpressed.

Female genitalia: Abdominal sternite VII with plica and fissura; plica wide, rectangular; gonocoxae I triangular, large, in caudal view opened; paratergite VIII subtriangular, with visible spiracle; paratergite IX squarish, larger than paratergite VIII.

Male: Unknown.

Etymology.—From the Greek *leptus,* meaning thin, delicate, and *pelios* meaning black.

Type species.—*Leptopelios ventus,* **new species**.

Leptopelios ventus Brailovsky, new species

(Figs. 1, 3)

Female.—*Measurements:* Head length 2.24; width across eyes 1.96; interocular space 1.00; interocellar space 0.40; preocular distance 1.28; length antennal segments: I, 2.64; II, 2.72; III, 2.12; IV, 3.16.

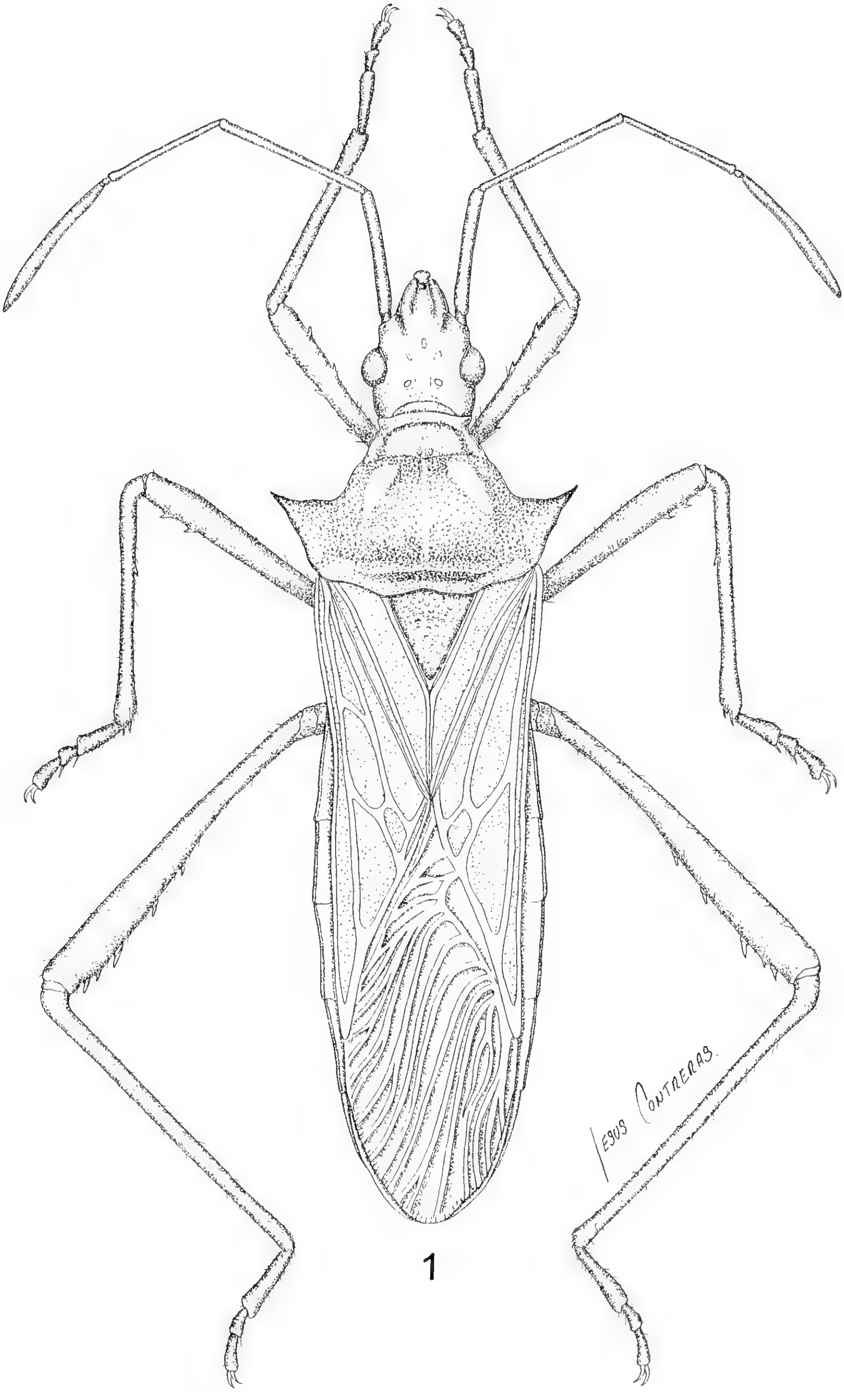
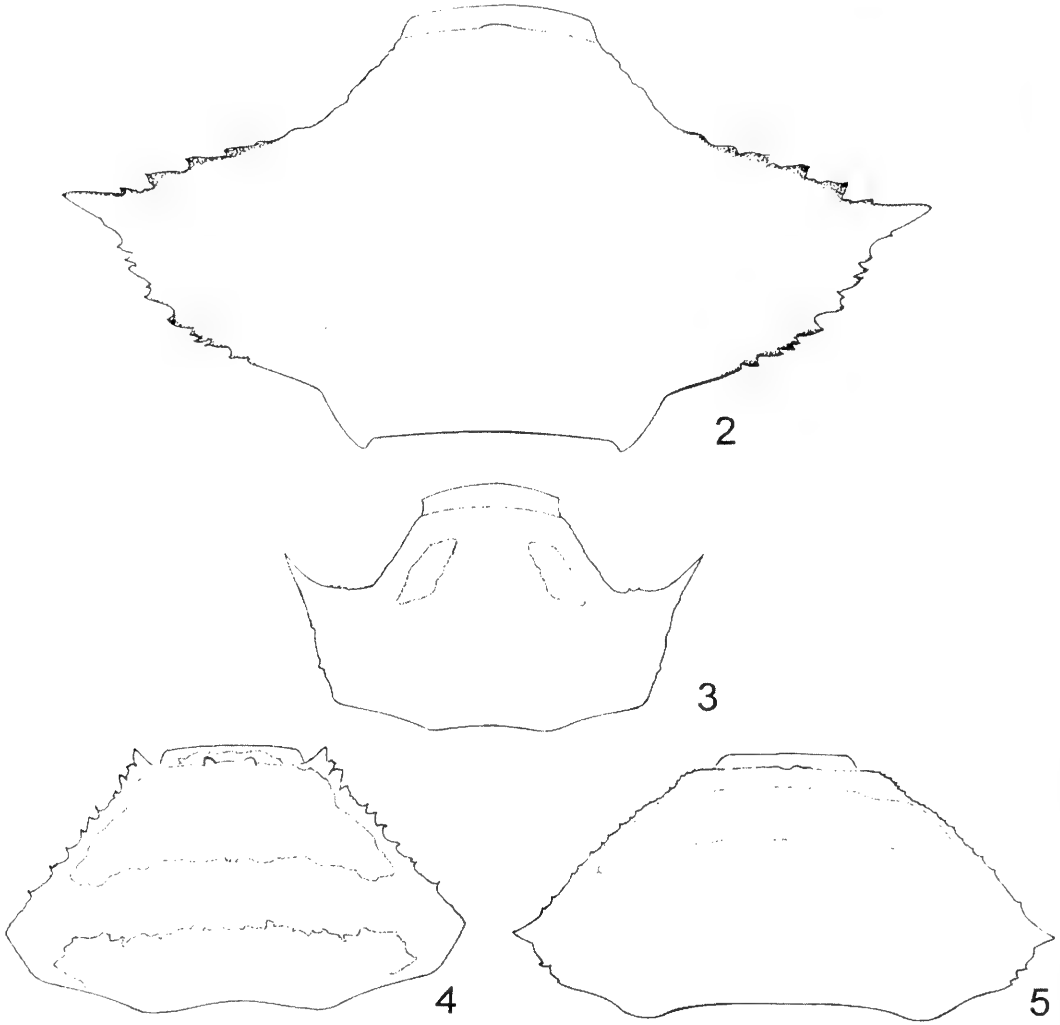


Fig. 1. Dorsal view of *Leptopelios ventus,* female.



Figs. 2–5. Pronotum. 2, *Malvana serrulata.* 3, *Leptopelios ventus.* 4, *Phthia picta.* 5, *P. decorata.*

Pronotum: Total length 2.88; width across frontal angles 1.48; width across humeral angles 4.60. Scutellar length 1.80; width 1.60; maximum width of abdomen 3.72. Total body length 15.45.

Dorsal coloration: Head dark with apex of tylus, a longitudinal stripe running between ocelli and eye, great portion of juga and antenniferous tubercle chestnut orange; antennal segment I with outer surface reddish orange, inner surface chestnut orange; segments II to IV chestnut orange with basal joint of IV chestnut brown; pronotum pale brown, with spine of humeral angle black and following areas yellow: two longitudinal and elongate stripes behind calli and running lateral to middle line and posterior third of posterolateral and posterior margin of pronotal disc; scutellum chestnut yellow with apex creamy yellow; clavus pale brown with vein dull yellow; corium pale brown with costal margin and apical angle yellow; hemelytral membrane smoky with basal angle darker; connexival segments bright orange yellow; dorsal abdominal segments III to VIII black with lateral margins bright orange yellow, and IX bright orange yellow. *Ventral coloration:* Yellow with lateral margins of mesosternum and metasternum pale brown, and scattered reddish spots on acetabulae and pleural abdominal sterna; coxae yellow with dark brown outer spot; fore trochanter yellow with dark brown spot; middle and hind trochanters yellow; fore and middle femora chestnut orange; hind femur with basal third yellow and distal third chestnut orange with spines dark brown; tibiae and tarsi chestnut orange yellow.

Male.—Unknown.

Holotype.—♀, Brazil, São Paulo, Teodoro Sampayo, November 1977, M. Alvarenga (American Museum of Natural History, New York).

Etymology.—From the latin *ventus,* meaning wind.

Distribution.—Known only from the type locality, in Brazil.

ACKNOWLEDGMENTS

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ON THE SUBGENUS *CERATOPHYLLUS* (*CELEOPHILUS* SMIT 1983), WITH A REDESCRIPTION OF ITS TWO SPECIES (SIPHONAPTERA: CERATOPHYLLIDAE: CERATOPHYLLINAE)

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Abstract.—The ceratophylline subgenus *Celeophilus* is redefined based upon collections of *Ceratophyllus* (*Celeophilus*) *adustus* Jordan 1932 and *C.* (*C.*) *zhovtyii* Yemel'yanova and Goncharov 1966, collected from woodpecker nests in Alaska. The two species are redescribed, the diagnostic characters for both are illustrated, and their host preferences and distribution are discussed.

Key Words: *Ceratophyllus,* (*Celeophilus*), redescription, host preferences, geographic distribution

In his detailed study of the family Ceratophyllidae, Smit (1983) attempted to bring more order to the genus *Ceratophyllus* Curtis 1832 by dividing it into six subgenera. These included the nominate subgenus and *Amonopsyllus* Wagner 1938, *Celeophilus* Smit 1983, *Emmareus* Smit 1983, *Monopsyllus* Kolenati 1857, and *Rosickyiana* Smit 1972. In North America, *Amonopsyllus, Monopsyllus* and *Rosickyiana* are each represented by single species. The first two are mainly parasites of squirrels, and the latter is associated with mustelids in the Arctic. The remaining three subgenera contain species that parasitize birds, and these are represented in North America by 22 species (*Ceratophyllus* [17], *Celeophilus* [2] and *Emmareus* [3]). While pulicologists may not agree on the status of some of these taxa, those belonging to *Ceratophyllus* and *Emmareus* are mostly well known and relatively easily identified, at least in the male sex. This has not been the case with the two species assigned to *Celeophilus.*

In addition to the holotype female of *C.* (*C.*) *adustus,* Smit examined one male and three females from the Haas Collection. It is not clear whether he was able to examine specimens of *C.* (*C.*) *zhovtyii,* but we suspect not. In any case, beyond the illustrations in the original descriptions and Smit's (1983) figure 13 of the occipital setal row and figure 178 of the spermatheca and associated ducts, both of *C.* (*C.*) *adustus,* no other illustrations exist. While the illustrations of the male clasper and st IX of *C.* (*C.*) *zhovtyii* seem accurate, the drawing of the apex of the male st VIII is not complete and does not show one of the diagnostic characters of the species.

Finally, since the male of *C.* (*C.*) *adustus* has never been described, and the description of *C.* (*C.*) *zhovtyii* was published in an obscure journal series generally unavailable to western workers, it seems appropriate to recharacterize the subgenus and redescribe the two species. Following is a review of the subgenus.

Names of host birds are taken from the A.O.U. Checklist (1998) and Sibley and Monroe (1990).

Subgenus *Celeophilus* Smit 1983

Ceratophyllus Curtis 1832—*Celeophilus* Smit 1983: 14 (subgen. n.).

Ceratophyllus (*Celeophilus*): Haddow et al. 1983: 70; Smit 1983: 30; Lewis 1990, 44; 1993, 65.

Diagnostic characters.—*Head:* Frontal tubercle extremely small. Eye well developed, slightly oval, well pigmented. Frontal setal row of 0 to 5 setae, usually 3 in males, 2 in females. Ocular setal row of 3 setae. Postocular seta present, with about half its length projecting beyond genal lobe. Postantennal region of head usually with 1 long seta above row of minute setulae extending along dorsal margin of antennal fossa. Occipital setal row widely interrupted above ventralmost seta. Labial palpi extending almost to apex of forecoxae.

Thorax: Pronotal ctenidium usually of 28 to 30 spines. Mesepimeron usually with a few small setae. Metepimeron with 4 to 8 slender bristles, usually 5 or 6, arranged in 3 irregular rows. Caudal margin of metanotum usually without spinelets or when present, they are minute.

Legs: Forecoxa sparsely setose. Sulcus of midcoxa with a short dorsal interruption. Forefemur with small setae on its outer surface. Striation of mid- and hindfemora and tibiae of medium density. Chaetotaxy of hindtibia reduced. Figs. 15 and 16 show hindfemora of *Ceratophyllus* (*Ceratophyllus*) *hirundinis* (Curtis 1826) and *Ceratophyllus* (*Emmareus*) *columbae* (Gervais 1844) the type species for their respective subgenera. First and third pairs of lateral plantar setae slightly displaced on to plantar surface.

Abdomen: Abdominal tergites I–IV usually with 1 or 2 marginal spinelets per side. Outer and inner of 3 antesensilial setae minute in males, somewhat longer and slightly subequal in females. Male: Tergum VIII lacking a spiculose area along its dorsocephalic margin. Sternite VIII long and narrow, lacking any stout setae but with a few slender apical and preapical bristles and a small subapical fimbriated vexillum. Distal arm of st IX slender and curved. Fixed process of clasper rather short and with a triangular apex. Two acetabular setae arising on or above acetabular projection. Movable process long and narrow, lacking any stout or spiniform setae. Apex of penis plate bearing a long tendril that is coiled >360°. Apophysis of st VIII and penis rods describing at least 1 complete convolution. Female: Genital ducts weakly sclerotized, ductus bursae and ductus obturatus rather short. Basal portion of spermathecal duct wrinkled and somewhat enlarged. Bulga large, cylindrical, with an apical orifice. Hilla rather small, with a slight terminal papilla. Anal stylet normally with a dorsal as well as a ventrolateral seta.

Remarks.—This is a small subgenus with two species, both of which are Holarctic in distribution where they parasitize woodpeckers.

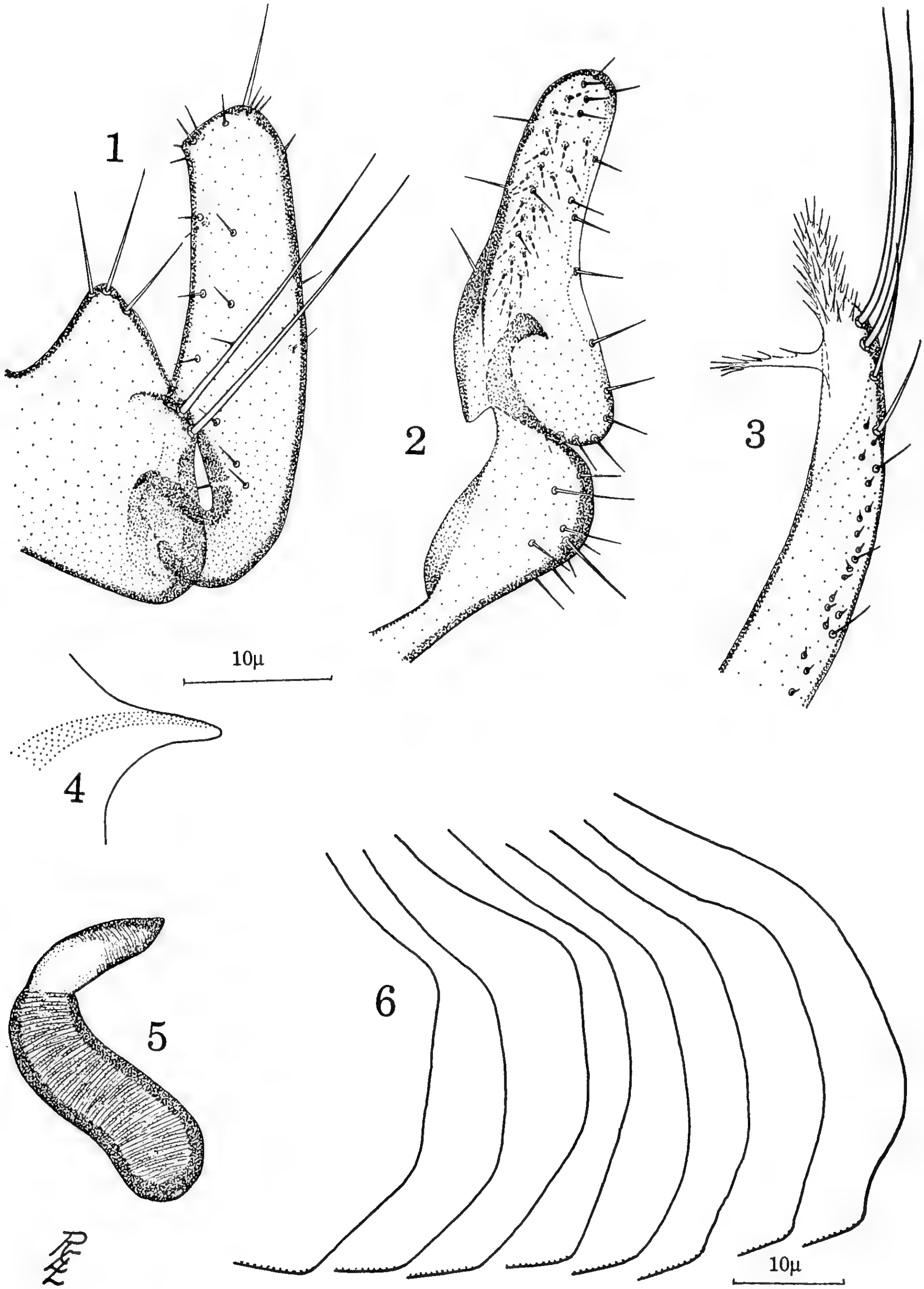
KEY TO SPECIES OF *CERATOPHYLLUS* (*CELEOPHILUS*)

1. Male movable process about 3.5× as long as wide at its widest point (Fig. 1); apex of st VIII terminated by a conical, fimbriated projection and subtended by a small, fimbriated vexillum (Fig. 3); apex of distal arm of st IX broadened basally, its apical half with parallel margins (Fig. 2); crochet acuminate and slightly sclerotized (Fig. 4); female st VII somewhat angled dorsally, its ventral margin usually smoothly rounded and lacking a ventral sinus (Fig. 6); spermathecal hilla tapering to a point (Fig. 5) . . . . *adustus*

– Male movable process >4× as long as wide at its widest point (Fig. 8); apex of st VIII terminated by a bulbous, fimbriated, subapical vexillum (Fig. 9); apex of distal arm of st IX not much expanded basally, its apical margins convergent (Fig. 8); crochet triangular with deflected apex (Fig. 10); female st VII somewhat more rounded dorsally and with at least a shallow ventral sinus (Fig. 12); spermathecal hilla with a trace of an apical papilla (Fig. 11) . . . . *zhovtyii*

Ceratophyllus (*Celeophilus*) *adustus* Jordan 1932
(Figs. 1–6, 14, 18, 21)

Ceratophyllus adustus Jordan 1932: 253, figs. 10–11. Canada, British Columbia,



Figs. 1–6. *Ceratophyllus* (*Celeophilus*) *adustus*. 1, Male clasper. 2, Male st IX. 3, Male st VIII. 4, Male aedeagal crochet. 5, Female spermatheca. 6, Female st VII variation.

Atlin, 59°31′N 133°41′W, from *Erethizon epixanthum* [= *dorsatum*], 3.IX.1931, H. S. Swarth leg. Holotype ♀, BMNH.

Ceratophyllus adustus: Holland 1949: 146; Lewis 1975: 660; Smit and Wright 1978: 20; Haas et al. 1980: 105; Haas 1983: 141; Haas and Wilson 1984: 127.

Ceratophyllus (*Ceratophyllus*) *adustus*: Holland 1985: 267.

Ceratophyllus (*Celeophilus*) *adustus*: Haddow et al. 1983: 70; Smit 1983: 30; Lewis 1990: 44.

Description.—*Head:* Frontal tubercle present but small and inconspicuous. Setae in frontal row 3 to 5 (~60% with 3) in male, 1 or 2 (90% with 2) in female. Setae in ocular row 3 in both sexes, rarely 1 or 4. Eye well developed in both sexes. Postocular seta present, about half of it extending beyond genal lobe. Most of long setae arising on antennal pedicel of female extending well beyond apex of clavus. Minute setulae extending along dorsal margin of antennal fossa 9 to 12 (50% with 12) in male, 9 to 15 (mostly 12 to 15) in female. Preoccipital setae 1 or 2 in both sexes (60% with 2 in male, 80% with 2 in female). When 2 present, they form a horizontal row above and parallel with antennal fossa. Setae in occipital row 4 to 6 per side (60% with 4) in male, 4 or 5 (50% with 4) in female. In both sexes, lowermost seta separated from other members of row by a wide space. Labial palpi extending almost to apex of forecoxae in both sexes. *Thorax:* Spines in pronotal ctenidium, 26 to 30 (70% with 27 to 29) in male, 27 to 30 (50% with 28 or 29) in female. Pseudosetae under mesonotal collar 8 to 10 in both sexes. Usually with 1 seta on mesepisternum in both sexes, occasionally with 2 or even 3. Mesepimeron with 1 or 2 setae (55% with 2, 45% with 1) in both sexes. Metanotal spinelets, when present, minute. Male with ~30% with 1/1 and another 30% with 0/1, while 80% of females were 0/0 and 20% were 0/1. Lateral metanotal setae present in only ~5% of both sexes. Usually only 1 seta on metepisternum in both sexes. Setae on metepimeron variable, 5 to 9 in male, 7 to 9 in female and not arranged in well defined rows. *Legs:* Forefemur with 4 to 8 fine setae on outer surface. Foretibia with 5 notches in caudal margin, including apical notch, bearing stout setae. With a submarginal row of 4 to 6 setae in inner surface in both sexes. Foretarsal segments I–III approximately equal in length, segment IV ~⅘ length of each of preceding 3. Segment V with 5 pairs of lateral plantar bristles, pairs I and III slightly shifted on to plantar surface. Midfemur with a submarginal row of 4 to 6 setae on inner surface. Midtibia with 6 notches in its caudal margin bearing stout setae, a submarginal row of ~6 to 8 setae on outer surface and 6 to 8 more on inner surface. Midtarsal segments I and II approximately equal in length, segment III ~½ length of each of preceding segments, segment IV ~¾ length of III. Segment V as with segment V of foretarsus. Hindfemur with a submarginal row of 4 or 5 fine setae on inner surface. Hindtibia (Fig. 14) with 5 notches in its caudal margin bearing strong setae, a submarginal row of ~8 setae on outer surface and ~6 on the inner surface. Hindtarsal segment II ~⅔ length of segment I, segment III ~½ length of segment II, segment IV slightly >½ length of segment III, segment V as with other legs. *Abdomen:* Tergal spinelets in male: t I (60% with 1/1, 40% with 3 or 4); t II (30% with 1/1, 70% with 3 or 4); t III (40% with 1/1, 60% with 3 or 4); t IV (90% with 1/1, 10% with 1/2); t V (20% with 0/1, 80% with 0/0). Tergal spinelets in female: t I (70% with 1/1, 30% with 3 or 4); t II (60% with 1/1, 40% with 3 or 4); t III (90% with 1/1, 10% with 0/1); t IV (20% with 0/0, 60% with 0/1, 20% with 1/1); t V (100% with 0/0). Median bristle of male antepygidial setae well developed, bordered dorsally and ventrally by single minute setulae. Median bristle of female antepygidial setae well developed, bordered dorsally and ventrally by single setae about ⅕ length of median. Remaining abdominal characters sexual in nature.

Male: Wagner's organ present but small and barely visible in some males. Penis rods coiled >360° but not as long as in *C.* (*C.*) *zhovtyii.* Apex of penis plate with a pronounced tendril that is coiled ~360°. Spiculose area on t VIII absent. Anal tergum blunt, shorter than conical anal sternite. Movable process of clasper (Fig. 1) ~3.5× as long as wide at its widest point, its cephalic incrassation arising ~⅔ down from apex. Dorsal apex of fixed process broadly triangular. Apex of st VIII (Fig. 3) terminating in a fimbriated, cone-shaped, membranous projection subtended by a few long setae and a fimbriated mesal vexillum. Distal lobe of apical arm of st IX (Fig. 2) expanded basally, cephalic and caudal margins of apical half roughly parallel. Crochet (Fig. 4) narrowly pointed and lightly sclerotized. Female: (Figs. 5–6, 18, 23). Spermatheca large and well sclerotized, its duct arising apically, its hilla with a slight apical projection. Fig. 6 illustrates variation in caudal margin of st VII. Anal stylet as in Fig. 18. Ventral anal lobe similar to that of *C.* (*C.*) *zhovtyii* but with a slightly more squared and angular apex. In absence of accompanying males, females difficult to separate from many members of subgenus *Ceratophyllus.*

Remarks.—This is the type species for the subgenus. As is frequently the case with rare species, much of the literature about it refers to previous references without adding materially to our knowledge. Originally described from a single female from an unusual host for a member of this genus, additional material was not published until Haas et al. (1980) reported 1 female and Haas and Wilson (1984) reported 66 males and 102 females. These collections came from various localities in Alaska, and until now the male has not been illustrated. However, it is now beyond doubt that this species is not a parasite of porcupines, as originally thought, but rather is a woodpecker flea infesting the nests of the flicker, *Colaptes auratus* Linnaeus 1758, the three-toed woodpecker, *Picoides tridactylus* (Linnaeus 1758) and probably other members of this genus in the extreme northwestern part of North America. Other members of the genus or their nests have yet to be reported as hosts.

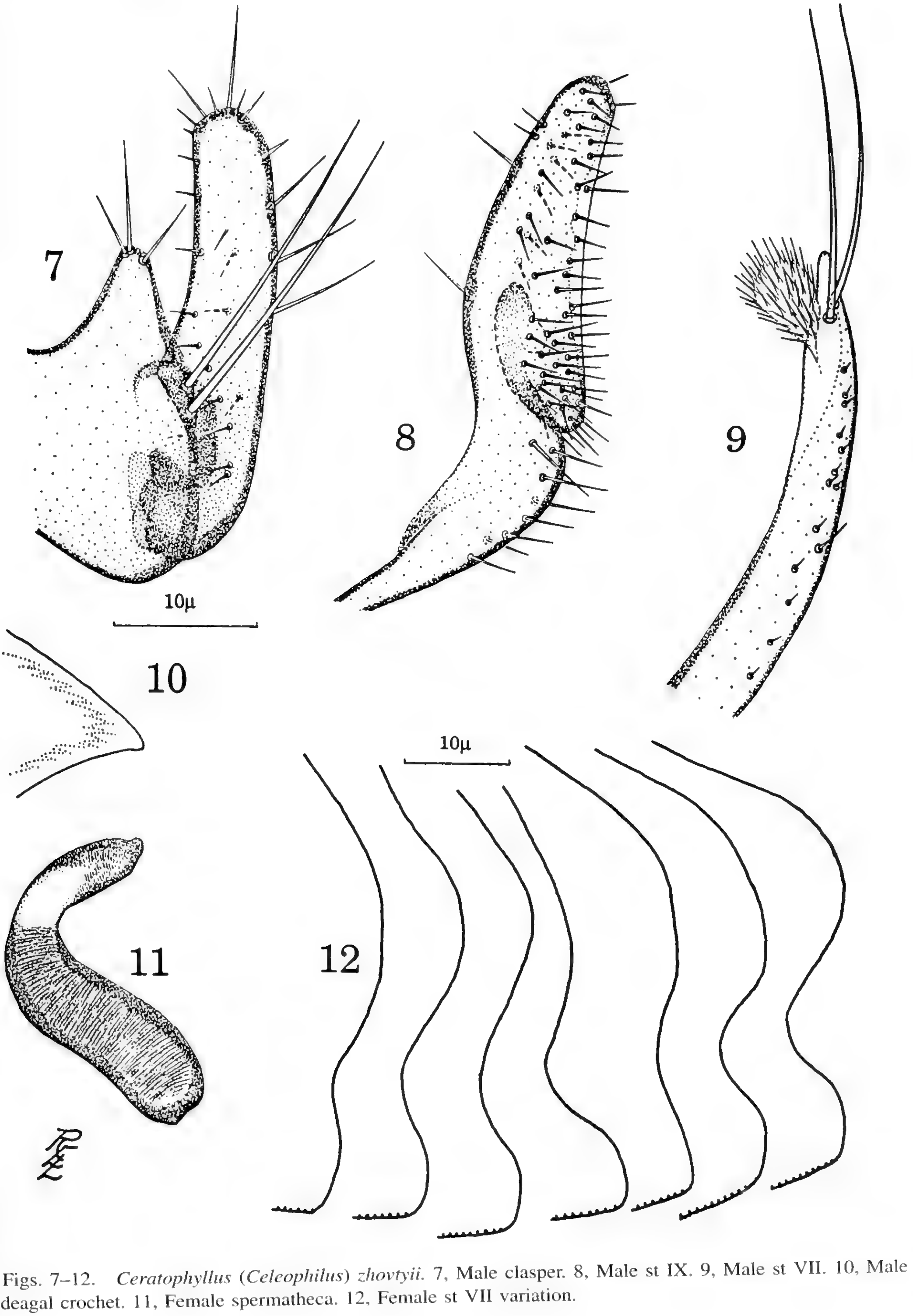
In his treatment of morphological anomalies in fleas, Haas (1983) described the presence of a vestigial second spermatheca in five of the 103 females he examined. While such anomalies are uncommon in ceratophyllid adults, they are not unknown, and over 25% of female *Nosopsyllus medus* Jordan 1938, from Iraq in the Lewis Collection have similar vestigial second spermathecae.

Distribution.—Collection records as cited in Haas and Wilson (1984) include the following localities: 4.8 km NE Cantwell; 22.5 km SW Chistochina; mile 10 Edgerton Highway; 3 km SE Eklutna Lake; 53 km W Glennallen; mile 119 Glenn Highway; 4.5 km NE Palmer; Knik River Road nr. Fox Lake; N shore Skilak Lake; 7.2 km NW Sterling; 2.9 km SE Talkeetna; 4.6 km E Wasilla and Lakeview Road nr. Kings Lake. All came from nests of *Colaptes auratus* or *Picoides* spp. in dead stubs of birch, spruce and poplar.

Host associations.—Only the flicker and the three-toed woodpecker have been identified with certainty as hosts. However, as Haas and Wilson (1984) point out, the downy (*Picoides pubescens* Linnaeus 1766), the hairy (*Picoides villosus* Linnaeus 1766) and the black-backed (*Picoides arcticus* (Swainson 1832)) woodpeckers also occur in the area where these fleas were collected. Of these, the downy and the hairy were considered to be the most likely preferred hosts, since they nest in dead tree stubs of birch, poplar and spruce similar to the recorded hosts while the latter species of woodpecker prefers to nest in living trees.

Ceratophyllus (*Celeophilus*) *zhovtyii* Yemel'yanova and Goncharov 1966 (Figs. 7–12, 13, 17, 21)

Ceratophyllus zhovtyii Yemel'yanova & Goncharov 1966: 309, figs. 1–4. USSR,

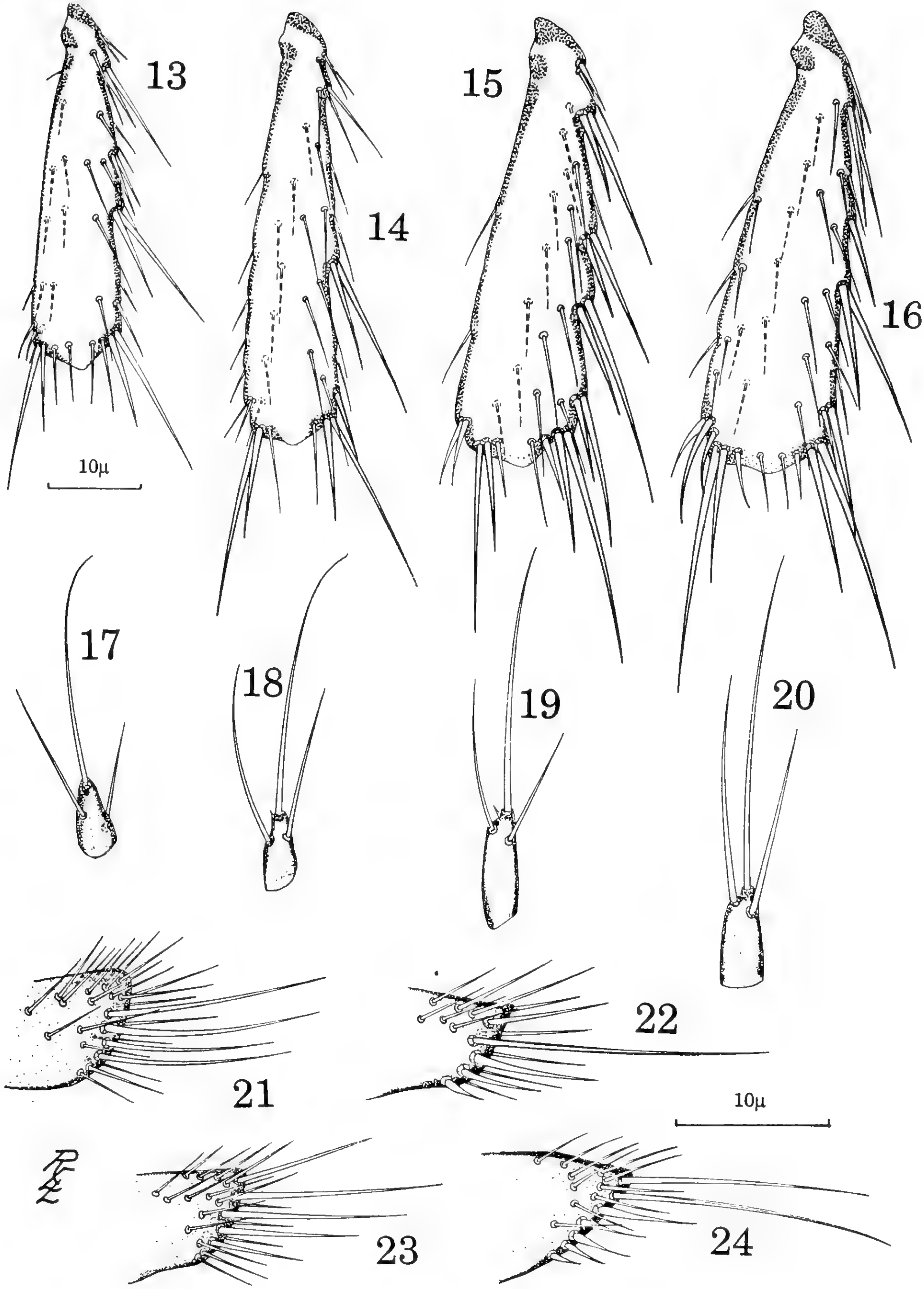


Figs. 7–12. *Ceratophyllus* (*Celeophilus*) *zhovtyii*. 7, Male clasper. 8, Male st IX. 9, Male st VII. 10, Male aedeagal crochet. 11, Female spermatheca. 12, Female st VII variation.

Irkutskaya Oblast, Cheremkhovsk Rayon, environs of Sakhir, ~53°08′N 103°01′E, from *Glaucidium passerinum,* 21.X.1962, V. D. Sonin leg. Holotype ♂, allotype ♀, Irkutsk Antiplague Institute, Russia.

Ceratophyllus zhovtyi: Lewis 1975: 660; Smit and Wright 1978: 41; Haddow et al. 1983: 70; Smit 1983: 14, 70; Haas and Wilson 1984: 127; Lewis 1990: 44; 1993: 65.

Description.—*Head:* Frontal tubercle present but small and inconspicuous. Setae per side in frontal row 1 or 2 (70% with 1) in male, 0 to 3 in female (15% with 0, 35% with 1, 50% with 2). Setae on ocular row 3 or 4 (92% with 3) in male, 3 (100%) in female. Eye well developed and pigmented in both sexes. Postocular seta present but < half of it extends beyond genal lobe. Most of long setae arising on antennal pedicel of female extend beyond apex of clavus. Minute setulae extending along dorsal margin of antennal fossa 10 to 18 in both sexes. In cases where number is low in female, row usually interrupted in middle. Preoccipital setae 1 or 2 (65% with 1, 35% with 2,) in male, 1 (100%) in female. When 2 present they form a row above and parallel with dorsal margin of antennal fossa. Setae per side in occipital row 4 or 5 (85% with 4, 15 % with 5) in male, 5 (100%) in female. Labial palpi extending ~⅘ length of forecoxae in both sexes. *Thorax:* Spines in pronotal comb 26 to 30 (50% with 30, 14% with 29, 21% with 28, 15% with 26 or 27) in male, 29 or 30 in female. Pseudosetae under mesonotal collar 7 to 12 in male, 10 to 12 in female. Usually 1 seta on mesepisternum, although 4 males lack any, another male has 2, and 2 other males have 4 minute setulae in this position, in female 0 to 2 (73% with 1, 13% with 2). Mesepimeron with 1 to 3 setae in both sexes (54% with 1, 38% with 2). With respect to spinelets on metanotal margin, all material was dead when collected and most specimens are damaged or contracted to extent that metanotal margin cannot be properly examined. However, based on *C.* (*C.*) *adustus* material at least a few probably with minute spinelets in this position. Lateral metanotal setae absent from 64% of males and 73% of females. Setae on metepisternum 1 or 2 in both sexes. Setae on metepimeron in male 3 to 5. In female number varies from side to side and ranges from 3 to 9. *Legs:* Forefemur with 6 to 9 fine setae on outer surface. Foretibia with 6 notches, including apical notch, in caudal margin bearing stout setae, and a submarginal row of 5 or 6 setae on outer surface in both sexes. Foretarsal segments I and II of equal length in both sexes, segment III ⅚ length in II in male, ⅝ length of II in female, segment IV ⅘ length of III in male, equal to III in female. Segment V with 5 pairs of lateral plantar bristles, pairs I and III slightly shifted on to plantar surface. Midfemur with a submarginal row of 3 to 6 setae on inner surface. Midtibia with 6 notches in caudal margin bearing stout setae, a submarginal row of 5 or 6 setae on outer surface and 6 to 8 more scattered over its inner surface. Midtarsal segments I and II almost equal in length in male, segment I ~⅕ longer than segment II in female, segment III ~⅓ shorter than segment II in both sexes, and segment IV ~¾ length of segment III in both sexes. Segment V as in foretarsus. Hindfemur with a submarginal row of fine setae on inner surface. Hindtibia (Fig. 13) with 5 notches in its caudal margin bearing strong setae in both sexes, plus a submarginal row of 6 to 8 setae on outer surface and 7 or 8 on inner surface. Hindtarsal segment III ~⅔ length of segment I in both sexes. In male hindtarsal segment II ~¾ length of III, and IV ~⅔ length of III. However, tarsomeres complete in only 3 legs in sample so analysis of variation limited. In female segments III and IV each ⅔ length of preceding segment. Hindtarsal segment V as in fore- and midtarsi. *Abdomen:* Tergal spinelets in male: t I (83% with 2/2, 17% with 1/2); t II (100% with 2/2); t III (83% with 2/2, 17% with 1/2); t IV (50% with 2/2, 17% with 1/2, 33% with 1/1). Due to condition



Figs. 13–24. Hindtibiae of males. 13, *Ceratophyllus* (*Celeophilus*) *zhovtyii*. 14, *C.* (*C.*) *adustus*. 15, *C.* (*Ceratophyllus*) *hirundinis*. 16, *C.* (*Emmareus*) *columbae* (Gervais 1844). 17–20, Female anal stylets. 17, *C.* (*C.*) *zhovtyii*. 18, *C.* (*C.*) *adustus*. 19, *C.* (*Emmareus*) *columbae*. 20, *C.* (*Ceratophyllus*) *hirundinis*. 21–24, Female ventral anal lobes. 21. *C.* (*C.*) *zhovtyii*. 22, *C.* (*C.*) *adustus*. 23, *C.* (*Emmareus*) *columbae*. 24, *C.* (*Ceratophyllus*) *hirundinis*.

of females only 5 of 12 specimens yielded an accurate count for tergal spinelets: t I 1/2 (1), 1/1 (1), 2/2 (3); t II 2/2 (5); t III 1/2 (3), 2/2 (2) and t IV 1/1 (5). Median bristle of male antepygidial setae well developed, bordered dorsally and ventrally by single, minute setulae. Median bristle of female antepygidial setae well developed, bordered dorsally and ventrally by single setae that are ~⅕ length of median. Remaining abdominal characters sexual in nature. *Male:* Wagner's organ present and more conspicuous than in *C.* (*C.*) *adustus.* Penis rods coiled approximately twice 360°, noticeably longer than in *C.* (*C.*) *adustus.* Apex of penis plate with a long tendril that is coiled ~360°. Spiculose area on t VIII absent. Anal tergum somewhat less blunt than in *C.* (*C.*) a*dustus,* shorter than conical anal sternite. Movable process of clasper (Fig. 7) over 4× as long as wide at its widest point, incrassation in its cephalic margin about halfway down from apex. Dorsal apex of fixed process more pointed than in *C.* (*C.*) *adustus.* Apex of st VIII (Fig. 9) terminating in a subapical, oval, fimbriated vexillum and 2 long setae. Distal lobe of apical arm of st IX (Fig. 8) not as expanded as in *C.* (*C.*) *adustus,* its cephalic and caudal margins converging to a rounded apex. Crochet (Fig. 10) triangular and slightly sclerotized. *Female:* (Figs. 11–12, 17, 21). Spermatheca large, well sclerotized, its duct arising apically, its hilla with a distinct apical papilla. Fig. 12 illustrates variation in caudal margin of st VII. Anal stylet as shown in Fig. 17. Ventral anal lobe similar to that of *C.* (*C.*) *adustus* but more rounded caudally and with a more rounded apex. As in case of female of *C.* (*C.*) *adustus,* in absence of accompanying males, females difficult to identify with any degree of certainty.

Remarks.—The Haas and Wilson (1984) reference to this species is the only mention of its occurrence in the Western Hemisphere. The series of 28 specimens came from 3 woodpecker nests in 3 different localities in Alaska. Two collections came from flicker nests and the third from the nest of a species of *Picoides.* Most of the specimens were dead when collected and are missing appendages and setae. They were taken in association with specimens of *C. adustus* and *C. rauschi* Holland 1960.

Distribution.—This species was described originally from a small series collected on the Eurasian pygymy owl (*Glaucidium passerinum* (Linnaeus 1758)) and a woodpecker, presumed to be the great spotted woodpecker (*Dendrocopos major* (Linnaeus 1758)) in the Irkutsk region of the Russia. Paratypes included 2 additional females from the type host and locality, 3 females from the Taishetskogo region of Irkutsk Oblast and 1 male and 3 females from the vicinity of Khudyakovo, 8 km NE of Irkutsk. The latter all came from woodpeckers. As with many other bird fleas, its apparent rarity is probably due to the infrequency with which bird nests, especially those of woodpeckers, are examined for fleas. So far this flea has only been collected in Alaska but it might be expected to occur in the northern parts of some of the Canadian provinces as well. Alaskan localities include mile 222.5 Glenn Highway; mile 151.3 Steese Highway and mile 31 Nabesna Road.

Host associations.—In addition to the pygmy owl and the great spotted woodpecker, this species has also been associated with the three-toed woodpecker (*Picoides tridactylus*) and the black woodpecker (*Dryocopus martius* (Linnaeus 1758)) according to Haddow et al. (1983: 70).

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IMMATURE STAGES AND BIOLOGY OF *TAYGETIS* HÜBNER (LEPIDOPTERA: NYMPHALIDAE)

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Abstract.—Although euptychiine butterflies are among the most diverse nymphalid group in the lowland neotropics, there is almost no information on their biology or classification. Chaetotaxy and descriptions of euptychiine immatures are presented for the first time. Immature stages of five *Taygetis* species, *T. mermeria* (Cramer), *T. cleopatra* C. Felder and R. Felder, *T. laches* (Fabricius), *T. thamyra* (Cramer), and *T. virgilia* (Cramer) are described, and head capsules of each stage are illustrated. Field observations of the adults and larvae are also presented, along with information on host use and habitat associations. All species except one were reared from hosts within Poaceae, *T. mermeria* and *T. virgilia* from *Guadua angustifolia* Kunth, *T. cleopatra* from *Olyra latifolia* Aublet and *Pariana* sp., and *T. laches* from *Andropogon* sp. *Taygetis thamyra* was reared from *Ischnosiphon* sp. (Marantaceae). Important characters for phylogenetic analysis are noted and the utility of larval characters in phylogenetic reconstruction is explored.

Key Words: Euptychiina, Satyrinae, Poaceae, bamboo, systematics, larvae

Euptychiine butterflies (Nymphalidae: Satyrinae: Euptychiina) are a large component of the lowland butterfly community, but their biology and early stages are mostly unknown and documented in only a handful of publications (Müller 1886, Weymer 1910, Singer et al. 1983, Young 1984). There are no published accounts of euptychiine first instar chaetotaxy and surprisingly, only one publication on any satyrine (Garcia-Barros 1987).

There is little information available on *Taygetis* species. Adults are fruit-feeders and are readily attracted to rotting fruit in baited traps or on the forest floor. Most species are not active during the day and usually are observed only when flushed from the forest floor. Once disturbed, these normally sedentary butterflies are agile, erratic fliers and often escape the net. In contrast, some species have been found to be active at dusk (DeVries 1987, Young 1972). *Taygetis* species are generally larger than other euptychiines and are dark brown with few markings except ocelli on the ventral wing surface. They occur from Mexico to northern Argentina and Paraguay, with the greatest diversity in the Amazon basin. There are 28 described species and at least three undescribed species (L. Miller, G. Lamas personal communication). For the immature stages, there are two published descriptions. Müller (1886) described a *Taygetis ypthima* (Hübner) larva, reared on bamboo. Young (1984) published descriptions of a *Taygetis* species [as *Taygetis andromeda* (Cramer)] reared in Costa Rica on grass. The taxonomic status of the form referred to as *T. andromeda* by Young is uncertain, as explained later in this paper.

I describe the chaetotaxy, immature stages, and natural history observations for five

Taygetis species. Host plants, noted for each species, were all Poaceae, mainly bamboos.

MATERIALS AND METHODS

Larvae and eggs were located in the field by searching known host plants and by observing female oviposition. Specimens were reared individually in plastic containers, and fresh host plant was added every two to three days. Notes on appearance, behavior, and development times were taken for all stages, and head capsules were preserved. When there were sufficient numbers of larvae, some were preserved in 95% ethanol after being immersed in boiling water for several seconds. When possible, photographs were taken of the larvae and pupae. Much of the work was conducted in Ecuador at Jatun Sacha Biological Station, Napo Province, during 1990 to 1993. Vouchers of larvae and adults are deposited in the National Museum of Natural History, Smithsonian Institution, Washington DC. Some comments on adult natural history, in particular observations on habitat associations, are taken from data gathered during a year long trapping study conducted at Jatun Sacha (see DeVries et al. 1997 for methodology).

Due to the absence of information on euptychiine immature stages, a basic morphological description of each *Taygetis* instar precedes the individual species descriptions. This will alleviate repetition in the species descriptions and avoid problems in establishing setal homologies with other satyrines, as Garcia-Barros (1987) relied on differing systems for naming primary setae.

Setal names for the head capsule follow Heinrich (1916), with modifications as incorporated by Stehr (1987). Body chaetotaxy follows Hinton (1946). Head capsule width is measured by the distance between the third stemmata. Diagnostic characters for individual species are given for mature instars only.

RESULTS

Euptychiine Morphology

Diagnosis.—*First instar:* Lobed setae (P1, P2, P3, L1, and A3) distinctly flattened and fanned in most *Taygetis* species, but see *Taygetis virgilia* (Cramer); A9 with two subventral setae; large head capsule.

Second and third instars: P1 and P2 equal in size, giving head horns two-pronged appearance; caudal filaments large, fleshy, and held together in a point.

Fourth instar: P1 and P2 equal in size, giving head horns two-pronged appearance; caudal filaments large, held together in a point for most species, but see *Taygetis mermeria* (Cramer).

Description.—*Egg:* Shiny, white, round, and smooth.

First instar: Head capsule with enlarged chalazae, referred to as lobes, on epicranium and laterally (Fig. 1); head horns on epicranium with fused chalazae of primary setae P1 and P2, forming two-pronged appearance; three lateral setae with enlarged chalazae, an unnamed seta on posteriodorsal area, a lateral seta, L1, and an anterior seta, A3 (the unnamed seta is labeled P3, following Heinrich (1916), who named setae by location on the head capsule); setae associated with lobed bases (P1, P2, P3, L1, and A3, referred to as lobed setae) curl anteriorly and possess oval setal insertions; stemmata setae S1, S2, and S3 also with enlarged bases, but never as large as previously mentioned setae; AF1 and AF2 located near frontal suture and not enlarged; stemmata 2, 3, 4 and 5 slightly raised; stemma 3 larger than other stemmata; on posteriodorsal and lateral area small ridges in the integument form a webbing pattern, not symmetrical on either side of the head capsule, absent on frontal area and lobes. Body shiny green; four lateral longitudinal lines, faint and white to yellow; prothoracic shield lightly sclerotized and small; dorsal setae D1 and D2 shorter on T1 than XD1 and XD2 (Fig. 2); one lateral seta on each thoracic segment; SD1 long and filamentous on T1; thoracic legs with secondary setae; D1 and D2 on abdominal segments equal in length and progressively larger from A1 to A10; on abdominal segments SD2 present only on A10 and two lateral setae present on each segment except A9 (Figs. 2–3); spiracle on A8 greatly enlarged and raised; A9 with two subventral setae; SD1 seta on A9 long and filamentous, as on T1; A10 with anal shield lightly sclerotized and bearing two caudal filaments, small and usually colorless.

Second and third instars: Lobed setae (P1, P2, P3, L1, and A3) flattened, narrowing sharply to a point, and reduced in relative size from first instar but larger than surrounding secondary setae; secondary setae on head capsule larger and more numerous around stemmata and mouthparts; some secondary setae large, with setal bases approximately equal in size to S1 and S3, located frontally on head horns between P1 and P2 (one on each headhorn), and basally on head capsule and head horns; shallow depressions or pits on epicranial and lateral areas of head capsule. Body green to bluish green; two thin lines on dorsum, undulating three times per segment, with bands of color between lines or surrounding them; overall appearance an ornate pattern, usually retained in fourth instar; four lateral lines; primary setae indistinguishable from secondary setae except XD1, XD2, and SD2 on T1 and SD1; SD1 long and filamentous on segments T1, T2, T3, A4, A5, A6, and A9; SD1 anterior and dorsal to spiracle on T1, more dorsal on T2 and T3, and posterior and ventral to spiracle on A4–A6 and A9; numerous secondary setae cover body with raised, slender setal bases approximately equal in length to setae; larvae with overall granular appearance from secondary setae; caudal filaments thick, fleshy, rounded without lateral edges, sloping downward, and held together.

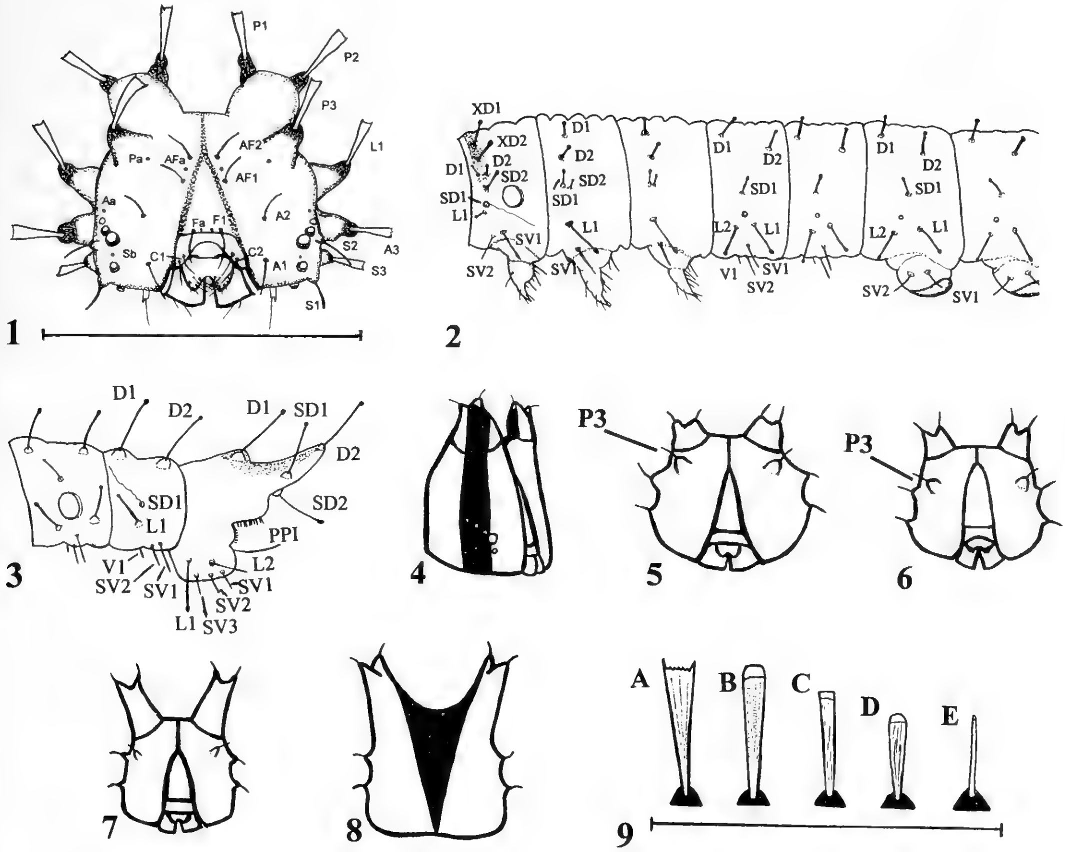
Fourth instar: Head capsule more variable than previous instars; head horns reduced or similar in relative size and shape to previous instars; lateral lobes reduced and more rounded than previous instars; secondary setae often more numerous than earlier instars but remain short. Body coloration and markings variable but always cryptic; thoracic median line darker than remainder of midline with thin, dark outline; specialized thin fan-shaped setae on thoracic median line only; chaetotaxy as in previous instars; caudal filaments usually long, three times as long as A9, and shaped as in earlier instars.

Remarks.—In first instar larvae XD, D, SD, and L setae are thickened with clubbed tips. These setae are possibly glandular, as described for some saturniid larvae (Aiello and Balcazar 1997). When alive, larvae viewed through a 10x lens appear to have small droplets at the apex of the dorsal setae. These are not seen in later instars. SV and V setae have pointed tips. As noted in the above descriptions, SD1 on certain segments is filiform, with setae long and filamentous. Bases are also modified, allowing for great flexibility of the setae. Garcia-Barros (1989) noted these setae on another satyrine, *Hipparchia fidia* Linnaeus. These filiform setae are probably sensory (Markl and Tautz 1975, Tautz 1977). Their serial homology to other non-sensory SD1 setae is questionable (Harvey 1991).

KEY TO KNOWN *TAYGETIS* FINAL INSTAR LARVAE

In addition to larvae described in this manuscript, the key also includes one unnamed species, referred to as *Taygetis andromeda* by Young (1984). Not enough information was provided in the description of *Taygetis ypthima* (Müller 1886) to include it in the key.

1. Head capsule and head horns without lateral markings 2
– Head capsule and head horns with lateral markings (Fig. 4) 3
2. P3 located at or above apex of frons (Fig. 5); body with black oblong spot dorsolaterally on T3; head capsules as in Fig. 10 . . . . *T. mermeria* (Cramer)
– P3 located below apex of frons (Fig. 6); head



Figs. 1–9. 1–3, *Taygetis* chaetotaxy. 1, Head chaetotaxy of *Taygetis mermeria* (scale = 2.0 mm). 2, Body chaetotaxy of *T. cleopatra,* T1 through A3. 3, Body chaetotaxy of *T. cleopatra,* A8 through A10. 4–8, Head capsule of *Taygetis* sp. 4, Lateral view. 5, Location of P3. 6, Location of P3. 7, Frontal view. 8, Basal view. 9, First instar P1 seta. A, *T. mermeria.* B, *T. cleopatra.* C, *T. laches.* D, *T. thamyra.* E, *T. virgilia* (scale = 2.0 mm).

capsule and body green; head capsules and larva as in Figs.14, 17 . . . . . . *T. virgilia* (Cramer)
3. Head horns approximately equal in length to frons length (Fig. 7); without broad "m" shaped marking on head capsule 4
– Head horns distinctly less than length of frons (Fig. 5); broad "m" shaped marking on head capsule; head capsules and larva as in Figs. 11, 15 . . . . *T. cleopatra* C. Felder and R. Felder
4. Base of head capsule without darkly colored triangle between head horns 5
– Base of head capsule with darkly colored triangle between head horns (Fig. 8); head capsules as in Fig. 13 . . . . . . *T. thamyra* (Cramer)
5. Body with faint longitudinal lines; no other markings; head capsules and larva as in Figs. 12, 16 . . . . *T. laches* (Fabricius)
– Body with many longitudinal lines forming broad bands dorsally and laterally; irregular black markings on dorsum; *T. andromeda* of Young (1984) . . . . *Taygetis* sp.

Taygetis mermeria (Cramer)
(Figs. 9A, 10)

Diagnosis.—Head capsule and head horns without lateral markings; P3 located at apex of frons; black oblong spot dorsolaterally on T3; caudal filaments triangular with lateral edge.

Description.—*First instar:* Head capsule 1.3 mm; dark reddish brown; mandibles and primary setae black; lobed setae (P1, P2, P3, L1, and A3) and S3 widely fanned, widest at apex (Figs. 9A, 10A); apex with uneven ends and no white coloration; lobed setal bases black. Body shiny blue green; caudal filaments colorless (n = 5).

Second instar: Head capsule 1.8 mm; bright green; two faint spots in epicranial area (Fig. 10B); faint yellow basal stripe; lobed setae light brown with red setal bases; secondary setae short and sparse. Body blue green; median dorsal stripe dark green, fading between A1 and A5, and broadly outlined with faint white undulating lines; dorsolaterally and laterally with two thin white lines; caudal filaments dark pink and tapering to point (n = 2).

Third instar: Head capsule 2.7 mm; green, paler basally; no markings (Fig. 10C); head horns with pale yellow basal stripe; setae as in previous instar. Body green to blue green; median dorsal stripe dark green, broadly outlined by wide white to yellow band, on thorax band purple, fading to white as instar progresses; dorsolaterally with two white undulating lines; one narrow white line laterally; spiracles pink; caudal filaments as in previous instar (n = 2).

Fourth instar: Head capsule 5.4 mm; dark reddish brown dorsally, paler ventrally; epicranial markings light brown (Fig. 10D); head horns with white to orange basal stripe; lobed setae fine, short, pale, and smaller than other *Taygetis* species; lobed bases flattened and round with tuberculate surface. Body light brown and gray, darker brown on thorax and laterally; dark prominent markings on T3 (oblong spot dorsolaterally) and A5 (dark slash mark dorsolaterally); median dorsal stripe faint brown with black outline on T1–T3 and broad outline of undulating white and brown bands on abdomen; dorsolaterally each abdominal segment with slash mark traversing almost entire segment and black dot at anterior edge of segment; slash marks form broad broken V in dorsal view, more prominent on anterior half of abdomen; two undulating white lines laterally; caudal filament white with lateral brown stripe, filaments triangular, separated, with lateral margins, and two times as long as A9 (n = 3).

Pupa: Round; smooth; no projections; mottled brown with black spots.

Biology.—*Taygetis mermeria* occurs throughout the neotropics from Mexico to Brazil and Bolivia. Although common in lowland forests, adults are not often seen during the day. Approximately 30 minutes before dark males can be found in localized open areas near their host plant, the bamboo *Guadua angustifolia* Kunth (Poaceae), vigorously defending sites. When one male encounters another, they fly in tight, quick circles with one or both leaving the clearing. Twirling males sometimes ascend 10 m above the clearing. Perched males often shiver to elevate their body temperature, a strategy also used by crepuscular brassolines before reproductive periods (Srygley 1994). Constant, vigorous flight of *T. mermeria* may also keep their body temperatures elevated. No mating attempts were observed, however, females were observed ovipositing just before dark in the canopy of the bamboo.

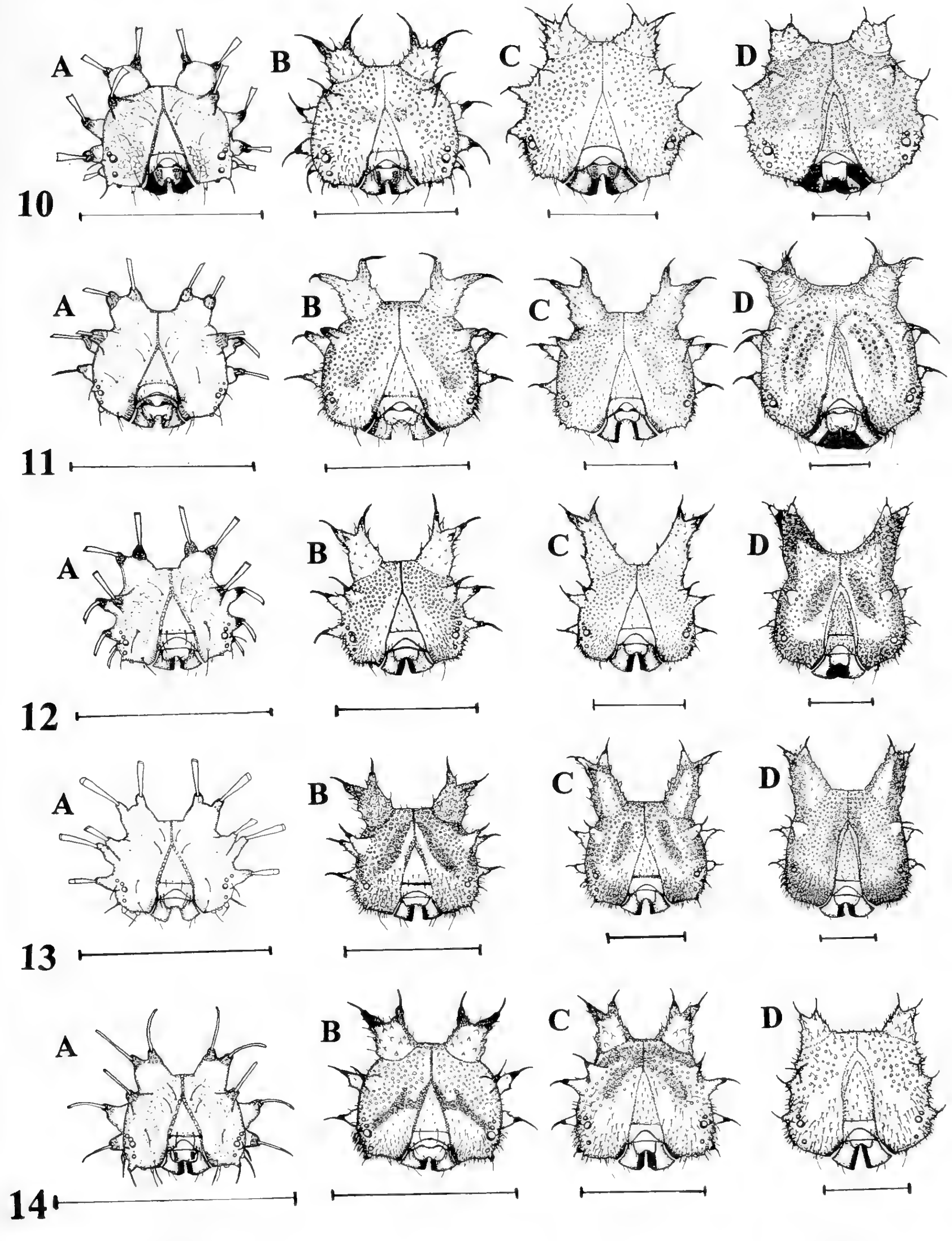
Taygetis mermeria is closely associated with its host plant. Trapping data show that most (95% or 114 out of 120) *T. mermeria* adults were collected within 100 m of their host plant (D. Murray and P. DeVries unpublished data). These trapped individuals were divided between two adjacent habitats, pasture and old growth forest, with stands of bamboo near each. Mark/recapture studies at Jatun Sacha suggest that individuals can have lengthy life spans of up to three months.

Eggs and larvae of *T. mermeria* were collected throughout the year and were found only on *G. angustifolia.* I never found this species on herbaceous bamboos or grasses, though they were searched regularly. Eggs and larvae were collected from cut bamboo trees 7–20 m in height, except two eggs found on understory bamboo resprouts at the edge of the Rio Napo.

Taygetis cleopatra C. Felder and R. Felder

(Figs. 9B, 11, 15)

Diagnosis.—Head capsule and head horns with gray to dark brown lateral mark-



Figs. 10–14. Head capsules of all instars (scale = 2.0 mm). 10, *Taygetis mermeria*. A, First instar. B, Second instar. C, Third instar. D, Fourth instar. 11, *T. cleopatra*. A, First instar. B, Second instar. C, Third instar. D, Fourth instar. 12, *T. laches*. A, First instar. B, Second instar. C, Third instar. D, Fourth instar. 13, *T. thamyra*. A, First instar. B, Second instar. C, Third instar. D, Fourth instar. 14, *T. virgilia*. A, First instar. B, Second instar. C, Third instar. D, Fourth instar.

ings; head horns distinctly less than length of frons; broad "m" shaped marking on head capsule; dark brown to rust colored patch on dorsum beginning on A3.

Description.—*First instar:* Head capsule 1.4 mm; reddish brown; primary setae black and twisted once; lobed setae (P1, P2, P3, L1, and A3) fanned, widest at apex, and black with a white band at apex (Figs. 9B, 11A); S3 flattened and twisted; webbing on head capsule light. Body shiny blue green with faint lateral white lines; caudal filaments colorless tipped pink (n = 11).

Second instar: Head capsule 2.0 mm; brown to greenish pink, darker basally and brown laterally; brown markings on epicranial area faint to absent; if present, markings incomplete fourth instar pattern (Fig. 11B); head horns pink with black setal bases and setae; fewer depressions than other *Taygetis* species; small, fine secondary setae. Body green; dorsal median stripe dark green, broadly outlined by white band forming undulating ornate pattern; dorsolaterally with faint purple line outlined in white; laterally white line thinly outlined in dark green; ventrolateral line reddish purple on thorax to A4, becoming bluish posteriorly; caudal filaments bright pink, tapering to point, becoming purple as instar progresses; premolt larvae bright green (n = 11).

Third instar: Head capsule 2.8 mm; pale green, darker basally and brown laterally; dark green to greenish-brown epicranial markings; ground plan of markings same as fourth instar, but sometimes only portions of pattern visible; most common pattern one simple stripe, as illustrated (Fig. 11C); lobed setae as in previous instar; setal bases tipped pink. Body color as in previous instar but ventrolateral line dark reddish purple for length of body; thorax, A9, and caudal filaments colored purple which intensifies as instar progresses and extends laterally along body; caudal filaments tapering to smooth point; premolt larvae bright green with no purple coloration (n = 13).

Fourth instar: Head capsule 4.9 mm; pale green gray to gray, dark gray laterally; dark gray to brown epicranial markings (Fig. 11D); head horns pale brown tipped yellowish white; lobed setae flat and pale brown, not greatly reduced; secondary setae and depressions sparse. Body cryptically colored in shades of brown; dorsum pale brown with darker patch beginning abruptly on A3 (Fig. 15), variable in color from slightly darker than body to dark brown or rust; patch undulates in each segment forming dark half moons dorsolaterally; median dorsal stripe on thorax brown outlined in gray or black, on abdomen gray; black spot present adjacent to median stripe on posterior edge of each segment, with darkest spots on A4; median stripe broadly outlined with pale brown and black lines forming undulating ornate pattern; pattern often irregular posteriorly; laterally dark brown to rust patches on thorax and A7 to A9; lateral band gray; caudal filaments purple gray to gray brown, three times as long as A9, and held together (n = 13).

Pupa: Round; smooth; no projections; green with black dots on abdomen; wingpads with faint red web-like markings; outlined in red; spiracles red (n = 8).

Biology.—*Taygetis cleopatra* occurs throughout the Amazon basin. This species is common in forested habitats, flying low in deep shade, and is most active at dusk. It was the most abundant *Taygetis* species collected at Jatun Sacha (DeVries et al. 1997). Adults were trapped in all habitats and varied in coloration from dark purplish gray to brown. Mature larvae from the area varied slightly, but this variation did not correlate with adult variation.

Larvae were collected from two herbaceous bamboos, *Olyra latifolia* Aublet and *Pariana* sp. (Poaceae). Eggs and larvae were commonly found on *O. latifolia* throughout the year. Eggs found on *Pariana* sp. were more difficult to locate, probably due to the greater abundance and more even distribution of the host plant. No eggs or larvae of *T. cleopatra* were found on woody bamboo, however one field collected larva was reared in the laboratory on this host plant. There were no variations in development times compared to a larva reared concurrently on *O. latifolia.*

Taygetis laches (Fabricius)
(Figs. 9C, 12, 16)

Diagnosis.—Head capsule and head horns with heavy dark reddish-brown markings; body smooth, green, with only faint longitudinal markings.

Description.—*First instar:* Head capsule 1.2 mm; light reddish brown; primary setae dark brown; lobed setae (P1, P2, P3, L1, and A3) gradually fanned, widest at apex (Figs. 9C, 12A); S3 fanned, but narrowed to point at apex, tipped white. Body shiny green; caudal filaments colorless (n = 3).

Second instar: Head capsule 1.4 mm; green to pale green without markings (Fig. 12B); head horns pale yellow; lobed setae black. Body bright green; on dorsum two thin undulating yellow lines; dorsolaterally two bright yellow stripes; laterally one pale yellow line; caudal filaments green gray, large, and tapering to point (n = 4).

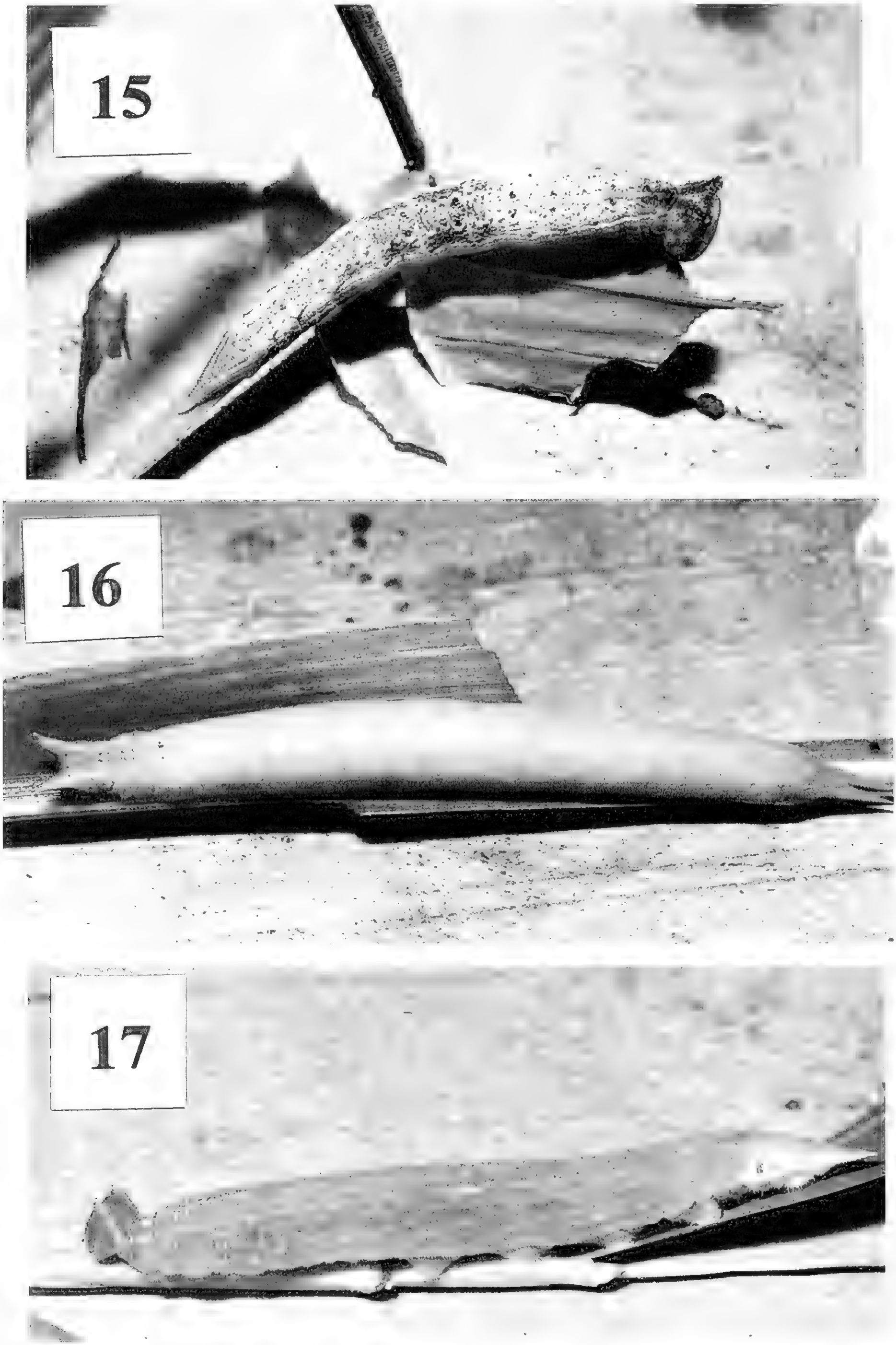
Third instar: Head capsule 2.3 mm; green to pale yellow, basally dark green; faint epicranial markings sometimes present; head horns large and pinkish brown, basally yellow; secondary setae sparse. Body green; median dorsal stripe dark green surrounded by white undulating bands outlined thinly in purple and forming ornate pattern on dorsum; dorsolaterally with two white stripes surrounding yellow band; ventrally one yellow line extending to caudal filament; filaments dark green, large, tapering to point (n = 3).

Fourth instar: Head capsule 3.6 mm; green, basally greenish brown with two black dots; brown laterally; brown epicranial markings (Fig. 12D); head horns large, green and tipped white with pale green basal stripe. Body smooth, green with few markings (Fig. 16); yellow-green coloration over thorax and green over abdomen; median dorsal stripe on thorax irregular and purple, becoming more orange in color as instar progresses; median stripe on abdomen pale bluish-green band, surrounded by thin purple to red undulating lines; ornate pattern not discernable except on close examination; lateral white bands outlined thinly in red; ventrally dark red to purple band, not present on thorax, and brighter posteriorly; caudal filaments dark green, three times as long as A9, and held together in point; (n = 3).

Pupa: Round; smooth; no projections; bright green; streaks of white and red; wingpads and head outlined in red (n = 2).

Biology.–*Taygetis laches* belongs to a species complex whose adults are phenotypically easy to distinguish from other *Taygetis* species. There are three named species within the complex, although it is unclear how many may be included. *Taygetis andromeda* (Cramer), although commonly used in the literature, is an unavailable name (junior primary homonym of *Papilio andromeda* Fabricius) and is currently considered a synonym of *T. laches* by L. Miller (personal communication). References to *T. andromeda* from Central America may be a separate species distinct from *T. laches,* and therefore unnamed. This unnamed species is common throughout the year and prefers disturbed habitats such as second growth forests, cacao plantations, and forest edges (DeVries 1987, D. Murray personal observation). *Taygetis laches,* found in lowland forests in the Amazon basin, has similar habitat preferences, but divergent immature stages.

Larval stages for "*T. andromeda*" in Costa Rica were reported by Young (1984) and DeVries (1987). These descriptions do not match larvae of *T. laches* that I reared at Jatun Sacha and Yasuni National Park, Ecuador, although overall head capsule shape and body form were similar. As with *T. thamyra,* another species in the complex, head horns retain the two-pronged shape of earlier instars and lengthen through the instars. The bodies of all three species are long and slender with smoothly tapering caudal filaments in second and third instars,



Figs. 15–17. Mature instars. 15, *Taygetis cleopatra*. 16, *T. laches*. 17, *T. virgilia*.

but diverging in shape in the mature instars. Clearly the species are related, but color patterns on the head capsule and body are strikingly different.

All *T. laches* individuals were reared on exotic pasture grasses of the genus *Andropogon* sp. (Poaceae), and I have observed females ovipositing on an unidentified wide-bladed grass in the open swampy pampas of Peru. As with "*T. andromeda,*" diet breadth appears broader for *T. laches* than for other *Taygetis* species. This trait may have allowed them to exploit the diversity of native and exotic grasses found in more disturbed areas. *T. laches* is also crepuscular. Males become active first, from one hour to half an hour before sunset, searching populations of host plants for females and patrolling and defending perches. Females of *T. laches* oviposit at dusk. I observed one male attempting to mate with a female while she was ovipositing, but he was rejected. Females were highly selective concerning oviposition sites and often oviposited on blades already containing eggs. Parasitoid pressure appears high within host plant patches. *Trichogramma* spp. (Hymenoptera: Trichogrammatidae) were common on individual host plants. One egg collected within thirty seconds of oviposition was parasitized, suggesting that *Trichogramma* wasps travel with females or are found in high numbers on the host plant. Once an oviposition site was selected, females rested on the blade, at times close to a minute, before curling their abdomen to the underside.

Taygetis thamyra (Cramer)
(Figs. 9D, 13)

Diagnosis.—Head capsule dark brown with darker brown lateral markings and epicranial yellow stripe; base of head capsule with darkly colored triangle; body dark brown with dorsolateral creme coffee-colored band and bright white ventral stripe.

Descriptions.—*First instar:* Head capsule 1.1 mm; brown; lobed setae (P1, P2, P3, L1, and A3) and S3 fanned, widest near apex, tipped white (Figs. 9D, 13A). Body green, slender; caudal filaments pink (n = 3).

Second instar: Head capsule 1.5 mm; dark red brown; head horns dark brown; darker and lighter epicranial markings; (Fig. 13B); P3, L1, and A3 setal bases pale brown. Body greenish red, red laterally and ventrally; ventrally one bright white line from A8 to A10; caudal filaments pinkish red, large, tapering to point (n = 3).

Third instar: Head capsule 2.9 mm; dark red; dark brown laterally; darker and lighter epicranial markings (Fig. 13C); lobed setal bases pale yellow. Thorax purple; abdomen green without markings or lines; caudal filaments pinkish purple, large, tapering to smooth point (n = 1).

Fourth instar: Head capsule 4.1 mm; dark brown; darker brown laterally; light yellow epicranial stripe (Fig. 13D); head horns with pale coffee-colored basal stripe; lobed setae bases white. Body dark brown; median dorsal stripe on thorax coffee colored, surrounded by thin band of dark brown; no dorsal stripe on abdomen; dorsum with thin white undulating lines forming ornate pattern; dorsolaterally coffee-colored band on abdomen to A7, darkening A8 to A10; ventrally bright white line; caudal filaments dark brown, three times as long as A9, and held together in point; setal bases on body white and larger than on other *Taygetis* species, forming a light powdery appearance on thorax and laterally on body (n = 1).

Pupa: Round; smooth; no projections; green with white flecks; head and wingpads with red outline (n = 1).

Biology.—*Taygetis thamyra* occurs in the Amazon basin from Columbia to Brazil. Adults are similar to *T. laches,* although the larvae are different. At Jatun Sacha, *T. thamyra* was less common than *T. laches* and never collected in butterfly traps. I reared this species twice, both times from *Ischnosiphon* sp. (Marantaceae). One female was observed ovipositing at dusk near the edge of an old growth forest. Unlike *T. laches,*

Table 1. Egg and larval durations in days for immature stages of *Taygetis* species. A "+" sign signifies eggs encountered in the field without observing oviposition.

Species	Egg	First	Second	Third	Fourth	Pupa	Total	Number
Taygetis mermeria	5+	7	6	10	15	16	54	n = 2
Taygetis thamyra	5.0	13	12	13	29	14	86	n = 1
Taygetis cleopatra	5.5	8	9	10	18	14.5	65	n = 5
Taygetis laches	5.5	7	6	7.5	12.5	11	49.5	n = 2
Taygetis virgilia	5+	6	5	7	7	10	40	n = 1

the female *T. thamyra* landed on the underside of the leaf to oviposit. This behavior may be dictated by the shape of the leaf since *Ishnosiphon* leaves are at least three times broader than *Andropogon* blades.

Durations of immature stages were longer than any other *Taygetis* species reared (Table 1). Although silica in grasses has been hypothesized to slow the growth of satyrines (DeVries 1987), *T. thamyra,* the one non-grass feeder in the group, offers no support for this. However, silica content may play a role in the feeding pattern of *Taygetis* and other grass-feeding euptychiines. The typical pattern is neat rectangular cuts in the leaf margin, easily recognized in the field. First instar *T. thamyra* larvae make several jagged, irregular "c" shaped cuts into the leaf margin. Later instars show little pattern. Larval colorations for *T. thamyra* were overall much darker than grass-feeding species and were well camouflaged against the dark red and green coloration of the host plant.

Taygetis virgilia (Cramer)
(Figs. 9E, 14, 17)

Diagnosis.—Head capsule and head horns without lateral markings; P3 located below apex of frons; body brightly colored green with yellow, orange, and brown leaf spot markings.

Description.—*First instar:* Head capsule 0.9 mm; dark brown; primary setae dark brown; lobed setae (P1, P2, P3, L1, and A3) long, thin, flattened, blunt tipped with thin white apical band (Figs. 9E, 14A). Body shiny yellowish green; four yellow lateral lines; caudal filaments colorless (n = 2).

Second instar: Head capsule 1.2 mm; pale brown; head horns laterally reddish brown; reddish-brown arch beginning at stemmata and bisecting frons (Fig 14B); secondary setae large and more numerous than other *Taygetis* species. Body bluish green; four yellow lines laterally; caudal filaments dark pink, large, tapering to a point (n = 2).

Third instar: Head capsule 2.0 mm; green, and laterally brownish yellow; two reddish-brown arcs near epicranium (Fig. 14C); lateral and basal primary setal bases yellow; secondary setae as in previous instar. Body bluish green; four yellow lines laterally, with faint red between; caudal filaments same as previous instar (n = 2).

Fourth instar: Head capsule 3.0 mm, smaller than other *Taygetis* species; bright green without markings (Fig. 14D); head horns with bright yellow basal stripe; orangish-yellow primary setal bases; secondary setae as in previous instars. Body bright green with very fine granulations; median dorsal stripe yellow and present only on thorax; yellow line dorsolaterally with variable patterns, from a number of colorful spots of brown surrounded by bright yellow and orange to reduced yellow smudges on T1, T2, A3, and A4 (Fig. 17); from A8 to A10 largest spot, present on all larvae consisting of a brown or black spot outlined in orange and surrounded by a large yellow patch; four yellow lines laterally; caudal filaments three times as long as A9, held together in a point; larva smaller and more brightly colored than other *Taygetis* larvae (n = 2).

Pupa: Round; smooth; no projections; bright green with no markings (n = 1).

Biology.—*Taygetis virgilia* adults are similar in appearance and habits to *T. rufomarginata* Staudinger and the two are sometimes treated as one species (DeVries 1987). Their current status is unclear, but they appear to be separate species based on larvae. The general larval description of *T. virgilia rufomarginata* (DeVries 1987) from Costa Rica and larvae of *T. virgilia* that I reared are not similar.

Taygetis virgilia adults are seldom seen during daytime unless they are flushed from the forest floor. Although more commonly encountered near its host plant *Guadua* sp. (Poaceae), adults are found in a variety of habitats, from undisturbed forests to forest edges. Surprisingly, although this species was not as abundant as other bamboo-feeding satyrines, it was frequently recaptured in mark/recapture studies at Jatun Sacha.

Eggs and larvae were found only in the canopy of bamboo, *G. angustifolia,* and were uncommon. Weymer (1910) also reported this species from bamboo. The duration of immature stages is shorter than other *Taygetis* species (Table 1), although *T. virgilia* adults are of similar size. In contrast to other large bamboo feeders, *T. virgilia* is not cryptic brown in the final instar, but retains the bright green coloration of earlier instars. This suggests that larvae usually rest on the leaves of bamboo, as opposed to species of *Pseudodebis* Forster and *Taygetis* that rest on the brown stems and sheaths.

DISCUSSION

The euptychiine morphology presented here serves as a basis for future phylogenetic studies that are critically needed. Unresolved taxonomic problems occur in many euptychiine genera, including *Taygetis.* Forster (1964) erected several genera for species once included in *Taygetis.* Unfortunately, generic limits were not defined in his manuscript, and the validity of his genera have been questioned (DeVries 1987). Based on my preliminary character analysis of both molecular and morphological data, the sister taxon to *Taygetis* is *Pseudodebis,* a genus comprising six neotropical species. The diagnostic characters I found for *Taygetis* species do not provide a great deal of evidence for separating *Taygetis* from closely related *Pseudodebis.* Further investigation into the immature stages of *Pseudodebis* are needed to resolve the validity of this genus.

The immature stages of species presented here share many of the same characteristics as given in previous publications on *Taygetis* species, with one main exception. All *Taygetis* species I reared had four larval instars, a trait noted by Singer et al. (1983) for other euptychiine genera and found by Müller (1886) for *T. ypthima.* However, Young (1984) reported five instars for "*T. andromeda.*" Because Young did not fully document larval durations for each stadium, future rearings are needed to clarify this issue. Larval duration for "*T. andromeda*" was reported by Young as about 48 days, which is similar to *T. laches* (Table 1).

Adults of many *Taygetis* species are phenotypically similar, creating taxonomic nightmares. However, for species described here and previously, identifying mature larvae is relatively simple. Head horn length, head capsule markings, and body color and pattern are all useful in identifying species. Immature stages may prove to be more informative than adult characters for sorting out difficult species complexes (i.e., *T. laches* and *T. virgilia*).

Because adult phenotypes can be highly variable within euptychiines, the intraspecific variability of immature stages may be logically questioned. In general I have found some variation in euptychiine larvae, but without careful observations, differences between larvae can be misinterpreted. *Taygetis cleopatra* larvae were reared multiple times under different conditions, and these larvae were variable in color pattern and intensity, but in a controlled manner. For example, the underlying head capsule and body patterns were the same, but at times the patterns were incomplete or faint. Colors can change throughout the instars, and without careful observation, this can result in incomplete larval descriptions. In general the pattern can darken within the first two days and then darken or lighten in the final two to three days of the stadium. Finally, the overall size and shape of the lobed setae and larger secondary setae do not seem to vary among individuals. However, deformities of head horns and caudal filaments are not rare. I have found deformities both in reared and field collected individuals.

The natural history information presented here highlights interesting aspects of euptychiine biology. Males are crepuscular and exhibit territorial behaviors in loose leks. Females are also crepuscular and oviposit close to darkness. This behavior is similar to that reported by Young and Muyshondt (1975) for *Caligo* and *Opsiphanes* species. I have observed crepuscular activity in all species discussed in this paper and also in *T. sosis* and *T. echo.* Young (1972) also reported crepuscular activity for *Taygetis* species. Undoubtably, this is a trait shared by most *Taygetis* species. With their supposed lack of chemical defenses and their dark colorations and large size, flying close to darkness may provide some protection from visual predators, as hypothesized by Young and Muyshondt (1975) for crepuscular brassoline species. The formation of leks and the courtship by males are areas of potential research in reproductive biology. Another area for investigation is the population dynamics of bamboo-feeding specialists. These species appear to be ideal organisms for examining metapopulation theory, given their high habitat associations and the clumping nature of the host plant. Many bamboos flower and die in mass. How is the population structure of bamboo-feeding specialists affected by this?

As more life histories are described and host use recorded, a clearer picture will emerge of the basic ecology and evolutionary history of the group. With a foundation of baseline data, we can then begin to test hypotheses on the evolutionary relationships within euptychiines, their diversification within Amazonia, and sister taxa relationships.

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RESOURCE UTILIZATION IN THE SIBLING SPECIES *TRUPANEA NIGRICORNIS* (COQUILLETT), A POLYPHAGE, AND THE NARROWLY OLIGOPHAGOUS *T. BISETOSA* (COQUILLETT) (DIPTERA: TEPHRITIDAE) IN SOUTHERN CALIFORNIA

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Abstract.—The flower heads of the hosts of the sympatric, morphologically similar, probable sister species, *Trupanea nigricornis* (Coquillett) and *T. bisetosa* (Coquillett) offer an annual, stable food source in southern California. In this study, larger flower heads supported the development of more larvae per head than smaller flower heads. The size of the puparia of *T. nigricornis* was found to vary among the different hosts and with the density of larvae per flower head. The larvae of *T. nigricornis* and *T. bisetosa* exploited the flower heads in a similar way, eating their way downward from the florets first, then into the achenes. The only difference detected was in the second instars of *T. bisetosa* which continued to feed on the florets compared to the second instars of *T. nigricornis* which fed on the achenes. This variation reflected the larger achene size of the hosts of *T. bisetosa.* The percentage of damaged achenes per flower head was found to be proportional to the size of the flower head. In general, a single *T. bisetosa* larva damaged fewer achenes per head than a *T. nigricornis* larva because of the relatively larger achene size and flower head diameter of *T. bisetosa* hosts. Larvae of both tephritids did not exhaust all their food resources in a particular flower head regardless of the size of the flower head and the density of the infesting larvae. In general, the percentage of flower heads infested by *T. bisetosa* was lower than the percentage of flower heads infested by *T. nigricornis.* Plant hosts with larger flower heads did not support more insect species than hosts with smaller heads. There was little evidence of interspecific competition between the various insect species exploiting the flower heads of *T. nigricornis* and *T. bisetosa* because of the many evasion strategies adopted by those insects to minimize interspecific contact.

Key Words: Insecta, *Trupanea,* cryptic species, sympatry, resource utilization, intraspecific competion, interspecific competition

The flower-head infesting tephritids, *Trupanea nigricornis* (Coquillett) and *T. bisetosa* (Coquillett), occur in sympatry in southern California. They also are probable sister species that have morphological and genetic similarities in the immature and adult stages (Knio et al. 1996a, b), but show major ecological and behavioral differences (Knio et al. 1996a, b). For example, *Trupanea nigricornis* is a generalist, infesting plants belonging to eight tribes in the Asteraceae (Goeden 1992, unpublished data), whereas *T. bisetosa* is narrowly oligophagous, restricted to one tribe, the Heliantheae, mainly to three *Helianthus* spp. (Cavender and Goeden 1983, Goeden 1992). Also, the eggs of *T. nigricornis* are inserted deep in the flower heads of host plants, often puncturing tissues, while those of *T. bisetosa* are deposited loosely among florets (Knio et al. 1996b). The ultrastructure of the ovipositor of these species also reflects the observed behavioral differences (Knio and Goeden, unpublished data). Further, *T. nigricornis* females lay eggs singly, with more eggs occurring per flower head later in the flowering cycle when resources are scare than earlier in the season. *T. bisetosa* females lay eggs in clusters (Knio et al. 1996b).

Because *T. nigricornis* and *T. bisetosa* are sympatric, probable sister species (Knio et al. 1996a), comparative studies, reported as a series of papers, on their biology, morphology, genetics, and ecology were undertaken to shed light on the differences that separate them. This current paper is intended to clarify the nature of polyphagy/oligophagy in *T. nigricornis* and *T. bisetosa* by addressing the question of resource utilization and interspecific interactions within the flower head guild. The objective is a comparative analysis of the strategies adopted by *T. nigricornis* and *T. bisetosa* for resource usage, resource sharing, and intraspecific and interspecific competition within the context of current evolutionary theory.

MATERIALS AND METHODS

Resource utilization by *Trupanea nigricornis* and *T. bisetosa* was studied by examining field-collected flower heads in the laboratory. Samples of flower heads of *T. nigricornis* and *T. bisetosa* host plants were collected at each of 22 desert and interior-valley locations in southern California during 1987–1992. The host plants of *T. nigricornis* sampled were *Encelia farinosa* Gray, *E. fructescens* Gray, *E. virginensis* A. Nelson, *Haplopappus acradenius* (Greene) Hall, *Viguiera deltoidea* Gray, and *Geraea viscida* (Gray) Blake. The host plants of *T. bisetosa* sampled were *Helianthus annuus* L., *H. niveus* (Bentham), and *Geraea canescens* Torrey & Gray.

Each plant sample consisted of a 1-l plastic bag containing 100–700 mature flower heads. Flower heads sampled were taken at random from several plants at each collection site. They were transported to the laboratory in ice chests via air-conditioned vehicles and stored under refrigeration until dissection. Subsamples of 25 infested heads and 25 non-infested heads were examined with a stereomicroscope.

The total number of heads dissected to obtain both subsamples was recorded in order to calculate percent infestation. The following parameters for infested flower heads were measured: number, stage, size (diameter and length) of larvae and puparia of *T. nigricornis/T. bisetosa*; state of the larvae (healthy, feeding, parasitized, sluggish, dead); number of achenes damaged by *T.nigricornis/T. bisetosa* larvae; relative position of the larvae and puparia within the flower heads; number, stages, sizes and orientation of other insect species; number of achenes damaged by other species of insects; and number of intact achenes remaining per flower head.

The following parameters for uninfested flower heads were measured: widest diameter of individual flower heads (measured with dial calipers); length of the flower heads (from the outer base of the receptacle to the tip of the florets); widest internal diameter of the receptacle; total number of achenes per flower head; oven dry weight of all 25 flower heads as a unit.

The remaining flower heads in every sample were counted and placed in (34 × 32 × 35 cm) glass-topped, sleeve cages in the insectary at the University of California, Riverside at 60% RH and 12/12 (L D) photoperiod from 0500–1700 h. The numbers and identities of the emerging insects were recorded.

One-way ANOVA and Tukey's test were

Table 1. Summary of the flower-head characteristics of the host plants of *Trupanea nigricornis* and *T. bisetosa* in southern California.

	Means ± SE[a], and range (in parentheses)					
	Number of Heads	Diameter (mm)	Length (mm)	Receptacle Width (mm)	Number of Seeds/Head	Dry Weight of 25 Heads (gm)
T. nigricornis:						
H. acradenius	125	3.7 ± 0.2a (2.5–6)	12 ± 0.4b (9.4–15.2)	2.1 ± 0.1a (1.3–3.3)	15.3 ± 0.9a (9–22)	0.5 ± 0.1 (0.4–0.8)
E. fructescens	425	12.9 ± 0.4d (8–18.5)	15 ± 0.4c (9–24)	5.5 ± 0.2c (3–8.4)	39.9 ± 2.3b (19–75)	6.1 ± 0.5 (3.2–9.3)
V. deltoidea	150	10.4 ± 0.3b (6.7–13)	11.4 ± 0.3ab (8–13.9)	4.1 ± 0.1b (2.5–5.4)	50.4 ± 4.7c (28–93)	3.3 ± 0.5 (2.4 ± 5.5)
E. farinosa	425	11.9 ± 0.2c (8.7–16.4)	10.9 ± 0.2a (8.3–15)	4.3 ± 0.1b (2.5–6.4)	61.7 ± 2d (28–112)	3.3 ± 0.1 (2.2–4.3)
G. viscida	25	21 ± 0.3g (18.4–24.3)	23.3 ± 0.3d (20.2–25.7)	9.2 ± 0.2d (8–11)	82.6 ± 2.3e (60–102)	18.5 —
E. virginensis	225	16.5 ± 0.4e (10–22.3)	14.5 ± 0.3c (19.4–18.3)	8.6 ± 0.2d (5.6–13.4)	89.6 ± 6e (45–152)	8.4 ± 0.6 (4–10)
Hosts of *T. bisetosa:*						
H. niveus	50	11.8 ± 0.2c (10.5–14.7)	13.6 ± 0.2c (11.6–15.1)	9.1 ± 0.4d (6.8–11.2)	45.9 ± 1bc (28–74)	4.4 ± 0.2 (4.2–4.5)
G. canescens	175	12.1 ± 0.6c (7.7–16.8)	13.5 ± 0.2c (10–16.7)	5.7 ± 0.2c (3.8–7.5)	46.3 ± 4.6bc (22–86)	4.6 ± 0.6 (2.4–6.5)
H. annuus	200	19.2 ± 0.2f (8.5–23.5)	19.1 ± 0.9c (10–31.5)	10.8 ± 0.2e (7–16.7)	120 ± 2.5f (83–130)	21 —

[a] SE = standard error. Means followed by the same letter are not significantly different at the 95% confidence level using Tukey's test.

used to compare differences between means. Regression analysis was done using Statistica. Mean ± standard errors are provided throughout unless otherwise noted.

RESULTS

Flower-head characteristics.—Characteristics of *Trupanea nigricornis* and *T. bisetosa* flower heads are summarized in Table 1. There were significant differences in the sizes of the flower heads of *T. nigricornis* hosts, i.e., *H. acradenius* had the smallest heads (ca. 4 mm in mean width), followed by *V. deltoidea* (10 mm), *E. farinosa* (ca. 12 mm), *E. fructescens* (ca. 13 mm), *E. virginensis* (16.5 mm), and *G. viscida* (21 mm). Among *T. bisetosa* hosts, *H. niveus* and *G. canescens* had smaller heads (ca. 12 mm) than the significantly larger heads of *H. annuus* (19.2 mm).

Among the hosts of *T. nigricornis, H. acradenius* had small, ovoid flower heads, with the smallest mean receptacle diameter and the lowest mean dry weight, followed by *V. deltoidea, E. farinosa, E. fructescens,* that are medium-sized, globose flower heads, and *E. virginensis,* and *G. viscida,* that are large, globose flower heads (Table 1). With respect to the number of achenes per flower head, *H. acradenius* had the lowest mean value of ca. 15 followed by *E. fructescens, V. deltoidea, E. farinosa, G. viscida,* and *E. virginensis* with mean values that ranged from ca. 40–90 achenes per flower head.

Among *T. bisetosa* hosts, *H. niveus* and *G. canescens* had shorter flower heads with smaller receptacle diameter and lower dry weight than *H. annuus* (Table 1) Also, *H. niveus* and *G. canescens* had only one-third the mean number of achenes per head than *H. annuus.*

As expected, there was a high correlation between the outside diameter of the flower

Table 2. Frequency distributions of larvae of *Trupanea nigricornis* in heads of different host plant species.

Hosts: Number of Larvae per Head	*E. virginensis* Count (%)	*E. farinosa* Count (%)	*E. fructescens* Count (%)	*H. acradenius* Count (%)	*V. deltoidea* Count (%)
1	44 (23.7)	274 (71.4)	210 (75.5)	60 (89.5)	65 (73)
2	53 (28.5)	86 (22.4)	53 (19.4)	5 (7.5)	21 (23.6)
3	36 (19.4)	22 (5.7)	13 (4.7)	1 (1.5)	2 (2.3)
4	18 (9.7)	2 (0.5)	0	1 (1.5)	1 (1.1)
5	15 (8.1)	0	1 (0.4)	0	0
6	9 (4.8)	0	0	0	0
7	4 (2.1)	0	0	0	0
8	4 (2.1)	0	0	0	0
9	3 (1.6)	0	0	0	0
Total number of heads:	186	384	278	67	89
Number of samples:	9	19	17	5	5

head and the number of achenes per flower head (R = 0.86) and the diameter of the receptacle and the number of achenes per flower head (R = 0.81). The length of the flower head had little relationship with achene number per flower head (R = 0.38).

Host plant phenology.—Collectively, the flower heads of *T. nigricornis* and *T. bisetosa* hosts offered continuous food resources for both tephritids. The hosts of *T. nigricornis* bloom in different seasons, such that there is a continual supply of flower heads for most of the year. They bloom mainly in two seasons, spring (e.g., *Encelia* sp.) and fall (e.g., *H. acradenius*), and for periods of 2–3 mo. depending on rainfall. The main host of *T. bisetosa, H. annuus,* blooms throughout the year in the absence of frost, and, thus, is a continuously available resource for this species.

Resource utilization by *T. nigricornis.*—The number of *T. nigricornis* larvae that fed and completed their development in a single head varied among different host plants. Regression analysis showed that flower head diameter (R = 0.47) was a moderate indicator of the number of larvae completing development per flower head; however, dry weight (R = 0.28) was a poor indicator of the number of larvae per flower head. The small heads of *H. acradenius* contained mainly one larva per head (89.5%); 7.5% contained two larvae and 3% had three or four larvae (Table 2). The number of *T. nigricornis* larva(e) per flower head in the hosts with medium-sized heads (*E. farinosa, E. fructescens,* and *V. deltoidea*) collectively were: 71–75% of the flower heads contained one larva, 19–24% had two larvae and 3–6% had three to five larvae (Table 2). In the large heads of *E. virginensis,* the number of larva(e) per head were: ca. 24% of the flower heads had one larva, ca. 48% had two or three larvae, ca. 18% had four or five larvae, ca. 7% had six or seven larvae and ca. 4% had eight or nine larvae (Table 2). Larger flower heads supported the development of a greater number of larvae than did smaller flower heads.

Resource utilization by *T. bisetosa.*—The number of *T. bisetosa* larvae that completed their development in the large flower heads of *H. annuus* ranged from one to 12 larvae per head. Thirty percent of *H. annuus* flower heads contained only one larva, 47% contained two or three larvae, 13.2% contained four or five larvae, 6.6% contained six or seven larvae and ca. 3% contained eight to 12 larvae (Table 3). Again, flower head diameter (R = 0.4) and dry weight (R = 0.38) were moderate and poor indicators, respectively, of the number of *T. bisetosa* larvae able to complete their development within a flower head.

The relatively smaller heads of *G. canescens* contained two to four *T. bisetosa* larvae per head and those of *H. niveus* con-

Table 3. Frequency distributions of larvae of *Trupanea bisetosa* in heads of *Helianthus annuus, Geraea canescens,* and *H. niveus.*

Number of Larvae per Head	*H. annuus* Count (%)	*G. canescens* Count (%)	*H. niveus* Count (%)
1	41 (30.1)	0	3 (75)
2	38 (27.9)	2 (50)	1 (25)
3	26 (19.1)	0	0
4	12 (8.8)	2 (50)	0
5	6 (4.4)	0	0
6	4 (2.9)	0	0
7	5 (3.7)	0	0
8	1 (0.7)	0	0
9	1 (0.7)	0	0
10	1 (0.7)	0	0
11	0	0	0
12	1 (0.7)	0	0
Total number of heads:	136	4	4
Number of samples:	10	1	1

tained one to two larvae per head (Table 3). On the other hand, the large heads of *H. annuus* resembled those of *E. virginensis* in supporting higher number of larvae than the smaller heads of other host plants.

Puparia size.—The size of *T. nigricornis* puparia was found to vary by host plant flower head diameter (Table 4). The smallest puparia were found in the small heads of *H. acradenius*; whereas, the largest puparia were found in the medium-sized, but long heads of *E. fructescens.* All *T. nigricornis* puparia were significantly smaller than *T. bisetosa* puparia, irrespective of host plant species (Table 4).

In some host plant species of *T. nigricornis* variation between the size of male and female puparia occurring singly in flower heads was noted (Table 5). For example, in *E. farinosa,* puparia that produced females were longer than those that yielded males. However, in *E. fructescens,* female *T. nigricornis* puparia were wider than male puparia, but not longer. In *E. virginensis,* the size of the puparia of *T. nigricornis* did not differ between males and females, although adult females of this tephritid species were generally larger than the males.

The size of *T. nigricornis* puparia varied with the density of the larvae per medium-sized flower head (Table 6). In *E. fructescens,* the puparia of *T. nigricornis* in flower heads infested by one larva were wider on average than puparia in heads infested with four or five larvae (Table 6). However, density of the larvae per head did not affect the length of the puparia dissected from *E. fructescens,* which had longer flower heads than its congeners (Table 6). No difference in the sizes of puparia was detected in *E. farinosa* flower heads with one larva and those with two to three larvae. Flower heads with four to five puparia were rare in the medium-sized heads of *E. farinosa* (Table 6). In the large flower heads of *E. vir-*

Table 4. Sizes of *Trupanea nigricornis* and *T. bisetosa* puparia in different host plants.

Host Plants	Number of Puparia Measured	Size of Puparia	
		D[a] ± SE (Range) mm	L[a] ± SE (Range) mm
T. nigricornis:			
E. farinosa	310	1.26 ± 0.002 (1–1.5) a	2.76 ± 0.01 (2.2–3.25) b
E. fructescens	270	1.28 ± 0.01 (1–1.55) c	2.84 ± 0.01 (2.16–3.25) c
E. virginensis	134	1.25 ± 0.003 (1–1.35) ab	2.73 ± 0.01 (2.2–3) b
H. acradenius	28	1.22 ± 0.01 (1–1.25) a	2.42 ± 0.03 (2.1–2.75) a
V. deltoidea	37	1.25 ± 0.01 (1.1–1.48) ab	2.72 ± 0.02 (2.5–3) b
G. viscida	4	1.25 ± 0 (1.25–1.25) ab	2.75 ± 0 (2.75–2.75) b
T. bisetosa:			
H. annuus	221	1.43 ± 0.01 (1.2–1.6) d	3.11 ± 0.01 (2.5–3.55) d

[a] D = diameter; L = length; SE = standard error.
Means followed by the same letter are not significant at the 95% confidence level, using Tukey's test.

Table 5. Sizes of male versus female *Trupanea nigricornis* puparia dissected from flower heads of different *Encelia* species.

Sex	Number of Puparia	Mean Diameter ± SE (range)[a] mm	Mean Length ± SE (range)[a] mm
E. farinosa:			
Females	38	1.27 a ± 0.01 (1.25–1.5)	2.85 a ± 0.02 (2.5–3.2)
Males	24	1.26 a ± 0.01 (1.2–1.45)	2.72 b ± 0.04 (2.2–3)
E. virginensis:			
Females	20	1.24 a ± 0.003 (1.2–1.25)	2.8 a ± 0.03 (2.5–3)
Males	10	1.25 a ± 0.005 (1.25–3)	2.8 a ± 0.03 (2.75–3)
E. fructescens:			
Females	7	1.43 a ± 0.04 (1.3–1.55)	2.89 a ± 0.12 (2.25–3.25)
Males	14	1.25 b ± 0.02 (1.1–1.5)	2.73 a ± 0.05 (2.5–3.1)

[a] SE = standard error. For every plant species: means followed by the same letter are not significantly different at 95% confidence level, using Tukey's test.

ginensis, the size of the puparia did not significantly differ between heads with one or two larvae and heads with four to nine larvae.

In *H. annuus,* no difference in the size of *T. bisetosa* puparia was detected between flower heads with one to three larvae and flower heads with higher larval densities (4–12) (Table 6).

Feeding behaviors by instar.—*Trupanea nigricornis* and *T. bisetosa* larvae exploited flower heads as a food source in a similar manner, except as second instars. First instars of both species tunneled and fed in the

Table 6. Sizes of *Trupanea nigricornis* and *T. bisetosa* puparia in heads infested with one to several larvae.

Sizes[a] of Puparia (mm)	Number of Larvae per Head[b]:		
	One	Two–Three	Four and More
T. nigricornis:			
E. farinosa:			
D ± SE	1.26 ± 0.01 (1–1.5)a	1.25 ± 0 (1.25–1.3)a	—
L ± SE	2.75 ± 0.01 (2.25–3.25)a	2.75 ± 0.01 (2.5–3.08)a	—
N	136	106	—
E. fructescens:			
D ± SE	1.32 ± 0.01 (1–1.55)a	1.27 ± 0.02 (1–1.3)ab	1.24 ± 0.02 (1–1.48)b
L ± SE	2.87 ± 0.03 (2.16–3.25)a	2.84 ± 0.03 (2.2–3.2)a	2.84 ± 0.05 (2.5–3.2)a
N	80	44	19
E. virginensis:			
D ± SE	1.25 ± 0 (1.25–1.25)a	1.24 ± 0.01 (1–1.35)a	1.23 ± 0 (1–1.3)a
L ± SE	2.81 ± 0.04 (2.75–3)a	2.71 ± 0.02 (2.2–3)a	2.72 ± 0.03 (2–3)a
N	8	44	54
T. bisetosa:			
D ± SE	1.46 ± 0.02 (1.25–1.55)a	1.42 ± 0.01 (1.25–1.6)a	1.44 ± 0.01 (1.2–1.6)a
L ± SE	3.08 ± 0.04 (2.55–3.5)a	3.14 ± 0.02 (2.8–3.5)	3.16 ± 0.02 (2.8–3.55)a
N	29	79	84

[a] D = Diameter; L = Length; SE = Standard error; N = Number of puparia measured.

[b] For each host, means followed by the same letter are not significantly different at the 95% confidence level using Tukey's test.

Table 7. Number of achenes damaged by *Trupanea nigricornis* and *T. bisetosa* third instar larvae in different host plants.

Host Plant	Number of Larvae	Mean of Damaged Achenes per Larva ± SE (Range)[a]: Number	Mean of Damaged Achenes per Larva ± SE (Range)[a]: Achenes per Head (%)
Hosts of *T. nigricornis:*			
Encelia farinosa	225	8.8 ± 0.2 (3–16) c	18.2 ± 0 (7.1–43.5)
Viguiera deltoidea	50	8.5 ± 0.5 (4–19) bc	21.9 ± 0.01 (9.4–52)
E. virginensis	165	8 ± 0.2 (4–14) b	10.3 ± 10 (4–27.1)
E. fructescens	225	7.9 ± 0.2 (3–16) b	24.3 ± 0.01 (8–58.3)
Haplopappus acradenius	56	7.3 ± 0.3 (3–13) a	50.6 ± 0.02 (23–83)
Hosts of *T. bisetosa:*			
Helianthus annuus	225	6.4 ± 0.1 (3–11) a	6.3 ± 0 (2.4–13.8)
Geraea canescens	12	5.2 ± 0.2 (4–6) a	16.3 ± 0.02 (9–23)

[a] SE = Standard error.

Means followed by the same letter are not significantly different at the 95% confidence level according to Tukey's test.

floral tubes. Second instars of *T. nigricornis* fed in the soft achenes while second instars of *T. bisetosa* fed in the floral tubes, close to the achene-floret junction. Third instars of both species fed upon and destroyed several adjacent achenes. When more than one larva of either species were present in a flower head, they were usually located centrally, but fed on different achenes, and were separated by one or several achenes.

A single larva of *T. nigricornis* damaged from three to 19 achenes, depending on the host plant species (Table 7). During larval feeding, *T. nigricornis* consumed ca. 9 achenes in *E. farinosa,* 8 achenes in *E. virginensis* and *E. fructescens,* 8.5 achenes in *Viguiera deltoidea,* and 7 achenes in *Haplopappus acradenius* (Table 7). The number of achenes damaged by a larva in the small flower heads of *H. acradenius* was significantly less than the number of achenes damaged in the other plant species (Table 7).

The percentage of achenes consumed or damaged in a flower head by a single *T. nigricornis* larva was proportional to the size of the flower head. Damage was highly correlated with the diameter (R = 0.91) and the dry weight (R = 0.86) of the heads of *T. nigricornis* hosts. Percent achenes damaged by a single larva was highest in the small heads of *H. acradenius* (51%), which contained the fewest achenes per head, and lowest in the large heads of *E. virginensis* (10.3%), which contained the most achenes per head (Table 7). Achene damage ranged between 18 and 24% in the medium-size heads of *E. farinosa, V. deltoidea,* and *E. fructescens* (Table 7).

The number of achenes consumed by a single *T. bisetosa* larva was less than that of *T. nigricornis.* During larval feeding *T. bisetosa* consumed a mean of 6.4 ± 0.1 achenes in *H. annuus* and a mean of 5.2 ± 0.2 achenes in *G. canescens* (Table 7). There was no significant difference in the number of achenes damaged in *H. annuus* and *G. canescens.* The number of achenes damaged by a single *T. bisetosa* larva was highly correlated with the diameter (R = 0.99) and the dry weight (R = 0.46) of the heads.

The percentage of achenes consumed or damaged per flower head by a single *T. bisetosa* larva was higher (16%) in the medium-size flower heads of *G. canescens* than the larger heads of *H. annuus* (6%) (Table 7). Also, this percentage was highly correlated with the diameter (R = 0.91) and dry weight (0.86) of the heads.

Trupanea nigricornis and *T. bisetosa* larvae did not exhaust all the achene resources

Table 8. Number of achenes per head that remained intact in flower heads infested with one or more *Trupanea nigricornis* third instar larva.

	Number of Intact Achenes ± SE[a] per Head (Range) in Heads Infested with the Following Number of Larva(e):						
Host Plant, N[b]	1	2	3	4	5	6–7	8–9
E. fructescens	25.7 ± 0.9	23.3 ± 1.5	17.4 ± 2.1	—	7 ± 0	—	—
	(9–65)	(4–45)	(8–35)	—	—	—	—
N	157	46	14	—	1	—	—
E. farinosa	41.1 ± 0.0	32.4 ± 1.4	30.7 ± 2.2	26 ± 0	—	—	—
	(13–78)	(11–60)	(12–55)	(26–26)	—	—	—
N	201	62	23	2	—	—	—
E. virginensis	69.7 ± 3.7	73.3 ± 3.6	77.7 ± 4.5	67.8 ± 8.1	59.9 ± 6.1	53 ± 11.8	28.5 ± 12
	(34–127)	(20–121)	(42–132)	(18–132)	(15–105)	(15–93)	(5–69)
N	41	49	33	13	15	11	8
V. deltoidea	31.2 ± 0.9	38 ± 4	—	—	—	—	—
	(15–48)	(25–52)	—	—	—	—	—
N	50	6	—	—	—	—	—
H. acradenius	6.9 ± 0.3	—	—	—	—	—	—
	(2–12)	—	—	—	—	—	—
N	57	—	—	—	—	—	—

[a] SE = standard error.
[b] N = number of flower heads analyzed.

in a given flower head regardless of the size of the flower head or larval density. The mean number of intact achenes remaining in hosts infested with one to several *T. nigricornis* larvae are summarized in Table 8. The medium-sized flower heads of *E. farinosa, E. fructescens,* and *V. deltoidea* infested with one to two larvae still contained 23–41(ca. 62–68%) undamaged achenes (Table 8). However, in *H. acradenius,* ca. seven (47%) achenes remained intact after infestation with a single larva (Table 8). The large flower heads of *E. virginensis* had 28–77 (ca. 32–89%) intact achenes whether they were infested with one or several larvae. However, there was a gradual decrease in the number of undamaged achenes when more than four larvae were present in *E. virginensis* (Table 8). Similarly, in *T. bisetosa* hosts, the mean number of intact achenes in *H. annuus* remained high (63–103; 53–86%), whether they were infested with 1–12 larvae (Table 9). Again, there was a gradual decrease in the number of intact achenes as the density of *T. bisetosa* larvae increased from one to 12 per head (Table 9).

Interspecific interactions.—The mean numbers of intact achenes remaining in heads infested concurrently with *T. nigricornis* and other herbivorous insects are summarized in Table 10. The medium-sized flower heads of *E. farinosa* and *E. fructescens* with multiple infestations still contained 24–51 (ca. 40–85%) and 4–22 (10–55%) intact achenes, respectively (Table 10). *Encelia virginensis* flower heads with multiple infestations retained 22–95 (ca. 25–100%) intact achenes suggesting little interspecific competition for achenes.

The mean numbers of intact achenes in heads infested with *T. bisetosa* and other insects are summarized in Table 11. The flower heads of *H. annuus* with multiple infestations retained 56–106 (47–88%) intact achenes. The flower heads of *G. canescens* with multiple infestations retained 20–21 (ca. 43%) intact achenes (Table 11).

The percentage infestation by *T. nigricornis* was highest in *E. virginensis* (44.2 ± 5.7%) and moderate to high in *E. farinosa* (32.5 ± 2.8%), *V. deltoidea* (29.6 ± 5.3%), and *E. fructescens* (25.5 ± 4.7%). Percentage infestation was lowest in the

Table 9. Number of achenes per head that remained intact in flower heads infested with one or more *Trupanea bisetosa* third instars.

	Number of Intact Achenes ± SE[a] per Head (Range) in Heads Infested with the Following Number of Larva(e):						
Host Plant, N[b]	1	2	3	4	5–6	9–10	11–12
H. annuus:	102.8 ± 3.8	96.9 ± 5.4	84.1 ± 6.5	78.8 ± 5.8	68.3 ± 6	70.7 ± 7	62.8 ± 6
	(55–142)	(56–124)	(58–105)	(56–107)	(48–102)	(35–95)	(45–82)
N	40	13	9	10	9	10	6
G. canescens:	36	15 ± 5	—	21.5 ± 3.5	—	—	—
	—	(10–20)	—	(18–25)	—	—	—
N	1	2	—	2	—	—	—

[a] SE = standard error.

[b] N = number of flower heads analyzed.

small heads of *H. acradenius* (12.3 ± 5.9%), which unlike the other hosts, bloomed in the fall instead of the spring. The percentage of *E. virginensis* flower heads with *T. nigricornis* plus at least one other species ranged from 28.4 to 71.4% (49.3 ± 4.8%); which was higher than the range found in the medium-sized flower heads of *E. farinosa, E. fructescens,* and *V. deltoidea*; 16.0 to 71.0% (40.1 ± 3.2%), 9.6 to 83% (35.7 ± 4.4%), 14.3 to 43% (31.5 ± 6.0%), respectively. Samples of *H. acradenius* with multiple insect infestations were rare. The insects that co-occurred with *T. nigricornis* in the host plant species examined were *Melanagromyza viridis* (Frost)

Table 10. Number of achenes per head that remained intact in flower heads with multiple infestations of insects including *Trupanea nigricornis.*

Host Plant	Number of Heads Examined	Mean Number of Intact Achenes per Head ± SE[a] (Range)	Number of Insects[b] per Head					
			T.n.	M.v.	N.f.	Lep.	C.g.	C.f.
E. farinosa	22	30.1 ± 2.6 (12–58)	1	—	1	—	—	—
	3	24.3 ± 5.4 (18–35)	2	1	—	—	—	—
	2	51 ± 1 (50–52)	1	1	—	—	—	—
	3	39.3 ± 9 (22–52)	1	—	—	1	—	—
	1	26	2	—	—	1	—	—
E. fructescens	3	21.7 ± 3.8 (16–29)	1	—	—	—	—	—
	6	20.3 ± 4.2 (10–40)	1–2	1	—	—	—	—
	1	10	1	1	—	—	6	—
	2	19 ± 6.9 (13–25)	1	—	—	—	—	1
	1	4	1	—	—	—	—	11
E. virginensis	8	89.5 ± 7 (66–121)	1	1	—	—	—	—
	3	95.3 ± 18.7 (59–121)	1	2–3	—	—	—	—
	10	67 ± 6.6 (32–105)	2–4	1–2	—	—	—	—
	2	73.5 ± 18.5 (55–92)	3–5	—	1	—	—	—
	1	90	4	2	1	—	—	—
	1	22	1	—	1	1	—	—
	2	49 ± 1 (48–50)	1–4	1	—	1	—	—
	2	24.5 ± 15.5 (9–40)	2–5	—	—	1	—	—
	4	62.8 ± 7 (40–99)	1	—	—	—	1–3	—
	4	74.3 ± 5.1 (61–89)	2–3	—	—	—	1–2	—

[a] SE = standard error.

[b] T.n. = *Trupanea nigricornis*; M.v. = *Melanogromyza viridis*; N.f. = *Neotephritis finalis*; Lep. = Lepidoptera larva (Noctuidae); C.g. = Cecidomyidae galls; C.f. = Cecidomyidae free-living larvae.

Table 11. Number of achenes per head that remained intact in flower heads with multiple infestations of insects including *Trupanea bisetosa*.

Host Plant	Number of Heads	Number of Intact Achenes per Head ± SE[a] (Range)	Number of Flies[b]/Head		
			T.b.	M.v.	N.f.
Helianthus annuus	3	105.7 ± 2.3 (102–110)	1–2	1	—
	3	56.3 ± 3 (52–62)	2–4	—	1
Geraea canescens	1	20	2	1	—
	1	21	1	2	—

[a] SE = standard error.

[b] T.b. = *Trupanea bisetosa*; M.v. = *Melanagromyza viridis*; N.f. = *Neotephritis finalis*.

(Agromyzidae), *Neotephritis finalis* (Loew) (Tephritidae), an undetermined species of *Smycronix* (Curculionidae), an undetermined Noctuidae species, and undetermined Cecidomyiidae gall formers and free-living, presumably predaceous, species.

The percentage flower head infestation by *T. bisetosa* and other insects in 15 *H. annuus* samples ranged from 9.1 to 61.9% (23 ± 4.2%). These were lower than the total percentage infestation of *T. nigricornis* hosts, with the exception of *H. acradenius.* The percentage of infested flower heads of *H. annuus* with *T. bisetosa* ranged from 3.6 to 59.5% (18.6 ± 4.3%). Few heads, 0–25% (3.0 ± 1.7%), were infested with *T. bisetosa* and other insects contemporaneously. The other insects that occurred with *T. bisetosa* in *H. annuus* flower heads were *M. viridis, N. finalis, Paracantha cultaris* (Coquillett) (Tephritidae), and an undetermined species of Noctuidae.

Only one sample of *H. niveus* yielded *T. bisetosa* with 4% of heads infested solely by this species. An additional 4% had mainly *M. viridis* occuring in flower heads.

The percentages of flower heads of *G. canescens* that yielded *T. bisetosa* were low, ranging from 1.2 to 13.3% (5.5 ± 4%), and there were few heads, 0–4% (1.3 ± 1.3%), with multiple infestations. The samples of *G. canescens* mainly yielded *M. viridis.*

Trupanea nigricornis and *T. bisetosa* populations showed several differences in the manner in which they infested their hosts. 1) The percentage flower heads infested by *T. bisetosa* was lower on average than the percentage of flower heads infested by *T. nigricornis,* except in *H. acradenius.* 2) The number of samples of *T. bisetosa* hosts that did not yield any *T. bisetosa* was greater than the number of samples of *T. nigricornis* hosts that did not yield any *T. nigricornis.* Among samples of *T. nigricornis* hosts, one of 10 (10%) *E. virginensis,* two of 17 (10.5%) *E. fructescens,* three of eight (37.5%) *H. acradenius* and two of eight (25%) *V. deltoidea* samples were not infested with *T. nigricornis.* All samples taken of *E. farinosa* yielded *T. nigricornis.* Among samples of *T. bisetosa* hosts, 19 of 33 (57.6%) samples of *H. annuus,* two of four (50%) *H. niveus,* and six of nine (66.7%) *G. canescens* were not infested with *T. bisetosa.* 3) Percentage infestation by *T. bisetosa* varied during the year. Infestations of *H. annuus* heads by *T. bisetosa* were highest late in the fall, when the densities of the plants in flower decreased. Percentage infestations were low to moderate in the spring, depending on the availability of soil moisture, and were low in the summer.

The total numbers and identities of other insects reared from flower heads of samples of *T. nigricornis* and *T. bisetosa* hosts are listed in Table 12. Members of other guilds including polyphagous, phytophagous insects and general predators and parasites were not listed. The agromyzid, *M. viridis,* and the tephritid, *N. finalis,* infested most plant species that host *T. nigricornis* and *T. bisetosa.* Adults of *M. viridis* were reared

Table 12. Total numbers of insects, by species, that were reared from samples of flower heads of *Trupanea nigricornis* and *T. bisetosa* hosts collected during 1987–1992.

Hosts, Number of Samples	Insect Species[a]:						Parasite Species[b]:					
	T.n.	T.b.	N.f.	M.v.	T.w.	P.c.	H	P	C	Pr	E	Others
E. farinosa:	1,379	—	934	55	1	—	517	241	46	2	8	—
N = 29	29	—	26	8	1	—	29	20	6	2	2	—
E. fructescens:	212	—	15	62	—	—	59	40	9	2	1	C, C.f.
N = 18	18	—	4	11	—	—	10	8	3	1	1	4, 1
E. virginensis:	204	—	22	40	—	—	30	31	82	—	5	C, C.f.
N = 10	10	—	4	6	—	—	6	7	7	—	2	6, 3
V. deltoidea:	26	—	—	20	—	—	2	2	—	—	—	C.f.
N = 5	5	—	—	3	—	—	2	1	—	—	—	1
H. acradenius:	63	—	—	—	1	—	1	39	—	—	—	2U.f
N = 4	4	—	—	—	1	—	1	3	—	—	—	1
G. viscida:	1	—	—	5	—	—	—	—	—	—	—	—
N = 1	1	—	—	1	—	—	—	—	—	—	—	—
G. canescens:	—	21	—	1,256	—	—	—	—	—	—	—	—
N = 7	—	3	—	7	—	—	—	—	—	—	—	—
H. annuus:	—	763	278	127	—	26	—	107	—	—	—	—
N = 34	—	34	9	9	—	7	—	18	—	—	—	—
H. niveus:	—	2	—	12	—	—	—	—	—	—	—	—
N = 2	—	1	—	2	—	—	—	—	—	—	—	—

[a] T.n. = *Trupanea nigricornis* (Tephritidae); T.b. = *Trupanea bisetosa* (Tephritidae); N.f. = *Neotephritis finalis* (Tephritidae); M.v. = *Melanogromyza viridis*; *T. wheeleri* = *Trupanea wheeleri* (Tephritidae); P.c. = *Paracantha cultaris* (Tephritidae).

[b] H = *Halticoptera* sp. (Pteromalidae); P = *Pteromalus* sp. (Pteromalidae); C = *Colotrechnus ignotus* Burks (Ptermalidae); Pr = Perilampidae; E = *Eurytoma* sp. (Eurytomidae); C = gall-forming Cecidomyiidae; C.f. = free-living Cecidomyiidae; U.f. = *Urophora formosa* (Tephritidae).

from all *T. nigricornis* hosts studied, except *Haplopappus acradenius.* They were also common in *T. bisetosa* hosts, and heavily infested all samples of flower heads of *G. canescens.* Adults of *N. finalis* were reared from all *Encelia* spp. studied as hosts of *T. nigricornis,* as well as from *H. annuus.* Less common species that occurred in *T. nigriconis* hosts were the tephritid *Trupanea wheeleri* Curran, found in one sample each of *H. acradenius* and *E. farinosa,* and the tephritid, *Goedenia* (formerly *Urophora*) *formosa* (Coquillett), that emerged from one sample of *H. acradenius.* Gallicolous as well as free-living, probably predaceous, cecidomyiid larvae were found in flower heads of *E. fructescens, E. virginensis,* and *V. deltoidea.* The tephritid *Paracantha cultaris* (Coquillett) was only reared from *H. annuus.*

Among the hosts of *T. nigricornis, E. farinosa,* and then *E. fructescens* and *E. virginensis,* were richer in numbers and abundance of associated insect species, as well as their parasites, than *V. deltoidea, H. acradenius,* and *G. viscida* (Table 12). The flower heads of *E. farinosa* and *E. fructescens* were exploited mainly by three dipterous species, *T. nigricornis, N. finalis,* and *M. viridis,* and their five species of pteromalid parasites. Flower heads of *E. virginensis* were utilized by the same three species of flies, but yielded only four species of parasites. Two other hosts of *T. nigricornis* studied, *V. deltoidea* and *H. acradenius,* were infested with mainly two species of flies, *T. nigricornis* and *M. viridis* in *V. deltoidea,* and *T. nigricornis* and *T. wheeleri* in *H. acradenius,* and two species of parasites (Table 12).

Among the three *T. bisetosa* host plants studied, the flower heads of *H. annuus* had the most species infesting them (Table 12). They were utilized by four species of flies, but only one species of parasite. The other hosts, *H. niveus* and *G. canescens,* were infested with two species of flies, and no parasites were reared from them.

Flower guild resource utilization.—The most common insects that fed within flower heads and shared space and food resources with *T. nigricornis* and *T. bisetosa* were *M. viridis, N. finalis* and a noctuid larva. Other insects like *P. cultaris* and larvae of the weevil, *Smicronyx* sp., infested host plants of *T. bisetosa* and *T. nigricornis,* respectively, but they did not share the same flower heads.

The agromyzid, *M. viridis,* was common in host plants of both *T. nigricornis* and *T. bisetosa.* Its larvae fed mainly in the upper part of the achenes and in the florets. The puparia were slightly smaller than those of *T. nigricornis*; averaging 1.1 ± 0.02 (0.8–1.3) mm in width and 2.5 ± 0.03 (1.5–3.1) mm in length (n = 60). They were easily recognized by their yellow color and their long posterior spiracles. The number of achenes damaged by one *M. viridis* larva ranged between 2 and 15. Among *T. nigricornis* hosts, the mean number of damaged achenes was 6.3 ± 0.6 (n = 12; range = 3–10) in *E. farinosa,* 6.6 ± 0.3 (n = 38; range 4–12) in *E. virginensis,* and 8.4 ± 0.5 (n = 27; range 4–15) in *E. fructescens.* This was less than the mean number of achenes damaged by *T. nigricornis* in these hosts (6–8 for *M. viridis* as opposed to 8–9 for *T. nigricornis*). In *T. bisetosa* hosts, the average number of achenes damaged by a single *M. viridis* larva was 5.1 ± 0.3 (n = 15; range = 4–8) in *H. niveus,* 5.4 ± 0.2 (n = 75; range = 3–9) in *G. canescens,* and 3.8 ± 0.6 (n = 10; range = 2–9) in *H. annuus.* Like *T. bisetosa,* agromyzid larvae caused less damage in *H. annuus* heads; however, a full size *T. bisetosa* larva destroyed more *H. annuus* achenes (6.5/per larva) than a full-sized *M. viridis* larva.

Like *T. nigricornis* and *T. bisetosa, M. viridis* did not use all of the achene resources present in a flower head. The numbers of intact achenes that remained in heads of different hosts infested with one or several *M. viridis* larvae are summarized in Table 13. The data show that *M. viridis* destroyed only a portion of the achenes in a given flower head, even when several larvae developed in the same head.

The tephritid *Neotephritis finalis* also was a common associate in both *T. nigricornis* and *T. bisetosa* hosts. Its larvae fed in the achenes, sometimes producing a little frass during their feeding. The puparia of *N. finalis* were easy to recognize; they were brown and measured 1.5 ± 0.02 (1.4–1.6) mm in diameter and 3.4 ± 0.02 (3–3.8) mm in length (n = 65). The mean number of achenes damaged by one larva of *N. finalis* was 13.3 ± 0.4 (n = 65; range = 9–22) in *E. farinosa.* This was higher than the damage caused by a single *T. nigricornis* larva. The mean number of achenes left intact in heads of *E. farinosa* infested with *N. finalis* was 33.7 ± 1.9 (n = 31; range = 13–55) in heads with one larva and 25.9 ± 1.8 (n = 23; range = 11–47) in heads with two larvae. The mean number of achenes damaged by one larva of *N. finalis* in *H. annuus* was 5.7 ± 0.4 (n = 10; range = 4–8). The mean number of undamaged achenes per head infested with one *N. finalis* larva in *H. annuus* was 94.6 ± 5.4 (n = 10; range 59–120). Thus, *N. finalis* also did not utilize all the achenes present in the flower heads of its hosts.

Noctuid larvae co-infested host plants of both *T. nigricornis* and *T. bisetosa.* Each noctuid larva fed within several flower heads over the course of its development. The average number of achenes damaged per flower head by one noctuid larva was (21.5 ± 1.7) (range = 9–40) in *E. farinosa*; and ranged from 3–20 achenes in *E. virginensis*; from 10 to all achenes, plus receptacles, in *E. fructescens*; from 10 to all achenes in *H. acradenius,* and from 7–60 achenes in *H. annuus.*

Curculionid larvae, *Smycronix* sp., infested the small flower heads of *H. acradenius.* Upon completion of its development each weevil larva had destroyed all

Table 13. Numbers of achenes remaining intact in flower heads of *Trupanea nigricornis* and *T. bisetosa* host plants infested with one or several *Melanogromyza viridis* third instars.

	Number of Intact Achenes ± SE[b] per Head (Range) in Heads Infested with:				
Host Plant	1 Larva	2 Larvae	3 Larvae	4 Larvae	5 Larvae
G. canescens:	30.9 ± 2.4	26 ± 1.9	18.4 ± 2.5	17 ± 3.3	17.3 ± 3.9
	(17–58)	(10–45)	(4–38)	(9–25)	(12–25)
N[a]	25	23	13	4	3
H. niveus:	31.6 ± 1.7	33.3 ± 3.4	—	—	—
	(20–40)	(23–40)	—	—	—
N	24	7	—	—	—
H. annuus:	99 ± 10	—	—	—	—
	(60–140)	—	—	—	—
N	10	—	—	—	—
E. virginensis:	83.7 ± 8.2	88.6 ± 10.9	71 ± 6.7	—	—
	(58–122)	(51–121)	(48–105)	—	—
N	7	7	9	—	—
E. fructescens:	25.1 ± 1.6	—	—	—	—
	(12–43)	—	—	—	—
N	27	—	—	—	—
E. farinosa:	56.3 ± 4.1	—	—	—	—
	(34–82)	—	—	—	—
N	12	—	—	—	—

[a] N = number of analyzed flower heads.
[b] SE = standard error.

the achenes in *H. acradenius.* Thus, unlike *T. nigricornis,* the weevil exhausted all the food resources present in the flower head of its hosts.

The height above the surface of the receptacle at which *T. nigricornis* and other insects associated with *T. nigricornis* hosts were found in the flower heads varied according to the plant and insect species. In the medium-size heads of *E. farinosa,* most (81%) puparia and third instars of *T. nigricornis* were found between 0.4 and 1 mm above the receptacle. A few (7%) third instars fed upon and later formed puparia atop the receptacle. In six of 15 cases (40%), these latter larvae slightly scored the receptacle after destroying the achene in which they fed before moving to adjacent achenes. In the medium-size, elongate heads of *E. fructescens,* very few (0.8%) third instars were found feeding on the receptacle and consequently no scoring of the receptacle occurred. Most larvae in *E. fructescens* were found between 0.6–2 mm above the receptacle. In the large heads of *E. virginensis,* few (1.2%) larvae fed on the receptacle and the majority were found at various levels, between 0.8 and 3.2 mm above the receptacle. Contrary to *Encelia* spp., most (90%) of the larvae and puparia in the small heads of *H. acradenius* were found at the surface of the receptacle. Consequently, the receptacle was scored 57% of the time. In the medium-size heads of *V. deltoidea,* larvae were found between 0 and 1.2 mm above the receptacle; however, no scoring of the receptacle was observed.

The heights above the receptacle at which *Trupanea bisetosa* larvae and puparia were found also varied among the host species. In *G. canescens,* the larvae fed mainly between 1 and 2 mm above the receptacle. In the large heads of *H. annuus,* 89% of the larvae and puparia were found between 0.8 and 2 mm above the receptacle and only 2% were found at the surface of the receptacle. No scoring of the receptacle by *T. bisetosa* was observed in *H. annuus* flower heads.

Third instars and puparia of *M. viridis* were mainly found near the achene/floret junction in the flower heads of *T. nigricornis* hosts. Third instars of *M. viridis* were found at 1–2, 0.4–2 and 0.4–2.8 mm above the receptacle in heads of *G. viscida, V. deltoidea* and *E. farinosa,* respectively. There was no scoring of the receptacle by *M. viridis* larvae in any host.

The positions of *M. viridis* larvae and puparia in the flower heads of *T. bisetosa* hosts varied according to the plant species. The larvae and puparia of *M. viridis* were found at 2–3.2 mm above the receptacle in *H. annuus* heads, which was higher than in *G. canescens* heads at 0–2 mm above the receptacle. This was because the larvae fed in the florets in the large heads of *H. annuus,* but mainly fed in the soft achenes and lower parts of the florets in the medium-size heads of *G. canescens.*

The levels at which *N. finalis* larvae and puparia were found in the flower heads of *T. nigricornis* and *T. bisetosa* also varied among its hosts. In *E. farinosa* heads, most *N. finalis* third instars fed, then pupariated, atop the receptacle. Half of the time, they scored the receptacle creating a shallow cavity (0.5–1 mm deep) that was wider (1.5–1.8 mm in diameter, N = 16) than that of *T. nigricornis.* In other hosts, *N. finalis* larvae and puparia were found at various levels above the receptacle: 0.8–2 mm in *E. fructescens,* 0.8–1.6 mm in *H. annuus,* and 0.8–3.2 mm in *E. virginensis.* No scoring of the receptacle was observed in the large heads of *E. virginenis.*

In *H. acradenius* and *E. fructescens,* noctuid larvae fed on the receptacle after destroying the achenes; whereas, in *H. annuus,* they fed inside the receptacle either without damaging the achenes or damaging the achene bases. In *E. virginensis* and *E. farinosa,* noctuid larvae were found at various levels and destroyed the achenes, but without feeding in the receptacles.

DISCUSSION

Comparison of *T. nigricornis* and *T. bisetosa* resource utilization and interspecific interactions did not illuminate any major differences that could be implicated in the "why" these two probable sister species have diverged so intricately in their host associations. Hosts of *T. nigricornis,* such as *Encelia* spp., grow right next to *H. annuus,* the primary host of *T. bisetosa,* yet the two tephritid species do not interact in any way that we have observed.

How these species used their resources included subtle differences. *Trupanea nigricornis* females apparently adjusted the number of eggs laid according to the size of the flower heads in order to avoid intraspecific competition (Headrick and Goeden 1998). Zwölfer (1973) reported that "... the intensity of competition within an individual flower head is dependent on the size of the head, the numbers and sizes of competing individuals, and their mode of feeding." Further, Zwölfer (1988) found a significant correlation between the body size of insects exploiting thistle flower heads and the diameter of the flower heads. Similar results were observed herein as *T. nigricornis* puparia were generally larger in larger sized flower heads, but not as large as *T. bisetosa* puparia that occurred in the large flower heads of *H. annuus.*

The flower heads of *H. annuus* did not support more species of insects than the smaller heads of the other hosts studied. Regression analysis showed that the number of species was poorly correlated with the diameter (R = 0.06) and dry weight (R = 0.07) of the flower heads of *T. nigricornis* and *T. bisetosa* host plants. This phenomenon has been observed for other tephritid systems and is summarized by Headrick and Goeden (1998).

Scoring of the receptacle is a facultative mode of resource exploitation that can provide extra nutrients to allow for continued development within a flower head. In *T. nigricornis* receptacle scoring is different from what Headrick and Goeden (1990) originally reported for *Paracantha gentilis.* Third instars of *P. gentilis* scored the receptacle at the center of the flower heads when they occurred at high densities (three or more larvae per head). These depressions provided the larvae with enough sap and nutrients to complete their development when the central achenes were depleted (Headrick and Goeden 1990). The occasional scoring of the receptacle by *T. nigricornis* produced smaller cavities than those of *P. gentilis,* and contrary to *P. gentilis,* a *T. nigricornis* larva produced three to four small cavities instead of a large one and the cavities were not located at the center of the flower head but they were found at the base of the three to four achenes in which the larva had fed. Also, occasional scoring of the receptacle by *T. nigricornis* was observed in heads with one larva as well as in heads with two to four larvae. Hence, this process in *T. nigricornis* is not related to larval density as in *P. gentilis,* but still may provide nutrients for development not otherwise obtained.

Interspecific competition among the different insect species infesting the flower heads of *T. nigricronis* and *T. bisetosa* hosts was low because few heads sampled had multiple infestations and where they occurred many achenes were left intact. Several strategies may be utilized to minimize interspecific competition. First, the timing of infestations differed among the different insect species. Noctuid larvae infested the heads of *H. annuus* early in the fall (September); whereas, *T. bisetosa* larval populations increased later in the fall. *Paracantha cultaris* infested the young heads of *H. annuus* late in the spring and in the summer when *T. bisetosa* populations were low. *Neotephitis finalis* infested the flower heads of *E. farinosa* later in the season than *T. nigricornis.* Both *T. nigricornis* and *M. viridis* attacked the flower heads of *E. farinosa* early in the season.

The second strategy may be temporal partitioning. Oviposition in different stages of flower heads may lead to exploitation of different stages of the flower heads by larvae of different species. In *H. annuus,* the eggs and first instars of *P. gentilis* developed in mature heads, whereas eggs and first instars of *T. bisetosa* developed in the closed immature heads. However, eggs of *T. bisetosa* and *N. finalis* were often found in the same stage heads. Females of both species may deposit a short term oviposition-deterring pheromone; however, there is no evidence yet of the presence of such pheromones. The larvae of unidentified noctuids infested mature heads of all *T. nigricornis* hosts. The heads infested by noctuids often contained puparia from which *T. nigricornis* adults had emerged.

The third strategy may involve spatial partitioning of the flower heads. In *Encelia* sp., most larvae of *M. viridis* fed in the florets, while *T. nigricornis* and *N. finalis* larvae fed in the achenes, closer to the receptacle. When larvae of *T. nigricornis* and *N. finalis* occurred in the same heads, they fed either at different depths in the achenes, with most *N. finalis* larvae at the base of receptacle, or at similar levels but separated by one or several achenes. In the large heads of *H. annuus,* the larvae of *T. bisetosa* and those of *N. finalis* occurred at different depths and also were separated by several achenes.

All three strategies used to minimize competition in this study fall under the "evasion strategy" described by Zwölfer (1979). He reported that insects sharing food resources have to follow one of two strategies for survival: evasion strategy or by maximizing their competitive capacity. Evasion strategies work to reduce competitive contacts between congeneric species. They involve processes like adopting a different time for oviposition, changing the time of larval development, or changing the feeding site. Such processes can create ecological character displacements. The disadvantage of these evasion strategies is that they promote specialization and narrow the food base of a species (Zwölfer 1979). If *T. nigricornis* and *T. bisetosa* are sister species, such evasion strategies could have been one of the factors accounting for the shift, i.e., adoption of a new host and specialization of *T. bisetosa* on *H. annuus* in order to avoid competition. Evasion strategies have been observed in the tephritid *P. gentilis* feeding on thistles and other tephritid systems (Headrick and Goeden 1998).

Interspecific competition is an important factor structuring insect communities (Strong et al. 1984). It was low among insect species exploiting the flower heads of *T. nigricornis* and *T. bisetosa* host plants because of the many evasion strategies adopted by these insects that reduced interspecific contacts and because so very few heads had multiple infestations and many achenes were left intact in these heads. Interspecific competition among phytophagous insects for food and space is generally uncommon and feeble (Strong et al. 1984). It is not the most important factor that shapes phytophagous insect communities. Most insect populations exist at low densities as a result of predation and parasitism. Consequently, natural enemies reduce interspecific competion because of their impact on insect populations (Strong et al. 1984).

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A NEW SPECIES OF *XIPHYDRIA* LATREILLE (HYMENOPTERA: XIPHYDRIIDAE) REARED FROM RIVER BIRCH, *BETULA NIGRA* L., IN NORTH AMERICA

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Abstract.—***Xiphydria decem*, n. sp.**, is described and separated from other North American species. It was reared from branches of river birch, *Betula nigra,* L. (Betulaceae) in Illinois.

Key Words: Symphyta, woodborer, woodwasp, hardwood, birch, Illinois

Larvae of *Xiphydria* Latreille bore and feed in the wood of small, dying or weakened tree branches. Most specimens are obtained by rearing, although adults sometimes show up in Malaise trap collections. Some species are relatively host specific; consequently, discovering an undescribed species in a host plant for which the wood-boring fauna has not been studied can be expected. NMS reared several specimens of an unusual *Xiphydria* from river birch, *Betula nigra* L., in southern Illinois. Although only three specimens have been reared, both sexes differ morphologically from all previously described species, and the species of host plant has not been recorded previously for *Xiphydria.* Here we describe and name this species in support of ongoing research by NMS on wood-boring Hymenoptera and their associated fungi.

Xiphydria decem Smith and Schiff, new species

(Figs. 1–4)

Female.—Length, 9.0 mm. Head black with narrow apex of mandible; small oval spot posterior to each lateral ocellus; and broad stripe from lower gena near malar area extending on gena, but not adjacent to eye, to top of head behind eye white. Thorax black with only narrow white spot on posterior corner of pronotal angles. Legs black with extreme base of foretibia, basal third of mid- and hindtibiae, and basal half of outer surface of mid- and hindbasitarsus white. Abdomen orange with basal plates, sheath, and cercus black, and with infuscate spot on apical sternite. Wings lightly, uniformly blackish; veins and stigma black.

Antenna 14-segmented. Reticulate sculpturation on head extending posterior to ocelli by about same distance as breadth of an ocellus; few ridges lateral to ocelli; reticulate sculpture on frons above antennae and between eyes (Fig. 1). Head in lateral view with 4–5 major striae on genae, few widely separated large punctures behind eyes; anteriorly protuberant; malar space (distance from eye to malar depression) less than width of first antennal segment (Fig. 2). Thorax with pronotum lacking sculpture on lower lateral half; punctures of mesepis-

Figs. 1–4. *Xiphydria decem.* 1, Head, dorsoanterior view. 2, Head, lateral view. 3, Thorax, lateral view. 4, Apex of lance and lancet.

ternum relatively dense and closely set, sparser on lower posterior margin and area between mesepisternum and mesosternum (Fig. 3). Lancet with 7 distinct serrulae, serrulae 1–3 rounded, serrulae from 4–7 flat and serrate (Fig. 4); apical 5 annuli straight. Sawsheath shorter than basal plate and about two-thirds length of hindtibia.

Male.—Length, 7.5 mm. Antenna with segments 1–5 orange to dark orange, segments 2–4 paler orange than segments 1 and 5; segments 6 to apex black. Head black with following white: mandible (except reddish apex); round spot on each side of clypeus; oval spot posterior to area between each lateral ocellus and eye; broad stripe from lower inner orbit continuing through malar area and extending on gena, but not adjacent to eye, to top of head behind each eye. Thorax black with following white: undersurface of cervical sclerite; posterior lateral margin of pronotum; lower third of pronotum laterally; tegula; oval streak on anterior margin of mesepisternum; oval spot on posterior margin of mesepisternum at center; elongate spot at junction of mesepisternum and mesosternum. Forecoxa black with white outer surface; midcoxa black with apical half white; hindcoxa mostly black with narrow white apex; rest of legs orange with fore- and midtarsi infuscate to black and apical 4 hindtarsal segments infuscate, darker than orange basitarsus. Abdomen orange with basal plates and anterior third of second tergum black; cercus brownish, darker than orange abdomen; small, faint, lateral yellowish-white spots on tergites 4–6. Wings lightly, uniformly blackish; veins and stigma dark brown to black.

Antenna 16 segmented. Sculpturation similar to that of female. Genitalia similar to that of *X. tibialis* Say (Smith 1976, figs. 28, 29).

Types.—Holotype ♀ labeled "USA: Illinois: Pope Co.: Hwy 145, 10 km S of Dixon Springs, Logs, April 3, 1999, Colls. Nathan M. Schiff & B. Planade," "emerged ex Betula nigra, May 1, 1999." Paratypes, 1 ♀ and 1 ♂ with the same data. All deposited in the National Museum of Natural History, Smithsonian Institution, Washington, DC.

Host and biological notes.—*Betula nigra* L. (Betulaceae), river birch. NMS collected three pieces of fallen, recently dead *Betula nigra* branches, only one of which contained *Xiphydria decem.* The piece that contained the larvae was 127 cm long, but the distal tip was broken when found. The end closest to the tree was 4.3 cm in diameter, and the distal end was 2.8 cm in diameter. There were three emergence holes (1.5, 1.6, and 1.6 mm in diameter) at branch diameters of 3.8, 3.8, and 3.2 cm, respectively. The first two emergence holes were 19.3 mm apart. The third emergence hole was 54 cm from the next nearest hole. The bark of mature *B. nigra* peels off the trunk like sheets of paper. The *X. decem* were in a younger distal shoot where the bark resembles young basswood or cherry. The wood samples with the exit holes are stored in the Jim Solomon Hardwood Borer Damage Collection at the Center for Bottomland Hardwoods, U.S. Forest Service, Stoneville, MS.

Etymology.—The specific epithet, "*decem,*" meaning ten in Latin, refers to the tenth species of *Xiphydria* known in North America.

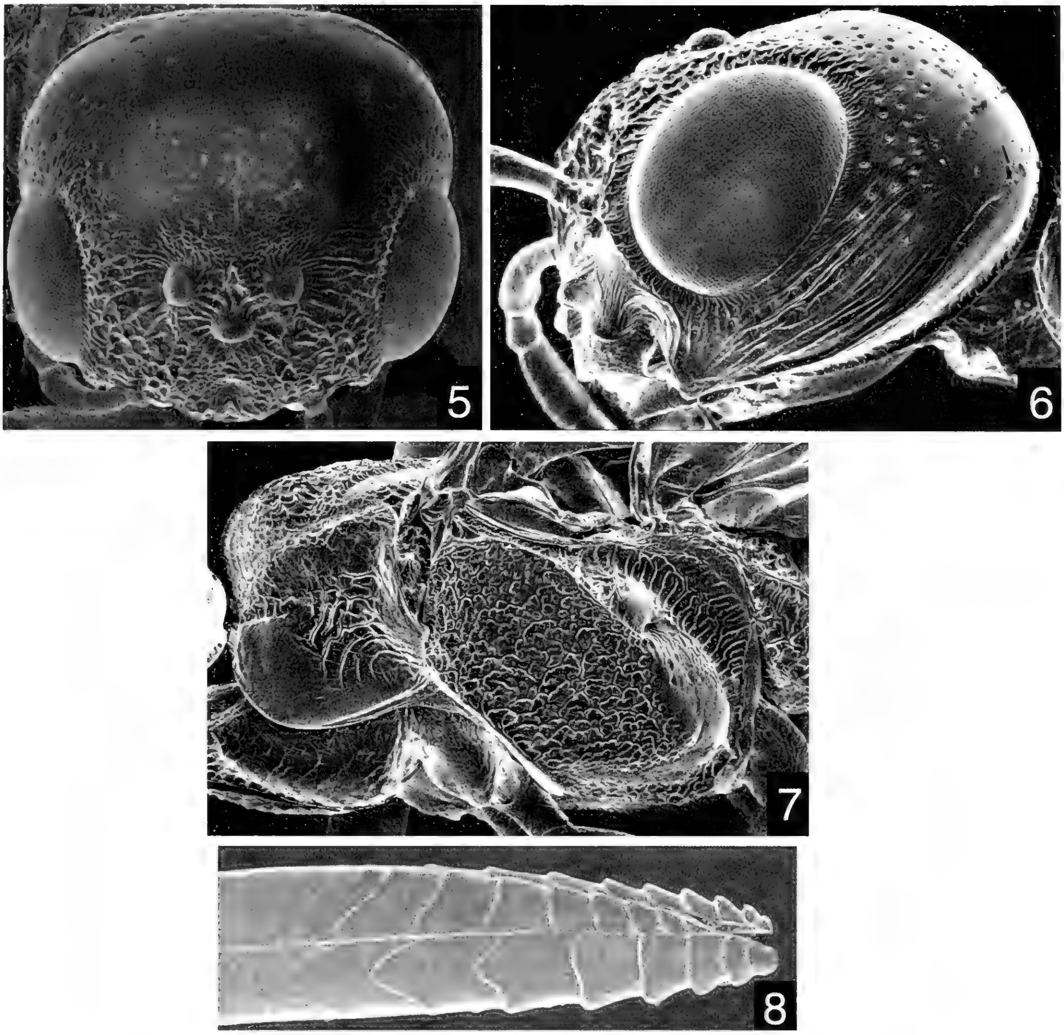
Remarks.—We have compared this new species with Palearctic and other Nearctic *Xiphydria,* but it is distinct from all species known to us.

The host, *Betula nigra* is restricted to stream banks and moist places at low to medium elevations from New Hampshire to northern Florida west through Ohio, Indiana, central Illinois, southern Wisconsin, to southern Minnesota, eastern Kansas eastern Oklahoma, and eastern Texas. Therefore, *X. decem* could be widely distributed in North America.

The female will run to couplet 6, *X. abdominalis* Say and *X. tibialis* Say in Smith's (1976) key. The male will not run past couplet 1 because of its almost entirely orange abdomen and mostly black mesepisternum. In coloration, *X. decem* is most similar to *X. abdominalis* and the red-abdomen form of *X. tibialis,* but structurally it is closest to *X. tibialis.* Coloration can be used to separate *X. decem,* but structure, especially sculpturation, also should be examined.

The female *Xiphydria abdominalis* has a long white streak on the head posterior to the area between the lateral ocellus and the eye, yellowish inner orbits, usually yellowish suprantennal area, usually reddish anterior portion of the pronotum, a white spot on the posteior margin of the pronotum, and pale orange tarsi. The male of *X. abdominalis* usually has the head, mesonotum, and mesepisternum extensively yellow with various sized black spots, and the legs entirely yellowish.

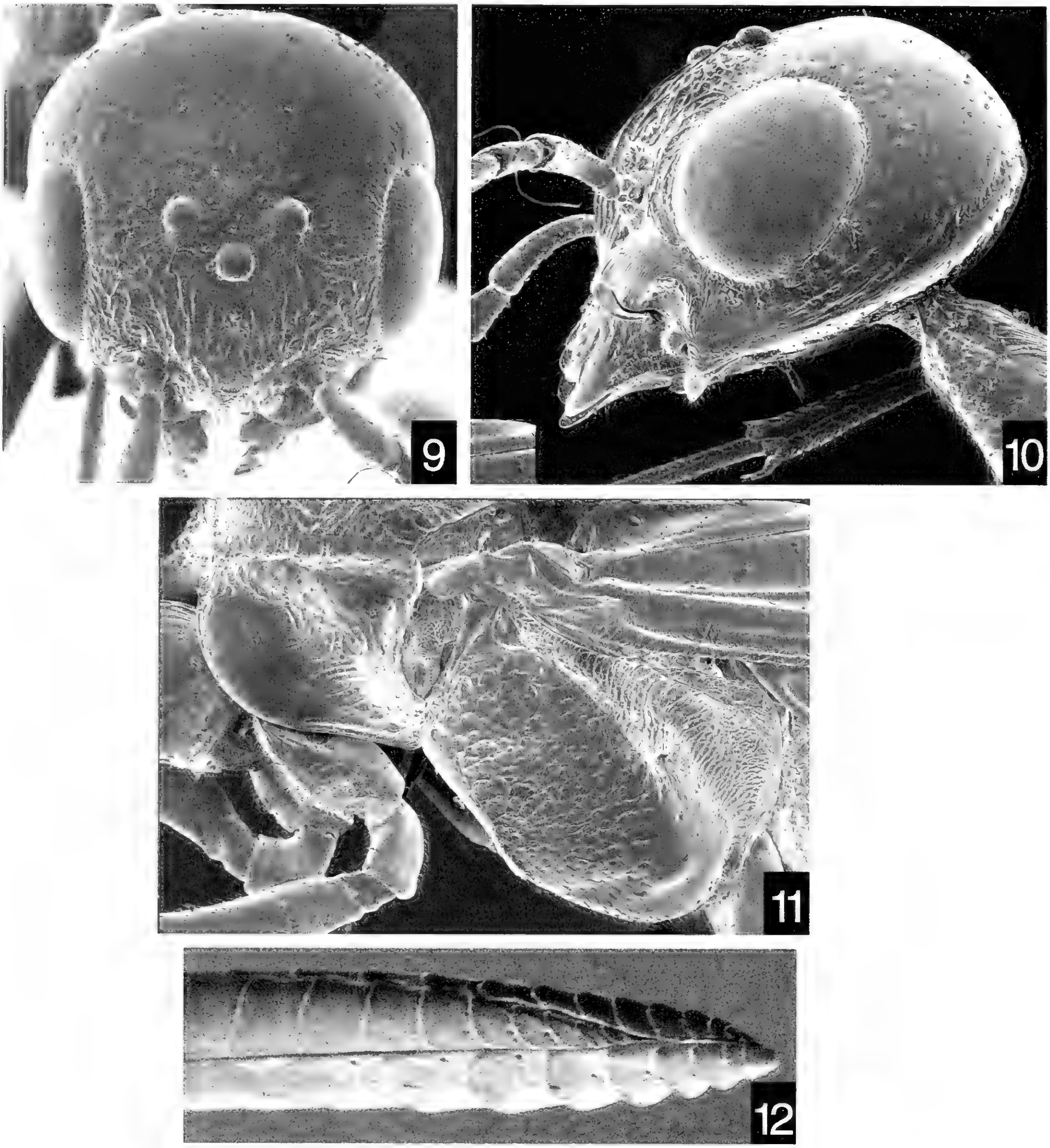
The female of the red-abdomen form of *X. tibialis* has lateral yellow spots on abdominal segments 2–5, the tibiae usually half or more white, the basitarsi and sometimes the second tarsal segments white, and



Figs. 5–8. *Xiphydria tibialis.* 5, Head, dorsoanterior view. 6, Head, lateral view. 7, Thorax, lateral view. 8, Apex of lance and lancet.

uniformly hyaline wings. The paler colored forms of *X. tibialis* males have extensive yellow on the head between the eyes, yellow antennae, and clypeus, yellow spots on the mesonotum, and mostly yellow mesipesternum and coxae.

Both *X. decem* and *X. tibialis* share the protuberant anterior part of the head when viewed in profile (Figs. 2, 6), extensive sculpturation on the head behind and lateral to the ocelli and on the gena (Figs. 1–2, 5–6), closely set sculpturation of the mesepisternum (Figs. 3, 7), similarly shaped serrulae of the lancet (Figs. 4, 8), and similar male genitalia. *Xiphydria abdominalis* has the front part of the head rounded when viewed in profile, none or weak sculpturation on the head behind and lateral to the ocelli and on the genae (Figs. 9–10), weaker sculpturation on the mesepisternum with wider shining interspaces and little or none on the lower mesepisternum and mesoster-



Figs. 9–12. *Xiphydria abdominalis*. 9, Head, dorsoanterior view. 10, Head, lateral view. 11, Thorax, lateral view. 12, Apex of lance and lancet.

num (Fig. 11), more rounded than serrate serrulae of the lancet (Fig. 12), and the valve of the male genitalia straighter and with a broad apical lobe (Smith 1976, fig. 34). As opposed *to X. tibialis, X. decem* has fewer striae and reticulations on the head behind and lateral to the ocelli, has fewer striae on the gena (Figs. 1–2, 5–6), lacks sculpturation on the lower half or more of the pronotum, has weaker sculpturation on the mesepisternum, especially at the junction of the mesepisternum and mesosternum (Figs. 3, 7), and has a sawsheath that is shorter than the basal plate.

The only other species of *Xiphydria* recorded from birch is *Xiphydria mellipes* Harris (Smith 1976). Its hosts are *Betula populifolia* Marsh., *B. papyrifera* Marsh., *B. lenta* L., *B. alleghaniensis* Britt. (= *B. lutea*), and *B. occidentalis* Hook. "Dead Betula nigra" was recorded as a host of *X. tibialis* by Smith (1976), but label data such as this sometimes need confirmation. *Xiphydria abdominalis* is mostly restricted to basswood, *Tilia americana* L., and the most common hosts recorded for *X. tibialis* are *Ulmus* sp. and *Prunus* sp., although NMS reared it from *Acer* sp. A number of other hosts have been recorded for *X. tibialis*, but these await confirmation (Smith 1976).

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GLYPHIDOCERA WALSINGHAM (LEPIDOPTERA: GELECHIOIDEA: GLYPHIDOCERIDAE) OF CERRO DE LA NEBLINA AND ADJACENT AREAS IN AMAZONAS, VENEZUELA

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Abstract.—Sixteen **new species** of *Glyphidocera* from Cerro de la Neblina and adjacent areas in Amazonas, Venezuela are described: ***G. acuminae, G. alexandrae, G. basipunctella, G. brevisella, G. brocha, G. brunnella, G. castanella, G. chungchinmookara, G. dentata, G. digitella, G. garveyi, G. glowackae, G. hamatella, G. janae, G. lunata,*** and ***G. mumiella.*** Figures of the male antennal notch are given for three species, male abdominal sex scales, male and female genitalia, and imagos. A key is provided to facilitate identification of the species.

Key Words: Glyphidoceridae, Cerro de la Neblina, tropical rainforest, Venezuela, Amazonas, taxonomy, genitalia

Species of *Glyphidocera* Walsingham (1892) are small to medium-sized brownish moths that occur only in the New World. Based on studies by the first author, their greatest diversity is in the tropics where the number of described and undescribed species exceeds that of the temperate region by a ratio of nearly 10:1. The total number of recorded species for the genus is about 100. Host associations are unknown for all but *Glyphidocera juniperella,* which feeds on *Juniperus horizontalis* Moench (Cupressaceae) (Adamski and Brown 1987).

The genus *Glyphidocera* was proposed and its type-species, *G. audax,* was described from Saint Vincent Island in the West Indies and placed in the Gelechiidae by Walsingham (1892). The genus remained within Gelechiidae until Hodges (1978) transferred *Glyphidocera* and several other genera with perplexing characters to Symmocinae within Blastobasidae. Hodges later (1998) transferred Symmocinae to Autostichidae, except for *Glyphidocera,* which he elevated to Glyphidoceridae based upon 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 gelechioid genera, *Ptilostonychia* Walsingham and *stibarenches* Meyrick as junior synonyms of *Glyphidocera.*

Glyphidoceridae usually can be recognized by a combination of the following characters: male with 4th flagellomere with tuft of setiform scales on dorsal surface, extending over concavity with sex scales on 5th and 6th flagellomeres; valva narrowed basally, abruptly widened apically, with protracted apex, and base of costa with dig-

Fig. 1. Base camp seven at Cerro de Neblina, Venezuela.

itate protraction; sacculus twisted apically; gnathos projecting dorsally from beneath tuba analis; juxta basally narrow, fused to vinculum, expanded distolaterally, forming a ventral support for aedeagus; aedeagus curved, with medium to large cornutus or cornuti; female ductus bursae large, sclerotized, with funnel-shaped antrum; ductus seminalis spiralled from posterior half of corpus bursae, with internal sclerotized support; and corpus bursae with spinules, especially at the anterior end, and a sclerotized plate opposite base of ductus seminalis.

The purpose of this paper is to describe 16 new species of *Glyphidocera* from Cerro de la Neblina and San Carlos de Rio Negro in Amazonas, Venezuela. Although the sample size for each species treated herein is very low the authors feel it important to recognize these organisms because little is known of the family and little is known of the area from which they were collected. Moreover, it is unlikely that other collecting expeditions will be made to Cerro de la Neblina in the near future.

All specimens were collected during the U.S. Scientists' Expedition to the Neblina tepuis during 1984. Specimens from San Carlos de Rio Negro (1°55′00″N 67°04′00″W) were collected about 0.5 km southeast of the village in lowland tropical rainforest. Specimens from Cerro de la Neblina were collected either at the basecamp (00°49′50″N 66°09′40″W; 140 m elevation) in lowland tropical forest or at Camp VII (00°50′40″N 65°58′10″W; 1,730–1,850 m elevation) on the tepuis. Camp VII was located on a rock outcrop covered by dense *Brocchinia tatei* L.B. Smith (Bromeliaceae) and scattered trees and shrubs, and broadened on one side by a gallery cloud forest (Fig. 1).

Kornerup and Wanscher (1978) was used as a color standard for descriptions of adult vestiture. Genitalia were dissected as described by Clarke (1941), except mercurochrome and chlorazol black were used as stains. Pinned specimens and genital preparations were examined with dissecting and compound microscopes. Measurements of wings were made using a calibrated ocular micrometer.

All specimens treated herein are in the National Museum of Natural History, Smithsonian Institution, Washington, D.C. (USNM).

The following species are described as part of several studies planned for the future that will help to estimate the species richness and provide data for hypotheses about phylogenetic relationships within the Glyphidoceridae and related Gelechioidea.

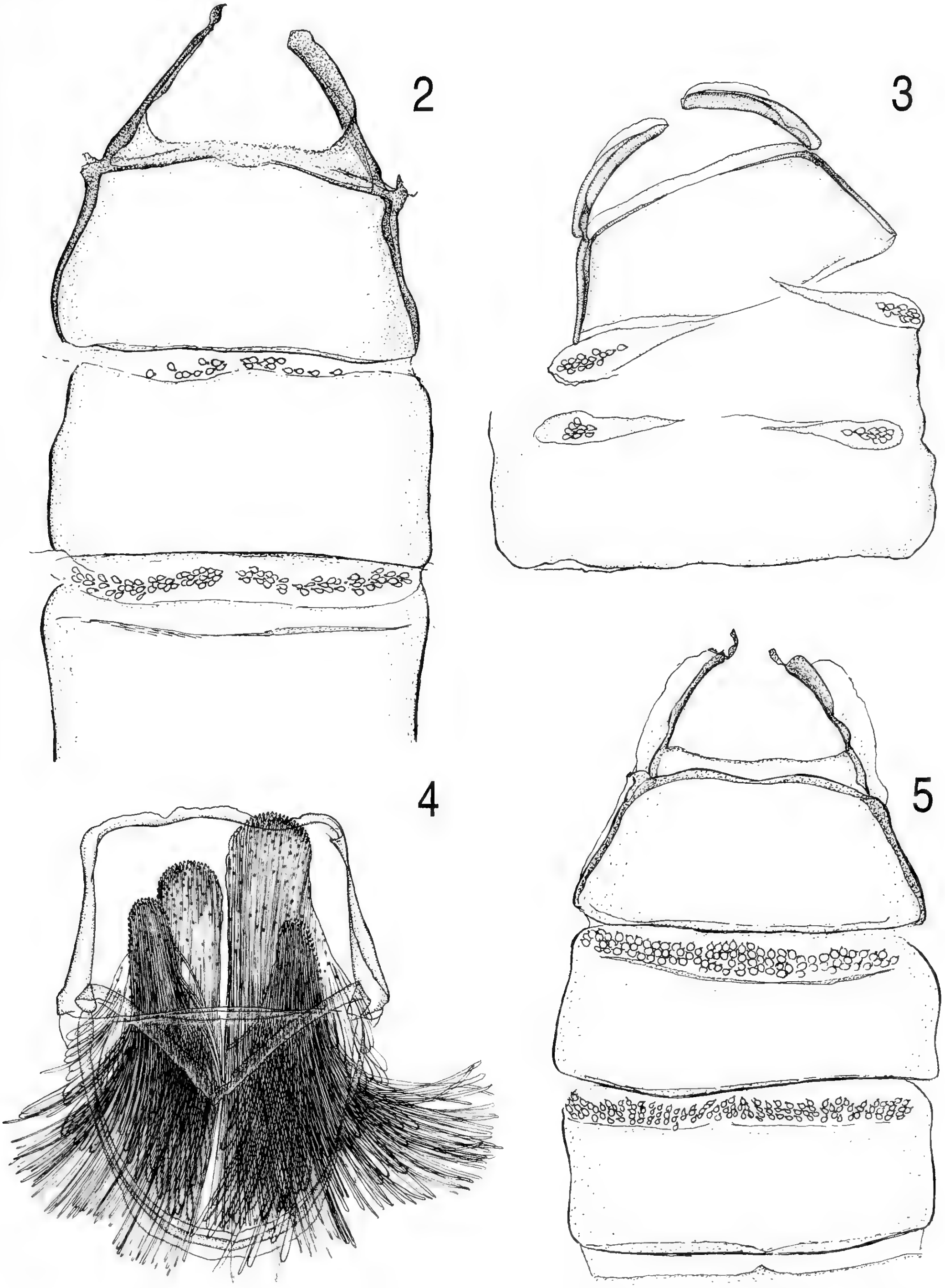
Key to Adult *Glyphidocera* of Cerro de la Neblina

1\. Male 2
– Female 14
2\. Forewing dark brown 3
– Forewing brown, pale brown, or brownish orange 4
3\. Anal area of hindwing with elongate patch of raised scales; outer margin of valva acuminate; vesica of aedeagus with large cornutus (Figs. 34–35) . . . . *mumiella*
– Anal area of hindwing without patch of raised scales; outer margin of valva broad, nearly truncate; vesica of aedeagus with small cornutus (Figs. 32–33) . . . . *garveyi*
4\. Dorsum of abdomen with specialized sex scales between segments 2–3, or 2–3 and 3–4 (Figs. 2–4, 6–9) 5
– Dorsum of abdomen without specialized sex scales 12
5\. Abdominal sex scales squamiform (Figs. 2–3, 6–9) 6
– Abdominal sex scales piliform (Fig. 4) . . . . *digitella*
6\. Abdominal sex scales restricted to lateral area of intersegmental membrane 7
– Abdominal sex scales not restricted to lateral area of intersegmental membrane (Figs. 2, 5–8) 8
7\. Abdominal sex scales on intersegmental membrane between terga 2-3 and 3-4 (Fig. 3); valva long, distally acuminate (Fig. 16); vesica of aedeagus with a cornutus (Fig. 17) . . . . *acuminae*
– Abdominal sex scales on intersegmental membrane between terga 2-3 (Fig. 9); valva short, distally truncate (Fig. 30); vesica of aedeagus with 10 cornuti (Fig. 31) . . . *brevisella*
8\. Abdominal sex scales separated by a small median space (Figs. 2, 6) 9
– Abdominal sex scales continuous (Figs. 5, 7–8) 10
9\. Apex of valva acuminate; apex of median lobe of gnathos rounded; aedeagus without apical spine (Figs. 14–15) . . . . *glowackae*
– Apex of valva bifurcate; apex of median lobe of gnathos pointed; aedeagus without apical spine (Figs. 22–23) . . . . *chungchinmookara*
10\. Abdomen with sex scales only between terga 2-3 . . . . *alexandrae*
– Abdomen with sex scales between terga 2-3 and 3-4 (Figs. 5, 7) 11
11\. Outer margin of valva with hooklike projection; uncus narrow; aedeagus parallel sided (Figs. 20–21) . . . . *hamatella*
– Outer margin of valva bifurcate; uncus wide; distal half of aedeagus broadened (Figs. 24–25) . . . . *basipunctella*
12\. Distal half of valva narrow (Fig. 36) . . *dentata*
– Distal half of valva broad (Figs. 12, 28) . . 13
13\. Lobe of dorsal articulation nearly straight; outer margin of valva with a large median toothlike projection (Fig. 12) . . . . *brocha*
– Lobe of dorsal articulation distally curved; outer margin of valva crescentshaped (Fig. 28) . . . . *lunata*
14\. Forewing dark brown . . . . *mumiella*
– Forewing brown, pale brown, or brownish orange 15
15\. Antrum narrow posteriorly (Figs. 38, 42) 16
– Antrum broad posteriorly (Figs. 39, 41, 43) 17
16\. Corpus bursae with large spinules near base of ductus seminalis; internal plate of corpus bursae distally narrowed (Fig. 38) . . *glowackae*
– Corpus bursae without large spinules near base of ductus seminalis; internal plate of corpus bursae broad throughout length (Fig. 42) . . . . *janae*
17\. Base of ductus seminalis narrow (Fig. 39) . . . . *hamatella*
– Base of ductus seminalis wide (Figs. 41, 43) 18
18\. Internal support of ductus seminalis short; internal plate of corpus bursae posteriorly broadened (Fig. 41) . . . . *brunnella*
– Internal support of ductus seminalis elongate; internal plate of corpus bursae subequal in width (Fig. 43) . . . . *castanella*

Glyphidocera brocha Adamski and Brown, new species

(Figs. 12–13, 44)

Diagnosis.—*Glyphidocera brocha* can be distinguished from other species of *Glyphi-*



Figs. 2–5. Male abdominal sex scales of *Glyphidocera*. 2, *G. glowackae*. 3, *G. acuminae*. 4, *G. digitella*. 5, *G. hamatella*.

docera by its small size (less than 5 mm wing length), pale brownish-orange ground color with three brown forewing spots, emarginate outer margin of the valva with a large median dentition, and a wide cornutus in the vesica. *Glyphidocera brocha* appears closest to *G. crocogramma* Meyrick but differs from the latter in having paler forewings and a more pointed median dentition on the outer margin of the valva.

Description.—*Head:* Vertex and frontoclypeus pale brownish orange intermixed with a few brown scales; labial palpus with outer surface pale brownish orange intermixed with a few brown scales, inner surface similar but with fewer brown scales; scape and flagellum pale brownish orange intermixed with brown scales, male 4th flagellomere with tuft of setiform scales on dorsal surface, extending over concavity with sex scales on 5th and 6th flagellomeres; proboscis pale brownish orange.

Thorax: Tegula and mesonotum brownish orange intermixed with some brown scales; legs pale brownish orange intermixed with some brown scales, white near apices of all segments and tarsomeres. Forewing (Fig. 44) length 4.9 mm (n = 1), mostly brownish orange intermixed with some brown scales; two brown discal spots present, one near base, one near apical end; one brown spot on CuP basad to spot near base of cell; marginal scales brown, fringe scales brown; undersurface pale brown except area between CuP and inner margin pale brownish orange. Hindwing with upper surface pale brown except area between cubitus and inner margin with elongate pale yellow scales; undersurface pale brown.

Abdomen: Male without specialized sex scales.

Male genitalia (Figs. 12–13): Uncus elongate, apically acuminate; ganthos laterally setose, with median lobe apically rounded; valva with apicoventral half beyond sacculus membranous and setose, apical margin with small dentitions dorsally and a single large dentate projection medially, base of costa with digitate projection, sacculus twisted apically; vesica with many microspinules and a large, wide cornutus.

Female genitalia: Unknown.

Holotype.—♂, "VENEZUELA: T[erritorio] F[ederal] Amaz[ona], Cerro de la Neblina, Basecamp, 0°50′N, 66°9′44″W, 140 m[eters], 13–20 Feb[ruary] 1984, D. Davis & T. McCabe"; "♂ Genitalia Slide by D A[damski] 3489, USNM 81642" [green label]. Deposited in the USNM.

Etymology.—The species epithet is derived from the Latin *brochus,* meaning "projecting teeth," and refers to the dentitions on the dorsal margin of the valva.

Glyphidocera glowackae Adamski and Brown, new species

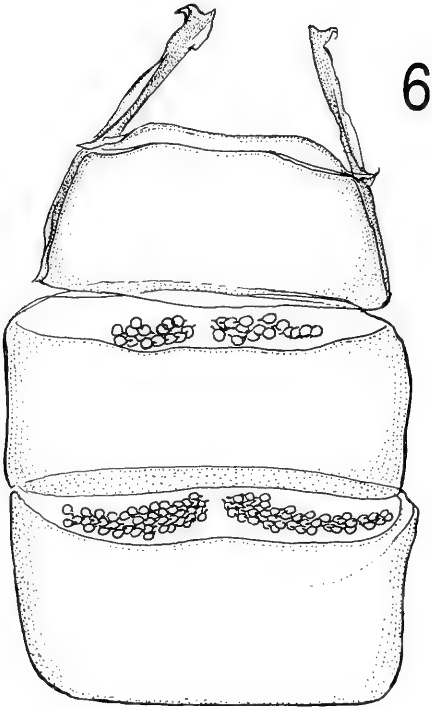
(Figs. 2, 14–15, 38, 45)

Diagnosis.—*Glyphidocera glowackae* can be distinguished from other species of *Glyphidocera* by its large size (about 11 mm or greater), widely rounded apex of the gnathos, elongate and slightly widened apex of the valva, and vesica with a wide cornutus. *Glyphidocera glowackae* appears closest to *G. acuminae* but differs from the latter by its larger size of the moth, slightly broader apical area of the costa of the valva, shorter and more apically rounded gnathos, and larger cornutus rather than a pair of subequal cornuti.

Description.—*Head:* Vertex and frontoclypeus brown tipped with pale brown; labial palpus with outer surface pale brownish orange intermixed with brown scales; inner surface similar but with more pale brownish-orange scales; scape brown intermixed with some brownish-orange scales, flagellum brown; male 4th flagellomere

→

Figs. 6–9. Male abdominal sex scales of *Glyphidocera.* 6, *G. chungchinmookara.* 7, *G. basipunctella.* 8, *G. alexandrae.* 9, *G. brevisella.*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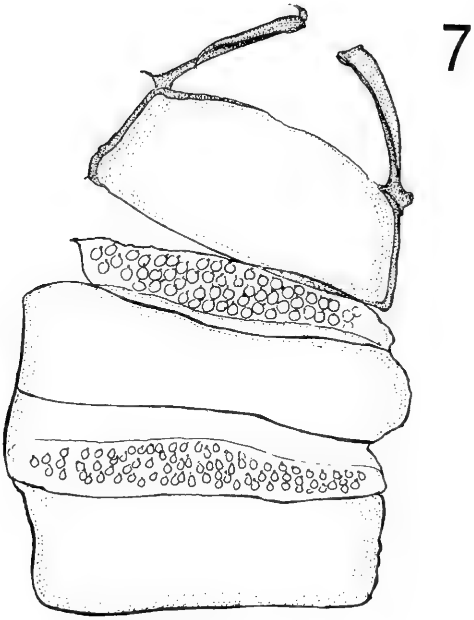
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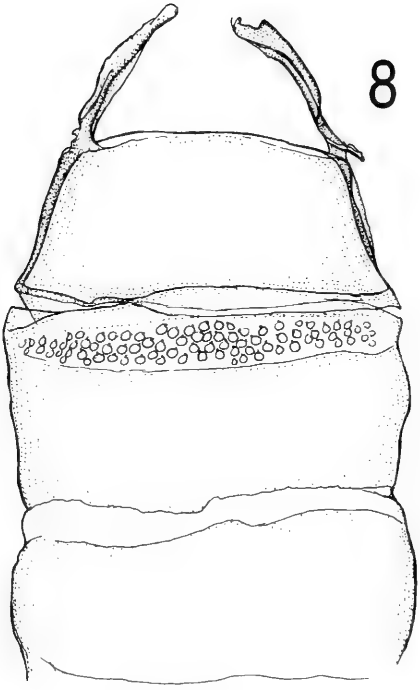
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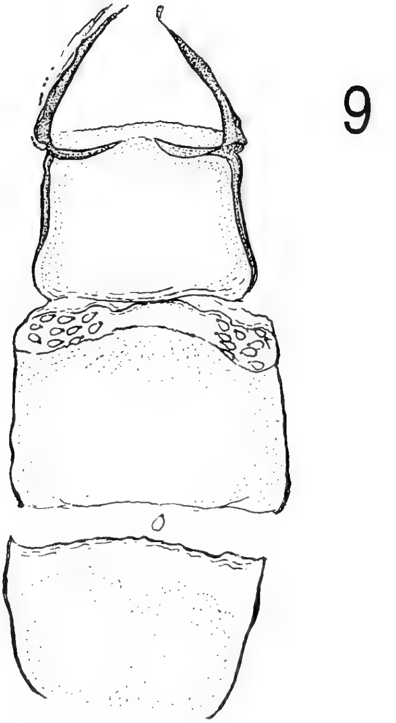
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with a tuft of setiform scales on dorsal surface, extending over concavity on 5th and 6th flagellomeres; inner surfaces of 5th and 6th flagellomeres smooth, demarcated with sex scales with decumbent apices (Figs. 62–63); proboscis pale brownish orange.

Thorax: Tegula and mesonotum brownish orange intermixed with brown scales; legs brown intermixed with brownish-orange scales on midsegment and to near apices of all segments and tarsomeres. Forewing (Fig. 45) length 10.9–12.2 mm (n = 5), pale brownish orange intermixed with several brown scales; two brown discal spots, one near base, the other near apical end; one brown spot on CuP basad to spot near base of cell; marginal scales brown, fringe scales pale brownish orange tipped with brown; undersurface pale brown. Hindwing with upper surface pale brown, area posterior to cubitus with some elongate scales; undersurface pale brown.

Abdomen (Fig. 2): Male with fewer squamiform sex scales on intersegmental membrane between terga 2-3 than between terga 3-4.

Male genitalia (Figs. 14–15): Uncus elongate, flattened dorsoventrally; gnathos with median lobe apically rounded; valva with apicoventral half beyond sacculus and basal area between costa and sacculus membranous, apicoventral area densely setose, apex attenuate, base of costa with digitate projection, sacculus twisted apically; vesica with many microspinules and a wide cornutus.

Female genitalia (Fig. 38): Papillae anales conical, with long and short setae intermixed; eighth segment with tergum longer than sternum; anterior apophyses posteriorly bifurcate, connecting with eighth tergum and eighth sternum; antrum funnel-shaped, slightly spinulate, with two internal flanges anteriorly; ductus seminalis spiralling from posterior end of corpus bursae, with long, spiralled internal support; corpus bursae spinulate, larger spinules near base of ductus seminalis, a large sclerotization opposite base of ductus seminalis, which constricts corpus bursae to form a protuberant lobe.

Holotype.—♂, "VENEZUELA: T[erritorio] F[ederal] Amaz[ona], Cerro de la Neblina, Camp VII, 1,850 m[eters], 0°51′N, 65°58′W, 2–4 Dec[ember] 1984, R.L. Brown"; "♂ Genitalia Slide by D. A[damski] 4070, USNM 81200" [green label]. Deposited in the USNM.

Paratypes.—3 ♂, 1 ♀. All paratypes with same label data as holotype except, "♂ Genitalia Slide by DA 4068, USNM 81198" [green label]; "♂ Genitalia Slide by DA 3477, USNM 81630" [green label]; "♂ Genitalia Slide by DA 4069, USNM 81199" [green label]; "♀ Genitalia Slide by DA 3478, USNM 81631" [green label]. All paratypes are in the USNM.

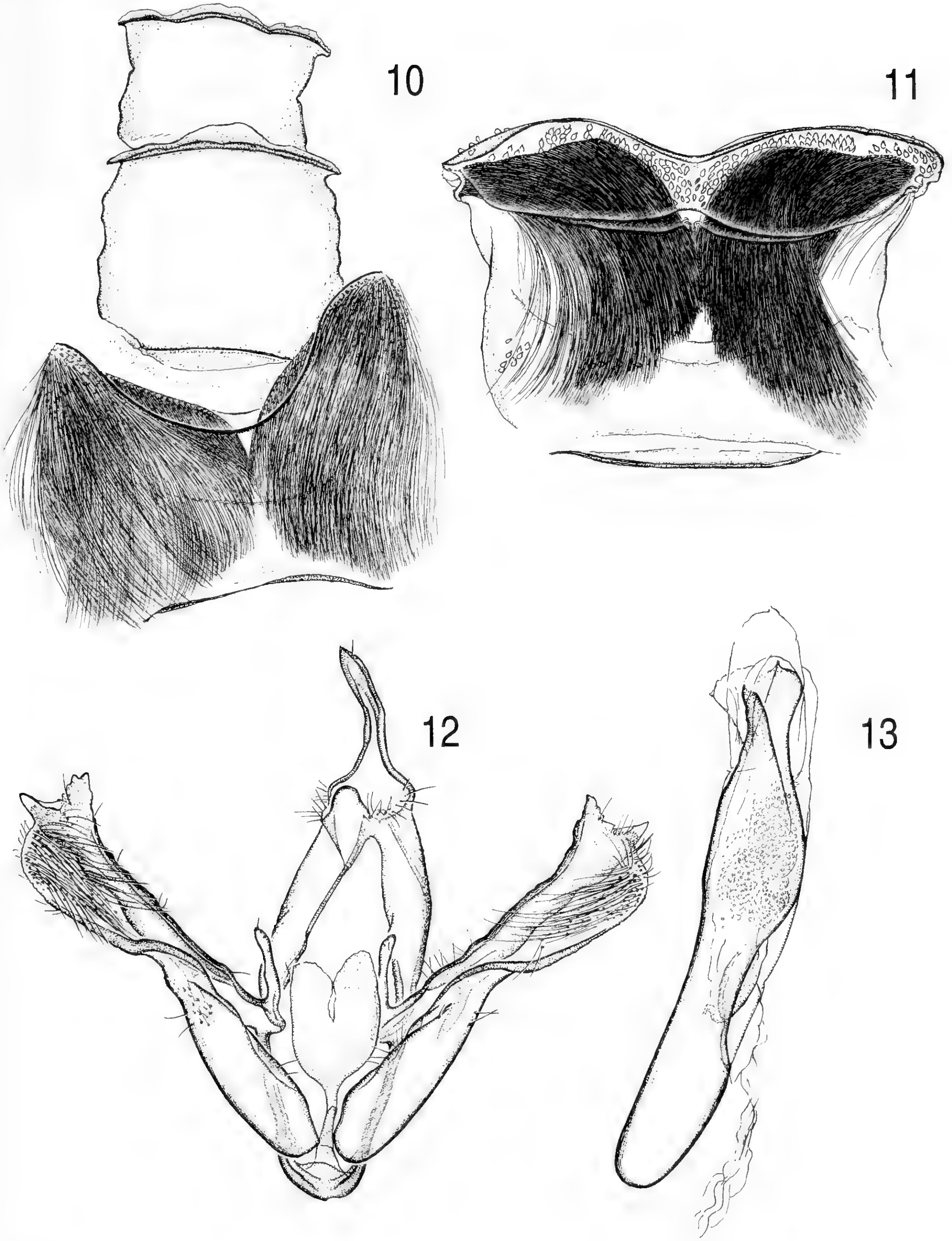
Etymology.—*G. glowackae* is named in honor of Anna Margaret Glowacka De-Corleto.

Glyphidocera acuminae Adamski and Brown, new species

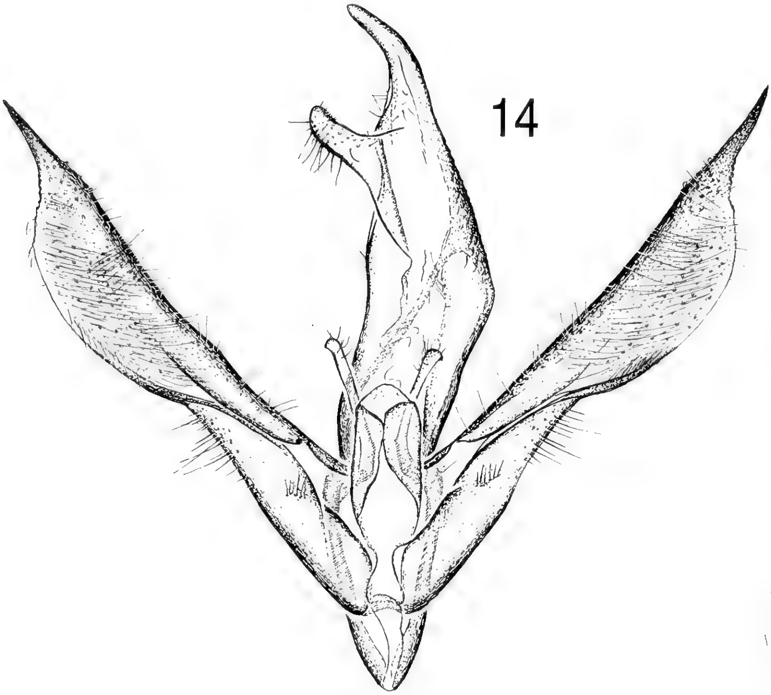
(Figs. 3, 16–17, 46)

Diagnosis.—*Glyphidocera acuminae* can be distinguished from other *Glyphidocera* by the presence of specialized abdominal sex scales on the lateral area of the intersegmental membrane between terga 2-3 and between terga 3-4 of the male, elongate lobe of gnathos, narrowly elongate distal part of the costa of the valva, and aedeagus with two subequal cornuti. *G. acuminae* is most similar to *G. glowackae* but the former has a more elongate lobe of gnathos lobe, narrower and more elongate apical area of the costa, broader digitate projection of the base of the costa, and narrower aedeagus with a pair of subequal cornuti and a single internal basal sclerotization.

Description.—*Head:* Vertex and frontoclypeus with brown scales tipped with brownish orange; labial palpus with outer surface brown intermixed with pale brownish-orange scales near apical area of second and third segments; inner surface similar but with more pale brownish-orange scales; scape brown intermixed with some brown-



Figs. 10–13. Male abdominal sex scales and male genitalia of *Glyphidocera*. 10, *G. garveyi*. 11, *G. mumiella*. 12, 13, *G. brocha*.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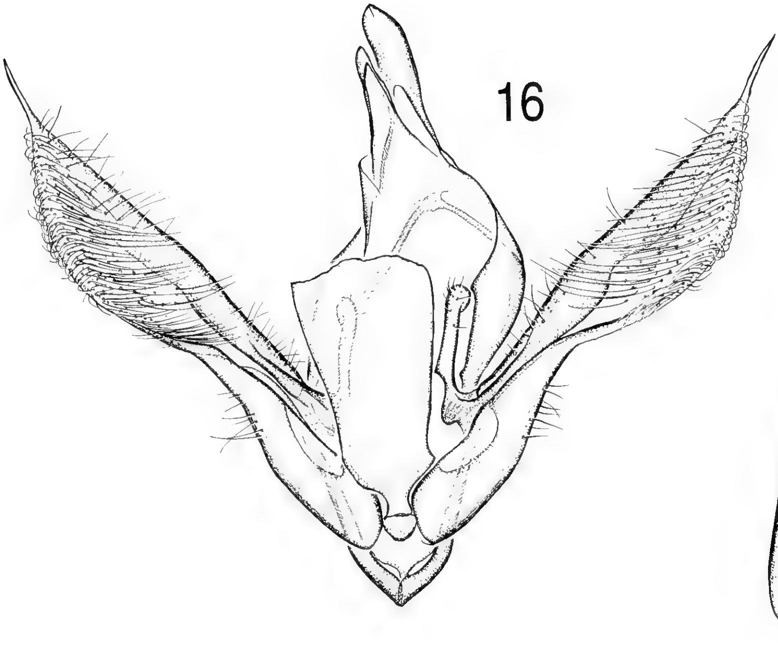
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Figs. 14–17. Male genitalia of *Glyphidocera*. 14, 15, *G. glowackae*. 16, 17, *G. acuminae*.

ish-orange scales basally and apically, flagellum brown; male 4th flagellomere with a tuft of setiform scales on dorsal surface, extending over concavity on 5th and 6th flagellomeres; proboscis pale brownish orange.

Thorax: Tegula brown intermixed with pale brownish-orange scales; legs brown intermixed with pale brownish-orange scales near midsegment and near apices of all segments and tarsomeres. Forewing (Fig. 46) length 5.9 mm (n = 1), brown and dark-brown scales intermixed with mostly pale brownish-orange scales from base to apical end of discal cell; a single brown discal spot near apical end of discal cell; marginal scales dark brown, fringe scales brown; undersurface pale brown. Hindwing with upper surface pale brown, area posterior to cubitus with elongate scales; undersurface pale brown.

Abdomen (Fig. 3): Male with squamiform sex scales on lateral part of intersegmental membrane between abdominal terga 2-3 and 3-4.

Male genitalia (Figs. 16–17): Uncus elongate, slightly widened basally; ganthos slightly shorter in length than uncus; valva with apicoventral half beyond sacculus and basal area between costa and sacculus membranous, apicoventral area densely setose, apex attenuate, base of costa with digitate projection, slightly widened apically; sacculus twisted apically; vesica with many microspinules and two subequal cornuti, and a large sclerotization near the basal opening of the aedeagus.

Female genitalia: Unknown.

Holotype.—♂, "VENEZUELA: T[erritorio] F[ederal] Amaz[ona], Cerro de la Neblina, Basecamp, 0°50′N, 66°9′44"W, 155 m[eters], Canopy 23–29 Feb[ruary] 1984, D. Davis & T. McCabe"; "♂ Genitalia Slide by D. A[damski] 3490, USNM 81643" [green label]. Deposited in the USNM.

Etymology.—The species epithet is derived from the Latin *acuminatus,* meaning "pointed," and refers to the pointed apical area of the costa of the valva.

Glyphidocera digitella Adamski and Brown, new species
(Figs. 4, 18–19, 47)

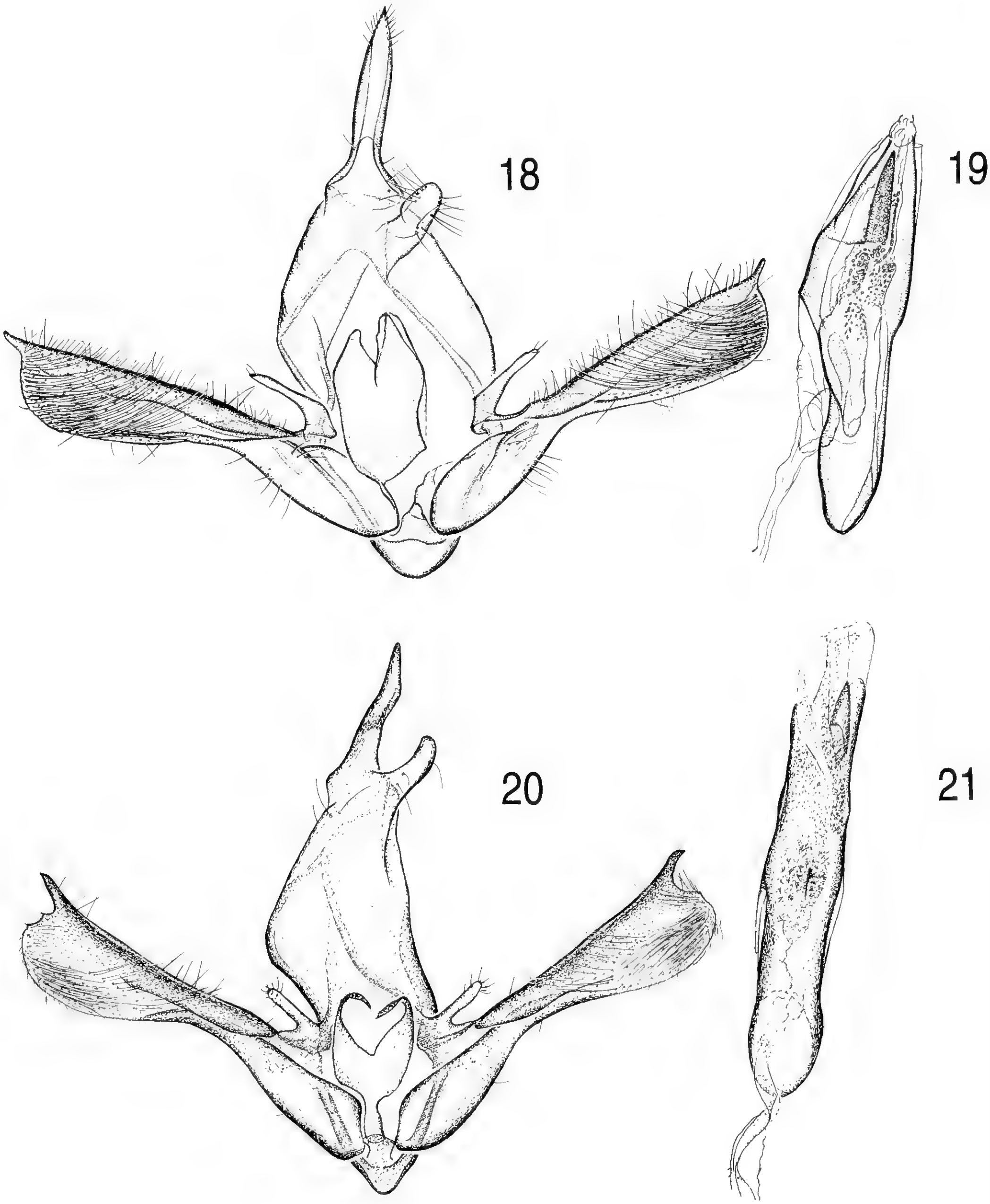
Diagnosis.—*Glyphidocera digitella* can be distinguished from other species of *Glyphidocera* by having a long uncus, wide and setose median lobe of gnathos, and a short digitate projection on the apical area of the apex of valva. *G. digitella* differs from *G. orthotenes* Meyrick, a similar species that ocurs in Colombia, by having its paler ground color, longer uncus, longer digitate projection on the costal base, and narrower apical area of the valval apex.

Description.—*Head:* Vertex and frontoclypeus with brown scales tipped with pale brown; labial palpus with outer surface brown intermixed with pale-brown scales; inner surface similar but with more pale-brown scales; scape pale brown intermixed with brown scales, flagellum brown; male 4th flagellomere with tuft of setiform scales on dorsal surface, extending over concavity on 5th and 6th flagellomeres; proboscis pale brown.

Thorax: Tegula and mesonotum with brown scales tipped with pale brown; legs brown intermixed with pale-brown scales near midsegments and apices of all segments and tarsomeres. Forewing (Fig. 47) length 4.9 mm (n = 1), pale brown intermixed with a few brown scales; discal cell with two spots, one near base, one near distal end; a brown spot on CuP basad to basal spot near cell; marginal scales brown, fringe scales pale brown. Hindwing with both surfaces pale brown.

Abdomen (Fig. 4): Male with four internal bundles of long piliform sex scales within segment two, and an external opening between terga 2-3.

Male genitalia (Figs. 18–19): Uncus elongate, apically acuminate; gnathos with median lobe apically rounded; valval apicoventral area beyond sacculus membranous and densely setose, apical margin



Figs. 18–21. Male genitalia of *Glyphidocera.* 18–19, *G. digitella.* 20–21, *G. hamatella.*

widely rounded ventrally and with short digitate projection dorsally, base of costa with digitate projection, sacculus twisted apically; aedeagus apically narrowed, vesica with many microspinules and an elongate cornutus.

Female genitalia: Unknown.

Holotype.—♂, "VENEZUELA: T[erritorio] F[ederal] Amaz[ona], San Carlos de Rio Negro, 1°36′N, 62°03′W, 6–12 Dec[ember] 1984, R.L. Brown"; "♂ Genitalia Slide by D. Adamski 2949, USNM

81459" [green label]. Deposited in the USNM.

Etymology.—The species epithet is derived from the Latin *digitus,* meaning "finger," and refers to the fingerlike process of the apical part of the valval costa.

Glyphidocera hamatella Adamski and Brown, new species

(Figs. 5, 20–21, 39, 48)

Diagnosis.—*Glyphidocera hamatella* can be distinguished from other species of *Glyphidocera* by the slightly recurved uncus, hooklike apical area of the costa of the valva, parallel sided aedeagus, and vesica with a stout cornutus. *Glyphidocera hamatella* is most similar to a North American species, *G. democratica* Meyrick, but differs from the latter by having a darker brown ground color, narrower and hooklike apical area of the costa of the valva, a narrower aedeagus, and vesica with a larger cornutus.

Description.—*Head:* Vertex and frontoclypeus with brown scales tipped with pale brown; labial palpus with outer surface brown intermixed with pale-brown scales from base to near apex of second and third segments; inner surface similar but with more pale-brown scales; scape pale brown intermixed with brown scales, flagellum pale brown; male 4th flagellomere with tuft of setiform scales on dorsal surface, extending over concavity on 5th and 6th flagellomeres; inner surfaces of 5th and 6th flagellomeres smooth, some marginal sex scales with acuminate apices (Figs. 64–65); proboscis pale brown.

Thorax: Tegula and mesonotum with brown scales tipped with pale brown; legs brown intermixed with pale-brown scales near apices of all segments and tarsomeres. Forewing (Fig. 48) length 7.1–8.0 mm (n = 4), brown scales tipped with pale brown intermixed with brown and some dark-brown scales; two brown discal spots, one large spot, the other small, near distal end of cell; marginal scales dark brown, fringe scales pale brown; undersurface pale brown except area between CuP and inner margin yellowish brown. Hindwing pale brown.

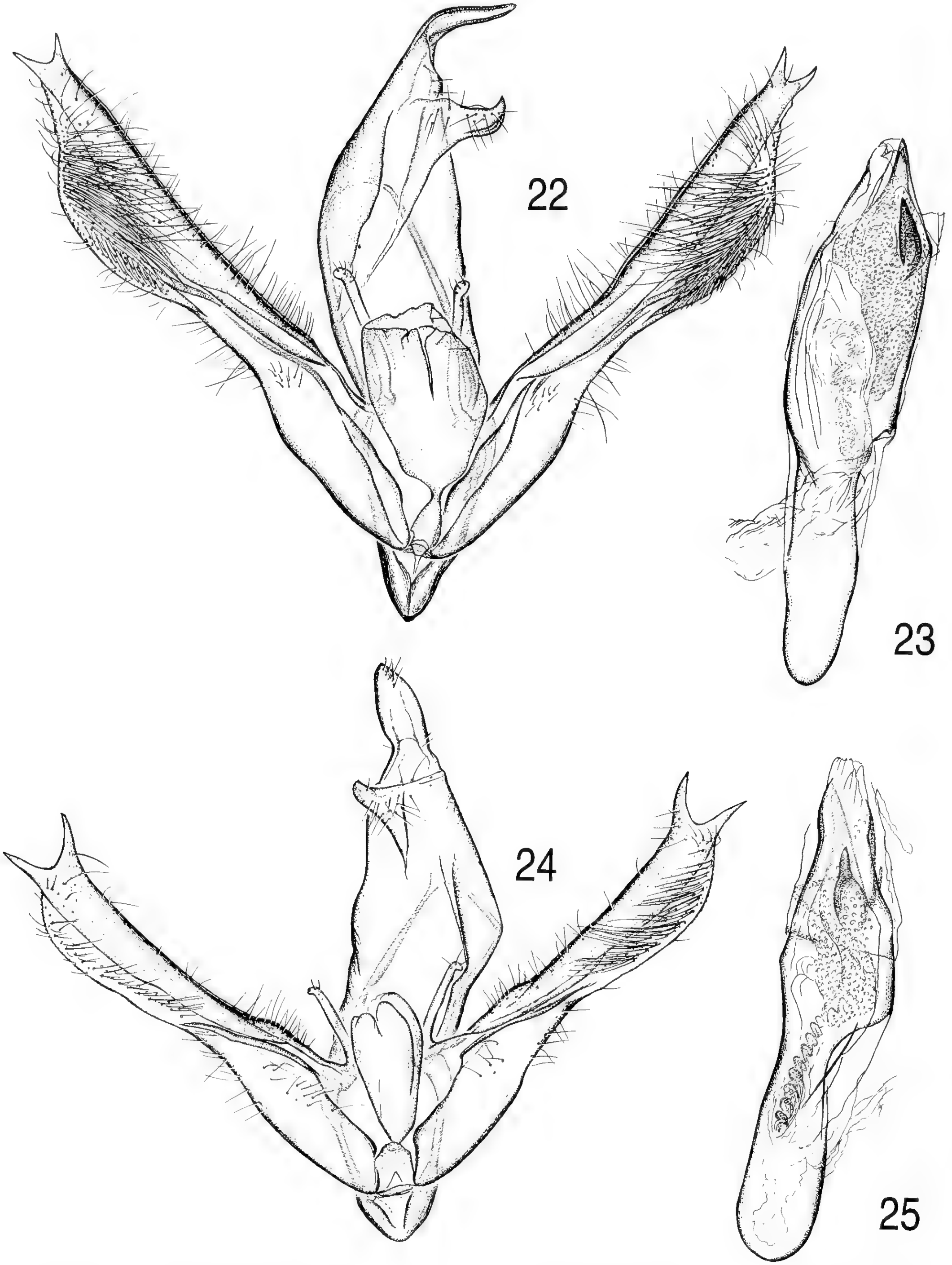
Abdomen (Fig. 5): Male with several transverse rows of specialized sex scales on intersegmental membrane between terga 2-3 and terga 3-4; scales between terga 2-3 slightly larger than those between terga 3-4.

Male genitalia (Figs. 20–21): Uncus elongate, slightly recurved; median lobe of gnathos shorter than uncus; valva with apicoventral half beyond sacculus and basal area between costa and sacculus membranous, apicoventral area densely setose, apical margin hooklike, base of costa with digitate projection, sacculus twisted apically; aedeagus parallel sided, vesica with many microspinules and a large cornutus.

Female genitalia (Fig. 39): Papillae anales conical, with short and long setae intermixed; eighth tergum with posterior margin broadly emarginate, eighth sternum with posterior margin broadly rounded; anterior apophyses posteriorly bifurcate, connecting eighth tergum and sternum; antrum funnelshaped, slightly spinulate, with a wide median lobe and two wide lateral lobes, two internal flanges near anterior end; ductus seminalis spiralled from near middle of corpus bursae; ductus seminalis with internal support; corpus bursae with wide accessory lobe on posterior end opposite ductus seminalis; corpus bursae spinulate, larger spinules near base of ductus seminalis and on anterior end, constricted on one side near middle by accessory lobe.

Holotype.—♂, "VENEZUELA: T[erritorio] F[ederal] Amaz[ona], Cerro de la Neblina, Basecamp, 0°50′N, 0°9′44″W, 140 m[eters], 4–12 Feb[ruary] 1984, D. Davis & T. McCabe"; "♂ Genitalia Slide by D A[damski] 3479, USNM 81632" [green label]. Deposited in the USNM.

Paratypes.—1 ♂, 1 ♀, Same label data as holotype except, "♂ Genitalia Slide by D A[damski] 4071, USNM 81201" [green label]: "♀ Genitalia Slide by D A[damski] 3480, USNM 81633" [green label]: 1 ♂, Same label data as holotype except, "21–



Figs. 22–25. Male genitalia of *Glyphidocera*. 22, 23, *G. chungchinmookara*. 24, 25, *G. basipunctella*.

29 Feb[ruary]", "♂ Genitalia Slide by D A[damski] 4072, USNM 81202" [green label]. All paratypes are in the USNM.

Etymology.—The species epithet is derived from the Latin *hamatus,* meaning "hooked," and refers to the hooklike apical area of the costa of the valva.

Glyphidocera chungchinmookara Adamski and Brown, new species
(Figs. 6, 22–23, 49)

Diagnosis.—*Glyphidocera chungchinmookara* can be distinguished from other species of *Glyphidocera* by its brown longitudinal streaks of the forewing; median lobe of gnathos dorsally curved and pointed; valva with a bifurcate apex; aedeagus apically widened, with a spine on apical end, and vesica with a large cornutus. *Glyphidocera chungchinmookara* is most similar to *G. lepidocyma* Meyrick but differs from the latter in having a narrower uncus, gnathos dorsally curved and pointed, and a broader aedeagus and larger cornutus.

Description.—*Head:* Vertex and frontoclypeus with brown scales tipped with pale brown; labial palpus with outer and inner surfaces brown intermixed with pale-brown scales to apices of second and third segments; scape pale brown intermixed with some brown scales, flagellum pale brown; male 4th flagellomere with tuft of setiform scales on dorsal surface, extending over concavity on 5th and 6th flagellomeres; proboscis pale brown.

Thorax: Tegula and mesonotum pale brown intermixed with brown scales and brown scales tipped with pale brown; legs pale brown intermixed with several brown scales from bases to near apices of all segments and tarsomeres. Forewing (Fig. 49) length 8.6–10.0 mm (n = 2), pale brown intermixed with a few dark-brown scales and dark-brown scales tipped with pale brown; major veins (radials, medials, and cubitals) demarcated with dark-brown scales; discal spots absent; marginal scales brown; fringe scales pale brown tipped with brown; undersurface pale brown. Hindwing pale brown with elongate scales on basal ⅔ of upper surface.

Abdomen (Fig. 6): Male with squamiform sex scales on intersegmental membrane between terga 2-3 and between terga 3-4; scales between terga 2-3 larger and less numerous than those between terga 3-4.

Male genitalia (Figs. 22–23): Uncus elongate, narrow; median lobe of gnathos with apex dorsally curved and pointed; valva with apicoventral half beyond sacculus and basal area between costa and sacculus membranous, apicoventral area densely setose, apical margin narrowly bifurcate, base of costa with digitate projection, sacculus twisted apically; aedeagus with apical ⅔ widened, apex pointed, vesica with many microspinules and a large cornutus.

Female genitalia: Unknown.

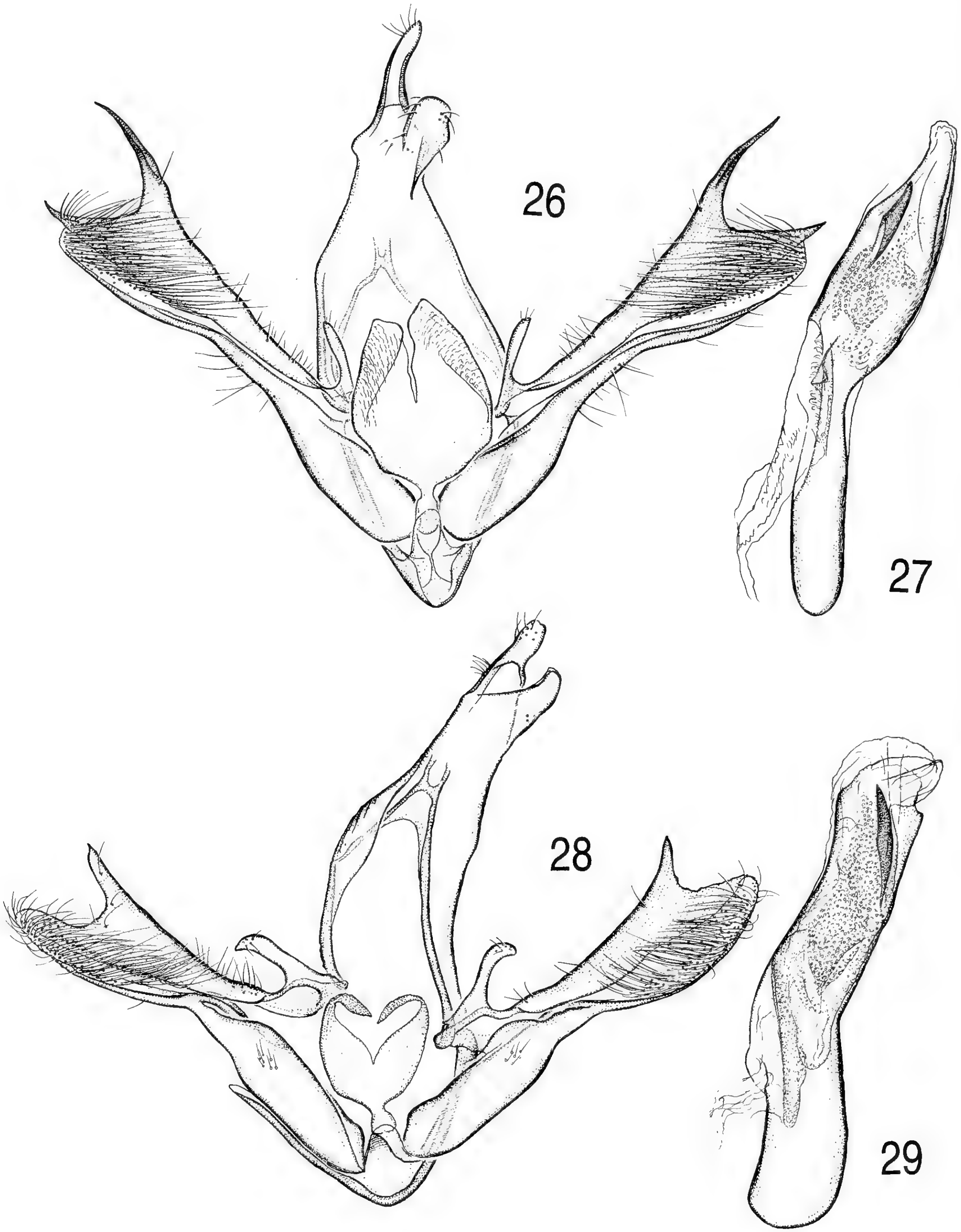
Holotype.—♂, "VENEZUELA: T[erritorio] F[ederal] Amaz[ona], Cerro de la Neblina, Camp VII, 1,850 m[eters], 0°51′N, 65°58′W, 2–4 Dec[ember] 1984, R.L. Brown"; "♂ Genitalia Slide by D. Adamski 2947, USNM 81457" [green label]. Deposited in the USNM.

Paratype.—1 ♂, Same label data as holotype except, "♂ Genitalia Slide by D A[damski] 4075, USNM 81205" [green label]. Deposited in the USNM.

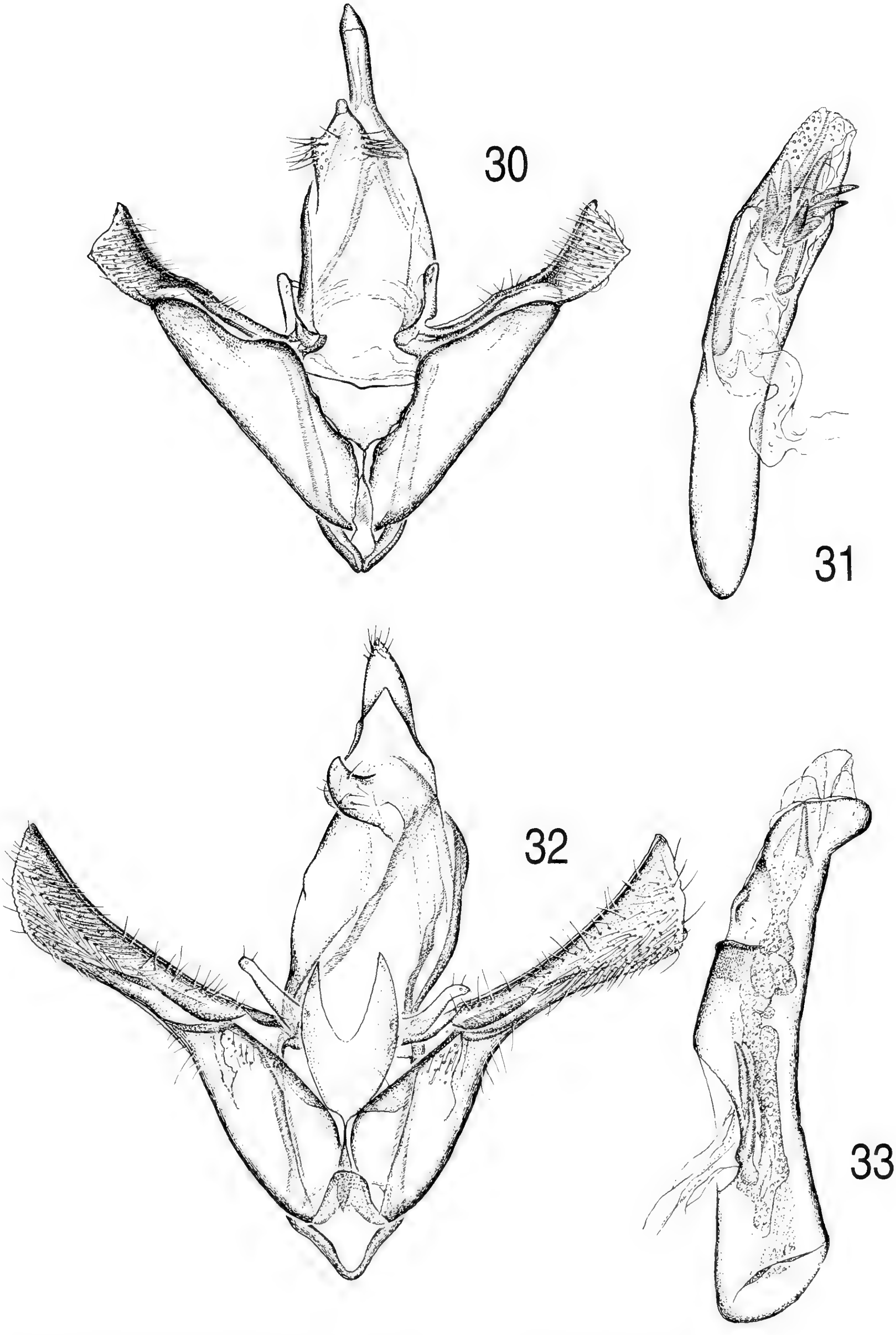
Etymology.—The species is named in honor of Chung Chin Mook.

Glyphidocera basipunctella Adamski and Brown, new species
(Figs. 7, 24–25, 50)

Diagnosis.—*Glyphidocera basipunctella* can be distinguished from other species of *Glyphidocera* by the small dark-brown elliptical spot at the base of the forewing, wide uncus, narrower median lobe of the gnathos, wide bifurcation of the apical margin of the valva, and vesica with a pair of large cornuti. *Glyphidocera basipunctella* appears closely related to *G. chungchinmookara* but differs from the latter by having a broader uncus, narrower median lobe of the gnathos, a wider bifurcation of the



Figs. 26–29. Male genitalia of *Glyphidocera*. 26, 27, *G. alexandrae*. 28, 29, *G. lunata*.



Figs. 30–33. Male genitalia of *Glyphidocera*. 30, 31, *G. brevisella*. 32, 33, *G. garveyi*.

outer margin of the valva, and vesica with two cornuti.

Description.—*Head:* Vertex and frontoclypeus with scales brown tipped with pale brown; labial palpus with outer surface pale brown intermixed with some brown scales, pale-brown scales from base to near apex of second segment; inner surface similar but with more pale-brown scales; scape pale brown intermixed with few brown scales, flagellum pale brown alternating with brown scales; male 4th flagellomere with a tuft of setiform scales on dorsal surface, extending over concavity on 5th and 6th flagellomeres; proboscis pale brown.

Thorax: Tegula pale brown intermixed with a few brown scales; legs pale brown intermixed with brown scales, pale-brown scales at midsegments and near apices of all segments and tarsomeres. Forewing (Fig. 50) length 6.9 mm (n = 1), brownish orange intermixed with brown scales; discal spots present, one near base, one near apical end; wing base with a small dark-brown elliptical spot near middle; marginal scales brown; fringe scales pale brown; undersurface pale brown. Hindwing: pale brown, basal ⅔ with elongate scales on upper surface.

Abdomen (Fig. 7): Male with squamiform sex scales between terga 2-3 and terga 3-4; scales between terga 2-3 slightly larger than those between terga 3-4.

Male genitalia (Figs. 24–25): Uncus wide; median lobe of gnathos slightly constricted near middle; valva with apicoventral third beyond sacculus and basal area between costa and sacculus membranous, apicoventral area densely setose; apical margin widely bifurcate; base of costa with digitate projection; sacculus twisted apically; aedeagus abruptly dilated near midlength, vesica with many microspinules and two large cornuti.

Female genitalia: Unknown.

Holotype.—♂, "VENEZUELA: T[erritorio] F[ederal] Amaz[ona], Cerro de Neblina, Base Camp, 140 m[eters], 0°50′N, 66°9′W, 24 Nov[ember]−1 Dec[ember] 1984, R. L. Brown"; "♂ Genitalia Slide by D. Adamski 2950, USNM 81460" [green label]. Deposited in the USNM.

Etymology.—The species epithet is derived from the Latin, *basi,* meaning "base," and *punctum* meaning "small dot," and refers to the dark brown elliptical spot at the base of the forewing.

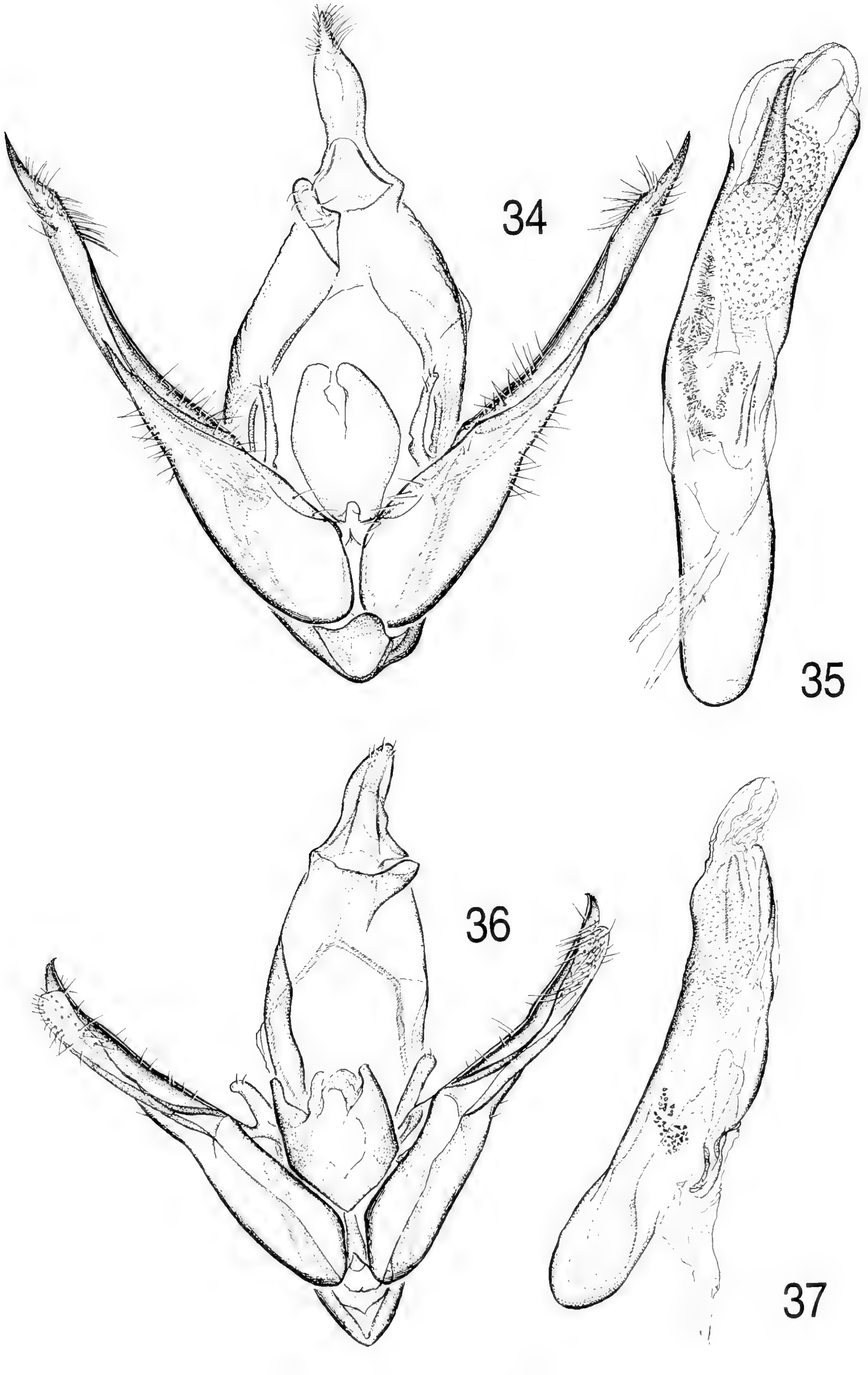
Glyphidocera alexandrae Adamski and Brown, new species

(Figs. 8, 26–27, 51)

Diagnosis.—Males of *Glyphidocera alexandrae* can be distinguished from those of other *Glyphidocera* by having squamiform sex scales between abdominal terga 2-3 but none between terga 3-4, a gnathal lobe with a widely rounded apex, widely bifurcate outer margin of the valva, and vesica with a large cornutus. *Glyphidocera alexandrae* is similar to *G. zophocrossa* Meyrick but differs from the latter by having squamiform male sex scales only between abdominal terga 2-3. Male *G. zophocrossa* have squamiform sex scales between abdominal terga 2-3 and 3-4.

Description.—*Head:* Vertex and frontoclypeus pale brown; labial palpus with outer surface dark brown intermixed with a few pale-brown scales; inner surface with second segment pale brown intermixed with a few dark-brown scales, terminal segment dark brown intermixed with a few pale-brown scales, scape pale brown intermixed with a few dark-brown scales, flagellum pale brown; male 4th flagellomere with a tuft of setiform scales on dorsal surface, extending over concavity on 5th and 6th flagellomeres; proboscis pale brown.

Thorax: Tegula and mesonotum pale brown intermixed with a few pale-brown scales; legs pale brown intermixed with a few dark-brown scales. Forewing (Fig. 51) length 6.4 mm (n = 1), brownish orange intermixed with few dark-brown scales along costal area and apical ⅓; two dark-brown discal spots, one near base, the other near apical end; one dark-brown spot along CuP basad of spot near base of cell; a small



Figs. 34–37. Male genitalia of *Glyphidocera*. 34, 35, *G. mumiella*. 36, 37, *dentata*.

dark-brown patch of scales near base; marginal scales dark brown; fringe scales dark brown; undersurface pale brown, except yellowish brown near posterior margin. Hindwing pale brown.

Abdomen (Fig. 8): Male with squamiform sex scales between terga 2-3.

Male genitalia (Figs. 26–27): Uncus elongate, apex rounded; median lobe of gnathos with rounded apex; valva with apicoventral ⅕ beyond sacculus and basal area between costa and sacculus membranous; apicoventral area densely setose; apical margin widely bifurcate; base of costa with digitate projection; sacculus twisted apically; aedeagus slightly widened near midlength, vesica with many microspinules and a large cornutus.

Female genitalia: Unknown.

Holotype.—♂, "VENEZUELA: T[erritorio] F[ederal] Amaz[ona], Cerro de la Neblina, Basecamp, 0°50′W, 66°9′4″W, 155 m[eters], Canopy, 23–29 Feb[ruary] 1984, D. Davis & T. McCabe"; "♂ Genitalia Slide by D A[damski] 3487, USNM 81640" [green label]. Deposited in the USNM.

Etymology.—This species is named in honor of Alexandra Kelly Levy.

Glyphidocera lunata Adamski and Brown, new species
(Figs. 28–29, 52)

Diagnosis.—*Glyphidocera lunata* can be distinguished from other species of in the genus by its short uncus, tegumen of the genital capsule elongate, apical margin of valva crescentshaped, and vesica with an elongate cornutus. *Glyphidocera lunata* is similar *G. eurrhipis* Meyrick, but differs from the latter by having a more elongated tegumen of the genital capsule, shorter uncus, more protuberant median lobe of the gnathos, shorter ventrodistal part of the valva, and broader aedeagus.

Description.—*Head:* Vertex and frontoclypeus with brown scales tipped with pale brown; labial palpus with outer surface brown intermixed with a few pale-brown scales from base to near apex of second segment; inner surface similar but with more pale-brown scales; scape pale brown intermixed with a few brown scales, flagellum pale brown; male 4th flagellomere with a tuft of setiform scales on dorsal surface, extending over cavity on 5th and 6th flagellomeres; proboscis pale brown.

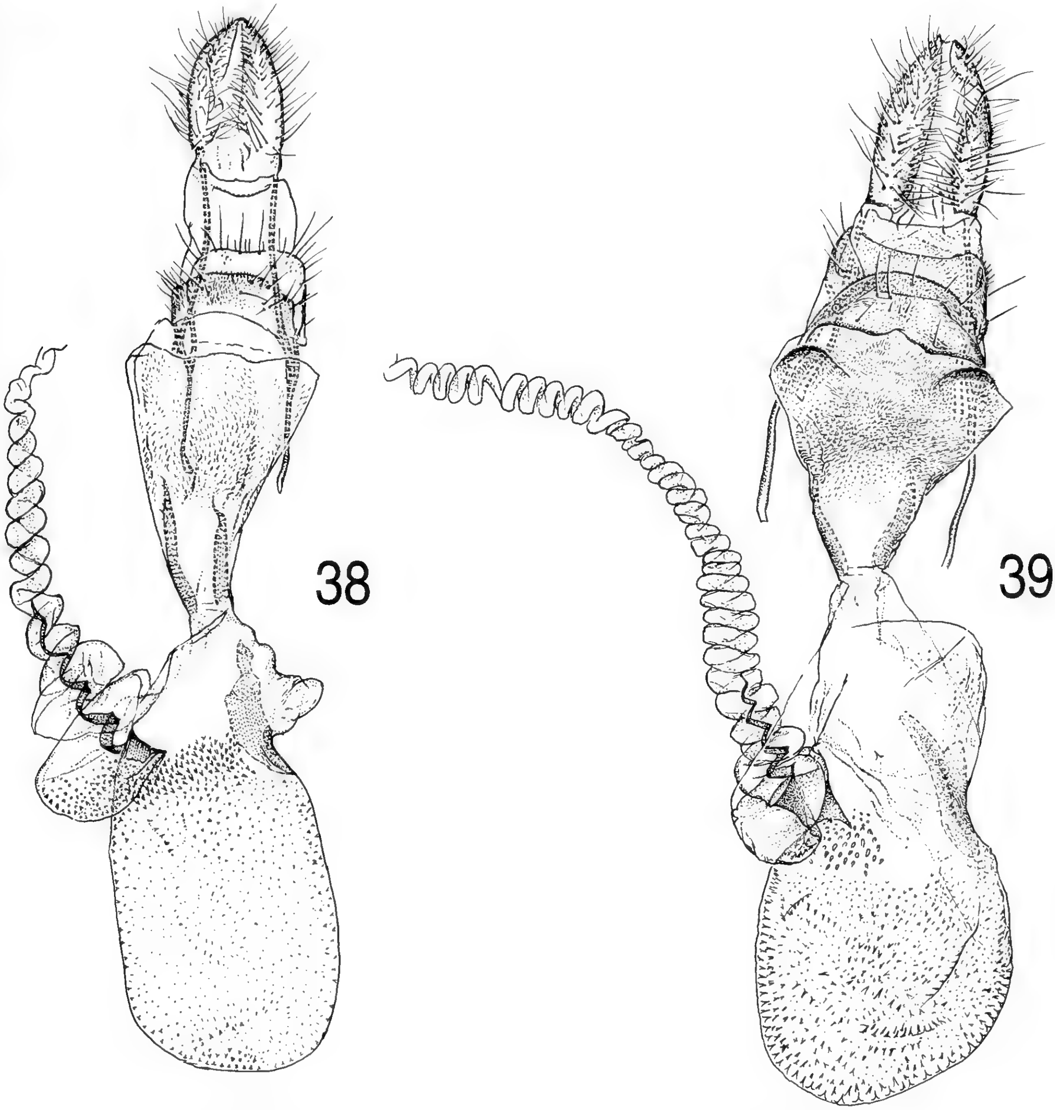
Thorax: Tegula with brown scales tipped with brownish orange; mesonotum brownish orange intermixed with a few brown scales; legs pale brown intermixed with brown scales, pale brown scales on midsegments and all tarsomeres. Forewing (Fig. 52) length 6.2 mm (n = 1), brownish orange intermixed with dark-brown scales mostly along costal margin and apical ⅓; two discal spots present, one near base, one near apical end; marginal scales dark brown; fringe scales dark brown with pale-brown base; undersurface pale brown. Hindwing pale brown, with elongate scales on basal ⅔ of upper surface.

Male genitalia (Figs. 28–29): Tegumen elongate, narrow; uncus short, apically rounded; median lobe of gnathos dorsally curved, apically rounded; valva with apicoventral half beyond sacculus and basal area between costa and sacculus membranous; apicoventral area densely setose; apical margin of valva widely bifurcate; base of costa with digitate projection, apically curved; sacculus twisted apically; aedeagus widened apically, vesica with many microspinules and an elongate cornutus.

Female genitalia: Unknown.

Holotype.—♂, "VENEZUELA: T[erritorio] F[ederal] Amaz[ona], San Carlow de Rio Negro, 1°56′N, 67°03′W, 6–12 Dec[ember] 1984, R.L. Brown"; "♂ Genitalia Slide by D A[damski] 3486, USNM 81639" [green label]. Deposited in the USNM.

Etymology.—The specific epithet is derived from the Latin *lunatus,* meaning "crescentshaped," and refers to the shape of the outer margin of the valva.



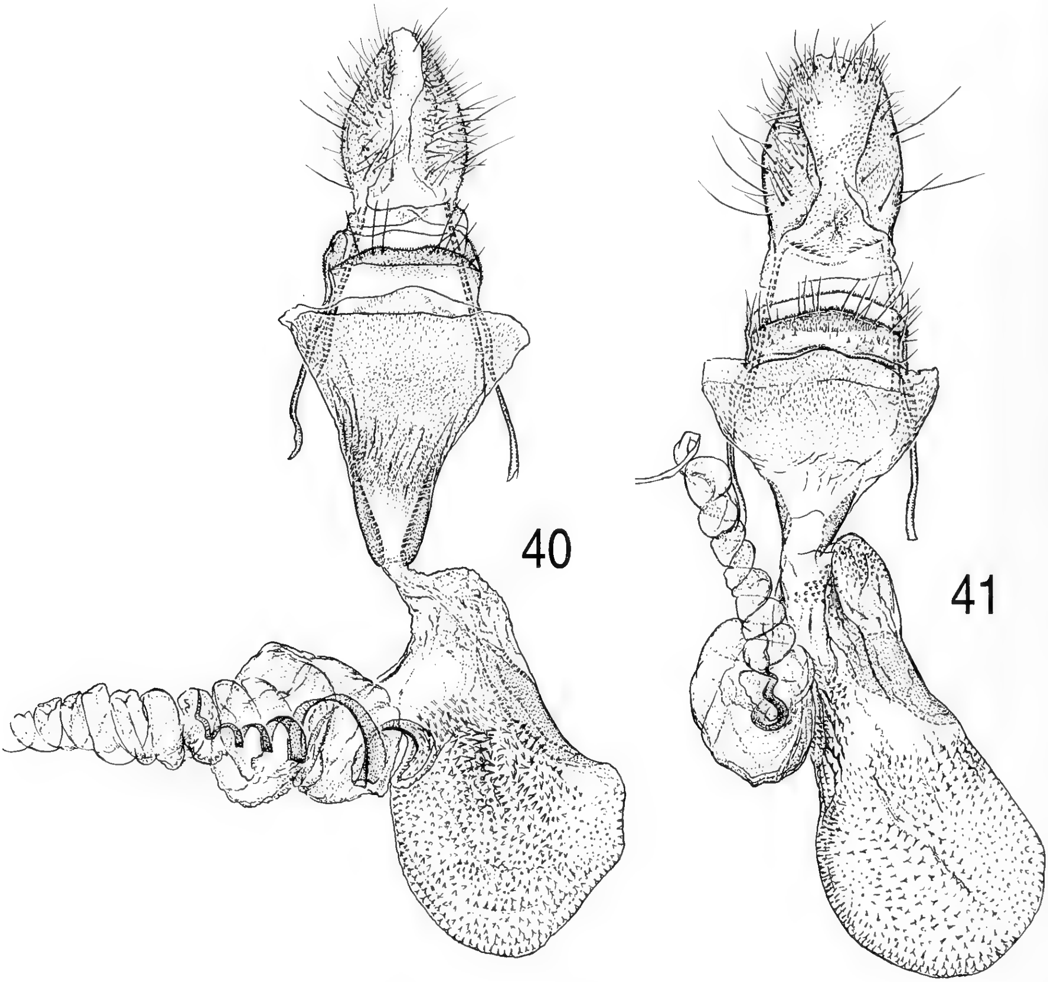
Figs. 38–39. Female genitalia of *Glyphidocera*. 38, *G. glowackae*. 39, *G. hamatella*.

Glyphidocera brevisella Adamski and Brown, new species

(Figs. 9, 30–31, 53)

Diagnosis.—*Glyphidocera brevisella* can be distinguished from other species of *Glyphidocera* by the presence of male abdominal squamiform sex scales on lateral intersegmental membrane between abdominal terga 2-3 and a few between terga 3-4, a wide median lobe of the gnathos with a short nipplelike apex, short valva, and vesica with 10 cornuti. *Glyphidocera brevisella* is superficially similar to *G. notolopha* Meyrick by having short valvae but differs from the latter by having a broader median lobe of gnathos with a short nipplelike apical process.

Description.—*Head:* Vertex and frontoclypeus pale brownish orange; labial palpus with outer and inner surfaces pale brownish



Figs. 40–41. Female genitalia of *Glyphidocera*. 40, *G. mumiella*. 41, *G. brunnella*.

orange intermixed with a few brown scales; scape pale brown intermixed with a few brown scales, flagellum alternating pale brown and brown; male 4th flagellomere with a tuft of setiform scales on dorsal surface, extending over concavity on 5th and 6th flagellomeres; proboscis pale brownish orange.

Thorax: Tegula and mesonotum pale brownish orange intermixed with a few brown scales; legs pale brown intermixed with brown scales, pale-brown scales at midsegments near apices of all segments and tarsomeres. Forewing (Fig. 53) length 4.6–4.8 mm (n = 2), pale brownish orange intermixed with brown scales mostly along costal area and apical ⅓; three discal spots present, one near base and two near distal end; premarginal spots present; marginal scales brown; fringe scales pale brown tipped with brown; undersurface pale brown, veins demarcated with pale yellowish-brown scales. Hindwings pale brown.

Abdomen (Fig. 9): Male with squamiform sex scales on lateral intersegmental membrane between terga 2-3 and a few between 3-4.

Male genitalia (Figs. 30–31): Uncus

elongate; median lobe of gnathos wide, with nipplelike apex; valva short, apical area beyond sacculus membranous except for costa; apical margin truncate; base of costa with digitate projection; sacculus wide, slightly twisted apically; aedeagus gradually widened from base, vesica with ten cornuti of varying sizes.

Female genitalia: Unknown.

Holotype.—♂, "VENEZUELA: T[erritorio] F[ederal] Amaz[ona], San Carlos de Rio Negro, 1°56′N, 67°02′W, 6–12 Dec[ember] 1984, R.L. Brown"; "♂ Genitalia Slide by D A[damski] 3481, USNM 81634" [green label}. Deposited in the USNM.

Paratype.—♂, Same label data as holotype except, "♂ Genitalia Slide by D A[damski 4073, USNM 81203" [green label]. Deposited in the USNM.

Etymology.—The specific epithet is derived from the Latin *brevis,* meaning "short," and refers to the short valva of this species.

Glyphidocera garveyi Adamski and Brown, new species

(Figs. 10, 32–33, 54)

Diagnosis.—*Glyphidocera garveyi* can be distinguished from other species of *Glyphidocera* by the dark-brown color of the moth, male with a pair of lateral bundles of piliform sex scales between abdominal terga 3-4, wide uncus, dorsally curved median lobe of the gnathos, short valva with outer margin entire, and aedeagus with truncate apex. *Glyphidocera garveyi* is similar to *G. lophandra* Meyrick but differs from the latter by having a darker ground color, less setose median lobe of gnathos, and aedeagus with a truncate apex.

Description.—*Head:* Vertex and frontoclypeus with scales dark brown, many tipped with pale brown; labial palpus with outer and inner surfaces dark brown intermixed with brownish-orange scales to apex of second segment; scape dark brown intermixed with a few brownish-orange scales, flagellum dark brown; male 4th flagellomere with tuft of setiform scales on dorsal surface, extending over concavity on 5th and 6th flagellomeres; inner surfaces and marginal scales of 5th and 6th flagellomeres with sex scales with fringelike scutes (Figs. 60–61); proboscis dark brown intermixed with brownish-orange scales.

Thorax: Tegula and mesonotum dark brown; legs dark brown intermixed with brownish-orange scales at midsegments and apices of all segments and tarsomeres. Forewing (Fig. 54) length 5.6–6.8 mm (n = 8), dark brown intermixed with a few brownish-orange scales, mostly on distal ⅓; marginal scales dark brown; fringe scales pale brown tipped with dark brown; undersurface pale brown. Hindwing upper surface pale brown except, basal ⅔ with elongate dark-brown scales; undersurface pale brown.

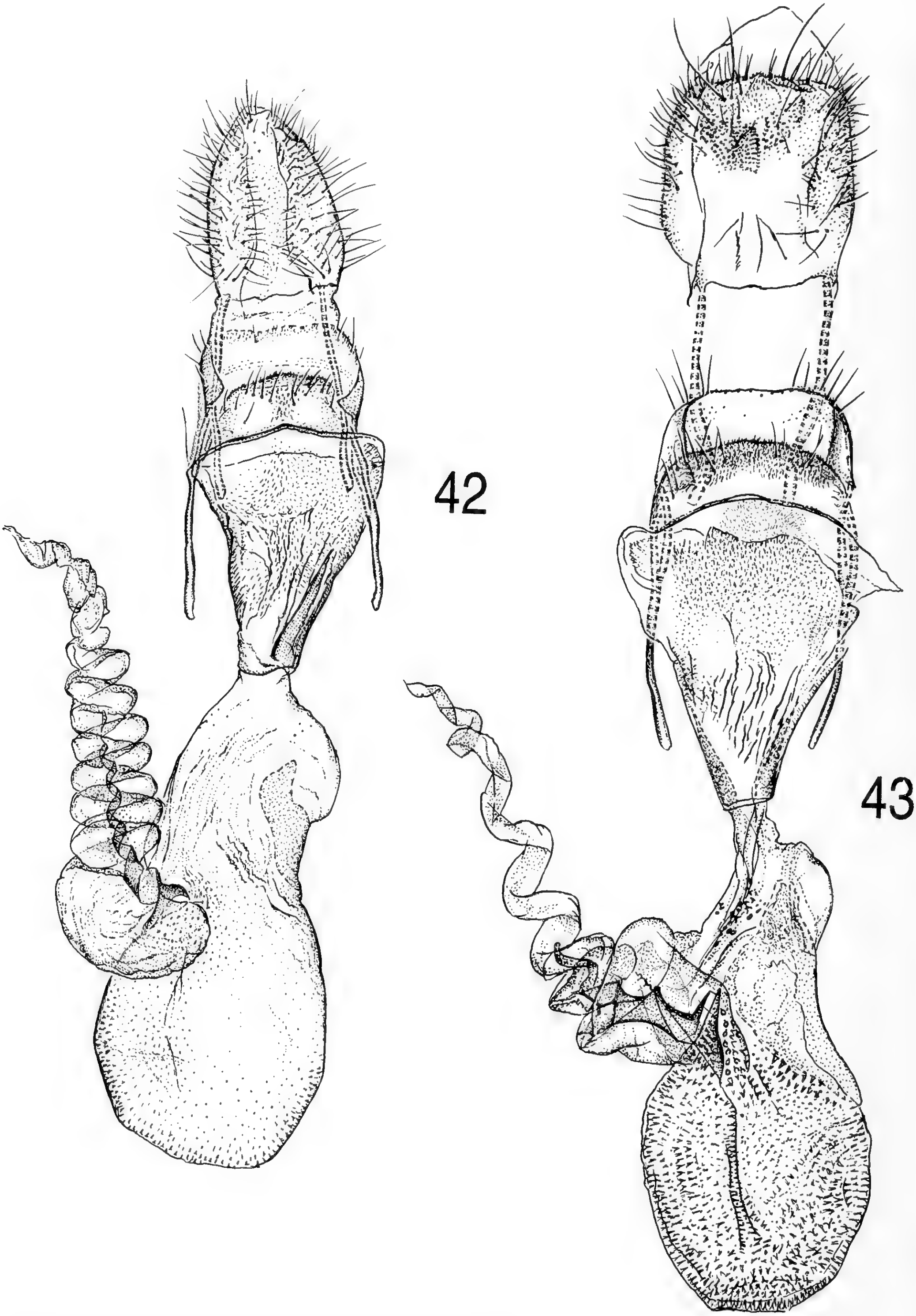
Abdomen (Fig. 10): Male with a pair of lateral bundles of piliform sex scales between abdominal terga 3-4.

Male genitalia (Figs. 32–33): Uncus wide, with acuminate apex; median lobe of gnathos abruptly curved dorsally, setose; valva membranous beyond sacculus except for costa, apical margin of valva entire; base of costa with digitate projection; aedeagus wide throughout length, truncate apex; vesica with a large cornutus.

Female genitalia: Unknown.

Holotype.—♂, "VENEZUELA: T[erritorio] F[ederal] Amaz[ona], Cerro de Neblina, Base Camp, 140 m[eters], 0°50′N, 66°9′W, 24 Nov[ember]−1 Dec[ember] 1984, R.L. Brown;" "♂ Genitalia Slide by D. Adamski 2948, USNM 81458" [green label]. Deposited in the USNM.

Paratypes.—4 ♂, Same label data as holotype (specimens not dissected): 2 ♂, Same label data as holotype except, "Basecamp, 0°50′N, 66°9′44″W, 155 m[eters], Canopy, 1–10 Mar[ch] 1984, D. Davis & T. McCabe": (specimens not dissected); 1 ♂, Same label data as holotype except, "Basecamp, 0°50′N,66°9′44″W, 140 m[eters] 21–29 Feb[ruary 1984, D. Davis & T. Mc-



Figs. 42–43. Female genitalia of *Glyphidocera*. 42, *G. janae*. 43, *G. castanella*.

Cabe" (specimen not dissected). Deposited in the USNM.

Etymology.—The species is named in honor of Jon Wheatley Garvey.

Glyphidocera mumiella Adamski and Brown, new species

(Figs. 11, 34–35, 40, 55)

Diagnosis.—*Glyphidocera mumiella* can be distinguished from other species of *Glyphidocera* by the following combination of features, male with specialized squamiform sex scales between terga 2-3 and between terga 3-4, internal bases of a pair of large internal bundles of piliform scales within segment two, opening within intersegmental membrane between 2-3, anal area of hindwing with elongate cluster of raised scales, valva narrow, vesica with a large cornutus. Relationships of *Glyphidocera mumiella* to other species of *Glyphidocera* are difficult to determine because of the unique shape of the valva.

Description.—*Head:* Vertex and frontoclypeus brown or vertex brown intermixed with pale brownish orange to clypeus; labial palpus with outer and inner surfaces pale brownish orange intermixed with some brown scales, pale brownish-orange scales near apex of second segment; scape and flagellum brown; male 4th flagellomere with tuft of setiform scales on dorsal surface, extending over concavity on 5th and 6th flagellomeres; proboscis pale brownish orange.

Thorax: Tegula and mesonotum brown; legs brown intermixed with pale brownish orange at midsegments and apices of all segments and tarsomeres. Forewing (Fig. 55) length 7.2–7.9 mm (n = 2), brown intermixed with a few pale brownish-orange scales; undersurface pale brown. Hindwing pale brown, upper surface with elongate cluster of raised scales on anal area of upper surface.

Abdomen (Fig. 11): Male with squamiform sex scales between terga 2-3 and between terga 3-4, with internal pair of large bundles of piliform scales between terga 2-3.

Male genitalia (Figs. 34–35): Uncus widest at about ⅔ length, slightly narrowed basally, apex acuminate; median lobe of gnathos with a rounded apex; valva narrow, pointed apically; base of costa with digitate projection, sacculus not twisted apically; aedeagus wide, vesica with many microspinules and a large cornutus.

Female genitalia (Figs. 40): Papillae anales conical, with short and long setae intermixed; eighth sternum narrow, trapezoidal; anterior apophyses posteriorly bifurcate, connecting eighth tergum and sternum; antrum funnelshaped, spinulate, wide, posterior margin entire, with two internal flanges near anterior end; ductus seminalis spiralled from posterior half of corpus bursae, with spiralled internal support basally; corpus bursae spinulate, larger spinules near base of ductus seminalis, slightly constricted on one side by a plate with pointed ends.

Holotype.—♂, "VENEZUELA: T[erritorio] F[ederal] Amaz[ona], Cerro de Neblina, Base Camp, 140 m[eters], 0°50′N, 66°9′W, 24 Nov[ember]–1 Dec[ember] 1984, R.L. Brown"; "♂ Genitalia Slide by D A[damski] 3482, USNM 81635" [green label]. Deposited in the USNM.

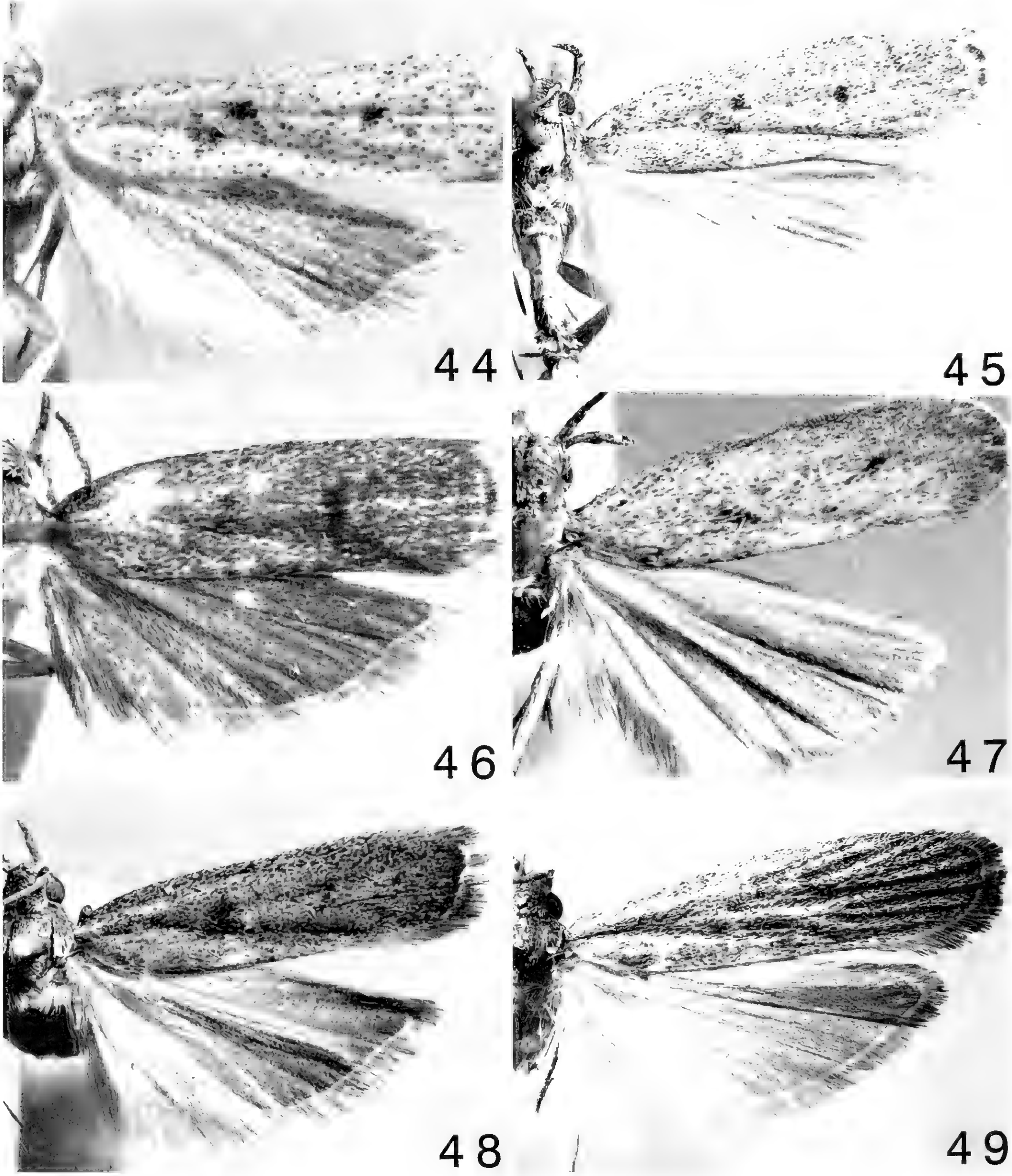
Paratype.—1 ♀, Same label data as holotype except, "1–10 March 1984, D. Davis & T. McCabe"; "♀ Genitalia Slide by D A[damski] 3483, USNM 81636" [green label]. Deposited in the USNM.

Etymology.—This species is named in honor of Megan "Mumi" Meridith Harrigal.

Glyphidocera dentata Adamski and Brown, new species

(Figs. 36–37, 56)

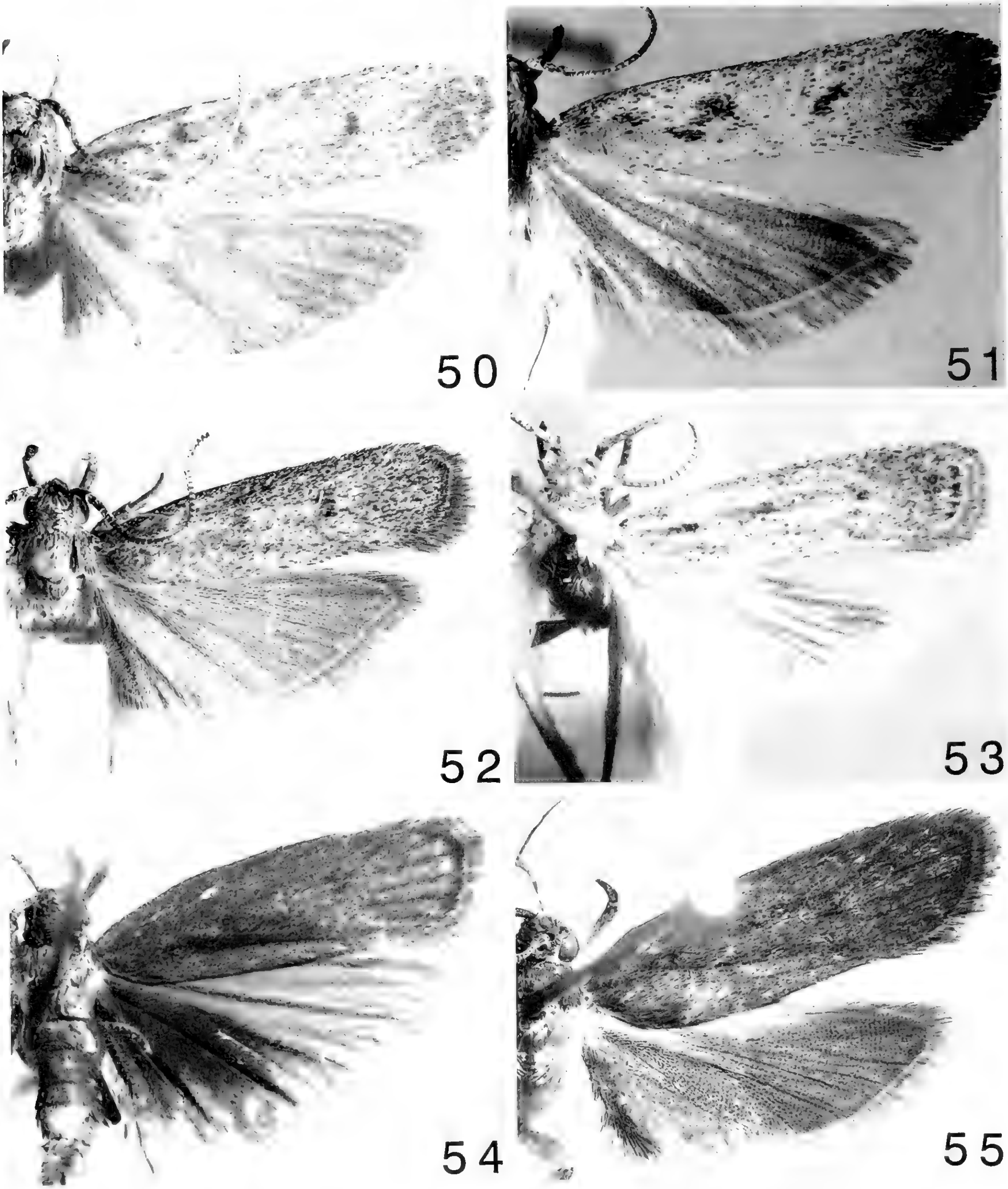
Diagnosis.—*Glyphidocera dentata* can be distinguished from other species of *Glyphidocera* by having a wide uncus, toothlike apical area of the valva; slightly narrowed basal area of the valva, and vesica with a large cornutus. *Glyphidocera dentata*



Figs. 44–49. Adults of *Glyphidocera*. 44, *G. brocha* (holotype). 45, *G. glowackae* (holotype). 46, *G. acuminae* (holotype). 47, *G. digitella* (holotype). 48, *G. hamatella* (holotype). 49, *G. chungchinmookara* (holotype).

is most similar *G. muniella*, but differs from the latter by having a shorter valva, paler ground color, broader uncus; toothlike apical area of the valva, and a smaller cornutus.

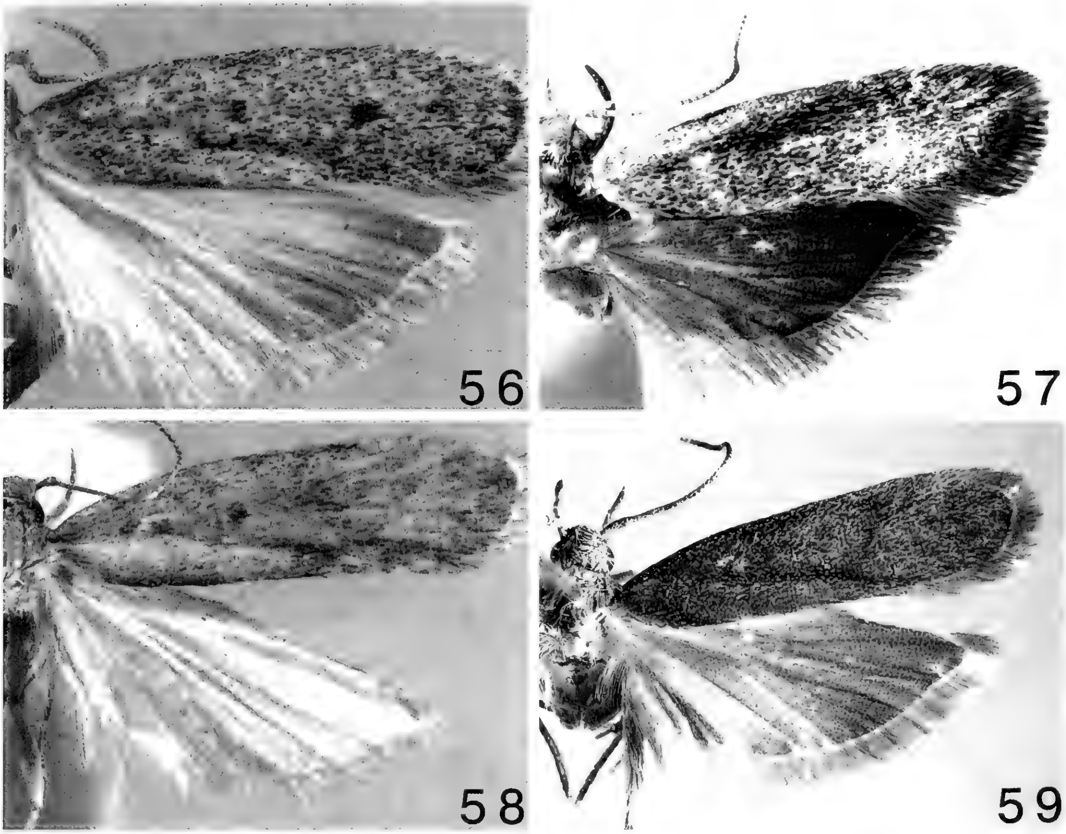
Description.—*Head:* Vertex and frontoclypeus with scales brown tipped with pale brown; labial palpus with outer surface brown intermixed with pale-brown scales; inner surface similar but with more pale-brown scales; scape pale brown intermixed with a few brown scales, flagellum pale brown and brown intermixed; male 4th flagellomere with tuft of setiform scales on



Figs. 50–55. Adults of *Glyphidocera*. 50, *G. basipunctella* (holotype). 51, *G. alexandrae* (holotype). 52, *G. lunata* (holotype). 53, *G. brevisella* (holotype). 54, *G. garveyi* (paratype). 55, *G. mumiella* (holotype).

dorsal surface, extending over concavity on 5th and 6th flagellomeres; proboscis pale brown.

Thorax: Tegula and mesonotum pale brownish orange intermixed with brown scales; legs pale brown intermixed with brown scales, pale-brown scales on midsegments and near apices of all segments and tarsomeres. Forewing (Fig. 56) length 6.0 mm (n = 1), pale brownish orange intermixed with brown scales; discal cell with two spots, one near base, one near apical



Figs. 56–59. Adults of *Glyphidocera*. 56, *G. dentata* (holotype). 57, *G. brunnella* (paratype). 58, *G. janae* (holotype). 59, *G. castanella* (holotype).

end; one small spot on CuP basad to spot near base of cell; marginal scales brown; fringe scales pale brown tipped with brown; undersurface pale brown. Hindwing pale brown.

Male genitalia (Figs. 36–37): Uncus wide, with slightly rounded apex; median lobe of gnathos rounded apically; valva short and narrow, membranous beyond sacculus except for costa; costal sclerotization narrowing apically, apical margin toothlike; sacculus narrow, slightly twisted apically; base of costa with digitate projection; aedeagus slightly narrowed distally, vesica with many microspinules and a large cornutus.

Female genitalia: Unknown.

Holotype.—♂, "VENEZUELA: T[erritorio] F[ederal] Amaz[ona], Cerro de la Neblina, Basecamp, 0°50′N, 66°9′44″W, 140 m[eters], 4–12 Feb[ruary] 1984, D. Davis & T. McCabe"; "♂ Genitalia Slide by D A[damski] 3488, USNM 81641" [green label]. Deposited in the USNM.

Etymology.—The species epithet is from the Latin *dentatus,* meaning "tooth," or "bearing a tooth," and refers to the toothlike apical area of the valva.

Glyphidocera brunnella Adamski and Brown, new species

(Figs. 41, 57)

Diagnosis.—*Glyphidocera brunnella* can be distinguished from other species of *Glyphidocera* by the dark-brown color of the moth; narrow eighth sternum, with anterior margin broadly rounded; antrum with a wide median lobe, and corpus bursae with a large plate enlarged on posterior end. Females of *Glyphidocera brunnella* and *G. hamatella* share an abruptly constricted antrum, anterior to mid-length, but the antrum in the latter species has lateral lobes on the posterior margin.

Description.—*Head:* Vertex and frontoclypeus brown; labial palpus with outer surface dark brown intermixed with a few pale-brown scales from base to near apex of second segment, terminal segment dark brown; scape dark brown intermixed with a few pale-brown scales, flagellum dark brown alternating with pale-brown scales; proboscis pale brown intermixed with dark-brown scales.

Thorax: Tegula and mesonotum brown intermixed with a few pale-brown scales; legs dark brown intermixed with pale-brown scales near midsegments and near apices of all segments and tarsomeres. Forewing (Fig. 57) length 5.6–5.8 mm (n = 1), dark brown intermixed with pale-brown scales mostly on basal half near cell; discal cell with faint spot near apical end; marginal scales dark brown; fringe scales brown; undersurface pale brown. Hindwing pale brown.

Male genitalia: Unknown.

Female genitalia (Fig. 41): Papillae anales conical, with short and long setae intermixed; eighth sternum narrow and broadly rounded distally; anterior apophyses posteriorly bifurcate, connecting eighth tergum and sternum; antrum funnelshaped, spinulate, with a wide median lobe, two internal flanges anteriorly; ductus seminalis spiralled from posterior end of corpus bursae, with spiralled internal support basally; corpus bursae spinulate, larger spinules near base of ductus seminalis, slightly constricted posteriorly on one side by a large plate.

Holotype.—♀, "VENEZUELA: T[erritorio] F[ederal] Amaz[ona], Cerro de Neblina, Base Camp, 140 m[eters], 0°50′N, 66°9′W, 24 Nov[ember]−1 Dec[ember] 1984, R.L. Brown"; "♀ Genitalia Slide by D A[damski] 4074, USNM 81204" [green label]. Deposited in the USNM.

Paratype.—1 ♀, Same label data as holotype except, "♀ Genitalia Slide by D A[damski] 3484, USNM 81637" [green label] (specimen is missing head). Deposited in the USNM.

Etymology.—The specific epithet is derived from the Latin *brunneus,* meaning "brown," and refers to the color of the moth.

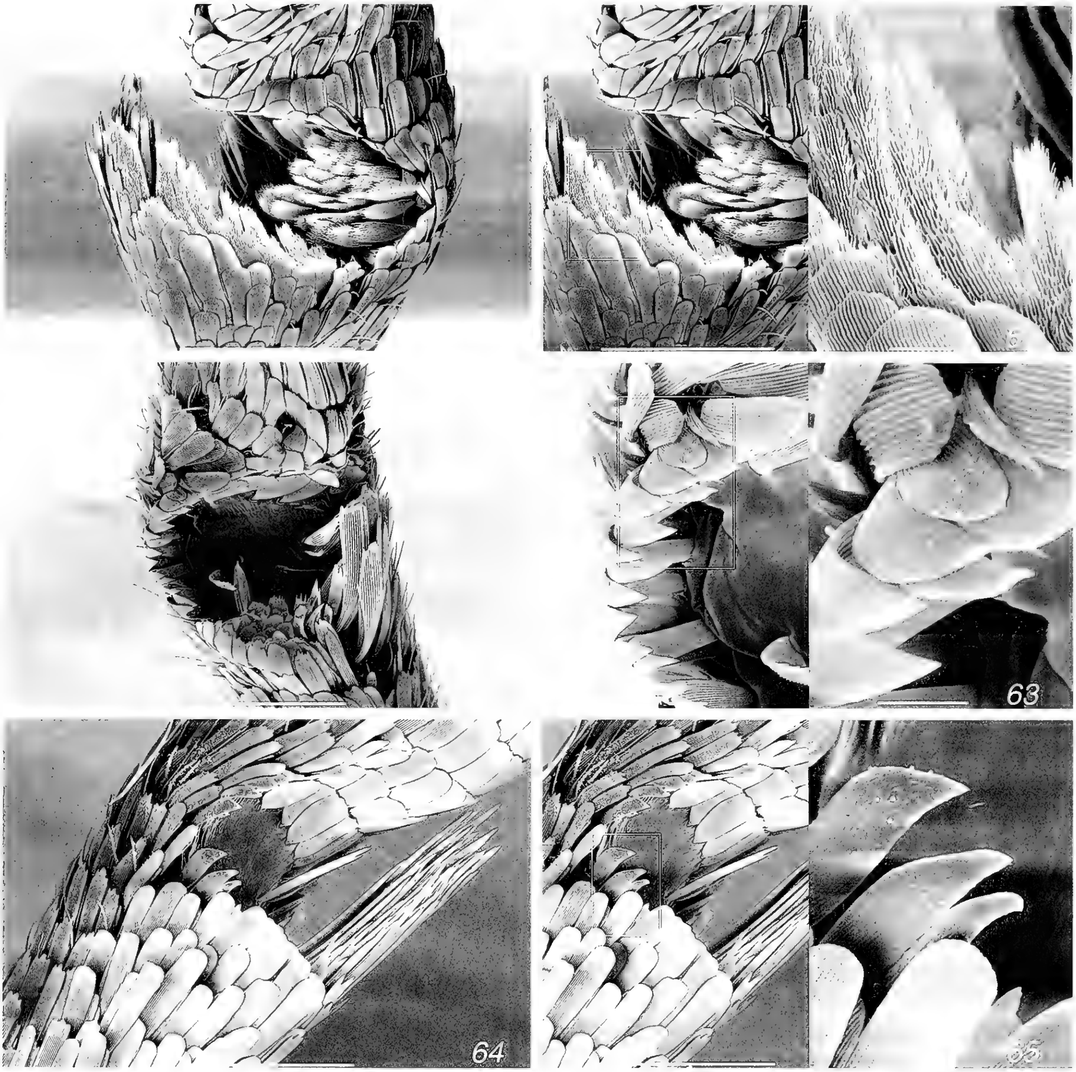
Glyphidocera janae Adamski and Brown, new species

(Figs. 42, 58)

Diagnosis.—*Glyphidocera janae* can be distinguished from other species of *Glyphidocera* by having a narrowed antrum; wide eighth sternum, with a broadly rounded posterior margin; elongate internal support of ductus seminalis; a large internal plate in corpus bursae, with shallow lateral emargination. *Glyphidocera janae* is most similar to *G. glowackae* in the possession of a slightly narrowed antrum and a broadly rounded posterior margin of the eighth sternum. The two differ in the length of the eighth sternum and the degree of spinulation near the base of the ductus seminalis.

Description.—*Head:* Vertex and frontoclypeus with brown scales tipped with pale brown; labial palpus with outer surface brown intermixed with pale-brown scales from base to near apex of second segment; inner surface similar except with more pale-brown scales; scape brown intermixed with a few pale brown scales, flagellum brown and pale brown alternating with each flagellomere; proboscis pale brown.

Thorax: Tegula and mesonotum brown; legs brown intermixed with pale brown scales near midsegments and near apices of all segments and tarsomeres. Forewing (Fig. 58) length 6.1 mm (n = 1), pale brown intermixed with some brown scales (many scales are missing); marginal scales brown; fringe scales mostly absent; undersurface pale brown. Hindwing pale brown.



Figs. 60–65. Antennal notch of *Glyphidocera*. 60, 61, *G. garveyi*. 62, 63, *G. glowackae*. 64, 65, *G. hamatella*.

Male genitalia: Unknown.

Female genitalia (Fig. 42): Papillae anales conical, with short and long setae intermixed; eighth sternum forming a wide band, broadly rounded posteriorly; anterior apophyses posteriorly bifurcate, connecting eighth tergum and sternum; antrum funnel-shaped, spinulate, and narrow, two internal flanges near constricted end; ductus seminalis spiralled from posterior end of corpus bursae, with elongate spiralled internal support; corpus bursae with microspinules throughout, constricted on one side by a large plate that has a slight emargination on posterior end.

Holotype.—♀, "VENEZUELA: T[erritorio] F[ederal] Amaz[ona], Cerro de la Neblina, Basecamp, 0°50′N, 66°9′44″N, 140 m[eters], 4–12 Feb[ruary] 1984, D. Davis & T. McCabe"; "♀ Genitalia Slide by D A[damski] 3491, USNM 81644" [green label]. Deposited in the USNM.

Etymology.—This species is named in honor of Jan Coleman-Knight, the first author's "second" seventh grade teacher.

Glyphidocera castanella Adamski and Brown, new species

(Figs. 43, 59)

Diagnosis.—*Glyphidocera castanella* can be distinguished from other species of *Glyphidocera* by having a broadly rounded posterior margin of the eighth sternum, antrum narrowed, elongate internal support of ductus seminalis spiralled, and internal plate with a slightly emarginate lateral margin. The female genitalia of *castenella* are similar to *G. mumiella* in having a highly spinulate corpus bursae and wide antrum. The two differ in the shape of the posterior margin of the eighth sternum and shape of the internal support of the ductus seminalis.

Description.—*Head:* Vertex and frontoclypeus with brown scales tipped with pale brown; labial palpus with outer surface brown intermixed with pale-brown scales from base to near apex of second segment; inner surface pale brown intermixed with a few brown scales; scape pale brown intermixed with a few brown scales, flagellum with basal half pale brown, distal half brown; proboscis pale brown.

Thorax: Tegula and mesonotum with brown scales tipped with pale brown; legs brown intermixed with pale-brown scales near midsegments and apices of all segments and tarsomeres. Forewing (Fig. 59) length 7.3 mm (n = 1), brown scales tipped with pale brown and brown scales along costal area; discal spots faint; marginal scales brown; fringe scales pale brown tipped with brown. Hindwing pale brown.

Male genitalia: Unknown.

Female genitalia (Fig. 43): Papillae anales conical, with short and long setae intermixed; eighth sternum a wide band, broadly rounded posteriorly; anterior apophyses posteriorly bifurcate, connecting eighth tergum and sternum; antrum funnel-shaped, spinulate, and narrowed, two internal flanges near anterior; ductus seminalis spiralled from posterior end of corpus bursae, with elongate internal support; corpus bursae with microspinules throughout, constricted on one side by large sclerotized plate that has an emargination on posterior end.

Holotype.—♀, "VENEZUELA: T[erritorio] F[ederal] Amaz[ona], Cerro de la Neblina, Basecamp, 0°50′N, 66°9′44″W, 140 m[eters], 4–12 Feb[ruary] 1984, D. Davis & T. McCabe"; "♀ Genitalia Slide by D A[damski] 3485, USNM 81638" [green label]. Deposited in the USNM.

Etymology.—The species epithet is derived from the Latin *castaneus,* meaning "brown," and refers to the brown color of the moth.

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TWO ATYPICAL NEW SPECIES OF *LACHESILLA* WESTWOOD IN THE *PEDICULARIA* GROUP (PSOCOPTERA: LACHESILLIDAE)

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Abstract.—Two **new species, *Lachesilla xalapensis*** and ***L. oaxacana,*** in the *pedicularia* group, from Xalapa, Veracruz, Mexico, and from Santa Catarina Lachatao, Oaxaca, Mexico, respectively, are here described and illustrated. Both species possess long processes arising from the claspers, an apomorphy that sets them apart from the other species in the group.

Resumen.—Dos **nuevas especies, *Lachesilla xalapensis*** y ***L. oaxacana,*** en el grupo *pedicularia,* de Xalapa, Veracruz, México, y de Santa Catarina Lachatao, Oaxaca, México, respectivamente, son aquí descritas e ilustradas. Las dos tienen un largo proceso en cada clasper, apomorfía que las separa de las otras especies del grupo.

Key Words: *Lachesilla, pedicularia* group, new species, Psocoptera, Mexico

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In the large, cosmopolitan psocid genus *Lachesilla* Westwood (with 228 described species, and 142 undescribed ones), 15 species groups have been phenetically recognized (García Aldrete 1974). One of these groups is the *pedicularia* group with 53 described species, mostly from Africa, South America, North America, Europe, and the Oriental region. Many undescribed species are known to occur in South and North America. The group has been diagnosed by García Aldrete (1974) and by Mockford (1993). The diagnosis of the males notes that the claspers are closely joined laterally to the hypandrium; the phallic apodeme is Y-shaped; the paraprocts have relatively long processes; the epiproct has single or double processes directed posteriorly; and the clunium may or may not have processes in the proximity of the epiproct. In the 80 known species in the group (described and undescribed), projections on the basal part of the claspers have not been observed, and the purpose of this paper is to describe two Mexican species of *Lachesilla* in this group that possess a long, slender process on each clasper, thus constituting a distinct subunit in the group. Both species are closely related, presenting basically the same color and pattern of head and body pigmentation and similar morphology of the female gonapophyses, but differ clearly in genital morphology of both sexes.

MATERIAL AND METHODS

The material studied consists of 26 specimens (3 males and 5 females of one species and 6 males and 12 females of the other). Color was recorded by observation of the specimens in 80% alcohol under a stereoscopic microscope at 100×, illuminated with yellow light. Specimens for microscopic study were dissected in 80% alcohol, and the head, right wings and legs, and genital parts were mounted on slides in Balsam of Canada. Measurements of parts mounted on slides were taken with an AO filar micrometer, with a measuring unit of 1.36 microns for wings and 0.53 microns for other parts. Abbreviations of parts measured, or counted, are as follows: FW and HW, lengths of fore and hind wings; F, T, t_1 and t_2, lengths of femur, tibia and tarsomeres of hind leg; ctt_1, number of ctenidobothria on t_1 of hind leg; Mx4, length of fourth palpomere of right maxillary palp; $f_1 \ldots f_n$, length of flagellomeres 1 . . . n; IO, minimum distance between compound eyes; D, antero-posterior diameter of right compound eye; d, transverse diameter of right compound eye; PO, d/D. The types are deposited in the National Insect Collection, housed in the Instituto de Biología, UNAM, Mexico City, Mexico.

Lachesilla xalapensis García Aldrete, new species

(Figs. 1–7)

Female.—*Color* (in 80% alcohol): Pale brown, with dark brown areas as indicated below. Compound eyes black, ocelli hyaline, with reddish-brown centripetal crescents. Antenna and maxillary palp dark brown. Head pattern (Fig. 2) with two dark brown spots (muscle insertions) on vertex, on each side of longitudinal midline. An irregular brown band from each compound eye to fronto-clypeal sulcus, above antennal fossae. Postclypeus with well defined ochre diagonal stripes. A wide, transverse, ochre band on each lower gena. Tergal lobes of meso- and metathorax reddish brown. Thoracic pleura with two irregular ochre stripes, one from behind compound eyes to abdomen and other from behind genal bands to abdomen. Legs pale brown. Wings (Fig. 1) hyaline, veins reddish brown. Abdomen pale brown, with ochre, transverse subcuticular bands, more distinct dorsally.

Morphology: Wing venation (Fig. 1). Subgenital plate setose as illustrated (Fig. 3), projected posteriorly in middle, projection deeply concave apically, with a field of short spines next to margin. Gonapophyses (Fig. 7) acinaciform, setose as illustrated; ninth sternum weakly pigmented between them. Paraprocts (Fig. 6), with 9–10 trichobothria, a peripheral one without basal rosette, setae as illustrated. Epiproct (Fig. 6) rounded posteriorly, with setal field on posterior third.

Measurements: FW: 2193, HW: 1685, F: 431, T: 807, t_1: 256, t_2: 88, ctt_1: 19, Mx4: 106, f_1: 327, f_2: 294, f_3: 247, f_4: 164, f_5: 106, f_6: 97, f_7: 86, f_8: 84, f_9: 71, f_{10}: 76, f_{11}: 82, IO: 318, D: 176, d: 119, IO/D: 1.8, PO: 0.67.

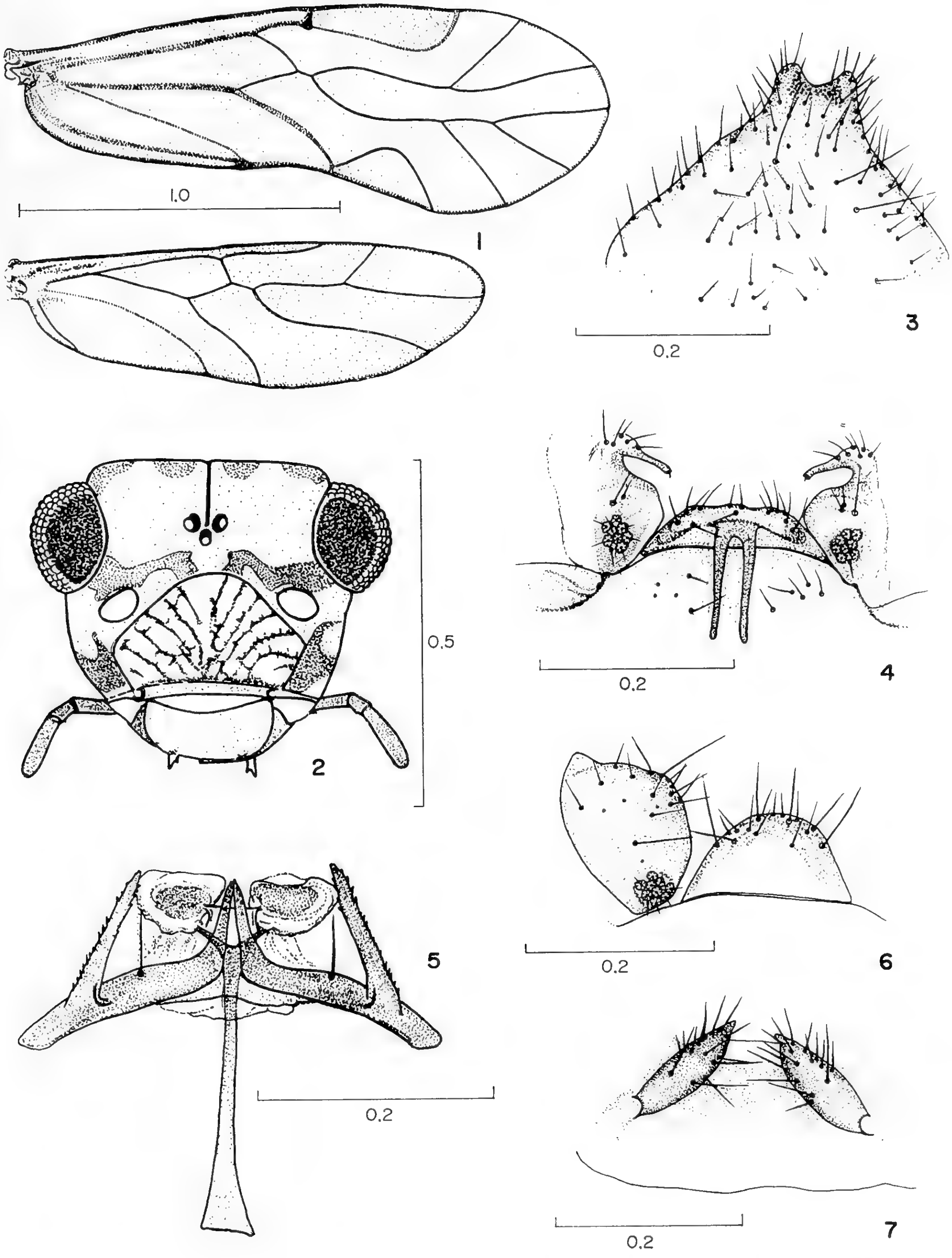
Male.—*Color* (In 80% alcohol): Same as female.

Morphology: Hypandrium (Fig. 5) small, triangular; claspers slender, with distal ends pointed, each with a field of short spines terminally. A long seta mesally on outer edge of each base; on each basal 3rd arises a stout, distally truncate, spiny projection. Phallic apodeme long, slender, wider proximally, diverging posteriorly, each arm ending in an irregular, membranous sac (Fig. 5). Paraprocts (Fig. 4) setose, with slender mesal projections, each with a small seta on apex; sensory fields with 9–10 trichobothria, a peripheral one without basal rosette; setae as illustrated. Epiproct (Fig. 4) wide, narrow antero-posteriorly, setose as illustrated, with a biramous, moderately long median projection.

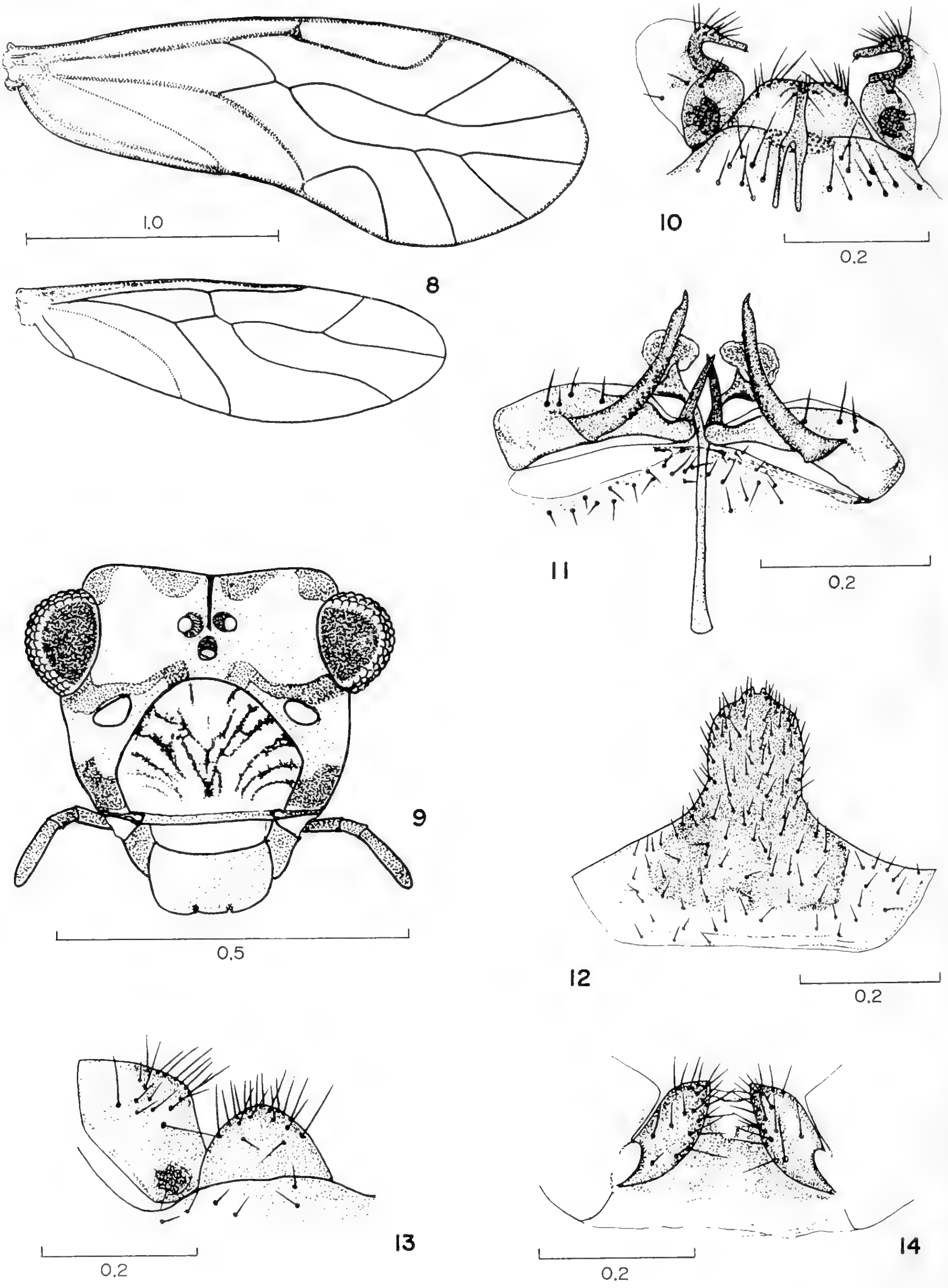
Measurements: FW: 2026, HW: 1554, F: 392, T: 750, t_1: 265, t_2: 95, ctt_1: 19, Mx4: 99, f_1: 303, f_2: 304, f_3: 269, f_4: 177, f_5: 133, f_6: 106, f_7: 97, f_8: 95, f_9: 78, f_{10}: 75, f_{11}: 108, IO: 300, D: 165, d: 115, IO/D: 1.81, PO: 0.69.

Types.—Holotype ♂, México. Veracruz. Xalapa. Km. 2.5, old road to Coatepec, Ecological Park Francisco Javier Clavijero, next to Instituto de Ecología, A.C., 1,250 m., 22.V.1998, beating dead fern fronds, J.A. Casasola. Allotype ♀, paratype ♂ with same data. Same locality, date and collector, but beating *Cupressus,* 3 ♀, paratypes.

Other specimens.—México. Veracruz, Chavarillo, Emiliano Zapata, 850 m., 21.V.1998, beating fallen branches with dead leaves, J.A. Casasola, 1 ♂. Las Hayas Ecological Park, 1,300 m., 22.V.1998, on dead, hanging leaves of *Yucca,* J.A. Casasola, 1 ♀.



Figs. 1–7. *Lachesilla xalapensis.* 1, Fore and hind wings, ♀. 2, Front view of head, ♀. 3, Subgenital plate, ♀. 4, Posterior margin of clunium, paraprocts and epiproct, ♂. 5, Phallic apodeme, hypandrium and claspers, ♂. 6, Right paraproct and epiproct, ♀. 7, Gonapophyses and ninth sternum, ♀. Scales in mm.



Figs. 8–14. *Lachesilla oaxacana.* 8, Fore and hind wings, ♀. 9, Front view of head, ♂. 10, Posterior margin of clunium, paraprocts and epiproct, ♂. 11, Phallic apodeme, hypandrium and claspers, ♂. 12, Subgenital plate, ♀. 13, Right paraproct and epiproct, ♀. 14, Gonapophyses and ninth sternum, ♀. Scales in mm.

Lachesilla oaxacana García Aldrete, new species

(Figs. 8–14)

Female.—*Color* (in 80% alcohol): Body color and head pattern of pigmentation (Fig. 9) essentially as in *L. xalapensis.*

Morphology: Wing venation (Fig. 8). Subgenital plate (Fig. 12), setose and pigmented as illustrated, columnar, with a small, concave, apical promontory. Gonapophyses (Fig. 14) acinaciform, setose; ninth sternum pigmented between them as illustrated. Paraprocts (Fig. 13) broad, semi-elliptic; sensory fields with 9 trichobothria, a peripheral one without basal rosette; setae as illustrated. Epiproct (Fig. 13) approximately semicircular, field of setae on distal third.

Measurements: FW: 2514, HW: 1913, F: 456, T: 896, t_1: 303, t_2: 92, ctt_1: 18, Mx4: 112, f_1: 319, f_2: 294, f_3: 238, f_4: 176, f_5: 112, f_6: 92, f_7: 82, f_8: 86, f_9: 62, f_{10}: 73, f_{11}: 99, IO: 328, D: 160, d: 106, IO/D: 2.04, PO: 0.66.

Male.—*Color* (in 80% alcohol): Same as female.

Morphology: Hypandrium wide, setose (Fig. 11). Claspers (Fig. 11) proximally wide, narrowing distally to end in smooth, slender, acuminate processes. A field of 3-4 setae mesally on outer edge of each clasper. Each clasper mesally with a stout, curved, acuminate projection, each with a field of short spines on inner edge. Phallic apodeme (Fig. 11) long, slender, distally forked, each arm wide distally, ending in a small, rounded, membranous sac. Paraprocts (Fig. 10) , each with a mesal, slender process; sensory fields with 11-12 trichobothria, a peripheral one without basal rosette; setae as illustrated. Epiproct trapezoidal (Fig. 10) with a median, slender, distally forked projection; setae as illustrated. Clunium with an elliptic field of short spines next to epiproct (Fig. 10).

Measurements: FW: 2518, HW: 1837, F: 434, T: 908, t_1: 299, t_2: 89, ctt_1: 19, Mx4: 110, f_1: 355, f_2: 336, f_3: 282, f_4: 212, f_5: 135, f_6: 111, f_7: 99, f_8: 94, f_9: 79, f_{10}: 73, f_{11}: 106, IO: 321, D: 167, d: 113, IO/D: 1.92, PO: 0.67.

Types.—Holotype ♂, México. Oaxaca. Santa Catarina Lachatao (Sierra de Juárez). 15.VII.1996, beating branches and foliage of *Quercus,* J.A. Casasola & T. Martínez. Allotype ♀, 11 ♀ and 5 ♂ paratypes, same data as holotype.

Comments.—*Lachesilla oaxacana* is very close to *L. xalapensis,* with which it shares similar body color, pattern of head pigmentation, general wing shape and venation, general shape of the gonapophyses, and having distinct, long processes on the claspers. The two species differ in the shape of the subgenital plates; in details of the shape of the gonapophyses (more elongate and pointed in *L. xalapensis*); in the shape of the claspers; number of setae on the outer margin and at the distal ends of the claspers; in the processes of the claspers; in details of the phallic apodemes; in the structure of the epiproctal process; and by the presence in *L. oaxacana* of a field of small spines in the posterior border of the clunium, next to the epiproct, absent in *L. xalapensis* (compare the pairs of Figs. 3 and 12, 7 and 14, 5 and 11, and 4 and 10).

The apomorphic presence of processes on the claspers places *L. xalapensis* and *L. oaxacana* distinctly apart from the other species in the *pedicularia* group. In life, the clasper processes extend almost perpendicular to the body, and probably function as accesories in copulation.

ACKNOWLEDGMENTS

I thank J. Arturo Casasola and Tomás Martínez, for collecting the specimens here studied, and Javier García, Felipe Villegas and Silvia López, of the Instituto de Biología, UNAM, for technical and secretarial support in the preparation of this paper.

LITERATURE CITED

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REVIEW OF THE GENUS *CIMOLUS* STÅL, WITH THE DESCRIPTION OF A NEW SPECIES (HETEROPTERA: COREIDAE: COREINAE)

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Abstract.—***Cimolus luteus*****, n. sp.**, collected in French Guiana, Panama, Suriname, and Venezuela, is described, illustrated, and compared with the two previously known species, *C. obscurus* Stål and *C. vitticeps* Stål. New localities are given for *C. vitticeps,* and a key is provided for the known species of *Cimolus.*

Key words: Insecta, Heteroptera, Coreidae, Coreini, *Cimolus,* new species, Neotropical Region

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The Genus *Cimolus,* proposed by Stål (1862), has never been reviewed. *Cimolus* is characterized by the robust, ovoid body; the head, with a small dorsal spine behind base of each antenniferous tubercle; short rostrum, reaching the anterior edge of mesosternum; and the legs, at most slightly enlarged, densely granulate, and with no more than a few scattered tubercles ventrally on the femora.

Anasa Amyot and Serville and *Catorhintha* Stål are somewhat similar to *Cimolus,* but the rostrum in these genera attains or extends beyond the middle of the mesosternum.

Previously, only two species of *Cimolus, C. obscurus* Stål (1870) and *C. vitticeps* Stål (1862) were known. In this contribution, one new species collected in French Guiana, Panama, Suriname, and Venezuela is described, and new distributional records for *C. vitticeps* are included.

The following abbreviations are used for the institutions cited in this paper: AMNH (American Museum of Natural History, New York); CAS (California Academy of Sciences, San Francisco); INBIO (Instituto Nacional de Biodiversidad, Costa Rica); LACM (Los Angeles County Museum, California); MELN (Muséo Entomológico, León, Nicaragua); MNHN (Muséum National d' Histoire Naturelle, Paris, France); RMNH (Nationaal Natuurhistorisch Museum, Leiden, The Netherlands); TAMU (Texas A&M University, College Station, Texas); UCV (Universidad Central de Venezuela, Escuela de Agronomía, Maracay, Venezuela); UGA (University of Georgia, Athens, Georgia); UMC (Wilbur R. Enns Entomology Museum, University of Missouri, Columbia, Missouri); UNAM (Colección Entomológica, Instituto de Biología, Universidad Nacional Autónoma de México, México D.F.); USU (Utah State University, Logan, Utah).

All measurements are given in millimeters.

Cimolus obscurus Stål
(Figs. 4, 5)

Cimolus obscurus Stål 1870: 189.

This species may be distinguished by the dorsally dull yellow head, with numerous black punctures coalescing to form two irregular stripes lateral to midline, the yellowish femora, with numerous, conspicuous reddish-brown to black dots never coalescing to form a continuous black stripe, and the yellow to orange abdominal sterna, with scattered black dots. Parameres as Figs. 4–5.

Distribution.—Florida, Louisiana, South Carolina, and Texas (Baranowski and Slater 1986, Froeschner 1988).

Material examined.—UNITED STATES OF AMERICA: 1 ♂, 1 ♀, Florida, Alachua Co., 4 mi N of La Crosse, 21 May 1989, L. R. Davis Jr. (UNAM); 1 ♂, Louisiana, Baton Rouge, 24 August 1920, T. H. Jones (UNAM); 1 ♂, 1 ♀, Texas, Brazos Co., College Station, 2 September 1979, J. E. Eger, and 22 September 1979, C. W. Agnew (UNAM); 1 ♂, Texas, Austin, Travis Co., 27 August 1976, P. L. Levin (UNAM); 1 ♀, Texas, Brazos Co., Bryan, 13 September 1976, J. C. Schaffner (UNAM).

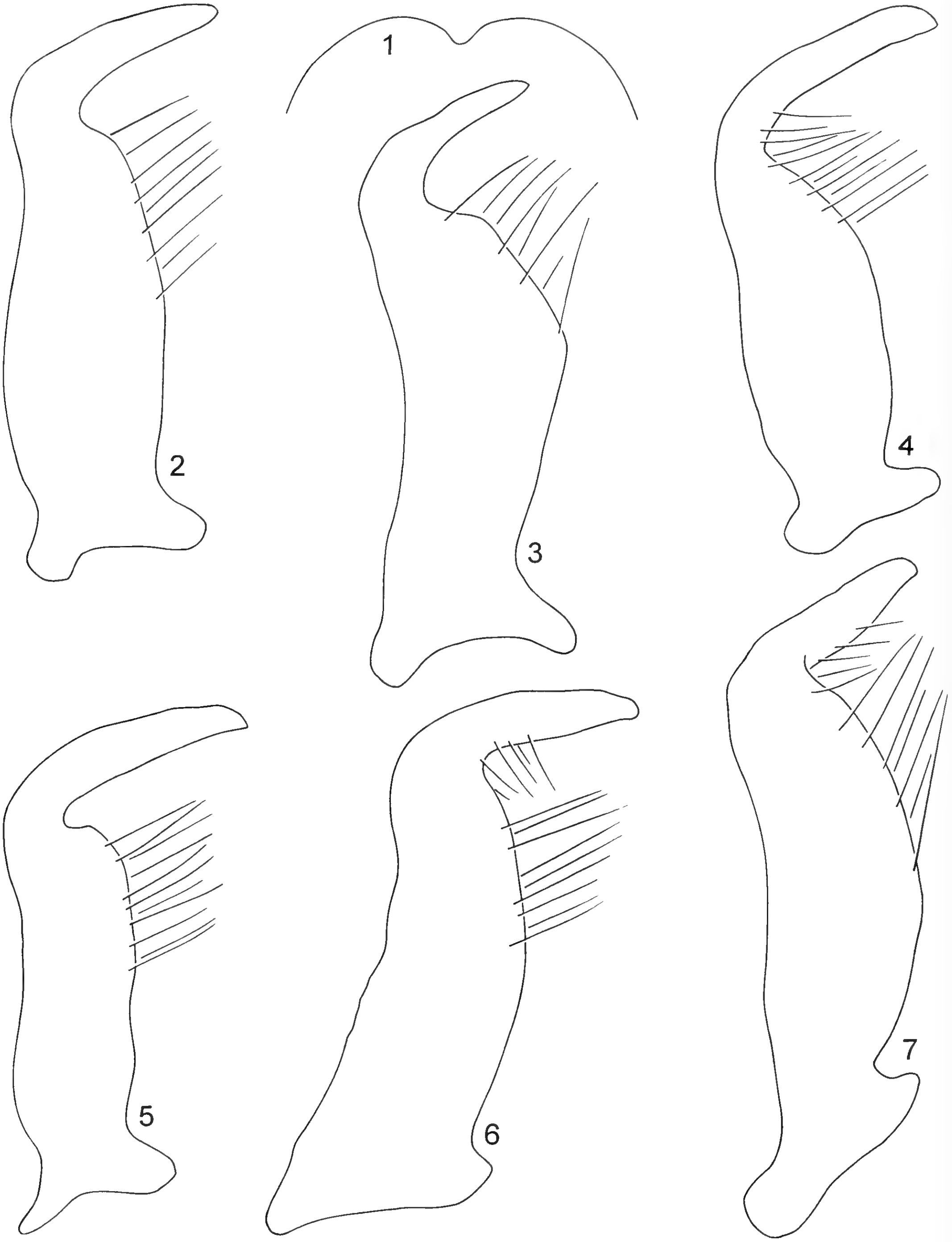
Cimolus vitticeps Stål
(Figs. 6–7)

Cimolus vitticeps Stål 1862: 302.

Differs from other species of the genus by the dorsally black head, with two lateral yellow stripes running between eye and ocelli; the femora dorsally black and ventrally dull yellow, with numerous black to reddish-brown dots; and the yellow to orange abdominal sterna, heavily mottled with irregularly distributed dark brown to black dots. Parameres as Figs. 6–7.

Distribution.—Belize, Guatemala, México, and Panama (Distant 1880–1893). New country records are Costa Rica, El Salvador, Honduras, and Nicaragua.

Material examined.—BELIZE: 1 ♀, Cayo Xunantunich, 14 August 1977, C. W. O'Brien and Marshall (AMNH). COSTA RICA: 1 ♀, Siquirres, December 1931, C. P. Dodge (AMNH); 1 ♂, Prov. Limon, Estación Hitoy Cerere, R. Cerere, Reserva Biologica Hitoy Cerere (100 m), November 1992, G. Carballo (INBIO); 2 ♀, Provincia Guanacaste, 8 km NO de Nacaome, P. N. Barra Honda (100 m), 8–25 August 1992, M. Reyes and April 1993, M. Reyes (INBIO); 1 ♀, Provincia Guanacaste, Santa Rosa National Park (300 m), December 1985, D. H. Janzen and W. Haliwacha (UNAM); 1 ♂, 14 km S Cañas, 20–29 May 1991, F. D. Parker (USU); 1 ♀, Provincia Guanacaste, Finca Jenny, 31 km N Liberia (300 m), October 1988 (INBIO); 1 ♀, Provincia Guanacaste, Estación Murciegalo, 8 km SO of Cuajiniquil (100 m), 17 July–2 August 1993, F. Quesada (INBIO). EL SALVADOR: 1 ♀, Armeria, 20 April 1954 (UNAM); 1 ♀, Union, 10 May 1954 (UMC). GUATEMALA: 1 ♂, Ayutla, 19 August 1947, B. Malkin (AMNH). HONDURAS: 1 ♂, Departamento Morazan, Escuela Agricola Panamericana Zamorano (2,650′), 22 July 1948, Hubbell (UCM); 1 ♂, Lago Jojoa, 19 July 1974, G. B. Marshall and C. W. and L. O'Brien (UGA). MEXICO: 1 ♂, Sinaloa, Mazatlan, 20 September 1976, J. Carayon (UNAM). 1 ♀, Nayarit, San Blas, 2–4 September 1976, C. D. George and R. R. Snellin (LACM); 2 ♀, Nayarit, Jalcocotan, 30 July 1984, M. Garcia and E. Barrera (UNAM). 1 ♂, 1 ♀, Durango, Mapimi, 11 March 1979, O. Mata (UNAM). 1 ♀, Tamaulipas, Bocatoma, 7 mi SSE Gomez Farias, 15 October 1985, R. Turnbow (UGA). 3 ♂, 1 ♀, Jalisco, Estación Biologica Chamela; 18–22 December 1987, H. Brailovsky and 5 November 1989, G. Ortega Leon and A. Cadena (UNAM). 1 ♂, Michoacan, Apatzingan, S Santillan, 29 July 1971 (UNAM); 1 ♀, Michoacan, Tinganbato, 10 December 1980, H. Brailovsky (UNAM). 1 ♀, Guerrero, Teocalco (1,100 m), 2 February 1989, E. Barrera, L. Cervantes and A. Cadena (UNAM); 1 ♀, Guerrero, 15 Km N of Iguala, Estación de Microondas Tuxpan, 24 May 1986, H. Brailovsky and E. Mariño (UNAM). 3 ♂, 3 ♀, Estado de México, Malinalco, 19 November 1980, H. Brailovsky and E. Barrera (UNAM). 1 ♂, Hidalgo, Autlan, Otongo (3,400′), C. W. and L. O'Brien and G. Wibmer (UNAM). 1 ♀, Morelos, Cañon de Lobos, 24 August 1976, H. Brailovsky (UNAM). 1 ♀, Oaxaca, Tamazulapan, 22 August 1959, A. S. Menke and L. A. Stange (LACM); 1 ♀, Oaxaca, Pluma Hidalgo,



Figs 1–7. *Cimolus* spp. 1, Caudal view of male genital capsule of *C. luteus.* 2–7. Parameres. 2–3, *C. luteus.* 4–5, *C. obscurus.* 6–7, *C. vitticeps.*

16 October 1985, E. Barrera (UNAM). 1 ♂, Veracruz, Pastorias, 14 April 1975, H. Brailovsky (UNAM); 4 ♂, 5 ♀, Veracruz, Jalapa, 25 August 1984, J. Peña, 3 October 1984, J. Peña, 1–8 September 1985, J. Peña and 25 April, E. Barrera (UNAM); 1 ♀, Veracruz, Tlapacoyan, 13 September 1986, E. Mariño (UNAM); 1 ♂, Veracruz, 3 mi NE Huatusco, 23 July 1989, Carroll, Schaffner and Friedlander (TAMU); 1 ♀, Veracruz, Cañon de Metlac, 3 km W of Fortin de las Flores, 6 July 1981, E. M. Fischer (CAS). 1 ♂, Chiapas, Palenque, 31 January 1985, M. Vertiz (UNAM); 1 ♀, Chiapas, Finca Prusia, 31 January 1985, M. Vertiz (UNAM). 1 ♀, Quintana Roo, Chetumal, Calderitas, 30 October 1981, E. Barrera (UNAM). 20 April 1954 (UNAM); 1 ♀, Union, 10 May 1954 (UMC). NICARAGUA: 1 ♀, Leon, August 1996, Zamira (MELN).

Cimolus luteus Brailovsky, new species
(Figs. 1–3, 8)

Male.—*Measurements:* Head length in dorsal view 1.40; width across eyes 1.76; interocular space 1.03; interocellar space: 0.50; preocular distance 0.84; length antennal segments: I, 1.96; II, 2.40; III, 2.08; IV, 1.88. Pronotum: Length 3.20; width across frontal angles 1.76; width across humeral angles 4.92. Scutellar length 1.80; width 2.00. Body length 13.20.

Coloration: Ground color, including legs, dull yellow with numerous black to dark red punctures and tubercles over entire dorsal and ventral surface; antennal segments dark chestnut orange with tubercles, apical third of segment III and basal third of segment IV dark red; head dorsally with numerous black punctures coalescing to form two irregular stripes with a narrow pale yellow median line and a shorter yellow stripe on each side between eyes and ocelli; anterolateral margins of pronotum, apex of scutellum, and anterior and posterior lobe of metathoracic peritreme creamy to pale yellow; hemelytral membrane yellowish white, with veins pale brown; connexivum alternating dark brown and yellow patches, with central portion of brown area suffused with yellow; abdominal segments I to VI black, and segment VII black with a yellow quadrangular spot running from middle to posterior margin; pleural abdominal margin yellow with two black dots, one close to middle third, the other near posterior angle.

Structure: Body robust, ovoid. Head declivent anteriorly, not extending appreciably forward of antenniferous tubercle; dorsally with a small spine behind base of each antenniferous tubercle; postocular tubercle moderately exposed; rostrum short, barely reaching anterior edge of mesosternum. Pronotum moderately declivous, with a distinct collar; frontal angles produced forward as blunt teeth; anterolateral edge irregularly crenulate, clearly emarginate; humeral angles rounded, scarcely expanded; posterolateral and posterior edge smooth; calli flat; anterior lobe of metathoracic peritreme reniform, posterior lobe sharp, small. Scutellum: Triangular, flat, apically subacute. Hemelytra: Macropterous, reaching apex of last abdominal segment. Abdomen: Connexival segments strongly elevated; posterior angles without spines. Legs. Unarmed, densely granulate; tibiae sulcate. Genital capsule: Posteroventral edge laterally produced into short blunt lobes, area between lobes with a slight or deep u-shaped concavity (Fig. 1). Parameres: Shaft robust with sides almost parallel; apical lobe elongate, distally narrowly rounded (Figs. 2–3).

Female.—*Measurements:* Head length in dorsal view 1.50; width across eyes 1.92; interocular space 1.12; interocellar space 0.52; preocular distance 0.92; length antennal segments: I, 2.20; II, 2.68; III, 2.48; IV, 1.92. Pronotum: Length 3.52; width across frontal angles 1.92; width across humeral angles 5.80. Scutellar length 2.24; width 2.28. Body length 14.83.

Coloration: Similar to male. Connexival segments VIII and IX dark chestnut orange with posterior margin black; abdominal

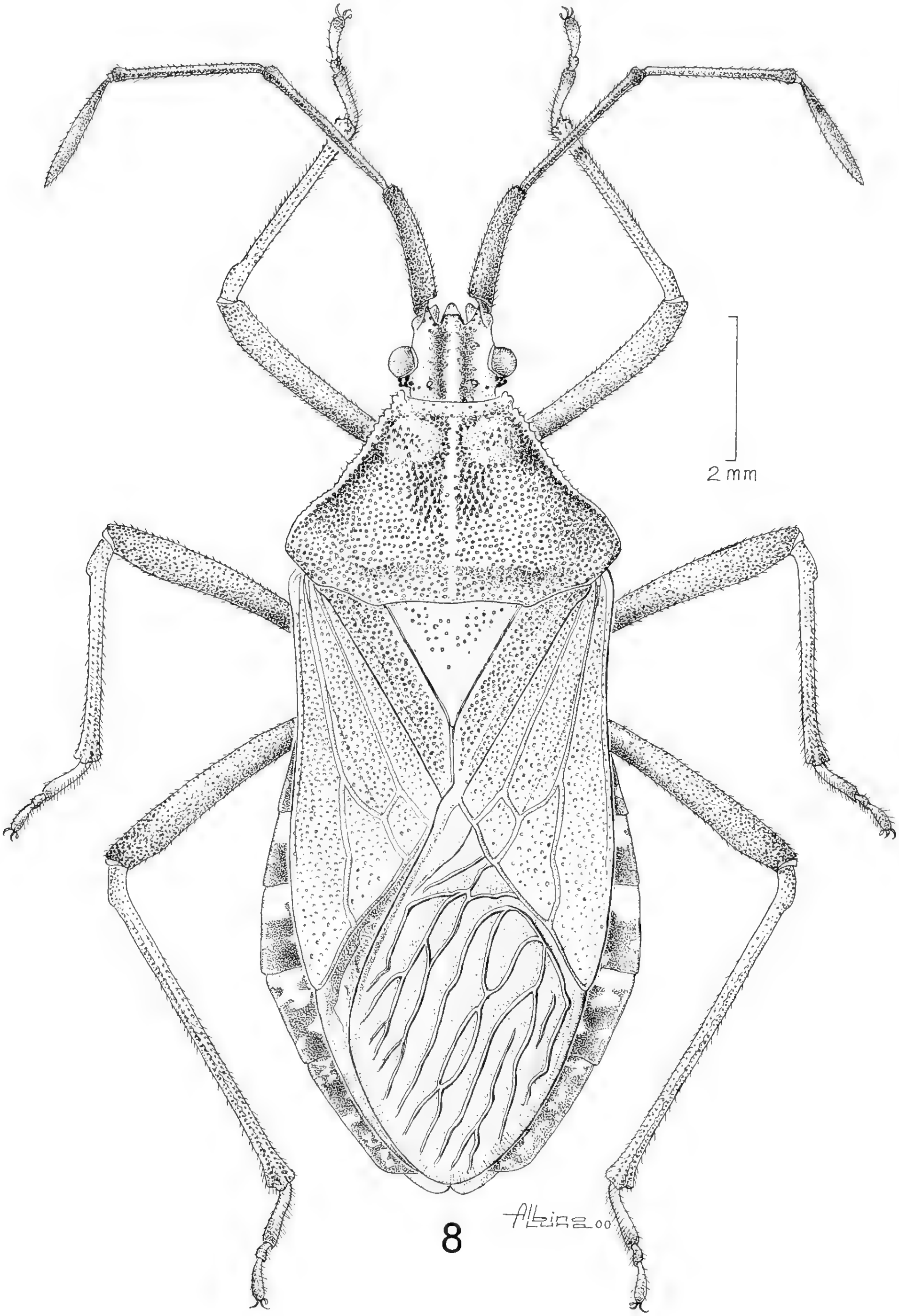


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Fig. 8. Dorsal view of *Cimolus luteus.*

segment VII black, VIII and IX dark chestnut orange suffused with irregular black spots; genital plates dull yellowish with punctures, tubercles, and upper and inner face of paratergite VIII and IX black. *Genital plates:* Abdominal sternite VII with a narrow longitudinal opening; fold rectangular, transversely straight; gonocoxae I triangular, closed in caudal view; paratergite VIII short, triangular with visible spiracle; paratergite IX square, weakly longer than paratergite VIII.

Integument (♂ *and* ♀): Body surface rather dull, clothed with short and usually decumbent, silvery, bristlelike setae; pronotum, scutellum, clavus, corium, head ventrally, thorax, abdomen, and male and female genitalia densely punctate; head dorsally, connexival segments, mesopleura, and metapleura scattered punctate; antennal segments I to III and legs densely tuberculate.

Variation.—1, Ground color dull orange; 2, antennal segments I and II black to dark reddish brown; 3, evaporative area black to orange yellow; 4, abdominal segments VIII and IX of female yellow with black spots.

Type material.—Holotype: ♂, VENEZUELA, Aragua, Rancho Grande, 2 May 1980, J. M. Ayala (UNAM). Paratypes: 1 ♂ FRENCH GUIANA, 1899, R. Oberthur (MNHN); 1 ♂, 1 ♀, PANAMA (without data) (MNHN, UMC); 2 ♂, 1 ♀, SURINAME, Paramaribo, 3 July 1963, P. H. van Doesburg, 24–31 March 1966, J. Geijskes, 1911 (without data) (RMNH); 1 ♂, 2 ♀, VENEZUELA, Tachira, San Cristobal, 13 May 1984 and 9 September 1981 (without colector) (UCV, UNAM); 1 ♀, Rancho Grande, Portachuelo, 28 May 1980, J. A. Clavijo and A. Chacon (UCV); 1 ♀, Aragua, Ocumare de la Costa, 24 August 1970, R. Casares and C. Padron (UCV); 1 ♀, Barinas, Cañas, 10 April 1949 (without colector) (UCV); 1 ♂, Venezuela (without data) (UNAM).

Notes.—*Cimolus luteus* is structurally similar to *C. vitticeps,* and *C. obscurus.* The three species can be separated by the greatly differing coloration of hemelytral membrane and femora, shape of parameres (Figs. 2–7), and distribution. In *C. luteus* the hemelytral membrane is yellowish white with the veins pale brown, and the femora are dull yellow with the tubercles black to dark red, never coalescing on irregular stripes or fused on a entirely black surface. This species occurs in French Guiana, Panama, Suriname and Venezuela. *Cimolus obscurus* apparently is confined to the south and southeastern United States (Florida, Louisiana, South Carolina and Texas) (Baranowski and Slater 1986, Froeschner 1988), and *C. vitticeps* widespread in Belize, Costa Rica, El Salvador, Guatemala, Honduras, México, Nicaragua, and Panama (Distant 1880–1893 and new additional records), has the hemelytral membrane black, and the femora dull yellow with numerous black dots over entire dorsal and ventral surfaces, the most dense being on the dorsal surface.

Etymology.—Named for its pale yellow ground color.

KEY TO SPECIES OF *CIMOLUS*

1. Hemelytral membrane yellowish white with veins pale brown . . . . *luteus,* n. sp.
– Hemelytral membrane black 2
2. Head dorsally dull yellow with numerous black punctures coalescing to form two irregular stripes lateral to midline; femora yellowish with numerous reddish-brown dots never coalescing on a black continuous stripe; abdominal sterna orange or yellow with few black dots . . . . *obscurus* Stål
– Head dorsally black with two lateral yellow stripes running between eye and ocelli; femora with dorsal surface entirely black and ventral surface yellow with numerous black to reddish-brown dots; abdominal sterna orange to yellow, heavily mottled with dark brown to black dots . . . . *vitticeps* Stål

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EXOTIC WOODBORING COLEOPTERA (MICROMALTHIDAE, SCOLYTIDAE) AND HYMENOPTERA (XIPHYDRIIDAE) NEW TO OREGON AND WASHINGTON

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Abstract.—Concerns about the unintentional introduction of exotic woodboring insects prompted surveys of high-risk sites in Washington in 1996 and Oregon in 1997 and 1998. Ports, port areas, mills and businesses known to have received or handled imported wood or wood products were monitored using Lindgren funnel traps and/or Scots pine bait logs. Seven species of beetles, *Micromalthus debilis* LeConte (Micromalthidae), *Gnathotrichus materiarius* (Fitch), *Hylastes opacus* Erichson, *Xyleborinus alni* (Niisima), *Xyleborus californicus* Wood, *Xyleborus pfeili* (Ratzeburg), *Xyloterinus politus* (Say) (Scolytidae), and one species of wood wasp, *Xiphydria prolongata* (Geoffroy) (Xiphydriidae), are recorded from Oregon, Washington, the western United States, or North America for the first time. These species are native to Asia, Europe, or the eastern United States. Most probably pose little immediate threat to the overall health of our forests, agricultural systems, and urban or rural environments. *Hylastes opacus*, a Palearctic species previously established in the eastern U.S., is a known pest of pines. *Xiphydria prolongata* has been implicated as a passive carrier of watermark disease of willows. Six (75%) of these species have hardwood hosts, implicating dunnage and solid wood packing material as probable pathways of introduction. Thirty-eight percent of the sites monitored in Oregon produced one or more new species records. These detections underscore the need for 1) effective regulations and certification, quarantine, and port inspection programs to prevent the introduction of exotic woodboring insects and 2) for systematic surveys of high-risk areas to determine which introduced organisms may already be established.

Key Words: exotic, woodborers, Micromalthidae, Scolytidae, Xiphydriidae

Woodboring beetles, particularly bark and ambrosia beetles (Scolytidae), are the most frequently intercepted insects on wood articles at U.S. ports of entry (Haack and Cavey 1997). Typical modes of introduction include raw logs, lumber, and solid wood packing material and dunnage associated with a wide range of commodities from Europe, Asia, and other foreign sources. Pest risk assessments identifying wood-associated pests, their likelihood of introduction, probability of establishment, and potential impacts have been recently completed in response to the demand for foreign timber and wood products (USDA Forest Service 1991, 1992, 1993, 1998). Regulations designed to mitigate potential pest risks have been developed as organisms or pathways of introduction were identified. Among the most recent are those regulating solid wood packing material from China (USDA-APHIS 1998). These regulations, along with port inspection, certification, and monitoring programs, serve as the first line of defense against the introduction of exotic organisms.

Despite such efforts, the number of exotic bark beetles established in North America has steadily increased (Marchant and Borden 1976, Wood 1977, Atkinson et al. 1990, Hoebeke 1994, L. M. Humble, unpublished data). While the impact of many of these recently introduced species is unknown, the pine shoot beetle, *Tomicus piniperda* (L.) (Scolytidae), has prompted intensive research, regulatory, and management programs (Haack et al. 1997). Recent discoveries of Asian longhorned beetle, *Anoplophora glabripennis* (Motschulsky) (Cerambycidae), in New York and Chicago prompted large-scale emergency quarantine, survey, and eradication programs (Haack et al. 1996, Poland et al. 1998). Exotic organisms such as these threaten the health of North American forests, agricultural systems, and urban and rural environments (US Congress, OTA 1993, Liebhold et al. 1995).

Increasing volumes of imported wood, wood products, and other foreign commodities have been arriving at Pacific Northwest ports. In Oregon, over 50 million board feet of logs, green lumber, railroad ties, and wood chips from New Zealand, Chile, Brazil, Mexico, and Russia were imported from 1991–1998 (Oregon Dept. Agriculture, unpublished data). In response to the increasing number of non-indigenous species becoming established in the northeastern U.S., the United States Department of Agriculture targeted six exotic bark beetle species for survey through its Cooperative Agricultural Pest Survey (CAPS) program beginning in 1994 (Cavey 1993). Consequently, CAPS surveys for exotic woodboring beetles and wood wasps were conducted at high-risk sites in Washington in 1996 and Oregon in 1997–98. Target species included the bark beetles (Scolytidae) *Hylastes opacus* Erichson, *Hylurgus ligniperda* (F.), *Ips typographus* (L.), and *T. piniperda,* and the European wood wasp, *Sirex noctilio* (F.) (Siricidae).

MATERIALS AND METHODS

Trapping surveys were conducted in the Washington port areas of Seattle, Tacoma, Olympia, Aberdeen, Longview, and Vancouver in 1996, and the Oregon ports of Portland and Coos Bay in 1997 and 1998. Additional high-risk sites surveyed in Oregon included a site across from the port of Longview, WA, several mills receiving foreign wood products, an exotic woods importer, warehouses receiving imported commodities, and wood recyclers. Lindgren traps (8-, 12-, or 16-funnel) baited with exotic bark beetle lure (EBB: ipsdienol, methylbutenol, and cis-verbenol), pine shoot beetle lure (AP: alpha-pinene), woodborer lures (AP-EtOH: alpha-pinene and ethanol ultra-high release [UHR] pouches), or ethanol UHR lures (EtOH), (Phero Tech Inc., Delta, BC) were the primary survey means. Traps were monitored weekly from late March to June 4 in Washington and biweekly from February through September and early October in Oregon. Bait logs of Scots pine (*Pinus sylvestris* L.), a preferred host for pine shoot beetle, were also placed at all Oregon trap sites in 1997 and 1998 and at additional high-risk sites in 1998. Upon removal, bait logs were placed in emergence tubes and monitored biweekly for insect emergence. Unless otherwise noted, all collection records refer to specimens collected in Lindgren funnel traps and are reported by: state, county, city (site type), lure, collection date, collector(s), and (number of specimens collected).

Non-scolytid beetles from the Oregon surveys were generally identified by LaBonte, based upon available literature and comparison with identified material in the insect collection of the Oregon Dept. of Agriculture (ODAC), Salem, OR, or the Oregon State Arthropod Collection (OSAC), Oregon State University, Corvallis, OR. Scolytidae and Xiphydriidae identifications were provided or confirmed by several taxonomic authorities (see Acknowledgments). Unless otherwise stated, specimens collected in the Oregon surveys are housed in the ODAC. Washington survey specimens were deposited in the William F. Barr Entomological Museum (WFBM) at the University of Idaho.

RESULTS

Two hundred and sixty-three species of woodboring or wood-associated beetles and wood wasps were identified in Oregon, totalling 26,986 specimens. Approximately 2,100 specimens comprising 29 species of wood-associated beetles were identified from the Washington survey. Seven species of beetles, *Micromalthus debilis* LeConte (Micromalthidae), *Gnathotrichus materiarius* (Fitch), *Hylastes opacus* Erichson, *Xyleborinus alni* (Niisima), *Xyleborus californicus* Wood, *Xyleborus pfeili* (Ratzeburg), *Xyloterinus politus* (Say) (Scolytidae), and one species of wood wasp, *Xiphydria prolongata* (Geoffroy) (Xiphydriidae), are recorded from Oregon, Washington, the western United States, or North America for the first time. New Oregon county records for *Xyleborus californicus* and *Xyleborus xylographus* (Say) are included as well.

NEW OREGON AND WASHINGTON RECORDS

Coleoptera
Micromalthidae

Micromalthus debilis LeConte

Records.—Oregon: Lane Co., Jasper (mill site), EtOH, 2 IX 1998, W. R. Estabrook & M. T. Savelich (1). Washington: King Co., Federal Way, V 1998 (exact date unavailable), in bank building, associated with bank vault, R. Mix (100's); Kitsap Co., Poulsbo, 17 VII 1998, in bank building, associated with bank vault, D. Suomi (100's).

Comments.—These data represent new northwestern U.S. and state records. This species is indigenous to North America east of the Rocky Mountains (Lawrence 1991). Larvae occur in decaying wood, predominantly hardwoods such as chestnut and oak, but also in conifers such as Douglas-fir and pine (Atkins 1982). This beetle has been spread via commerce to many parts of the world (Atkins 1982), presumably via wooden building and packing material. The sole member of the family Micromalthidae, *M. debilis* has one of the most complex life cycles of any insect, including three types of paedogenetic larvae (Lawrence 1991).

Micromalthus debilis has been found infesting the wood panels forming the walls and floors of bank vaults and safes (Weintraub 1995). The high moisture content of this wood apparently provides ideal conditions for these beetles. *Micromalthus debilis* is known from safes in Las Vegas (16 V 1994, P. Bowerman), and Carson City (VI 1993, E. Benes), NV (J. Knight, personal communication).

Micromalthus debilis is probably established in Oregon and Washington. Although the Oregon record is represented by only a single specimen, a substantial population was probably present in order for an individual to be trapped. The Washington populations have been resident in the bank buildings for up to seven years. The beetles accumulated in great numbers at windows and other locations, and it seems likely some escaped into the surrounding woods, which have ample suitable host material (D. Suomi, personal communication). The status of the Nevada populations is unknown.

Scolytidae

Gnathotrichus materiarius (Fitch)

Records.—Oregon: Wasco Co., The Dalles (mill site), AP-EtOH, 4 V 1998 (2); EBB, 14 IX 1998 (1). All specimens collected by T. A. Stafford.

Comments.—These data represent new western North American and state records. This species is indigenous to eastern North America, extending west to SD, and it has been introduced in France and adjacent European countries, as well as the Dominican

Republic (Wood 1977, 1982, in litt.). *Gnathotrichus materiarius* may have reached Oregon through natural dispersal since this species was found in western SD in 1962 (S. L. Wood, in litt.). Hosts are pine, spruce, and Douglas-fir (Wood 1982, Bright and Skidmore 1997). One specimen has been deposited in the National Museum of Natural History, Smithsonian Institution (USNM).

Hylastes opacus Erichson

Records.—Oregon: Linn Co., Sweet Home (mill site), W. R. Estabrook and M. T. Savelich (1); Multnomah Co., Portland (port vicinity), T. A. Stafford (1); Wasco Co., The Dalles (industrial site), T. A. Stafford (4). All specimens were found 22 III 1998 dead in emergence tubes containing bait logs of *Pinus sylvestris* placed in early 1997.

Comments.—These data represent new western North American and state records. This Palearctic species was recently recorded from ME, NH, NY, WV (Hoebeke 1994, Rabaglia and Cavey 1994), and ON and PQ (Bright and Skidmore 1997). It is a noxious pest in nurseries and pine plantations in Europe and is occasionally intercepted in pine dunnage at major U.S. ports (Hoebeke 1994). The hosts are primarily pines, especially *P. sylvestris,* although other conifers are sometimes attacked (Hoebeke 1994, Bright and Skidmore 1997). Two specimens have been deposited in the USNM.

Xyleborinus alni (Niisima)

Records.—Oregon: Columbia Co., Rainier (port vicinity), 25 IV 1997 (2), (AP-EtOH, 1; EBB, 1); 9 V 1997 (11) (AP-EtOH, 9; EBB, 2), G. I. Fowles; Multnomah Co., Portland (port area and warehouse sites) (3), AP-EtOH (27 III 1998, 2; 22 V 1998, 1), G. I. Fowles. Washington: Pierce Co., Tacoma (port areas), 3-11 IV 1996 (3) (AP, 1; EtOH, 1; EBB, 1), EBB, 11-17 IV 1996 (1); Thurston Co., Olympia (port areas), 12 III-1 IV 1996 (5) (EtOH, 4; EBB, 1), 27 III-9 IV 1996 (11) (EtOH, 10; EBB, 1). All Washington specimens were collected by H. Kamping.

Comments.—These data are the first published North American and state records for this species. The previous known distribution includes Europe (Austria, Germany, Poland, and Czechoslovakia) and Asia (Japan and eastern Russia) (Wood and Bright 1992, Bright and Skidmore 1997). At least the Oregon specimens appear to be the result of an introduction from Japan (S. L. Wood, in litt.). Subsequent to these records, *X. alni* was identified from voucher material collected in 1995 at four sites around Vancouver, BC (L. M. Humble, unpublished data). Hosts are alder, birch, hazel, linden, oak, and willow (Wood and Bright 1992, Bright and Skidmore 1997). Examination of potential host material near the Port of Olympia in April, 1997, verified a breeding population from wind-thrown alder, *Alnus rubra* Bongard. One Oregon specimen has been deposited in the USNM and the Washington specimens have been deposited in the WFBM.

Xyleborus californicus Wood

Records.—Oregon: Lane Co., Jasper (mill site), AP-EtOH, 29 V 1997, W. R. Estabrook (1); AP-EtOH, 29 IV 1998, W. R. Estabrook & M. T. Savelich (3); 2 VI 1998, W. R. Estabrook & M. T. Savelich (2) (AP-EtOH, 1; EtOH, 1); Multnomah Co., Portland (warehouse site), AP-EtOH, 29 IV 1998, K. A. Puls (2). Washington: Clark Co., Vancouver (port vicinity), EtOH, 1–10 IV 1996, H. Kamping (1).

Comments.—These data represent new Washington state and Oregon county records. This species was previously recorded from CA (8 specimens) and OR, Marion Co. (2 specimens) (Furniss et al. 1992). It was also recently recorded from the eastern U.S. in AR, DE, MD, and SC (Vandenberg et al. 2000). Despite the specific epithet, this species is now known to be indigenous to the northern Palearctic (Vandenberg et al. 2000), based upon specimens from Siberia examined by S. L. Wood. Its hosts are unknown (Hobson and Bright 1994), but this species can probably be found in species of oak (S. L. Wood, in litt.) and was found in an oak stump in AR (Vandenberg et al. 2000). One specimen has been deposited in the USNM and the Washington specimen has been deposited in the WFBM.

Xyleborus pfeili (Ratzeburg)

Records.—Oregon: Lane Co., Jasper (mill site); AP-EtOH (2) (10 VI 1997, 1; 16 VI 1998, 1); EtOH (9) (18 V 1998, 6; 16 VI 1998, 1; 29 VI 1998, 1; 2 IX 1998, 1); EBB, 27 VII 1998 (1). All specimens were collected by W. R. Estabrook and M. T. Savelich.

Comments.—These data are new western North American and Oregon records. This species is indigenous to Africa, Asia, Europe, and has been introduced into New Zealand (Wood and Bright 1992). It has been recently recorded as an introduction into the eastern U.S., in MD (Vandenberg et al. 2000). Its hosts include a wide variety of deciduous trees, including alder, beech, elm, maple, oak, and poplar, as well as several conifers (Wood and Bright 1992). One specimen has been deposited in the USNM.

Xyleborus xylographus (Say)

Records.—Oregon: Lane Co., Goshen (mill site), AP-EtOH, (2) (16 VI 1998, 1; 2 VII 1998, 1). Both specimens were collected by W. R. Estabrook & M. T. Savelich.

Comments.—These data represent a new Oregon county record. This species is indigenous to the Antilles and eastern North America from ON and PQ to the Gulf Coast (Wood and Bright 1992). The previous records from western North America (BC, CA, OR) represent introductions (Wood and Bright 1992). The prior OR record was based upon a single specimen from Yamhill Co. (Furniss et al. 1992). The hosts of this species are primarily oaks, rarely other deciduous trees and some conifers (Wood and Bright 1992, Solomon 1995). One specimen has been deposited in the USNM.

Xyloterinus politus (Say)

Records.—Washington: King Co., Seattle (port vicinity), EBB, 6 V – 4 VI 1996, H. Kamping (1).

Comments.—This is a new record for the western U.S. and Washington. This species is native to eastern Canada and the eastern U.S. (Wood 1982, Bright 1976). It has been recently recorded from BC (L. M. Humble, unpublished data). Its hosts are primarily deciduous trees, including maple, alder, birch, and oak, although it has been rarely found in conifers (Wood 1982). The specimen has been deposited in the WFBM.

HYMENOPTERA

Xiphydriidae

Xiphydria prolongata (Geoffroy)

Records.—Oregon: Multnomah Co., Portland (wood recycling facility), AP-EtOH, 19 VIII 1998, T. A. Stafford (1).

Comments.—This is a new western North American and state record. Previous North American records include MI and NJ (Smith 1983). This European species is known as the "willow wood wasp." It has been recorded from Finland south to Italy and from England east to Siberia (Smith 1978). Its hosts are deciduous trees, including maple, alder, birch, plane tree, poplar, oak, willow, and elm (Smith 1983). Unlike other insects in this paper, xiphydriids are primarily associated with partially decayed wood (Furniss and Carolin 1977). *Xiphydria prolongata* has been implicated as a passive carrier of watermark disease of willows (Gray 1940).

DISCUSSION

We record eight species of exotic wood-boring insects from Oregon, Washington, the Pacific Northwest, the western U.S., western North America, or North America, for the first time. They are native to several regions of the world, including Asia, Europe, and the eastern U.S., indicating both inter- and intra-continental pathways of introduction. While much attention has been paid to organisms introduced from foreign sources and their impacts, the same is not true for introductions from domestic sources. The potential ecological and economic impacts of "regional exotics" are a significant cause for concern as well (Pimentel et al. 2000) as regions of the country with distinct faunal components are becoming increasingly homogeneous.

Six of the sixteen sites surveyed in Oregon (38%), yielded new U.S. or state records of exotic woodboring insects. These are sobering results. While all the sites surveyed had a high potential for introduction (ports, mills, warehouses, and wood recyclers), only a modest portion of such sites were surveyed. Other systematic surveys for exotic bark beetles have also produced new state, U.S., or Canadian records (Atkinson et al. 1990, Hoebeke 1994, Rabaglia 1998, Vandenberg et al. 2000, L. M. Humble, unpublished data). These detections emphasize the need for surveys to determine which introduced organisms may already be established, particularly in high-risk areas, and to assess the efficacy of port inspection, certification, treatment, and quarantine programs. As further surveys are conducted, detections of additional non-indigenous species are expected.

Seventy-five percent of the exotic species documented in this paper have hardwood hosts, implicating dunnage and solid wood packing material as probable introduction pathways. Woodboring ambrosia beetles and wood wasps are most likely transported within the wood itself. Bark beetles and the wood-associated *Micromalthis debilis* probably hitchhike under bark, in cracks or crevices, or are otherwise associated with wood, wood products, packing material, or raw wood craft items. Live adults of two species of exotic longhorned beetles (Coleoptera: Cerambycidae) have recently been intercepted in Oregon with goods imported from China. *Monochamus alternatus* Hope was found inside a shrink-wrapped wooden pallet of transformers at an electronics manufacturing company. *Callidiellum villosulum* (Fairmaire) was intercepted after emerging from trunks of manufactured Christmas trees (cedar logs with bark and artificial limbs) in Oregon and ten other states. These interceptions illustrate the ease with which woodboring pests can escape detection at ports-of-entry and be distributed to other locations.

Whether or not detections represent established populations in all cases is uncertain. Records of only a single individual are suspect. However, it seems likely that substantial populations must be present in order for an individual to be trapped. Lindgren funnel trap recapture efficiency for several species of scolytids was extremely low, ranging from 0–10% (Turchin and Odendaal 1996, Barclay et al. 1998, E. A. Allen, unpub. data). The scolytids *Hylastes opacus, Xyleborinus alni, Xyleborus californicus,* and *X. pfeili,* are clearly established as these records stem from multiple individuals, multiple collection sites, multiple years, or a combination of all three. An effort to find an established population of *Micromalthis debilis* at the Jasper, Lane Co., site in February 1999 was unsuccessful.

Despite preventative measures, exotic organisms continue to accumulate in North American forests and ecosystems at an alarming rate. More than 400 species of exotic insects are known to be naturalized on woody plants in the United States (Mattson et al. 1994). Rearing studies of Scolytidae from native trees collected at two locations in British Columbia found that non-indigenous species comprised the majority of the total scolytid fauna recovered (Humble et al. 1998). Bark beetle trapping surveys in Maryland found that 31% of species were exotics, and, even more disturbing, 94% of individuals were exotics (Rabaglia 1998). Two long-established exotics, *Xyleborus dispar* (F.) and *Xyleborinus saxeseni* (Ratzeburg), were the most numerous scolytids at several sites in Oregon. These two species together accounted for 32% (n = 4,942) of all Scolytidae trapped (n =

15,592) during Oregon's 1997 and 1998 surveys. This proportion would have been much higher if not for the results from several relatively pristine sites.

Once established, exotic species forever alter the nature of an ecosystem, and may act as "contributing" or "inciting" factors, or in the worst case, "final straws" leading to irreversible ecological impacts (Mattson 1997). Several publications have recently outlined the impacts exotic species have on biodiversity, the economy, and the overall health of our forests, agricultural ecosystems and urban and rural environments (U.S. Congress, OTA, 1993, Campbell and Schlarbaum 1994, Liebhold et al. 1995, Wallner 1996). Recent estimates of losses due to exotic insect pests are $13.9 billion per year for crop pests, and $2.1 billion for forest pests (Pimentel et al. 2000). While most of these new exotics in Oregon and Washington are not expected to have significant economic or ecological consequences, we cannot afford to be complacent. *Tetropium fuscum* (F.) (Coleoptera: Cerambycidae) known to attack stressed or dying spruce in Europe and Asia, was recently found to be attacking large numbers of live, healthy red, white and Norway spruce in Halifax, Nova Scotia (CFIA 2000). Clearly we have much to learn about the impacts and prevalence of exotic species in our forests and urban and rural environments.

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FIRST REPORT OF *GYPSONOMA ACERIANA* (DUPONCHEL) (LEPIDOPTERA: TORTRICIDAE), AN OLD WORLD POPLAR PEST, IN NORTH AMERICA

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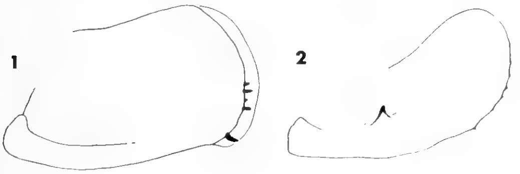
Abstract.—Three adult males of *Gypsonoma aceriana* (Duponchel) were collected in two counties in western Washington State during 1998–99. Although superficially similar to the cottonwood twig borer, *G. haimbachiana* (Kearfott), of eastern North America, *G. aceriana* is easily recognized by its distinctive male genitalia. *G. aceriana* is a notable pest of *Populus* (Salacaceae) species and hybrids in plantations and nurseries in Europe, where it is known as the poplar shoot borer. Young larvae mine leaves, and older larvae bore into terminal shoots, often causing gall-like swellings. The species may be established in western Washington State, and could become a significant pest in North America.

Key Words: *Gypsonoma aceriana,* Tortricidae, Lepidoptera, *Populus,* immigrant

Known abroad as the poplar shoot borer, *Gypsonoma aceriana* (Duponchel) ranks high among pests affecting *Populus* (Salacaceae) plantations and nurseries in Europe (Arru 1975, Georgiev and Velcheva 1999). During 1998–99, three male adults of *G. aceriana* were collected in western Washington State. One (#6719801) was found in the Seattle port area (5430 Marginal Way SW, King Co., 122°20.192′W 47°33.101′N, in a mercury vapor light trap, 28 July 1998, M. Allen, collector). The second (#1319901) was found at a tree nursery (Silva Seed, P. O. Box 118, Roy, Pierce Co., 122°32.690′W 47°0.000′N, in a trap baited with European pine shoot moth, *Rhyacionia buoliana* [D. & S.], lure [*E*9–12:Oac, from Phero Tech Inc., 7572 Progress Way, Delta, B. C., Canada V4G 1E9], 5 August 1999, D. Mangun collector). The third (#7892167) emerged inside a cage placed over leaf litter beneath plants of the hybrid *Populus deltoides* Bartr. ex Marsh X *P. trichocarpa* Torr. & Gray (Wash. State Univ., Puyallup, Pioneer St. & Corwin Rd., Pierce Co., 122°19.793′W 47°11.357′N, 16 July 1999, T. Murray, collector). These sites are more than 25 km from one another (Fig. 3). The records suggest that at least one of the collected adults developed locally, and that the species may have a foothold in western Washington State. The specimens and associated genital preparations are deposited in the National Museum of Natural History, Smithsonian Institution, Washington, DC, the University of Minnesota Entomology Museum, St. Paul, and the Washington State Department of Agriculture collection, Olympia.

In exterior appearance, adults of *G. aceriana* (Bassus et al. 1975, Bentinck and Diakonoff 1968, Bradley et al. 1979, Kuznetsov 1987) are very similar to those of the North American cottonwood twig borer, *G. haimbachiana* (Kearfott) (Miller 1987). Genital anatomy provides the most reliable



Figs. 1–2. Male genital valvae of *Gypsonoma.* 1, *G. aceriana* (drawn from genitalia slide MS 00377, specimen #6719801, Seattle, Washington State, in University of Minnesota Entomology Museum, St. Paul). 2, *G. haimbachiana* (drawn from genitalia slide PB 88, specimen from Sioux City, Iowa, col. 6 July 1928, in University of Minnesota Entomology Museum, St. Paul).

means of distinguishing the two species, the *G. aceriana* male valvae being highly unique in shape and diagnostic in both shape and arrangement of spines (Figs. 1–2). Injury symptoms and damage caused by *G. aceriana,* as reviewed below, are likewise similar in many ways to those of *G. haimbachiana* (Solomon 1995).

In Europe, the species has been reported feeding on *Populus alba* L., *P. deltoides, P. nigra* L., *P. nigra* var. *italica* Muenchh, *P. tremula* L., and others, as well as many hybrids among Old and New World poplars (Bradley et al. 1979, Georgiev and Velcheva 1999, Heymans et al. 1983, Panetsos and Kailidis 1969, Templin 1971). *Acer* and *Ulmus* also have been mentioned as foodplants (Bentinck and Diakonoff 1968, Pinto Coelho Heitor and Maia Santos 1979), but these records need confirmation.

It should be noted that the European foodplant *P. deltoides* is the eastern cottonwood of North America. This species was introduced long ago to Europe for ornamental and hybridizing use. Also, the Lombardy poplar, cultivated in much of North America, is a clone of the European *P. nigra* var. *italica* (Little 1979). Some hybrid poplars affected in Europe also occur in North America.

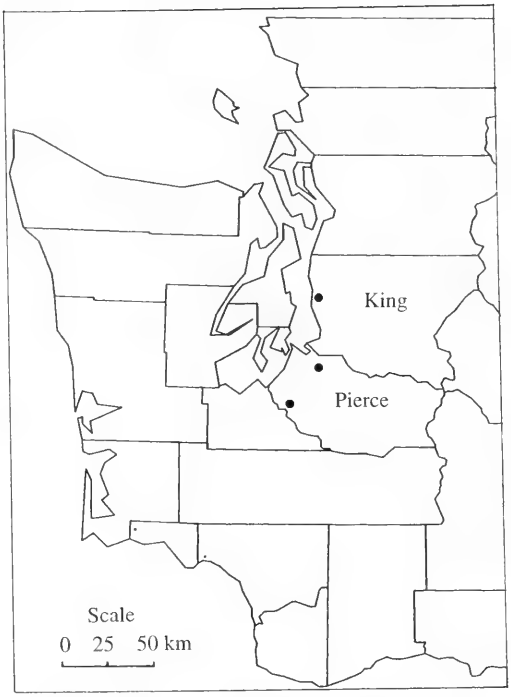


Fig. 3. Map of western Washington State showing *Gypsonoma aceriana* collection sites in King and Pierce Counties.

The following summary of the life cycle, injury, and residual damage is drawn mainly from Bassus et al. (1975), Blankwaardt (1955), Bradley et al. (1979), Heymans et al. (1984), Schefer-Immel (1959), and Templin (1971). The species is univoltine in the northern part of its range and bivoltine in the southern part. Eggs are laid in summer on the undersides of foodplant leaves near the veins. Young larvae feed first as leaf miners, creating hook-shaped mines. They move to bark crevices for wintering. The most severe injury occurs in the spring when larvae leave wintering sites and climb higher to bore into terminal shoots. Frass is extruded from infested shoots through a small hole into an erect, frass-covered silken tube. A single larva may bore several successive galleries in a shoot, the affected parts often swelling and forming rudimentary galls. Damaged shoots are unsuitable for use as cuttings. In older trees, shoot injury may result in deformities such as forks and bushes, which lead to crookedness in as many as 30% of stems. Useful illustrations of injury and life stages can be found in Attard (1979), Bassus et al. (1975), Bentinck and Diakonoff (1968), Blankwaardt (1955), and Bradley et al. (1979).

The European distribution of *G. aceriana* ranges from Ireland eastward to Russia, and from Sweden southward to Greece—virtually the whole of Europe (Razowski 1996). Booij and Voerman (1984) have characterized an effective sex attractant: *E*10–12: OAc + *E*10–12:OH [7:3]. Swatschek (1958) described the larva taxonomically and provided a key to larvae of the European species of *Gypsonoma.*

The high rank of *Gypsonoma aceriana* among poplar pests in Europe, its wide European distribution, and similarities in the poplar floras of Europe and North America suggest that the insect could become a significant pest in North America.

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NOTE

First Report of *Amblyomma supinoi* Neumann (Acari: Ixodida: Ixodidae) from the Arakan Forest Turtle, *Geoemyda depressa* Anderson (Reptilia: Testudines: Emydidae), with Additional Records of this Tick from the Union of Myanmar

Despite the intensity with which the tick fauna of Southeast Asia has been studied (Kohls 1957. Studies from the Institute for Medical Research, Federation of Malaya. No. 28: 65–94; Tanskul et al. 1983. Journal of Medical Entomology 20: 330–341; Wassef and Hoogstraal 1988. Journal of Medical Entomology 25: 315–320, and references cited therein), new host and distribution records, and even new species, continue to be reported from this region (Kolonin 1993. Journal of Medical Entomology 30: 966–968; Robbins et al. 1997. Entomological News 108: 60–62; Kollars and Sithiprasasna 2000. Journal of Medical Entomology 37: 640; Robbins and Platt 2000. Proceedings of the Entomological Society of Washington 102: 225–226). Between 21 January and 14 February 2000, one of us (SGP) participated in an expedition to central Rakhine (formerly Arakan) State in western Myanmar (formerly Burma), with the primary objective of obtaining data on the conservation status, ecology and exploitation of the exceedingly rare Arakan forest turtle, *Geoemyda depressa* Anderson, hitherto known from only seven specimens (Iverson and McCord 1997. Chelonian Conservation and Biology 2: 384–389). Rakhine State is located in extreme western Myanmar on the border with Bangladesh and encompasses much of the densely forested Arakan Yoma range, a southern extension of the Himalayas that is one of the most sparsely populated areas in mainland Southeast Asia (Henderson et al. 1982. Burma: a country study. DA Pam 550-61, Headquarters, Department of the Army, Washington, DC; Salter 1983. Wildlife in the southern Arakan Yomas. Survey report and interim conservation plan. FO: BUR/80/006, Field Report 16/83, Food and Agriculture Organization of the United Nations, Rome). Although specific locality data are lacking, five of the seven previously known specimens of *G. depressa* are thought to have been collected in the Arakan Yomas. In 1994, two additional living specimens were purchased near Po Shang (23°42N, 100°01E) in western Yunnan Province, China, though Iverson and McCord (1997) suggest that these were imported for the Chinese food market and are therefore extralimital.

The central Rakhine State expedition yielded a single living male specimen of *G. depressa* (carapace length 22.0 cm, mass 1,300 g) with 18 plastral annuli (whose relationship to this animal's age is uncertain) that had been found by a hunter's dog on 7 February at a site about 30 m from a small stream in bamboo (*Melocanna bambusoides* Trinius) forest on Salu Taung, along the western slope of the Arakan Yoma range (coordinates unavailable, approximately 19°10N, 94°20E). The carapace of this turtle was grossly deformed and appeared to have been partially crushed, with subsequent abnormal healing. Two male ticks removed from folds of skin around the right foreleg were identified as *Amblyomma supinoi* Neumann and constitute the first record of any parasite from *G. depressa.* This tick collection (RML 123074) has been deposited in the U.S. National Tick Collection, Institute of Arthropodology and Parasitology, Georgia Southern University, Statesboro. The turtle was deposited in the Yangon Zoo, Yangon, Myanmar.

Amblyomma supinoi is a distinctive

Table 1. Collections of *Amblyomma supinoi* made from *Indotestudo elongata* in the Arakan Yoma, central Rakhine State, Myanmar, 31 January–7 February 2000, S.G. Platt.

Tortoise No.	Sex/Carapace Length (cm)	Tick Totals	Tick Attachment Sites (No. of Ticks)	Date
7	♂ 24.2	4♂	left (2) and right (2) rear legs	31 January
8	♂ 27.5	9♂, 1♀	left (7) and right (3) rear legs	31 January
10	♂ 24.0	9♂	left (1) and right (8) rear legs	31 January
11	♀ 27.9	7♂, 1♀	left (5) and right (3) rear legs	3 February
12	♂ 29.5	6♂	left (5) and right (1) rear legs	3 February
13	♀ 26.3	4♂	left (2) and right (2) rear legs	3 February
14	♀ 28.5	6♂	left (3) and right (3) rear legs	3 February
15	♀ 15.9	2♂	left (1) and right (1) rear legs	3 February
16	♀ 20.0	2♂	left (1) and right (1) rear legs	3 February
26	♀ 13.4	1♂	right (1) rear leg	7 February

though uncommonly collected tick species that probably occurs throughout mainland Southeast Asia but that has only been recorded from Myanmar (Neumann 1911. Ixodidae. Das Tierreich. No. 26: 1–169; Robinson 1926. Ticks: a monograph of the Ixodoidea. Part IV. The genus *Amblyomma.* Cambridge University Press, London), Thailand (Tanskul et al. 1983), and Vietnam (Kolonin 1995. Journal of Medical Entomology 32: 276–282). It also occurs in India (Sharif 1928. Records of the Indian Museum 30: 217–344; Petney and Keirans 1995. Tropical Biomedicine 12: 45–56). This tick typically parasitizes tortoises, especially the yellow tortoise, *Indotestudo elongata* (Blyth), for which there are early published records (Neumann 1911; Robinson 1926; Toumanoff 1944. Les tiques (Ixodoidea) de l'Indochine. Instituts Pasteur de l'Indochine, Saigon). During the central Rakhine State expedition, 50 males and two females of *A. supinoi* were removed from 10 of 11 living adults of *I. elongata* that were examined for ectoparasites. Collection data for these tortoises are shown in Table 1, where tortoises 7–10 were captured in the vicinity of Mae Sadwe village (19°37.19N, 94°09.23E), tortoises 11–16 were found in and around Pyaung Chaung village (19°32.64N, 94°06.70E), and tortoise 26 was taken in Datun Taung village (19°33.89N, 93°56.05E). Note that ticks were not sorted by sex when they were removed from their hosts. Because nothing is known about the life history of *A. supinoi* (Camicas et al. 1998. Les tiques du monde (Acarida, Ixodida): nomenclature, stades décrits, hôtes, répartition. ORSTOM, Paris), we are unable to account for the preponderance of male ticks in our collections or for the absence of ticks on the forelegs of tortoise hosts. All 10 tick collections have been deposited in the American Museum of Natural History, New York, New York.

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NOTE

Ochlerotatus tormentor (Dyar and Knab) (Diptera: Culicidae), A New Confirmed Mosquito Record for Virginia

During 1996 and 1997, personnel of the Department of Entomology, North Carolina State University, Raleigh, NC, were contracted by the U.S. Army Corps of Engineers to monitor and make control recommendations for mosquitoes on and adjacent to John Kerr Reservoir. This reservoir straddles the border of North Carolina and Virginia. Between 1 April and 30 September in both years systematic larval, adult landing, and light trap (Centers for Disease Control) collections were made in Halifax County, Virginia. The collection sites were at or near the headwaters of the reservoir and adjacent to the Bannister, Dan, and Hyco rivers. Although monitoring and control recommendations were the primary concerns, these surveys permitted the documentation of a faunal list for mosquitoes in the headwaters of John Kerr Reservoir.

Mosquitoes collected during the surveys were transported to Raleigh where they were identified using Slaff and Apperson (1989) and temporarily stored at North Carolina State University. The identity of the specimens of *Ochlerotatus tormentor* (Dyar and Knab) was confirmed by the junior author, and they are preserved in the Department of Entomology Insect Collection, North Carolina State University, Raleigh, NC. Use of the genus name, *Ochlerotatus* Lynch Arribalzaga, and its abbreviation, *Oc.*, follows Reinert (2000).

In 1996, 31 mosquito species were collected, while 27 were collected in 1997. Included were three collections of larvae of *Oc. tormentor*, one in 1996 and two in 1997. These represent the first confirmed specimens of this species collected in Virginia. Two fourth-instar larvae were collected on May 6, 1996, at a wildlife hunting access area about 1 km south of the Dan River and 1.6 km east of the junction of highways U.S. 58 and VA 360 in South Boston, Virginia. These larvae were collected in a temporary pool with a thick mat of pine needles. In 1997, one second-instar larva was collected on July 17 in a shallow leaf-filled depression in a hardwood forest. This site is on a creek flood plain near the confluence of the creek with the Hyco River, and is about 9 km east of the above highway junction in South Boston and 2 km south on State Road 601. An additional two fourth-instar larvae were collected at this last site on July 25.

Other species collected as larvae with the *Oc. tormentor* include: *Aedes vexans* (Meigen), *Oc. atlanticus* (Dyar and Knab), *Oc. canadensis* (Theobald), *Psorophora ferox* (von Humboldt), and first and second instars of *Ochlerotatus* spp. and *Anopheles* Meigen species.

Previous lists of the mosquitoes of Virginia published by Dorer et al. (1944), Carpenter and LaCasse (1955), Bickley (1957), Gladney and Turner (1969) and Darsie and Ward (1981) did not mention or provide published records for *Oc. tormentor* in Virginia. However, map number 24 (p. 249) of Darsie and Ward (1981) shows *Oc. tormentor* occurring in the eastern half of Virginia, based on records of this species from Maryland and North Carolina, not on published Virginia records or confirmed specimens from Virginia.

The collection of *Oc. tormentor* larvae in May and July agrees with the late spring-early summer collection periods normally seen for this species in North Carolina (Harrison et al. 1998). This species also probably occurs further west in Virginia, because it has been collected in Forsyth County, NC (Harrison et al. 1998) approximately 150 km west and slightly south of Halifax County, Virginia.

Virginia has had active mosquito surveillance and control programs for many years. The absence of a confirmed record for *Oc. tormentor* in the state was almost certainly affected by the fact that adult female *Oc. tormentor* cannot be separated morphologically from those of *Oc. atlanticus*. Scanlon and Yates (1970) and Roberts and Scanlon (1979), using pristine reared specimens, found characters to separate the females of these two species in Texas. Unfortunately, *Oc. tormentor* larvae are uncommon in the Mid-Atlantic Region and are difficult to rear. Thus, those characters have not been confirmed on reared females in this region. Although the male genitalia of these two species are easily separated we found it easiest to separate them by characters in the larval stage (Carpenter and LaCasse 1955). The siphon of *Oc. tormentor* has seta 1-S inserted within evenly spaced pectin (see Darsie and Ward 1981: 137, fig. 566), not distal to pecten as on *Oc. atlanticus* (see Darsie and Ward 1981: 132, fig. 541). Also, there are 9–13 spine-like comb scales on *Oc. tormentor* instead of 4–6 spine-like comb scales as on *Oc. atlanticus*. Live larvae of these two species in the Mid-Atlantic Region usually exhibit a black and cream banded pattern with the thorax and abdominal segments 7–8 pale, while the remainder of the body is dark (Harrison et al. 1998), which helps in field identification.

Finding *Oc. tormentor* in south central Virginia fills a gap in the distribution of this species in the Mid-Atlantic Region, adds another species to the Virginia mosquito list, and reaffirms the value of collecting larvae during mosquito surveys.

We are very grateful to C. S. Apperson, who designed and initiated these surveys and reviewed the manuscript. We also gratefully acknowledge A. A. McCaskill and Nhan Duc Nguyen for assistance in the laboratory and field.

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NOTE

Deletion of *Calliodis pallescens* (Reuter) from the United States Fauna (Hemiptera: Heteroptera: Anthocoridae)

The genus *Asthenidea* was described by Reuter (1884) to include *Cardiastethus clarus* White and four new species described by him: *maculipennis, pallescens, punctatostriata,* and *temnostethoides.* Subsequently, the type species of the genus, *Asthenidea temnostethoides* Reuter, was designated by Kirkaldy (1906). Carayon (1972) synonymized *Asthenidea* Reuter 1884 with *Calliodis* Reuter (1871) and placed *Calliodes* into his new subtribe Calliodina. *Asthenidea pallescens* Reuter was described by him from Veracruz, Mexico. Champion (1990) examined the types from Mexico and added Guatemala and Nicaragua. Blatchley (1926) reported *Asthenidea pallescens* from Royal Palm Park, Florida, and included some habitat notes. Later, Blatchley (1928) described *Cardiastethus flaveolus* from Florida, based on the same series from Royal Palm Park, the type being a male, and included additional material from Paradise Keys (Florida). Blatchley indicated that W. E. China of the British Museum had stated that the Royal Palm Park specimens were not *Asthenidea pallescens* Reuter but an undescribed species, related to *Cardiastethus tropicalis* Champion, that had been reported from Guatemala, Panama, and Grenada.

Henry (1988) cited both *Calliodis pallescens* (Reuter) from Florida and Mexico and *Cardiastethus flaveolus* Blatchley from Florida. In light of the information given in Blatchley (1928), *Calliodis pallescens* should be deleted from the United States fauna and the record of it from Royal Palm Park referred to *C. flaveolus.*

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NOTE

A Replacement Name for *Freemania* A. Warren, with Notes on the Higher Classification of the Genus (Lepidoptera: Hesperiidae)

Recently, I proposed the genus *Freemania* for a diminutive Andean species of skipper, *Freemania rawlinsi* A. Warren (Lepidoptera: Hesperiidae, Heteropterinae) (Warren 2001: 144). I inadvertently overlooked prior descriptions of that genus-group name for water mites from Ireland (*Freemania* Halbert 1944: 84; type species, *Freemania dispar* Halbert 1944: 84 (Arachnida: Acarina: Pionidae)) and for marine flatworms from the Pacific coast of California, Washington, and British Columbia (*Freemania* Hyman 1953: 336; type species, *Phylloplana litoricola* Heath and McGregor 1912: 472 (Platyhelminthes: Polycladida: Leptoplanidae)). *Freemania* A. Warren, is therefore preoccupied, and the following replacement name is here proposed: ***Freemaniana* A. Warren, new name** for *Freemania* A. Warren, 2001 (type species: *Freemania rawlinsi* A. Warren 2001: 144).

Olaf. H. H. Mielke (personal communication), has brought to my attention the existence of eight additional *Freemaniana rawlinsi* specimens, all from Ecuador: Environs de Loja, 1893 (2 ♂, USNM); Gualaceo, Azuay Prov., 2,800 m (1 ♂, Mielke collecion), Sayausi, Azuay Prov., 2800 m., 26-X-1994 (1 ♂), 23-IX-1994 (4 ♂—all from the Piñas collection in Quito).

Freemaniana rawlinsi was originally described as a member of the subfamily Cyclopidinae Speyer. The rationale for using the name Cyclopidinae instead of Heteropterinae Aurivillius (Warren 2001) is in principle correct (see also Warren 2000). Article 40.2 of the ICZN (1999) states that if a family-group name was replaced before 1961 because of the synonymy of the type-genus, the substitute name is to be maintained if it is in prevailing usage. At the time I prepared the 2001 manuscript, I knew of no replacement name for Cyclopidinae having been proposed before 1961. After reading Warren (2001), Dr. G. Lamas (personal communication) brought the actions of Verity (1940: 86) to my attention. For Cyclopidinae and Heteropterinae, Verity noted that their respective type genera, *Cyclopides* Hübner and *Heteropterus* Duméril, were subjective synonyms, *Cyclopides* being junior, and therefore chose to use Heteropterinae. Cyclopidinae had a short history of usage (see Warren 2001), and the more frequently applied Heteropterinae prevails in usage. Satisfying Article 40.2 by taking Verity (1940) into account, the valid subfamily name for *Freemaniana* and related genera is Heteropterinae.

About 15 genera are currently placed in Heteropterinae although the monophyly of that group is not confirmed and requires further study. Those genera are: *Apostictopterus* Leech; *Argopteron* Watson; *Barca* de Nicéville; *Butleria* Kirby; *Carterocephalus* Lederer; *Dardarina* Evans; *Dalla* Mabille (including *Eumesia* Felder and Felder); *Freemaniana*; *Heteropterus* (includes *Cyclopides*); *Hovala* Evans; *Lepella* Evans; *Leptalina* Mabille; *Metisella* Hemming; *Piruna* Evans; *Tsitana* Evans.

Thanks to Gerardo Lamas Muller (Universidad Nacional Mayor de San Marcos, Lima, Peru) for sharing his extensive knowledge on zoological nomenclature. Olaf H. H. Mielke (Universidade Federal do Paraná, Curitiba, Brazil) generously shared information on additional *Freemaniana* specimens. Thanks to John E. Rawlins (Carnegie Museum of Natural History, Pittsburgh, PA) for helping to obtain literature cited herein, providing valuable technical advice, and carefully reviewing a draft of this paper. Hideyuki Chiba (Fukuoka, Japan) kindly shared information on Old World members of the Heteropterinae. Thanks also to Andrew V. Z. Brower, Darlene D. Judd (Oregon State University), Charles V. Covell, Jr. (Louisville University) and an anonymous reviewer for valuable comments and suggestions. This research was supported by the Ferguson Endowment for Systematic Entomology at Oregon State University.

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BOOK REVIEWS

A Dictionary of Entomology. Compiled by Gordon Gordh with assistance by David H. Headrick. $112. CABI Publishing, 10 E 40th St., Suite 3203, New York, NY 10016, USA. ISBN 0 85199 291 9. E-mail: cabi-nao@cabi.org.

This dictionary is a large, double-column, 1,032 page book. It begins with a 2½ page foreword, but let us go right to the contents, which evidently cover all categories of words and names related to entomology, including some common names, scientific names, entomologists, diseases, adjectival terms, even pesticides. I search first for the name Kieffer. His given name Jean-Jacques is unhyphenated here, but the entry gives birth and death dates, a few biographical highlights, including the names of three of the groups he studied, and two biographical citations (of the six I know), the author of one of them misspelled here as "Travares." I next look for Tavares, which I find misspelled as "Tauares." This item has birth and death dates and cites four obituaries, but gives no further biographical data. I then look up Rübsaamen, a contemporary of Kieffer's, but his first name Ewald is misspelled Edwald. Most other biographical entries list only obituaries, but some, possibly when there were no obituaries to cite, e.g., Wigglesworth, are listed only with some biographical data. One included person died in 1994, so the book seems fairly up to date. At least one entry treats a living person and I wonder why others at least as eminent are not included. Eleanor H. Slifer, deceased in 1987, is treated as a living person "specializing in . . ." with no birth and death dates.

I then browse group names. "Diptera" has a five inch entry giving author and date, time when present in the geological record (Permian-Recent), derivation of the name, and a good diagnostic summary. "Cecidomyiidae" has a two inch summary paragraph. It indicates that the name is a plural noun, which I hope stops people from using the incorrect and annoying "Cecidomyiidae is." "Gall midges" is used for the common name at the top of the entry but "midges" is used later in the paragraph. There is no separate entry for "midge," but there is for "midges," which narrowly restricts the word to the following: "See Chironomidae. Cf. Biting Midges." Contrary to information in the family entry, many cecidomyiids have at least one crossvein. Author and date are provided for about half of the family names.

Then to morphological terms. The entry "gonostylus" helpfully gives the part of speech, derivation, and plural form, but reference is made to the "gonostylus generally modified to form . . . harpagones." There is no separate listing for harpagones, although there is one for "harpes," under which, in definition 2, we find "Diptera: See Dististylus; Harpagones; Parameres." Neither dististylus nor harpagones has an entry. The entry "gonocoxite" refers one to "gonocoxa," contrary to use in McAlpine et al., 1981, *Manual of Nearctic Diptera,* a book that has provided dipterists with a lingua franca for anatomical terms. The good work of that authoritative book was not absorbed by this dictionary. The term "hypoproct," part of the proctiger, is listed only under "hypandrium" as the "hypoproct of Needham," and is not listed in the "proctiger" entry. Halter is spelled "haltere," the British spelling, but both spellings should have been given because "halter" is the spelling used in North America. I suspect that was an editorial change because other British spellings, e.g., "colour," are used throughout.

The dictionary includes words not particular to entomology, e.g., "effluvium" and "refuse." A typo occurs on pg. 282, column 1, line 7 from bottom, "maine" for "marine," and same column, line 3 from bottom, type-species is improperly hyphenated, even though the main entry for "type species" is not. "Screw-worm" is hyphenated here, contrary to use as "screwworm" in the Entomological Society of America's *Common Names of Insects & Related Organisms,* 1997. The dictionary includes two appendices, one a partial list of full journal titles referred to in abbreviated form in the text, chiefly for obituaries, the other a list of compendia of insect common names.

Definitions of names and terms I know little about seem apt and generally look good, and the dictionary includes a world of information, but, as I have indicated, a user will need to be critical in the use of this dictionary. Contrary to the publisher's blurb on the back cover, the book is not comprehensive or fully cross-referenced, and in my estimation it is not finished or authoritative. The foreword by Dr. Gordh recognizes that there may be omissions and errors of fact. Three times in the foreword, mention is made of a future, next, or second edition, which, e.g., "will provide many new definitions, some definitions will be refined and errors will be corrected." The idea is, I suppose, for us to buy this book and support a work in progress.

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Embia. Contributions to the Biosystematics of the Insect Order Embiidina. Part 1. Origin, Relationships and Integumental Anatomy of the Insect Order Embiidina. Part 2. A Review of the Biology of the Embiidina. By Edward S. Ross, 2000. Occasional papers of the California Academy of Sciences No. 149. Part 1. 53 pp.; Part 2. 36 pp. Soft bound. 8.5 × 11 inches. ISSN 0068-5461. $18.60, including shipping. Available through California Academy of Sciences, Scientific Publications, Golden Gate Park, San Francisco, CA 94118.

The web-spinners of the order Embiidina (most authors still use Embioptera), are unique in the insect world in that they live in silk tubes spun with their feet. Their bodies and biologies are completely defined by adaptations wrought from living within the narrow confines of these tubes. Web-spinners have received relatively scant attention due to their inconspicuous nature and the fact that they are not capable of damaging structures or living plants.

Dr. Edward S. Ross, Curator Emeritus at the California Academy of Sciences, has spent much of his life studying these long neglected insects. For the past 60 years he has traveled throughout the world, amassing a web-spinner collection exceeding 300,000 specimens, representing more than 1,000 species. His latest contribution to their study appears in a new publication called *Embia,* which contains some of the author's long-shelved monographs originally intended to appear as chapters in a series of volumes on web-spinners. *Embia* is superbly illustrated with line drawings and biting-sharp black and white photographs.

The first section of Part 1 entitled "Origin and Relationships" covers the evolutionary origin of web-spinners. Fossil evidence dates from the Tertiary, although the author suggests that there is evidence that the Embiidina and their alleged sister order, the Plecoptera, probably evolved from a common ancestor early in the Carboniferous period. The Tertiary fossils exhibit evidence of adaptations found in all extant species which allow for easy, backwards movement through narrow silk galleries spun from glands housed in oversized protarsal segments.

The chapter "Integumental Anatomy" offers a detailed analysis of the external morphology of *Oligotoma,* a genus of nearly cosmopolitan distribution whose males are frequently attracted to light and easily collected for comparative study. Sections include the head, eyes, antennae, cervix, prothorax, pterothorax of males, meso- and metathorax of females, legs (including the nature of embiid silk), and wings. Flexibility, reduction and loss of the wings, along with short legs are all a result of the need to move quickly inside the galleries. The chapter concludes with sections on the web-spinner abdomen, detailing both male and female genitalia. All sections are peppered with the author's observations on the adaptive significance and diagnostic value of various anatomical features.

Part 2 begins with "A review of the biology of Embiidina," based primarily on observations acquired during the author's world travels and in the laboratory. Following a section on general biology, the author presents information on the subsocial behavior of web-spinners. Typical web-spinner colonies consist of gynopaedia—parental females living in galleries with their offspring. Mazes of branched galleries often house large groups of individuals in all stages of development. As the young develop they search for food by continually expanding the galleries within or on edible surfaces. Mature female and developing web-spinners feed mostly on dead plant materials, including weathered bark, dead leaves, lichen, and moss. Adult males do not feed.

There is no evidence of cooperation among individuals, but females do guard their eggs and young in a manner similar to earwigs. The behavior of males, mating behavior, egg protection, development, parthenogenesis, diet, movement, and habits are presented.

Web-spinners are found in a wide variety of situations. The author lists various natural and artificial habitats where web-spinners occur: tropical evergreen forests, tropical cloud forests, seasonally-dry grassy woodlands, semi-arid, open grasslands, desert areas, and human habitats. There is a wonderful photo here of the author extricating an undescribed taxon of web-spinner from the root surfaces of Welwitchia plants in the Namib Desert. The caption of another photo at the end of the work states that the orange and black nymphs of an undescribed *Dihybocercus* from Zambia are mimics of a poisonous paederine staphylinid beetle, but this observation is not elaborated in the text. Sections on geographic and ecological range, natural and artificial dispersal are followed by a look at the natural hazards that befall web-spinners, including predators, parasitoids, and pathogens. Predator avoidance is one of the primary advantages of gallery life, especially for those species constructing their galleries beneath stones or within log crevices.

Both parts 1 and 2 are followed by bibliographies, neither of which is extensive since much of the work presented here is drawn from the author's own unpublished work. Curiously, a pertinent review paper on the order, the author's own "Biosystematics of the Embioptera" (1970, Annual Review of Entomology 15: 157–172) is not cited in either bibliography.

In the preface, the 86 year old author states, "If I live long enough, many issues of Embia—mostly on systematics—will appear in rapid succession." I wish the author good health and look forward to future issues detailing this fascinating group of insects. This and future editions of *Embia* are essential for students of web-spinners and welcome editions for devotees of literature revealing lesser known orders of insects. The series is sure to spur interest in these secretive animals.

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SOCIETY MEETINGS

1052nd Regular Meeting—January 4, 2001

The 1052nd 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 new President John Brown at 7:00 p.m. The meeting was attended by 19 members and 11 guests. The minutes of the 1051st meeting were approved as read.

No names of new applicants for membership were read. Two visitors were introduced.

In miscellaneous business, Edd Barrows had an insect display dating from the 1930's and mentioned that the Hirshhorn Museum has on exhibit some art constructed mostly from beeswax. David Furth displayed: an issue of *Wings,* the Xerces Society journal, filled with exceptional insect pictures by the renowned researcher and photographer Ed Ross; the Entomological Society of America's 2001 calender; noted that the ESW website is up (http://entomology.si.edu:591/ESW/ESWMenus.html) and encouraged members to add information to their records; and presented specimens forming the basis of tonight's presentation.

Program Chair Ted Schultz introduced the speaker, former ESW president and Smithsonian Entomology Collection Manager David G. Furth. His talk, entitled "Searching for Sumacs and Flea Beetles: from African Poison Arrows to Mexican Poison Ivy," was essentially a travelog by an entomologist whose long-distance jumps between research sites surpass, relative to his body length, even those of his study organisms. Flea beetles (Chrysomelidae: Alticinae) get their name from their ability to leap great distances, thanks to an efficient spring-like extensor apodeme in their hind femora. The *Blepharida*-group is cosmopolitan and includes 16 genera. Although backed up by morphological minutia, the best feature uniting them is food plant use. As far as known, almost all feed on either Anacardiaceae or Burseraceae. Other unusual features of these beetles are: egg masses are covered by feces; larvae are translucent and trail their spiral-form feces; pupal cells are able to survive for years. Dr. Furth showed pictures of people, beetles, habitats, and cities from Israel, Africa, Hong Kong, and Mexico. In Namibia, the bushmen use *Blepharida* pupae to coat the sides of their arrows. A single coating is sufficient to kill large mammals such as giraffes and lasts three months. Unlike the poisons of the Monarch butterfly and other insects, the poison of *Blepharida* is manufactured, not sequestered. Most of Dr. Furth's work is in Mexico, where 31 of the 38 species present are found nowhere else. The beetles' host plant preference was the source for some amusing anecdotes.

The meeting was adjourned at 8:10 p.m. Refreshments were provided by Ted Schultz.

Respectfully submitted,
Stuart H. McKamey,
Recording Secretary

1053rd Regular Meeting—February 1, 2001

The 1053rd 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 7:03 p.m. The meeting was attended by 26 members and 9 guests. The minutes of the 1052nd meeting were approved as read.

Steve Lingafelter read the names of three new applicants for membership: Dan Kjar, Vyvy Pham, and Oscar Pérez. Four visitors were introduced.

For exhibits, Chris Thompson displayed the book "*Dípteros de Costa Rica*" by M.

Zumbado, and slides from a recent trip to Attu, of the Aleutian Islands. Ralph Eckerlin displayed "*Sifonápteros do Brasil*" by P. M. Linardi and L. R. Guimarães. Ted Schultz displayed "*Ants: Standard Methods for Measuring and Monitoring Biodiversity*" edited by D. Agosti, J. D. Majer, L. E. Alonso, and T. R. Schultz. Dave Furth had his hands full with "*Biodiversidad, Taxonomía y Biogeografía de Artrópodos de México Vol. II*" edited by J. Llorente B., E. G. Sopiano, and N. Papavero and the beautifully pictured "*The Natural World of Bugs and Insects*" by K. and R. Preston-Mafham.

Program Chair Ted Schultz introduced the speaker, Dr. Brian M. Wiegmann of North Carolina State University, who presented his "Phylogenetic Insights into the Natural History of Flies." The early evolutionary radiation of major fly lineages occurred simultaneously as that of flowering plants, about 140 million years ago. To better understand the details of this, Dr. Wiegmann and his colleagues have undertaken three large projects: cladistics of the higher taxa of Brachycera using molecules and morphology; a more detailed examination of the ancient family Therevidae; and sequencing fossils to improve chronology estimates of evolutionary radiation. Morphological features that had never been analyzed together were gleaned from the literature and additional features were discovered in larvae as well as male and female external and internal anatomy, for example ganglionic fusion along the nerve chord. Molecular data was derived from the conservative, mitochondrial 28S rDNA, about 3,000 nucleotides long. Six outgroup species from Nemotocera and 105 species representing all major families of lower Brachycera were sequenced. His team analyzed the data using the Parsimony Rachet method, which covers tree space better for large trees. Despite the abundance of data, basal lineages lacked solid support. Surprisingly, the combined morphological and molecular analysis resembled the purely morphological tree, but still the basal lineages remained largely a mystery. In the future they intend to run the analysis on subsets of the tree. The analysis of Therevidae, which has about 900 species, went surprisingly better. Total evidence analyses provided good support for monophyly of Therevidae and for major clades within the family.

The meeting was adjourned at 8:10 p.m. Refreshments were provided by Ted Schultz.

Respectfully submitted,
Stuart H. McKamey,
Recording Secretary

1054th Regular Meeting—March 1, 2001

The 1054th 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 7:00 p.m. The meeting was attended by 19 members and 9 guests. The minutes of the 1053rd meeting were approved with minor modification.

Steve Lingafelter read the names of one new applicant for membership: Gordon F. Pratt. Five visitors were introduced.

For exhibits, Gabriela Chavarria displayed a beetle-and-flower motif scarf. Ted Schultz displayed the 1999 issues of *Zoologica Scripta* devoted to higher classification of Hymenoptera and the book "*Hymenoptera: Evolution, Biodiversity and Biological Control,*" edited by A. D. Austin and M. Dowton. Jill Swearingan brought a copy of her "Bug Bites" column in the community newsletter of Cheverly, Maryland. Diane Calabrese displayed a saturniid painting. Steve Lingafelter displayed the book "*List of Chinese Insects, Volume I*" by Hua Li-Zhong. Edd Barrows had on hand the new book he edited, "*Animal Behavior Desk Reference: Dictionary of Animal Behavior, Ecology and Evolution, 2nd edition.*"

Program Chair Ted Schultz introduced

the speaker, Dr. Dolores Savignano, of the U.S. Fish and Wildlife Service, who presented "Potential Impacts of Pesticides on Pollinators." It is estimated that 90% of all plants and 30% of all crops need pollinators, giving them ecological and economic importance. Dr. Savignano focused on insects and, particularly, bees. Pesticides are only part of the danger facing pollinators. In the United States, we use 4.5 billion pounds of pesticide per year, consisting of over 20,000 formulations of 900 active ingredients. While federal regulations require testing for effects on pollinators, it is not always completed prior to registration. Of the 357 pesticides tested for bee toxicity, 30% were considered toxic. Although information is scant, pesticides have been documented to reduce crop production due to fewer pollinators (e.g., a 4 million pound decline in a blueberry crop). Because pesticides have been detected up to 750 meters downwind from spray areas, the potential impact on non-target insects, including pollinators, and their natural ecosystems is at risk. But there was good news too. To reduce the impact of pesticides on pollinators, Dr. Savignano suggested reducing the need for pesticides through crop rotation, biological control, etc., using less toxic alternatives, using direct application when possible rather than aerial spraying, using liquid formulations rather than dust, and, lastly, minimizing pesticide application when plants are blooming.

The meeting was adjourned at 8:00 p.m. Refreshments were provided by Ted Schultz.

Respectfully submitted,
Stuart H. McKamey,
Recording Secretary

1055th Regular Meeting—April 5, 2001

The 1055th 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 Gabriela Chavarria at 7:00 p.m. The meeting was attended by 19 members and 14 guests. The minutes of the 1054th meeting were approved as read.

No names of new applicants for membership were read. Five visitors were introduced.

For exhibits, Warren Steiner had two recent issues of *Science News* with articles on insects and the book "*Tiger Beetles of Alberta: Killers on the Clay, Stalkers on the Sand,*" a fun book by John Acorn. Arthur Evans had two issues of "*Fauna,*" one about katydids and another on onychophorans. Diane Calabrese displayed a Saks Fifth Ave. advertisement for insect-like jewelry in the *New Yorker.* Dave Furth had two new books: "*Protecting Biodiversity: National Laws Regulating Access to Genetic Resources in the Americas*" edited by S. Perkoff and M. Ruiz Muller; and "*Coleópteros de Chile*" by E. Arias Tobor. Furth then showed slides he had recently taken in Egypt of hand-woven carpets with insect images, of bee images abundant in the 3,000–4,000 year old hieroglyphics of temples and tombs, and of a four-foot long stone scarab sculpture.

Program Chair Ted Schultz introduced the speaker, Dr. Rex Cocroft, University of Missouri, who presented his work on "Communication and Cooperation in Group-living Insects." After explaining that the tight social organization of the well studied honeybees represents just one extreme in a wide array of behaviors, Dr. Cocroft introduced his study organisms: treehoppers (Membracidae), which communicate by vibrational signals sent through the substrate. He then proceeded to play a number of them on a stereo, giving us quite a different audial perspective of a forest. Dr. Cocroft discussed and contrasted the social structures of two species that are distant relatives in one subfamily. He has delved mostly into a species of *Umbonia,* which exhibits a high degree of parental investment in its offspring. In this system the primary ecological challenge is apparently predation by wasps; branches with aggregations lacking attendant adults are quickly picked clean, as the synchronous waves of calls of the helpless immatures go unanswered. In the other example, a species of the genus *Calloconophora,* the ecological challenge appears to be finding high quality food resources on a rapidly growing plant. Adults frequently abandon the nymphs, and when the meristem ages, the aggregation breaks up, only to regroup at a new mersitem once the excited calls from a lucky individual are felt. Dr. Cocroft backed up these just-so stories with results from abundant playback, lab-controlled experiments, but left us with even more questions about these complex systems. He closed by posing a general hypothesis: that because cooperation and communication allow individuals to survive group-living on plants, substrate-born vibrational communication may be a widespread adaptation.

The meeting was adjourned at 8:25 p.m. Refreshments were provided by Ted Schultz.

Respectfully submitted,
Stuart H. McKamey,
Recording Secretary

Minutes of the 1056th Regular Meeting—May 3, 2001

The 1056th 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 7:00 p.m. The meeting was attended by 23 members and 6 guests. The minutes of the 1055th meeting were approved as read.

Membership Chair Steve Lingafelter read the names of five new applicants for membership: Matthew L. Buffington, John Strazanac, Robert E. Roughley, John Franclemont, and Michael Philip. No new members were present. One visitor was introduced.

In miscellaneous business, Dave Furth announced that the ESW Annual Banquet will be held June 28rd at the Uniformed Services University of Health Sciences in Bethesda, Maryland. Quentin Wheeler is the invited speaker. For exhibits, Ray Gagné had "*Dictionary of Entomology*" by G. Gordh and D. H. Headrek and noted that it is comprehensive in scope but appears unfinished and unauthoritative. Prospective buyers should look at it first to see whether it will fill their needs. Arthur Evans showed slides of spring insects and spiders from Virginia, tarantulas from around the world, and had a recent issue of the journal "*Fauna*" that featured web sites for beetles. Chris Thompson had the new MYIA publication, Volume II, "*World Catalogue of Stratiomyidae*" by N. E. Woodley. Dave Furth had several new books on display: the field guide "*Insects, Spiders, and Other Terrestrial Arthropods*" by G. C. McGavin; "*Dragonflies of North America*" by J. G. Needhamm, M. J. Westfall, Jr., and M. L. May; "*Native Bees on Wildflowers in Western Australia*" by T. F. Houston; the "*Identification Guide to Butterflies Protected by the CITES Convention and the European Union,*" in Spanish and English by J. E. Tormo Muñoz and V. Roncero Corrochono; and "*Fauna Ibérica*" Volume 13, on Chrysomelidae.

Program Chair Ted Schultz introduced the speaker, Stephen D. Gaimari of the National Museum of Natural History, who presented "Searching for the Elusive Broad-headed Fly, *Eurychoromyia mallea* (Diptera: Eurychoromyiidae)." He held in one hand the few references that contain any information on the family, which has one species represented by four specimens collected in the Andean foothills near Mapiri, Bolivia. Stephen and colleagues mounted an expedition to find additional specimens and perhaps biological information in order to ascertain the relationship of this species to other flies, which at present is based mostly on shared reductions that are homoplasious within the superfamily. The staff of the Colección Boliviana de

Fauna in La Paz helpfully arranged permits beforehand so the group could immediately head down the purportedly most dangerous road in the world in search of their flighty quarry. The trials and tribulations of collecting in the tropics played out dramatically for this raggedy band of dipterists. Despite sacrificing liters of blood to the fly god Simulia, the broad-headed fly eluded them. They did, however, collect many good specimens of other target taxa. The next step: return for more punishment (and fun).

The meeting was adjourned at 8:11 p.m. Refreshments were provided by Ted Schultz.

Respectfully submitted,
Stuart H. McKamey,
Recording Secretary

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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 *Blephariceга* 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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