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BIOLOGY AND SEASONAL HISTORY OF *ELASMOSTETHUS ATRICORNIS* (VAN DUZEE) (HEMIPTERA: ACANTHOSOMATIDAE), WITH DESCRIPTIONS OF THE IMMATURE STAGES AND NOTES ON PENDERGRAST ORGANS

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Abstract.—Details of the seasonal history and habits, and duration of the immature stages of *Elasmostethus atricornis* (Van Duzee), a specialist acanthosomatid stink bug on spikenard (*Aralia racemosa* L.; Araliaceae) are presented and discussed. The bug's seasonal cycle is univoltine throughout its North American range, with peak adult emergence nearly synchronous with the first appearance of host plant inflorescences in early July. The egg and five nymphal instars are briefly described, with emphasis on color patterns, and all life stages are photographed. A brief review and illustrations of Pendergrast organs, unique to the Acanthosomatidae, are also provided.

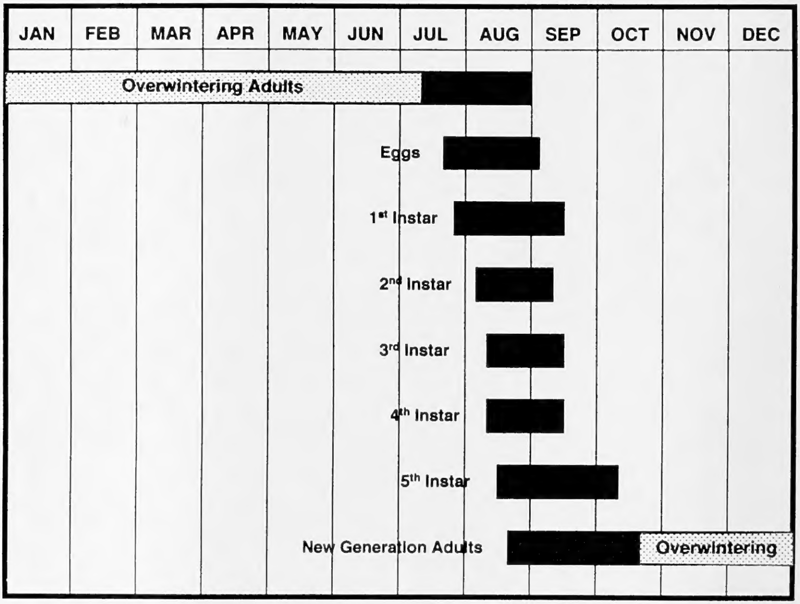
Key Words: Hemiptera, Acanthosomatidae, *Elasmostethus atricornis,* seasonal history, immature stages, Pendergrast organs

The Acanthosomatidae, a group often considered by earlier workers as a subfamily or a tribe of an inclusive Pentatomidae, comprise three subfamilies, approximately 47 genera, and 180 species worldwide (Kumar 1974, Schuh and Slater 1995). All are phytophagous, feeding on a variety of plants characteristic of mid- to late-successional stages, with several genera feeding upon members of one of the oldest angiosperm subclasses, Hamamelidae (orders Utricales, Fagales, and Hamamelidales) (Schaefer and Ahmad 1987). Six species, three each in the genera *Elasmostethus* Fieber and *Elasmucha* Stal, occur in North America (Thomas 1991).

Elasmostethus atricornis (Van Duzee) is known from Montana to Quebec and south to South Carolina (Jones and McPherson 1980, McPherson 1982). Its primary host plant, *Aralia racemosa* L. (Araliaceae), is commonly referred to as American spikenard, which describes the elongated panicles of fragrant, greenish-white flowers. Leaves are divided and subdivided into 6 to 21 heart-shaped leaflets. It is a perennial shrub often found on ravine banks (Wiegand and Eames 1926), growing 1–2 m each summer and dying back completely in the fall. Maturing fruits (berries) become a deep crimson red to purple in the fall. American spikenard has a geographic distribution somewhat sympatric with that of *E. atricornis,* except the former is recorded farther south to Georgia and New Mexico.

The objective of this study is to document the biology and seasonal history of this little-studied species through field observations over multiple seasons; to photograph its unique habitat, host plant, and various life stages; and to describe and illustrate its immature stages.

Table 1. Seasonal history of *Elasmostethus atricornis* on American spikenard, *Aralia racemosa,* in New York. (Note: Stippled bars indicate period when adults are overwintering in duff and leaf litter, and black bars indicate period when life stages are on host plants.)



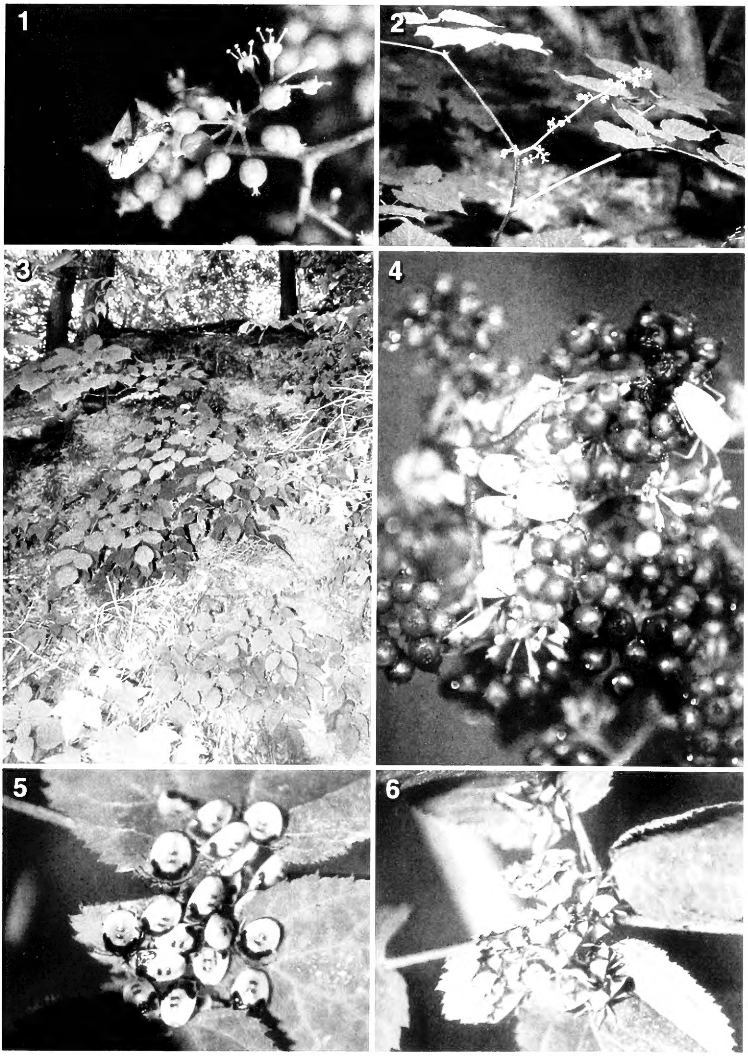
METHODS AND MATERIALS

The seasonal history of *E. atricornis* was studied at several sites in Ithaca (Tompkins Co.), New York. Observations were made over four seasons, at irregular intervals (but usually every few days) from early to mid July through October, in 1987 and again from 1999 to 2001. The primary study sites included natural areas near Beebe Lake on the Cornell University campus and also along Fall Creek adjacent to the Cornell University Arboretum, and at two local state parks (Buttermilk Falls and Robert H. Treman).

Developmental times were based on laboratory rearing in 2001, maintained at room temperature (ca. 20–22° C) under natural photoperiod (July–September). Nymphs were placed with spikenard inflorescences and fruits (in aquapics) in plastic boxes. Fruits were changed every 1–2 days, but developmental stages and molts were recorded daily.

BIOLOGY

Seasonal history and habits.—The generalized field history (Table 1) of *E. atricornis* is based on populations found on American spikenard in the Ithaca area. New host plant shoots appear by mid May, and by mid July the plant produces large flowering stalks (Fig. 2). Overwintered adults (Fig. 1) began to appear on foliage of American spikenard (Fig. 3) after the plants



Figs. 1–6. The acanthosomatid stink bug *Elasmostethus atricornis* and its host plant, American spikenard, *Aralia racemosa*. 1, Adult feeding on host fruits. 2, Elongated flower panicle of host plant in early July. 3, Typical ravine bank habitat of host plant. 4, Cluster of fifth instars and two teneral adults on maturing fruits of host plant. 5, Aggregation of fifth instars on upper leaf surface of host plant, just prior to molting to new generation adults. 6, Adults clustered on host leaves, prior to overwintering.

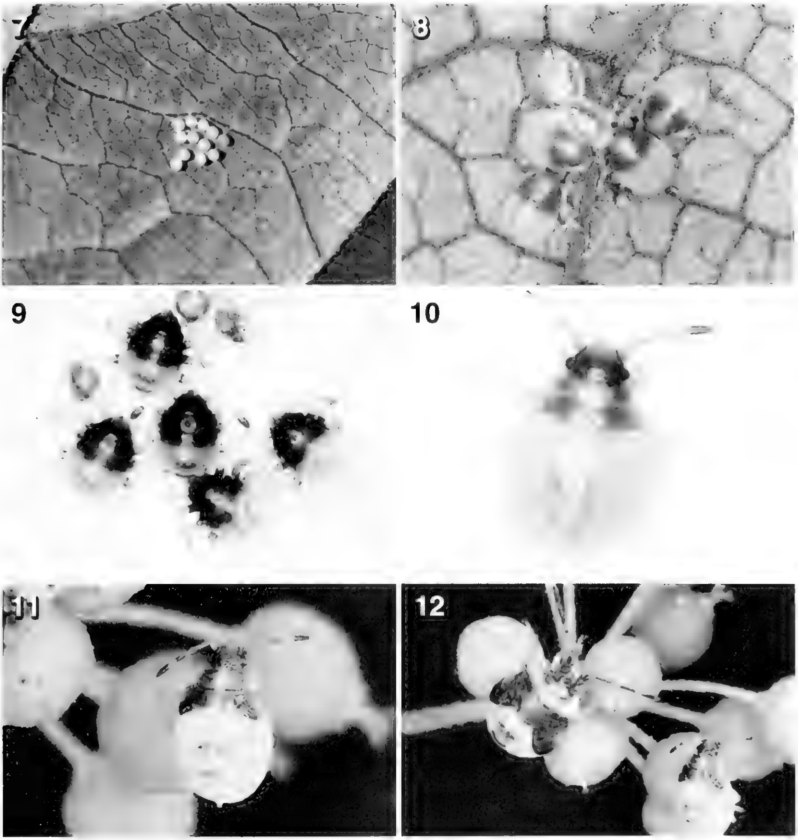
produced inflorescences and small, developing fruits. During all years studied, bugs generally were not observed until the first or second week of July. In 1987, adults were first noticed on July 10. In 1999, overwintered adults were seen on July 14, with matings taking place on July 16. Adults were not seen on plants until July 20 in 2001. Soon after they emerged from overwintering sites, adults began to feed, probing flowers and developing reproductive structures; they also sought mates. Soon after mating, egg deposition began. When oviposition began before fruits were available (i.e., late July to early August), eggs were deposited on the lower leaf surfaces, usually arranged (Fig. 7) in small tight clusters of 12–25 eggs, or often as individual eggs. After early to mid August, the majority of eggs were laid on the surface of individual fruits or on the pedicels. Eggs were observed as early as July 22 in 1999 and July 30 in 2000, and females continued to lay eggs as late as September 15 in 2001. Eggs hatched approximately 2–3 days after deposition. First instars, which hatched synchronously in a clutch, were found in the field as early as July 25 in 2001. First instars do not stray from the egg shells (Fig. 8), but remain motionless in place; they apparently did not feed on their host plant during this life stage. After molting to the second instar (Fig. 9), nymphs dispersed to host fruits. Second instars were observed by early August (ca. August 2) in 1999, closely followed by third instars (Fig. 10) and fourth instars (Fig. 11) (August 14 in 2000; August 11 in 2001), and then fifth instars (Fig. 12) (August 15 in 2001). Second through fifth instars fed on fruits after probing with their stylets. Fourth and fifth instars, highly polymorphic in coloration (Figs. 4–5, 11–12), often clustered among the maturing berries (Fig. 4), where they were essentially camouflaged by the very similar fruit shape and coloration (Aldrich 1988); this crypsis might protect the nymphs from predation. Fifth instars often aggregated on upper leaf surfaces, in folded-over leaves, and in large numbers just prior to adult eclosion (Fig. 5). Adults also clustered on leaves in the fall (Fig. 6). Adults of the new generation began to appear by late August (August 23 in 1987 and 2001) and continued to appear until early to mid October (October 7 in 2001 and October 11 in 1999). In 1999, new adults were present as late as October 19. By late October, or after the first hard frosts, most adults disappeared from host plants, presumably having moved to overwintering sites in and under the deep leaf litter below and around the senescing hosts, as observed for *E. interstinctus* (L.) in Alaska (Barnes et al. 1996). Only a single generation was produced annually in central New York, as is the case elsewhere in its range in North America (Jones and McPherson 1980).

Duration of immature stages.—In the laboratory at 20–22° C (n = 6 egg clusters observed), the incubation time for eggs of *E. atricornis* ranged from 4–6 days after clutch deposition; by contrast, in the field the majority of eggs hatched 2–3 days after deposition. Nymphal development (from egg hatch to adult eclosion) ranged from 11 to 39 days. The earliest appearance of new adults (from egg hatch) averaged 18.8 days (range 11–27) and the latest averaged 32.4 days (range 28–39). Each of the first two nymphal stadia generally lasted 2–3 days, while the third and fourth nymphal stadia required 2–4 days (10–11 days for some individuals). The fifth nymphal stadium averaged 9 days (range 2–14). As in a natural setting, nymphs of all instars remained on the clusters of maturing host fruits throughout the period of nymphal development.

DESCRIPTION OF IMMATURE STAGES

Egg (Fig. 7).—Length, 0.88–0.93 mm (n = 4); width, 0.64–0.73 mm (n = 7). Ovoid, slightly pointed apically, pale translucent green. Red eye spots visible through egg chorion just prior to egg hatch.

First instar (Fig. 8).—Length, 0.97–1.18 mm; width, 0.52–0.98 mm (n = 12). Head, thorax, and dorsal plates (= abdominal



Figs. 7–12. Life stages of *Elasmostethus atricornis*. 7, Cluster of eggs on lower leaf surface of *Aralia racemosa*. 8, Newly hatched first instars. 9, Second instars. 10, Third instar. 11, Fourth instar. 12, Fifth instar (left).

scent gland openings) uniformly brownish, except ecdysial lines of head and median line of thorax pale, subhyaline. Eye dark red. Antenna pale brown. Legs pale yellow; tarsi darker. Abdomen uniformly yellowish green.

Anterior wing pads undeveloped. Approximate ratio of lengths along median line of pro-: meso-: metanotum = 4.0: 3.0: 1. Antennomere ratio (approximate) of I: II: III: IV = 1: 1.2: 1.2: 2.2.

Second instar (Fig. 9).—Length, 1.67–2.54 mm.; width, 1.26–1.67 mm (n = 12). Head, thorax, and dorsal plates mostly dark brown to black. Anterior dorsal plate with some reddish highlights. Abdomen pale yellowish. Eye dark red to black. Antenna pale yellow, subhyaline, except basal antennomere infuscated and apical antennomere darkened (reddish black) on apical half or more. Legs pale yellowish, except femora dark brown. Apical tarsal segment (bearing claws) slightly darkened.

Anterior wing pads undeveloped. Approximate ratio of lengths along median line of pro-: meso-: metanotum = 7.1: 4.9: 1. Antennomere ratio (approximate) of I: II: III: IV = 1: 1.2: 1.3: 1.6.

Second instar very similar to first instar, except head and thorax of latter darker; sternal plates of thorax also darkly pigmented as well as femora and tip of rostrum. Distal half or more of apical antennomere piceus or black.

Third instar (Fig. 10).—Length, 2.59–4.75 mm; width, 1.32–3.61 mm (n = 11). Head, thorax, and dorsal plates dark brown, except anterior portion of head (including juga and tylus), lateral margins and middle of pronotum and mesonotum, and central portions of dorsal plates (only narrow anterior and lateral margins dark) pale yellowish. Abdomen mostly yellowish green. Narrow darkened anterior margins of dorsal plates with some reddish highlights. Eye dark red or black. Antenna infuscated, basal antennomere mostly dark brown, antennomeres 2 and 3 centrally darkened, apical (4th) antennomere dark reddish brown. Legs blackish brown except bases of femora and middle of tibiae pale yellowish.

Anterior wing pads undeveloped. Approximate ratio of lengths along median line of pro-: meso-: metanotum = 4.5: 4.0: 1. Antennomere ratio (approximate) of I: II: II: IV = 1: 1.5: 1.7: 2.2.

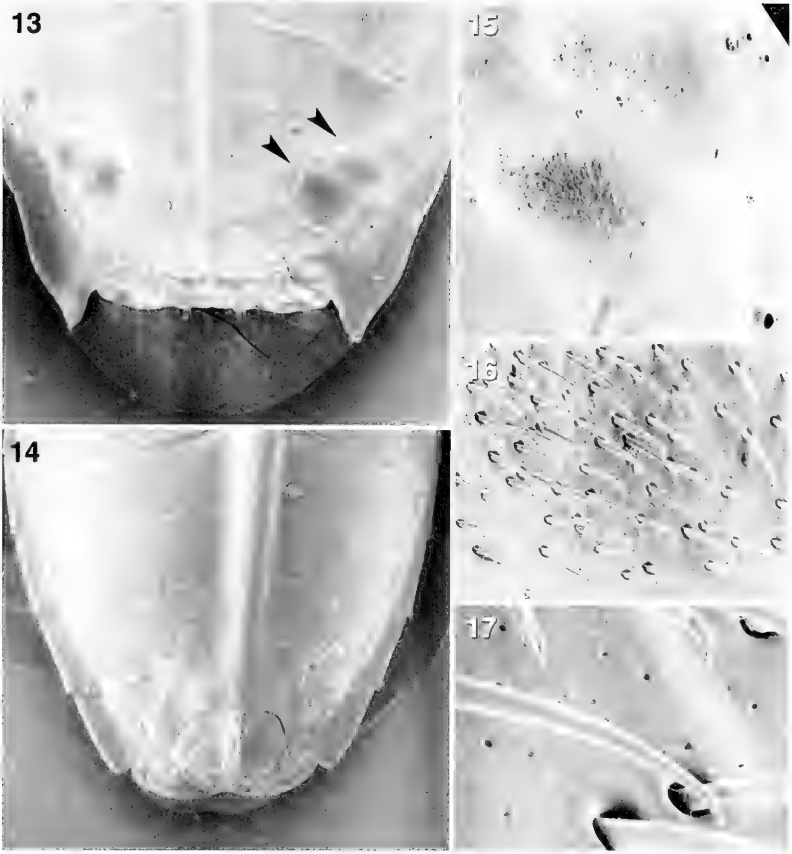
Fourth Instar (Fig. 11).—Length, 3.45–5.16 mm; width, 2.73–4.01 mm (n = 14). Coloration of head and thorax highly variable, ranging from pale green to blackish. Dorsal plates also variable in color, from pale yellowish to dark reddish brown with reddish and black highlights. Abdominal segments pale yellowish green. Eye generally reddish. Antennomere reddish brown to dark brown to blackish. Legs pale green to reddish brown; apical tarsal segment generally darker.

Anterior wing pads developed, attaining posterior margin of metanotum; posterior wing pads undeveloped. Approximate ratio of lengths along median line of pro-: meso-: metanotum = 4.0: 7.1: 1. Antennomere ratio (approximate) of I: II: III: IV = 1: 2.1: 1.8: 2.3.

Fifth Instar (Figs. 4–5, 12).—Length, 6.61–8.55 mm; width, 4.54–5.49 mm (n = 14). As in preceding instar, coloration of head, thorax, and dorsal plates highly variable. In non-maculated specimens, head, thorax, and abdomen pale yellowish green, except antennomeres reddish to reddish brown, tarsal segments reddish brown, and dorsal plates highlighted with some red and black. In maculated specimens, head and thorax (including well-developed wing pads) variously marked with black. Dorsal plates mostly dark reddish or black around perimeters, greenish yellow centrally. Abdomen generally pale green. Ocelli and eye dark reddish. Antennomeres mostly dark reddish brown. Femora mostly pale greenish; tibiae generally brownish; apical portion of terminal tarsal segment dark red to black.

Scutellum well developed, attaining posterior margin of metanotum. Anterior wing pads highly developed, extending to third or fourth abdominal tergite. Posterior wing pads conspicuously developed. Approximate ratio of lengths along median line of pro-: meso-: metanotum = 13.7: 20.7: 1. Antennomere ratio (approximate) of I: II: III: IV = 1: 1.8: 1.9: 1.7.

Note: Beginning with the fourth instar, which is nearly synchronous with fruit ripening (fruits become dark red to purple), and continuing with the fifth instars, the dorsal coloration is generally highly variable, with pale morphs of mostly yellowish green with no dark markings to maculated morphs with red and black highlights on the head and thorax, including dark red, brownish or black wing pads. Late in the season (September into October), this variable dor-



Figs. 13–17. Scanning electron photomicrographs of abdominal venters of acanthosomatid adults. 13, Abdominal venter and Pendergrast organs (arrows) of *Elasmostethus cruciatus*. 14, Abdominal venter of *Elasmucha lateralis*. 15, Close-up of Pendergrast organs on sterna 6 & 7 of *E. cruciatus*. 16–17, Magnification of setae (16) and cuticular pores (17) of the Pendergrast organs of *E. cruciatus*.

sal coloration makes nymphs difficult to see among the ripening fruits on which they feed (see Fig. 4).

PENDERGRAST ORGANS

Pendergrast organs, structures on the abdominal venter of females only, are unique to the Acanthosomatidae. They have been used as one of the characters defining 26 genera (Kumar 1974), although a similar structure exists in at least one other hemipteran family, the Lestoniidae (Fischer 2000). In observing the oviposition behavior of *E. atricornis*, we found that the female, after depositing an egg, brushes each hind tarsus alternately and repeatedly against the Pendergrast organs, followed by an apparent tapping of the egg. This sequence of behavior was repeated 5–10 times continuously for 30–60 seconds. Pendergrast (1952) noted similar behavior for the New Zealand species *Rhopalimorpha lineolaris* Pendergrast.

In both *E. atricornis* and *E. cruciatus* (Say), the Pendergrast organs are circular, depressed areas located laterally on the sixth and seventh abdominal sterna, a pair of depressions on either side of the midline (Fig. 13). Under high magnification, these depressed cuticular areas are clothed with short setae (Figs. 15–16) interspersed with minute pores (Fig. 17). Microscopic examination (Breddin 1903, Pendergrast 1953, Carayon 1981, Staddon 1990) and SEM and transmission electron microscopy (Fischer 1994) of cuticular preparations of other acanthosomatid species indicate that the pores are connected by ducts to glandular tissue.

Several hypotheses have been promoted that speculate on the function of the Pendergrast organs, including their involvement in copulation (Breddin 1903, Pendergrast 1953), in pheromone production (Staddon 1990), and in the secretion of compounds that deter egg predation (Aldrich 1988, Fischer 1994). Acanthosomatids in genera that lack Pendergrast organs instead brood or guard their eggs and young. For example, females of *Elasmucha lateralis* (Say), a common North American acanthosomatid in which Pendergrast organs (Fig. 14) are absent, exhibits brooding behavior. Females of *E. lateralis*, and those of other species in this worldwide genus, guard their eggs, first instars and sometimes later instars (Frost and Haber 1944; Kudô 1990, 2000; Kudô and Nakahira 1993; Kaitala and Mappes 1997).

Discussion

The absence of apparent feeding in first instars and the late-season appearance of overwintered adults are not unique to *Elasmostethus*. These biological attributes are shared by other heteropteran taxa.

Lack of feeding by first instars is not unusual among pentatomomorphan Heteroptera. In many instances, first-instar nymphs of seed-sucking species, such as the southern green stink bug (*Nezara viridula* (L.)), the rice stink bug (*Oebalus pugnax* (F.)) (Bowling 1979, 1980), and the green stink bug (*Acrosternum hilare* (Say)) (Simmons and Yeargan 1988), remain clustered on the eggs shells and do not feed on plant tissue; however, occasionally the nymphs have been observed probing the egg shells with their stylets. First instars of many predatory pentatomids (subfamily Asopinae) do not feed, or feed only on unhatched eggs of their own species (Wheeler 2001), such as *Euthyrhynchus floridanus* (L.) (Oetting and Yonke 1975), *Podisus maculiventris* (Say) and *P. placidus* Uhler (Mukerji and LeRoux 1965, Oetting and Yonke 1971), and *Stiretrus fimbriatus* (Say) and *S. anchorago* (F.) (Oetting and Yonke 1971, Waddill and Shepard 1974). Some first-instar coreoids also do not feed (Pupedis et al. 1985). For example, first instars of *Leptoglossus fulvicornis* (Westwood), a magnolia fruit-feeding specialist, do not feed or do so only minimally on foliage (Wheeler and Miller 1990), while first instars of *L. occidentalis* Heidemann, the western conifer-seed bug, often are able to reach the second stadium without feeding (Koerber 1963).

Several heteropterans also are characterized by the late-season appearance of overwintered adults. Wheeler and Miller (1990) documented that the coreid *Leptoglossus fulvicornis* overwinters in the adult stage in Pennsylvania and remains in hibernation sites until mid-June to early July at which time adults then colonize host trees when small, cone-like fruits begin to appear. Other specialist Heteroptera that overwinter as adults and do not become active until late in the season when inflorescences or developing fruits of their host plants are available include the lygaeid *Ochrimnus mimulus* (Stål) (Palmer 1986) and the pentatomid

Proxys punctulatus (Palisot de Beauvois) (Vangeison and McPherson 1975).

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NOMENCLATURAL CHANGES IN PTEROMALIDAE, WITH A DESCRIPTION OF THE FIRST NEW WORLD SPECIES OF *ORMOCERUS* WALKER (HYMENOPTERA: CHALCIDOIDEA)

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Abstract.—The new species ***Ormocerus americanus*** **Dzhanokmen and Grissell** is described based on specimens reared from cynipid galls on oak in Texas. The following **new synonymies** are proposed: *Abyrsomele* Dzhanokmen 1975a = *Halticopterina* Erdös 1946; *Halticopterina penthocoryne* Dzhanokmen 1975a = *H. moczari* Erdös 1954; *Homoporus longiventris* Dzhanokmen 1999 = *H. cupreus* Erdös 1953; *Phaenocytus heptapotamicus* Dzhanokmen 1990 = *P. glechomae* (Förster 1841); *Pseudocatolaccus amegallus* Dzhanokmen 1989 = *P. nitescens* (Walker 1834); *Pteromalus maculatus* Dzhanokmen 1998 = *P. vopiscus* Walker 1839; *Stenoselma haplogastra* Dzhanokmen 1975a = *S. nigrum* Delucchi 1956; *Stenoselma armeniaca* Dzhanokmen and Herthevtzian 1990 = *S. nigrum* Delucchi 1956; *Stirogenium* Dzhanokmen 1985 = *Paracarotomus* Ashmead 1894; *Stirogenium asiaticum* Dzhanokmen 1985 = *Paracarotomus cephalotes* Ashmead 1894. The following are **new combinations**: *Chlorocytus arkansensis* (Girault) from *Habrocytus* Thomson; *C. languriae* (Ashmead) from *Habrocytus* Thomson; *C. rhodobaeni* (Ashmead) from *Habrocytus*; *C. simillimus* (Gahan) from *Habrocytus*; *C. vassiliefi* (Ashmead) from *Homoporus* Thomson; *Halticopterina lauta* (Dzhanokmen) from *Abyrsomele* Dzhanokmen; *Mesopolobus elymi* (Dzhanokmen) from *Platneptis* Bouček; *Neocatolaccus carinatus* (Howard) from *Catolaccus* Thomson.

Key Words: Chalcidoidea, Pteromalidae, cynipid galls, oak

The family Pteromalidae is worldwide in distribution and is numerically the third largest family within the superfamily Chalcidoidea (Noyes 2001). Currently there is virtually no worldwide consensus of opinion on the ranks of taxa composing the family or of the definition of subfamilies that should be recognized. The status of a great many higher level taxa have not been evaluated and most of the genera and species remain unstudied. We take this opportunity to make some changes in the nomenclature of Holarctic pteromalids based upon examination of the types and collection material from the Canadian National Collection, Ottawa (CNC); The Natural History Museum, London (NHM, London); National Museum of Natural History, Smithsonian Institution, Washington D.C. (USNM); Natural History Museum, Budapest (NHM, Budapest); Zoological Institute, St. Petersburg (ZI); and Institute of Zoology, Almaty, Kazakhstan. We also describe a new species of *Ormocerus* Walker, reared from cynipid galls on oak, which is the first reported species of the genus in the New World.

NEW SYNONYMIES

Halticopterina Erdös

Halticopterina Erdös 1946: 160.

Type species: Halticopterina triannulata Erdös. Original designation. (NHM, Budapest, examined.)

Abyrsomele Dzhanokmen 1975a: 627. **New synonymy**.

Type species: Abyrsomele lauta Dzhanokmen. Original designation. (ZI, examined.)

The type species of *Abyrsomele* does not differ from *Halticopterina* in generic characters and is herein considered a subjective junior synonym of the latter genus.

Halticopterina moczari Erdös

Halticopterina moczari Erdös 1954: 153–154. (NHM, Budapest, examined.)

Halticopterina penthocoryne Dzhanokmen 1975a: 625–627. **New synonymy**. (ZI, examined.)

Examination of the type specimens leaves no doubt that *H. penthocoryne* is a subjective junior synonym of *H. moczari*.

Homoporus cupreus Erdös

Homoporus cupreus Erdös 1953: 245. (NHM, Budapest, examined.)

Homoporus longiventris Dzhanokmen 1999: 183–185. **New synonymy**. (ZI, examined.)

Homoporus longiventris was distinguished from *H. cupreus* chiefly by having lighter colored antennae and legs and by its narrower gaster. These differences, based upon an examination of several series of specimens, now appear to occur within the range of variation of a single species and we consider *H. longiventris* a subjective junior synonym of *H. cupreus*.

Phaenocytus glechomae (Förster)

Pteromalus glechomae Förster 1841: 21.

Phaenocytus glechomae: Graham 1969: 562–563.

Phaenocytus heptapotamicus Dzhanokmen 1990: 65–67. **New synonymy**. (ZI, examined.)

The genus *Phaenocytus* Graham was created for *Pteromalus glechomae* Förster. Although we have not seen the type, we compared *P. heptapotamicus* with specimens of *P. glechomae* housed in the NHM, London. The two are identical and we consider the former a subjective junior synonym of *P. glechomae*.

Pseudocatolaccus nitescens (Walker)

Amblymerus nitescens Walker 1834: 347. (NHM, London, examined.)

Pseudocatolaccus nitescens: Graham 1969: 694–696.

Pseudocatolaccus amegallus Dzhanokmen 1989: 45–46. **New synonymy**. (ZI, examined.)

Examination of the type and additional series of *Pseudocatolaccus nitescens* (Walker) convinces us that it is the same as *P. amegallus. Pseudocatolaccus nitescens* is a rather variable species (Graham 1969), and it seems that *P. amegallus* is just a form of *P. nitescens* having the postmarginal vein shorter than normal. Thus we consider *P. amegallus* a subjective junior synonym of *P. nitescens*.

Pteromalus vopiscus Walker

Pteromalus vopiscus Walker 1839: 274. (NHM, London, examined.)

Pteromalus maculatus Dzhanokmen 1998: 494–496. **New synonymy**. (ZI, examined.)

Examination of the type of *Pteromalus vopiscus* Walker showed that *P. maculatus* is almost certainly the same species. It differs from the latter in small details that we consider to fall within the range of individual variability of *P. vopiscus*. For this reason we place *P. maculatus* as a subjective junior synonym of *P. vopiscus*.

Paracarotomus Ashmead

Paracarotomus Ashmead 1894: 335–336.

Type species: Paracarotomus cephalotes Ashmead. Monobasic. (USNM, examined.)

Stirogenium Dzhanokmen 1985: 152. **New synonymy**.

Type species: Stirogenium asiaticum Dzhanokmen. Original designation. (ZI, examined.)

Based upon an examination of the type species of *Paracarotomus* and *Stirogenium*, the latter differs in no morphological way and so is now considered a subjective junior synonym of *Paracarotomus*.

Paracarotomus cephalotes Ashmead

Paracarotomus cephalotes Ashmead 1894: 335. (USNM, examined.)
Stirogenium asiaticum Dzhanokmen 1985: 152–153. **New synonymy**. (ZI, examined.)

After comparing the type specimens of *Stirogenium asiaticum* and *Paracarotomus cephalotes* we found that they differ in no way. Therefore we consider *Stirogenium asiaticum* a subjective junior synonym of *Paracarotomus cephalotes*.

Stenoselma nigrum Delucchi

Stenoselma nigrum Delucchi 1956: 66–68.
Stenoselma haplogastra Dzhanokmen 1975b: 1096–1097. **New synonymy**. (ZI, examined.)
Stenoselma armeniaca Dzhanokmen and Herthevtzian 1990: 139–142. **New synonymy**. (ZI, examined.)

We examined all the determined specimens of *S. nigrum* in NHM, London. The differences between *Stenoselma nigrum* and *S. haplogastra* appear to fall within the range of variation of a single species, and we have no hesitation in placing *S. haplogastra* as a subjective junior synonym of *S. nigrum*. The differences given in the description of *armeniaca* also fall within the range of variation of *nigrum* and we place *S. armeniaca* as a subjective junior synonym of *S. nigrum*.

NEW COMBINATIONS

As a result of the examination of the types of additional pteromalid species, we propose the following new combinations:

Chlorocytus arkansensis (Girault 1917), **n. comb.** from *Habrocytus* Thomson
Chlorocytus languriae (Ashmead 1896), **n. comb.** from *Habrocytus* Thomson
Chlorocytus rhodobaeni (Ashmead 1896), **n. comb.** from *Habrocytus* Thomson
Chlorocytus simillimus (Gahan 1919), **n. comb.** from *Habrocytus* Thomson
Chlorocytus vassiliefi (Ashmead 1903), **n. comb.** from *Homoporus* Thomson
Halticopterina lauta (Dzhanokmen 1975a), **n. comb.** from *Abyrsomele* Dzhanokmen
Mesopolobus elymi (Dzhanokmen 1984), **n. comb.** from *Platneptis* Boucek
Neocatolaccus carinatus (Howard 1897), **n. comb.** from *Catolaccus* Thomson

The genus *Chlorocytus*, established by Graham (1956), was not formally reported in the Nearctic until 1997 (Bouček and Heydon 1997). No described species were included at that time, and the above new combinations are the first species reported for the Nearctic. These taxa were described much earlier when such important characteristics as the shape and structure of the prepectus and propodeum were not critically analyzed. In *Chlorocytus* the prepectus is large and uniformly reticulate, the propodeum is nearly always large (more than half as long as the scutellum) and with irregular carinae and shallow spiracular sulci. Additionally, in *Chlorocytus* the antennal clava in profile is often asymmetrical, its upper edge strongly curved. These characters distinguish *Chlorocytus* from the morphologically similar genus *Pteromalus* Swederus (and its synonym *Habrocytus*, which some may regard as a subgenus).

Ormocerus Walker

Burks (1979) placed the genus *Ormocerus* Walker in the subfamily Miscogasterinae, tribe Ormocerini and included *O. flora*

(Girault) and *O. vulgaris* (Ashmead) in the genus. Heydon and Bouček (1992) examined the types of these two species and determined that neither belonged to *Ormocerus*. For *O. flora* they established the genus *Ficicola* Heydon and Bouček; they transferred *O. vulgaris* to the genus *Seladerma* Walker. As a result of these actions, none of the described Nearctic species remained in the genus *Ormocerus*. In their key to Nearctic genera of Pteromalidae, Bouček and Heydon (1997) cited *Ormocerus* as having "at least 4 spp." based apparently on their knowledge of undescribed species in the region. Frankie et al. (1992: Table 17.6) listed, but did not discuss, "*Ormocerus* n. sp." as a parasitoid of the sexual generation of a cynipid gall on oak in Texas. It is this material, representing the first known species of the genus from the New World, that we describe herein.

Ormocerus americanus **Dzhanokmen and Grissell, new species**

(Figs. 1–4)

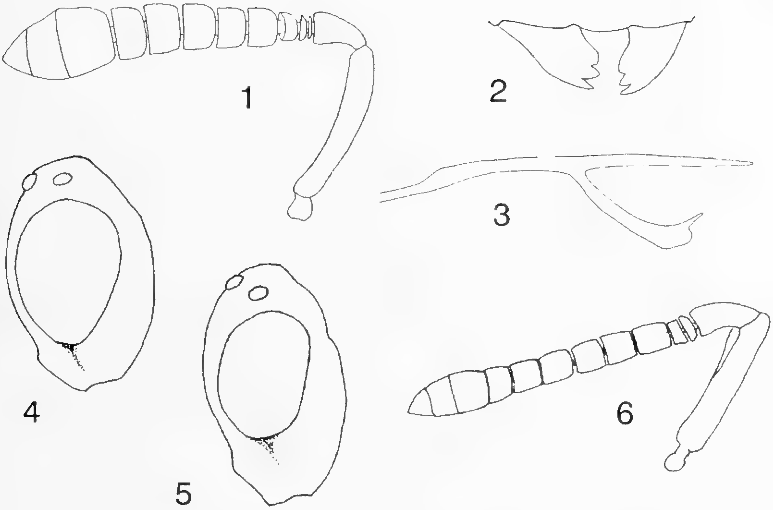
Female holotype.—Body length 2.1 mm. Head, mesosoma, and coxae dark green with metallic gloss. Metasoma dark fulvous. Antenna dark: scape dark with metallic tinge, pedicel dark brown, flagellum brown. Femora mainly brown to black with metallic green tinge, tibiae fuscous except at apices, remaining parts of legs testaceous, apices of tarsi fuscous. Forewing appearing hyaline, but with slight fuscous cloud below stigmal vein extending below marginal to parastigmal vein; venation brownish testaceous.

Head in dorsal view 2.3 times as broad as long. POL about 2.3 OOL. head transversely oval in frontal view. Gena relatively short (Fig. 4), very slightly curved, converging strongly towards mouth. Anterior margin of clypeus (Fig. 2) evenly curved forward. Eyes relatively large, height about 2.5× height of gena (Fig. 4). Antennae inserted low on face, toruli at or slightly above level of ventral eye margin. Antennal flagellum clavate (Fig. 1); 2 transverse anelli, anellus barely as wide as first funicle segment; first funicle segment shorter and narrower than second; second and third segments slightly transverse; following segments strongly transverse. Both mandibles with three teeth (Fig. 2). Maxillary palp 4-segmented, labial palp 3-segmented.

Mesosoma about 1.4× as long as broad. Mesoscutum with reticulate sculpture, interspersed with numerous minute pits from which arise setae, which cover mesoscutum. Notaulus complete and deep, not interrupted by sculpture. Scutellum distinctly longer than broad, convex, sculptured like mesoscutum though with more conspicuous pits among reticulation on lateral sides and base. Frenum weakly delimited. Propodeum medially nearly ⅙ scutellum length, weakly alutaceous, almost smooth, with distinct median carina, without plicae. Callus with several hairs; spiracles subcircular, separated by nearly ¾ their greatest diameter from metanotum. Upper mesopleuron large, polished and smooth. Prepectus finely reticulate. Spur of midtibia longer than first tarsal segment. Forewing with speculum closed below, not extending farther than beginning of marginal vein; disc beyond speculum densely setose. Lower surface of costal cell with only a few setae in distal ⅓. Basal cell with some setae proximally and distally along cubital vein; basal vein a conspicuous transparent tract, with only one or two setae at junction dorsally with parastigma. Apical margin of wing with fringe. Postmarginal vein slightly longer than marginal, latter 1.2× longer than stigmal (Fig. 3).

Metasoma about as long as mesosoma, 1.8× as long as broad, acute apically, narrower than mesosoma. Basal tergite occupying ⅓ total length, its hind margin medially emarginate. Gaster ventrally keeled, hypopygium extending nearly ½ distance from base of gaster to tips of ovipositor sheath, which project slightly at most.

Male.—Body length 2.0 mm. Agreeing with female except as follows: forewing completely hyaline; stigmal vein elongately triangular (instead of linear), widening from



Figs. 1–6. *Ormocerus* spp. 1–4, *Ormocerus americanus*, female. 1, Antenna. 2, Mandibles and anterior margin of clypeus. 3, Forewing venation. 4, Head, lateral view. 5–6, *Ormocerus latus*, female. 5, Head, lateral view. 6, Antenna.

marginal vein to junction with stigma where it is subequal in width; flagellum cylindrical, clothed with dense, semierect setae, funicular segments strongly transverse and nearly twice width of anellus.

Variation.—Female specimens vary from 1.8 to 2.1 mm in length. There is little variation in color except the general metallic green tinge of the femora may disappear, leaving them dark brown in color. The forewing infuscation is obscure at best; in some specimens it is little more than a slight darkening posterior to the stigma; in others it is barely visible but extends to the parastigma. The eye height ranges from 2.5 to 3 times the genal length. Only one male is known.

Type material.—Holotype ♀, Dallas, Dallas County, Texas, coll. 2-IV-1974, em. 1–15-V-1974, coll. Gordon Frankie, ex bisexual generation *Disholcaspis cinerosa* (Bassett) [Hymenoptera: Cynipidae] on *Quercus virginiana* Mill [Fagaceae] (USNM); 15 ♀, 1 ♂ paratypes same data as holotype; 3 ♀ paratypes same data except collected 29-III-1974 (no emergence date) (USNM; 1 ♀ paratype in ZI, 2 ♀ paratypes in CNC).

Host.—The species was reared from the bisexual generation of *Disholcaspis cinerosa* on *Quercus virginiana*.

Discussion.—*Ormocerus americanus* differs from the two European species, *O. latus* Walker and *O. vernalis* Walker chiefly in its shorter gena and larger eye (Fig. 4). The eye is 2.5 to 3 times the genal length in *O. americanus*, whereas in *O. latus* and *O. vernalis* it is about 2 times the genal length (Fig. 5). Both *O. americanus* and *O. latus* differ from *O. vernalis* in several features including: the presence of an apical wing fringe (absent from *O. vernalis*), the basal cell has many setae and the basal vein is relatively bare (basal cell bare but the basal vein with several rows of setae in *O. vernalis*), forewing with pale infuscation sometimes seen only with difficulty (darkly infuscated in *O. vernalis*), the stigmal vein is curved (straight in *O. vernalis*), and the propodeum is lightly reticulate (coarsely rugulose in *O. vernalis*). *Ormocerus americanus* differs from *O. latus* by the basal flagellomeres being wider than long (Fig. 1) (longer than wide in *O. latus,* Fig. 6); the notauli sharply defined as nearly smooth grooves (ill-defined and interrupted by sculpture in *O. latus*); and the median area of the propodeum less reticulately sculptured (almost alutaceous) than the lateral areas (nearly uniformly sculptured in *O. latus*).

The three known species of this genus attack cynipid gall-formers on oak.

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BIOLOGY OF *RHYNENCINA LONGIROSTRIS* JOHNSON (DIPTERA: TEPHRITIDAE)

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Abstract.—Adults of *Rhynencina longirostris* Johnson were successfully reared from larvae in the achenes of *Smallanthus uvedalius* (L.) Mackenzie (Asteraceae), the first confirmed host plant record for this fly. Adults of *R. longirostris* are univoltine with a flight-time corresponding to the flowering period of *S. uvedalius,* which is July–September in the Great Smoky Mountains National Park. *Heteroschema* sp. (Hymenoptera: Pteromalidae) parasitoids and *Homoeosoma* sp. (Lepidoptera: Pyralidae) feeding in capitula of the host are probably significant sources of mortality of *R. longirostris* immature stages.

Key Words: *Smallanthus uvedalius,* Great Smoky Mountains National Park, All Taxa Biological Inventory, host plant

In connection with the All Taxon Biological Inventory (ATBI) that was initiated in the Great Smoky Mountains National Park (GSMNP) in 1997, Gary Steck (GJS) and Bruce D. Sutton (BDS) joined a dipterists' 'collecting blitz' in late May, 1999. During this visit, GSMNP collections curator, Don DeFoe (DD), kindly allowed us to peruse the collection in the Natural History Museum (GSNP) at the park headquarters at Sugarlands, where we noted the presence of six specimens of a rarely collected tephritid fly, *Rhynencina longirostris* Johnson. These specimens are the first known record of *R. longirostris* in the state of Tennessee (Steck and Sutton 2000), with label data as follows: "Tennessee: Sevier Co., Park HQ, 1520′ elev., 5 Aug 1996." DD, as collector of the specimens, was able to take us directly to the location and the plants upon which the adult flies had been taken; this was a small patch of *Smallanthus uvedalius* (L.) Mackenzie (Asteraceae) in a disturbed, shaded area next to a parking lot. The flies had been on the flower heads at the time of capture. That discovery prompted all of the following investigations reported here.

Rhynencina is a small genus comprising only five New World species: three species are present in South America, one in Mesoamerica, and one, *R. longirostris,* in eastern North America (Freidberg and Norrbom 1999). The latter has been recorded from Pennsylvania, Maryland, North Carolina, and Georgia (Foote et al. 1993), and Tennessee (Steck and Sutton 2000). Limited host plant information is available for the genus. *Rhynencina emphanes* (Steyskal) (Colombia) has been reared from flowers of *Espeletia* sp.; adults of *Rhynencina dysphanes* (Steyskal) (Andean countries), *Rhynencina spilogaster* (Steyskal) (Mexico, Central America), and *R. longirostris* have all been collected on *Polymnia* sp. and/or the closely related genus *Smallanthus*; and *R. spilogaster* has been observed ovipositing into flowers of *Smallanthus* sp. (Freidberg and Norrbom 1999) (host genera are all of Asteraceae, tribe Heliantheae); finally, *R. longirostris* was reared for the first time from *Smallanthus uvedalius* (Steck and Sutton 2000) as more fully described below.

Smallanthus uvedalius (formerly *Polymnia uvedalia*), commonly known as leafcup or bearsfoot, is an herbaceous perennial that is widespread in woods and meadows of the eastern United States and flowers from summer to fall. Disk flowers are sterile, and thick achenes are produced from the ray flowers (Cronquist 1980).

MATERIALS AND METHODS

Most data were gathered from two patches of the host plant, *Smallanthus uvedalius*, in the GSMNP, one at Metcalf Bottoms and another at Sugarlands. The former stand of plants was spread along about 250 m of roadside and contained an estimated 1,300–1,800 plants. The patch at Sugarlands was about 20 m × 3 m with an estimated 150–200 plants.

Data on immature stages was obtained by dissections of flower and seed heads that were collected from 1999 to 2001. On 24 and 27 September 1999, DD collected mature seed heads from Metcalf Bottoms and Sugarlands, respectively, packaged them in brown paper bags, and sent them by overnight delivery to Gainesville, Florida; two additional collections of dried seed heads, from Sugarlands on 5 October, and from Metcalf Bottoms on 13 October 1999, were also sent to Gainesville in the same manner. In total about 50 dried seed heads were collected in 1999. Dissection of these heads revealed the presence of likely tephritid larvae inside achenes, as described more fully below. In an attempt to rear adults, several 100s of unopened achenes were held dry and at room temperature in the laboratory until mid-November, 1999. At that time they were placed on damp sphagnum moss in a loose-lidded plastic container and kept in a refrigerator at about 4°C to break diapause. In mid-April, 2000, the achenes in their bed of damp sphagnum moss were transferred to a glass terrarium with screened top and bottom. At this time, some of the achenes were observed to be completely softened and disintegrating, while others were still very hard as before. Thereafter the terrarium was kept in a shaded area outdoors under ambient Gainesville conditions (likely much warmer and drier than Smoky Mountains conditions), or alternatively under fluorescent lighting in a garage utility room with more moderate temperature and humidity conditions. The terrarium was watered sporadically.

Further dissections were made from seed heads collected from Metcalf Bottoms and Sugarlands 4–8 September 2000 (Lionel Stange); from buds and flowering heads collected on 13 July 2001, Metcalf Bottoms (GJS, Victor M. Steck); and from buds, flower heads, and seed heads collected 2–4 September 2001 (GJS, BDS), Metcalf Bottoms.

Observation and collection of adult stages were made during 12–13 July 2000 (GJS, BDS), 2 and 13 July 2001 (GJS, VMS), and 2–4 September 2001 (GJS, BDS).

All life stages of *R. longirostris* are vouchered at the Museum of Entomology, Florida State Collection of Arthropods (FSCA) in Gainesville. A full description of all immature stages will be published at a later date.

RESULTS

Rearing to adult stage.—Seeds held for overwintering in 1999 began germinating in mid-May, 2000. In mid-July the terrarium was brought back into the laboratory in Gainesville for closer observation, and between 24 and 27 July 2000 three adult *R. longirostris* flies emerged, thus proving *S. uvedalius* to be a host of the immature stages. On 12 July 2000, GJS and BDS carefully combed the litter below the host plants at Sugarlands looking for remains of the previous year's achenes. A few dozen intact achenes were located (along with numerous fragments) and held for rearing, but nothing came of them.

Immature stages in flower and seed heads.—On 28 September 1999, GJS and BDS dissected and examined the contents of some of the seed heads collected by DD on September 24 and 27 at Metcalf Bottoms and Sugarlands, respectively. There were no exposed tephritid immature stages present in the heads. Most seed heads retained a peripheral ring of black, dry, and well-filled achenes (disk flowers are sterile, and a maximum of 11–12 seeds per head develop from the peripheral ray flowers). Achenes were very hard, and only with considerable difficulty did we manage to open them to examine the contents. Some achenes, often slightly lighter-colored and smaller, contained a bright yellow larva. In each case, a single larva filled the seed cavity, with only the thin, but hard, pericarp surrounding it. A total of seven 3rd instar larvae (based on mouthhook size; body lengths varied from about 1.6 to 3.7 mm) and five puparia was extracted in this fashion. Two of the puparia were held dry in a vial; in May 2001, it was noted that two adults of a *Heteroschema* sp. (Hymenoptera: Pteromalidae) had emerged. In addition, of the three puparia preserved in alcohol, two clearly contained hymenopteran larvae. Thus, the latter are likely larval-pupal parasitoids. There were no signs of exit holes or 'windows' prepared by the *R. longirostris* larvae for later escape from the achene. The larvae were preserved in 70% alcohol after killing in hot water. Numerous seeds contained frass and tiny Lepidoptera larvae. There were also a few small, non-tephritid Diptera pupae in the dry seed heads, but not in the achenes.

From the Sugarlands (5 October 1999) and Metcalf Bottoms (13 October 1999) seed head collections, we attempted to get a more quantitative estimate of their contents. To avoid destroying the achene contents, a small hand-held drill with a fine, bur bit was used to grind away enough of the pericarp to determine the contents. Of 221 achenes examined in this manner, a total of 11 live *R. longirostris* 3rd instars, one dead 2nd instar, and 12 live pupae was obtained. The larvae had consumed the seed only. Two of the puparia were held dry for emergence—one yielded an adult *Heteroschema* sp., and the other an unemerged adult *R. longirostris*; five of the other ten puparia clearly contained hymenopteran larvae. Thus, this limited sample indicates a parasitism rate of 50%. Of the remaining achenes, 102 contained seemingly viable seeds (46%) and 89 appeared non-viable (empty or shriveled) (40%); another six achenes were full of insect frass (3%). The 221 achenes examined were not selected randomly, as we were trying to maximize the number *R. longirostris* specimens found, and so chose smaller, discolored achenes; thus, these numbers do not accurately reflect actual infestation rates. See Table 1 for a summary of achene contents.

Because of the time, effort, and difficulty encountered in dissecting dried achenes, the seed heads collected in year 2000 were treated differently: achenes were separated from their capitula, placed into a beaker of water, and gradually heated to about 70°C; after cooling they were transferred to 70% isopropanol. After a few months of storage in alcohol, the achenes were much more easily dissected with forceps without damaging their contents. One hundred achenes from each site were randomly selected and dissected. From the Metcalf Bottoms collection, these yielded 24 immature specimens of *R. longirostris* (three 1st instars, seven 2nd instars, four 3rd instars, ten pupae; nine of the ten puparia clearly contained a hymenopteran larva) (Table 1). As noted above, only a single *R. longirostris* larva or puparium was present in a given achene. Each of the immature specimens, excepting one of the 1st instars, was inside the seed coat. In the case of the 1st and 2nd instars, the surrounding seed coat was merely a shrivelled bag. (These could not be distinguished from the seed coat of numerous other inviable but uninfested seeds.)

Table 1. Immature stages of *Rhynencina longirostris* in seed heads of *Smallanthus uvedalius*.

Contents	Oct 1999	Sept 2000	July 2001	Sept 2001
No. achenes examined	221	100	237	ca. 117
No. eggs	0	0	46	0
No. 1st instars	0	4	0	2
No. 2nd instars	1	7	0	1
No. 3rd instars	11	4	0	0
No. puparia	12	10	0	0
% parasitized puparia	50%	90%	—	—
Lepidoptera frass	+	11*	0	ca. 70

+ Indicates present, but not quantified.

* Does not represent total damage from Lepidoptera feeding, because only intact achenes were selected for dissection.

There was nothing resembling an obvious oviposition scar on the achene exterior, suggesting that oviposition occurs directly into the flower ovary at a very early stage of development. Of the 100 achenes dissected, only 32 contained what appeared to be viable seeds. Of the remainder, 11 had been destroyed by Lepidoptera larvae as evidenced by their frass; other seed coats were empty or only partially filled for no apparent reason. Infested achenes were indeed smaller than those with viable seeds. Average diameter of infested achenes was 4.7 mm (range 3.3–5.4 mm, N = 24), while that of achenes with viable seed was 5.1 mm (range 4.2–6.0 mm, N = 32). Infestation at the Sugarlands site was very low: of 100 achenes, only two contained *R. longirostris* (one 1st instar and one 2nd instar), while 71 contained apparently viable seeds.

Plant collections made in year 2001 were treated somewhat differently from before. Entire capitula (rather than culled, intact achenes) were subjected to hot water treatment, then preserved in alcohol. This provided data on *R. longirostris* egg deposition and the full impact of Lepidoptera larvae on seed production.

On 2 July 2001 there were only a very few buds of *S. uvedalius* to be found at Metcalf Bottoms, and none was larger than about 5 mm in diameter. By 13 July, a small number of buds had developed to the stage where capitula disks were exposed and petals of ray flowers partially developed. All of the capitula (88 total) in the most advanced stage of development were collected, preserved in alcohol, and examined under a microscope (see Table 1). Oviposition and probe punctures, where an aculeus had penetrated the outer phyllaries and young achenes, were easily visible. Dissected heads ranged in size from unopened buds as small as 4 mm diameter to the most developed capitulum in the population, which had a 12 mm-diameter receptacle (measured with outer phyllaries removed) and petals of 12 mm length. Six capitula (7%) were found with eggs oviposited into achenes as follows: (1) two of ten achenes with one egg each in a 12 mm-diameter capitulum with petals expanded, which was the most developed capitulum present at Metcalf Bottoms; (2) nine of nine achenes with a range of two to five eggs per achene in a 10 mm-diameter capitulum with outer phyllaries reflexed and one petal just beginning to unfurl; (3) five of 11 achenes with one egg each in a 10 mm-diameter capitulum with none of the petals unfurled; (4) four of nine achenes with one to two eggs each in a 10 mm-diameter capitulum with bracts partly reflexed and no petals; (5) four of 11 achenes with one egg each in a 10 mm-diameter capitulum with none of the petals unfurled; and, (6) one of 12 achenes with one egg in a 9 mm-diameter capitulum with disk exposed and no petals. The achenes containing eggs ranged from 1.2 to 2.8 mm long. Two capitula of 9 mm diameter had punctures that indicated probing by an aculeus but no eggs. There were no probing punctures found on achenes of unopened buds or heads with a receptacle diameter of less than 9 mm, although a few probing punctures were found in the phyllaries of smaller capitula (two 8-mm and one 6-mm capitula). None of the eggs had yet hatched. Thus, the few days before 13 July at the time when capitula of *S. uvedalius* first began to open and attained about 9 mm diameter, marked the very beginning of the reproductive period of *R. longirostris* at Metcalf Bottoms for the year 2001.

By 2 September 2001, the *S. uvedalius* population at Metcalf Bottoms was found to be highly senescent, i.e., fewer than 1% of all flower heads remained in bud or the flowering stage. No adult flies were observed at this time, but oviposition had occurred probably not long before, as 1st instar larvae were still to be found in developing achenes (Table 1). A notable observation at this time was the very extensive feeding damage by larvae of a *Homoeosoma* sp. (Lepidoptera: Pyralidae). Of the 14 capitula examined, 11 had been fed upon by *Homoeosoma*; seven were 90–100% consumed, and three were 33–50% consumed. Thus, it is likely that some, perhaps many, late season *R. longirostris* immature stages were eaten by larvae of *Homoeosoma* sp.

Observations on adult flies.—During 12–13 July 2000, GJS and BDS found male and female adult *R. longirostris* in abundance on *S. uvedalius* foliage and flower heads at the Metcalf Bottoms site. Plants were well developed at this site, many to 1 m or more in height, and some were in flower. A smaller number of adult *R. longirostris* was observed at Abram's Creek campground, also on *S. uvedalius,* but no adults were found at the Sugarlands site, where *S. uvedalius* was not yet in flower.

On 2 July 2001, very few or no flower buds were present at Metcalf Bottoms and Sugarlands, respectively, and no adults were observed. On 13 July 2001, one female and three males were observed at Metcalf Bottoms. One male was observed mounted on the female on the most developed flower head at this site, and a second male was facing them on the periphery of the same flower head. Therefore, courtship and mating apparently occur on the host plant, as is typical for many tephritid flies. By 2 September 2001, no adults were to be found at Metcalf Bottoms, where flowering of host plants was nearly finished. However, in other areas, such as Cades Cove and Abrams Creek campground, many plants were still in full flower, and adult *R. longirostris* were collected at Abrams Creek campground on 4 September 2001.

DISCUSSION

Based on our rearings and collections from 1996 to 2001, we conclude that *R. longirostris* is univoltine with a flight-time corresponding to the flowering period of *S. uvedalius,* i.e., July–September in the GSMNP. Local populations of *S. uvedalius* flower at somewhat different times. It remains to be determined whether the emergence and disappearance of the associated fly populations are locally synchronized with their hosts, or whether flies disperse among local host populations according to the presence/absence of capitula at an appropriate stage for oviposition. Courtship and mating occur on the host plant. Oviposition probably begins as soon as achenes of *S. uvedalius* develop to the minimum size needed to support larval development. At the beginning of the flowering season, when buds are scarce, a single achene may have several eggs oviposited; thereafter, females lay only a single egg into an achene. Only one larva develops per achene. Parasitism by hymenopteran larval-pupal parasites may be very high. Given the extreme hardness of the mature, dry achenes, hymenopteran parasites may be able to attack only during the early stages of achene development. Late in the flowering season, Lepidoptera larvae feed voraciously on capitula and probably also inflict significant mortality on immature stages of *R. longirostris.* Many achenes from the preceding year's seed crop that were found under host plants at Sugarlands appeared to have been cracked open leaving only very hard fragments. It is possible that vertebrate seed predation is another significant cause of mortality, particularly if rodents, such as squirrels or mice, or seed-feeding birds, are targeting the slightly more easily opened, protein-rich, infested achenes. By what means the adult flies escape the achene remains unknown. Dried achenes are very hard and it is difficult to imagine an adult extricating itself without a pre-thinned 'window' in place. Perhaps they rely on simple weathering from the elements to decompose the pericarp to a point where adults can eclose and escape successfully.

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IMMATURE STAGES AND BIOLOGY OF *POSTTAYGETIS PENELEA* CRAMER (LEPIDOPTERA: NYMPHALIDAE: SATYRINAE)

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Abstract.—*Posttaygetis penelea* Cramer larvae are common in bamboo understory, present year round, and can be found in a wide variety of habitats. Larvae specialize on woody bamboos within the genus *Guadua* (Poaceae), and adults are highly associated with bamboo groves. The presence of the host plant is the only important habitat requirement for this species, in that they can be found within bamboo groves in forest habitats, forest edges, and pastures. The immature stages of *P. penelea* are described and head capsules and chaetotaxy are illustrated. Both larvae and pupae possess distinct features which separate this monotypic genus from the closely related genera *Taygetis* Hübner and *Pseudodebis* Forster.

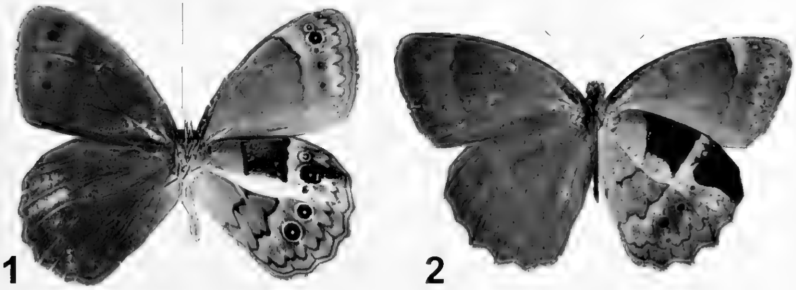
Key Words: Euptychiina, Satyrinae, *Taygetis, Pseudodebis,* bamboo, larvae, specialist, chaetotaxy

Posttaygetis Forster (1964) is a monotypic butterfly genus within the diverse satyrine subtribe Euptychiina (Nymphalidae: Satyrinae). *Posttaygetis penelea* (Cramer 1777) occurs throughout the Amazon basin to southern Brazil and was recently collected as far north as Nicaragua (Maes 1995). Individuals are normally encountered within lowland *Guadua* bamboo groves (Poaceae), although I collected a worn specimen from premontane forest (Wilson Botanical Garden, Costa Rica, elevation 1,110 m).

Posttaygetis penelea is easy to recognize by the combination of somber satyrine markings and a bright yellow band traversing the ventral hind wing (Fig. 1). This yellow band is greatly reduced or absent in the one named form, *P. penelea* var. *penelina* (Staudinger 1888), found in southern Brazil (Fig. 2). Forster (1964) provided no information on delineation of the *Posttaygetis* other than commenting that it is distinguished by structures of the male genitalia. However, larvae possess several distinctive features which separate this species from the closely related genera *Taygetis* Hübner and *Pseudodebis* Forster. These diagnostic characters, along with the immature stages, are described in this paper.

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. Appearance, behavior, and development times were noted for all stages. Larvae were preserved in 95% ethanol after being immersed in boiling water for several seconds. Vouchers are deposited in the National Museum of Natural History, Smithsonian Institution, Washington DC. Much of the work for this study was conducted in Ecuador at Jatun Sacha Biological



Figs. 1–2. Adults, dorsal view on left, ventral view on right. 1, *Posttaygetis penelea*, male, Ecuador, Napo Prov., Puerto Misahuallí. 2, *P. penelea* var. *penelina*, male, Brazil, Mato Grosso, Chapada [BNHM].

Station, Napo Province, during 1990 to 1993. 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 that site (DeVries et al. 1997).

Setal names for the head capsule follow Heinrich (1916), with modifications as incorporated by Stehr (1987). Body chaetotaxy follows Hinton (1946). More detailed information on euptychiine morphology can be found in Murray (2001). Head capsule width is measured by the distance between the third stemmata. Instar durations are given as averages of five individuals.

RESULTS

Posttaygetis penelea Cramer

Diagnosis.—*First instar:* No unique features separate species from other euptychiines other than combination of larger size, head capsule primary setae terminating in a fine point, and extremely dense pattern of ridges on head capsule surface, which extend medially to A2 (Fig. 3).

Second and third instar: White band bisecting dorsal aspect of head capsule, expanding medially; four large apical setae on head horns, P1, P2, and two secondary setae (Fig. 4–5); slender green body with white, broad dorsolateral stripe; caudal filaments projecting dorsolaterally.

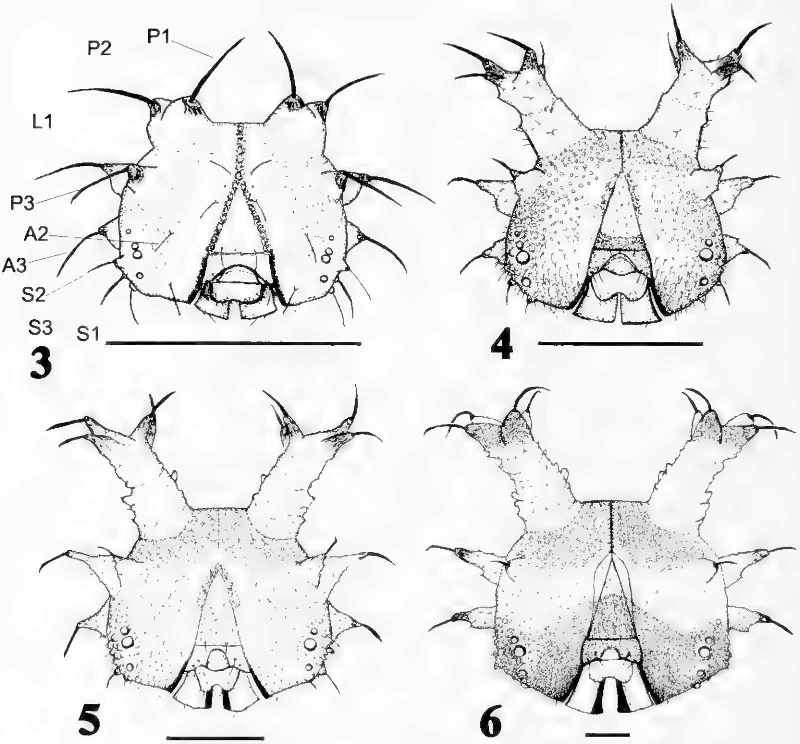
Fourth instar: White band bisecting dorsal aspect of head capsule; head horns and lateral lobe setal bases elongated; four large apical setae on head horns, P1, P2, and two secondary setae with large setal bases and long, recurved setae (Fig. 6); specialized setae bordering epicranial suture terminating at apex of adfrontal area; body with green and brown dorsolateral slashes forming broad inverted "v" in dorsal view.

Pupa: Four prominent pairs of tubercles dorsally on abdomen (Fig. 10).

Description.—*Egg:* Shiny, round, semitransparent, pale white to pale green (n = 28). Duration 6.0 days.

First instar: Head capsule 0.8 mm; black; lobe setae (P1, P2, P3, L1, and A3) long, narrow, terminating in a fine point; lobe setae basally thick but not flattened; P1 located more basal than P2; dense dendritic pattern of ridges on the head capsule integument (Fig. 3). Body shiny dark green; D1 and D2 shorter than XD1 and XD2 on prothoracic segment (Fig. 7); SD1 on T1 and A9 sensory with long, filamentous seta; D1 and D2 approximately equal on all abdominal segments except A8 and A9, where D1 larger than D2 (Fig. 8); caudal filaments short, rounded (n = 17). Duration 4.8 days.

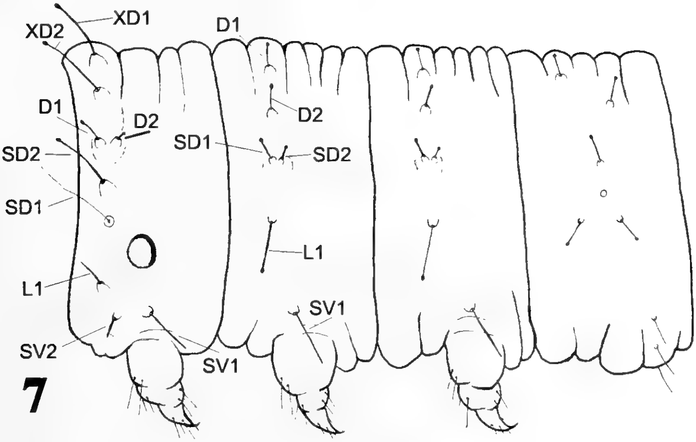
Second instar: Head capsule 1.2 mm; light brown darkening to brown one to two days after molting; head horns and lateral

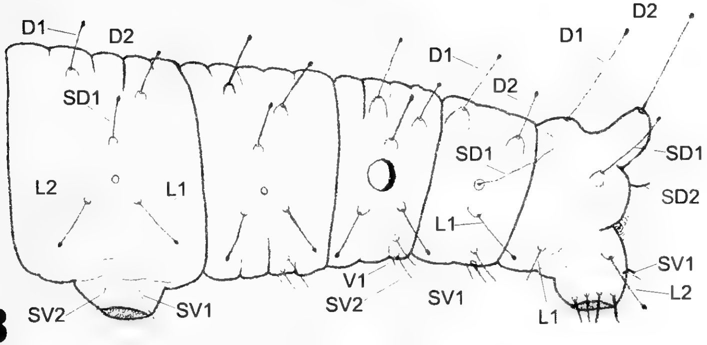


Figs. 3–6. Head capsules of *Posttaygetis penelea*, frontal view (scale = 2.0 mm). 3, First instar. 4, Second instar. 5, Third instar. 6, Fourth instar.

head capsule dark brown; apical portion of frons outlined in dark brown; lateral setal lobes white; distinctive white band extending between P3 setae, widening medially (Fig. 4); head horns large, projecting slightly anteriorly, with two large apical secondary setae in addition to P1 and P2; lobe setae long, flattened, and twisted, at least as long as sclerotized base; P3 thinner and shorter than other setae; lateral lobe setal bases white; S2 setae long, flattened, and twisted. Body bright green with bright white dorsolateral stripe; caudal filaments pink and projecting dorsolaterally; numerous secondary setae on body; primary setae indistinguishable from surrounding secondary setae except for SD1 sensory setae on T1–T3, A4, A5, and A9; integument covered with fine microgranulations (n = 14). Duration 4.9 days.

Third instar: Head capsule 1.9 mm; same as in previous instar except dark brown, basally reddish brown; head horns with white basal stripe; P3 considerably smaller than other lateral lobe setae (Fig. 5). Body dark green; median dorsal stripe faint reddish green, outlined by undulating white lines on abdomen only; dorsolateral band

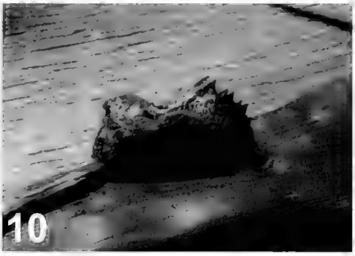




Figs. 7–8. Body chaetotaxy of first instar *Posttaygetis penelea*. 7, T1–A1. 8, A6–A10.

broad, bright white to yellow, and extending laterally on caudal filaments; thin white line laterally; caudal filaments pink apically and projecting dorsolaterally; body chaetotaxy same as previous instar (n = 18). Duration 5.0 days.

Fourth instar: Head capsule 3.1 mm; dark brown; reddish brown basally and laterally; white basal stripe; white band as in previous instar; P1 and P2 flattened, recurved, and one and a half times length of setal base; two secondary apical setae on head horns as large as P1 and P2; specialized setae bordering epicranial suture from apex of adfrontal area to head capsule base, curving over suture and criss-crossing setae on opposing side (Fig. 6). Body pale brown (Fig. 9); prothoracic shield green; dorsal median stripe on thorax rust brown outlined thinly in dark brown; dorsal median stripe on abdomen green, often fading to greenish brown as instar progresses, outlined with thin white undulating lines; green coloration extends dorsolaterally on each seg-



Figs. 9–10. *Posttaygetis penelea.* 9, Mature larva, dorsal view. 10, Pupa, lateral view.

ment, forming a broad "v" pattern in dorsal view; fine lines of brown and white laterally; black spots dorsolaterally, two per segment, on T2, T3, A1, and A9; spots variable in size and may not be present; large prominent dark brown spot laterally on A3 to A4, tapering smoothly to form a line on A5 through A6 and bordered ventrally by bright cream line; caudal filaments green; chaetotaxy of SD1 sensory setae same as previous instar; secondary setal bases on body covered in fine microgranulations; specialized setae within thoracic dorsal midline stripe, setae similar in morphology to specialized setae on head capsule, not found elsewhere on body (n = 23). Duration 8.8 days.

Pupa: Dark brown with green and pale brown markings (Fig. 10); compressed; dorsal apical point on thorax knobbed, projecting anteriorly; four prominent tubercles dorsally on abdomen (n = 12). Pupates flat against substrate. Duration 9.8 days.

Biology.—*Posttaygetis penelea* adults are encountered in and around *Guadua* bamboo groves. At Jatun Sacha, Ecuador, adults were present in all months of the year, but were never abundant (DeVries et al. 1997). All individuals trapped were from sites in forest habitats containing bamboo (n = 25). Within the bamboo groves males defend small sunlit patches but do not exhibit lekking behavior that occurs in many *Taygetis* species (Murray 2001). Females oviposit in late afternoon, usually from 4:00 until dusk, and often remain in small, localized areas to select oviposition sites.

Larvae specialize on bamboo (*Guadua* sp.). Mature larvae provided with two herbaceous bamboos (*Olyra latifolia* L. and *Pariana* sp.) and one grass species (*Orthoclada laxa* (Rich) P. Beauv.) did not feed. Eggs are laid singly on small bamboo shoots in the understory. Although bamboo groves are comprised of a substantial amount of plant biomass, most is in the canopy, with only isolated resprouts, young plants, or new growth in the understory. For butterflies restricted to understory sites, the number of oviposition sites can be limiting. There can be up to a half dozen *P. penelea* eggs on the underside of some leaf blades.

Although adults are not commonly encountered in the field, the immature stages of *P. penelea* are often easily located in suitable bamboo habitat. This species does not appear to go into reproductive diapause in the upper Napo region of Ecuador, as larvae are present year round. Systematic searches for larvae were conducted at Jatun Sacha, including bamboo groves located in forests, forest edges, and open pastures. *Posttaygetis penelea* larvae were found in all habitats and were the only euptychiine bamboo feeders found in isolated bamboo groves in pastures.

DISCUSSION

Despite the paucity of information provided by Forster (1964), several unique larval characters were found that support *Posttaygetis* as a valid genus. *Posttaygetis penelea* was originally placed within *Taygetis,* and the larvae share many morphological traits. Most notable of these traits are the retention of both P1 and P2 setae at the apex of the head horns and the enlarged primary setae on the head capsule. However, *P. penelea* differs from closely related species by the presence of two large apical secondary setae between P1 and P2 on the head horns, the distinct white or dark brown band transversing the head capsule, and the widely spaced caudal filaments, which project dorsolaterally, albeit weakly, in later instars. In the fourth instar, the distribution of specialized setae bordering the epicranial suture is also an important diagnostic character, with the setae terminating at the apex of the adfrontal suture. Other euptychiines either do not possess these setae, or the setae are found on the adfrontal area and/or frons. *Posttaygetis penelea* pupae differ from *Taygetis* and *Pseudodebis* pupae by their compressed shape and large tubercles on the abdominal dorsal surface. There are differences in ecological traits as well. Most *Taygetis* species are crepuscular and many males exhibit lekking behavior (Young 1984, Murray 2001). In contrast, *P. penelea* is diurnal and males do not form leks. Also, females of *Taygetis* bamboo specialists oviposit at dusk in the canopy, not in the understory as *P. penelea.*

There is only slight color change within each instar as the larvae develop, a trait commonly found in *Taygetis* larvae (Murray 2001). Unlike many satyrines, *P. penelea* larvae and pupae are not polymorphic. Other than the previously noted named form, *P. penelea* var. *penelina,* there is also little variation in wing pattern, which can be highly variable in related *Taygetis* species. This form is reported to occur near the southern edge of the species' distribution, but I have collected individuals from the Ecuadorian rainforest that also lack the distinctive band, although I have never reared an individual. Most likely this form is present in many *P. penelea* populations, but in low numbers.

The fact that the immature stages of *P. penelea* have not been described yet is somewhat surprising. As noted earlier, larvae are common in the bamboo understory, present year round, and can be found in a wide variety of habitats, including pasture, as long as bamboo is present. Indeed, the presence of bamboo is the only important habitat requirement, suggesting that this species is not heavily impacted by habitat disturbance. This result was also found by Singer and Ehrlich (1991) for several other specialist euptychiines.

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Alejandro Suarez and Gabriel Tapuy provided valuable assistance in collecting and rearing larvae. I also thank Gerardo Lamas, Giovanni Onore, the Organization for Tropical Studies, and Jatun Sacha Biological Station for assistance with logistics and fieldwork. David Neil identified host plants and Jon Seals translated sections of manuscripts, and these services were much appreciated. Helpful suggestions to this manuscript came from Chris Carlton, Gerardo Lamas, Lee Miller, and Dorothy Prowell. The following organizations provided invaluable support for this research project: Fundacíon Jatun Sacha, the United States Peace Corps, the Organization for Tropical Studies, and American Women in Science.

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A NEW SPECIES OF *CONASPIDIA* KONOW (HYMENOPTERA: TENTHREDINIDAE) FROM INDIA AND REVIEW OF THE INDIAN SPECIES

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Abstract.—***Conaspidia maculosa*, new species**, is described from Sikkim, India. It is the fourth species of this Asian genus known from India, the other species being *C. dubiosa* Forsius, *C. fasciatipennis* Turner, and *C. sikkimensis* Konow. The new species belongs in the *scutellaris* group of *Conaspidia* and is separated from related species in that group and the other Indian species.

Key Words: India, *Conaspidia*, sawfly, Tenthredininae

Conaspidia Konow is an exclusively eastern and southeastern Asian genus of the subfamily Tenthredininae. It is known from eastern Russia and Japan, through China to northeastern India, Myanmar, and Vietnam. The first compilation of species with a key was that by Malaise (1945), who treated eight species. In the most recent treatment, Wie and Nie (1997) recognized five groups and keyed 18 species. Here we describe a fourth species from India, the others being *C. sikkimensis* Konow 1898 (type species), *C. fasciatipennis* Turner 1919, and *C. dubiosa* Forsius 1931, all recorded from Sikkim. The genus has been characterized by Malaise (1945) and Wie and Nie (1997).

Conaspidia maculosa Smith and Saini, new species
(Figs. 1–4)

Female.—Unknown.

Male.—Length, 10.0 mm. Antenna yellow with apical 3 segments black dorsally. Head and mouthparts reddish brown with black markings as follows: postocellar area, large spot lateral to postocellar area; small spot lateral to lateral ocellus; stripes from clypeus to just above antennae between antenna and eye and between antennae, connected by a transverse stripe dorsal to antennal insertions. Thorax black with cervical sclerites laterally, dorsal half of pronotum, tegula, and parapterum reddish brown; small spots on mesonotal lateral lobe opposite mesoprescutum, on lateral margin, and on metanotum posterior to each cenchrus. Metanotum lateral to cenchri reddish brown. Abdomen orange with anterior margin of first segment, anterior margin of 2nd segment and segments 5 to apex black; apical tergum reddish brown at center. Legs orange yellow with hind tibia blackish. Forewing yellow orange with black macula at base of wing, black stripe from stigma to posterior margin at center of wing, and large black macula at apex (Fig. 3); base of costa reddish brown, all other veins and stigma black, with veins orange yellow in orange-yellow portion; hind wing uniformly clear.

Figs. 1–3. *Conaspidia maculosa.* 1, Dorsal view of head. 2, Antenna. 3, Forewing.

Antenna (Fig. 2) filiform, length 1.7× head width; scape slightly less than 2× longer than broad and longer than pedicel; pedicel slightly longer than broad; 3rd segment 1.3× longer than 4th segment. Head impunctate, shining; and broad behind eyes in dorsal view (Fig. 1); eyes slightly converging below, with lower interocular distance 1.1× eye length. Clypeus with deep emargination about half its medial length, lateral lobes narrow and rounded; labrum about 2× broader than long, anterior margin rounded; malar space nearly linear, less than half diameter of front ocellus; postocellar area about 1.2× longer than broad; genal carina present, extending to top of head but

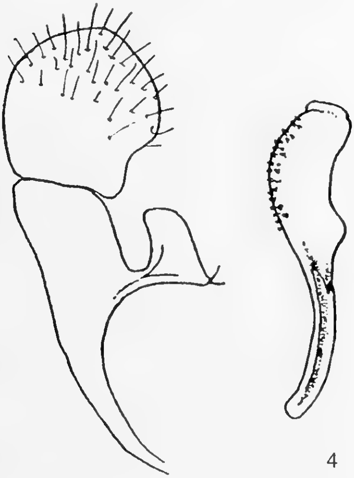

Fig. 4. Male genitalia of *Conaspidia maculosa*; ventral view of left half of genital capsule on left, lateral view of penis valve on right.

not including postocellar area. Mesoprescutum and mesonotal lateral lobes shining, with fine, widely spaced punctures; mesoscutellum in lateral view produced as a high conical projection, its height equal to length of posttergite, with deep, large punctures laterally and separating scutellum from posttergite; posttergite uniformly punctate. Punctures on mesepisternum large, close, irregular, extending to mesosternum; mesosternum not punctate, shining; mesosternal area rounded, without mesosternal postero-lateral thorn or projection. Hind basitarsus about 0.8× length of following tarsal segments combined, about equal to following three segments. Inner tooth of tarsal claw longer than outer tooth and placed lateral to it on inner side. Abdomen shining, without surface sculpture. Hind wing without peripheral vein; cells M and Rs present; anal cell petiolate, with petiole length about equal to widest width of anal cell. Genitalia in Fig. 4.

Holotype.—♂, Chungthang, Sikkim, India, May 1995, 1800 m, M.S. Saini. Deposited in the National Pusa Collections, Division of Entomology, India Agricultural Research Institute, New Delhi.

Etymology.—The species name is from the Latin *maculosus,* spotted, referring not only to the three maculae of the wings but extensive black markings on the head and body.

Discussion.—This species belongs to the *scutellaris* group of Wei and Nie (1997). The *scutellaris* group includes *C. guttata* (Matsumura 1912) from Japan, *C. kalopanacis* Xiao and Huang 1983 from China, *C. liui* Wei 1997 from China, *C. murotai* Togashi 1984 from Japan, and *C. scutellaris* Malaise 1945 from China and Myanmar. The *scutellaris* group is separated from other groups of *Conaspidia* by the strongly infuscate cross bands of the forewing with black maculae at the base and apex, the basal tooth of the left mandible small and obtuse, the scutellum strongly elevated, and the lance without a spine near the annuli (Wie and Nie 1997).

This new species will key to *C. liui* Wei from Hunan, China, in the key to species by Wie and Nie (1997), as it shares the following characters: short hind basitarsus, shorter than the following tarsal segments combined; third antennal segment longer than the fourth; hind wing of the male without a peripheral vein; head subparallel behind the eyes; maculation of the forewing; elevated mesoscutellum; small, obtuse basal tooth of the left mandible; punctures laterally on the mesoscutellum; dense, large punctures of the mesepisternum; impunctate mesosternum; and inner tooth of the tarsal claws longer than the outer tooth. The genitalia are also very similar to *C. liui* (see Wie and Nie 1997, fig. 37) though they are difficult to compare since they might not be drawn from exactly the same aspect. The new species differs from *C. liui* by the black apical segments of the antenna, black mesonotum, black mesopleuron, black anterior margins of the first and second abdominal terga, black apical segments of the abdomen, lower interocular distance slightly longer than eye length, postocellar area longer than broad, and more slender, and curved penis valve.

Very few *Conaspidia* have the inner tooth longer than the outer tooth. This occurs only in *C. liui* and *C. latifasciata* Wei 1997, the latter assigned to the *bicuspis* group.

The coloration of *C. maculosa* is very similar to *C. guttata,* but *C. guttata* has large, isolated punctures on the mesepisternum, mesosternum with dense small punctures, the inner tooth of the tarsal claws shorter than the outer tooth, and mesoscutellum lower and more convex and smoother without the large lateral and posterior punctures.

SPECIES IN INDIA

In India, *Conaspidia* is known only from Sikkim. *Conaspidia maculosa* is the only species with the basal, central, and apical maculae of the forewing. *Conaspidia sikkimensis* has only the apex of the forewing infuscated, *C. fasciatipennis* has only the central band and apical macula, and the forewing of *C. dubiosa* is uniformly yellowish. The species are included in the keys by Malaise (1945) and Wie and Nie (1997).

Conaspidia dubiosa.—Both sexes of this species were described from "Sikkim" by Forsius (1931). The forewing is uniformly yellowish, the third antennal segment is slightly shorter than the fourth segment, and the hind basitarsus is longer than the remaining tarsal segments combined. We have not seen additional specimens.

Conaspidia fasciatipennis.—This species was described from "Tong Lap, Haut Mekong" by Turner (1919). Only the female was treated by Turner (1919) and Malaise (1945); however, Wie and Nie (1997) indicated that both sexes are known. It was recorded from "Sikkim" by Wie and Nie (1997). The forewing has the central dark band and apical macula but lacks the basal macula present in *C. maculosa.* We have not seen specimens from India.

Conaspidia sikkimensis.—Konow (1898) described this species from "Sikkim." He described only the female, and only the female was included by Malaise (1945), but Wie and Nie (1997) stated that both sexes are known. Only the apex of the forewing is black. The species is figured by Malaise (1945, pl. IIb). We have seen the following specimens from India: Sikkim, Gangtok, 2200 m, 12.V.1983 (2 ♀, 6 ♂).

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TWO NEW SPECIES OF *PHYLLOPHAGA* HARRIS (COLEOPTERA: SCARABAEIDAE: MELOLONTHINAE) FROM SOUTH CENTRAL MEXICO

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Abstract.—***Phyllophaga* (*Chlaenobia*) *rzedowskiana*, new species**, is described from remnants of deciduous tropical forests at 940–1,145 m altitude at seven localities of southwestern Puebla and eastern and southeastern Morelos, México; it is included in the species group "*vexata*." ***Phyllophaga* (*Listrochelus*) *barrerana*, new species**, is described from remnants of deciduous tropical forests at 1,000–1,210 m altitude at five localities of southern State of Mexico, southeastern Morelos, and southwestern Puebla, México; it is included in the species group "*cavata*." Drawings of the head, pronotum, abdomen, tarsal claws, and genital structures are provided.

Resumen.—Se describe ***Phyllophaga* (*Chlaenobia*) *rzedowskiana* nueva especie**, procedente de los remanentes de bosques tropicales caducifolios localizados entre los 940 y 1,145 m de altitud en siete localidades del suroeste de Puebla, del este y sureste de Morelos, México; la que se agrega al grupo de especies "*vexata*." También se describe ***Phyllophaga* (*Listrochelus*) *barrerana* nueva especie**, procedente de los remanentes de bosques tropicales caducifolios ubicados entre los 1,000 y 1,210 m de altitud en cinco localidades al sur del Estado de México, el sureste de Morelos y el suroeste de Puebla, México; la cuál se incorpora al grupo de especies "*cavata*." Se incluyen ilustraciones de la cabeza, pronoto, abdomen, uñas tarsales y estructuras genitales.

Key Words: May beetles, *Phyllophaga*, taxonomy, deciduous tropical forests, México

A large area between the Mexican states of Morelos, Puebla, Guerrero, and Oaxaca (approximately 17°30′–19°N 98°–99°45′W) is known as the upper basin of the Rio Balsas. This area is especially interesting because it represents a transition between species from the tropical deciduous forests, widely extended along the lower Pacific slopes and lower basin of the Balsas River, species from the pine-oak forests located along the Neovolcanic Axis and Sierra Madre del Sur, and species from the xeric scrubs extended across the Tehuacan, Acatlán, and Huajuapan valleys.

Thirty species of the genus *Phyllophaga* Harris (*sensu lato*) have been listed from southwestern Puebla (Morón and Aragón 1997; Morón 1992, 1998; Aragón et al. 1998; Morón et al. 2000), and twenty species have been found in southeastern Morelos (Deloya and Morón 1994, 1998; Pérez-García 1999), but the adjacent areas of Guerrero and Oaxaca included in the upper basin of the Balsas River remain poorly collected.

Field work during 1999 at Puebla localities and curatorial work of some Mexican collections during 2000–2002 led to the discovery of two undescribed species of *Phyllophaga,* apparently restricted to the upper basin of the Balsas River. Below, we give descriptions of males and females of one new species of *P.* (*Chlaenobia* Blanchard), and males and females of one new species of *P.* (*Listrochelus* Blanchard).

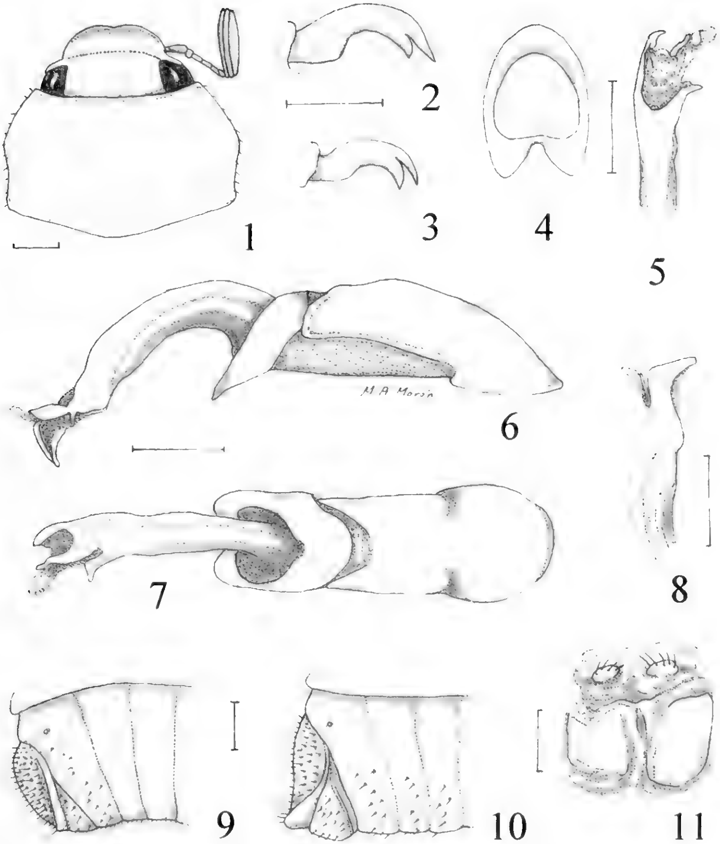
The characters and terms used in the descriptions are those of Chapin (1935), Saylor (1940), and Morón (1986, 1992). Drawings were made with the aid of a camera lucida and Zeiss stereomicroscope; measurements were obtained with an ocular micrometer or caliper.

Acronyms used in the text are as follows: CAS, California Academy of Sciences, San Francisco; CNC, Canadian National Collection, Ottawa; HAHC, Henry and Anne Howden, Canadian Museum of Nature, Ottawa; IBUNAM, Instituto de Biología, UNAM, México City; IEXA, Instituto de Ecología, Xalapa, México; MHNM, Museo de Historia Natural, México City; MXAL, private collection M.A. Morón, Xalapa, México; UNSM, University of Nebraska State Museum, Lincoln.

Phyllophaga (*Chlaenobia*) *rzedowskiana* Aragón and Morón, new species

(Figs. 1–11)

Description.—*Holotype male:* Clypeus and frons yellowish brown; pronotum shiny yellowish; elytron straw yellowish without macroscopic vestiture, glabrous; mouthparts, sterna, pygidium and legs shiny straw yellowish. Clypeus 2.5× wider than long, anterior border slightly sinuate, with elevated margin (Fig. 1), disk surface glabrous, slightly concave at sides, with many uniformly distributed, deep, rounded punctures. Frontoclypeal suture slightly sinuate and deeply impressed. Frons 2.1× wider than long, glabrous, convex, regularly and deeply punctate. Vertex without punctures. Antenna 9-segmented (Fig. 1), with 3-segmented club, lamellae 1.5× longer than length of preceeding five segments combined. Frons 3.1× wider than dorsal diameter of each eye. Eye canthus long and narrow, with 11–12 setae. Labrum bilobed, deeply sinuate, with scattered long, slender setae on borders. Mentum slightly concave, impunctate, with scarce lateral setae, anterior border slightly sinuate. Pronotum 1.6× wider than long and 2.5× wider than frons. Pronotal disk shiny, with round, moderately deep punctures, irregularly distributed; lateral borders widely angulated, lateral marginal bead with scattered, short, slender setae; basal bead strongly indicated, inclusive in front of scutellum where indicated by deep punctures; anterior angles obtuse, not prominent; posterior angles not directed downward, obtuse. Scutellum 1.2× wider than long, with small punctures irregularly distributed. Elytron 2.7× longer than wide, shiny, glabrous, densely rugo-punctate; punctures small, shallow, separated by 1–2 diameters; epipleural border progressively narrowed along complete margin, with a nearly homogeneous fringe of slender setae; humeral callus rounded, prominent; apical callus rounded. Metathoracic wings completely developed. Propygidium slightly shiny, yellowish with shallow punctuation and scattered short setae. Pygidium convex, mainly towards basal border (Fig. 9), shiny, densely punctate, with many short, erect setae on disk; apical margin with 8 long, slender setae; basal margin incomplete at middle. Pterosternum with moderately dense, long yellowish setae. Visible abdominal sternites II to IV of similar length, slightly flattened, with dense, short setae at middle; sternite V flattened, slightly longer than preceeding sternite, with short setae at middle and one row of long setae toward posterior border. Anal plate nearly as long as preceeding sternite, convex, slightly fur-



Figs. 1–11. *Phyllophaga* (*Chlaenobia*) *rzedowskiana*. 1, Male head and pronotum, dorsal view. 2, Male protarsal claw, lateral view. 3, Female protarsal claw, lateral view. 4, Parameres, distal view. 5, Apex of aedeagus, ventral view. 6, Genital capsule, right lateral view. 7, Genital capsule, dorsal view. 8, Apex of aedeagus, left lateral view. 9, Male abdomen, lateral view. 10, Female abdomen, lateral view. 11, Female genital plates, ventral view. Scale lines = 1 mm, except Figs. 2–3 = 0.5 mm.

rowed at midline, with scattered, long setae, posterior margin poorly indicated at sides. Protibia shorter than protarsus (0.53:1), with external border tridentate, proximal tooth much shortened, preapical spur narrow, nearly straight, apex acute, half as long as 2nd protarsomere. Mesotibia with one oblique, sharp, setiferous carina on external side; upper apical spur straight, narrow, and 1.1× longer than lower spur. Metatibia shorter than metatarsus (0.75:1), with one oblique, sharp, setiferous carina on external side; upper apical spur lanceolate, slightly curved, apex acute, nearly as long as basal metatarsomere, and 1.3× longer than lower spur; lower apical spur articulated with tibial border, with acute apex. Tarsomeres nearly cylindrical, elongate, with enlarged apices, with some setae apically and two lines of thick setae on ventral side. Protarsal claws narrowly cleft (Fig. 2), with lower tooth shorter than upper tooth; meso- and metatarsal claws with lower tooth slightly shorter than upper tooth. Genital capsule with short parameres (Figs. 4, 6–7), dorsally and ventrally fused, symmetrical, apex of each paramere widely rounded and directed downward. Aedeagus with sclerotized, tubelike support, and three, angled, apical projections, one of them notably largest, with apex directed downward (Figs. 5–8). Tectum enlarged, widely convex. Length of genital capsule from apex of parameres to border of basal piece: 3.7 mm. Total body length: 12.0 mm. Humeral width: 5.0 mm.

Allotype female: Similar to male except as follows: antenna with lamella of segments 7–9 slightly shorter than the length of five preceeding segments combined. Visible abdominal sternites II to V convex, with scattered setiferous punctures near middle; anal plate convex, with scattered setiferous punctures, and 6 slender setae at posterior border. Complete surface of pygidium with many erect setae; basal half convex, distal half with deep concavity at middle, with 8 slender setae along apical border (Fig. 10). Protibia with teeth of external border slightly longer than in male. Both apical spurs of metatibia articulated, wide, lanceolate and curved. Protarsus slightly longer than protibia (1.12:1). Tarsal claws similar on all legs; lower tooth slightly shorter than upper (Fig. 3). Ventral genital plates convex, poorly sclerotized, nearly symmetrical, without setae, apical borders briefly sinuated; dorsal genital plates small, with long setae on distal border (Fig. 11). Total body length: 12.1 mm. Humeral width: 5.0 mm.

Variation.—*Male:* Similar to holotype except as follows: sclerotized preapical projections of aedeagus more or less narrower or longer. Total body length: 11.8–12.3 mm; humeral width: 4.9–5.2 mm. *Female:* similar to allotype except head and pronotum light reddish brown, disc and apical border of anal plate with more or less setae. Total body length: 12.0–12.5 mm; humeral width: 5.0–5.3 mm.

Type material.—Described from 51 ♂, 54 ♀. Holotype ♂ MXAL: México: Puebla, Atencingo, Chietla, 1,145 m, 30-V-1999, A. Aragón. Allotype ♀ MXAL: same data as holotype. Paratypes CAS, CNC, HAHC, IBUNAM, IEXA, MXAL, MHNM, UNSM: México: Morelos, Emiliano Zapata, 10-VI-78, F. Cervantes (3 ♂); Huautla, 2.5 km N and 4 km W Estación CEAMISH, 940 m, 8/12-VI-1996, A. Pérez (3 ♂ 2 ♀); Huahutla, Estacion CEMISH, 2.5 km N 4 km W, 940 m, 8-12-VI-1996, luz, A. Pérez (11 ♂, 5 ♀); Zacatepec, Galeana, 28-VI-1983, C. Deloya (6 ♂ 8 ♀); same data except 27-VI-1983 (3 ♂ 6 ♀); 3-VII-1983 (1 ♂ 1 ♀); 4-VII-1983 (1 ♂); Acamilpa, Tlaltizapan, 27-VI-1983, C. Deloya (1 ♂); Jojutla, Cerro del Higuerón, 4-VII-1982, C. Deloya (1 ♂); Jojutla, 9-VIII-1983, C. Deloya (1 ♂ 1 ♀); 26-VI-1983 (1 ♂); Jojutla, Unidad Morelos, VI-1988, C. and G. Deloya (18 ♂ 30 ♀).

Type locality.—Chietla, Atencingo municipality, State of Puebla, México (approx. 18°31′N; 98°35′W).

Distribution.—Southwestern Puebla, eastern and southeastern Morelos, México (Fig. 12).

Biological Data.—Males and females of *P. rzedowskiana* were collected at white fluorescent lights and Hg lights near remnants of tropical deciduous forests, that include species of *Bursera, Pseudosmodingium, Amphipterygium. Lysiloma, Ceiba, Acacia, Ipomoea, Lemaireocereus, Cephalocereus,* and *Pachycereus* (Rzedowski 1978), surrounded by sugarcane plantations, at 940–1,145 m altitude. Phenology: May (2), June (97), July (4), August (2). Other species of *Phyllophaga* flying at the same time and place were *P.* (*Chlaenobia*) *howdeniana* Morón, *P.* (*Phyllophaga*) *bre-*

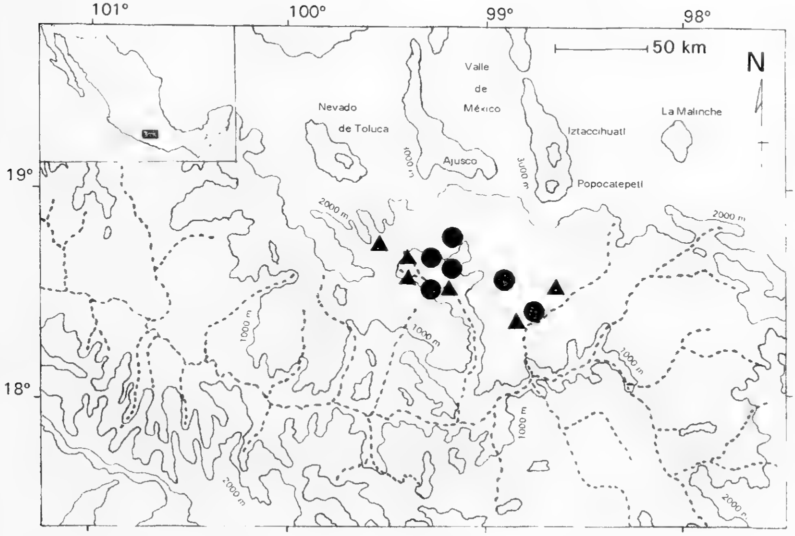


Fig. 12. Distribution of *Phyllophaga* (*C.*) *rzedowskiana* (●) and *P.* (*L.*) *barrerana* (▲) in the Upper Basin of Balsas River, México. Dotted lines represent the approximate flow of the Balsas River and its main tributaries. Map adapted from García and Falcón (1974).

videns (Bates), *P.* (*Phyllophaga*) *ilhuicaminai* Morón, and *P.* (*Listrochelus*) *barrerana*, n.sp.

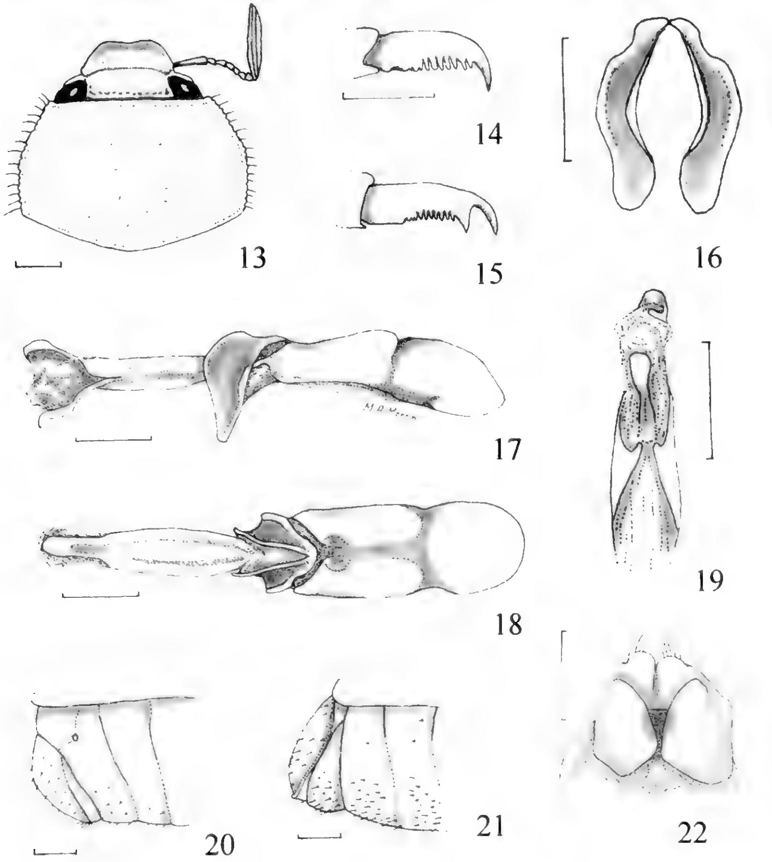
Remarks.—*Phyllophaga* (*Chlaenobia*) *rzedowskiana* belongs to the species group "*vexata*" (*sensu* Morón 1986). By body shape, size, color, general vestiture, punctuation on the clypeus, pronotum and elytra, as well as the general shape of the male genital capsule, it is similar to *P.* (*Chlaenobia*) *howdeniana* Morón. But the short parameres with rounded apex, the three irregular projections at the apex of the sclerotized support of aedeagus (see Morón 1992, figs. 8–10) and the shallow, preapical depression in the pigydium of the female, with small, rounded prominences at each side separate *P. rzedowskiana* from *P. howdeniana*.

Etymology.—This new species is dedicated to Dr. Jerzy Rzedowski, a well-known Mexican botanist, whose pioneering studies on the xeric vegetation and deciduous tropical forests from México are continuous references to scientists and students.

Phyllophaga (*Listrochelus*) *barrerana* Aragón and Morón, new species

(Figs. 13–22)

Description.—*Holotype male:* Clypeus and frons reddish brown; pronotum shiny reddish yellow; elytron straw yellowish without macroscopic vestiture, glabrous; mouthparts, sterna, pygidium and legs shiny reddish yellow. Clypeus 2.8× wider than long, anterior border brief and widely sinuate, with elevated margin (Fig. 13), disk surface glabrous, slightly concave at sides, with uniformly distributed, deep, rounded punctures. Frontoclypeal suture slightly sinuate and finely impressed. Frons 2.7× wider than long, glabrous, nearly flattened, irregularly and deeply punctate; transverse carina of vertex strongly indicated; surface



Figs. 13–22. *Phyllophaga* (*Listrochelus*) *barrerana*. 13, Male head and pronotum, dorsal view. 14, Male protarsal claw, lateral view. 15, Female protarsal claw, lateral view. 16, Parameres, distal view. 17, Genital capsule, right lateral view. 18, Genital capsule, dorsal view. 19, Apex of aedeagus, ventral view. 20, Male abdomen, lateral view. 21, Female abdomen, lateral view. 22, Female genital plates, ventral view. Scale lines = 1 mm, except fig. 14 = 0.5 mm.

behind carina with scattered, small punctures. Antenna 10-segmented (Fig. 13), with 3-segmented club, lamellae 1.4× longer than length of preceeding six segments combined. Frons 2.5× wider than dorsal diameter of each eye. Eye canthus long and narrow, with 12 setae. Labrum bilobed, widely sinuate, with scattered long, slender setae on borders. Mentum slightly concave, impunctate, with scarce lateral setae, anterior border briefly sinuate. Pronotum 1.5× wider than long and 2.6× wider than frons. Pronotal disk shiny, with round, shallow punctures, irregularly distributed, leaving an impunctate mesial strip on anterior half; lateral borders widely angulated, lateral marginal bead crenulate, with slender setae; basal bead strongly indicated, inclusive in front of scutellum where it is indicated by deep punctures; anterior angles obtuse, slightly prominent; posterior angles obtuse, widely rounded. Scutellum 1.2× wider than long, with small punctures apically. Elytron 2.4× longer than wide, shiny, glabrous, rugo-punctate; punctures small, shallow, separated by 2–4 diameters; epipleural border progressively narrowed along complete margin, with a fringe of slender setae; humeral callus rounded, prominent; apical callus rounded. Metathoracic wings completely developed. Propygidium slightly shiny, yellowish with shallow and scattered setiferous punctures. Pygidium uniformly convex (Fig. 16), shiny, with scattered, shallow punctures and short setae on disk; apical margin with 10 slender setae; basal margin incomplete at middle. Pterosternum with dense, long yellowish setae. Visible abdominal sternites II to IV of similar length, slightly flattened, with scattered, short setae near middle; sternite V flattened, slightly longer than preceeding sternite, with scarce, short setae, shallowly furrowed at midline of posterior half, and with posterior border briefly notched. Anal plate much narrowed (Fig. 16), with scattered, shallow setiferous punctures, briefly furrowed at midline. Protibia shorter than protarsus (0.51:1), with external border tridentate, proximal tooth much shortened, preapical spur narrow, nearly straight, apex acute, 0.6× as long as 2nd protarsomere. Mesotibia with one oblique, sharp, setiferous carina on external side; upper apical spur straight, narrow, as long as lower spur. Metatibia shorter than metatarsus (0.8:1), with one oblique, sharp, setiferous carina on external side; upper apical spur sinuate, apex acute, 1.4× longer than basal metatarsomere, and 1.2× longer than lower spur; lower apical spur articulated with tibial border, with acute apex. Tarsomeres nearly cylindrical, elongate, with enlarged apices, with some setae subapically, and scattered setae on ventral side. All tarsal claws irregularly unipectinate (Fig. 14). Genital capsule with short parameres (Figs. 15, 18–19), dorsally fused, symmetrical, with strong carinae along dorso-distal border and lateral border, apex of each paramere widely rounded and directed downward. Tectum with shallow, wide sulcus along midline and rounded prominences basally (Fig. 18). Aedeagus with sclerotized, tubelike support, with dorsal preapical projection, and one subapical, slightly asymmetrical sclerite (Figs. 17–19). Length of genital capsule from apex of parameres to border of basal piece: 3.8 mm. Total body length: 11.2 mm. Humeral width: 5.0 mm.

Allotype female: Similar to male except as follows: antenna with lamella of segments 8–10 0.8× longer than length of preceeding seven segments combined. Anal plate large and convex, with short setae. Pygidium moderately convex with scattered setiferous punctures (Fig. 21). Tarsal claws with acute tooth before the middle of ventral border, and posterior border unipectinate (Fig. 15). Ventral genital plates with posterior border narrowed, with rounded apex, glabrous. Dorsal genital plates with apical border widely curved, briefly notched, with erect setae at apex (Fig. 22). Total body length: 13.2 mm. Humeral width: 5.8 mm.

Variation.—Male specimen from Ixtapan de la Sal similar to holotype except as follows: pronotal and elytral punctures deeper; carinae of the parameres more elevated. Total body length in both sexes: 13.0–13.5 mm; humeral width in both sexes: 5.6–5.9 mm.

Type material.—Described from 24 ♂ 3 ♀. Holotype ♂ MXAL: México: Puebla, Tilapa, Casa Blanca, 1,210 m, 30-V-1999, A. Aragón. Allotype ♀ MXAL: México: Morelos, Acamilpa, Tlaltizapán, 27-VII-1983, C. Deloya. Paratypes CAS, CNC, HAHC, IBUNAM, IEXA, MXAL, MHNM, UNSM: same data as holotype (2 ♂); México: Puebla: Chietla, Atencingo, 1,145 m, 30-V-1999, A. Aragón (2 ♂); Estado de México, Ixtapan de la Sal, 29-V-1971, A. Barrera (1 ♂); México: Morelos: Jojutla, Unidad Morelos, VI-1988, C. and G. Deloya (1 ♂); Jojutla, 9-VIII-1983, C. Deloya (1 ♂); Zacatepec, Galeana, 28-VI-1983, C. Deloya (5 ♂); same data except 27-VI-1983 (1 ♂); Acamilpa, Tlaltizapan, 27-VII-1983, C. Deloya (10 ♂ 2 ♀).

Type locality.—Tilapa, Atencingo municipality, state of Puebla, México (aprox. 18°34′N; 98°32′W).

Distribution.—Southwestern Puebla, southern México and southeastern Morelos, México (Fig. 12).

Biological Data.—Males of *P. barrerana* were collected at white fluorescent lights near remnants of tropical deciduous forests, that include species of *Bursera, Pseudosmodingium, Amphipterygium. Lysiloma, Ceiba, Acacia, Ipomoea, Lemaireocereus, Cephalocereus,* and *Pachycereus* (Rzedowski 1978), surrounded by sugarcane plantations, or avocado and mango plantations, at 1,145–1,210 m altitude. Phenology: May (6), June (7), July (13), August (1). Other species of *Phyllophaga* flying at the same time and place were *P.* (*Chlaenobia*) *howdeniana* Morón, *P.* (*Chlaenobia*) *rzedowskiana* Aragón and Morón, *P.* (*Phyllophaga*) *brevidens* (Bates), and *P.* (*Phyllophaga*) *ilhuicaminai* Morón.

Remarks.—*Phyllophaga* (*Litrochelus*) *barrerana* belongs to the species group "*cavata*" (*sensu* Morón 1986). By body shape and size, punctuation on the clypeus, pronotum and elytra, structure of pygidium, as well as the general shape of the male genital capsule, it is similar to *P.* (*Listrochelus*) *valia* Saylor and *P.* (*L.*) *cochisa* Saylor. But the pruinose elytra with basal, erect setae; pruinose and setiferous pygidium; parameres with acute apices curved inward; and wide sclerotized support of the aedeagus with the apex abruptly narrowed, separate *P. valia* from *P. barrerana.* The male antennal club as long as the preceeding six segments combined; non-furrowed anal plate; parameres with enlarged, nearly parallel, acute apices; and narrow sclerotized support of aedeagus without apical reduction, separate *P. cochisa* from *P. barrerana.*

Etymology.—This new species is dedicated to the late Dr. Alfredo Barrera (1926–1980), well known Mexican entomologist, ethnobiologist, teacher and promoter of the biological sciences, whose publications on the taxonomy of Siphonaptera, scientific collections, natural history museums, ecology of tropical vegetation, and Mayan ethnobotanical nomenclature, are classical references.

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A REVISION OF THE NEOTROPICAL BITING MIDGES OF THE GENUS *PARADASYHELEA* INGRAM AND MACFIE (DIPTERA: CERATOPOGONIDAE)

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Abstract.—This revision of the Neotropical biting midges of the genus *Paradasyhelea* Ingram and Macfie recognizes three species of this rare genus in southern South America and includes a key for the recognition of both sexes of all Neotropical species. In addition to the previously described *P. brevipalpis* (Ingram and Macfie), which is redescribed and illustrated, two **new species** are described and illustrated: ***P. ingrami***, from Argentina, and ***P. macfiei***, from Argentina and Chile.

Resumen.—En esta revisión de las especies patagónicas del curioso género *Paradasyhelea* Ingram & Macfie, se reconocen tres especies para América del Sur, incluyéndose asimismo una clave identificatoria de todas las especies Neotropicales, para ambos sexos. Además de la especie previamente descripta *P. brevipalpis* (Ingram y Macfie), la cual es redescripta e ilustrada, se describen e ilustran dos **especies nuevas**: ***P. ingrami*** de la Argentina, y ***P. macfiei*** de la Argentina y Chile.

Key Words: Diptera, Ceratopogonidae, *Paradasyhelea,* biting midges, new species, Neotropical

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A single, very unusual biting midge that was collected by Frank W. Edwards during an expedition to Patagonia in 1926 was subsequently described as *Dasyhelea brevipalpis* by Ingram and Macfie (1931). However, Ingram and Macfie noted that "This species falls into that group of insects still included in the genus *Dasyhelea* Kieffer in which the antennal segments are not sculptured, and segments 12–14 in the male are not binodose. It differs moreover from a typical species in the genus in having small humeral pits, a rather long petiole to the median fork, a fringe on the alula, a T. R. (tarsal ratio of hind leg) less than 2, and in the peculiar form of the palp." Perhaps because this species was otherwise so different from other species of *Dasyhelea,* Macfie (1940) designated it as the type species of the new genus *Paradasyhelea,* which he included in his "*Dasyhelea* Group" in his classic paper "The genera of Ceratopogonidae."

Subsequently, Wirth and Lee (1959) assigned *Dasyhelea egregia* Macfie (1932) from New Zealand to *Paradasyhelea* Macfie when they described two new species in this genus from eastern Australia. They noted that species of *Paradasyhelea* were unique among three apparently related genera in having both radial cells obsolete, a short costa extending less than 0.5 of wing length and otherwise resembling these three genera as follows: 1) *Forcipomyia* Meigen, because of its broadly separated eyes, oblique r-m crossvein, hind tarsal ratio less than 2.0, the presence of slender hyaline sensilla on the flagellum, and the shape of the male gonostylus and parameres; 2) *Dasyhelea,* because of its 4-segmented palpus, pubescent eyes, short proboscis with vestigial mandibles, and the shape of the apicolateral processes of male genitalia; and 3) *Culicoides* Latreille, by the presence of humeral pits and sensory pits (sensilla coeloconica) on some flagellomeres and terminal flagellomere without a terminal papilla. Wirth and Blanton (1969) essentially reiterated what Wirth and Lee had said about the relationships of these four genera but noted that "*Paradasyhelea* seems to be a relict ceratopogonid of an extremely annectant type with characters cutting across three subfamily lines."

Wirth et al. (1974) were the first workers to include *Paradasyhelea* in the tribe Culicoidini of the subfamily Ceratopogoninae in their list and key of world genera. They noted that "The genera placed in the tribe Culicoidini appear to be as primitive and non-specialized as any in the family . . . We believe it is no accident that the annectant genera *Paradasyhelea* and *Austroconops* Wirth and Lee from Australia, New Zealand, and Patagonia fall here." Wirth and Lee (1959) described the pupae of two species of *Paradasyhelea,* however, Kettle and Elson (1975) first noted the nearly identical nature of pupae in that genus to those of *Culicoides.* Furthermore, when Kettle and Elson described and illustrated the larvae of *P. minuta* they noted ". . . it is clear that larvae of *P. minuta* cannot be separated from those of *Culicoides,* with which they share (1) a head ratio of about 1.5; (2) inconspicuous antennae; (3) an absence of multiple setae on the head; (4) a poorly developed ventral suture on the head; and (5) with most *Culicoides,* an absence of long perianal bristles." Subsequently, when Elson-Harris and Kettle (1985) described the adults and immature stages of their new Australian species *P. reyei,* they noted "The immatures of *P. reyei* confirm this close similarity between *Paradasyhelea* and *Culicoides.*" Elson-Harris and Kettle also listed several features of the immature stages of *Paradasyhelea* that differed from those in *Culicoides.* Perhaps a study in progress by Borkent (personal communication) on all available immature stages of Ceratopogonidae will help resolve questions of intergeneric relationships between these two genera.

Using modern phylogenetic methods involving detailed outgroup comparisons to determine polarity of character states, Borkent (1995) implied a sister group relationship between *Culicoides* and *Paradasyhelea* when he noted "The presence of a number of flagellomeres with sensilla coeloconica in at least some members of this genus may indicate that the derived condition is actually a synapomorphy of *Culicoides* + *Paradasyhelea.*" Using the same phylogenetic methods, Borkent and Grogan (1995) determined, based on the absence of palisade setae on tarsomere 1 of the hind leg in adults, that "the earliest lineage of the Ceratopogoninae are *Culicoides, Paradasyhelea* Macfie, and *Washingtonhelea* Wirth and Grogan." Finally, while the monophyly of *Paradasyhelea* has not yet been firmly established, it is the only genus in the tribe Culicoidini in which the adult females of all species have reduced, vestigial mandibles, thereby, at least making them unique within the tribe. While some species of *Culicoides* are autogenous (non-feeding) with reduced, vestigial mandibles, this is almost certainly a derived condition for these species in that genus and is not evidence of a sister group relationship of these two genera.

Currently, there are nine known species of *Paradasyhelea,* eight of which are from the southern hemisphere (Borkent and Wirth 1997): *P. albipunctata* Wirth and Lee (1959), from New South Wales, Australia; *P. boucheti* Clastrier (1989), from New

Caledonia; *P. brevipalpis* Ingram and Macfie (1931), from Argentina; *P. egregia* (Macfie) (1932), from New Zealand; *P. harrisoni* Wirth (1981), from New Zealand; *P. minuta* Wirth and Lee (1959), from New South Wales and Queensland, Australia; *P. neocaledoniensis* Clastrier (1989), from New Caledonia; and *P. reyei* Elson-Harris and Kettle (1985), from Queensland, Australia. Only one species, *P. olympiae* Wirth and Blanton (1969), is known from the northern hemisphere, but only from the original specimens that were collected on the Olympic Peninsula in Olympic National Park, Washington, USA, by Willis Wirth in 1968. However, Wirth and Blanton were not entirely confident of the generic assignment of *P. olympiae* and noted when they compared it with the then four other known species of *Paradasyhelea* that it "differs from all of them in the shape of the apicolateral processes of the ninth tergum, the aedeagus, and the median sclerite of the parameres."

A recent collecting trip to Patagonia in Argentina and Chile by GRS produced some specimens of *Paradasyhelea* that differed from those of *P. brevipalpis.* Art Borkent kindly lent us additional specimens of *Paradasyhelea* in the Canadian National Collection of Insects (CNCI) in Ottawa, Canada. In addition, GRS recently re-examined the holotype of *P. brevipalpis* in The Natural History Museum (BMNH) in London, United Kingdom. A careful examination of these specimens revealed two undescribed species that we describe and illustrate herein, we also redescribe and illustrate *P. brevipalpis* and provide a key for the recognition of all Neotropical species. Clastrier (1989) provided a key to the world species of *Paradasyhelea,* but, inexplicably, failed to include *P. egregia.*

Unless otherwise noted, all recently acquired specimens were mounted on microscope slides in Canada balsam in the manner of Wirth and Marston (1968). Types are deposited in the Museo de La Plata, Argentina (MLPA) or in the CNCI, as indicated. General terms follow those in Downes and Wirth (1981). We dedicate this article to our recently departed colleague, Dr. Larry Quate, in recognition of his important contributions to the study of primitive Diptera.

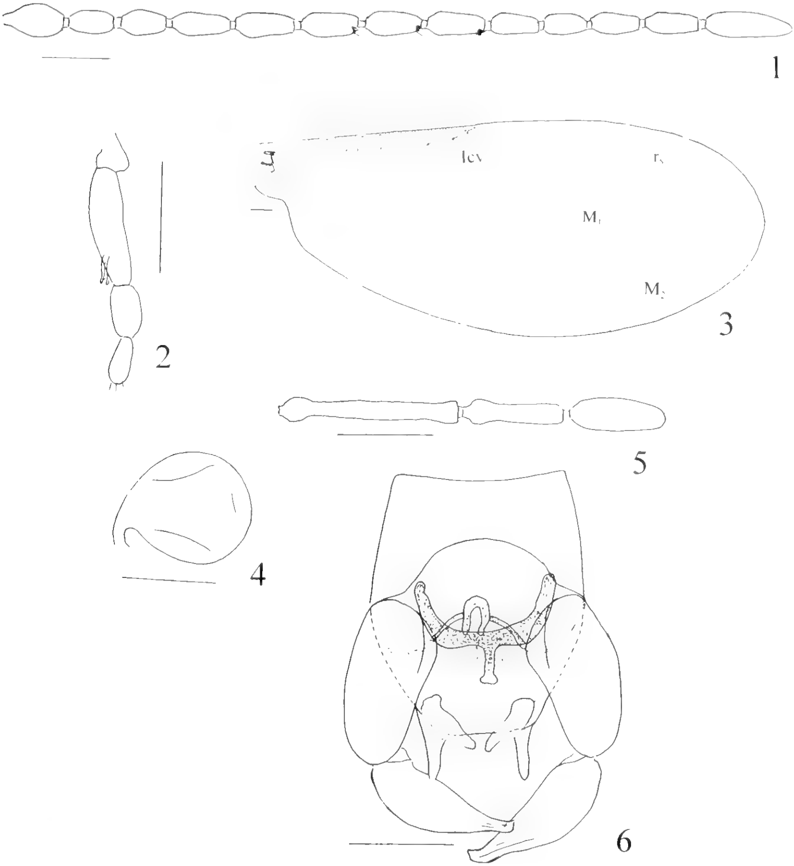
KEY TO NEOTROPICAL SPECIES OF *PARADASYHELEA*

1. Female 2
– Male 4
2. Palpus 5-segmented, third segment with capitate sensilla enclosed in a rounded pit (Fig. 14); spermatheca small, ovoid . . . . *Paradasyhelea macfiei,* n. sp.
– Palpus 4 or 5-segmented, capitate sensilla not enclosed in a pit (Figs. 2, 8); spermatheca large, retort-shaped 3
3. Palpus 5-segmented; flagellomere 9 of female unusually short and narrow, shorter than 10 (Fig. 7) . . . . *Paradasyhelea ingrami,* n. sp.
– Palpus 4-segmented; flagellomere 9 of female longer than 10 (Figs. 1, 13) . . . . *Paradasyhelea brevipalpis* (Ingram and Macfie)
4. Gonostylus abruptly narrowed at midlength (Fig. 18), nearly straight to blunt tip; distal portion of aedeagus tapering to pointed tip (Fig. 18); parameres with inverted U-shaped basal sclerite and a pair of posteriorly projecting processes (Fig. 19) . . *Paradasyhelea macfiei,* n. sp.
– Gonostylus stout, flask-shaped (Fig. 6) or progressively tapering to almost pointed tip (Fig. 12); distal portion of aedeagus with knob-like tip (Figs. 6, 12); parameres reduced to a stout inverted U-shaped sclerite (Figs. 6, 12) 5
5. Gonostylus progressively tapering to almost pointed tip; apicolateral process of male genitalia stout (Fig. 12) . . . . *Paradasyhelea ingrami,* n. sp.
– Gonostylus flask-shaped; apicolateral process of male genitalia long and slender (Fig. 6) . . *Paradasyhelea brevipalpis* (Ingram and Macfie)

Paradasyhelea brevipalpis (Ingram and Macfie)
(Figs. 1–6)

Dasyhelea brevipalpis Ingram and Macfie 1931: 178 (♂; Argentina, Lake Nahuel Huapi).

Paradasyhelea brevipalpis: Macfie 1940: 17 (comb.); Wirth 1981: 386 (in key); Spinelli 1987: 667 (♀; Argentina, Neuquén and Río Negro provinces); Spinelli and Grogan 1999: 709 (Argentina, Tierra del Fuego).



Figs. 1–6. *Paradasyhelea brevipalpis.* 1, Flagellum of female. 2, Palpus of female. 3, Wing of female. 4, Spermatheca. 5, Flagellomeres 11–13 of male. 6, Genitalia of male. Scales = 0.05 mm. Icv = Intercalary vein; M_1 = Vein M_1; M_2 = Vein M_2; r_5 = Cell r_5.

Diagnosis.—Only Neotropical species of *Paradasyhelea* with a 4-segmented palpus. Female with flagellomere 9 longer than 10; capitate sensilla of palpus not enclosed in a pit; scutellum with 9 stout setae; vein M_2 present or absent; costal ratio 0.41–0.43; spermatheca large, retort-shaped; halter brownish. Male with apicolateral process long and slender; gonostylus flask-shaped; distal portion of aedeagus with knoblike tip; parameres reduced to a stout inverted U-shaped sclerite.

Female.—*Head:* Dark brown. Eyes pubescent, separated by breadth of 2 ommatidia. Antennal flagellum (Fig. 1) brown; flagellomere 9 longer than 10; sensilla coeloconica on flagellomeres 1, 6–8, or rarely 9; scape pale, with 9–11 setae; antennal ratio 0.70 (0.65–0.75, n = 6). Palpus (Fig. 2) 4-segmented, pale; segment 2 (fused primitive 2nd & 3rd) with scattered capitate sensilla on surface of distal third. *Thorax:* Uniformly brown. Scutum with sparse vestiture of setae; scutellum with 9 stout setae in row plus 20 smaller setae. Legs brownish including tarsi, femorotibial joints darker; hind tibial comb with 4 bristles; hind tarsal ratio 1.65 (1.52–1.82, n = 6); claws short, slightly curved. Wing (Fig. 3) densely covered with mactrotrichia (as determined by their insertions, not illustrated); radial cells obliterated; vein M_2 nearly imperceptible or absent; a conspicuous, forked intercalary vein present in cell r_5; wing length 1.20 (1.10–1.32, n = 6) mm, breadth 0.50 (0.47–0.55, n = 6) mm; costal ratio 0.42 (0.41–0.43). Halter brownish. *Abdomen:* Pale brown. One retort-shaped, very heavily sclerotized spermatheca (Fig. 4) with slender oblique neck, measuring 0.070 by 0.061 mm, neck 0.008 mm.

Male.—Similar to female with usual sexual differences. Lengths of distal three flagellomeres (Fig. 5) in μm 97-56-52. Hind tarsal ratio 1.47 (1.42–1.60, n = 5). Wing length 1.10 (1.08–1.17, n = 5) mm; breadth 0.36 (0.34–0.37, n = 5) mm; costal ratio 0.45 (0.44–0.46, n = 5). Genitalia (Fig. 6): Sternite 9 with moderately deep, broad caudomedian excavation; tergite 9 moderately long, distal margin nearly straight; apicolateral process very slender, each with a minute apical seta; cercus elongated, tip truncate. Gonocoxite short, twice as long as broad with poorly developed mesobasal tubercle; gonostylus stout, flask-shaped, as long as gonocoxite, tapering abruptly on distal half, tip pointed, beaklike. Aedeagus Y-shaped; basal arms heavily sclerotized, subparallel; distal portion nearly straight with slightly expanded, knoblike tip. Parameres reduced to stout, inverted U-shaped basal sclerite; basal apodemes curved, heavily sclerotized.

Distribution.—Argentina, in subantarctic *Nothofagus* forests, from 40°S south to Tierra del Fuego.

Type.—Holotype male, Argentina, Río Negro Province, eastern end of Lake Nahuel Huapi (BMNH). Examined during the present study.

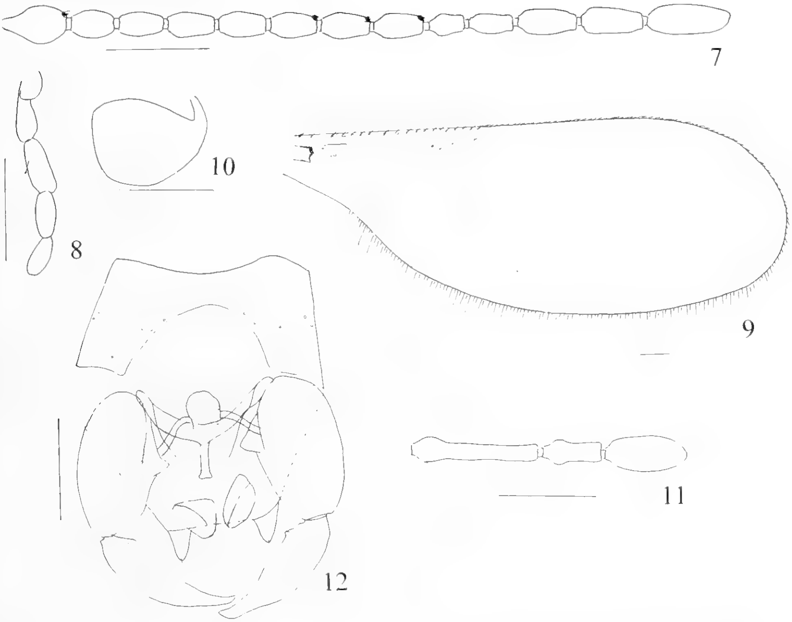
Other specimens examined.—Argentina, Neuquén, 10 km N San Martin de Los Andes, 24-XI-1984, G. Spinelli, 4 ♀, 1 ♂; Neuquén, 6–7 km S San Martin de Los Andes (900 m), 26-XI-1986, G. Spinelli, 1 ♀, 3 ♂; Neuquén, Lanin National Park, Lake Queñi, 6/8-II-1999, P. Marino, 1 ♂; Nahuel Huapi National Park, Chall-huaco, 6-XII-1992, G. Spinelli, 1 ♀, CDC light trap; Nahuel Huapi National Park, Lake Escondido, 29-XI-1984, G. Spinelli, 1 ♀; same data except 3-XII-1988, D. Añon Suárez, 2 ♂ CDC light trap; Chubut, Los Alerces National Park, lake Futalaufquen, 22-II-1994, G. Spinelli, 1 ♀, sweep net; Chubut, Los Alerces National Park, Puerto Mermoud, 23-II-1994, G. Spinelli, 1 ♀, 1 ♂, sweep net; Santa Cruz, Río Turbio, mina I, 14-I-1992, A. Estévez-J. Muzón, 2 ♀, 4 ♂, sweep net; Tierra del Fuego, lake Escondido (140 m), 2-III-1993, G. Spinelli, 1 ♀; Tierra del Fuego National Park, Lapataia, 9/10-I-1995, G. Spinelli, 6 ♀, CDC light trap.

Paradasyhelea ingrami Spinelli and Grogan, new species

(Figs. 7–12)

Diagnosis.—Only species of *Paradasyhelea* with female flagellomere 9 unusually short; palpus 5-segmented, capitate sensilla on segment 3 not enclosed in a pit; scutellum with 9 stout setae; vein M_2 absent; costal ratio 0.35; halter brownish; spermatheca large, retort-shaped; apicolateral process of male genitalia stout; gonostylus progressively tapering; distal portion of aedeagus with knoblike tip; parameres reduced to a stout inverted U-shaped basal sclerite.

Female.—*Head:* Dark brown. Eyes pubescent, separated by breadth of 2 ommatidia. Antennal flagellum (Fig. 7) brown; flagellomere 9 unusually shorter, narrower



Figs. 7–12. *Paradasyhelea ingrami.* 7, Flagellum of female. 8, Palpus of female. 9, Wing of female. 10, Spermatheca. 11, Flagellomeres 11–13 of male. 12, Genitalia of male. Scales = 0.05 mm.

than those immediately proximad, distad; sensilla coeloconica on flagellomeres 1, 6–8; scape with 7 setae; antennal ratio 0.74. Palpus (Fig. 8) 5-segmented, slightly paler than flagellum; segment 3 with few scattered capitate sensilla on mesal surface, not enclosed in a pit. *Thorax:* Uniformly brown. Scutum with sparse vestiture of setae; scutellum with 9 stout setae in a row, and 9 slender anterior setae. Legs brownish including tarsi, femorotibial joints darker; hind tibial comb with 4 bristles; hind tarsal ratio 1.60; claws short, slightly curved. Wing (Fig. 9) densely covered with mactrotrichia (as determined by their insertions, not illustrated); radial cells obliterated; vein M_2 absent; a conspicuous, forked intercalary vein present in cell r_5; wing length 0.85 mm, breadth 0.34 mm; costa very short, costal ratio 0.35. Halter brownish. *Abdomen:* Pale brown. One retort-shaped, very heavily sclerotized spermatheca (Fig. 10) with slender, curved, oblique neck, measuring 0.070 by 0.050 mm, neck 0.015 mm.

Male.—Similar to female with usual sexual differences. Lengths of distal three flagellomeres (Fig. 11) in μm 68-34-44. Hind tarsal ratio 1.60 (1.50–1.75, n = 5). Wing length 0.82 (0.74–0.88, n = 5) mm; breadth 0.28 (0.26–0.30, n = 5) mm; costal ratio 0.37 (0.36–0.38, n = 5). Genitalia (Fig. 12): Sternite 9 with deep, broad caudomedian excavation; tergite 9 large, distal margin nearly straight; apicolateral process stout, each with a minute apical seta; cercus conspicuous, tip bluntly rounded. Gonocoxite short, twice as long as broad with large blunt mesobasal tubercle; gonostylus stout, as long as gonocoxite, distal portion moderately curved, tapering distally to slender weakly pointed tip. Aedeagus Y-shaped; basal arch heavily sclerotized; distal portion nearly straight with slightly expanded, knob-like tip. Parameres reduced to a stout, inverted U-shaped basal sclerite, basal apodemes curved, heavily sclerotized.

Distribution.—Argentina (Chubut and Río Negro provinces).

Types.—Holotype ♂, Argentina, Río Negro, Somuncurá plateau, Chipauquil, 27-XI-1995, G. Spinelli, sweep net (MLPA). Paratypes, 1 ♀, 7 ♂ (MLPA), as follows: Argentina, Río Negro, Somuncurá plateau, Estancia El Rincón, 29-XI-1995, G. Spinelli, 1 ♀ (allotype), sweep net; same data, 1 ♂, CDC light trap; same data, 1 ♂, Malaise trap; Chubut, Sierra Cuadrada plateau, Estancia Don Eduardo, 1–2-XII-1996, G. Spinelli, 5 ♂, Malaise trap.

Etymology.—We are pleased to name this new species in honor of the late Alexander Ingram in recognition of his pioneering publication on Patagonian biting midges that he co-authored with J. W. S. Macfie (Ingram and Macfie 1931).

Discussion.—This is the only Patagonian species inhabiting steppe areas, which are located as far as 350 km from the *Nothofagus* forests.

Paradasyhelea ingrami resembles *P. brevipalpis* by virtue of the large, retort-shaped spermatheca, the distal portion of aedeagus with knoblike tip, and parameres reduced to a stout inverted U-shaped sclerite. However, it clearly differs from *P. brevipalpis* by its 5-segmented palpus, much shorter costa, flagellomere 9 unusually shorter and narrower than those immediately proximad and distad, the gonostylus progressively tapering to weakly pointed tip, and the stouter apicolateral process of the male genitalia. This new species keys to near couplets 5a (*P. boucheti*) and 5b (*P. brevipalpis*) in the world key by Clastrier (1989), but both of these species differ from *P. ingrami* in having 4-segmented palpi.

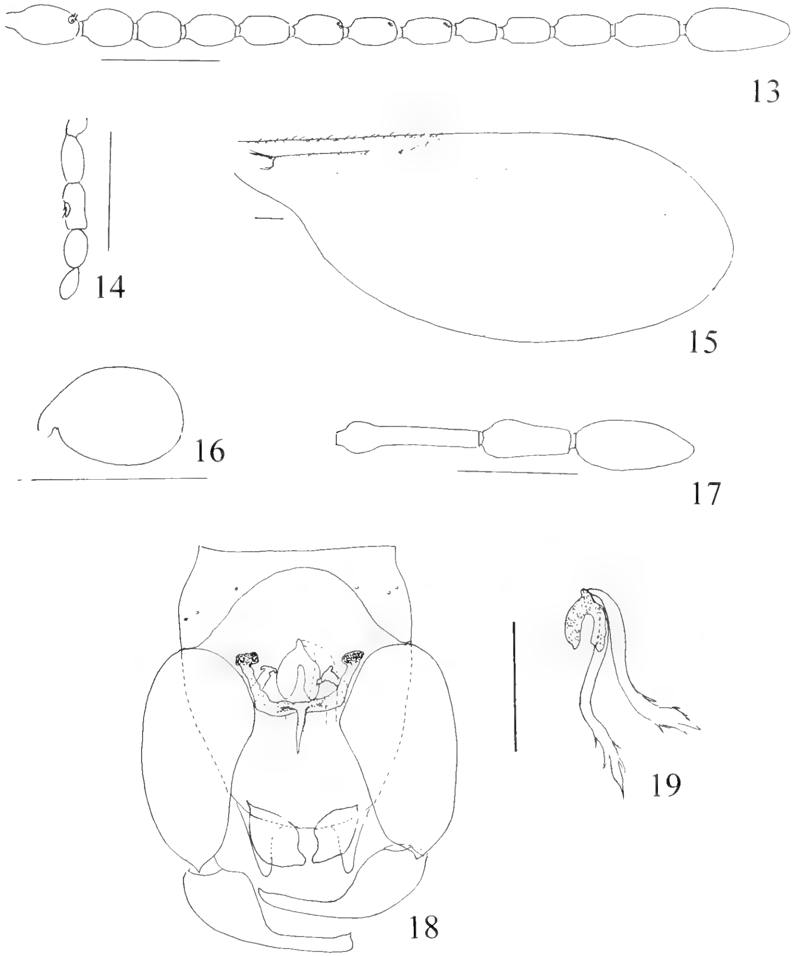
Two females collected from a forested area in the western portion of the Argentinean province of Neuquén (15 km E Caviahue, 13-XI-1994, G. Spinelli, 2 females, sweep net, (MLPA) are very similar to this species, apparently differing only by their more broadly separated eyes (by width of 4–5 ommatidia). Because of this difference in these two specimens and also because no males were found associated with them, we do not consider them as members of *P. ingrami* and, therefore, have not designated them as paratypes.

Paradasyhelea macfiei Spinelli and Grogan, new species

(Figs. 13–19)

Diagnosis.—Only species of *Paradasyhelea* with palpus 5-segmented, segment 3 with capitate sensilla enclosed in a rounded pit; vein M2 absent; halter whitish; spermatheca small, ovoid; gonostylus abruptly narrowed at midlength, nearly straight to blunt tip; distal portion of aedeagus tapering to pointed tip; parameres with inverted U-shaped basal sclerite and pair of posteriorly projecting processes.

Female.—*Head:* Dark brown. Eyes pubescent, separated by breadth of 2 ommatidia. Antennal flagellum (Fig. 13) brown; flagellomere 9 subequal to or slightly shorter than those immediately proximad, distad; sensilla coeloconica on flagellomere 1 very inconspicuous, these sensilla may be present or absent on flagellomeres 6–9; scape with 7 setae; antennal ratio 0.71 (0.68–0.75, n = 5). Palpus (Fig. 14) 5-segmented, slightly paler than flagellum; segment 3 with a rounded, shallow sensory pit bearing capitate sensilla. *Thorax:* Uniformly brown. Scutum with sparse vestiture of setae; scutellum not in position to count number of setae. Legs brownish including tarsi, femorotibial joints darker; hind tibial comb with 4 bristles; hind tarsal ratio 1.72 (1.68–1.82, n = 5); claws short, slightly curved. Wing (Fig. 15) densely covered with mactrotrichia (as determined by their insertions, not illustrated); radial cells obliterated; vein M_2 absent; a conspicuous forked intercalary



Figs. 13–19. *Paradasyhelea macfiei*. 13, Flagellum of female. 14, Palpus of female. 15, Wing of female. 16, Spermatheca. 17, Flagellomeres 11–13 of male. 18, Genitalia of male, parameres removed. 19, parameres. Scales = 0.05 mm.

vein present in cell r_5; wing length 0.80 (0.70–0.92, n = 5) mm, breadth 0.37 (0.32–0.42, n = 5) mm; costa short, costal ratio 0.36 (0.35–0.38, n = 5). Halter whitish. *Abdomen:* Pale brown. One small ovoid spermatheca (Fig. 16) with oblique neck, measuring 0.036 by 0.029 mm, neck 0.007 mm (n = 2).

Male.—Similar to female with usual sexual differences. Lengths of distal three flagellomeres (Fig. 17) in µm 54-35-46. Scutellum with 7 stout setae in row, 7 slender, more anterior setae. Hind tarsal ratio 1.70 (1.65–1.75, n = 5). Wing length 0.82 (0.77–0.86, n = 5) mm; breadth 0.32 (0.30–0.33, n = 5) mm; costal ratio 0.37 (0.36–0.39, n = 5). Genitalia (Figs. 18–19): Sternite 9 with very deep, broad caudomedian excavation; tergite 9 moderately long, distal margin nearly straight; apicolateral process long, slender, with minute apical seta; cercus conspicuous, conical, somewhat pointed at tip. Gonocoxite twice as long as broad with weakly developed mesobasal tubercle; gonostylus nearly as long as gonocoxite, stout at base, abruptly narrowed at midlength, nearly straight to bluntly rounded tip with ventral point. Aedeagus Y-shaped; basal arch heavily sclerotized, distal portion tapering to slender pointed tip. Parameres (Fig. 19) with inverted U-shaped basal apodemes heavily sclerotized and pair of posteriorly projecting processes arising basally at basal sclerite, distal half of each process bent ventrally, expanded apically with lateral tooth-like projections, tip pointed.

Distribution.—In subantarctic forests of Argentina (west of Chubut and Río Negro) and Chile.

Types.—Holotype ♂, Chile, Cautín (1150 m), Conguillio National Park, 4/5-II-1988, L. Masner (CNCI). Paratypes, 12 ♀, 8 ♂, as follows: same data as holotype, 12 ♀, 3 ♂ (CNCI); Chile, Llanquihue, 3 km N Ensenada, 4-XII-1994, L. Quate, 2 ♂, Malaise trap (MLPA); Argentina, Nahuel Huapi National Park, Chall-huaco, 6-XII-1992, G. Spinelli, 1 ♂, sweep net (MLPA); Argentina, Chubut, Los Alerces National Park, 9/12-XII-1994, L. Quate, 1 ♂, Malaise trap (MLPA); Neuquén, Laguna Epulafquen, 21/23-II-2001, G. Spinelli, 1 ♂, Malaise trap.

Etymology.—We are pleased to name this new species in honor of John William Scott Macfie in recognition of his pioneering paper on Patagonian biting midges that he co-authored with A. Macfie (Ingram and Macfie 1931) and his proposal of the genus *Paradasyhelea* (Macfie 1940).

Discussion.—This is the only species in the genus *Paradasyhelea* in which the males have a pair of posteriorly projecting processes arising from the basal sclerites of the parameres. This new species keys to near couplets 5a (*P. boucheti*) and 5b (*P. brevipalpis*) in the world key by Clastrier (1989), but both of these species differ from *P. macfiei* in having 4-segmented palpi.

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CHECKLIST OF THE TREEHOPPERS (HEMIPTERA: MEMBRACIDAE) OF GREAT SMOKY MOUNTAINS NATIONAL PARK

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Abstract.—This checklist of treehoppers (Hemiptera: Membracidae) from Great Smoky Mountains National Park documents a total of 53 species in 25 genera, based on examination of museum specimens and 3 collecting trips in association with the All Taxa Biodiversity Inventory (ATBI). The park's treehopper fauna represents roughly half of the treehopper species reported from North Carolina. Twenty-four new county records are given for North Carolina species. Moreover, 28 species are new state records (= first published records) for Tennessee, increasing its known treehopper fauna to 51 species (all listed herein). Fifty-two species are apparently new records for GSMNP. Cades Cove, an expansive meadow region in the western portion of the park, is especially species rich with 35 species, many of which feed on oaks.

Key Words: Membracidae, treehoppers, Great Smoky Mountains National Park, Smokies, ATBI, Tennessee, North Carolina, host plants

Great Smoky Mountains National Park (GSMNP), located in the Southern Appalachian Mountains, is among the most species-rich temperate environments in the world (Pedersen 1999, Brown 2000, Sharkey 2001). The park straddles the North Carolina–Tennessee border, occupying portions of five counties: Haywood and Swain in North Carolina and Blount, Cocke, and Sevier in Tennessee. It ranges in elevation from 256 m to 2,025 m (Clingmans Dome). Although certainly diverse, the precise numbers and kinds of organisms within the park, especially invertebrates, are largely undocumented (Pedersen 1999, Sharkey 2001). Additionally, the diversity of the park is threatened by invasive animals, plants, and diseases (Pederson 1999, Brown 2000, Sharkey 2001). The All Taxa Biodiversity Inventory (ATBI) was created to address this lack of knowledge of native fauna. Its major goal is to document every living organism in the park to provide a benchmark of the biodiversity prior to invasion by non-indigenous organisms (Sharkey 2001). The following checklist represents the first attempt to document the species richness of treehoppers within Great Smoky Mountains National Park.

Treehoppers, known for their interesting shapes (Figs. 1–6) and behaviors, are herbivorous insects common in the eastern deciduous forest (Dietrich et al. 1999) and other biomes worldwide (Wood 1993). Extensive research has been published on the systematics, taxonomy, and biology of the

Figs. 1–6. Representative treehoppers of Great Smoky Mountains National Park. 1, *Cyrtolobus fenestratus*. 2, *Atymna querci*. 3, *Telamona collina*. 4, *Entylia carinata*. 5, *Archasia belfragei*. 6, *Thelia bimaculata*. With the exception of *T. bimaculata*, all the above species are new state records for Tennessee. *C. fenestratus* (♀ shown), *A. querci* (♂), and *T. bimaculata* (♂) are sexually dimorphic in coloration. Photographs by M. S. Wallace and L. L. Deitz.

New World treehoppers (Kopp and Yonke 1973a–c, 1974; Deitz 1975; Deitz and Kopp 1987; Deitz 1989; Deitz and Dietrich 1993; Wood 1993; McKamey 1998; Dietrich et al. 2001). Numerous eastern North American treehoppers feed on various species in the family Fagaceae, especially oaks (*Quercus* spp.).

North Carolina's treehopper fauna is relatively rich and well known, with at least

Table 1. Collecting sites within Great Smoky Mountains National Park. Some locality records are incomplete because data labels were imprecise.

Sites H-1 to H-11, North Carolina, Haywood County, GSMNP	
H-1.	Cataloochee, grass field
H-2.	Cataloochee, Beach Grove School
H-3.	Cataloochee, Palmer Chapel
H-4.	Cataloochee, head of Rough Fork Ridge Trail
H-5.	Cataloochee, head of Big Fork Ridge Trail
H-6.	Chestnut Branch, 1 mi. upstream Ranger Station
H-7.	Cataloochee Creek, at USGS Gaging Station
H-8.	Cataloochee, elevation 853 m
H-9.	Harmon den, Pigeon River
H-10.	Sterling [=Mt. Sterling?]
H-11.	Cataloochee, Cataloochee Watershed, N35°35′10.50″ W83°04′53.61″, elevation 1382 m
SW-1 to SW-18, North Carolina, Swain County, GSMNP	
SW-1.	Hwy-441 at Smokemont Campground, N35°33.14′ W83°18.50′, elevation 701 m
SW-2.	Beetree Ridge, Thomas Divide Tr., 0.1 mi. S of Newfound Gap Rd.
SW-3.	Hwy-441 at Tow String Road, N35°32.37′ W83°17.73′, elevation 701 m
SW-4.	Hwy-441, 3.1 mi SE of NC/TN state line
SW-5.	Hwy-441, 7.3 mi. SE of NC/TN state line
SW-6.	Hwy-441 at Collins Creek Picnic Area, elevation 732 m
SW-7.	Clingmans Creek
SW-8.	nr. Shuckstack
SW-9.	nr. bunkhouse at Hazel Creek
SW-10.	Clingmans Dome
SW-11.	Bone Valley Creek
SW-12.	Mingus Creek (approx. 0.5 mi. N of Oconaluftee Visitors Center)
SW-13.	Big Cove Road, Malaise Trap Site #1, N35°31.15′ W83°17.77′
SW-14.	Big Cove Road, Malaise Trap Site #2, N35°31.12′ W83°17.45′
SW-15.	Big Cove Road, Malaise Trap Site #3, N35°30.76′ W83°17.89′
SW-16.	Big Cove Road, Malaise Trap Site #4, N35°30.64′ W83°17.87′
SW-17.	Andrews Bald, Noland Watershed, N35°32′19.77″ W83°29′39.02″, elevation 1757 m
SW-18.	Clingmans Dome, Noland Watershed, N35°33′37.14″ W83°29′43.40″, elevation 1944 m
Sites B-1 to B-22, Tennessee, Blount County, GSMNP	
B-1.	Cades Cove, N old field
B-2.	Cades Cove, Methodist Church, N35°36.44′ W83°48.99′, elevation 549 m
B-3.	Cades Cove, Primitive Baptist Church, N35°36.14′ W83°48.82′, elevation 549 m
B-4.	Cades Cove, Hyatt Road, N35°36.28′ W83°49.36′, elevation 533 m
B-5.	Cades Cove, Missionary Baptist Church, N35°36.43′ W83°49.63′, elevation 573 m
B-6.	Cades Cove, Loop Road, near entry donation box, N35°36.45′ W83°47.22′, elevation 561 m
B-7.	Cades Cove, Sparks Lane
B-8.	Cades Cove, E of Cooper Road Trail, N35°36.30′ W83°50.07′, elevation 564 m
B-9.	Cades Cove Campground, N35°86.17′ W83°46.44′, elevation 573 m
B-10.	Cades Cove
B-11.	Cades Cove, Gregory Place
B-12.	Cades Cove, W of John Oliver Place, N35°36.34′ W83°47.88′, elevation 549 m
B-13.	Cades Cove, Abrams Creek
B-14.	Cades Cove, 0.3 km E of Primitive Baptist Church
B-15	Cades Cove West
B-16	Cades Cove, Cable Mill Visitor Center, N35°35.28′ W83°50.52′, elevation 536 m
B-17.	Foothills Parkway, N Look Rock
B-18.	along Lynn Camp Prong, elevation 649 m
B-19.	Rich Mountain Trail/Road
B-20.	Cades Cove, Abrams Watershed, N35°35′31.05″ W83°50′16.94″, elevation 520 m
B-21.	Cades Cove, N35.60° W83.78°, elevation 576 m
B-22.	Tremont Env[ironmental] Sta[tion]

Table 1. Continued.

Sites C-1 to C-5, Tennessee, Cocke County, GSMNP	
C-1.	Albright Grove, Indian Camp Watershed, N35°43′59.76″ W83°16′50.23″, elevation 1034 m
C-2.	Snakeden Ridge, Cosby Watershed, N35°44′36.23″ W83°13′11.99″, elevation 993 m
C-3.	Cosby Ranger Station, N35.78° W83.21°, elevation 533 m
C-4.	Sutton Ridge Overlook, Mt. Cammerer
C-5.	Cosby
Sites SE-1 to SE-16, Tennessee, Sevier County, GSMNP	
SE-1.	Sugarlands Visitor Center, elevation 488 m
SE-2.	Park Headquarters
SE-3.	Mount LeConte
SE-4.	Twin Creeks Natural Resources Center, N35°41′05.97″ W83°29′56.61″, elevation 594 m
SE-5.	Greenbrier [=Greenbriar Pinnacle?]
SE-6.	Mid. Prong Little Pigeon River, nr. Park Boundary, elevation 419 m
SE-7.	Grotto Falls trailhead, N35°40′ W83°28′, elevation 687 m
SE-8.	Little River Road, 3.1 mi. SW of Visitors Center
SE-9.	Baskins Creek Trail
SE-10.	Hwy-441
SE-11.	Brushy Mountain, Middle Prong Little Pigeon Watershed, N35°40′35.64″ W83°25′50.89″, elevation 1467 m
SE-12.	Goshen Prong, East Prong Little Pigeon Watershed, N35°36′38.22″ W83°32′33.77″, elevation 895 m
SE-13.	Indian Gap, West Prong Little Pigeon Watershed, N35°36′39.00″ W83°26′37.44″, elevation 1672 m
SE-14.	Foothills Parkway, Wears Valley
SE-15.	Elkmont
SE-16.	nr. Gatlinburg

89 confirmed species and another 13 species reported but not confirmed by voucher material (Dietrich et al. 1999). By comparison, Tennessee's fauna is poorly documented with only 23 membracid species reported in the literature (Lawson 1922; Funkhouser 1927; Ball 1931; Meyer 1937; Metcalf and Wade 1965; Kopp and Yonke 1973a–c, 1974 [distribution maps])—of which only two species were listed with specific locality data (Meyer 1937).

With the exception of *Helonica excelsa* (Fairmaire 1846) (Wallace and Deitz 1999), we have found no published records of treehoppers from GSMNP, although numerous identified specimens were present in the park's collection. Whittaker (1952) listed the number of specimens (but not species) he collected from the family Membracidae in his study of foliar insects of GSMNP. The objectives of the present project were to investigate the species richness of treehoppers in the park and to provide an authoritative checklist of the known species.

MATERIALS AND METHODS

The treehopper species records listed in the Results and Discussion section are based on specimens in the following collections: the North Carolina State University Insect Collection (NCSU), Raleigh; Museum Collection of Great Smoky Mountains National Park (GSNP [= GSMNP Collection]), Gatlinburg, Tennessee; Department of Zoology and Entomology Collection, University of Tennessee (ECUT), Knoxville; and the National Museum of Natural History (USNM), Smithsonian Institution, Washington, D.C. (collection codons follow Arnett et al. 1993). Many specimens deposited at GSNP were collected by Dmitri Novikov who surveyed the park's treehoppers in 1995. Also, some specimens were collected at UV-lights, Malaise traps,

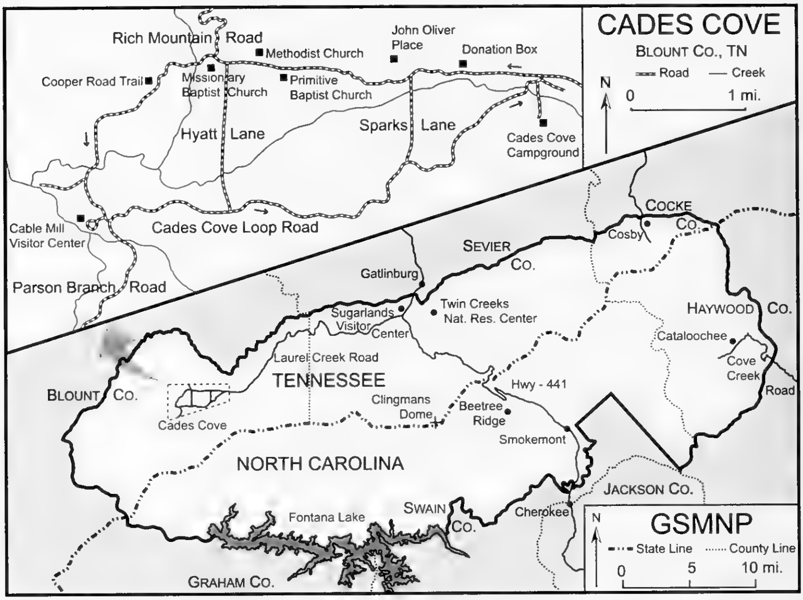

Fig. 7. Diagrammatic map of Great Smoky Mountains National Park showing state and county borders, with selected details of Cades Cove. Delineated by K. H. Spieler.

or insecticidal fogging of *Quercus rubra* L. Most of the specimens deposited at NCSU are from recent collecting by the authors in May 1999, June 2000, and October 2001 in association with the ATBI. A majority of our specimens were collected by sweeping and beating foliage and branches using sweep nets and by hand picking. No attempt has been made to compare the effectiveness of various collecting methods.

Species records are based on adult and nymphal specimens and are organized alphabetically by genus and species. For each species, localities from which the specimens were collected are listed, organized by state, county, and the site codes listed in Table 1. Site descriptions were compiled from specimen labels and major sites are indicated in Fig. 7 (sites from some early specimens were too imprecise to map). In a few instances, data not explicitly stated on the labels, such as "Malaise trap," is indicated in square brackets by the authors if known. Data on the date(s) of collection, sex, host plant(s), and site of deposition (collection) are listed for each site record when available. Host plant nomenclature is based on Dietrich et al. (1999: see host index, pp. 258–261) who listed the common and scientific names for hosts of North Carolina treehoppers and on Radford et al. (1968). Hosts from which both nymphs and adults are reported are likely true hosts; hosts from which only adults are known are less certain. The sex could not be determined for a number of specimens with broken or parasitoid-damaged abdomens. Metcalf and Wade (1965), Kopp and Yonke (1973a–c, 1974), McKamey (1998), and Dietrich et al. (1999) were used to verify nomenclature, check synonymies, and identify new state and county records. The photographs of live treehoppers (Figs. 1–6) were made using an MTI® DC330E digital video camera, Image Pro Plus® version 3.0, and Adobe Photoshop® version 5.0. The term "new record" is used here in the sense of "the first published record" rather than the "first occurrence" or "first collection" of a species. Undoubtedly, most of the species listed here have flourished in the park for a very long time.

Results and Discussion

Our examination of museum specimens and three seasons of collecting in association with the ATBI produced a total of 53 species in 25 genera from the park. These records represent 60% of the treehopper species known (at least 89) in North Carolina (Dietrich et al. 1999). None represented new species records for the state, but 24 species are noted as new county records for North Carolina. Twenty-eight species are noted as new state records for Tennessee. A total of 51 treehoppers are now recorded for Tennessee, 47 given in the checklist below and 4 others not yet found in the park: *Cyrtolobus fuliginosus* (Emmons 1854), *Heliria mexicana* Stål 1869, *Stictocephala taurina* (Fitch 1856), and *Tortistilus trilineatus* (Funkhouser 1918) (Funkhouser 1927, Ball 1931, Kopp and Yonke 1973a–c). All records from Blount, Cocke, and Sevier Counties, Tennessee, appear to be the first published records for these counties (not individually noted as new county records in the checklist). Of the 53 treehoppers listed below, 52 are apparently the first published records for GSMNP. *Helonica excelsa*, previously recorded from the park (Wallace and Deitz 1999), is not yet known from North Carolina.

Treehoppers are known from 72 sites in the park (Table 1, Fig. 7), notably Cades Cove (TN: Blount County), Cataloochee (NC: Haywood Co.), Cosby (TN: Cocke Co.), and several sites off Hwy-441 (NC: Swain and TN: Sevier counties), including Smokemont Campground (NC: Swain Co.). Thirty-five species were collected from sites within Cades Cove, toward the park's western border (12 of these species have yet to be collected elsewhere in the park).

Although the genera *Entylia* Germar, *Micrutalis* Fowler, and *Publilia* Stål were collected primarily from herbaceous plants, 13 treehopper genera were collected from various oak species. Nearly half of the North Carolina treehopper fauna are known to feed on plants within the Fagaceae, especially oaks (Dietrich et al. 1999). Based on our collecting in the eastern United States, *Cyrtolobus* Goding (represented by 9 species in this checklist), *Ophiderma* Fairmaire, *Smilia* Germar, and *Xantholobus* Van Duzee feed exclusively on oaks (Dietrich et al. 1999, MJR unpublished observations). Although Wood (1993) reported that *Platycotis vittata* (Fabricius) is also restricted to oaks, MJR has collected populations, including nymphal aggregations, on *Betula*, *Castanea*, *Fagus*, and *Platanus*.

Cades Cove (Fig. 7) is an ideal habitat for treehoppers because much of its area is open grassland with oaks occurring singly in open fields, along roadsides, in association with restored historic structures, and at the edge of open fields and forests. Treehoppers are thought to show positive phototaxis on their host plants (Johnson and Freytag 1997) and thus are often collected towards the tips of branches or on other areas of the plant exposed to sunlight.

Most treehoppers were collected from branches and foliage well within the reach of ordinary collecting nets. Attempts to collect from areas of continuous forest were limited due to the height of the foliage in these areas. Thus, the relative distribution and numbers of treehoppers listed in this study, especially the many species collected in Cades Cove, are likely proportional to the intensity of our collecting efforts in particular areas. Indeed, in an early study of foliar insects of the Smokies, Whittaker (1952) collected 21 membracid specimens (unidentified) from various habitats in the park including "cove forest, oak-chestnut forest, heath bald, pine forest, spruce forest, and pine heath." Johnson and Freytag (1997), using sticky traps, found treehoppers to be most commonly associated with the top and middle levels of pin oak canopies in Kentucky. Therefore, the potential for discovering more species in various habitats within the park and at higher levels within the various host plants is appreciable. Notably, species such as *Archasia auriculata* (Fitch 1851), *Cyrtolobus tuberosus* (Fairmaire 1846), *Ophiderma grisea* Woodruff 1919, and *Telamona extrema* Ball 1903 are not reported in Tennessee or GSMNP, yet they occur commonly in neighboring states (Kopp and Yonke 1973a–c, 1974; Dietrich et al. 1999) and thus are likely to occur in the park.

CHECKLIST OF THE TREEHOPPERS OF GREAT SMOKY MOUNTAINS NATIONAL PARK

Acutalis tartarea (Say 1830). TN: Blount County.: Site B-1 (see Table 1): 11 July 1995, 3 ♀, 2 ♂ (GSNP). Sevier Co.: Site SE-1: 27 Sept. 1982, 1 ♀ (GSNP). Site SE-16: 25 June 1947, 1 ♀, on *Erigeron* sp. (NCSU).

Archasia belfragei Stål 1869. Fig. 5. TN (NEW STATE RECORD): Blount Co.: Site B-2: 28 May 1999, 3 ♀, 1 ♂, on *Quercus alba* L. and *Q. falcata* Michaux (NCSU). Site B-3: 28 May 1999, 2 ♀, 1 ♂, on *Q. alba* (NCSU). Site B-4: 15 June 2000, 2 ♂, 1 ♀, on *Platanus occidentalis* L. and *Robinia pseudoacacia* L. (GSNP, NCSU). Site B-21: 20 May 2001, 1 ♀ (GSNP).

Atymna castaneae (Fitch 1851). NC: Swain Co.: Site SW-10: 21 June 1941, 1 ♂ (USNM). TN (NEW STATE RECORD): Blount Co.: Site B-19: 15 May 1995, 3 nymphs, on *Castanea dentata* (Marshall) Borkh.; 8 June 1995, 7 ♀, 16 ♂, on *C. dentata*; 7 July 1995, 1 ♀ (GSNP).

Atymna querci (Fitch 1851). Fig. 2. NC: Swain Co. (NEW COUNTY RECORD): Site SW-1: 14 June 2000, 1 ♀, on *Quercus* sp. (NCSU). Site SW-14: 19–26 May 2001, 2 ♀, [Malaise trap] (GSNP). Site SW-17: 3–17 July 2001, 1 ♀, [Malaise trap] (GSNP). TN (NEW STATE RECORD): Blount Co.: Site B-5: 15 June 2000, 1 ♀, on *Q. stellata* Wangenh. (NCSU). Site B-8: 15 June 2000, 1 ♀, on *Q. alba* (NCSU). Site B-10: 14 June 1995, 4 ♀, on *Q. alba* (GSNP). Cocke Co.: Site C-3: 16 May 2001, 1 ♀ (GSNP); 17 May 2001, 1 ♂ (GSNP).

Campylenchia latipes (Say 1824). NC: Haywood Co.: Site H-9: 24 June 1995, 1 ♀, 1 ♂, sweeping; 13 July 1995, 1 ♀, 1 ♂, sweeping (GSNP). Swain Co.: Site SW-11: 21–24 July 1964, 2 ♀, 7 ♂ (NCSU). Site SW-16: 21–28 July 2001, 1 ♂, [Malaise trap] (GSNP). TN: Blount Co.: Site B-20: 30 July–Aug. 2001, 1 ♂, [Malaise trap] (GSNP). Sevier Co.: Site SE-1: 21 May 1943, 1 nymph (GSNP). Site SE-3: July 1959, 1 ♀ (GSNP).

Carynota mera (Say 1830). TN: Blount Co.: Site B-2: 28 May 1999, 1 nymph, on *Carya* sp. (NCSU).

Cyrtolobus arcuatus (Emmons 1854). TN: Blount Co.: Site B-20: 21 May 2001, 1 ♀, [Malaise trap] (GSNP). Cocke Co.: Site C-3: 16 May 2001, 1 ♀ (GSNP).

Cyrtolobus auroreus Woodruff 1924. TN (NEW STATE RECORD): Blount Co.: Site B-19: June 1995, 1 ♀, on *Q. rubra*, insecticidal fogging (ECUT); 8 June 1995, 1 ♂, on *Quercus* sp. (GSNP). Sevier Co.: Site SE-4: 25 May 2000, 1 ♂, [Malaise trap] (GSNP).

Cyrtolobus fenestratus (Fitch 1851). Fig. 1. NC: Haywood Co. (NEW COUNTY RECORD): Site H-10: 17 June 1994, 1 ♀, 1 ♂, on *Quercus rubra*, insecticidal fogging (ECUT). Swain Co. (NEW COUNTY RECORD): Site SW-2: 10 June 1994, 4 ♀, 1 ♂, 1 [sex?], on *Q. rubra*, insecticidal fogging (ECUT, GSNP). Site SW-17: 3–17 July 2001, 1 ♀, [Malaise trap] (GSNP). Site SW-18: 3–17 July 2001, 1 ♀, [Malaise trap] (GSNP). TN (NEW STATE RECORD): Blount Co.: Site B-9: 14 June 2000, 1 ♀, on *Q.* sp. (NCSU). Site B-19: 31 May 1994, 1 ♂, on *Q. rubra*, insecticidal fogging (ECUT).

Cyrtolobus flavolatus Woodruff 1924. TN

(NEW STATE RECORD): Blount Co.: Site B-10: 10 June 1995, 1 ♀, on *Quercus alba* (GSNP).

Cyrtolobus fuscipennis Van Duzee 1908. NC: Swain Co. (NEW COUNTY RECORD): Site SW-1: 29 May 1999, 1 ♀, on *Quercus alba* (NCSU). Site SW-13: 30 June to 7 July 2001, 1 ♀, [Malaise trap] (GSNP). Site SW-14: 19–26 May 2001, 1 ♀, [Malaise trap]; 7 July 2001, 1 ♀, [Malaise trap]; 21–28 July 2001, 1 ♀, [Malaise trap] (GSNP). TN (NEW STATE RECORD): Blount Co.: Site B-9: 14 June 2000, 1 ♀, 2 ♂, on *Q.* sp., blacklighting; 15 June 2000, 1 ♂, blacklighting (NCSU). Site B-10: 14 June 1995, 1 ♀, on *Q. stellata* (GSNP). Site B-11: 8 June 1995, 1 ♀, on *Q. alba* (GSNP). Cocke Co.: Site C-2: 9–22 May 2001, 1 ♂, [Malaise trap] (GSNP). Site C-3: 16 May 2001, 1 ♀ (GSNP).

Cyrtolobus maculifrontis (Emmons 1854). NC: Swain Co. (NEW COUNTY RECORD): Site SW-17: 3–17 July 2001, 1 ♀, [Malaise trap] (GSNP). TN (NEW STATE RECORD): Blount Co.: Site B-2: 28 May 1999, 3 ♀, 1 ♂, on *Quercus alba* and *Q. stellata*; 15 June 2000, 3 ♀, 1 ♂, on *Q.* sp. (NCSU). Site B-5: 15 June 2000, 3 ♀, 7 ♂, on *Q. stellata* and *Q.* sp. (GSNP, NCSU). Site B-6: 28 May 1999, 1 ♀, on *Q. alba* (NCSU). Site B-9: 14 June 2000, 1 ♂, blacklighting (NCSU). Site B-19: 31 May 1994, 1 ♀, on *Q. rubra,* insecticidal fogging (ECUT).

Cyrtolobus pallidifrontis (Emmons 1854). NC: Swain Co. (NEW COUNTY RECORD): Site SW-18: 6–25 June 2001, 2 ♀, [Malaise trap] (GSNP). TN (NEW STATE RECORD): Blount Co.: Site B-3: 15 June 2000, 2 ♀, on *Quercus alba* (NCSU). Site B-5: 15 June 2000, 1 ♀, on *Q. alba* (NCSU). Site B-7: 28 May 1999, 1 ♂, on *Q. alba* (NCSU). Site B-8: 15 June 2000, 1 ♀, on *Q. alba* (NCSU). Site B-9: 14 June 2000, 2 ♀, 1 ♂, on *Q.* sp. (NCSU). Site B-10: 10 June 1995, 1 ♀, on *Q. alba*; 14 June 1995, 4 ♀, 1 ♂, on *Q. alba* (GSNP). Site B-19: 31 May 1994, 1 ♀, 1 ♂, on *Q. rubra,* insecticidal fogging; 8 June 1995, 1 ♂, 1 [sex?], on *Q. rubra,* insecticidal fogging (ECUT). Sevier Co.: Site SE-4: 8–15 Oct. 2001, 1 ♀, [Malaise trap] (GSNP). Site SE-12: 22 Oct.–5 Nov. 2001, 1 ♀, [Malaise trap] (GSNP).

Cyrtolobus togatus Woodruff 1924. NC: Swain Co. (NEW COUNTY RECORD): Site SW-3: 14 June 2000, 1 ♀, on *Quercus* sp. (NCSU).

Cyrtolobus vau (Say 1830). NC: Haywood Co.: Site H-11: 20 Aug–11 Sept. 2001, 3 ♀, [Malaise trap] (GSNP). Swain Co. (NEW COUNTY RECORD): Site SW-1: 14 June 2000, 1 [sex ?], on *Quercus* sp. (NCSU). Site SW-17: 3–17 July 2001, 1 ♂, [Malaise trap] (GSNP). TN (NEW STATE RECORD): Blount Co.: Site B-8: 15 June 2000, 1 ♀, on *Q. alba* (NCSU). Site B-9: 14 June 2000, 1 ♀, 1 ♂, on *Q.* sp., blacklighting; 15 June 2000, 1 ♀, on *Q. alba* (NCSU). Site B-10: 10 June 1995, 2 ♀, on *Q. alba* and *Ostrya virginiana* (Miller) K. Koch; 14 June 1995, 1 ♀, on *Q. alba* (GSNP). Site B-19: 8 June 1995, 2 ♂, on *Q.* sp.; 7 July 1995, 1 ♀ (GSNP). Sevier Co.: Site SE-4: 25 May 2000, 1 ♀, [Malaise trap] (GSNP).

Enchenopa binotata (Say 1824) complex. NC: Swain Co. (NEW COUNTY RECORD): Site SW-9: 14 Oct. 1986, 1 ♀, sweeping (GSNP). TN: Blount Co.: Site B-10: 2 July 1995, 1 ♀, 3 ♂, on *Liriodendron tulipifera* L. (GSNP). Site B-12: 15 June 2000, 1 ♀, 3 ♂, on *Robinia pseudoacacia* (NCSU). Cocke Co.: Site C-1: 14 Nov. 2000, 1 ♀, [Malaise trap] (GSNP).

Entylia carinata (Forster 1771). Fig. 4. NC: Haywood Co.: Site H-9: 9 June 1995, 2 ♂, on *Betula nigra* L. (GSNP). Swain Co.: Site SW-1: 13 Oct. 2001, 3 ♀, 2 ♂, on *Eupatorium* (as Joe-pye-weed) sp. and *Solidago* sp. (NCSU). Site SW-5: 29 May 1999, 1 ♀, 1 ♂, on *Erigeron* sp. (NCSU). Site SW-11: 21–24 June 1964, 5 ♀, 2 ♂ (NCSU). Site SW-16: 9–16 June 2001, 1

♀, [Malaise trap] (GSNP). TN (NEW STATE RECORD): Blount Co.: Site B-3: 28 May 1999, 7 ♀, on *Verbesina alternifolia* (L.) Britton ex Kearney (NCSU). Site B-5: 14 Oct. 2001, 1 ♀, on *V. alternifolia* (NCSU). Site B-6: 28 May 1999, 3 ♀, 3 ♂, on *Quercus alba*, sweeping, sweeping weeds (NCSU). Site B-7: 28 May 1999, 1 ♀, on *V.* sp.; 14 Oct. 2001, 3 ♀, *V. alternifolia* (NCSU). Site B-10: 19 April 1995, 1 ♀ on *V. alternifolia*; 26 April 1995, 2 ♀, on *Acer rubrum* L. (GSNP). Site B-15: 19 April 1995, 3 ♀, 5 ♂, on grass (GSNP). Site B-20: 21 May 2001, 2 ♀, [Malaise trap] (GSNP). Sevier Co.: Site SE-1: 21 May 1943, 1 ♀ (GSNP). Site SE-2: 15 June 1950, 1 ♀ (GSNP).

Glossonotus univittatus (Harris 1841). TN (NEW STATE RECORD): Blount Co.: Site B-2: 28 May 1999, 1 ♀, on *Quercus falcata* (NCSU). Site B-13: 13 June 1981, 1 ♂ (GSNP).

Hadrophallus borealis (Fairmaire 1846). NC: Swain Co.: Site SW-11: 21–24 July 1964, 1 ♀, 2 ♂ (NCSU). TN: Sevier Co.: Site SE-4: 3 July 1995, 1 ♀ (GSNP).

Helonica excelsa (Fairmaire 1846). TN: Blount Co.: Site B-2: 28 May 1999, 1 ♀, on *Quercus alba* (NCSU). [First reported from GSMNP by Wallace and Deitz (1999) as *Helonica* treehopper].

Microcentrus caryae (Fitch 1851). TN (NEW STATE RECORD): Blount Co. Records: Site B-2: 14 Oct. 2001, 1 ♀, on *Carya* sp. (NCSU).

Microcentrus perditus (Amyot & Serville 1843). NC: Swain Co. (NEW COUNTY RECORD): Site SW-1: 29 May 1999, 1 ♀, *Quercus* sp. (NCSU). Site SW-3: 14 June 2000, 1 ♂, *Q.* sp. (NCSU). Site SW-14: 30 June to 30 July 2001, 1 ♂, [Malaise trap] (GSNP). TN (NEW STATE RECORD): Blount Co.: Site B-2: 15 June 2000, 1 ♀, on *Q.* sp. (NCSU). Site B-3: 15 June 2000, 1 ♀, on *Q. alba* (NCSU). Site B-8: 15 June 2000, 2 ♀, 3 ♂, on *Q. alba* (NCSU). Site B-10: 10 June 1995, 2 ♂, on *Q. alba*; 14 June 1995, 3 ♀, on *Q. alba*; 15 June 1995, 1 ♀, 1 ♂, on *Q. alba* (GSNP). Site B-16: 15 June 2000, 1 ♀, *Q. alba* (NCSU).

Micrutalis calva (Say 1830). NC: Swain Co.: Site SW-11: 21–24 June 1964, 4 ♀ (NCSU). Site SW-15: 9 July 1999, 1 ♀, [Malaise trap] (GSNP). TN: Blount Co.: Site B-2: 28 May 1999, 1 ♀, on *Quercus alba* (NCSU). Site B-5: 15 June 2000, 1 ♀, sweeping (NCSU). Site B-6: 28 May 1999, 1 ♀, on *Q. alba* (NCSU). Site B-7: 28 May 1999, 1 ♂, on *Robinia pseudoacacia* (NCSU). Site B-10: 24 May 1995, 1 ♂; 10 June 1995, 1 ♂; 14 June 1995, 1 ♀ (GSNP). Site B-16: 15 June 2000, 1 ♀, sweeping meadow (NCSU). [First recorded for TN in Davidson Co. (Meyer 1937).]

Micrutalis dorsalis (Fitch 1851). NC: Swain Co.: Site SW-11: 21–24 July 1964, 1 ♀, 2 ♂ (NCSU).

Ophiderma definita Woodruff 1919. NC: Swain Co. (NEW COUNTY RECORD): Site SW-2: 10 June 1994, 1 ♀, 1 ♂, on *Quercus rubra*, insecticidal fogging (ECUT). TN (NEW STATE RECORD): Blount Co.: Site B-2: 28 May 1999, 1 ♀, on *Q. falcata* (NCSU). Site B-7: 28 May 1999, 1 ♀, on *Q. imbricaria* Michaux (NCSU). Site B-12: 15 June 2000, 1 ♂ (NCSU). Site B-19: 31 May 1994, 3 ♀, 2 ♂, 1 [sex ?], on *Q. rubra*, insecticidal fogging (ECUT). Cocke Co.: Site C-3: 16 May 2001, 1 ♂ (GSNP). Sevier Co.: Site SE-4: 25 May 2000, 2 ♀, [Malaise trap] (GSNP).

Ophiderma evelyna Woodruff 1919. TN: Blount Co.: Records: Site B-2: 28 May 1999, 3 ♀, 1 ♂, on *Quercus falcata*; 15 June 2000, 6 ♀, on *Q.* sp. (GSNP, NCSU).

Ophiderma flava Goding 1893. NC: Haywood Co.: Site H-10: 17 June 1993, 4 ♂, on *Quercus rubra*, insecticidal fogging; 22 July 1993, 1 ♀, on *Q. rubra*, insecticidal fogging; 12 Aug. 1993, 1 ♀, on *Q. rubra*, insecticidal fogging; 17 June 1994, 1 ♀, on *Q. rubra*, insecticidal fogging; 1 July 1994, 1 ♂, on *Q. rubra*, insecticidal fogging (ECUT). Swain Co. (NEW COUNTY RECORD): Site SW-2: 1 Sept. 1992, 1 ♀, on *Q. rubra,* insecticidal fogging; 23 July 1993, 1 ♀, on *Q. rubra,* insecticidal fogging; 9 Aug. 1993, 1 ♀, on *Q. rubra,* insecticidal fogging (ECUT); 10 June 1994, 4 ♀, 15 ♂, on *Q. rubra,* insecticidal fogging (ECUT, GSNP). Site SW-17: 3–17 July 2001, 1 ♂, [Malaise trap] (GSNP). TN (NEW STATE RECORD): Blount Co.: Site B-19: 2 June 1993, 2 ♀, on *Q. rubra,* insecticidal fogging; 18 June 1993, 3 ♀, on *Q. rubra,* insecticidal fogging; 31 May 1994, 4 ♀, 3 ♂, on *Q. rubra,* insecticidal fogging; 26 Aug. 1994, 1 ♀, on *Q. rubra,* insecticidal fogging (ECUT). Cocke Co.: Site C-3: 16 May 2001, 2 ♂; 18 May 2000, 1 ♂ (GSNP).

Ophiderma flavicephala Goding 1893. NC: Swain Co. (NEW COUNTY RECORD): Site SW-1: 29 May 1999, 1 ♀, sweeping (NCSU). Site SW-6: 29 May 1999, 1 ♀, on *Quercus* sp. (NCSU).

Ophiderma pubescens (Emmons 1854). TN (NEW STATE RECORD): Blount Co.: Site B-19: 31 May 1994, 1 ♀, on *Quercus rubra,* insecticidal fogging (ECUT).

Ophiderma salamandra Fairmaire 1846. NC: Haywood Co. (NEW COUNTY RECORD): Site H-10: 1 July 1994, 1 ♂, on *Quercus rubra,* insecticidal fogging (ECUT). Swain Co. (NEW COUNTY RECORD): Site SW-13: 9–16 June 2001, 1 ♂, [Malaise trap] (GSNP). TN (NEW STATE RECORD): Blount Co.: Site B-19: 2 June 1993, 1 ♀, on *Q. rubra,* insecticidal fogging (ECUT).

Platycotis vittata (Fabricius 1803). NC: Haywood Co.: Site H-2: 29 May 1999, 1 ♀, on *Quercus* sp. (NCSU). Site H-3: 29 May 1999, 1 ♀, on *Liriodendron tulipifera* (NCSU). Site H-6: 5 June 1986, 1 ♀ (GSNP). Site H-7: 30 May 1990, 1 ♂ (GSNP). Site H-11: 26 Mar. 2001, 1 ♀, [Malaise trap] (GSNP). Swain Co.: Site SW-1: 29 May 1999, 1 ♀, 2 ♂, on *Q.* sp.; 13 Oct. 2001, 1 ♂, on *Q. falcata* (NCSU). Site SW-2: 1 Sept. 1992, 2 ♀, on *Q. rubra,* insecticidal fogging; 5 Oct. 1993, 1 ♀, on *Q. rubra,* insecticidal fogging (ECUT); 15 July 1994, 1 ♀, on *Q. rubra* (GSNP). Site SW-7: 28 June 1995, 1 ♂, on *Betula alleghaniensis* Britton (GSNP). Site SW-14: 21–28 June 2001, 1 ♂, [Malaise trap] (GSNP). Site SW-17: 12 Nov. 2000, 1 ♀, [Malaise trap]; 3–17 July 2001, 1 ♂, [Malaise trap] (GSNP); 9–24 Oct. 2001, 5 ♀, 3 ♂, [Malaise trap] (GSNP); 8–24 Nov. 2001, 1 ♀, [Malaise trap] (GSNP). Site SW-18: 13 Nov. 2000, 1 ♀, [Malaise trap]; 24 May–6 June 2001, 1 ♀, [Malaise trap]; 6–25 June 2001, 1 ♀, [Malaise trap] (GSNP). TN: Blount Co.: Site B-2: 28 May 1999, 1 ♀, on *Q. falcata* (NCSU). Site B-3: 28 May 1999, 22 ♀, 19 ♂, on *Q. stellata* (NCSU). Site B-5: 14 Oct. 2001, 6 ♀, 1 ♂, 5 nymphs, on *Q. alba* and *Q. stellata* (NCSU). Site B-6: 14 Oct. 2001, 7 ♀, 3 ♂, 7 nymphs, on *Platanus occidentalis* and *Q. imbricaria* (NCSU). Site B-7: 28 May 1999, 2 ♀, 1 ♂, on *Q. alba* (NCSU). Site B-8: 15 June 2000, 2 ♀, on *Q. alba* (NCSU). Site B-10: 8 June 1995, 1 ♀, on *Q. alba* (GSNP). Site B-11: 8 June 1995, 2 ♀, 1 ♂, on *Q. alba* (GSNP). Site B-14: 14 Oct. 2001, 1 ♂, on *Q. alba* (NCSU). Site B-17: 15 June 1995, 1 ♀ (GSNP). Site B-19: 8 June 1995, 1 ♂, on *Q. velutina* Lam.; 7 July 1995, 1 ♀, on *Q. alba* (GSNP). Site B-20: 14–26 Feb. 2001, 1 ♂, [Malaise trap] (GSNP). Cocke Co.: Site C-1: 14 Nov. 2000, 1 ♀, [Malaise trap]; 19 Jan. 2001, 1 ♂, [Malaise trap] (GSNP); 8–19 June 2001, 1 ♂, [Malaise trap] (GSNP); 27 Sept.–16 Oct. 2001, 1 ♂, [Malaise trap] (GSNP). Site C-2: 13 Dec. 2000, 1 ♂, [Malaise trap]; 30 Jan.–16 Feb. 2001, 1 ♀, [Malaise trap] (GSNP). Site C-4: 2 Oct. 1995, 6 nymphs, on *Castanea dentata* (GSNP). Site C-5: 27 Sept. 2000, 1 ♀ (GSNP). Sevier Co.: Site SE-4: 3 July 1995, 1 ♀; 8 Nov. 1999, 1 ♀, [Malaise trap]; 29 Mar. 1999, 1 ♀, [Malaise trap]; 2 Aug. 2000, 1 ♀, [Malaise trap]; 12 Sept. 2000, 1 ♀, [Malaise trap]; 12 Oct. 2000, 1 ♀, [Malaise trap]; 24 Oct. 2000, 4 ♀, 3 ♂, [Malaise trap]; 27 Nov. 2000, 2 ♀, 2 ♂ [Malaise trap]; 12 Dec. 2000, 2 ♂, [Malaise trap]; 16 Jan. 2001, 1 ♀, 5 ♂, [Malaise trap]; 29 Jan.–12 Feb. 2001, 1 ♀, [Malaise trap]; 16–30 July 2001, 1 ♂, [Malaise trap] (GSNP); 10 Sept. 2001, 1 ♂, [Malaise trap] (GSNP); 15 Oct.–5 Nov. 2001, 1 ♂, [Malaise trap] (GSNP). Site SE-5: 6 Sept. 1940, 13 ♀, 5 ♂, on *Castanea* sp. (GSNP). Site SE-11: 23 Oct.–6 Nov. 2000, 3 ♀, 3 ♂, [Malaise trap]; 6 Nov. 2000, 1 ♀, 1 ♂, [Malaise trap] (GSNP); 21 June–5 July 2001, 1 ♂, [Malaise trap] (GSNP); 13–27 Oct. 2001, 1 ♀, 2 ♂, [Malaise trap] (GSNP). Site SE-12: 10 Nov. 2000, 2 ♀, 1 ♂, [Malaise trap]; 14 Feb. 2001, 1 ♀, [Malaise trap]; 28 Mar.–9 Apr. 2001, 1 ♀, [Malaise trap] (GSNP). Site SE-13: 10 Nov. 2000, 1 ♀, 1 ♂, [Malaise trap] (GSNP); 26 Sept.–24 Oct. 2001, 1 ♂, [Malaise trap] (GSNP). Site SE-14: 1 Oct. 1986, 9 ♀, 11 ♂, 7 nymphs, on *C. dentata* (GSNP).

Publilia concava (Say 1824). NC: Haywood Co.: Site H-4: 29 May 1999, 1 ♂, on *Eupatorium* sp. (NCSU). Swain Co.: Site SW-1: 29 May 1999, 6 ♀, 2 ♂, on *Erigeron* sp. and sweeping; 13 Oct. 2001, 17 ♀, 5 ♂, on *Eupatorium* sp. (as Joe-pye-weed) and *Solidago* sp. (NCSU). Site SW-6: 29 May 1999, 9 ♀, 2 ♂, on *Eupatorium* sp., *Solidago* sp., and sweeping (NCSU). Site SW-11: 21–24 July 1964, 1 ♀ (NCSU). TN: Blount Co.: Site B-3: 28 May 1999, 1 ♀, on *Verbesina alternifolia* (NCSU). Sevier Co.: Site SE-6: 5 Sept. 1995, 1 ♀, 2 ♂, sweeping riparian vegetation (GSNP). Site SE-7: 28 May 1999, 1 ♀ (GSNP). Site SE-8: 28 May 1999, 2 ♀, 3 ♂, sweeping herbaceous plants (NCSU). Site SE-10: 28 May 1997, 1 ♂ (NCSU). [First recorded for TN in Davidson Co. (Meyer 1937)].

Publilia reticulata Van Duzee 1908. NC: Haywood Co.: Site H-3: 29 May 1999, 1 ♂ (NCSU). Site H-4: 29 May 1999, 2 ♀, on *Eupatorium* sp. (NCSU). Swain Co. (NEW COUNTY RECORD): Site SW-16: 9–16 June 2001, 1 ♀, [Malaise trap] (GSNP). TN: Sevier Co.: Site SE-8: 28 May 1999, 5 ♀, 2 ♂, sweeping weeds, sweeping herbaceous plants (NCSU). Site SE-15: 15 June 1946, 1 ♀, 1 ♂ (USNM).

Smilia camelus (Fabricius 1803). NC: Swain Co. (NEW COUNTY RECORD): Site SW-1: 29 May 1999, 1 ♀, on *Quercus* sp. (NCSU).

Spissistilus festinus (Say 1830). TN: Blount Co.: Site B-1: 11 July 1995, 1 ♂ (GSNP). Site B-10: 6 April 1995, 2 ♂; 24 May 1995, 1 ♂; 10 June 1995, 1 ♂ (GSNP).

Stictocephala brevitylus (Van Duzee 1908). NC: Haywood Co.: Site H-3: 29 May 1999, 2 ♀, on *Quercus* sp. (NCSU). Site H-4: 29 May 1999, 1 ♀, 1 ♂, on *Sambucus canadensis* L., sweeping weeds (NCSU). Site H-5: 29 May 1999, 3 ♀, 2 ♂, on *Q.* sp. (NCSU). Site H-8: 29 May 1999, 1 ♀, on *Ostrya virginiana* (NCSU). Swain Co.: Site SW-1: 29 May 1999, 6 ♀, 4 ♂, on *Erigeron* sp., *Q.* sp., *Robinia pseudoacacia,* and sweeping; 14 June 2000, 3 ♀, on *R. pseudoacacia* (NCSU). Site SW-6: 29 May 1999, 5 ♀, 3 ♂, *Eupatorium capillifolium* (Lam.) Small and *E.* sp. (NCSU). Site SW-11: 21–24 July 1964, 1 ♀ (NCSU). Site SW-12: 10 July 1980, 1 ♂ (GSNP). Site SW-15: 9–16 June 2001, 1 ♂, [Malaise trap] (GSNP). Site SW-16: 9–16 June 2001, 1 ♂, [Malaise trap] (GSNP). TN (NEW STATE RECORD): Blount Co.: Site B-2: 28 May 1999, 1 ♀, 1 ♂, on *Rubus* sp. (NCSU). Site B-4: 15 June 2000, 3 ♀, on *R. pseudoacacia* (NCSU). Site B-7: 28 May 1999, 1 ♀, 1 ♂, on *Gleditsia triacanthos* L., sweeping (NCSU). Site B-10: 10 June 1995, 1 ♀ (GSNP). Sevier Co.: Site SE-4: 9 May 1995, 1 ♀ (GSNP). Site SE-8: 28 May 1999, 1 ♀, sweeping herbaceous plants (NCSU).

Stictocephala diceros (Say 1824). NC: Haywood Co.: Site H-1: 20 July 1995, 1 ♂ (GSNP). TN: Sevier Co.: Site SE-2: 15 Aug. 1947, 1 ♂ (GSNP).

Stictocephala lutea (Walker 1851). NC:

Haywood Co.: Site H-1: 16 May 1995, 1 ♀, 1 ♂ (GSNP). Swain Co. (NEW COUNTY RECORD): Site SW-3: 14 June 2000, 2 ♀, 1 ♂, on *Quercus* sp. (NCSU). TN: Blount Co.: Site B-6: 28 May 1999, 1 ♀, sweeping herbaceous plants (NCSU). Site B-19: 15 May 1995, 2 ♀, 1 ♂, on *Q. velutina*; 26 May 1995, 3 ♀, on *Q. velutina* and *Quercus* sp. (GSNP). Sevier Co.: Site SE-4: 25 May 2000, 1 ♂, [Malaise trap] (GSNP). Site SE-9: 17 June 1995, 1 ♀ (GSNP).

Stictocephala militaris (Gibson and Wells 1917). TN (NEW STATE RECORD): Blount Co.: Site B-22: 20 Aug. 1999, 5 ♂, moth trap—blacklighting (GSNP).

Telamona collina (Walker 1851). Fig. 3. NC: Haywood Co. (NEW COUNTY RECORD): Site H-9: 9 June 1995 [found dead], 1 [sex ?] (GSNP). TN (NEW STATE RECORD): Blount Co.: Site B-6: 28 May 1999, 1 nymph, on *Platanus occidentalis* (NCSU). Site B-7: 28 May 1999, 1 ♂, 1 nymph, on *P. occidentalis* (NCSU). Sevier Co.: Site SE-4: 22 June 1999, 1 ♀, 1 ♂, [Malaise trap]; 4 July 1999, 1 ♀, [Malaise trap] (GSNP).

Telamona decorata Ball 1903. TN (NEW STATE RECORD): Blount Co.: Site B-3: 28 May 1999, 1 ♂, on *Quercus stellata* (NCSU). Site B-19: 31 May 1994, 1 ♂, on *Q. rubra*, insecticidal fogging (GSNP). Sevier Co.: Site SE-4: 27 Nov. 2000, 1 ♀, [Malaise trap] (GSNP).

Telamona maculata Van Duzee 1908. NC: Swain Co. (NEW COUNTY RECORD): Site SW-14: 30 June to 7 July 2001, 1 ♂, [Malaise trap] (GSNP).

Telamona monticola (Fabricius 1803). NC: Haywood Co. (NEW COUNTY RECORD): Site H-10: 17 June 1993, 2 ♂, 1 ♀, 1 [sex ?], on *Quercus rubra*, insecticidal fogging (ECUT, GSNP); 17 June 1994, 1 ♀, on *Q. rubra*, insecticidal fogging (ECUT). TN (NEW STATE RECORD): Blount Co.: Site B-2: 28 May 1999, 1 ♀, on *Q. alba* (NCSU). Site B-5: 15 June 2000, 1 ♀, 1 ♂, on *Q. stellata* and *Robinia pseudoacacia* (NCSU). Site B-9: 14 June 2000, 1 ♂, on *Q.* sp. (NCSU). Cocke Co.: Site C-3: 18 May 2000, 1 ♀, 1 ♂ (GSNP).

Telamona reclivata Fitch 1851. NC: Swain Co. (NEW COUNTY RECORD): Site SW-2: 1 Sept. 1992, 1 ♀, on *Quercus rubra*, insecticidal fogging (ECUT).

Telamona unicolor Fitch 1851. TN (NEW STATE RECORD): Blount Co.: Site B-2: 28 May 1999, 1 ♂, on *Carya* sp. (NCSU). Site B-6: 28 May 1999, 1 ♀, on *C.* sp. (NCSU).

Thelia bimaculata (Fabricius 1794). Fig. 6. NC: Swain Co.: Site SW-8: [no date], 1 ♀ (GSNP). TN: Blount Co.: Site B-4: 15 June 2000, 2 ♀, 1 ♂, on *Robinia pseudoacacia* (NCSU). Site B-12: 15 June 2000, 1 ♀, 1 ♂, on *R. pseudoacacia* (NCSU). Site B-18: 1 Sept. 1988, 1 ♂ (GSNP). Sevier Co.: Site SE-2: 2 Sept. 1937, 1 ♀ (GSNP). Site SE-4: 3 July 1995, 1 ♀ (GSNP). Site SE-15: 11 Aug. 1947, 1 ♂ (USNM).

Tortistilus abnormus (Caldwell 1949). TN (NEW STATE RECORD): Blount Co.: Site B-2: 15 June 2000, 2 ♂, on *Quercus* sp., sweeping (GSNP, NCSU).

Tortistilus inermis (Fabricius 1775). TN: Blount Co.: Site B-16: 15 June 2000, 2 ♂, sweeping (GSNP, NCSU).

Tylopelta gibbera (Stål 1869). NC: Swain Co.: Site SW-11: 21–24 July 1964, 1 ♀, 2 ♂ (GSNP, NCSU). TN: Sevier Co.: Site SE-2: 15 Aug. 1947, 1 ♀ (USNM).

Vanduzea arquata (Say 1830). NC: Swain Co.: Site SW-1: 28 May 1999, 1 [sex ?], 70 nymphs [ethanol], on *Robinia pseudoacacia*; 14 June 2000, 15 ♀, 2 ♂, on *R. pseudoacacia*; 13 Oct. 2001, 1 ♂, on *Q. alba*? (NCSU). Site SW-3: 14 June 2000, 4 ♀, 1 ♂, on *R. pseudoacacia* (NCSU). Site SW-4: 29 May 1999, 2 nymphs, on *R. pseudoacacia* (NCSU). Site SW-8: [no date], 2 ♀ (GSNP). TN: Blount Co.: Site B-2: 28 May 1999, 2 ♀, 7 ♂, [1 ♀, 1 ♂, and 10 nymphs in ethanol], on *R. pseudoacacia* (NCSU). Site B-10: 20 July 1995, 1 ♂ (GSNP). Site B-12: 15 June 2000, 3 ♀, 6 ♂, on *R. pseu-*

doacacia (NCSU). Site B-19: 7 July 1995, 1 ♀ (GSNP). Sevier Co.: Site SE-4: 8 July 1995, 1 ♀ (GSNP); 15 Oct. 2001, 7 ♀, 1 ♂, 2 nymphs, on *R. pseudoacacia* (NCSU). Site SE-8: 28 May 1999, 1 ♂, on *R. pseudoacacia* (NCSU).

Xantholobus intermedius (Emmons 1854). NC: Haywood Co. (NEW COUNTY RECORD): Site H-10: 17 June 1994, 5 ♀, 2 ♂, on *Quercus rubra,* insecticidal fogging; 1 July 1994, 3 ♀, 1 [sex ?], on *Q. rubra,* insecticidal fogging (ECUT, GSNP). Swain Co. (NEW COUNTY RECORD): Site SW-2: 1 Sept. 1992, 1 ♀, on *Q. rubra,* insecticidal fogging; 9 July 1993, 1 ♂, on *Q. rubra,* insecticidal fogging; 10 June 1994, 1 ♀, 1 ♂, on *Q. rubra,* insecticidal fogging; 28 June 1994, 1 ♀, 4 ♂, on *Q. rubra,* insecticidal fogging; 15 July 1994, 1 ♀, on *Q. rubra,* insecticidal fogging (ECUT, GSNP). Site SW-17: 3–17 July 2001, 1 ♀, [Malaise trap] (GSNP). Site SW-18: 6–25 June 2001, 1 ♀, [Malaise trap] (GSNP). TN (NEW STATE RECORD): Blount Co.: Site B-19: 31 May 1994, 2 ♀, on *Q. rubra,* insecticidal fogging; 26 Aug. 1994, 1 ♀, on *Q. rubra,* insecticidal fogging (ECUT).

Xantholobus lateralis Van Duzee 1908. TN (NEW STATE RECORD): Blount Co.: Site B-19: 15 May 1995, 1 ♀, on *Quercus velutina* (GSNP).

Xantholobus muticus (Fabricius 1777). TN (NEW STATE RECORD): Blount Co.: Site B-5: 15 June 2000, 1 ♀, on *Quercus* sp. (NCSU).

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A NEW SPECIES OF SOCIAL WASP IN THE GENUS *APOICA* LEPELETIER (HYMENOPTERA: VESPIDAE: POLISTINAE: EPIPONINI)

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Abstract.—***Apoica ambracarina*, n. sp.**, is described from queens, workers, and males. It is known from Rio Branco, Brazil, São Felix do Xingu, Brazil, and Tuparro Cerro Tomas, Colombia. Male genitalia and descriptive characters of all castes are illustrated. This is the ninth described species of the nocturnal genus *Apoica*.

Key Words: *Apoica ambracarina,* new species, Vespidae, Polistinae

Apoica Lepeletier is a genus of large-bodied, swarm-founding social wasps (Hymenoptera: Vespidae; Polistinae, Epiponini) distributed from Mexico to Argentina. *Apoica* are distinguished from other epiponines by their unusually large ocelli and associated nocturnality. Some *Apoica* are light in overall color, including the yellow *A. flavissima* Vecht, the cream-colored *A. pallens* (F.), and the white *A. gelida* Vecht. Some *Apoica* (*A. arborea* de Saussure and *A. strigata* Richards) have a "striped" appearance on the metasoma, generated by pale areas of the terga. Others are more or less uniformly dark brown to black in color with few pale markings, including *A. pallida* (Olivier), *A. thoracica* du Buysson, and *A. albimacula* (F.). Richards (1978) last revised the group, discussing these eight species. Although the species described here is generally a dark amber color, it is easily distinguished from other dark-bodied *Apoica* by its possession of a unique suite of characters.

Apoica ambracarina Pickett, new species
(Figs. 1–9, 10A, 11B)

Diagnosis.—Predominantly amber colored. Posterior border of terminal metasomal tergum pale yellow. Metanotum rounded, with longitudinal, median carina. Propodeal bristles erect, not curved. Eye bristles present and prominent over the entire surface of the eyes. Scutal bristles reaching posterior margin of scutum. Habitus of queen, worker, and male shown in Fig. 1.

Queen.—*Morphology:* Average wing length 1.78 cm (n = 5, ±0.027). Prominent longitudinal carina between antennal sockets (Fig. 2A). Median scutal sulcus wide, flaring anteriorly. Metanotum rounded, with obvious carina (as in Fig. 5). *Color:* Terminal two flagellomeres of antenna pale. Body almost entirely amber colored, with mesosoma slightly darker amber than metasoma. Scutum with two dark brown parapsidal furrows, fusing posteriorly (Fig. 3A). Posterior border of the terminal metasomal tergum pale yellow (Fig. 4A).

Worker.—*Morphology:* Average wing length 1.85 cm (n = 5, ±0.035). Prominent carina between antennal sockets, as in queen (Fig. 2B). Median scutal sulcus as in queen. Metanotum rounded, with obvious carina (Fig. 5). *Color:* Scutum with two dark brown parapsidal furrows, fusing posteriorly (Fig. 3B). Posterior border of the

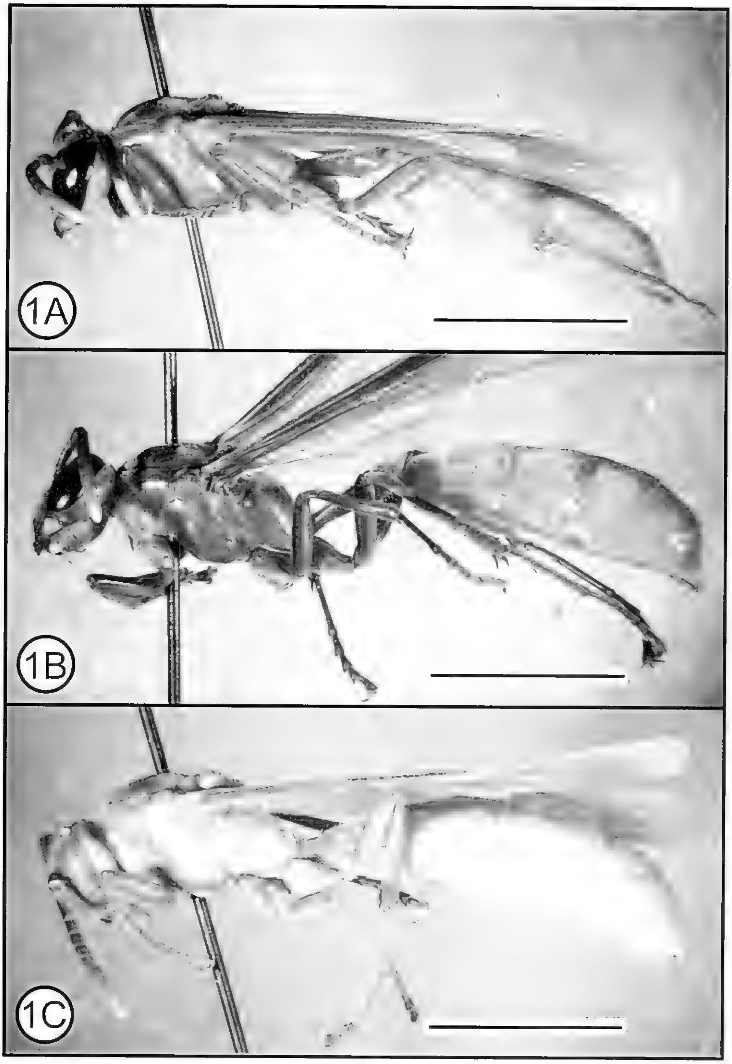
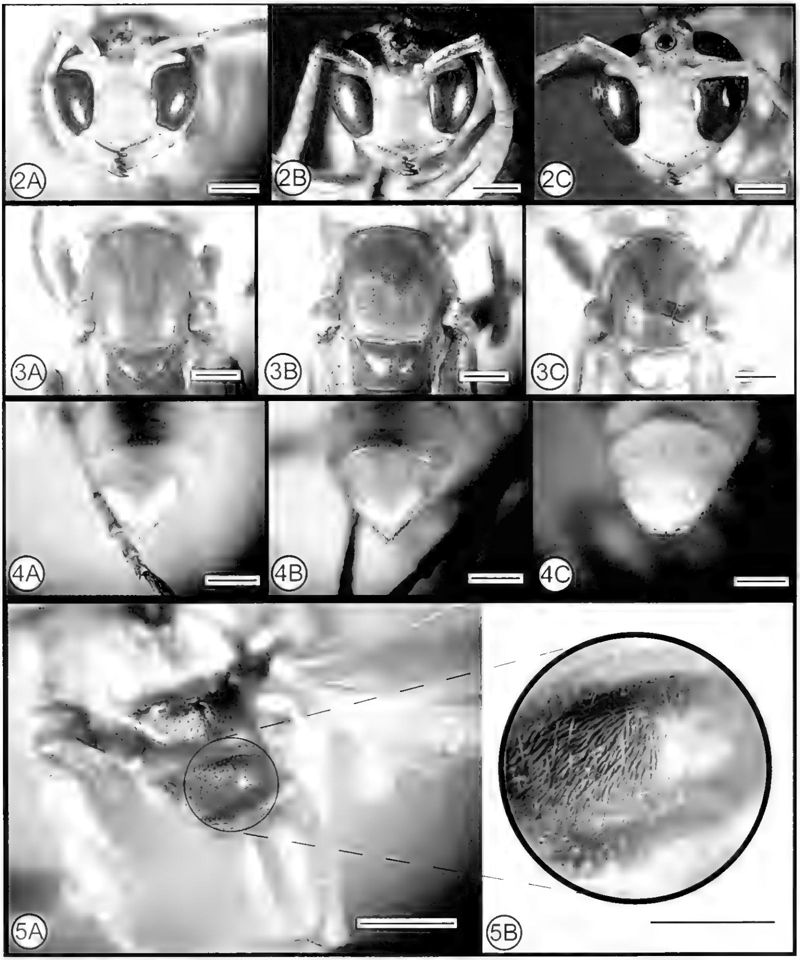


Fig. 1. Habitus of a queen (A), worker (B), and male (C) of *Apoica ambracarina*. Scale bars = 5.0 mm.



Figs. 2–5. *Apoica ambracarina.* 2. Frontal view of heads of a queen (A), worker (B), and male (C) showing carina between antennal sockets; scale bars = 3.0 mm (A), 3.0 mm (B), and 2.0 mm (C). 3. Dorsal view of mesosoma of a queen (A), worker (B), and male (C) showing dark brown parapsidal furrows; scale bars = 1.0 mm. 4. Dorsal view of terminal metasomal tergum of a queen (A), worker (B), and male (C) showing pale (yellow) posterior edge; scale bars = 2.0 mm. 5. (A) Oblique posterior view of mesosoma of worker holotype of *A. ambracarina* showing metanotal carina, enlarged in (B) for clarity; scale bars = 2.0 mm (A) and 1.0 mm (B).

terminal metasomal tergum pale yellow (Fig. 4B). Metasoma slightly darker than in queen.

Male.—*Morphology:* Average wing length 1.63 cm (n = 5, ±0.044). Prominent carina between antennal sockets (Fig. 2C). Median scutal sulcus less developed than in female. Many prominent bristles on entire scutum, all curving medially. Metanotal carina slight, nearly absent. *Genitalia:* Distal end of aedeagus punctured, with sensilla emerging from punctures (Fig. 6a). Central region of aedeagus with numerous denticles (Fig. 6B). Parameral spine extending far below body of paramere (Fig. 8) Paramereal spine with setae straight or curving slightly (Fig. 8A). Tip of digitus attaches to cuspis; digitus rounded and curved at tip (Fig. 9). Cuspis with prominent, curved setae (Fig. 9). *Color:* Scutellum and metanotum mostly pale yellow. Scutum with two dark brown parapsidal furrows, fusing posteriorly (Fig. 3C). Posterior border of terminal metasomal tergum pale yellow (Fig. 4C). Generally lighter in overall color than female.

Type material.—Holotype worker, labeled "Rio Branco, Acre State, Brazil, coll. S. Mateus and F. B. Noll, 10 X 1998" All paratypes from same colony, same data as holotype. Paratypes include 80 workers, 11 males, and 9 queens, labeled as such. Holotype and 40 worker, 5 male, and 5 queen paratypes are deposited in the Museu de Zoologia, Universidade de São Paulo, Brasil. The remaining paratypes are deposited in the Ohio State University Insect Collection, Columbus (20 workers, 3 males, 2 queens) and the American Museum of Natural History, New York (20 workers, 3 males, 2 queens).

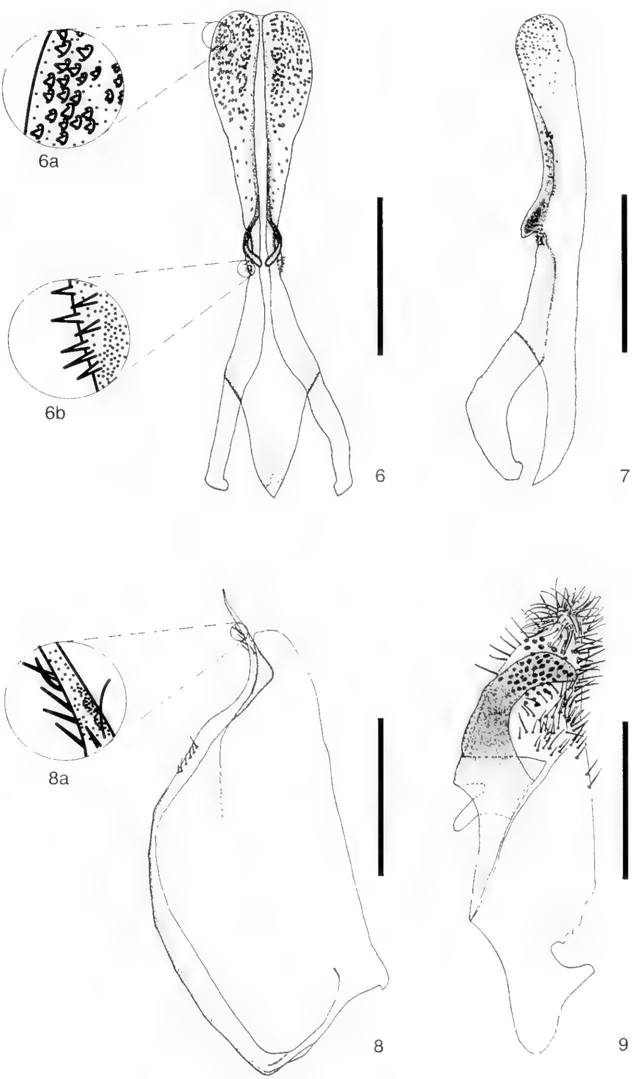
Distribution.—*Apoica ambracarina* is known from the type locality; São Felix do Xingu, Brazil; and Tuparro Cerro Tomas, Colombia.

Other material examined.—1 ♀: "Columbia Vicnada PNN, Tuparro Cerro Tomas 140 m, 5°21′00″N 67°51′36″W, 8–28 aug 2000 W. Villalba, Sample No 513" (pers. coll. C. Sarmiento); 1 ♀: "Columbia Vicnada PNN, Tuparro Cerro Tomas 140 m, 5°21′00″N 67°51′36″W, 18–28 aug 2000 W. Villalba, Sample No 516" (pers. coll. C. Sarmiento); 1 ♀: "Columbia Vicnada PNN, Tuparro Cerro Tomas 140 m, 5°21′00″N 67°51′36″W, 29 jun – 15 jul 2000 Malaise, Sample No 269 W. Villalba" (pers. coll. C. Sarmiento); 5 ♀: "Moyen XINGU (Brésil), Mission M. Boulard, P. Jauffret et P. Pompanon, Museum PARIS, SAO FELIX DO XINGU, 1–4-X-1975" (MNHN); 4 ♀: "Moyen XINGU (Brésil), Mission M. Boulard, P. Jauffret et P. Pompanon, Museum PARIS, SAO FELIX DO XINGU, 29–30-IX-1975" (one determined *A. thoracica* B. Sigwalt 1984) (MNHN).

Nest.—The nest was not collected with the colony of *A. ambracarina,* so a precise description is not possible. However, I was told that the nest was approximately 15 m high in a tree and appeared to be a typical *Apoica* subgenus *Apoica* (c.f., *Apoica arborea,* Vecht 1972: 738, photo I) nest in all other respects (pers. comm., F. B. Noll).

Etymology.—The name refers to the general amber color of the wasp and the presence of the longitudinal, medial metanotal carina.

Remarks.—*Apoica ambracarina* is distinguishable from other *Apoica* by its amber color and the presence of a longitudinal, median metanotal carina. Although the metasoma of some *Apoica* is light brown or yellowish, the presence of the carina distinguishes *A. ambracarina* from all other known *Apoica* species, except *A. albimacula. A. albimacula* also has a metanotal carina, but close examination of the carinae reveals that they are not homologous. The posterior margin of the metanotum is rounded in *A. ambracarina* (Fig. 10A), as is typical of most *Apoica,* whereas *A. albimacula* has a sharply angled metanotum posteriorly (Fig. 10B) and a much more prominent metanotal carina. Also, the carina of *A. albimacula* is near the posterior margin of the metanotum (Fig. 11A) whereas the carina of *A. ambracarina* is more an-



Figs. 6–9. Male genitalia of *Apoica ambracarina*. 6, Aedeagus (ventral view), with enlargements of sensilla (6a) and medial denticles (6b). 7, Aedeagus (lateral view). 8, Right paramere (interior view) with enlargement of spine showing setae (8a). 9, Right volsella. (lateral view). Scale bars for 6–8 = 0.01 mm. Scale bar for 9 = 0.005 mm.

Fig. 10. Lateral view of *Apoica ambracarina* (A) and *A. albimacula* (B). The metanotum of *A. ambracarina* is rounded posteriorly (see arrow), whereas the metanotum of *A. albimacula* is more sharply angled (see arrow). Scale bars = 2.0 mm.

terior (Fig. 11B). Although Richards (1978: 262) mentioned in his key to *Apoica* that *A. thoracica* has a "Metanotum usually rounded, rarely with traces of a keel," this is inaccurate. *A. thoracica* does not have a metanotal keel (Fig. 11C). Richards may have included *A. ambracarina* in his concept of *A. thoracica* if he had seen specimens. In particular, he may have seen some specimens of *A. ambracarina* in the Muséum National D'Histoire Naturelle that were identified as *A. thoracica* (see Material Examined).

In his discussion of *Apoica thoracica*, Richards (1978: 268) stated "In the collection at Paris are two females marked type, Guyane francaise: Camopi, 1900 (F. Geay). These are specimens of *A. albimacula*. The whole gaster, including the endband of gastral tergite 1 to tip of tergite 6 is yellowish brown (perhaps immature) but the pale yellow at the base of tergite 2, though faded, can still be distinctly seen if carefully looked for. Moreover, the metanotum has a distinct keel." When I first saw the colony of the species described here, I thought it was equivalent to the two unusual specimens described by Richards (1978), because they are light brown to amber colored and posses a metanotal carina. However, since studying these specimens, I have concluded that, although they are much lighter than any other *A. albimacula* specimens I have observed, they are indeed *A. albimacula* and not members of *A. ambracarina*. The posterior edge of the metanotum of Richards' specimens is sharply pointed, as in *A. albimacula* (Fig. 10B), but this edge is rounded in *A. ambracarina* (Fig. 10A). Also, *A. ambracarina* has a pale mark on the posterior tip of the terminal metasomal tergum and dark brown parapsidal furrows on the scutum,

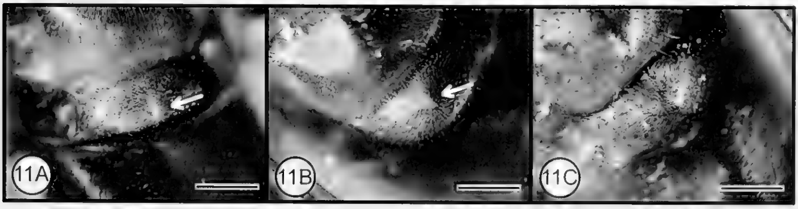


Fig. 11. Oblique posterior views of metanota of *Apoica albimacula* (A), *A. ambracarina* (holotype) (B), and *A. thoracica* (C). The carina of *A. albimacula* is near the posterior margin of the metanotum (see arrow) whereas the carina of *A. ambracarina* is more anterior and more blunt (see arrow); *A. thoracica* has no metanotal carina Scale bars = 1.0 mm.

but these are absent on *A. albimacula* and Richards' specimens.

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BRYOPHAGY IN THE AUCHENORRHYNCHA: SEASONAL HISTORY AND HABITS OF A MOSS SPECIALIST, *JAVESELLA OPACA* (BEAMER) (FULGOROIDEA: DELPHACIDAE)

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Abstract.—Specialization on mosses, previously unknown in the Fulgoroidea and apparently also for any auchenorrhynchan, is reported for the delphacid planthopper *Javesella opaca* (Beamer). New state records for this seldom-collected species are Alabama, Georgia, Massachusetts, New York, North Carolina, South Carolina, and Tennessee. Nymphs developed mainly on the gametophores of common hair-cap moss, *Polytrichum commune* Hedw. (Polytrichaceae), on granite flatrocks and in other communities, and once were found on another polytrichaceous moss, *Polytrichastrum alpinum* (Hedw.) G.L. Sm. At Boggs' Rock, a granite flatrock in northwestern South Carolina, late instars overwintered in mats of *Polytrichum commune*, and adults developed by mid- to late March. The only macropterous adults (n = 5) observed from June 1996 to July 1998 were found between 10 April and 2 May 1997; all other adults were brachypters. First instars of the season's first generation appeared from mid- to late May, with adults appearing from mid-June to early July. The first instars observed in August were those of an overwintering generation. Fluctuations in the numbers of planthoppers are discussed in relation to the condition of moss colonies (green vs. drought stressed) and weather (precipitation, temperature, and evaporation). In the laboratory, nymphs fed on thicker stems of the moss. The use of mosses is considered a derived host association in the evolution of the Delphacidae.

Key Words: Insecta, Delphacidae, moss feeding, *Polytrichum commune*, *Polytrichastrum alpinum*, granite outcrops

> The large gaps in our knowledge of the bryosystem, coupled with the ubiquity of mosses, leaves great scope for original research by bryofaunal ecologists.
>
> —I.M. Kinchin 1990

Studies on insect-plant interactions have emphasized vascular plants, the Tracheophyta, including seedless groups such as ferns, but especially the more economically important gymnosperms and angiosperms among the seed plants. Even though insects of nonvascular plants (Bryophyta) generally have been neglected by researchers (Gerson 1969, Lawrey 1987), the insect fauna associated with bryophytes evidently is not notably diverse when only those phytophages known to complete their development on these plants are considered. Among bryophytes, insects are found mainly on mosses—Bryophyta *sensu stricto*—rather than on hornworts and liverworts. Moss-inhabiting insects, which are recorded for most of the hemimetabolous and holometabolous orders (Gerson 1969), can be found on both aquatic and terrestrial mosses. In many cases, whether the species use mosses for food or only for shelter is not known.

In the Homoptera, used in its traditional sense (the group is paraphyletic [e.g., von Dohlen and Moran 1995]), moss feeders include several sternorrhynchan groups: aphids, such as species of *Melaphis* Walsh, *Muscaphis* Börner, and *Myzodium* Börner (e.g., Patch 1938, Börner 1952, Müller 1973, Smith and Knowlton 1975, Richardson 1981, Moran 1989, Dolling 1991, Thomas and Lombard 1991), as well as certain ensign scales (Ortheziidae) (e.g., Kozár and Miller 1999, 2000) and mealybugs (Pseudococcidae) (Williams 1985). The use of mosses as true hosts by ortheziids is largely undocumented (Dolling 1991).

Bryophagy apparently has remained unknown in the Auchenorrhyncha (evidently also a paraphyletic taxon [e.g., Campbell et al. 1994, Sorensen et al. 1995, Hamilton 1996]). Dolling (1991) stated that all auchenorrhynchans feed on vascular plants. Herein bryophagy in the auchenorrhynchan superfamily Fulgoroidea is reported. I summarize data on the seasonality and habits of the delphacid planthopper *Javesella opaca* (Beamer) on common hair-cap moss, *Polytrichum commune* Hedw., and record nymphs and adults from the moss *Polytrichastrum alpinum* (Hedw.) G.L. Sm.; discuss fluctuations in the numbers of planthoppers relative to the condition of host colonies (green vs. brown and drought stressed) and weather conditions: precipitation, temperature, and evaporation; and suggest that mosses represent an evolutionarily derived host association in the Delphacidae. Seven new state records also are given for this seldom-collected species.

This contribution is dedicated to my friend and colleague, Craig A. Stoops, who called my attention to a delphacid he collected from moss when we were in the field in June of 1996. He helped make field collections and laboratory observations before he left Clemson University in January 1997.

MATERIALS AND METHODS

Study area.—Boggs' Rock (34°48.4′N, 82°41.6′W) in northwestern South Carolina was the main study site. It is 2.1 km north of Liberty, Pickens County, and lies just west of the intersection of U.S. highway 178 with state secondary road S-39-317 (Quarry Road). This granite-gneiss flatrock ranges in elevation from 262 to 293 m (Knox 1974). Several plant species endemic to granite flatrocks in the southeastern United States (e.g., McVaugh 1943, Shure 1999) are found at Boggs' Rock, but because permanent depression pools are absent (Knox 1974), flatrock endemics restricted to such pools also are lacking.

Host plants.—*Polytrichum commune* (Musci: Polytrichales: Polytrichaceae) is a dark green, robust, perennial moss of wide distribution in the New and Old Worlds except in tropical areas. Its leafy stems, rigid and erect (acrocarpic), are connected by an extensive system of subterranean rhizomes. Stems of this tall moss can reach a height of 45 cm (Crum 1976, Crum and Anderson 1981, Derda and Wyatt 1990). This dioecious moss reproduces asexually by vegetative branching and propagation from plant fragments, with some populations being maintained entirely by vegetative reproduction; it can also become established sexually from spores (Leslie 1975, Derda and Wyatt 1990, Wyatt and Derda 1997). Found on various acidic substrates in disturbed and natural communities, *P. commune* often is abundant on granite flatrocks. It is an important soil builder of the annual-perennial herb community of granite outcrops and a characteristic plant of that community. Its colonies or mats are persistent and often extensive (Burbanck and Phillips 1983, Derda and Wyatt 1990, Quarterman et al. 1993).

The moss variety on which the planthopper *J. opaca* was collected at Boggs' Rock and other rock outcrops is *P. commune* var. *perigoniale* (Michx.) Hampe. Plants of this variety are shorter and grow in denser tufts than those of the nominate variety (Crum and Anderson 1981). Of the many varieties of *P. commune* that have been described, *perigoniale* has been the one most consistently recognized by authorities (Zouhair et al. 2000). *Polytrichum commune* var. *perigoniale*, however, is not genetically distinct from the nominate variety (Derda and Wyatt 1990). Overlapping in range with *P. commune* var. *commune*, *P. commune* var. *perigoniale* might represent only a "dry land phase" of a species that grows mainly in wet habitats (Crum and Anderson 1981). Derda (1998) considered *P. commune* var. *perigoniale* merely a phenotype of dry, exposed soils (cf. Zouhair et al. 2000).

In the southern Appalachians, *J. opaca* was found on *Polytrichum commune* var. *commune* and *Polytrichastrum alpinum*, a polytrichaceous moss that also has been placed in *Pogonatum* and *Polytrichum* (Smith 1971, Crum and Anderson 1981, Smith Merrill 1992). This coarse species, usually 4–16 cm high with erect stems, is Holarctic and particularly widespread at northern latitudes (Crum and Anderson 1981).

Field sampling.—After *J. opaca* was discovered at Boggs' Rock in June 1996, I surveyed other southeastern granite outcrops (flatrocks and monadnocks) for the presence of the delphacid on *Polytrichum* species. The seasonality of *J. opaca* was followed at Boggs' Rock, the study areas corresponding with granite outcrop divisions B and C in Knox's (1974) floristic study.

I (or C.A. Stoops) visited Boggs' Rock seven more times at irregular intervals in 1996 and collected planthoppers by placing a white enamel pan (28 × 40 cm) into a thick mat of the moss and using an axe handle to tap the overlying stems over the pan. Planthopper nymphs were field sorted by size and recorded as either early (I, II) or later (III–V) instars, and the sex of adults and the condition of the moss colonies were noted. The number of individuals of *J. opaca* observed was not standardized but generally was 10. Nearly all individuals were replaced on the moss, although voucher material of both nymphs and adults was collected and deposited in the Clemson University Arthropod Collection (CUAC); adults also were deposited in the collection of S.W. Wilson, Central Missouri State University, Warrensburg.

Sampling at Boggs' Rock was conducted similarly in 1997 and 1998 but at more regular intervals than in 1996. I recorded the stage of the first 10 individuals of *J. opaca*—as early or late instars and adult males or females—found on the moss in Knox's (1974) outcrop division C, a colony of the host plant that became desiccated and brown without frequent rain. I also often recorded the stage of the first 10 individuals encountered in a supplemental sample from moss in a wetter area of the outcrop (Knox's division B). In 1997, after an initial collection in early January, I sampled weekly or biweekly from early March to late August; I also sampled in mid-September and early November. In 1998, samples were taken weekly (occasionally biweekly or every three weeks) from late February to late July when no more planthoppers were being collected, presumably because of drought conditions. After that, I sampled six more times from late August to late November in an attempt to collect *J. opaca*. Six additional attempts to collect the planthopper at Boggs' Rock were made from early April 1999 to late May 2002.

Fluctuations in planthopper numbers.—Data from the two nearest weather-recording stations were used to better interpret the numbers of planthoppers observed relative to the condition of moss colonies. The weather station at Pickens (34°53′N, 82°43′W) is about 10 km north of Boggs' Rock; the Clemson station (34°41′N, 82°49′W) is about 18 km southeast of the sample site.

Laboratory observations.—The work with *J. opaca* in the laboratory involved placing nymphs of several instars in plastic petri dishes or snap-cap vials that contained the gametophyte (1–5 stems) of common hair-cap moss. The feeding behavior of nymphs, presence of exuviae, and number of days of observation were noted, but the duration of nymphal stadia was not determined.

Javesella opaca (Beamer)
(Fig. 1)

Javesella opaca was described in the genus *Delphacodes* Fieber from Connecticut by Beamer (1948), who selected as holotype a male collected at Willimantic on 8 August 1946. His type series also included adults taken from 3 August to 2 September 1946, at Storrs, Conn. (14 ♂, 8 ♀); Dingmans Ferry, Pa. (6 ♂, 5 ♀); and Mountain Lake, Va. (1 ♂). The only additional published record is that of Maw et al. (2000) from Quebec, Canada; this delphacid was listed as a provincial record without a specific locality and was recognized as belonging to the genus *Javesella* (as "*Javasella*") Fennah (Maw et al. 2000). According to K.G.A. Hamilton (personal communication, 2002), the Quebec record of *J. opaca* is based on a total of 13 males and 3 females from Covey Hill (5 June) and Laniel (5 June, 20–21 July). New state records, based on the present study (see Material examined), are Alabama, Georgia, Massachusetts, New York, North Carolina, South Carolina, and Tennessee.

The transfer of *opaca* to *Javesella* by Maw et al. (2000), made in a checklist without discussion of this nomenclatural change, is the appropriate generic placement (S.W. Wilson, personal communication, 1996). Mainly on the basis of genitalic characters, the polyphyletic genus *Delphacodes* should be restricted to about 10 Old World species (Asche 1985, Bartlett and Dietz 2000).

Seasonal history.—Late instars of *J. opaca* overwintered in mats of common haircap moss. In contrast to the yellow or yellow-brown nymphs found during spring and summer, the overwintered nymphs were darker and sometimes fuscous. The darker coloration, similar to that observed in certain other delphacids (e.g., Wilson and McPherson 1981), was observed at Boggs' Rock by early November in 1996 and 1997 (late instars collected in New York in mid-August and some early instars from Massachusetts in early September also were dark). Adults first were seen in 1997 during sampling on 16 March and were present on 29 March in 1998. In both years, males appeared first, but sex ratios usually became female biased within three weeks after adults began to appear. Overwintered fifth instars were last seen on 10 April in 1997 (2 in sample of 10) and 5 April in 1998 (1 of 20).

First instars of the season's new generation first were observed on 23 May in 1997 and 12 May in 1998. Adults of this generation, almost all males initially, first were seen in the 19 June sample in 1997 and the 22 June sample in 1998. Several late instars (7 of 20) of the new generation were still present in 1997 on 20 July. Early instars of a partial (overwintering) generation were found on 4 August 1997. In 1998, apparently because of drought conditions, no nymphs or adults could be collected after early July.

Nearly all the adults observed from June 1996 to July 1998 were brachypters. Only five macropters were seen during the study, all between 10 April and 2 May 1997; the three that were collected were females. Adults were not found after mid-August, with only nymphs observed from then until mid- to late March of the following year.

Fluctuations in planthopper numbers.—The numbers of *J. opaca* observed fluctuated widely during the period of study, depending mainly on the amount of precipitation at Boggs' Rock. Available moisture, in turn, affected the condition of the moss colonies inhabited by the planthopper.

Despite the wide variation in the numbers of planthoppers that could be beaten from *Polytrichum*, at least 10 individuals usually could be found on each sample date; few, however, were found in July of 1998. Precipitation that year was about 160 cm at Pickens and about 156 cm at Clem-

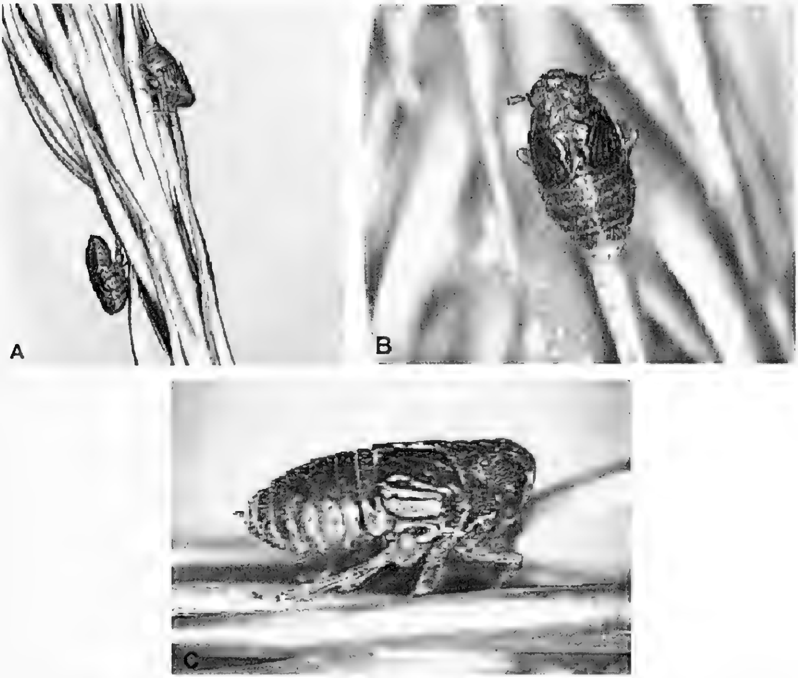

Fig. 1. *Javesella opaca.* (A) Females (brachypters) on leafy gametophyte of common hair-cap moss, *Polytrichum commune*; (B) dorsal and (C) lateral views of female.

son, figures that actually exceeded annual averages of 142 cm for Pickens (1952–2001) and 134 cm for Clemson (1930–2001). Looking only at total precipitation for 1998, however, is misleading; after substantial rains on 1 May (nearly 6 cm) and 8 May (>3.6 cm), rainfall was scant in the weeks preceding the planthopper's disappearance. At Pickens, precipitation for the last half of May was only 1.4 cm; rainfall for June totaled 13.6 cm, with nearly half of the total falling on the month's 20th day. After 20 June, only 0.3 cm of rain fell during the next 30 days, a period when daily maximum temperatures substantially exceeded normal highs. Temperatures were at least 32.2°C (90°F) from 21 June to 14 July, with nine consecutive days of 36.1–36.7°C (97–98°F). Evaporation at Clemson (data are unavailable for Pickens) exceeded rainfall by 15.2 cm for the 30 days following 20 June.

Only four adults and no nymphs were observed during regular sampling on 4 July 1998; seven adults were seen when a supplemental sample was taken on 6 July. No additional individuals were found during sampling on seven dates from 24 July to 29 November 1998. Two adult males were found in early April 1999, but *J. opaca* was not observed at Boggs' Rock in late March, mid-May, and mid-August 2000; in late March and early November 2001; or in late May 2002.

Habits.—*Javesella opaca* was found at Boggs' Rock in thick mats of common haircap moss in marginal areas of rock outcrops. Moss colonies harboring the planthopper grew beneath shrubs and small trees, particularly Chinese privet (*Ligustrum sinense* Lour.; Oleaceae) and eastern red-cedar (*Juniperus virginiana* L.; Cupressaceae). The delphacid was not found in more exposed colonies of the moss. Even when nymphs and adults were most numerous, they were difficult to detect on mats of *Polytrichum*; only occasionally were a few individuals observed on the surface of *P. commune* mats. The largest numbers of planthoppers—early instars only—were found on 8 June 1997. *Javesella opaca* had been difficult to find on 23 May 1997 when moss colonies were brown (a total of 9 individuals was observed in both the regular and supplemental samples), but on 8 June after recent rainfall, more than 30 first and second instars were found in each of three 1-pan samples from now green areas of moss. When nymphs were numerous, exuviae dislodged from moss also were observed during sampling.

In the southern Appalachians, *J. opaca* was found at an altitude of about 1,130 m on *Polytrichastrum alpinum* (Alleghany Co., NC). The moss was mostly obscured by various grasses. Populations of the planthopper also were found at about 1,685 m in mats of *Polytrichum commune* var. *commune* (Carter Co., TN).

When nymphs were placed in petri dishes or vials with sprigs of gametophyte from *Polytrichum commune*, they quickly (<5 min.) settled on the thicker stems and inserted their stylets. While feeding, nymphs (n = 10+) remained motionless, except for an occasional twitching of the legs, and typically stayed at one site for two hours or more. Only once was a clear drop of excretion or honeydew seen at the end of the anus. First instars were not reared to adulthood, but preliminary observations suggest that *J. opaca* could be easily reared on moss in the laboratory. Nymphs of various instars were maintained in a petri dish on the same sprigs of *P. commune* for 16 days and nymphal exuviae were observed. A first instar placed in a 4-dram vial with two moistened stems of moss molted once and was still alive after 27 days.

Material examined.—Adults from a locality are listed first, followed by a listing of any nymphs; when nymphs at Boggs' Rock were recorded in the field as early (I, II) and later (III–V) instars, the numbers of early and later instars are separated by a hyphen. An asterisk beside the word *nymph(s)* indicates that voucher material is housed in the CUAC. Collections were made by the author (no collector indicated), C.A. Stoops (C.A.S.), both of us (C.A.S. & A.G.W.), or W.K. Reeves (W.K.R.) from *Polytrichum commune,* except in Alleghany County, North Carolina, where the host was *Polytrichastrum alpinum* and in Pennsylvania where the host was identified as *Polytrichum* sp.

ALABAMA: Cherokee Co., Rt. 35, SE of Fort Payne, 31 Aug. 1996, 2 adults (sex undetermined), 10 Apr. 1997 (1 ♂, 9 ♀); Jackson Co., sandstone outcrop, Rt. 117, 0.3 km NW of jct. Rt. 71, Flat Rock, 10 Apr. 1997 (3 ♂, 4 ♀; 1 fifth instar). GEORGIA: Columbia Co., Heggie's Rock, E of Appling, 5 Apr. 1997 (4 ♂, 11 ♀), 26 Mar. 2002 (1 ♂; 1 fifth instar); Gwinnett Co., No Business Creek granitic outcrop, 2.6 km SSE of Snellville, 7 July 1996 (1 ♂), 26 Mar. 2002 (1 ♂, 4 ♀; 2 fifth instars). MASSACHUSETTS: Montague Sand Plains, 3.5 km N of Montague, 5 Sept. 2002 (1 ♂, 1 ♀; early instars). NEW YORK: Sullivan Co., Rt. 42, Forestburg, 3 Sept. 2002 (8 first through third instars); Ulster Co., Sam's Point Dwarf Pine Ridge Preserve, NE of Cragsmoor, 13 Aug. 2000 (12 ♂, 10 ♀; nymphs). NORTH CAROLINA: Alleghany Co., ca. 7 km ENE of Laurel Springs, 16 June 2002 (4 ♂, 1 ♀; late instars); Swain Co., Great Smoky Mountains National Park, nr. Ravens Fork, 8 Jan. 2001, W.K.R. (late instars). PENNSYLVANIA: Potter Co., NE of Keating Summit, 18 May 1997, C.A.S. (3 late instars). SOUTH CAROLINA: Pickens Co., Boggs' Rock, 2.1 km N of Liberty, 16–17 June 1996, C.A.S. & A.G.W. (adults, sex undetermined; 25+ nymphs); 22 June 1996, C.A.S. (adults; nymphs*: 1–2); 6 July 1996, C.A.S. & A.G. W. (7 ♂, 10 ♀; nymphs*:0–11); 20 July 1996, C.A.S. (adults; nymphs*:0–4); 18 Aug. 1996 (5 adults, sex undetermined; nymphs:11–4); 29 Sept. 1996, C.A.S. & A.G.W. (nymphs:3–7); 13 Oct. 1996, C.A.S. & A.G.W. (nymphs:10–0); 9 Nov. 1996, C.A.S. & A.G.W. (nymphs:10–0); 4 Jan. 1997 (nymphs*:0–19); 7 Mar. 1997 (nymphs*: 0–11); 16 Mar. 1997, C.A.S. & A.G.W. (2 ♂; nymphs: 0–10); 21 Mar. 1997 (3 adults, sex undetermined; nymphs: 0–7); 4 Apr. 1997 (4 ♂, 4 ♀; nymphs*:0–2); 10 Apr. 1997 (3 ♂, 5 ♀; nymphs: 0–2); 18 Apr. 1997 (4 ♂, 6 ♀); 25 Apr. 1997 (3 ♂, 7 ♀); 2 May 1997 (3 ♂, 7 ♀); 10 May 1997 (3 ♂, 6 ♀; nymph:0–1); 23 May 1997 (2 ♂, 4 ♀; nymphs:2–0); 8 June 1997 (nymphs*:7–4); 19 June 1997 (3 ♂, 2 ♀; nymphs*:0–9); 29 June 1997 (2 ♂, 4 ♀; nymphs*:1–3); 5 July 1997 (3 ♂; nymphs*: 2–5); 13 July 1997 (11 ♂, 3 ♀; nymphs*: 2–4); 20 July 1997 (10 ♂, 3 ♀; nymphs*: 2–5); 4 Aug. 1997 (6 ♂, 2 ♀; nymphs*:11–1); 17 Aug. 1997 (nymphs*:8–1); 14 Sept. 1997 (nymphs*:2–0); 2 Nov. 1997 (nymphs: first through third instars): 28 Feb. 1998 (nymphs*:0–6); 15 Mar. 1998 (nymphs:0–10); 22 Mar. 1998 (nymphs:0–10); 29 Mar. 1998 (3 ♂; nymphs:0–7); 5 Apr. 1998 (7 ♂, 3 ♀); 12 Apr. 1998 (5 ♂, 5 ♀); 24 Apr. 1998 (1 ♂, 9 ♀); 5 May 1998 (1 ♂, 2 ♀); 12 May 1998 (2 ♀; nymphs:8–0); 18 May 1998 (nymphs:10–0); 27 May 1998 (1 ♀; nymphs:9–0); 6 June 1998 (nymphs:8–12); 22 June 1998 (12 ♂, 1 ♀; nymphs:1–6); 4 July 1998 (3 ♂, 1 ♀); 6 July 1998 (6 ♂, 1 ♀); 4 Apr. 1999 (2 ♂); York Co., granite flatrock, Clover, 20 Apr. 1997 (3 ♀; 1 fifth instar). TENNESSEE: Carter Co., Carver's Gap, Roan Mountain, 27 October 2002 (late instars).

DISCUSSION

When *J. opaca* was first collected from mats of *Polytrichum* in June of 1996, its presence on moss was considered incidental. I was unaware of any moss-feeding fulgoroids, a group in which adults of many species, including delphacids, can be found on plants that do not support nymphal development (e.g., DuBose 1960, Wilson et al. 1994). Because seeds of various angiosperms accumulate, germinate, and survive in mats of mosses (McVaugh 1943), even the planthopper nymphs collected from moss might have been associated with vascular plants, such as grasses or sedges, that were growing within the *Polytrichum* colonies. Delphacids develop mainly on monocots, especially grasses and sedges (Wilson et al. 1994). *Javesella kilmani* (Van Duzee) and *J. stali* (Metcalf) are associated with an aberrant host, the vascular cryptogam (sphenophyte) horsetails, *Equisetum* spp. (Equisetaceae) (Strickland 1940, Ossiannilsson 1978).

A consistent collection of nymphs and adults of the delphacid from *P. commune* at Boggs' Rock and elsewhere, coupled with observations of its moss-feeding behavior in the laboratory, soon indicated that *J. opaca* was a true bryophage. It can be regarded as a bryophilous species or a bryobiont (*sensu* Gerson 1982)—that is, an animal associated exclusively with bryophytes. As such, *J. opaca* becomes the first known bryophagous fulgoroid and apparently also the first auchenorrhynchan known to develop on mosses. Somewhat similarly, the first known bryophagous species of the largest family of Heteroptera, the Miridae, only recently was discovered (Yasunaga 2000; see also Wheeler 2001).

My collection of *J. opaca* in North Carolina on *Polytrichastrum alpinum* might shed light on how Beamer (1948) was able to collect 22 adults of this planthopper at a locality in Connecticut and 11 adults in Pennsylvania without associating the species with mosses. When I collected the first specimens of *J. opaca* in North Carolina while sweeping grasses, I was unaware of the polytrichaceous moss growing under the grasses. Beamer probably would not have looked for delphacids in extensive mats of *Polytrichum commune* because no auchenorrhynchans were then known from mosses. He more likely would have swept the planthopper from the erect stems of *Polytrichastrum alpinum* (or another moss of similar growth habit) that grew beneath grasses, plants that are common hosts of Delphacidae. Delphacids should be more readily swept from a moss such as *Polytrichastrum alpinum* that grows in loose tufts than from one such as *Polytrichum commune* that has a more densely tufted (cespitose) growth habit. Even if Beamer had noticed the mosses while he swept grasses, he likely would not have associated the planthopper with a nonvascular plant.

The Delphacidae appear not to have diversified on mosses. Except for *J. opaca,* all other delphacids for which nymphal hosts are known develop on vascular plants. Fulgoroids and other homopterans that feed on plants other than angiosperms or on fungi likely are derived from angiosperm feeders (e.g., Wilson et al. 1994; see also Hamilton 1990). Even though *J. opaca* belongs to an "advanced" lineage (Stenocraninae-Plesiodelphacinae-Delphacinae) of the Delphacidae and belongs to the most morphologically advanced tribe of the most advanced delphacid subfamily (see Asche 1985, 1990; Emeljanov 1995), moss feeding by this planthopper might represent an ancient or relictual host relationship for the family. More likely, however, is that in the Delphacidae the use of mosses reflects a one-time host shift and an evolutionarily derived host association.

Bryophagy in the Delphacidae, a phloem-feeding group (e.g., O'Brien and Wilson 1985, Denno et al. 1987, Wilson et al. 1994, Watanabe and Kitagawa 2000), might have been predicted for polytrichaceous mosses. Although mosses are considered nonvascular plants (Buck and Goffinet 2000), the long-distance conducting systems of certain members of the Polytrichaceae are similar in structure and function to those of simple vascular plants (Tansley and Chick 1901, Thomas et al. 1988). Water moves in elements called hydroids; photosynthate, principally sucrose, moves in leptoids that are similar to sieve elements in the phloem of higher plants. Among mosses that have been studied, the conducting cells of *Polytrichum commune, Polytrichastrum alpinum,* and certain other polytrichaceous species are the most structurally complex (Collins and Oechel 1974, Behnke 1975, Scheirer 1980, Reinhart and Thomas 1981, Richardson 1981, Thomas et al. 1990).

The moss-feeding mirid described as a new species by Yasunaga (2000) belongs to a group of heteropterans that are mainly cell-content feeders on mesophyll rather than vascular-tissue feeders (Wheeler 2001). The mirid would not necessarily need to feed on a moss with a conducting system similar in structure to that of vascular plants. *Javesella opaca,* however, as a presumed phloem feeder, is likely restricted to polytrichaceous mosses with well-developed conducting cells. It might be more host restricted than are many other bryophagous insects (Gerson 1982, Lawrey 1987). In fact, most delphacids (74%) are recorded from a single plant genus (Wilson et al. 1994).

Javesella opaca might feed on gametophores of common hair-cap moss in a manner similar to that of the aphid *Myzodium modestum* Hottes on the same moss species (Thomas and Lombard 1991). The planthopper, however, does not feed in aggregations as does the aphid and might not alter the translocation of sugars in internal conducting tissues of the moss, as Thomas and Lombard (1991) demonstrated for the aphid. Occasional production of honeydew droplets by the sucrose-feeding *M. modestum* (Thomas and Lombard 1991) agrees with my observations on *J. opaca,* which presumably also feeds on photosynthate of common hair-cap moss.

Javesella opaca has been collected mainly on thick mats of *Polytrichum commune* in both natural and disturbed communities. This planthopper might also be found on *Polytrichastrum ohioense* (Ren. & Card.) G.L. Sm. In fact, Knox (1974) recorded *Polytrichastrum ohioense* as the only polytrichaceous moss at Boggs' Rock, but his voucher material actually is *Polytrichum commune* (L.E. Anderson, personal communication, 2002). Both polytrichaceous species can be found on granite outcrops (e.g., Oosting and Anderson 1939, McVaugh 1943), but *Polytrichum commune* is a characteristic plant of granite flatrocks and apparently is the dominant hair-cap moss in granite outcrop communities in Georgia and elsewhere in the southeastern states (e.g., Burbanck and Phillips 1983, Quarterman et al. 1993, Murdy and Carter 2000).

Given the persistence of *Polytrichum* colonies and the stability of granite flatrock communities, the observed low incidence (<3%) of macroptery might have been expected for *J. opaca* because dispersal might not be critical to the continuity of a planthopper population that lives in such a relatively stable or permanent habitat (e.g., Wagner and Liebherr 1992). From June 1996 to July 1998, the delphacid typically was observed at Boggs' Rock in small numbers when rainfall was scant and its host was metabolically inactive, but it could be collected in greater numbers from still green colonies of the moss in wetter areas of the flatrock. The more consistent availability of moisture in these wetter colonies apparently allowed egg hatch to continue, which sometimes led to asynchrony in the development of hopper populations in desiccated compared to greener host patches.

In 1998, a year of above-average precipitation, the delphacid was not found after early July. Apparently the low and uneven distribution of rainfall in late spring and early summer, combined with consecutive days of unusually high temperatures and evaporation, severely reduced the densities of *J. opaca* in the two sample areas at Boggs' Rock. Adults and nymphs were no longer seen, even in the usual wetter moss colonies, which had become desiccated. Although temperatures within green mats of *P. commune* generally are lower than those at the surface, desiccated mats are marked by internal temperatures higher than those of the ambient air (Leslie 1975). Other groups of arthropods, such as collembolans and mites, were scarce in 1998 when moss colonies were brown and dry. In contrast to the planthopper, collembolans and mites reappeared in numbers following abundant rainfall. That only two adults of *J. opaca* have been collected at Boggs' Rock since July 1998, even when moss was lush, suggests that its populations were substantially reduced during periods of low rainfall in the summer of 1998 rather than being found deeper in moss and, therefore, perhaps more difficult to dislodge from desiccated colonies of the host.

In the southern Appalachians, mats of *Polytrichum commune* in high-elevation mesic communities, such as grassy balds, would be constantly moist and should be considered an even more permanent habitat than the periodically dry mats of the moss in granite outcrops. The degree of brachyptery in *J. opaca* might be studied in populations occupying both permanent and less stable habitats. That this planthopper primarily ingests sucrose translocated in moss leptoids, as apparently is the case in several other moss-feeding hemipterans, requires verification. Also needed are surveys for additional moss species that might serve as hosts and studies of basic life-history parameters such as fecundity, longevity, and duration of the immature stages (eggs were not found in the present study), as well as observations on mating and oviposition behavior. In addition, the studies on nutritional ecology that Lawrey (1987) suggested be conducted on moss-feeding arthropods in general are appropriate to the research needs for *J. opaca*.

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THE AFROTROPICAL *OMMATIUS FLAVIPENNIS* SPECIES GROUP (DIPTERA: ASILIDAE), WITH DESCRIPTIONS OF SIX NEW SPECIES

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Abstract.—A new Afrotropical species group, *Ommatius flavipennis,* including six species (***O. angustus*, n. sp., *O. callidus*, n. sp., *O. flavipennis*, n. sp., *O. nigrantis*, n. sp., *O. pernecessarius*, n. sp.**, and ***O. perscientus*, n. sp.**) are reported. The species group and species are diagnosed, described, and compared with similar species. Illustrations of the right wing of the male and terminalia of all species and a key to the species are provided. Comments on the distribution are included.

Key Words: Diptera, Asilidae, *Ommatius* Wiedemann, *flavipennis* species group, new species, Afrotropical

Ommatius Wiedemann (1821) is a large, widespread Ommatiine (Diptera: Asilidae) genus in the Afrotropics that has received little attention until recently (Scarbrough and Marascia 1996, 2000; Scarbrough 2002a). Eighty species (Oldroyd 1980) are assigned to this genus of which 46 are from Africa. However, preliminary studies indicate that a considerable number of undescribed species from Africa will require formal names and descriptions. Several additional taxonomic problems exist within this genus that must be resolved before phylogenetic relations can be accessed and comprehensive keys to the African species can be constructed. Thus far the genus *Emphysomera* Schiner (1996, 1999) and the subgenus *Metommatius* (Scarbrough and Marascia 2000) have been revised. Further, we redescribed two species, designated types for *O. tenellus* van der Wulp and designated a replacement name (*O. abdelkuriensis* Scarbrough) for *O. tibialis* Richardo (Scarbrough 2002a). The purpose of this paper is to report a new Afrotropical species group, *O. flavipennis,* including six new species.

METHODS

The descriptive terminology follows McAlpine (1981). Dissections of the terminalia and preparation of illustrations of external and internal parts follow Scarbrough and Marascia (1999, 2000) and Scarbrough (2002b). Descriptions are composites of all specimens examined. In recording label data, each line is demarcated by a slash (/). Square brackets are used for additional information not present on labels. Ratios used in the descriptions are as follows: Head-face ratio [HFWR] = the greatest anterior distance across divided by the width of the face at the base of the antenna; flagellum width-length ratio [FWLR] = the length divided by the greatest width of the flagellum; cell m_1 width ratio [m_1WR] = width at the basal third [widest] and apical two-thirds [narrowest] divided by the basal width; hind femoral width-length ratio [HFWLR] = the length of the hind femur divided by its greatest width. All measurements were made of pinned specimens. Structures in illustrations are labeled only for the first species and are not repeated for comparable structures of the following species. Morphological structures illustrated in different positions have a single scale line.

Specimens used in this study are housed in the following Institutions: The Natural History Museum, London (BMNH); California Academy of Sciences, San Francisco (CASC); Canadian National Collection, Ottawa (CNCI); Natal Museum of South Africa, Pietermaritzburg (NMSA); Musée Royal de L'Afrique Centrale, Tervuren (MRAC); Muséum National d' Histoire Naturelle, Paris (MNHN); Hope Entomological Collection, The University Museum, Oxford (OXUM), and The Natural History Museum of Zimbabwe, Bulawayo (NMZB). Acronyms of institutions herein follow Arnett et al. (1993).

TAXONOMY

The Afrotropical *Ommatius flavipennis* species group

Diagnosis.—*Ommatius flavipennis* species are readily recognized by the following combination of characters. 1) Abundant, long setae below the head and proboscis, length about as long as proboscis; long flagellum, 1.7–3.0 longer than wide; dorsal facial setae usually long, ⅓–½ as long bristles. Anepimeral bristle present. 2) Wing (Figs. 1–6) mostly or entirely dense microtrichose. Cell r_4 long, narrowly triangular with base at or just beyond apex of cell d; vein R_4 strongly arched basally, slightly concave or angled posteriorly before wing margin. 3) Middle and femora with 2 ventral rows of stout bristles, those of hind femur extend from base to or near apex. 4) Apical sternites of abdomen with sparse erect bristles except in *nigrantis* and *perscientus.* 5) Epandrium (Figs. 7, 17, 27, 47, 57) usually narrow except wide apically in *nigrantis,* apex pointed, curved dorsally in *nigrantis* (Fig. 37). 6) Aedeagus (Figs. 10, 20, 30, 40, 50, 60) tubular, flattened dorsoventrally, with wide base and apex, narrowed medially; ventral keel and flared apex present Figs. 12, 22, 32, 42, 52, 62). 7) Spermatheca (Figs. 15, 25, 35, 55) long and tubular, with wide base and narrow apex, usually recurved or looped, except short, carrot-shaped in *nigrantis* (Fig. 45).

Remarks.—Whereas most *Ommatius* species are superficial similar externally, the structure of the terminalia is the primary means of identification of species and species groups. The long setation of the head, presence of two rows of ventral bristles below the middle and hind femora, length and shape of cell r_4, and shape of the aedeagus readily separate the *flavipennis* species group from all known Afrotropical congeners. The length and shape of cell r_4 of *O. longipennis* (Linder 1955) is similar to all members of the *O. flavipennis* but differs in the other characters listed above. It is further similar to *O. perscientus* in the the narrow, mostly sparse setose face, thin brown tomentose mesonotum, and brown veins and microtrichia. However, *Ommatius perscientus* differs significantly from *O. longipennis* in the combined characters of the terminalia. Species of the subgenus *Metommatius* Hull (Scarbrough and Marascia 2000) and *O. tenellus* van der Wulp (Scarbrough 2002a) also differ in the presence of glabrous stripes or spots on the mesonotum, wing venation, and characters of the terminalia. The former differs further in the absence of marginal scutellar bristles and rows of ventral bristles below the middle and hind femora.

Distribution.—The species group is widespread in middle Africa, ranging from southern Ethiopia westward to Nigeria and southward to Angola and Zimbabwe. However, five species (*O. callidus, O. flavipennis, O. nigrantis,* and *O. pernecessarius, O. perscientus*) are concentrated in the eastern half of the continent although *O. pernecessarius* ranges westward to Nigeria. *Ommatius angustus* is known only from the Lubango and Huambo regions of Angola. All species were captured [where data given] between 1100 and 2100 meters in savanne and low mountain forests.

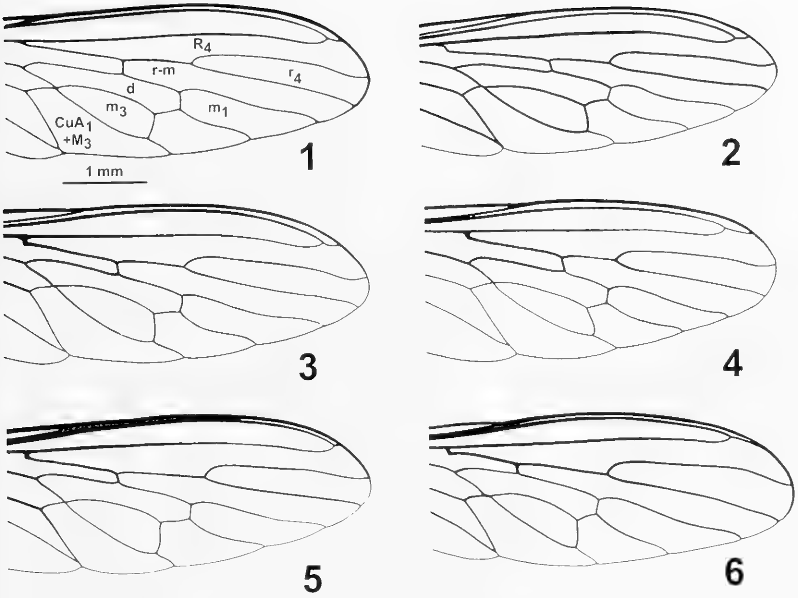


Fig. 1–6. *Ommatius* spp., right wing. 1, *O. angustus*. 2, *O. callidus*. 3, *O. flavipennis*. 4, *O. nigrantis*. 5, *O. pernecessarius*. 6, *O. perscientus*. R_4 = radial vein, r_4 = radial cell, r-m = radial-medial crossvein, d = cell d, m_1 = medial cell, m_3 = medial cell, CuA_1+M_3 vein.

KEY TO THE AFROTROPICAL *OMMATIUS FLAVIPENNIS* SPECIES GROUP

1. Mesonotum dorsally brown tomentose, diffused paramedial stripes sometimes present; ocellar tubercle with 4–5 long setae; postocular bristles long, thin, strongly proclinate, apex of bristles well forward of posterior margin of eye; sternites of female with only thin setalike bristles 2

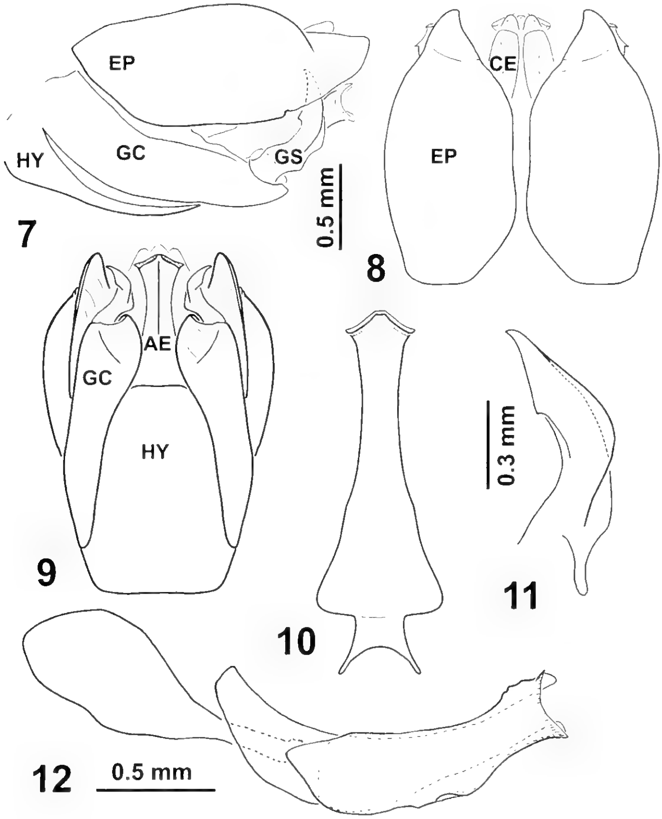
– Mesonotum dorsally with two, narrow, contrastingly brown tomentose paramedial stripes; ocellar tubercle with only 2 long setae; postocular bristles thick and short, tips usually just forward of eye margin posteriorly, well behind ocellar tubercle; body yellow tomentose; apical sternites of female with few to several yellow bristles 3

2. Fore and middle femora black, narrow base sometimes yellow; abdomen unusually flat, clavate apically; mesonotum posteriorly, scutellum entirely, and basal segments of abdomen gray tomentose; wing and terminalia as in Figs. 4, 37–46); Democratic Republic of Congo, Tanzania . . . . *nigrantis*, n. sp.

– Fore and middle femora yellow ventrally and posteriorly, dark brown dorsally and anteriorly; abdomen round in cross-section, neither flat nor spatulate; thorax and abdomen dorsally brown tomentose; wing and terminalia as in Figs. 6, 57–62); Zambia, Zimbabwe . . . . *perscientus*, n. sp.

3. Mesonotum with most lateral bristles yellow; gonostylus with a prominent concavity posteriorly (Figs. 11, 21, 31); aedeagus narrow apically, base much wider in dorsal view, midbasal 'shoulders' absent (Figs. 10, 20, 30), ventral keel variable (Figs. 12, 22, 32); sternite 8 of female with 1–4 prominent bristles apically, preapical, medioapical tubercle absent (Figs. 14, 24, 34); genital fork with narrow, constricted base (Figs. 26, 36, 46) 4

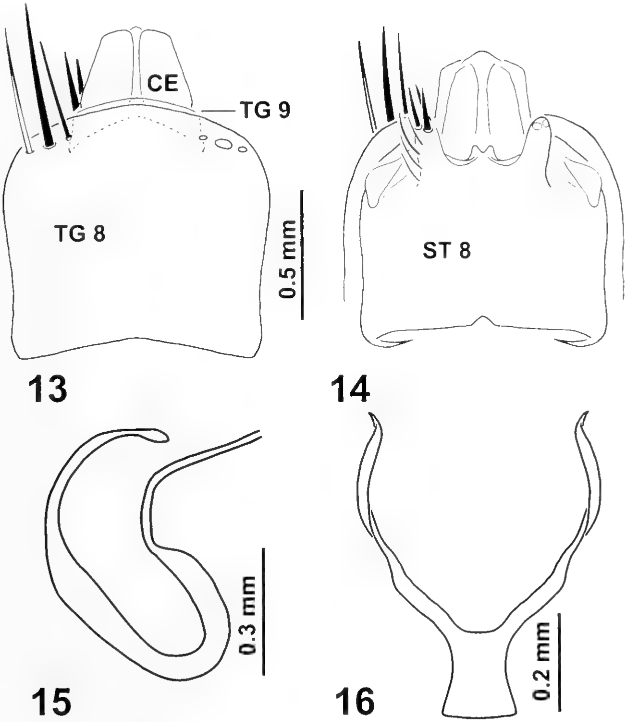
– Mesonotum usually with lateral bristles black; gonostylus without prominent concavity posteriorly (Fig. 51); aedeagus wide in dorsal



Figs. 7–12. *Ommatius angustus*, male terminalia. 7–9, Lateral, dorsal, and ventral views. 10, Aedeagus, dorsal view. 11, Left gonostylus. 12, Aedeagus, lateral view. AE = aedeagus, EP = epandrium, CE = cercus, GS = gonostylus, GC = gonocoxite, HY = hypandrium.

view, wide mid-basal 'shoulders' (Fig. 50) and strong ventral keel present (Fig. 52); sternite 8 of female without prominent bristles apically, a prominent, preapical, medioapical tubercle present (Fig. 54); spermatheca with a preapical constriction (Fig. 55); genital fork with wide base (Fig. 56); Burundi, Democratic Republic of Congo, Kenya, Malawi, Nigeria, Tanzania, Uganda, Zambia . . . . *pernecessarius*, n. sp.

4. Gonostylus angular (Figs. 27, 31); gonocoxite long, capitate apically in lateral view (Fig. 27); aedeagus unusually narrow in dorsal view, base abruptly wide (Fig. 30), prominent ventral keel present (Fig. 32); apical margin of sternite 8 of female evenly contoured, hornlike process absent, 2 flat bristles present (Fig. 34); spermatheca as in Fig. 35; Democratic Republic of Congo, Zambia, Zimbabwe . . . *flavipennis*, n. sp.
Gonostylus curved forward (Figs. 11, 21); gonocoxite shorter, sides even apically (Figs. 7, 9, 17, 19); aedeagus triangular in dorsal view, sides gradually widens posteriorly (Fig. 10, 20), keel as in Figs. 12, 22); apical margin of sternite 8 of female hornlike processes, each bearing prominent bristles (Figs. 14, 24); spermatheca as in Figs. 15, 25 5



Figs. 13–16. *Ommatius angustus*, female terminalia. 13–14, Dorsal and ventral views. 15, Spermatheca. 16, Genital fork. Abbr. TG8 = tergite 8, TG9 = tergite 9, CE = cercus, ST8 = sternite 8.

5. Gonostylus narrow, only slightly arched forward (Figs. 7, 11) aedeagus wide apically, apex oval, about as wide dorsally as laterally (Fig. 10), a moderate ventral keel present (Fig. 12); tergite 8 of female with lateral bristles oval, sides gradually narrowed from base to apex (Fig. 13); sternite 8 with deep, medioapical notch between prominent hornlike processes (Fig. 14); apex of spermatheca slightly swollen (Fig. 10); genital fork as in Fig. 11; Angola . . . . . *angustus*, n. sp.
– Gonostylus wide, strongly arched forward (Fig. 21); aedeagus narrow apically, apex much wider dorsally than laterally, a low ventral keel present (Figs. 20–22); tergite 8 of female with base of lateral bristles flat and wide, side abruptly narrows beyond (Figs. 23, 24); sternite 8 only slightly recessed, not strongly notched between short, hornlike processes (Fig. 24); apex of spermatheca not noticeable swollen (Fig. 25); genital fork as in Fig. 26; Democratic Republic of Congo . . *callidus*, n. sp.

TAXA

Ommatius angustus Scarbrough, new species

(Figs. 1, 7–16)

Male.—Body 15.9–17.0 mm; wing 12.3–12.5 mm. *Head:* Face yellow tomentose, dorsal half with black vestiture, dorsal setae abundant, ½–⅔ as long as bristles; FHWR 1.0:7.1–1.0:7.5. Antenna, frons, and ocellar tubercle black setose. Flagellum about as long as scape and pedicel combined; FWLR

1.0:2.0–1.0:3.2. Frons light-brown tomentose, setae longer than scape. Ocellar tubercle with 2 long setae, length subequal to scape and pedicel combined. Dorsal postocular bristles short, mostly black, longest seta with tip just forward of eye posteriorly.

Thorax: Mesonotum with 2 wide, brown, tomentose, paramedial stripes, fused anteriorly, and 2 lateral spots; 4 dorsocentral bristles present, most black, 1–2 yellow; 5 lateral bristles yellow, 1 notopleural bristle black. Scutellum with scattered, long, yellow setae and 2 yellow marginal bristles; weak preapical groove present. Anepimeral bristle yellow.

Wing (Fig. 1): Entirely yellow to yellowish-brown microtrichose. Anterior radial vein mostly yellow, brown apically. Cell m_1WR 1.0:1.8:1.6–1.0:1.9:1.6.

Legs: Femora mostly yellow with yellow bristles; fore and middle femora mostly black anteriorly, narrow apex black posteriorly; hind femur with narrow apex and narrow anterior stripe black, stripe present on apical ⅓–⅔; apical anteroventral bristle sometimes black. Middle femur with 4–5 ventral bristles in each row. HFWLR 1.0:4.3–1.0:5.1. Narrow apex of middle and hind tibiae brown. Tarsi yellow setose; basal 3 tarsomeres yellow, narrow apices sometimes brown; fore and middle tarsi with numerous yellow bristles laterally; hind tarsus with only 1 yellow bristle.

Abdomen: Mostly yellow to yellowish-gray tomentose, yellow setose; tergites 5–7 sparse, brown tomentose dorsally, black setose; apical corner of tergites 2–8 with 2–4 stout, usually yellow, bristles; sternites 2–7 usually with 1–4 stout yellow bristles apically.

Terminalia: Black (Figs. 7–12). Gonostylus narrow in lateral view, concave posteriorly. Aedeagus triangular dorsally, basal corners wide; wide in lateral view; low ventral keel present.

Female.—Differs as follows. Body 14.5–19.5 mm; wing 10.8–12.5 mm; FHWR 1.0:6.6–1.0:6.7; FWLR 1.0:2.8–1.0:2.9; m_1WR 1.0:2.1:1.9–1.0:2.5:2.4; HFWLR 1.0:5.1–1.0:5.6. *Head:* Occiput with 2–3 dorsal postocular bristles yellow. *Legs:* Fore tarsus with yellow bristles present on outer side only; hind femur with setigerous bristles only on basal ½; hind tarsus with only black bristles. *Abdomen:* Most tergites laterally and sternites apically with 2–4 stout, bristles, latter mostly yellow. *Terminalia* (Figs. 13–16): Sternite 8 mostly black, narrow apex red; apical margin strongly produced as hornlike processes, apex with 3–4 stout, black bristles.

Specimens examined.—Holotype ♂, ANGOLA: (A6)/Tundavala/9 mls NW Sa/da Bandeira [= Lubango, Huíla Plateau]/23.vii.1972/Southern/African Exp./B. M. 1972-1 (BMNH). Paratypes: 1 ♂, 3 ♀, same data as holotype (BMNH); 1 ♀, (A22), Nova Lisboa [= Huambo, Bié Plateau]/5–7.viii.1972/Southern/African Exp./B. M. 1972-1 (BMNH).

Etymology.—Latin *angustus* for narrow passage, referring to the gorge at Tundavala.

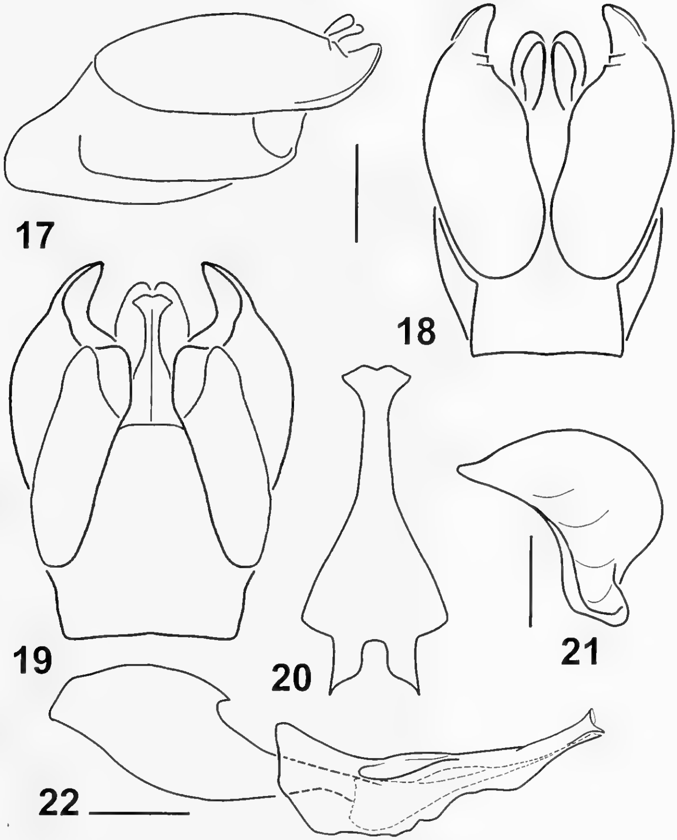
Distribution.—Montane species [elevation 1676 m] capture in July and August on the Huíla and Bié Plateaus of west central and south central Angola.

Remarks.—The long narrow flagellum, yellow thoracic and femoral bristles, and combined characters of the terminalia (Figs. 7–16) especially the gonostylus and aedeagus of the male and segment 8 and spermatheca of the female distinguish *O. angustus* from congeners.

Ommatius callidus Scarbrough, new species

(Figs. 2, 17–26)

Male.—Body 19.3–20.3 mm; wing 12.5–12.7 mm. *Head:* Face with yellow vestiture, setae on dorsal ⅔ short, ⅓ as long as bristles; HFWR 1.0:6.7–1.0:8.0. Antenna, frons, and ocellar tubercle black setose; pedical rarely scattered yellow setose. Flagellum less than scape and pedicel combined; FWLR 1.0:1.9–1.0:2.2. Frons ventrally with setae slightly longer than scape. Ocellar tubercle with 2 setae about ⅔ as



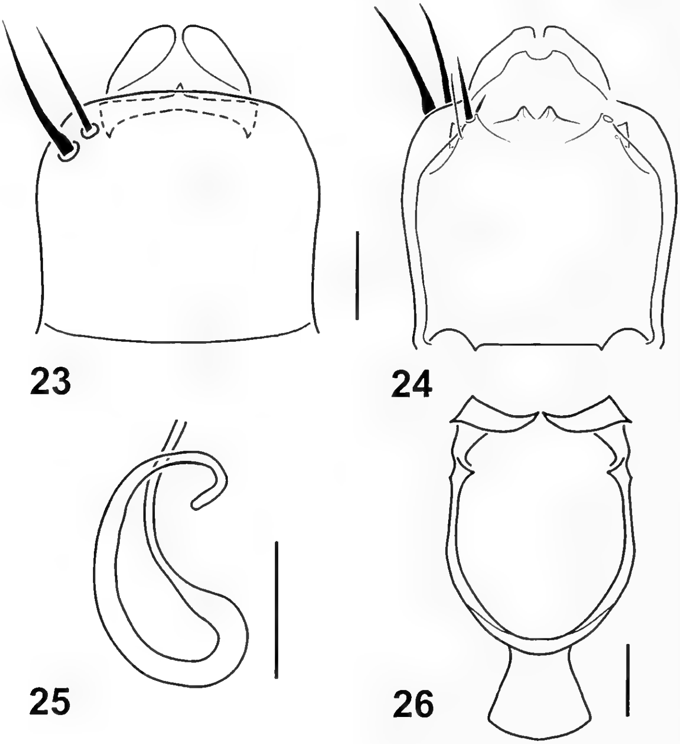
Figs. 17–22. *Ommatius callidus*, male terminalia. 17–19, Lateral, dorsal, and ventral views. 20, Aedeagus, dorsal view. 21, Left gonostylus. 22, Aedeagus, lateral view.

long as scape and pedicel combined. Postocular bristles yellow, rarely with 1–2 black; bristles short, longest with tip just forward of eye posteriorly.

Thorax: Mesonotum with 2 wide, brown, tomentose, paramedial stripes, fused anteriorly, and 2 lateral spots; bristles mostly yellow; 7–8 dorsocentral bristles present; 2–3 dorsocentral and 1 notopleural bristles usually black. Scutellum with long, yellow setae and yellow marginal bristles; preapical groove absent. Anepimeral bristle yellow.

Wing (Fig. 2): Entirely yellow to brownish-yellow microtrichose. Anterior radial veins yellow basally. Cell m_1WR 1.0:2.3: 2.0–1.0:2.8:2.3.

Legs: Femora mostly yellow, narrow apices brown; ventral bristles usually yellow; fore and middle femora mostly brown



Figs. 23–26. *Ommatius callidus*, female terminalia. 23–24, Dorsal and ventral views. 25, Spermatheca. 26, Genital fork.

anteriorly, hind femur anteriorly with narrow brown sometimes on apical ⅓–½. Middle femur with 2–3 black anteroventral bristles. HFWLR 1.0:4.1–1.0:4.3. Narrow apex of 2, sometimes 3, tibiae brown. Tarsi mostly yellow setose; basal 3 tarsomeres yellow, narrow apices often brown; each tarsus with several yellow bristles.

Terminalia (Figs. 17–22): Gonostylus wide, strongly arched forward, wide concavity posteriorly. Aedeagus with wide apex and base in dorsal view, triangular, narrow in lateral view; ventral keel weak.

Female.—Body 17.3–18.3 mm; wing 15.0 mm; HFWR 1.0:6.2–1.0:7.3; FWLR 1.0:2.3–1.0:2.6; m_1WR 1.0:2.3:3.0–1.0:3.0:2.6; HFWLR 1.0:4.9–1.0:5.3. *Thorax:* Two to 4 dorsocentral and 2 notopleural bristles sometimes black. *Legs:* Fore and middle femora yellow, only narrow apex black; middle femur with 1 anterior and 2 anteroventral bristles black. *Abdomen:* Lateroapical margin of tergites and scattered on most sternites with yellow bristles. *Terminalia* (Figs. 23–26): Sternite 8 red, apical margin produced medially, short processes with 1–2 black bristles apically, each process separated medially by shallow concavity bearing a divided tubercle.

Specimens examined.—Holotype ♂,

DEMOCRATIC REPUBLIC OF CONGO: Musée du Congo/Lulua Riv. Luele/1928/Dr. Walker (MRAC). Paratypes: 5 ♂, 4 ♀, same data as holotype (MRAC).

Etymology.—Latin *callidus*, meaning skillful, refers to the hunting ability of asilids.

Distribution.—Captured along the Lulua Rivers in southeastern Democratic Republic of Congo.

Remarks.—The short facial, frontal, and ocellar setae, the yellow postocular and mesonotal bristles, and combined characters of the terminalia (Figs. 17–26), especially the gonostylus and aedeagus of the male and segment 8 and spermatheca of the female distinguish *O. callidus* from congeners.

Ommatius flavipennis Scarbrough, new species

(Figs. 3, 27–36)

Male.—Body 13.9–17.3 mm; wing 9.8–11.2 mm. *Head:* Face with yellow and black setae dorsally, setae about ½ as long as bristles; FHWR 1.0:5.9–1.0:7.0. Antenna, frons, and ocellar tubercle black setose. Flagellum as long as scape and pedicel combined; FWLR 1.0:2.7–1.0:3.0. Frons brownish yellow to red-brown tomentose. Ocellar tubercle with longest setae about as long as scape and pedicel combined. Occiput with black postocular bristles usually extends to dorsolateral or midlateral margin of eye; dorsal bristles with apices just beyond posterior margin of eye.

Thorax: Mesonotum dorsally largely brown tomentose, paramedial stripes and lateral spots present in best specimens; 5 lateral and 5–6 dorsocentral bristles present, most black, often 2–3 dorsocentral and 2–3 lateral bristles yellow. Scutellum with scattered, long setae and yellow marginal bristles; shallow preapical groove present. Anepimeral bristles yellow.

Wing (Fig. 3): Entirely yellow to brownish-yellow microtrichose. Anterior 2–3 radial veins yellow basally. Cell m_1WR 1.0:3.2:2.6–1.0:3.0:2.7.

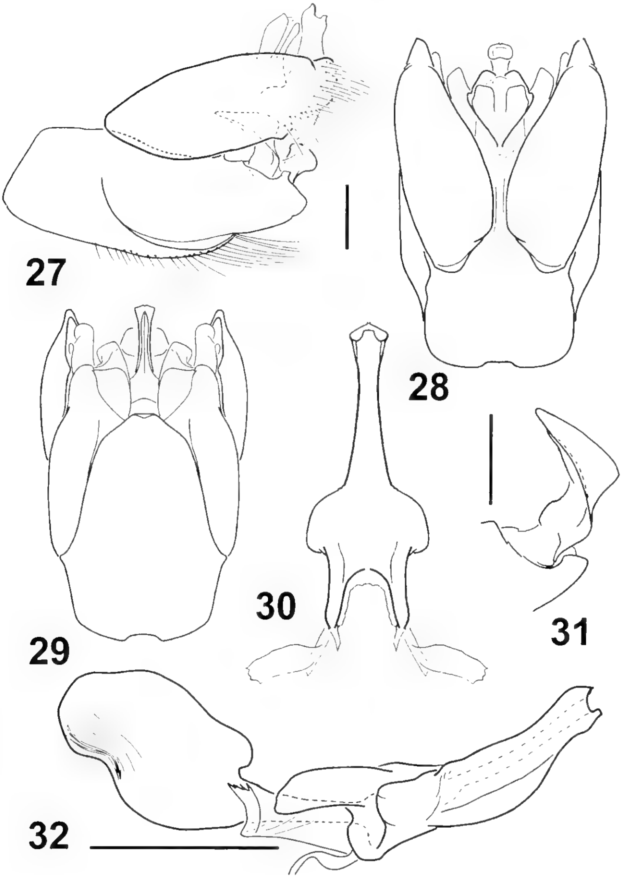
Legs: Fore and middle femora dark brown anteriorly and narrow apices posteriorly, yellow otherwise. Middle femur with 4 black bristles, 1 anteriorly and 3 anteroventrally; posteroventral bristles yellow. Hind femur yellow with narrow apex black, black variable anteriorly as a narrow or wide streak, often mostly black anteriorly; ventral bristles yellow; HFWLR 1.0:4.6–1.0:5.4. Tarsi mostly yellow setose; basal 2–3 tarsomeres light, usually yellow with apex brown; each tarsus with 5–12 yellow bristles.

Abdomen: Dark brown with yellow to yellowish-gray tomentum and yellow vestiture; each tergite dorsally with brown tomentum, light brown on basal segments, grading to dark tomentum on apical tergites. Apical margins of tergites 2–7 laterally with 2 yellow bristles; apical corner of sternites 3 and 4 with 1–2 thick yellow bristles, remaining sternites with bristly setae.

Terminalia (Figs. 27–32): Gonostylus strongly angular, L-shaped, deep concavity posteriorly. Gonocoxite apically capitate. Aedeagus narrow in dorsal view, base abruptly wide; wide in lateral view; prominently ventral keel present.

Female.—Differs from males as follows. *Face:* Dorsal ½–⅔ black setose; FWLR 1.0:3.1. *Legs:* Middle femur with only yellow bristles. Hind femur often with only narrow apex black. Basal 3 tarsomeres of fore and middle tarsi and basal 2 of hind tarsus mostly yellow. *Abdomen:* Apical margin of tergites 2 and 3 laterally with 3–4 and tergites 4–7 with 2 yellow bristles; tergite 8 with 3 black bristles. Sternites 3–7 with several, scattered, yellow bristles. *Terminalia* (Figs. 33–36): Sternite 8 with apical margin slightly produced medially, 2 flat, black bristles present mediolaterally.

Species examined.—Holotype ♂, ZAMBIA: Sakeji River [1400 m. elev.]/Ikelenge/N. Mwinilungo/Nat Mus Bulawayo/13–14.iv.1972/Pinley-de Moor Exp. (NMZB). Paratypes: DEMOCRATIC REPUBLIC OF CONGO: 1 ♂, 2 ♀, Congo Belge: P.N.U./Mbuywe-Bala (1,750 m)/25–31.iii.1948/Mis. G. F. de Witte (MRAC). ZAMBIA: 2



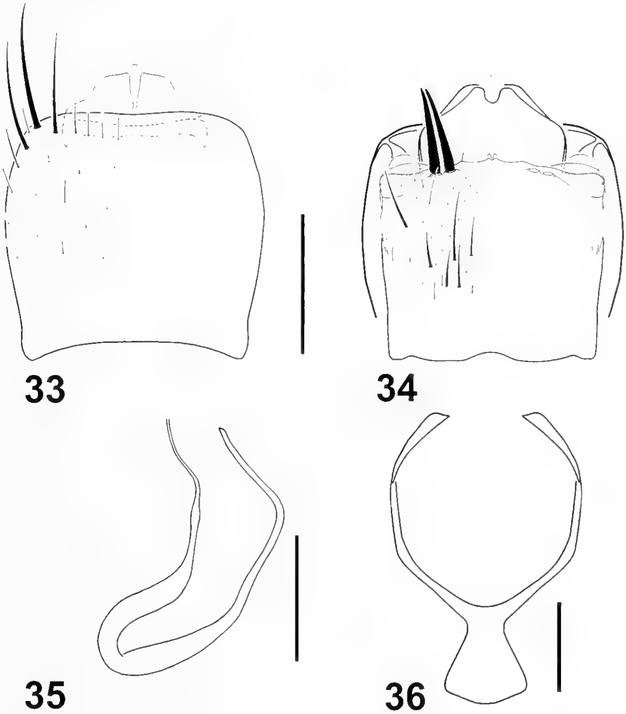
Figs. 27–32. *Ommatius flavipennis*, male terminalia. 27–29, Lateral, dorsal, and ventral views. 30, Aedeagus, dorsal view. 31, Left gonostylus. 32, Aedeagus, lateral view.

♂, 1 ♀, same data as holotype; 2 ♂, Mrushi R./80 m E of Kapiri/7.iii.1969/Pinhey-de Moor Exp (NMZB); 1 ♂, 35 mi S of Ndola/30.i.1965/Nat Museum S Rhodesia (NMZB). ZIMBABWE: 1 ♂, 1 ♀, Crocodile Pool Farm Blanket/Nat Museum S Rhodesia/15.xii.1977/D.K.B. Wheeler (NMZB).

Etymology.—Latin, *flavipennis*, combination of *flavus* for yellow and *pennis* for wing, referring to the color of the wing.

Distribution.—Captured from December through April at altitudes between 1400–1750 meters along the river basin Plateaus of southern Democratic Republic of Congo, Zambia, and Zimbabwe.

Remarks.—The narrow flagellum, black setae on the dorsal half of the face, and



Figs. 33–36. *Ommatius flavipennis,* female terminalia. 33–34, Dorsal and ventral views. 35, Spermatheca. 36, Genital fork.

combined characters of the terminalia (Figs. 27–36), especially the wide aedeagus with a midbasal constriction and prominent ventral keel, the short angular gonostylus, the capitate gonocoxite of the male and characters of segment 8 and spermatheca of the female distinguish *O. flavipennis* from congeners.

***Ommatius nigrantis* Scarbrough, new species**

(Figs. 4, 37–46)

Male.—Black body with unusually long, yellow and black setae, black femora, and a flat, spatulate abdomen. Body 11.7–12.9 mm; 7.8–10.0 mm. *Head:* Face entirely with long vestiture of uniform thickness, thick bristles absent; vestiture ventrally more dense, about as long as proboscis, and yellow; that on dorsal ¾ of face black; HFWR 1.0:6.2–1.0:6.5. Antenna, frons, and ocellar tubercle black setose. Flagellum subequal to scape and pedicel combined; scape with long ventral setae extending beyond base of flagellum; FWLR 1.0:2.1–1.0:2.2. Frons yellow brown to brown tomentose; setae as long as scape and pedicel combined. Ocellar tubercle with several long setae, apex of longer seta well beyond base of flagellum. Numerous black postocular bristles present, bristles extending to or beyond midlateral margin of eye; bristles thin and strongly proclinate with apex of longest dorsal bristle at or just before ocellar tubercle.

Thorax: Mostly yellow to yellowish-gray tomentose. Mesonotum with wide, brown tomentose stripe medially and 2 spots laterally, paramedial lines indistinct; prescutellum broadly gray tomentose; vestiture mostly black and thin, anterior setae about as long as pedicel and scape combined; 9–10 long, setalike dorsocentral bristles present; 5–6 thick lateral bristles present, 1 often yellow. Scutellum with scattered black or yellow setae and 2 thin black bristles; longest setae as long as marginal bristles. Anepisternum dorsally with scattered black setae. Anepimeral bristle yellow.

Wing (Fig. 4): Entirely brownish yellow microtrichose. Veins brown. Cell m_1 WR 1.0:1.7:1.3–1.0:1.7:1.6.

Legs: Femora usually mostly dark brown or black with narrow bases yellow, rarely entirely dark; most bristles and setae yellowish to white; long ventral setae of fore and middle femora sometimes black; HFWLR 1.0:5.6–1.0:5.8. Hind tibia with narrow apex black. Tarsi yellow setose; basal 2 tarsomeres yellow, narrow apices brown; bristles mostly black, 1–2 yellow fore tarsal bristles usually present.

Abdomen: Spatulate, junction of segments 2–3 ⅔ as wide as segments 6–7; tergites 1–4, tergite 5 narrow base and sides, and most sternites with thin gray tomentum, apical tergites shiny brown or black with purple highlights. Setae mostly yellow, long laterally with sparse black or yellow bristles on most tergites; tergites 1–3 entirely yellow setose, tergite 4 yellow setose basally and black apically, tergites 5–8 entirely black setose.

Terminalia (Figs. 37–42): Narrow, about ½ as wide as segment 6. Epandrium with apex flared, about as wide as base, small digitate ventroapical process present. Gonostylus narrowed apically, posterior concavity absent. Aedeagus narrow apically, sigmoid, apex flared.

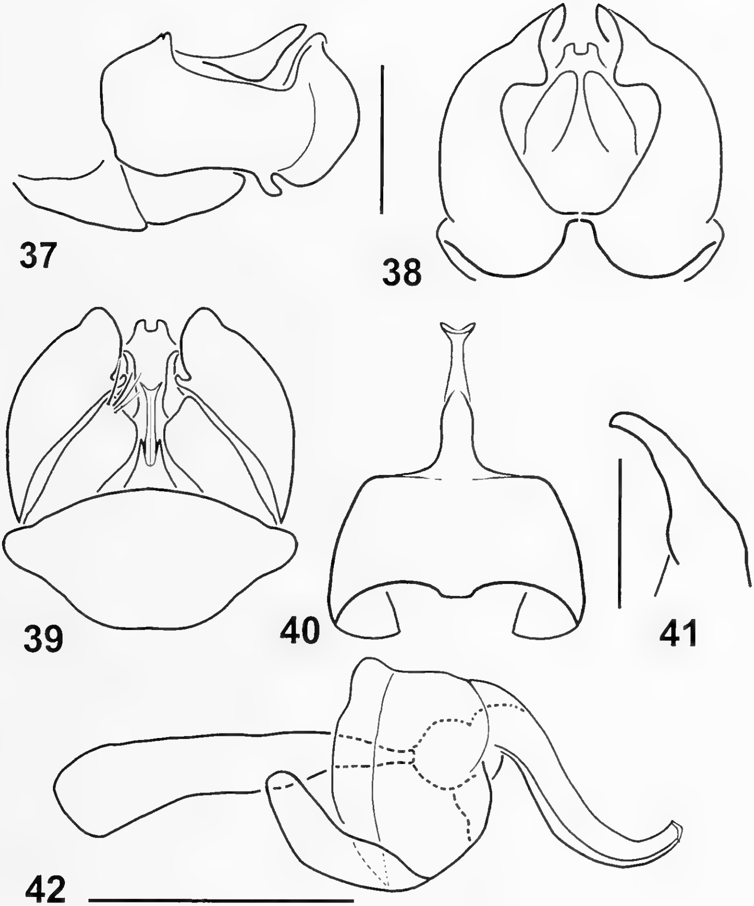
Female.—Differs as follows. Body 11.2–13.1 mm; wing 11.0–11.3 mm; FHWR 1.0:6.2–1.0:6.3; FWLR 1.0:2.2–1.0:2.7; m_1WR 1.0:2.4:2.0–1.0:2.3:2.1; HFWLR 1.0:5.3–1.0:5.4. *Abdomen:* Only slightly constricted at junction of segment 2–3, latter about ⅘ as wide as segments 6–7; tergites dorsally mostly black setose; dull gray tomentum gradually thinning apically, apical segments bare; sternites with only scattered yellow setae and sparse, thin bristles laterally. *Terminalia* (Figs. 43–46): Tergite 8 with only thin bristles. Sternite 8 evenly contoured apically. Spermatheca short, straight, carrot-shaped. Genital fork with apex of arms capitate.

Specimen examined.—Holotype ♂, TANZANIA: Iwawa/15 mls. N. W. of/Mwakete/7000 ft/21.i.52 WP (BMNH). Paratypes: DEMOCRATIC REPUBLIC OF CONGO: 1 ♂, Congo belge: P.N. U., Mukana (Lusanga) (1,810 m.)/6.iii.1948/Mis. G. F. de Witte. 1352a (MRAC); 2 ♀ [1 without tip of abdomen]/Congo belge: P.N. U./Mukana (1,810 m.)/4.iii.1948/22, 23.iv.1949/Mis. G. F. de Witte. 1389a/2550a (MRAC); 1 ♂, Congo belge: P.N. U./Kabwekanon (1,815 m.)/6.iii.1948/Mis. G. F. de Witte. 1367a (MRAC); 2 ♀, Congo belge: P.N. U./Lusanga (près Mukana) (1,810 m.)/4.vi.1945/Mis. G. F. de Witte. 80–81 (MRAC).

Etymology.—Latin *nigrantis* for black or dusky, referring to the color of the legs.

Distribution.—Captured in montane forests (1810 to 2121 m. elev.) during March and April in western Tanzania and eastern Democratic Republic of Congo.

Remarks.—The mostly black femora with yellow bristles; the unusually long, black setae of the head; gray tomentum of the thorax and basal abdominal segments; the flat, spatulate abdomen; and the combined characters of the terminalia (Figs. 37–46) distinguish *O. nigrantis* from congeners. The unusually wide, dorsally oriented apex of the epandrium; narrow gon-



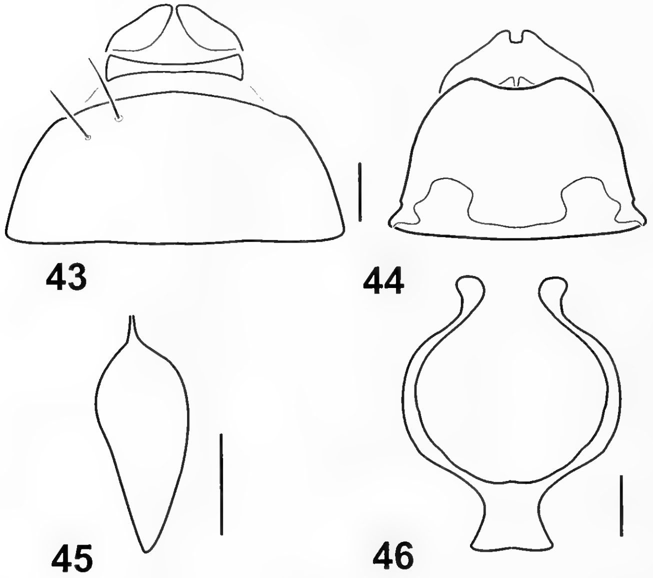
Figs. 37–42. *Ommatius nigrantis*, male terminalia. 37–39, Lateral, dorsal, and ventral views. 40, Aedeagus, dorsal view. 41, Left gonostylus. 42, Aedeagus, lateral view.

ostylus; and sigmoid aedeagus further distinguishes the male. Absence of scattered, stout bristles on the abdomen; a short, carrot-shaped spermatheca; and capitate arms of the genital fork further distinguish the female.

Ommatius pernecessarius Scarbrough, new species

(Figs. 5, 47–56)

Male.—Body 11.0–14.4 mm; wing 9.6–10.5 mm. *Head:* Dorsal ⅔ of face with



Figs. 43–46. *Ommatius nigrantis,* female terminalia. 43–44, Dorsal and ventral views. 45, Spermatheca. 46, Genital fork.

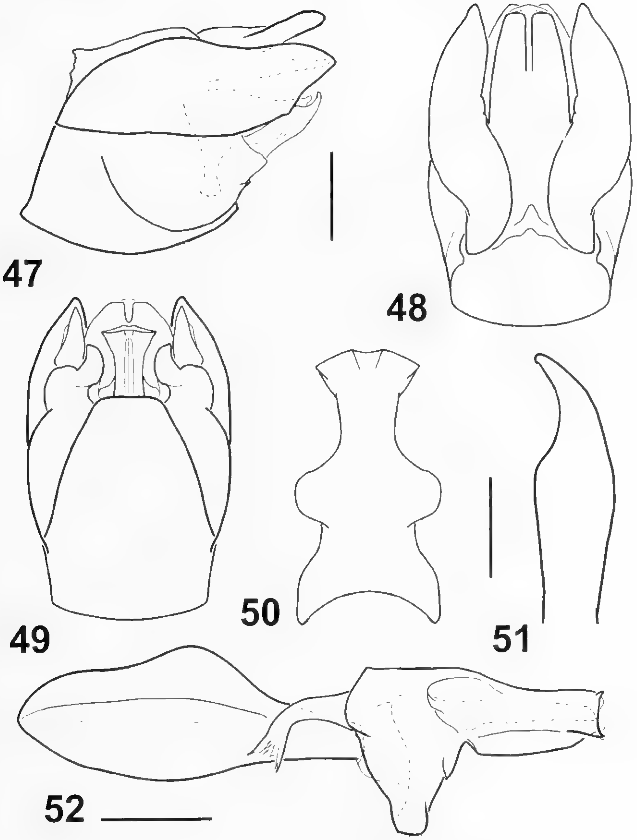
sparse black or mixed black and yellow setae, about ⅓ as long as 6 black bristles; FHWR 1.0:6.0–1.0:7.0. Antenna, frons, and ocellar tubercle black setose. Flagellum slighter shorter than scape and pedicel combined; FWLR 1.0:1.7–1.0:2.3. Frons with setae as long as scape. Ocellar tubercle with setae slightly shorter than scape and pedicel combined. Occiput dorsally with 6–8 black postocular bristles; apex of longest just beyond posterior margin of eye.

Thorax: Mesonotum with 2 wide, brown, tomentose, paramedial stripes, fused anteriorly, and 2 lateral spots; 5 lateral and 5–6 dorsocentral black bristles, 1–2 rarely yellow. Scutellum with scattered yellow setae and 2 black marginal bristles; preapical groove absent. Anepimeral bristle yellow.

Wing (Fig. 5): Dense yellow microtrichose; radial veins brownish yellow. Cell m_1WR 1.0:2.3:2.0–1.0:5.0:4.5.

Legs: Fore and middle femora anteriorly and narrow apices posteriorly black, otherwise yellow; hind femur variable, usually mostly yellow with narrow anterior streak and narrow apex black; all femora sometimes black anteriorly with narrow base yellow. Middle femur usually with only black bristles; 1–3 short black bristles usually present posteroventrally. Hind femur usually with most or all anterior and anteroventral bristles black, rarely bristles entirely yellow; posteroventral bristles usually yellow; HFWLR 1.0:4.4–1.0:5.0. Tibiae with narrow apices brown, sometimes light brownish yellow anteriorly. Tarsi yellow setose; basal tarsomere, sometimes second tarsomere, mostly yellow, apices narrowly brown; only black bristles present.

Abdomen: Mostly dense yellow tomentose, yellow setose; tergites medially brown with sparse black setae; sternites 3–7 and anterior margin of tergites laterally with yellow bristles.



Figs. 47–52. *Ommatius pernecessarius*, male terminalia. 47–49, Lateral, dorsal, and ventral views. 50, Aedeagus, dorsal view. 51, Left gonostylus. 52, Aedeagus, lateral view.

Terminalia (Figs. 47–52): Gonostylus narrow, posterior concavity absent. Gonocoxite long, narrow apically, tightly wrapped abound base of gonostylus. Aedeagus wide, strong prebasal constriction and prominent ventral keel present.

Female.—Differs as following. Body 10.8–14.2 mm; wing 10.5–11.7 mm: FHWR 1.0:5.8–1.0:6.3; FWLR 1.0:1.6–1.0:2.7; m$_1$ WR 1.0:2.5:2.4–1.0:4.7:4.7; HFWLR 1.0:5.0–1.0:5.4. *Head:* Face with 10–12 black bristles and dorsally mostly black setae. *Thorax:* Scutellum with marginal bristles always black, preapical groove often absent. *Wing:* Base of cell r$_4$ well beyond apex of cell d; r-m crossvein just beyond middle of cell d. *Legs:* Color of femora variable, blackish with narrow bases yellow to hind femur yellow with only narrow apex dark brown to black.

Hind femur posteroventrally with 3–5 longer, thinner yellow bristles. *Abdomen:* Most tergites apically with 3–4 thick, long, yellow bristles, tergite 8 with only short, black bristles; sternites 2–7 with few to several yellow bristles. Sternite 8 anteromedially reddish yellow to yellow, with a raised, oval tubercle, usually divided longitudinally. *Terminalia:* (Figs. 53–56). Sternite 8 with prominent medioapical tubercle; spermatheca constricted before apex, apex wider. Genital fork with short, wide base.

Specimens examined.—Holoype ♂, UGANDA: Budongo Forest nr Lk. Albert/ 1000 m/iv.1972/E. B. Babyetaqara (CNCI). Paratypes, DEMOCRATIC REPUBLIC OF CONGO: 1 ♂, 1 ♀, Musée Du Congo/Uelé Aba/14, 20.iv.1914/Dr. Rodhain (MRAC); 1 ♀, Musée Du Congo/Uelé: Van Kerkhevanville/Degreef (MRAC); 1 ♀, Musée Du Congo/Uala/xii.1932/A. Corbisier (MRAC); 1 ♀, Musée Du Congo/Iturl/Niarembe v.1921/Ch. Scops (MRAC); 1 ♀, Musée Du Congo/Dungu/iii.1920/P. Van den Plas (MRAC); 1 ♀, 7052 Lubwe/sur feuille Arbre/viv. 7.xii.55 Lips E' Villa, (MRAC); 1 ♀, 10 mi. S. of/ Kapona/13.i.58/1570 m/E. S. Ross &, R. E. Leech, (CASC). BURUNDI: 1 ♂, Mwaro/ Gigoli/21.x.80/J. G. Pointel (MNHN). ETHIOPIA: 1 ♂, Sidamo/Provience Dilla/ 3.vi.1974/Victor O. DeMasil/C. A. S. Accession (CASC). KENYA: 1 ♂, 2 ♀, Kakamega/ v–vi.1950/Mrs. Adamson (BMNH); 1 ♀, KENYA: Kapsabet/10.v.1991/A. Freidberg & Fini Kaplan (NMSA). MALAWI: 1 ♂, 1 ♀, Nyasaland/Usangha distr. 35–4500 ft/ 29.xi–15.xii.1910/S.A. Neave (BMNH). NIGERIA: 1 ♂, 2 ♀, Obridu cr/SE state/ 25.iii.1971/J.T. Medler (BMNH). RWANDA: 1 ♂, Gabiro, Kegera Park/1325 m 8.xii.57/E. S. Ross & R. E. Leech (CASC). UGANDA: 1 ♀, N. Uganda: van Someren/Madi Opei n. u/v.51/Com. Inst. Ent. coll No. 12301 (BMNH); 1 ♂, 1909/Col. Sir D. Bruce/1909-155 [terminalia on slide S.58] (BMNH); 1 ♀, May 1914/Uganda Uny-/oro Hoima/3700 feet/Coll. Kitter-/bergerd dd '19/C. A. Wiggins (OXUM). TANZANIA: 1 ♀, Njombe/ 6000–6500 ft/Tanganyika/9.xii.1957 W. P. (BMNH); 1 ♂, 1 ♀, 41 mi. N./of Kasulu 1150 m/19.xi.1967/K. S. Ross &/A. R. Stephan (CASC). ZAMBIA: 1 ♀, Lusaka/8.i.41/ Frank M. Hull Collection (CNCI). COUNTRY UNKNOWN: 1 ♀, Y1, presented by/ Imp. Bur. Ent./1921–9. [Prey mounted on separate pin] same data except *Lectis/bequaerti*/Lallen/det. in B. M./W. E. China [Cercopidae] (BMNH).

Etymology.—Latin *pernecessarius* for 'very close by relation' referring to its similarity to others in this group.

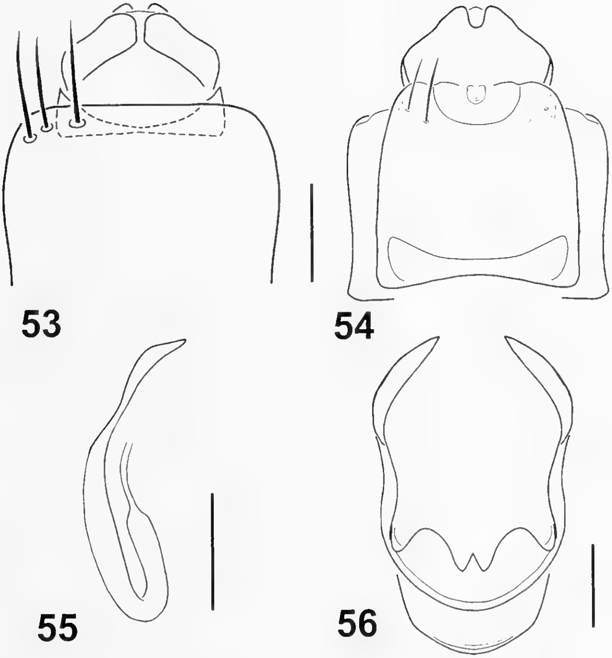
Distribution.—Captured in October through June at altitudes between 1150 to 1900 meters from Southern Ethiopia westward to Nigeria and southward to Zambia.

Remarks.—The short flagellum; sparse, short setae on the dorsal half of the face; black thoracic, femoral, and tarsal bristles; and combined characters of the terminalia (Figs. 47–56) distinguish *O. pernecessarius* from congeners. The shapes of the gonostylus, gonocoxite, and aedeagus readily characterize the male. The raised, oval, preapical tubercle on sternite 8, the preapically constricted spermatheca, and wide, short base of the genital fork further characterize the female.

Ommatius perscientus **Scarbrough, new species**

(Figs. 6, 57–62)

Male.—Body 8.7–14.2 mm; wing 7.3–9.8 mm. *Head:* Face yellow tomentose, several, thin, black bristles and sparse setae present on dorsal ⅔; thick yellow bristles and abundant long setae present on ventral ⅓; FHWR 1.0:8.1–1.0:9.8. Antenna, frons, and ocellar tubercle black setose. Flagellum short, as long as scape; FWLR 1.0:1.5. Frons yellowish-brown tomentose; setae short, longest seta slightly longer than scape. Ocellar tubercle with 2 setae as long as 3 antennomeres combined. Occiput mostly thin brownish-gray tomentose, eye margin narrowly dense yellowish gray; scattered black setae present dorsally; long, thin, black postocular bristles extend beyond midlateral margin of head, longest



Figs. 53–56. *Ommatius pernecessarius*, female terminalia. 53–54, Dorsal and ventral views. 55, Spermatheca. 56, Genital fork.

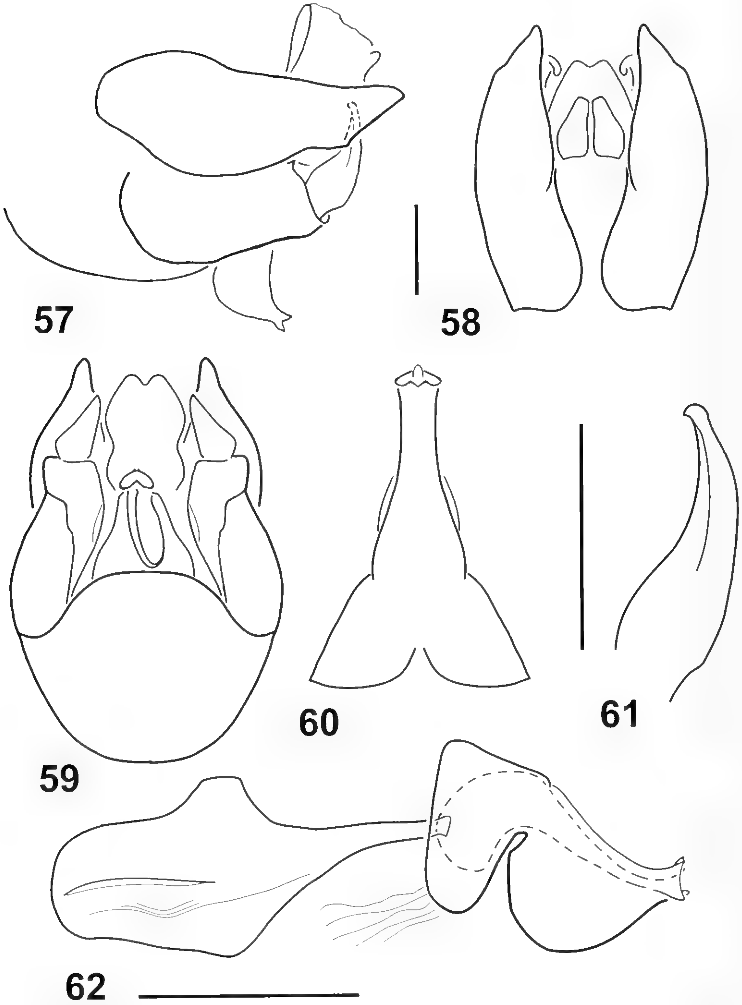
dorsal bristle with tip well before posterior margin of eye.

Thorax: Mesonotum brown tomentose dorsally, distinct paramedial stripes and lateral spots absent; bristles black; 4 dorsocentral bristles present, wide spaced with first at of just behind transverse suture. Scutellum brown tomentose dorsally, apical margin gray; scattered black setae and 2 black marginal bristles present; weak preapical groove present. Anepimeral bristle black; anepisternum dorsally scattered black setose.

Wing (Fig. 6): Dense, black microtrichia present beyond r-m crossvein; veins dark brown. Cell m_1WR 1.0:2.1:1.9–1.0:2.9:2.6.

Legs: Coxae with stout bristles. Femora mostly black; fore and middle femora yellow ventrally and posteriorly except at apex; hind femur yellow on basal fourth to third. Middle femur with black bristles anteriorly and anteroventrally; posteroventral bristles variable, all yellow, black, or mixed with apical bristles black. Hind femur with anterior and anteroventral bristles variable, entirely yellow or black, if mixed then 1–3 basal anteroventral bristles yellow; posteroventral bristles entirely yellow or 3–4 apical bristles black; HFWLR 1.0:5.0–1.0:5.2. Tibiae yellow except brown as follows: narrow apex of fore and middle tibiae and apical half of hind tibia; bristles black. Tarsi mostly black, basal tarsomere of fore and middle tarsi mostly yellow, narrow apex black; bristles black.

Abdomen: Black, apical margin of most segments dull yellow to yellowish brown.



Figs. 57–62. *Ommatius pernecessarius*, male terminalia. 57–59, Lateral, dorsal, and ventral views. 60, Aedeagus, dorsal view. 61, Left gonostylus. 62, Aedeagus, lateral view.

Terga mostly thin, brown tomentose, basal segments brownish gray laterally; black setose; apical corner of terga 4–8 with 1–4 thin, black bristles. Sterna brownish-gray tomentose, mostly pale yellow setose; sternites 6–7 with scattered, short, black setae; sternum 8 with only black vestiture.

Terminalia (Figs. 57–62): Gonostylus

narrow apically, posterior groove absent. Aedeagus slightly sigmoid with a prominent ventral keel.

Female.—Unknown.

Specimens examined.—Holotype ♂, ZIMBABWE: Mt. Selinda/Nov–Dec 1930/ R. H. R. Stevenson (OXUM). Paratype, ZIMBABWE: 1 ♂, [without abdomen], same data label as holotype (OXUM); 1 ♂, Vumba Mts./S. Rhodesia/29.xi.1934/Major Drysdale (OXUM). ZAMBIA: 1 ♂, Southern Rhodesia/Chitinda Forest/25.viii–2.v.1907/C. F. M. Swynnerton/1915-426 (BMNH).

Etymology.—Latin *perscientus* for 'very skillful', alluding to the predaceous habit of asilids.

Distribution.—A montane species captured during August and November–December in eastern Zambia and Zimbabwe.

Remarks.—In addition to the characters in the key, the narrow face with sparse setae dorsally; dorsal postocular bristles proclinate with apices well forward of the posterior margin of the eyes; mesonotum with thin brown tomentum, paramedial stripes absent; wing with dense brown microtrichia beyond r-m crossvein; hind femur black except for narrow yellow base; apical half of hind tibia black, and terminalia (Figs 57–62) characterize *O. perscientus.*

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THREE NEW GENERA, TWO NEW SPECIES, AND SOME RECTIFICATIONS IN NEOTROPICAL EULIINI (LEPIDOPTERA: TORTRICIDAE)

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Abstract.—Three **new genera** in the tortricid tribe Euliini are described and illustrated: ***Euryeulia***, with type species *E. biocellata* (Walsingham 1914), **new combination**, from Mexico; ***Pseudapina***, with type species ***P. lanceovalva*, new species**, from Venezuela; and ***Circapina***, with type species ***C. flexalana*, new species**, from Costa Rica. Three **new generic synonymies** are proposed: *Pycnospina* Razowski 1997 is a junior synonym of *Lobogenesis* Razowski 1990, with the **new combination** *L. centrota* (Razowski 1997); *Osmaria* Razowski 1991 is a junior synonym of *Anopina* Obraztsov 1962, with the **new combination** *A. psaeroptera* (Razowski and Becker 1991); and *Chirotes* Razowski and Becker 1999, along with its replacement name, *Prochirotes* Razowski 2001, are junior synonyms of *Strophotina* Brown 1998, with the **new combinations** *S. chorestis* (Razowski and Becker 1999) and *S. niphochondra* (Razowski and Becker 1999).

Key Words: genitalia, biodiversity, synonymy, new combinations, classification, *Euryeulia, Pseudapina, Circapina, Pycnospina, Lobogenesis, Osmaria, Anopina, Chirotes, Prochirotes, Strophotina*

Since 1980, more new genera (n = 107) have been proposed in the tribe Euliini than in any other tribe of the family Tortricidae. All of these new genera are restricted to the New World tropics, presenting compelling evidence of the hyperdiversity of the group within this large and complex geographic region. Based primarily on material collected by Vitor Becker of Planaltina, Brazil, the vast majority of these genera have been described by Jozef Razowski, who has nearly single-handedly created a generic framework into which new species of Neotropical Euliini can be placed. However, this task is far from complete, with numerous described and undescribed species still defying confident generic assignment. In contrast, for some of the monotypic genera, which are numerous (n = 49), relationships with other genera are becoming more clear, and there is a need to synonymize those that likely represent extremes within a single monophyletic lineage (i.e., genus). The purposes of this paper are to describe three new genera, propose the synonymy of three previously described genera, describe two new species, and propose five new combinations. The overall goal is to continue to build upon the growing generic framework for the tribe and to clarify relationships in an effort to establish a stable, meaningful classification.

MATERIALS AND METHODS

Specimens were obtained from or examined at the following institutions: The Natural History Museum, London, England

(BMNH); Instituto Nacional de Biodiversidad, Santo Domingo de Heredia, Costa Rica (INBio); Essig Museum of Entomology, University of California, Berkeley, California, U.S.A. (UCB); National Museum of Natural History, Smithsonian Institution, Washington, D.C., U.S.A. (USNM); and Zoological Museum, Copenhagen, Denmark (ZMC). Genitalia preparations of representative individuals were made following the methodology summarized in Brown and Powell (2000). Illustrations of genitalia are photographs of slide mounts taken with a SONY DKC5000® digital camera and enhanced using Adobe Photoshop® and Adobe Illustrator® software. Illustrations are of a single representative preparation, but some have been slightly modified where the parts are disarticulated. Descriptions are composite, based on all available specimens. Forewing measurements were made with a transparent millimeter ruler under low power of a Leica MZ12® dissecting microscope, and estimated to the nearest one-tenth millimeter. Terminology for wing venation and genitalia structures follows Horak (1984). Abbreviations are as follows: FW = forewing; HW = hindwing; DC = discal cell; n = number of individuals examined; $\bar{x}$ = mean; ca. = about (approximately). Elevations presented in feet on data labels are converted to meters and given in brackets.

SYSTEMATICS

Euryeulia Brown, new genus

Type species: *Tortrix biocellata* Walsingham 1914.

Diagnosis.—Superficially, *Euryeulia* is like no other genus in Euliini. Its forewing pattern, with a pair of rounded, maroon spots in the distal half of the wing (Fig. 1), is more similar to some species of *Episimus* Walsingham (Olethreutinae) than to other euliines. The genitalia, likewise, are moderately divergent from other members of the tribe. The elongate, sinuate accessory rods originating from the base of the gnathos (Fig. 4) are reminiscent of a similar structure in *Gnatheulia* Razowski; the capitate uncus is similar to that of *Anopina hilasma* (Walsingham) and *Gauruncus* Razowski; and the narrow valvae are reminiscent of *Ernocornutia* Razowski. The inflated apophyses posteriores in the female genitalia (Fig. 7) are similar to the those of *Paraptila* Meyrick. Putative autapomorphies include all the unusual characters mentioned above because most appear to be derived independently within *Euryeulia*. The relationship of *Euryeulia* to any of the mentioned genera is obscured by the large number of autapomorphies. *Euryeulia* is assigned provisionally to Euliini on the basis of its possible relationship with other genera in the tribe based on the characters mentioned above.

Description.—*Head:* Antennal cilia 1.2–1.3 times width of flagellomere in male; short, unmodified in female. Labial palpus (all segments combined) ca. 1.2–1.4 times horizontal diameter of compound eye, segment II weakly upturned, rough scaled, expanded distally by scaling; segment III ca. 0.2 times as long as II, smooth scaled, with tip exposed. Maxillary palpus rudimentary. Dorsal portion of frons with short overhanging tuft of scales; lower portion smooth scaled. Ocellus moderate in size. Chaetosemata present. Proboscis present, presumably functional. *Thorax:* Dorsum smooth scaled; legs unmodified, male without foreleg hairpencil. FW length ca. 2.5 times width; DC length ca. 0.65 times FW length; DC width 0.16–0.18 times DC length; CuA_2 originates ca. 0.7 along length of DC; all veins separate beyond DC; chorda absent; M-stem absent; CuP present only at margin. Raised scale tufts absent; male without costal fold. Hindwing with Sc+R and Rs approximate at base; Rs to termen; Rs and M_1 approximate at base; M_2 and M_3 separate; M_3 and CuA_1 connate. *Abdomen:* Dorsal pits absent; no modified corethrogyne scaling in female. Male genitalia (Fig. 4) with uncus weakly curved, enlarged and somewhat cordate apically. Socius moderately long, slender, ca. 0.9 times length of gnathos arms, pendant; not fused to gnathos.

Gnathos complete, arms joined distally into short triangular plate; an elongate, slender, sinuate, accessory arm arising at base of each arm of gnathos; accessory arms ca. 1.5 times length of gnathos proper. Subscaphium and hami absent. Transtilla a broad band, with a few small thorns. Valva narrow, costa curved ventrad just before apex; sacculus ill-defined, without free process. Pulvinus absent. Vinculum present; tegumen unmodified. Juxta an arrowhead-shaped, sclerotized plate. Aedeagus moderate in size, ca. 0.66 length of valva; vesica with small patch of tiny cornuti; phallobase simple, rounded. Female genitalia (Fig. 7) with papillae anales moderately slender; apophyses anteriores long and slender; apophyses posteriores slightly shorter, broadly inflated in anterior two-fifths, with narrow tip at anterior end. Sterigma a broad transverse band, narrowest at middle, dilated laterally; area immediately anterad of papillae anales a large, broad cup; antrum a large sclerotized bowl. Ductus bursae moderately long and broad, with a slender accessory bursa arising from right side at antrum. Corpus bursae relatively short, oblong, finely punctate; signum absent.

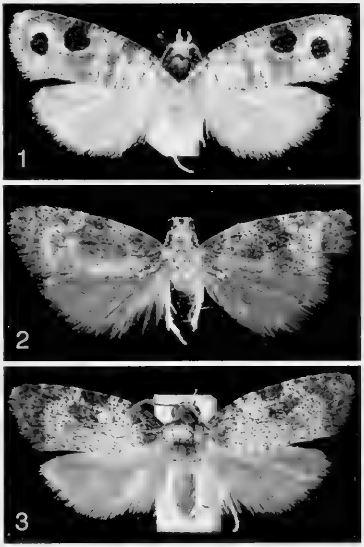
Etymology.—The genus name is derived from the Greek "eurys," meaning broad, and "*Eulia*", the type genus of the tribe, and is interpreted as feminine in gender.

Euryeulia biocellata (Walsingham 1914), **new combination**
(Figs. 1, 4, 7)

Tortrix biocellata Walsingham 1914: 278 (description and illustration of adult).

"*Eulia*" *biocellata:* Powell et al. 1995: 146 (checklist).

Diagnosis.—As mentioned above, *Euryeulia biocellata* cannot be confused with any other euliine. It is recognized easily by its *Episimus*-like facies and unique genitalia. The species, originally described in the Linnaean genus *Tortrix,* has nothing in common with that genus, which includes one species from Europe and one from Asia. Its transfer to "*Eulia*" in the Checklist of Neotropical Lepidoptera (Powell et al. 1995) was merely for convenience—a place for many species of Euliini that lacked meaningful generic assignment. *Eulia* is a monotypic genus that is Holarctic in distribution.



Figs. 1–3. Adults of new tortricid genera. 1, *Euryeulia biocellata.* 2, *Pseudapina lanceovalva.* 3, *Circapina flexalana*

Redescription.—Male. *Head:* Frons white; vertex cream; labial palpus cream on inner surface, cream and pale brown on outer surface. *Thorax:* Mixed cream and pale brown, with dark brown, V-shaped band bordered at posterior edge by cream; tegula red-brown. FW (Fig. 1) length 5.9–7.2 mm ($\bar{x}$ = 6.4; n = 4); ground color gray, with narrow, transverse, gray-brown lines, broadly bordered by pale yellow; two conspicuous, circular, tawny maroon spots, one at costa ca. 0.6 distance from base to apex, extending to lower angle of DC, the second smaller, situated midway between the costal spot and mid-termen. Fringe whitish. *Ab-*

domen: Pale brown. Genitalia (Fig. 4; based on 2 preparations) as described for genus.

Female. *Head and thorax:* As described for male. FW length 8.0 mm (n = 2); as described for male. *Abdomen:* Pale brown. Genitalia (Fig. 7; based on 2 preparations) as described for genus.

Types.—Lectotype ♀, Mexico, Guerrero, Amula, 6000′ [1846 m], Aug 1918, H. H. Smith (BMNH). Paralectotype ♂, same data as lectotype (BMNH). Walsingham (1914) stated "Type ♀ (66513); ♂ (66514)" which has been interpreted as the designation of a female type and a male type. Hence, a lectotype designation is necessary in order to stabilize the nomenclature and identity of this species. The female already bears a BM "lectotype" label. Walsingham's (1914) type series consists of the two specimens cited above; a third identically labeled specimen in BMNH was not included.

Additional specimens examined.—MEXICO: Durango: 3 mi E Revolcaderos, 11 Aug 1972, J. Powell (1 ♂, UCB). Guerrero: Amula, 6000′ [1846 m], Aug [no year], H. H. Smith (1 ♂, BMNH); 5 km W Tixtla, 1710 m, 18 Sep 1982, J. Powell & J. Chemsak (1 ♂, 2 ♀, UCB). Sinaloa: 2 mi SW Potrerillos, 4200′ [1285 m], 12 Aug 1986, J. Brown & J. Powell (1 ♂, UCB).

Distribution and biology.—*Euryeulia biocellata* has been recorded only from the middle elevations (1290–1850 m) of the Sierra Madre Occidental of western Mexico. The general habitat of the collecting localities in Durango and Sinaloa is pine-oak forest. Collection dates are August and September. All recent specimens were taken at blacklight.

Pseudapina Brown, new genus

Type species: *Pseudapina lanceovalva* Brown, new species.

Diagnosis.—Superficially, *Pseudapina* is nearly indistinguishable from *Circapina*, new genus (Figs. 2, 3), described below, and based on facies alone it is hard to imagine that they are not congeneric. However, characters of the male and female genitalia (Figs. 5–6, 8–9) provide convincing evidence that the two are distinct. Putative autapomorphies for *Pseudapina* include the slender, dorsally projecting socii and the broadly lanceolate valvae (Fig. 5). *Pseudapina* shares with *Odonthalitus bisetanus* Brown and *O. improprius* Brown a patch of strong, curved spines from the basal portion of the valva at the lateral base of the transtilla, and a distally attenuate valva (Brown 2000). The female genitalia of *Pseudapina* share with many species of *Odonthalitus* extremely short apophyses anteriores (Fig. 8). The erect, sclerotized structures from the dorsum of the tegumen interpreted as a modification of the socii in *Pseudapina* may be homologous with what has been interpreted as a paired or bifurcate uncus in *Odonthalitus*, but this is not without question. Their position and configuration also are reminiscent of the hami of Chlidanotinae, but it is highly unlikely that these structures are homologous with those found in Chlidanotinae. The putative homology of the spines of the valva and the socii/uncus, along with the extremely short apophyses, argue for a close relationship between *Odonthalitus* and *Pseudapina*. Assignment of *Pseudapina* to Euliini is based on the possession of a male foreleg hairpencil, which has been identified as a putative synapomorphy for the tribe (Brown 1990).

Description.—Male. *Head:* Antennal cilia 1.2–1.5 times width of flagellomere in male. Labial palpus (all segments combined) ca. 1.5 times horizontal diameter of compound eye; segment II weakly upturned, rough scaled, expanded distally by scaling; segment III ca. 0.5 times as long as II, smooth scaled, exposed. Maxillary palpus rudimentary. Dorsal portion of frons with short overhanging tuft of scales; lower portion smooth scaled. Ocellus small. Chaetosemata present. Proboscis present, presumably functional. *Thorax:* Dorsum smooth scaled; male with foreleg hairpencil. FW length ca. 2.5 times width; DC length 0.65–0.70 times FW length; DC width 0.16–0.18 times DC length; CuA_2 originating ca. 0.7 along length of DC; all veins separate beyond DC; chorda absent; M-stem absent; CuP present at margin. Raised scale tufts absent; male without costal fold. Hindwing with Sc+R and Rs approximate at base; Rs to termen; Rs and M_1 approximately at base; M_2 and M_3 separate; M_3 and CuA_1 connate or short-stalked. *Abdomen:* Dorsal pits absent; no modified corethrogyne scaling in female. Male genitalia (Fig. 5) with uncus weakly club-shaped, gradually expanded in distal three-fourths, sparsely setose in distal one-fourth. Structure interpreted as base of socius elongate, sclerotized, attenuate, projecting dorsally, hooked apically, nearly as long as uncus; lower portion of socius short, broad, pendant. Gnathos complete, somewhat membranous basally, arms joined distally into short, hoodlike process. Subscaphium and hami absent. Transtilla with stout, sclerotized lateral bases, membranous mesally. Valva broad at base, attenuate apically, with narrow apical beak; group of 10–15 stiff, curved setae arising near base of transtilla; sacculus not developed. Pulvinus absent. Vinculum complete, well developed. Juxta a sclerotized plate. Aedeagus moderately small, narrow, weakly curved in distal one-fifth, ca. one-half length of valva; phallobase slightly elongate, simple, rounded at base; vesica without cornuti. Female genitalia (Fig. 8) with papillae anales broadly slipper-shaped; apophyses extremely short, especially apophyses anteriores. Sterigma a narrow, spiculate, transverse band. Ductus bursae extremely long, slender. Corpus bursae round, densely and evenly spiculate; signum absent.

Etymology.—The genus name is a contraction of the Greek "pseudos," meaning false, and "*Anopina*," a genus with which *Pseudapina* is superficially similar. It is interpreted as feminine in gender.

Pseudapina lanceovalva Brown, new species

(Figs. 2, 5, 8)

Diagnosis.—As mentioned above, *P. lanceovalva* is superficially nearly indistinguishable from *Circapina flexalana*, described below. Male genitalia of *P. lanceovalva* are easily distinguished by the slender, attenuate, dorsally-projecting socius, weakly club-shaped uncus, broadly lanceolate valva, and unmodified aedeagus. The group of curved spines near the base of the valva is similar to that present in two species of *Odonthalitus* Razowski. Female genitalia are distinguished by the extremely long, slender ductus bursae, which is similar to that of *Odonthalitus poas* Brown.

Description.—Male. *Head:* Frons, vertex, and labial palpus with cream to pale tan scales. *Thorax:* Cream to pale tan. FW (Fig. 2) length 5.8–6.1 mm ($\bar{x}$ = 5.9; n = 2); ground color white, sprinkled with brown and red-brown scales; ill-defined basal patch of pale red-brown scales; a subrectangular patch of pale red-brown scales near middle of costa; three tiny dashes from costa between costal patch and apex; apex with ill-defined pale brown patch. Fringe alternating pale gray and pale orange. *Abdomen:* Pale brown. Genitalia (Fig. 5; based on 2 preparations) as described for genus.

Female. *Head:* As described for male. *Thorax:* FW length 7.0 (n = 1), pattern as described for male. *Abdomen:* Genitalia (Fig. 8; based on 1 preparation) as described for genus.

Holotype.—♂, Venezuela, Aragua, Rancho Grande [1100 m], 1–7 Aug 1967, R. W. Poole (USNM).

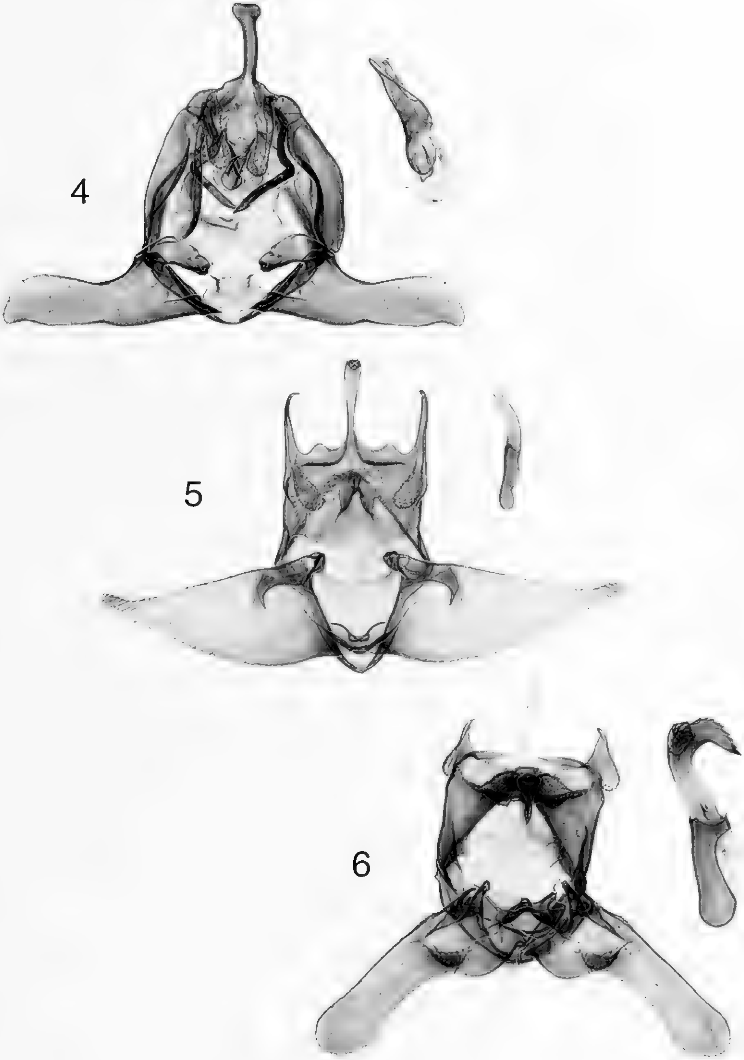
Paratypes.—Venezuela: Aragua: Rancho Grande, 1100 m, 24–31 Oct 1966, S. S. & W. D. Duckworth (1 ♀, USNM), 8–14 Jul 1967, R. W. Poole (1 ♂, USNM).

Distribution and biology.—*Pseudapina lanceovalva* is known only from the type locality. Nothing is known of the early stages. Adults have been collected in July, August, and October.

Etymology.—The species name refers to the broadly lanceolate shape of the valva in the male genitalia.

Circapina Brown, new genus

Type species: *Circapina flexalana* Brown, new species.



Figs. 4–6. Male genitalia. 4, *Euryeulia biocellata*. 5, *Pseudapina lanceovalva*. 6, *Circapina flexalana*.

Diagnosis.—Adults of *Circapina* are most similar to those of *Pseudapina* in forewing length and pattern—the two are nearly indistinguishable. However, as discussed above, the two are easily separated by numerous features of the male and female genitalia. Putative autapomorphies for *Circapina* include the slender, weakly sclerotized, sparsely hairy uncus; the erect, semicordate socii; and the broad, apically hooked aedeagus. It is likely that *Circapina* is related to *Anopina* on the basis of the elongate antennal cilia in the male, the presence of a male foreleg hairpencil, and the forewing pattern with a semicircular costal blotch, but the same could be said of *Pseudapina*. *Circapina* is assigned to Euliini on the basis of the male foreleg hairpencil, which may represent a synapomorphy for this tribe (Brown 1990).

Description.—Male. *Head:* Antennal cilia 1.2–1.5 times width of flagellomere in male; simple, unmodified in female. Labial palpus (all segments combined) ca. 1.5 times horizontal diameter of compound eye; segment II weakly upturned, rough scaled, expanded distally by scaling; segment III ca. 0.5 times as long as II, smooth scaled, mostly exposed. Maxillary palpus rudimentary. Dorsal portion of frons with short overhanging tuft of scales; lower portion smooth scaled. Ocellus small. Chaetosemata present. Proboscis present, presumably functional. *Thorax:* Dorsum smooth scaled; male with foreleg hairpencil. FW length ca. 2.5 times width; DC length 0.65–0.70 times FW length; DC width 0.16–0.18 times DC length; CuA_2 originating ca. 0.7 along length of DC; all veins separate beyond DC; chorda absent; M-stem absent; CuP present at margin. Raised scale tufts absent; male without costal fold. *Hindwing:* Sc+R and Rs approximate at base; Rs to termen; Rs and M_1 approximate at base; M_2 and M_3 separate; M_3 and CuA_1 connate or short-stalked. *Abdomen:* Dorsal pits absent; no modified corethrogyne scaling in female. Male genitalia (Fig. 6) with entire capsule somewhat robust, with tegumen broad, especially dorsally. Uncus simple, rodlike, very slender, weakly sclerotized, sparsely hairy. Socius sclerotized, short, erect, with fine hairs, semicordate, broad at base, attenuating apically, not fused to gnathos. Gnathos complete, arms moderately broad, short, joined distally into short, stout, hooklike mesal process. Subscaphium and hami absent. Transtilla digitate at lateral bases, membranous mesally. Valva broadly expanded at base, with rounded ventral portion, narrow, parallel-sided in distal two-thirds, rounded apically; densely hairy, semicircular flap in middle of basal one-third; sacculus not developed. Pulvinus absent. Vinculum complete, well developed. Juxta a sclerotized plate. Aedeagus moderately long, ca. as long as valva, broad, with distal one-fifth hooked and strongly toothed; phallobase elongate, simple, rounded. Female genitalia (Fig. 9) with papillae anales moderately broad, mostly parallel-sided; apophyses short, especially apophyses anteriores. Sterigma membranous, with quadrate lobe mesally. Ductus bursae moderate in width, weakly sinuate, lightly sclerotized, coiled one revolution. Corpus bursae oblong, finely punctate but without conspicuous spiculae; signum absent.

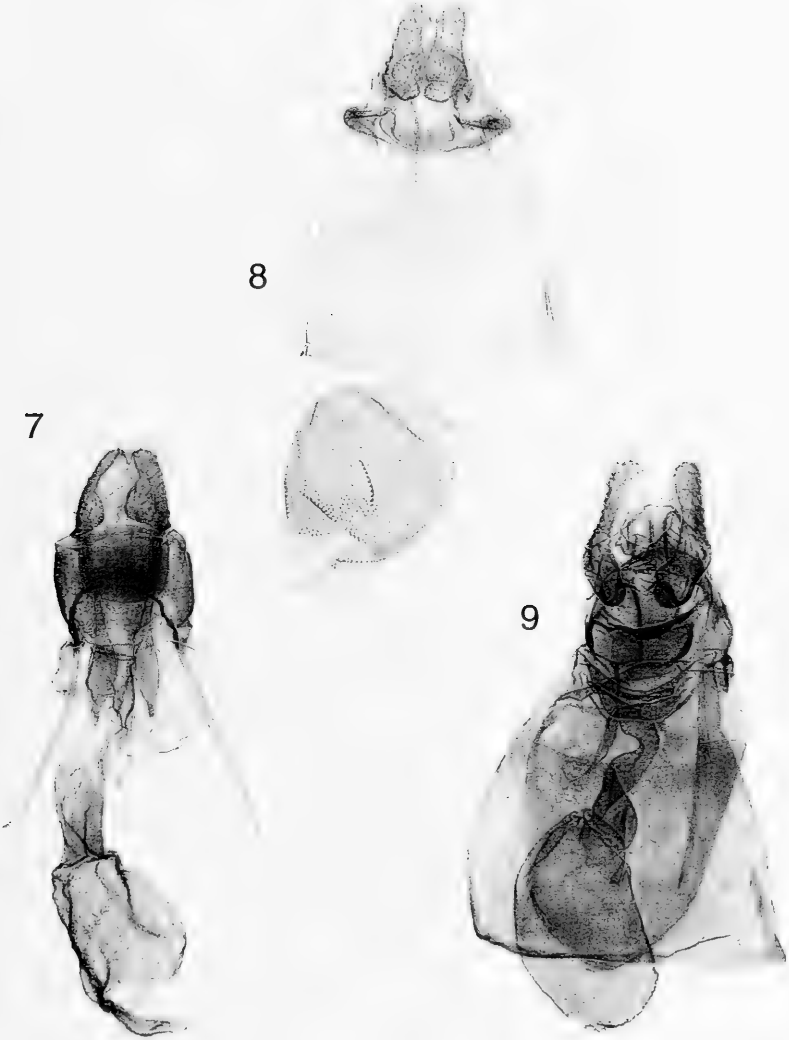
Etymology.—The genus name is a contraction of the Latin "circa," meaning near, and "*Anopina*," a genus with which *Circapina* is superficially similar. It is interpreted as feminine in gender.

Circapina flexalana Brown, new species

(Figs. 3, 6, 9)

Diagnosis.—Superficially, *Circapina flexalana* is most similar to *Pseudapina lanceovalva*. It can be distinguished from all other Euliini by the slender, hairy uncus, broad tegumen with erect semicordate socii, and broad aedeagus with curved and toothed apex. The latter feature is the most striking autapomorphy for this species.

Description.—Male. *Head:* Frons, vertex, and labial palpus cream to pale tan. *Thorax:* Pale tan with upraised posterior crest of shiny gray scales; tegulae whitish. FW (Fig. 3) length 4.9–6.6 mm ($\bar{x}$ = 5.8;



Figs. 7–9. Female genitalia. 7, *Euryeulia biocellata*. 8, *Pseudapina lanceovalva*. 9, *Circapina flexalana*.

n = 12); ground color white, sprinkled with brown and red-brown scales; ill-defined basal patch of pale brown scales; a semicircular patch of pale red-brown scales near middle of costa, with an irregular, pale brown, rectangular patch immediately below; apical patch extending to mid-tornus, pale brown with red-brown overscaling. Fringe alternating gray and bronze. *Abdomen:* Pale brown. Genitalia (Fig. 6; based on 3 preparations) as described for genus.

Female. *Head:* As described for male. *Thorax:* FW length 7.0 mm (n = 2); as described for male, except basal region of dorsum overscaled with gray. *Abdomen:* Genitalia (Fig. 9; based on 1 preparation) as described for genus.

Holotype.—♂, Costa Rica, Puntarenas Province, Monteverde, 1400 m, 22–24 Jul 1990, S. Meredith & J. Powell (UCB).

Paratypes.—Costa Rica: Guanacaste Province: Est. Cacao, lado suroeste del Volcan Cacao, 1000–1400 m, Sep 1989, C. Chavez (1♂, INBio), Jun 1990, II Curso Parataxon. (1♂, INBio), 25 Sep–11 Oct 1990, C. Chavez (1♂, INBio), Nov–Dec 1990, C. Chavez & R. Espinoza (1♂, INBio). Puntarenas Province: Monteverde, 1400 m, 22–24 Jul 1990, S. Meredith & J. Powell (4♂, 1♀, UCB), 29–31 Mar 1992, S. McCarty & J. Powell (2♂, 1♀, UCB, USNM), 8–10 Dec 1978, D. Janzen (1♂, INBio). San Luis, Monteverde, 1000–1350 m, Feb 1995, Z. Fuentes (1♂, INBio).

Distribution and biology.—*Cercapina flexalana* is known from 1000–1400 m elevation on the western side of the central cordillera of Costa Rica. All specimens examined are from two localities: Monteverde (Puntarenas Province) and SW side of Volcan Cacao (Guanacaste Province). Capture dates are scattered throughout the year from February to December.

Etymology.—The specific epithet refers to the reflexed or curved distal portion of the aedeagus.

Lobogenesis Razowski 1992

Lobogenesis Razowski 1992: 213; Powell et al. 1995: 144; Brown 2000: 25. Type species: *Lobogenesis lobata* Razowski 1992, by monotypy.

Pycnospina Razowski 1997: 84. Type species: *Pycnospina centrota* Razowski 1997, by monotypy. **New synonym.**

Razowski (1997) proposed *Pycnospina* to accommodate the species *P. centrota* Razowski, described in the same paper, known only from the holotype male. Based on the description and illustration (Razowski 1997), the species *centrota* belongs in *Lobogenesis* Razowski 1992; I overlooked this species in my revision of the latter genus (Brown 2000). *Lobogenesis centrota* (Razowski), **new combination**, shares the following synapomorphies with other *Lobogenesis*: (1) uncus bifurcate and finely spined in distal one half; (2) socius with a rounded lobe extending dorsad of the point of attachment to the tegumen; (3) valva with a linear row of tiny spinelike teeth extending from subbasal spinose lobe to near apex; and (4) valva with a strong, digitate flange from basal one-third of costa. The expanded arms of the uncus beyond the bifurcation, and the club-shaped enlargement at the distal ends of the gnathos arms indicate that *L. centrota* belongs to a species group that includes *L. peruviana* Brown, *L. antiqua* Brown, and *L. contrasta* Brown (Brown 2000). Inclusion of *centrota* in *Lobogenesis* relegates *Pycnospina* to a junior synonym of *Lobogenesis*.

Anopina Obraztsov 1962

Anopina Obraztsov 1962: 2, 1967: 2; Powell 1964: 118, 1983: 39, 1986: 374; Powell et al. 1995: 142; Brown and Powell 1991: 5, 2000: 12. Type species: *Tortrix triangulana* Kearfott 1908, by original designation.

Osmaria Razowski 1991: 177. Type species: *Phtheochroa psaeroptera* Razowski and Becker 1986, by monotypy. **New synonym.**

In 1986 Razowski and Becker described *Phtheochroa psaeroptera* from Huatusco, Veracruz, Mexico. In 1991, Razowski recognized that the species had been placed erroneously not only in *Phtheochroa*, but in the tribe Cochylini. To remedy this situation he described a new monotypic genus, *Osmaria*, and indirectly transferred it to Euliini (i.e., "it [*Osmaria*] belongs in the group of genera close to *Popayanita* Razowski.").

Based on the description and illustration (Razowski and Becker 1986), *psaeroptera* is almost certainly a member of the *triangulana* species group of *Anopina* Obraztsov, **new combination**, as defined by Brown and Powell (2000). The overall shape of the uncus, gnathos, and valva, and the elongate antennal cilia of the male are characteristic of *Anopina*. The shape of the sacculus and the white color of the forewing are synapomorphies supporting the relationship of *psaeroptera* to a group of white *Anopina* species that includes *A. desmatana* (Walsingham) (from Guerrero), *A. albominima* Brown and Powell (from Guerrero), and *A. albomaculana* Brown and Powell (from Sinaloa and Nayarit). See Brown and Powell (2000) for comparisons of genitalia. Inclusion of *psaeroptera* in *Anopina* relegates *Osmaria* to a junior synonym of *Anopina*.

Strophotina Brown 1998

Strophotina Brown 1998: 44. Type species: *Eulia strophota* Meyrick 1926, by original designation.

Chirotes Razowski and Becker 1999: 417. Preoccupied by *Chirotes* Cuvier 1817. Type species: *Chirotes chorestis* Razowski and Becker 1999, by original designation. **New synonym**.

Prochirotes Razowski 2001: 277. Replacement name for *Chirotes* Razowski and Becker 1999. **New synonym**.

I described *Strophotina* (Brown 1998) to accommodate *S. curvidagus* Brown (from Costa Rica) and *Eulia strophota* Meyrick (from Colombia, Ecuador, Peru, and Venezuela), with the latter designated as the type species. The following year, Razowski and Becker (1999) described *Chirotes* to accommodate *C. chorestis* Razowski and Becker (type species) (from Ecuador), *C. niphochondra* Razowski and Becker (from Ecuador), and *Eulia strophota* Meyrick. There is no doubt that the two genera represent the same concept, and the synonymy is the result of a lack of communication among the authors rather than differing taxonomic opinions. The synonymy of *Chirotes* and its replacement name, *Prochirotes*, with *Strophotina* results in two **new combinations**: *Strophotina chorestis* and *S. niphochondra*.

My interpretation of species limits within the genus differs from that presented by Razowski and Becker (1999). I treated all specimens (4♂, 6♀) from South America (i.e., Colombia, Ecuador, Peru, and Venezuela) as conspecific (i.e., *strophota*), although I indicated that it is possible that more than one species was represented in the material (Brown 1998). Razowski and Becker (1999) considered specimens (2♀) from Carchi, Maldonado, Ecuador, to represent *strophota*, and the specimen (♂) from Baeza, Napo, Ecuador, to represent *chorestis*. Although I suspect that the two names are synonyms, the paucity of material inhibits reliable conclusions. In addition, I suspect that *niphochondra* represents a different, undescribed genus closely related to *Strophotina*. I have examined two males from Chile (ZMC) that are congeneric with *niphochondra*. These males (including the type of *niphochondra*) have short, more attenuate valvae, a broad, stout aedeagus that is quite different from that of *Strophotina*, a unique tonguelike mesal portion of the transtilla, and lack the dense row of spines from the costa of the valva. While it is possible that these features are autapomophies at the species level, I suspect that they represent characters that define a new genus.

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REVIEW OF THE SOUTHEASTERN ASIAN SAWFLY GENUS *ANAPEPTAMENA* KONOW (HYMENOPTERA: TENTHREDINIDAE)

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Abstract.—*Anapeptamena* Konow (Tenthredinidae: Selandriinae) has been known only by its type species, *A. albipes* Konow, from India and Myanmar. Two new species have been discovered from India and are described: ***Anapeptamena darjeelingensis*, n. sp.**, and ***A. dhanoultiensis*, n. sp.** A male of the genus, that of *A. dhanoultiensis*, is described for the first time. Descriptions, illustrations, and a key are provided for identification of the species.

Key Words: India, Myanmar, Selandriinae

Intensive survey work in India by the first author has documented a large number of new records and resulted in the discovery of many undescribed sawflies. Many genera considered monotypic or to include few species have been found to be much larger and more diverse than previously thought. Such is the case for *Anapeptamena* Konow, a small genus in the Selandriinae known only from several specimens of a single species from northeastern India and Myanmar. Here we review the genus, describe two new species from India, and give a key to the species. A male of the genus also is described for the first time.

The history of *Anapeptamena* revolves around decisions of synonymy by two authors. A year after Konow (1898) described *Anapeptamena*, Cameron (1899) described the genus *Busarbia*. A year later, Konow (1900) proposed the synonymy of the two genera, and subsequent authors followed Konow's treatment, resulting in a number of additional species in *Anapeptamena*. The distinction between *Anapeptamena* and *Busarbia* was not studied until Malaise (1944) was able to examine the type species. He discovered and enumerated a number of differences between the two genera and thus treated them as separate. Based on Malaise's interpretation, all species described in *Anapeptamena* since Konow's (1900) proposed synonymy belong either to *Busarbia* or other genera. From Malaise (1944) to the present, *Anapeptamena* has remained monotypic. We concur with Malaise's (1944) separation of *Anapeptamena*.

Holotypes are deposited in the National Pusa Collections, Division of Entomology, India Agricultural Research Institute, New Delhi, India. Paratypes are at Punjabi University, Patiala, India (PUNJ) and the National Museum of Natural History, Smithsonian Institution, Washington, D.C., USA (USNM).

Abbreviations used in the descriptions are as follows: EL = eye length; IATS =

inner apical tibial spur; ICD = intercenchral distance; IDMO = interocular distance at level of median ocellus; ITD = intertegular distance; LID = lower interocular distance; MB = metabasitarsus; OATS = outer apical tibial spur; OCL = ocello-occipital line; OOL = oculo-ocellar line; POL = postocellar line.

Anapeptamena Konow

Anapeptamena Konow 1898: 271. Type species: *Anapeptamena albipes* Konow. By monotypy.

Description.—Antenna filiform; apical segments without ventral membranous areas; segments 3 and 4 subequal in length or 3 slightly longer than 4; following segments gradually decreasing in length to apex; pedicel 1.5–2.0× as long as its maximum width and almost as long or as long as scape. Mandible strongly bent, almost at right angle, with a subapical tooth; clypeus subconvexly bent from side to side with its anterior margin subtruncate to slightly circularly emarginate (Figs. 1–3); frontal area poorly defined, not surrounded by an acute, high carina; hind orbits carinate below only, with postgenal carina extending only part way up eye. Lateral furrows fine, diverging backwards, abruptly ending just before hind margin of head. Hind orbits very short, head from above narrowing behind eyes. Epicnemium strongly convex, separated from mesepisternum by a furrow. Mesepisternum in front view obtusely raised without carina, rounded at center. Forewing without anal crossvein; veins M and 1m-cu strongly converging, not parallel; vein Rs more or less faint. Hind wing with two closed cells, Rs and M; anal cell sessile. Metabasitarsus shorter than following tarsal joints combined, as about 5:6. Tarsal claws with long, slender inner tooth, nearly as long as outer tooth, without basal lobe (Figs. 4–6). Head, thorax, and abdomen smooth, shining and impunctate.

Remarks.—Several generic characters are slightly modified from previous characterizations of *Anapeptamena* (Malaise 1944, 1963). These include antennal segment 3 sometimes slightly longer than 4, the two not always equal in length; the anterior margin of the clypeus may be shallowly, roundly emarginate, not always subtruncate; and the frontal area is sometimes distinct due to well defined frontal ridges though not surrounded by a sharp carina and not always completely indistinct.

Anapeptamena may be keyed in Malaise's (1963) key to world genera of Selandriinae. It is distinguished from *Busarbia* (type species, *Busarbia viridipes* Cameron from Khasia Hills, India), the genus with which it has been confused, by the poorly defined frontal area, short postgenal carina on the hind orbits extending only part way up the eye, and the last four antennal segments without ventral membranous areas. *Busarbia* has a distinct, pentagonal frontal area, surrounded by an extremely acute and high carina with a transverse lateral carina to inner margin of each eye, the entire hind orbits with a postgenal carina, and the last four antennal segments with ventral membranous areas which give the segments the appearance of bulging downwards.

Anapeptamena is known only from Myanmar and northeastern India. Food plants are not known, but most Selandriinae feed on ferns.

KEY TO SPECIES

1. Malar space half diameter of front ocellus; labrum black, tegula white; intertegular distance 3.5× intercenchral distance; lance not strongly narrowing toward apex, with about 7 serrulae (Fig. 9); . . . . *A. albipes* Konow

– Malar space nearly linear; labrum and tegulae either both white or both black; intertegular distance 4.0× intercenchral distance; lancet either sharply narrowing toward apex (Fig. 10) or with fewer than 7 serrulae (Fig. 11) 2

2. Labrum and tegula white to yellow; clypeus subtruncate, anterior margin of labrum acute (Fig. 2); frontal ridges laterally connected to inner margins of eyes by a low transverse ridge; lancet sharply narrowing toward apex,

with about 8 serrulae (Fig. 10) . . . . *A. darjeelingensis*, n. sp.

– Labrum and tegula black; clypeus shallowly roundly emarginate, anterior margin of labrum rounded (Fig. 3); frontal ridges without transverse ridge to inner margins of eyes; lancet short, not strongly narrowing toward apex, with about 6 serrulae (Fig. 11) . . . . *A. dhanoultiensis*, n. sp.

Anapeptamena albipes Konow
(Figs. 1, 4, 9)

Anapeptamena albipes Konow 1898: 271.—Malaise 1944: 10–11 (Myanmar records).

Female.—Average length, 5.0 mm. Black with tegula and legs, except infuscated apical tarsal segments, yellow to whitish. Wings hyaline; costa, stigma, and venation dark brown to black.

Antennal length 2× head width; pedicel 2× longer than its apical width, almost as long as scape; segment 3 longer than 4, as 8:7. Anterior margin of clypeus subtruncate, labrum broader than long, as 2:1, with rounded anterior margin (Fig. 1); malar space equal to half diameter of front ocellus; inner margins of eyes parallel in middle, faintly converging below; LID:IDMO:EL = 2.0:2.4:1.9; OOL:POL:OCL = 1.7:1.0:2.0. Frontal area slightly higher than level of eyes; supraantennal tubercles and frontal ridges indistinct, without transverse ridge to inner margin of eye; supraantennal pits distinct and removed from antennal sockets by a distance equal to diameter of pit; median fovea indistinct; circum- and interocellar furrows distinct, postocellar furrow indistinct; postocellar area subconvex, broader than long (5:4 at maximum width). Mesoscutellum subconvex, appendage not carinate. ITD:ICD = 3.5:1.0. Tarsal claws as in Fig. 4. IATS:MB:OATS = 2.0:5.5:1.8. Abdomen with light golden pubescence. Lancet not distinctly narrowing toward apex, lateral teeth above serrulae distinct, with about 7 serrulae (Fig. 9).

Male.—Unknown.

Material examined.—INDIA: West Bengal: Darjeeling, 2200 m, 26.5.1989, coll. M.S. Saini (1 ♀, PUNJ); Sikkim: Gangtok, 1550 m, 14.5.93, coll. M.S. Saini (1 ♀, USNM); Khasia Hills (holotype ♀).

Distribution.—India (West Bengal, Sikkim); Myanmar (Kambaiti at 2000 m, close to the Yunnan frontier [Malaise 1944]).

Type.—The holotype female is at the Deutsches Entomologisches Institut, Eberswalde, Germany, labeled "Khasia Hills, Assam," "coll. Konow," "Holotypus [red]," "Anapeptamena albipes Knw., Assam," "TYPUS [red]," "Coll. DEI Eberswalde." The head is glued onto a piece of cardboard on the same pin; the antennae are missing.

***Anapeptamena darjeelingensis* Saini, Smith, and Saini, new species**
(Figs. 2, 5, 10)

Female.—Length, 5.0 mm. Black with labrum, tegula, coxae (except extreme bases), midleg (except last tarsal segment), and hind leg (except lightly infuscated apical 3 tarsal segments) yellow to whitish. Wings subhyaline; costa, stigma, and venation dark brown to black.

Antennal length 2× head width, pedicel 2× its apical width, almost as long as scape; segment 3 longer than 4, as 5:4. Anterior margin of clypeus slightly emarginate; labrum about as long as broad, with acuminate anterior margin (Fig. 2); malar space linear; inner margins of eyes parallel in middle, faintly converging below; LID:IDMO:EL = 2.0:2.4:2.1; OOL:POL:OCL = 1.5:1.0:1.5. Frontal area slightly higher than level of eyes; supraantennal tubercles indistinct but continue posteriorly similar to somewhat prominent frontal ridges; in middle, frontal ridge laterally connected to inner margins of eye by a low transverse ridge; supraantennal pits distinct and removed from antennal sockets by a distance equal to diameter of pit; median fovea distinct and gently curved in its posterior half with bottom almost flat; interocellar furrow distinct, circum- and postocellar furrows indistinct; postocellar area subcon-

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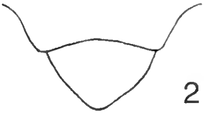

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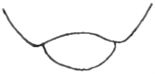

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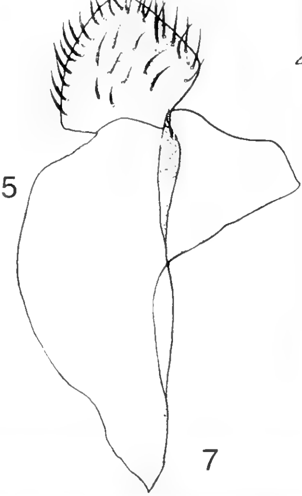

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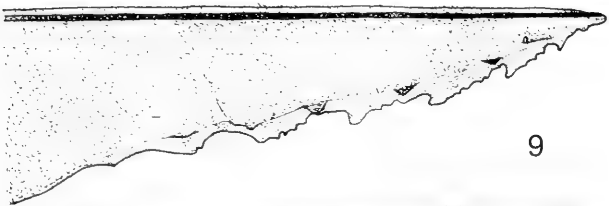

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vex, broader than long as 5:4 at its maximum width. Mesoscutellum subconvex, appendage not carinate. ITD:ICD = 4.0:1.0. Tarsal claws as in Fig. 5. IATS:MB:OATS = 2.0:6.0:1.8. Abdomen with brownish golden pubescence. Lancet strongly narrowing toward apex, lateral teeth above serrulae indistinct, with about 8 serrulae (Fig. 10).

Male.—Unknown.

Type.—Holotype ♀, West Bengal: Darjeeling, 2200 m, 8.5.1983, coll. M.S. Saini.

Distribution.—India (West Bengal).

Etymology.—The species name is derived from the type locality.

Anapeptamena dhanoultiensis Saini, Smith, and Saini, new species

(Figs. 3, 6–8, 11)

Female.—Length, 4.2 mm. Black with tibiae yellow and rest of legs fuscous. Wings lightly, uniformly infumated; costa, stigma, and venation brown.

Antenna (apical 2 segments missing) with pedicel 1.5× longer than broad, as long as scape, segment 3 longer than 4, as 4:3. Anterior margin of clypeus shallowly roundly emarginate; labrum broader than long, as 2:1 with rounded anterior margin (Fig. 3). Malar space linear. Inner margins of eyes converging below; LID:IDMO:EL = 2.0:2.5:2.0; OOL:POL:OCL = 1.3:1.0:1.0. Frontal area almost same height as eyes; supraantennal tubercles and frontal ridges indistinct; supraantennal pits distinct and removed from antennal sockets by 1.75× diameter of pit; median fovea indistinct in its posterior half and in anterior half represented by a deep median supraantennal pit; without transverse ridge extending to inner margin of eye; circum- and interocellar furrows distinct, postocellar furrow indistinct; postocellar area subconvex, broader than long, as 2:1 at its maximum width. Mesoscutellum flat, appendage not carinate. ITD:ICD = 4.0:1.0. Tarsal claws as in Fig. 6. IATS:MB:OATS = 2.0:7.5:1.6. Abdomen with brownish yellow pubescence. Lancet short, not strongly narrowing toward apex, without lateral teeth above serrulae, with about 6 serrulae (Fig. 11).

Male.—Average length, 4.5 mm. Similar to female except apical halves of coxae, basal half of fore- and midfemora, inner surface of hind femur on basal half, and apical tarsal segments black. Supraantennal pits removed from antennal sockets by 0.5× diameter of a pit. Genitalia as in Figs. 7, 8; harpe triangular, pointed at apex; parapenis produced into a narrow, rounded lobe at apex; penis valve oblong, finely serrate on dorsoapical margin.

Types.—Holotype ♀, Uttar Pradesh: Dhanoulti, 2000 m, 25.7.1993, coll. M.S. Saini. Paratypes: Same data as holotype except 3.6.1983 (2 ♂, PUNJ, USNM).

Distribution.—India (Uttar Pradesh).

Etymology.—The name is derived from its type locality.

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Figs. 1–11. *Anapeptamena.* 1–3, Clypeus and labrum. 1, *A. albipes.* 2, *A. darjeelingensis.* 3, *A. dhanoultiensis.* 4–6, Tarsal claw. 4, *A. albipes.* 5, *A. darjeelingensis.* 6, *A. dhanoultiensis.* 7, Male gonoforceps of *A. dhanoultiensis.* 8, Male penis valve of *A. dhanoultiensis.* 9–11, Female lancets. 9, *A. albipes.* 10, *A. darjeelingensis.* 11, *A. dhanoultiensis.*

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A REVISION OF THE NEOTROPICAL CLICK BEETLE GENUS *SEMIOTINUS* PJATAKOWA (COLEOPTERA: ELATERIDAE)

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Abstract.—Fifteen species, formerly placed in *Semiotus* Eschscholtz are transferred into the genus *Semiotinus*, which formerly included only *S. banghaasi* Pjatakowa. The 17 known species of the Neotropical genus *Semiotinus* Pjatakowa are described and keyed. *Semiotinus maculatus, n. sp.*, is described. *Semiotus straminious* Candèze is a **new synonym** of *S. brevicollis* Candèze, **n. comb**; *S. dyptichus* Candèze and *S. subvirescens* Schwarz are **new synonyms** of *S. quadricollis* Kirsch, **n. comb.**; *S. juvenilis* Candèze and *S. borrei* Candèze are **new synonyms** of *S. fusiformis* Kirsch, **n. comb.**; *S. elegantulus* Candèze is a **new synonym** of *S. trilineatus* Candèze, **n. comb.**; *S. pulchellus* Candèze is a **new synonym** of *S. quadrivittis* Steinheil, **n. comb.**; and *S. staudingeri* Pjatakowa is a **new synonym** of *S. aeneovittatus* Kirsch, **n. comb.** The three genera of the subfamily Semiotinae are also keyed.

Key Words: Coleoptera, click beetle, Elateridae, *Semiotus*, *Semiotinus*

The Neotropical click beetle genus *Semiotinus* was proposed by Pjatakowa (1941) to include a single species, *S. banghaasi* Pjatakowa from Colombia. It was distinguished from the related genus *Semiotus* Eschscholtz by having the pronotum wider than long, by the presence of carinae on the hind angles of the pronotum, and by the bulkier body.

Unfortunately, the type and only known specimen of this species was destroyed in a fire in Kiev in the 1940's along with several hundred other Pjatakowa types (V.G. Dolin, personal communication). In the process of revising the Neotropical genus *Semiotus*, it became clear that many of the smaller species assigned to that genus were similar to Pjatakowa's description of *Semiotinus*. A phylogenetic analysis of all species considered to be included in *Semiotus* indicated a basal monophyletic clade for a group of species sharing characters with *Semiotinus* (Wells 2002). These species are herein assigned to the genus *Semiotinus*. Additionally, one previously undescribed species is included in the genus.

Of the 17 species here recognized, only a few are represented by more than a few specimens. A total of only 33 specimens were available for study from 26 major institutions or museums. Accordingly, intraspecific variability is not well understood and must be inferred from the genus *Semiotus*. The best approach under these circumstances is to be conservative in delimiting species.

Materials and Methods

The following collections provided material for this study (involving both the genera *Semiotus* and *Semiotinus*). The recognized four-letter codens are from Arnett et al. (1993). Specimens of *Semiotinus* were present in only a few of these institutions.

The Natural History Museum, London (BMNH); California Academy of Sciences, San Francisco (CASC); Canadian Museum of Nature, Ottawa (CMNC); Canadian National Collection of Insects, Ottawa (CNCI); Colorado State University, C.P. Gillette Museum of Arthropod Biodiversity, Fort Collins (CSUC); Cornell University Insect Collections, Ithaca, New York (CUIC); Deutsches Entomologisches Institut, Eberswalde (DEIC); Escuela Agricola Panamericana, Zamorano, Tegucigalpa, Honduras (EAPZ); E.G. Riley Collection (EGRC); Essig Museum, University of California, Berkeley (EMEC); Field Museum of Natural History, Chicago (FMNH); Hungarian Natural History Museum, Budapest (HNHM); Instituto Nacional de Biodiversidad, Santo Domingo, Costa Rica (INBC); Institut Royal des Sciences Naturelles de Belgique, Brussels (ISNB); Museum für Naturkunde, Berlin (MNFD); Muséum National d'Histoire Naturelle, Paris (MNHN); Montana Entomology Collection, Montana State University, Bozeman (MTEC); Naturhistorisches Museum, Vienna (NHMW); The Ohio State University Collection, Columbus (OSUC); University of Oxford, Hope Entomological Collections, United Kingdom (OXUM); Peter Cate Collection, Vienna (PCCV); Snow Entomological Collections, University of Kansas, Lawrence (SEMC); Staatliches Museum für Tier-Kunde, Dresden (SMTD); Texas A&M University, College Station (TAMU); National Museum of Natural History, Smithsonian Institution, Washington, D.C. (USNM); Universitetets Zoologiske Museum, Copenhagen (ZMUC).

Male and female internal genitalia were examined after dissection and being cleared in a 1.0 molar solution of KOH at room temperature. Dissections were made on specimens from non-type material, except where available material was limited. The type material was too feeble to dissect. Color terminology was standardized by using the color charts in *A Dictionary of Color* (Maerz and Paul 1950) and then correlated with color descriptions found in W. T. Stern's *Botanical Latin* (1983). These sources should be consulted for precise identification of colors in this study. A general description of the main colors referred to herein include aerugineus: verdigris; aurantiacus: apricot orange; badius: dull chocolate brown; fulvus: dull yellow with a mixture of gray and brown; luteus: buttercup yellow; piceus: black as pitch; rufopiceus: reddish black (in this study more black than reddish); sanguineus: blood red; testaceus: brick red to brownish yellow (of unglazed earthenware); viridis: untinted green.

Measurements of body length were made from the anterior margin of the frons (including frontal spines when present) to the tip of the elytra (including spines, when present). Measurements of body width were made at the widest part of the body—generally on the basal third of the elytra. Pronotal length was measured along the center-line of the pronotum. Pronotal width was measured at the tip of the hind angles. Elytral length was measured along the suture. Elytral width was measured at the widest point—generally at the basal third. The relative width of the eyes was determined using the ocular index (Campbell and Marshall 1964). This is determined by measuring the narrowest distance between the eyes divided by the width of the head measured across the eyes. This quotient is then multiplied by 100.

Distributional data in the material examined sections are from the specimen labels. Exceptions to this include the dates, which have been standardized so as to be read: day—month (in Roman numerals)—year. In cases where these periods are uncertain, the data have remained exactly as indicated on the labels. Larger political divisions have also been added in cases where they have not appeared on labels (and where they could be determined). Duplicate specimens of the same species bearing identical labels are only listed once. All available type material was examined, including Chassain's recent lectotype designations. The Pjatakowa types have been destroyed (V.G. Dolin, personal communication).

DIAGNOSTIC CHARACTERS OF ADULTS

The genus *Semiotinus* is distinguished from all other genera in the Semiotinae by the straight or recurved lateral pronotal margin (as in Figs. 1, 14–18) that joins the dorsal surface of the pronotum and the hypomeron at an acute angle (Fig. 12). Other characters are also typical of the genus but are not, in themselves, diagnostic for all species. These characters include: the hind angles of the pronotum that are typically carinate or subcarinate, the prosternum that is typically straight in profile, the frons that is typically lobed and without projecting spines, the pronotum that is typically wider than long, the pronotal disk that is typically evenly convex across without depressions or tubercles, and the elytra that each typically terminate in an acute spine and either a sharp subapical angle or dentition. These characters are not typical of *Semiotus.*

Within the genus itself, the primary characters used to distinguish species are the presence or absence of frontal spines, shape of the lateral margin of the pronotum, color of the head, pronotum, and elytra, and shape of the apical elytral spines.

Male and female genitalic characters also differ interspecifically. The male parameres range from narrow to broad and bear an apical blade (Figs. 2–9). This blade varies significantly in size and shape ranging from triangular with sharp angles (Figs. 2–4) to sinuous with rounded edges (Fig. 6). Posteriorly the blade has lateral angles that differ in size and angle of projection. The anterior sclerite of the female bursa copulatrix also differs in the only two species examined. The pattern includes a median piece, or spine, flanked by two lateral arms, or spines (Figs. 10, 11).

Several species of *Semiotus* in the *S. caracasanus* group (Wells 2002) are superficially similar to the species of *Semiotinus* with frontal spines (*S. macer* (Candèze) and *S. aeneovittatus* (Kirsch)). Both groups lack

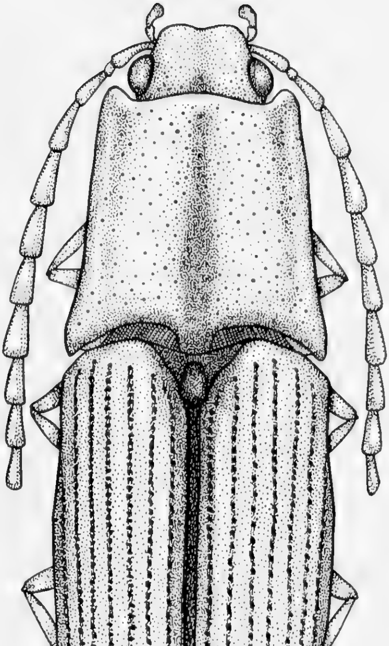

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Fig. 1. *Semiotinus maculatus.*

marginal sulci. In these cases, species of *Semiotus* can be recognized by the broader pronotal border (joining the hypomera in an even curvature (as in Fig. 13) and not acutely as in *Semiotinus*) and by the very finely punctate pronotum and elytra with faint striae. The pronotal punctures in *Semiotinus* are deeper, and the striae and strial punctures are clearly defined.

KEY TO GENERA OF SEMIOTINAE

1. Pronotum, viewed from above, with sides straight or recurved (Figs. 14–18); dorsal surface of pronotum meeting hypomeron at an acute marginal angle, without defining sulcus (Fig. 12) . . . . . . *Semiotinus* Pjatakowa
– Pronotum, viewed from above, with sides sinuate or rounded (Fig. 19); lateral pronotal margin rounded, incrassate, undulate, or sulcate, never acute (as in Fig. 13) 2
2(1). Tarsi with thick pubescent pads on segments 1 to 3 . . . . *Oistus* Candèze
– Tarsi with thin glabrous pads on segments 1 to 3 . . . . *Semiotus* Eschscholtz

Genus *Semiotinus* Pjatakowa

Semiotinus Pjatakowa 1941: 107 (type species, *Semiotinus Bang-Haasi* Pjatakowa, orig. desig.); Calder 1976: 107; Lawrence and Newton 1995: 853.

Description.—Length 7–23 mm, colored variously with combinations of orange, yellow, green, brown, and black. Frons with two spines or lacking frontal spines (as in Figs. 14–18). Antenna serrate extending one to four segments beyond hind angle. First two segments testaceus to piceus, remaining segments fulvus to piceus. Pronotum as wide as or wider than long, disk evenly convex; with or without setae, often glabrous, nitidus, punctation evenly scattered throughout, or becoming denser and umbilicate anterolaterally; lateral margins straight or recurved (in dorsal view), either parallel-sided or convergent anteriorly, without defining sulcus, pronotum and hypomeron joining at a sharp edge (Fig. 12), hind angles divergent or not. Hypomeron elongate, posterior border sinuous and often dentate, partially enclosing procoxae. Prosternal process lobed anteriorly, prosternal process straight or curved in profile, extending between procoxae to mesosternal fossa. Scutellum subquadrate to elongate, longer than wide, flat or convex on disk. Legs fulvus to piceus, tarsal segments 1–3 lobed beneath; tarsal claws broad at base, without basal setae. Elytron widest anteriorly then narrowing to apex. Intervals flat or convex; elytral base on same plane as pronotum, occasionally gibbous and rising above level of pronotum; color piceus to fulvus, often with alternating light and dark bands; glabrous or pubescent; abdomen fulvus to piceus, sternite 5 of females often with two foveae. Bursa copulatrix generally with two posterior platelike sclerites, and one spinose anterior sclerite. Parameres generally bearing an apical blade apically.

Larvae and pupae unknown.

KEY TO SPECIES OF *SEMIOTINUS* PJATAKOWA

1. Head with two frontal spines (as in Fig. 15) 2
– Head without two frontal spines (as in Figs. 14, 16–18) 3
2(1). Pronotum and elytra pale yellow to light brown with greenish blue (often metallic) maculae or bands; apex of each elytron with two subequal spines (Fig. 22) . . . . *aeneovittatus* (Kirsch)
– Pronotum and elytra light brown, if markings present, then without greenish blue markings; apex of each elytron with a single spine and a subapical tooth or angle (Fig. 23) . . . . *macer* (Candèze)
3(1). Pronotum with three dark longitudinal vittae (sometimes confluent posteriorly) . . . . *trilineatus* (Candèze)
– Pronotum with 0, 1, or 2 dark vittae . . . 4
4(3). Elytra unicolorous, at least on basal half 5
– Elytra not unicolorous, with light and dark contrasting vittae or patterns (or with pale elytra contrasting with infuscate striae or strial punctures) 10
5(4). Elytra black, or dark reddish black . . . . *morio* (Candèze)
– Elytra dull yellow, yellowish green, or light brown to orange 6
6(5). Pronotal margin (viewed from above) strongly recurved (Fig. 14) . . . . *conicollis* (Candèze)

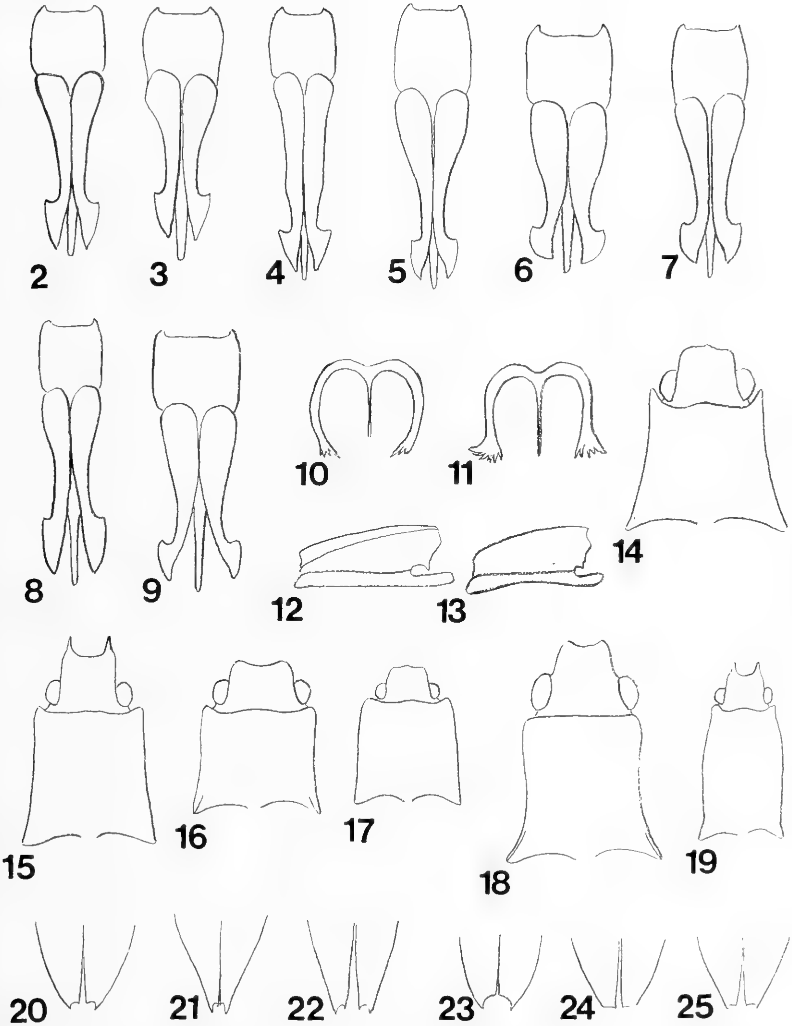

Fig. 2–25. *Semiotinus* and *Semiotus* species. 2–9, Male genitalia. 2, *Semiotinus quadricollis.* 3, *Semiotinus fussiformis.* 4, *Semiotinus boliviensis.* 5, *Semiotinus virescens.* 6, *Semiotinus limbaticollis.* 7, *Semiotinus aeneovittatus.* 8, *Semiotinus maculatus.* 9, *Semiotinus scitulus.* 10–11, Female anterior sclerite. 10, *Semiotinus aeneovittatus.* 11, *Semiotinus macer.* 12–13, Lateral aspect of pronotum. 12, *Semiotinus scitulus.* 13, *Semiotus zonatus.* 14–19, Head and pronotum. 14, *Semiotinus conicollis.* 15, *Semiotinus aeneovittatus.* 16, *Semiotinus nigricollis.* 17, *Semiotinus virescens.* 18, *Semiotinus boliviensis.* 19, *Semiotus nigriceps.* 20–25, Elytral apices. 20, *Semiotinus limbaticollis.* 21, *Semiotinus quadrivittis.* 22, *Semiotinus aeneovittatus.* 23, *Semiotinus macer.* 24, *Semiotinus nigricollis.* 25, *Semiotinus boliviensis.*

– Pronotal margin not strongly recurved (as in Figs. 1, 17) 7
7(6). Pronotum with two black vittae; elytra gibbous at base . . . . . *brevicollis* (Candèze)
– Pronotum without black bands or with a single black band; elytra not gibbous at base 8
8(7). Elytra (at least on basal half) orange to blood red . . . . *maculatus*, n. sp.
Elytra dull yellow to yellowish green 9
9(8). Lateral pronotal margins straight, hind angles divergent (Fig. 17); pronotum immaculate 17
Lateral pronotal margins straight and parallel, not diverging posteriorly; pronotum maculate . . . . *quadricollis* (Kirsch), in part
10(4). Elytral intervals all dull yellow, striae and/or strial punctures infuscate (dark brown to black) 11
Elytral intervals not all of same color 12
11(10). Pronotum with one dark discal macula or vitta . . . . *fusiformis* (Kirsch)
– Pronotum with two dark discal vittae . . . . *supplicans* (Kirsch)
12(10). Each elytron with four dark and four pale vittae—intervals 1, 3, 5, 7, and sometimes lateral margin, brown, intervals 2, 4, 6, 8 and 9 dull yellow . . . . *scitulus* (Candèze)
– Each elytron with fewer than four vittae of either color 13
13(12). Pronotum black, without yellow to light brown margins 16
– Pronotum black with yellow to light brown margins, or with discal band only black 14
14(13). Head black 15
– Head orange to pale brown . . . . *quadricollis* (Kirsch), in part
15(14). Elytra gibbous at base; lateral margin of elytra concave in outline near apex (Fig. 21) . . . . *quadrivittis* (Candèze)
– Elytra not gibbous, as wide (dorsoventrally) at base as on basal third; lateral margin of elytra evenly convex in outline near apex (Fig. 20) . . . . . *limbaticollis* (Candèze)
16(13). Pronotum narrow, length of anterior pronotal margin approximately ⅔ width of elytral humeri (Fig. 18); apex of each elytron bispinose, area between spines emarginate (Fig. 25) *boliviensis* (Candèze)
– Pronotum less narrow, length of anterior pronotal margin approximately ¾ or more width of elytral humeri (Fig. 16); apex of each elytron blunt and angulate, if small dentitions present, then without emargination (Fig. 24) . . . . . *nigricollis* (Candèze)
17(9). Body 4 mm wide at widest point . . . . *banghaasi* Pjatakowa
– Body less than 3.6 mm wide at widest point . . . . *virescens* (Candèze)

Semiotinus aeneovittatus (*Kirsch*), **n. comb.**

(Figs. 7, 10, 15, 22)

Semiotus aeneovittatus Kirsch 1884: 44 (lectotype, female (Chassain, in press): SMTD; type locality: Ecuador, Huamboya).

Semiotus staudingeri Pjatakowa 1941: 107 (holotype destroyed; type locality: Ecuador, Normandia). **New synonym.**

Description.—*Length* 13–16 mm (length/width ratio 4.4–4.8). *Head* badius to rufopiceus on disk, fulvus to testaceus peripherally, with faint dark metallic sheen aerugineus, with two spines anterolaterally (Fig. 15); fine decumbent setae scattered throughout, punctation subumbilicate and scattered throughout. *Antenna* serrate, reaching 2–3 segments beyond hind angle of pronotum in male, 1–2 segments in female; segments 1 and 2 testaceus, segments 3–11 rufopiceus. *Thorax* with pronotum 2–3 mm (length/width ratio 0.7–1.0) subtrapezoidal, hind angles slightly diverging; margin thin, clearly defined; badius to rufopiceus with dark metallic sheen aeruginosus; fine scattered setae and deep punctures throughout. Scutellum fulvus to badius, strongly convex, anterior margin declivitous and wider than rounded posterior margin. Prosternum linear in profile, apex of prosternal process not divided; fulvus to aurantiacus, with or without badius macula laterally; few erect setae anteriorly, denser and decumbent setae laterally, punctation fine medially, thicker laterally. Hypomeron fulvus to aurantiacus; glabrous, nitidus with fine decumbent setae and deep punctures near suture. Mesosternum depressed below plane of metasternum; fulvus to aurantiacus, fossa glabrous and impunctate, lateral areas with dense setae and fine punctures. Mesepisternum and epimeron fulvus to aurantiacus. Metasternum testaceus to aurantiacus with or without badius to piceus anterolateral areas; mostly glabrous with few erect setae and with fine decumbent setae anterolaterally, punctation fine medially, wider and denser anterolaterally. Femora fulvus to testaceus.

Elytron 9–12 mm (length/width ratio 3.1–3.3), gibbous anteriorly, subparallel on anterior half then narrowing to tip; ranging from a metallic aerugineus with circumscutellar area fulvus to luteus, to nearly entirely fulvus with fine aeruginous macula on intervals 6 and 8 basally; glabrous, nitidus, striae faint, strial punctures clearly defined; apex ending in a terminal spine and a large dentition along inner angle subapically (Fig. 22).

Abdomen testaceus to aurantiacus; fine setae and punctation becoming thicker laterally; female without foveae on sternite 5; anterior sclerite of bursa copulatrix with lateral arms enlarged apically, each bearing 2 to 3 large dentitions, lateral arms 1.2 times longer than median piece (Fig. 10). Male with parameres diverging apically, apical blades small, 20% length of parameres (Fig. 7).

Material examined.—ECUADOR: Huamboya, D. Stubel (lectotype of *S. aneovittatus*, SMTD); Napo, Baeza, 2,000 m., 25-II-1979, H. & A. Howden (1, CNCI); Napo, 7 km S. Baeza, 2,000 m, (20–28)-II-1979, H. & A. Howden (1, CNCI).

Diagnosis.—The two frontal spines (Fig. 15) and the verdigris metallic sheen distinguish *S. aeneovittatus* from all other *Semiotinus*. *Semiotinus macer* also bears frontal spines but is readily distinguished by the brown body (and lack of verdigris metallic sheen), larger size, and more elongate and parallel-sided elytra.

Note.—The type material of *Semiotus staudingeri* has been destroyed (Dolin, personal communication). Pjatakowa's description, though, does not differ from the type of *S. aeneovittatus*. There are no other known species of *Semiotus* (or *Semiotinus*) that have the bluish green metallic coloration.

Semiotinus banghaasi Pjatakowa

Semiotinus Bang-Haasi Pjatakowa 1941: 107 (holotype: lost; type locality: Colombia: San Antonio)

No specimens of this species were available for study, but it apparently represents a valid species. The holotype was destroyed (V.G. Dolin, personal communication). The following description is interpreted from Pjatakowa (1941).

Description.—*Length* 14 mm, 4 mm wide (length/width ratio 3.3). *Head* flat, fulvus to testaceus, shallowly tri-impressed, sparsely punctate. *Antenna* long, extending to hind angle, with segments 1 and 2 flavotestaceus, segments 3–11 fuscus. *Thorax* with pronotum wider than long, nearly quadrangular; testaceus with obscure fulvus to viridis border; moderate punctures, anterior angles rounded, hind angles short, little divergent, with a distinct carina. Scutellum oblong, anterior margin truncate, rounded behind, 3-angled, slightly wider posteriorly. Venter, except epipleura and lateral areas of prosternum luteus to aurantiacus. Femora fulvus to testaceus.

Elytron convex, striate, striae piceus, punctate; fulvus to luteus with viridis tint; glabrous; apex emarginate.

Material examined.—None.

Note.—Pjatakowa's description of *S. banghaasi* seems to place the species next to *S. virescens*. Both species are yellowish green and similar with respect to the characters listed by Pjatakowa in the description of *S. banghaasi*. The important difference between the two species is the width of the body, which in *S. banghaasi* is 4 mm, and in *S. virescens*, less than 3.6 mm. A specimen (in the BMNH) labelled as *S. banghaasi* is too narrow and should be considered *S. virescens*.

Semiotinus boliviensis (Candèze), **n. comb.**
(Figs. 4, 18, 25)

Semiotus boliviensis Candèze 1895: 16 (holotype, male: INSB; type locality: Bolivia).

Description.—*Length* 10–11 mm (length/width ratio 4.4–4.6). *Head* piceus, frontal margin with two angulate lobes anterolaterally, without spines; long setae and umbilicate punctures throughout. *Antenna* serrate, reaching 3–4 segments beyond hind angle; badius to piceus. *Thorax* with pronotum 2 mm (length/width ratio 0.8–0.9) parallel sided on anterior half then strongly diverging to hind angles (Fig. 18), margin thin, hind angles carinate; piceus; long setae and deep punctation throughout, becoming denser peripherally. Scutellum subrectangular, longer than wide, covered with long setae. Prosternum nearly straight in profile; piceus; long setae and scattered punctures throughout. Hypomeron rufopiceus. Mesosternum rufopiceus to piceus; long golden setae and scattered punctures throughout. Mesepisternum and metasternum rufopiceus to piceus; long aureus setae and scattered punctures throughout. Femora rufopiceus to piceus.

Elytron 8 mm (length/width ratio 3.2–3.4), subgibbous, subparallel on anterior ⅘ then narrowing to tip; badius to piceus with intervals 2–4 (or 5) fulvus; nitidus, with short setae, intervals convex, striae and strial punctures clearly defined; apex ending in a terminal spine and a smaller dentition along inner angle subapically (Fig. 25).

Abdomen badius to piceus; long aureus setae and scattered punctures throughout. Male with parameres sinuate along apical third (Fig. 4), apical blades subtriangular, approximately 20% length of parameres. Female unknown.

Material examined.—BOLIVIA: (1, INSB).

Diagnosis.—The completely black head, lack of frontal spines and very narrow anterior aspect of the pronotum (Fig. 18), and recurved pronotal margins distinguish *S. boliviensis* from all other *Semiotinus*.

Semiotinus brevicollis (Candèze), **n. comb.**

Semiotus brevicollis Candèze 1857: 332 (holotype: BMNH; type locality: N. Granada); Candèze 1874: 186.

Semiotus stramineus Candèze 1857: 333 (holotype: BMNH; type locality: Colombia); Candèze 1874: 188. **New synonym.**

Description.—*Length* 13–17 mm (length/width ratio 4.0–4.2). *Head* testaceus to aurantiacus, front without spines; fine decumbent setae scattered throughout and long erect setae over eyes and anterior margin, punctation scattered throughout; ocular index 75.0–78.0. *Antenna* reaching 1–3 segments beyond hind angle; segments 1 and 2 testaceus, segments 3–11 badius. *Thorax* with pronotum 2–4 mm (length/width ratio 0.7–0.9), sides straight, diverging to angles, hind angles subcarinate; margin thin, clearly defined; lateral and anterior margins testaceus, wide, sublateral bands piceus, median area aurantiacus to badius; dense decumbent setae throughout, punctation deep, especially deep and umbilicate on piceus bands. Scutellum fulvus to testaceus, longer than wide, hind margin rounded, anterior margin straight. Prosternum linear in profile, tip of prosternal process not divided; testaceus to aurantiacus medially with rufopiceus macula along suture extending onto hypomeron; nearly glabrous and impunctate medially, with erect setae and deep punctures anterolaterally. Hypomeron fulvus to aurantiacus laterally, with rufopiceus band along suture extending nearly to lateral margin; with dense decumbent setae and punctures along suture, nearly glabrous with very fine punctures laterally. Mesosternum testaceus to aurantiacus, fossa glabrous and impunctate, lateral areas with dense setae and fine punctures. Mesepisternum testaceus to aurantiacus. Metasternum aurantiacus to sanguineous, badius to piceus anterolaterally; with few setae medially becoming dense anterolaterally, punctation fine medially becoming denser anterolaterally. Femora testaceus.

Elytron 10–12 mm (length/width ratio 2.9–3.1), gibbous basally, subparallel on anterior ⅔ then narrowing to tip; fulvus, strial punctures darker; glabrous, nitidus, intervals convex, striae an strial punctures clearly defined; apex ending in a terminal spine and a smaller dentition along inner angle subapically.

Abdomen testaceus to aurantiacus with nebulous infuscation sublaterally; fine setae and punctation becoming denser laterally; female without foveae on sternite 5. Male unknown.

Material examined.—COLOMBIA: (1, BMNH); N. GRANADA (this could be anywhere in Ecuador, Colombia, Venezuela, or Panama) (1, BMNH).

Diagnosis.—*Semiotinus brevicollis* is distinct from other *Semiotinus* in having unicolorous elytra, a yellow to orange head, gibbous elytral base, and two pronotal vittae. The type of *S. stramineus* is larger (being just over 16 mm long) than other known examples of *S. brevicollis*. No other differences could be determined. The two are here considered conspecific.

Semiotinus conicollis (Candèze), **n. comb.**
(Fig. 14)

Semiotus conicollis Candèze 1857: 333 (holotype: BMNH; type locality: Colombia); Candèze 1874: 188.

Description.—*Length* 19–20 mm (length/width ratio 3.7–3.9). *Head* fulvus to testaceus, frontal margin often angled without spines; nitidus with few decumbent setae scattered throughout; ocular index 66.0–68.0. *Antenna* serrate, reaching 3–4 segments beyond hind angle; segments 1 and 2 testaceus, segments 3–11 testaceus to badius. *Thorax* with pronotum 3–4 mm (length/width ratio 0.7–0.8) wider than long, sides strongly recurved (viewed from above), hind angles divergent (Fig. 14); testaceus to aurantiacus, darker on disk; glabrous, nitidus. Scutellum testaceus to aurantiacus, subtriangular. Prosternum linear in profile; testaceus to aurantiacus, lobe paler; glabrous with fine punctation medially, denser setae and punctation laterally. Hypomeron fulvus; covered with fine setae and punctures throughout. Mesosternum fulvus to testaceus, fossa glabrous and impunctate, lateral areas with dense setae and fine punctures. Mesepisternum testaceus to badius. Metasternum testaceus to badius; sparse erect setae medially, denser decumbent setae laterally on dark area. Femora aurantiacus to testaceus.

Elytron 15 mm (length/width ratio 2.8–3.0) gibbous; unicolorous fulvus with faint viridis tint; glabrous, nitidus, striae faint to obsolete, strial punctures clearly defined; apex bearing two small spines or dentitions.

Abdomen testaceus; scattered erect setae medially, dense decumbent setae laterally, punctation fine becoming dense laterally. Genitalia not examined.

Material examined.—COLOMBIA: (1, BMNH).

Diagnosis.—The unicolorous elytra, recurved pronotal margin (Fig. 14), and yellow to light brown head readily distinguish *S. conicollis* from all other *Semiotinus*.

Semiotinus fusiformis (Kirsch), **n. comb.**
(Fig. 3)

Semiotus fusiformis Kirsch 1866: 181 (lectotype, female (Chassain, in press): SMTD; type locality: Bogotá); Steinheil 1875: 113; Candèze 1874: 185.

Semiotus juvenilis Candèze 1874: 187 (holotype: BMNH; type locality: Colombia). **New synonym**.

Semiotus borrei Candèze 1878: 9 (type: not found; type locality: Ecuador). **New synonym**.

Description.—*Length* 12–13 mm (length/width ratio 4.8–4.9). *Head* piceus, front without spines; fine decumbent setae and shallow subumbilicate punctures throughout. *Antenna* reaching 3–4 segments beyond hind angle in male; segments 1 and 2 testaceus, segments 3–11 rufopiceus to piceus, *Thorax* with pronotum 2–3 mm (length/width ratio 0.8.–0.9) subtrapezoidal, hind angles diverging; margin thin, clearly defined; fulvus to aurantiacus, with elliptical piceus macula medially; glabrous. Scutellum badius to piceus, longer than wide, posterior border rounded, anterior margin straight. Prosternum linear in profile, tip of prosternal process not divided; piceus, prosternal lobe and prosternal process fulvus to aurantiacus; few erect setae anteriorly, decumbent setae laterally, punctation fine medially, thicker laterally. Hypomeron fulvus to luteus, piceus laterally along suture; nitidus with or without few scattered setae throughout, punctation of few shallow subumbilicate punctures throughout. Mesosternum fulvus to testaceus medially, piceus laterally, fossa glabrous and impunctate, lateral areas with dense setae and fine punctures. Mesepisternum piceus. Metasternum badius to piceus throughout or with fulvus to testaceus median coloration; glabrous with fine punctation medially, with fine decumbent setae and denser punctation anterolaterally. Femora fulvus to testaceus.

Elytron 8–10 mm (length/width ratio 3.5–3.7), subparallel on anterior half then narrowing to tip; fulvus to luteus with strial punctures badius to rufopiceus; glabrous, nitidus, striae and strial punctures clearly defined, intervals convex; apex ending in a terminal spine and a smaller dentition along inner angle subapically.

Abdomen badius to rufopiceus, sternite 5, lateral areas of sternites 3 and 4 and medial area of sternite 1 lighter; fine setae and punctation becoming thicker laterally. Male with parameres subtriangular apically, lateral margins convex, aedeagus extending beyond apical tips of blades (Fig. 3).

Material examined.—COLOMBIA: Bogota, Kirsch (1, SMTD); ECUADOR: Pich., 35 km E Tandapi, 8,000–9,000 ft., 24-IV-1975, S. & J. Peck (1, CNCI); E. de Ville, 71 (1, INSB).

Diagnosis.—The single pronotal band and fulvus elytra with infuscate punctures separate *S. fussiformis* from all other *Semiotinus*.

Note.—The type of *S. borrei* has not been located. A specimen with the author's (Candèze) determination label was located in Brussels (INSB). This specimen is clearly a synonym of *S. fusiformis*.

Semiotinus limbaticollis (Candèze), **n. comb.**
(Figs. 6, 20)

Semiotus limbaticollis Candèze 1857: 336 (holotype: BMNH; type locality: Colombia); Candèze 1874: 188.

Description.—*Length* 9–10 mm (length/width ratio 4.1–4.3). *Head* piceus throughout without spines; few long setae and scattered shorter setae, punctation subumbilicate. *Antenna* serrate, reaching 3–4 segments beyond hind angle; piceus. *Thorax* with pronotum 2 mm (length/width ratio 0.8–1.0), subquadrate, margins straight, gradually widening posteriorly, hind angles subcarinate; piceus, with thin fulvus to aurantiacus margins becoming wider near angles. Scutellum badius to rufopiceus, parallel-sided, angles rounded, longer than wide. Prosternum linear in profile; piceus, lobe and prosternal process fulvus to testaceus; long pale setae, punctation becoming umbilicate laterally. Hypomeron piceus, with lateral margin fulvus to aurantiacus; long pale setae, punctation close and umbilicate throughout. Mesosternum aurantiacus medially, piceus laterally, covered with long pale setae. Mesepisternum piceus. Metasternum piceus; glabrous medially, with dense decumbent setae laterally, punctation fine becoming dense laterally. Femora fulvus to testaceus.

Elytron 6–8 mm (length/width ratio 3.0–3.1), subparallel on anterior ⅔ then narrowing to tip; badius to rufopiceus with intervals 1–4, 9, and margin fulvus to luteus on basal ⅔; glabrous, nitidus, with fine setae laterally, strial punctures well defined, striae fine to obsolete; apex ending in one spine apically and a smaller dentition subapically (Fig. 20).

Abdomen piceus, with lateral margin badius, sternite 5 testaceus; pale setae and fine punctation throughout. Male with parameres sinuate, apical blades with lateral margins strongly convex (Fig. 6).

Material examined.—COLOMBIA: (1, BMNH); ECUADOR: Chiquinda, Buckley (1, BMNH).

Diagnosis.—The combination of the

black head lacking frontal spines, contrasting elytral bands or patterns (fewer than 4 of each color per elytron), and evenly convex elytral margins distinguish *S. limbaticollis* from all other *Semiotinus.*

Semiotinus macer (Candèze), **n. comb.**
(Figs. 11, 23)

Semiotus macer Candèze 1889: 80 (holotype, female: INSB; type locality: Colombia).

Description.—*Length* 21 mm (length/width ratio 4.5–4.7). *Head* testaceus to aurantiacus, with two spines anterolaterally; fine decumbent setae and deep punctation throughout with longer setae over spines; ocular index 64.0–66.0. *Antenna* serrate, reaching 2–3 segments beyond hind angle; testaceus to piceus. *Thorax* with pronotum 4 mm (length/width ratio 1.0), sides straight, narrowly diverging posteriorly; margin thin, clearly defined; testaceus to aurantiacus, with piceus band extending from base to near apex; glabrous, nitidus with punctures widely separated. Scutellum strongly declivitous anteriorly, without clear anterior margin, lateral margins convex; testaceus to badius. Prosternum concave in profile, not divided at apex; testaceus to aurantiacus with or without badius to piceus maculae along suture; glabrous, nitidus medially with fine setae and deep punctures laterally. Hypomeron fulvus to aurantiacus; glabrous laterally with fine setae and deep punctures along suture. Mesosternum aurantiacus to badius, fossa glabrous and impunctate, lateral areas with dense setae and fine punctures. Mesepisternum badius to piceus. Metasternum testaceus to rufopiceus. Femora aurantiacus to badius.

Elytron 15 mm (length/width ratio 3.2–3.4), long and narrow, subparallel on anterior ¾ then rounded to tip; testaceus, strial punctures infuscate; mostly glabrous, nitidus with occasional setiferous punctures, intervals nearly flat, striae obscure to obsolete, strial punctures pronounced; apex ending in a terminal small spine and a smaller dentition or sharp angle along suture subapically (Fig. 23).

Abdomen testaceus to aurantiacus; fine setae and dense punctation throughout; female with two elliptical and very shallow piliferous foveae in center of sternite 5; anterior sclerite of the bursa copulatrix with lateral arms enlarged apically, each bearing two to three large dentitions, lateral arms 1.2 times longer than median piece (Fig. 11). Male unknown.

Material examined.—COLOMBIA: (1, INSB).

Diagnosis.—The very elongate and parallel-sided body (at least 4.5 times longer than wide) in combination with the two frontal spines distinguish *S. macer* from all other *Semiotinus. Semiotinus aeneovittatus* also bears frontal spines but is less elongate, and has a metallic bluish maculae on the pronotum and elytra which contrasts with the fulvus to testaceus base color. *Semiotinus macer* is darker testaceus and lacks metallic blue maculae.

***Semiotinus maculatus* Wells, new species**
(Figs. 1, 8)

Description.—*Length* 15 mm (length/width ratio 4.1–4.2). *Head* aurantiacus with basal piceus macula, without spines; glabrous, nitidus with few erect setae above eyes and anterior margin, punctation deep and scattered throughout. *Antenna* extending three segments beyond hind angle in male; segments 1 and 2 testaceus, segments 3–11 piceus. *Thorax* with pronotum 3–4 mm (length/width ratio 1.0–1.1); subtrapezoidal, sides straight, posterior margin wider than anterior margin, hind angles hardly divergent; margin narrowly incrassate without sulcus; aurantiacus to testaceus with narrow piceus band medially; glabrous, nitidus with deep punctation scattered throughout; scutellum piceus, narrowly ovate, nearly twice as long as wide; prosternum nearly straight in profile; aurantiacus to testaceus medially, piceus laterally; glabrous with fine punctation medially and with decumbent and erect setae and deep punctation laterally. Hypomeron aurantiacus to testaceus with piceus band along suture; glabrous, nitidus laterally with fine setae and deep punctation medially. Mesosternum finely punctate with fine setae, fossa glabrous and impunctate; aurantiacus to testaceus medially, piceus laterally. Mesepisternum piceus. Metasternum aurantiacus to testaceus medially, piceus laterally; glabrous with fine punctation medially, with decumbent setae and denser punctation laterally. Femora fulvus to testaceus.

Elytron 10–11 mm (length/width ratio 2.9–3.0) subparallel on anterior half then narrowing to tip; testaceus to aurantiacus with interval 1 infuscate on posterior half; glabrous, nitidus, striae and strial punctures deep to moderately deep; apex bearing one spine.

Abdomen aurantiacus to testaceus medially, badius laterally; nearly glabrous with fine punctation medially, with decumbent setae and denser punctation laterally; female unknown. Male with parameres narrow medially, apical blades 0.3 times length of parameres (Fig. 8).

Material examined.—Holotype (♂): ECUADOR: Napo, Baeza, 2000 m, 25-II-1979, H. & A. Howden (CNCI). Paratype: ECUADOR: Chiquinda, Buckley (1 ♂, BMNH).

Diagnosis.—*Semiotus maculatus* can be separated from all other *Semiotinus* by the uniform orange to light brown dorsal color (except the piceus scutellum and pronotal and frontal band and the darker infuscation on the apical half of the elytra in the paratype) and the concave outline of the elytral margin near the apex.

Note.—The specific name '*maculatus*' refers to the maculate pronotum.

Semiotinus morio (Candèze), **n. comb.**

Semiotus morio Candèze 1857: 336 (holotype: BMNH; type locality: Colombia); Candèze 1874: 189.

Description.—*Length* 10–11 mm (length/width ratio 3.5–3.6). *Head* piceus throughout without spines; few long setae and subumbilicate punctures. *Antenna* serrate, reaching 3–4 segments beyond hind angle; piceus. *Thorax* with pronotum 1–3 mm (length/width ratio 0.8–0.9) subcompanulate, lateral margin curving inwards to almost straight; margin thin, without sulcus, hind angles carinate; piceus; nitidus, with long pale setae laterally. Scutellum piceus, subtriangular, anterior margin not defined. Prosternum linear in profile; piceus; vestiture double, punctation becoming umbilicate laterally. Hypomeron piceus; long pale setae, punctation close and umbilicate throughout. Mesosternum piceus, vestiture double. Mesepisternum piceus. Metasternum piceus; vestiture double, punctation fine throughout. Femora testaceus to rufopiceus.

Elytron 8–9 mm (length/width ratio 2.3–2.5), subparallel on anterior ½ then narrowing to tip; deep sanguineous to rufopiceus throughout; glabrous, nitidus, with fine setae laterally, striae and strial punctures well defined; apex ending in two dentitions apically.

Abdomen piceus, without lateral pale areas, sternite 5 with or without testaceus to sanguineous patches; vestiture double, punctation fine throughout. Genitalia not examined.

Material examined.—COLOMBIA: (1, BMNH).

Diagnosis.—The small size and black to reddish black coloration of the body separate *S. morio* from all other *Semiotinus*.

Semiotinus nigricollis (Candèze), **n. comb.**
(Figs. 16, 24)

Semiotus nigricollis Candèze 1857: 335 (holotype: BMNH; type locality: N. Granada); Candèze 1874: 188.

Description.—*Length* 13 mm (length/width ratio 3.7–3.9). *Head* piceus throughout without spines; few long setae and subumbilicate punctures; ocular index 67.0–69.0. *Antenna* serrate, reaching 3–4 segments beyond hind angle; piceus. *Thorax* with pronotum 2–3 mm (length/width ratio 0.7–0.9) subcompanulate, lateral margin curving inwards to almost straight (Fig.

16); margin thin, without sulcus, hind angles carinate; piceus; nitidus, with long pale setae laterally. Scutellum piceus, longer than wide, subrectangular. Prosternum linear in profile; piceus; long pale setae, punctation becoming umbilicate laterally. Hypomeron piceus; long pale setae, punctation close and umbilicate throughout. Mesosternum piceus, covered with long pale setae. Mesepisternum and mesepimeron piceus. Metasternum piceus; glabrous medially, with long setae laterally, punctation fine throughout. Femora piceus.

Elytron 10–11 mm (length/width ratio 2.9–3.1), subgibbous anteriorly; interval 1 rufopiceus; intervals 2–5 (and part of 6 basally) fulvus to luteus, intervals 7–9 rufopiceus; glabrous, nitidus, with fine setae laterally, strial punctures well defined, striae fine to obsolete; apex ending in two dentitions apically (Fig. 24).

Abdomen piceus, with lateral margin and all of sternite 5 testaceus to sanguineous; pale setae and fine punctation throughout. Genitalia not examined.

Material examined.—N. GRANADA (this could be anywhere in Ecuador, Colombia, Venezuela, or Panama) (1, BMNH).

Diagnosis.—The blunt elytral apices (Fig. 24) and completely black pronotum distinguish *S. nigricollis* from all other *Semiotinus*.

Semiotinus quadricollis (Kirsch), **n. comb.** (Fig. 2)

Semiotus quadricollis Kirsch 1866: 181 (lectotype, female (Chassain, in press): SMTD; type locality: Bogotá); Candèze 1874: 187.

Semiotus diptychus Candèze 1874: 188 (holotype: BMNH; type locality: Ecuador). **New synonym.**

Semiotus subvirescens Schwarz 1904: 49 (syntype (1 found), female: DEIC; type locality: Ecuador, Balzapamba). **New synonym.**

Description.—*Length* 12–15 mm (length/width ratio 4.2–4.3). *Head* testaceus to aurantiacus, front without spines; fine decumbent setae scattered throughout and long erect setae over eyes and anterior margin, punctation scattered throughout; ocular index 69.0–72.0. *Antenna* reaching 0–2 segments beyond hind angle in female; segment one testaceus, segments 2–11 piceus. *Thorax* with pronotum 2–3 mm (length/width ratio 0.9–1.0), subtrapezoidal, nearly straight, hind angles hardly diverging, carinate; margin thin, clearly defined; aurantiacus with lateral margins paler, with median macula piceus; dense decumbent setae throughout, punctation deep becoming nearly contiguous along lateral margin. Scutellum testaceus, longer than wide, posterior border rounded, anterior margin straight. Prosternum linear in profile to slightly concave, tip of prosternal process not divided; testaceus to aurantiacus medially with or without a rufopiceus macula along suture extending onto hypomeron; nearly glabrous and impunctate medially, with erect setae and deep punctures anterolaterally. Hypomeron fulvus to aurantiacus laterally, occasionally rufopiceus along suture; with dense decumbent setae and punctures along suture, nearly glabrous with very fine punctures laterally. Mesosternum testaceus to aurantiacus, fossa glabrous and impunctate, lateral areas with dense setae and fine punctures. Mesepisternum testaceus to aurantiacus. Metasternum testaceus to aurantiacus medially, occasionally badius to piceus anterolaterally; with few setae medially becoming dense anterolaterally, punctation fine medially becoming denser anterolaterally. Femora testaceus, tibiae and tarsi darker infuscate.

Elytron 8–11 mm (length/width ratio 2.9–3.1), subparallel on anterior ⅔ then narrowing to tip; fulvus, strial punctures darker, with or without darker humeral bands; glabrous, nitidus, intervals convex, striae and strial punctures clearly defined; apex ending in a terminal spine and a smaller dentition along inner angle subapically.

Abdomen testaceus to aurantiacus with nebulous infuscation sublaterally; fine setae and punctation throughout; female without foveae on sternite 5. Male with apical blade of parameres subtriangular, lateral margins convex (Fig. 2).

Material examined.—COLOMBIA: (3, BMNH; 1, ISNB); N. de S. 2600 m, 30 km S Chinacota, 14-V-1974, H. & A. Howden (1, CNCI); ECUADOR: Balzapamba, R. Haensch S. (1, DEIC).

Diagnosis.—*Semiotinus quadricollis* is distinct from other *Semiotinus* in having a subquadrate pronotum with a yellow to orange head and a single pronotal band. *Semiotinus conicollis* and *S. brevicollis* also have yellow to light brown heads but have two dark pronotal bands (*S. brevicollis*) or have a strongly recurved pronotum (*S. conicollis*).

Note.—As with most other *Semiotinus, S. quadricollis* is known from very few specimens. Only six specimens were seen in this study, two of which are the types of the synonyms *S. subvirescens* and *S. diptychus*. The venter of the type of *S. diptychus* is paler and the frontal macula is darker than in *S. quadricollis*. This difference, however, has not proven to be of value when comparing variability of other *Semiotinus* nor in the sister genus *Semiotus*.

Semiotinus quadrivittis (Steinheil), **n. comb.**
(Fig. 21)

Semiotus quadrivittis Steinheil 1875: 113 (lectotype (Chassain, in press): MNHN; type locality: N. Granada).

Semiotus pulchellus Candèze 1889: 81 (holotype: INSB; type locality: Colombia). **New synonym**.

Description.—*Length* 12–16 mm (length/width ratio 3.9–4.0). *Head* piceus throughout, front without spines; fine decumbent setae scattered throughout; ocular index 64.0–66.0. *Antenna* serrate, reaching 2–3 segments beyond hind angle; segments 1 and 2 testaceus, segments 3–11 rufopiceus to piceus. *Thorax* with pronotum 2–4 mm (length/width ratio 0.9–1.1), margins straight, subparallel, hind angles hardly diverging; margin thin, clearly defined; fulvus to aurantiacus laterally with large maculae on disk extending from base to (or near to) anterior margin; glabrous or with very fine setae scattered throughout. Scutellum testaceus to piceus, longer than wide. Prosternum nearly linear in profile; piceus, prosternal process and lobe testaceus to aurantiacus. Hypomeron badius to piceus along suture, fulvus to luteus laterally. Mesosternum testaceus to aurantiacus medially, piceus laterally, fossa glabrous and impunctate, lateral areas with dense setae and fine punctures. Mesepisternum piceus. Metasternum testaceus to aurantiacus medially, piceus laterally (or completely piceus). Femora testaceus to piceus.

Elytron 8–12 mm (length/width ratio 2.8–2.9), slightly gibbous; fulvus to aurantiacus with three piceus bands (one along interval 1, one around interval 8, and one band between intervals 1 and 8); glabrous, nitidus; apex ending in a terminal spine and a smaller dentition along inner angle subapically (Fig. 21).

Abdomen testaceus to aurantiacus with scattered piceus maculae. Genitalia not examined.

Material examined.—COLOMBIA: Medellin, 1915-38 (1, BMNH); N. Granada (1, INSB; 1, MNHN).

Diagnosis.—The dark brown to black pronotal band with yellow to light brown margins, fewer than four alternating light and dark elytral bands, gibbous elytra, and narrow (concave in outline) elytral apices distinguish *S. quadrivittis* from all other *Semiotinus*.

Semiotinus scitulus (Candèze), **n. comb.**
(Figs. 9, 12)

Semiotus scitulus Candèze 1874: 186 (holotype: BMNH; type locality: Ecuador).

Description.—*Length* 12–13 mm (length/width ratio 4.0–4.4). *Head* piceus throughout or with anterolateral angles aurantiacus, front without spines; fine decumbent setae scattered throughout, punctation subumbilicate and scattered throughout; ocular index 64.0–67.0. *Antenna* serrate, reaching 2–3 segments beyond hind angle in male; segments 1 and 2 testaceus, segments 3–11 rufopiceus to piceus. *Thorax* with pronotum 2–4 mm (length/width ratio 0.8–1.1), subtrapezoidal, hind angles hardly diverging; margin thin, clearly defined (Fig. 12); fulvus to aurantiacus with large suborbicular to subquadrate piceus macula on disk (often pointed apically); glabrous or with fine setae scattered throughout. Scutellum badius to piceus, longer than wide, posterior border rounded, anterior margin straight. Prosternum linear in profile, tip of prosternal process not divided; piceus, prosternal process and lobe fulvus to testaceus; few erect setae throughout becoming denser and decumbent laterally, punctation fine medially, thicker laterally. Hypomeron badius to piceus along suture, fulvus to luteus laterally; glabrous, nitidus, or with few scattered setae, punctation of few shallow subumbilicate punctures throughout. Mesosternum fulvus to testaceus medially, piceus laterally, fossa glabrous and impunctate, lateral areas with dense setae and fine punctures. Mesepisternum piceus. Metasternum badius to piceus throughout or with fulvus to testaceus median coloration; glabrous with fine punctation medially, with fine decumbent setae and denser punctation anterolaterally. Femora aurantiacus to testaceus.

Elytron 9–10 mm (length/width ratio 2.9–3.1), subparallel on anterior half then narrowing to tip; fulvus to luteus with intervals 1, 3, 5, 7, and lateral margin badius to piceus; glabrous, nitidus, striae faint, strial punctures clearly defined; apex ending in a terminal spine and a smaller dentition along inner angle subapically.

Abdomen aurantiacus to rufopiceus with fulvus areas on sternites 1 and 5; fine setae and punctation becoming thicker laterally; female not seen. Male with parameres narrowing apically before blades, apices divergent, apical blades small, less than 20% length of parameres (Fig. 9).

Material examined.—ECUADOR: (1, BMNH); VENEZUELA: Merida, Tabay, Mucuy, Send. Lag. Suero cloud forest, 225 m, (VI–VII)-1989, S & J Peck (1, CMNC); Merida, S. Briceno (1, USNM).

Diagnosis.—The presence of alternating light and dark elytral bands (4 each per elytron) distinguishes *S. scitulus* from all other *Semiotinus*.

Semiotinus supplicans (Kirsch), **n. comb.**

Semiotus supplicans Kirsch 1884: 45 (lectotype, male (Chassain, in press): SMTD; type locality: Colombia, Pasto, 2800 m).

Description.—*Length* 18 mm (length/width ratio 2.9–3.1). *Head* fulvus to testaceus, without piceus maculae; frons with anterolateral areas rounded to angled, without spines; scattered setae throughout. *Antenna* serrate, reaching 2–3 segments beyond hind angle; segments 1 and 2 testaceus, segments 3–11 piceus. *Thorax* with pronotal margins straight, hind angles not, or hardly, diverging; fulvus to testaceus with two sinuate piceus bands sublaterally; with dense setae, especially over piceus bands. Scutellum subtriangular, fulvus to testaceus. Femora testaceus.

Elytron subparallel on anterior ⅔ then narrowing to tip; fulvus to testaceus with strial punctures infuscate; glabrous, nitidus, striae and strial punctures distinct; apex bearing two subequal spines. Male genitalia not examined.

Material examined.—COLOMBIA: Pasto, 2800 m., D. Stubel (1, SMTD).

Diagnosis.—The uniform pale elytral color interrupted by infuscate strial punctures, the two pronotal bands, and the two subequal spines on each elytron separate *S. supplicans* from all other *Semiotinus*.

Semiotinus trilineatus (Candèze), **n. comb.**

Semiotus trilineatus Candèze 1857: 324 (syntypes (3), female: BMNH; type locality: Colombia); Steinheil 1875: 112; Candèze 1874: 182.

Semiotus elegantulus Candèze 1857: 325 (syntypes (2): BMNH; type locality: Colombia); Candèze 1874: 182. **New synonym.**

Description.—*Length* 11–15 mm (length/width ratio 4.2–4.6). *Head* fulvus to testaceus, frontal margin often angled without spines; nitidus with few decumbent setae scattered throughout; ocular index 72.0–75.0. *Antenna* serrate, extending 0–1 segments beyond hind angle in female; segments 1 and 2 testaceus, segments 3–11 testaceus to badius. *Thorax* with pronotum 2–4 mm (length/width ratio 0.9–1.2), subquadrate, lateral margins straight, hind angles diverging; fulvus to aurantiacus with long thin median band (extending length of pronotum) and two sublateral shorter and sinuate badius to rufopiceus bands, hind angles often obscure; glabrous, nitidus. Scutellum fulvus to testaceus, longer than wide, posterior border rounded. Prosternum linear in profile; testaceus to aurantiacus, lobe paler, with or without piceus marking along suture; glabrous with fine punctation medially, denser setae and punctation laterally. Hypomeron fulvus, hind angles with or without piceus macula; glabrous, nitidus, punctation very fine throughout. Mesosternum testaceus, fossa glabrous and impunctate, lateral areas with dense setae and fine punctures. Mesepisternum testaceus. Metasternum testaceus, often piceus anterolaterally; sparse erect setae medially, denser decumbent setae laterally on dark area. Femora aurantiacus to testaceus.

Elytron 8–12 mm (length/width ratio 2.9–3.6), subparallel on anterior ⅔ then narrowing to tip; intervals 2, 4, 6, and 8 fulvus, intervals 1, 3, 5, and 7 either fulvus vitreus or badius vitreus; glabrous, nitidus, striae faint to obsolete, strial punctures clearly defined; apex ending in a terminal spine and a smaller dentition along inner angle subapically.

Abdomen testaceus medially, badius laterally; scattered erect setae medially, dense decumbent setae laterally, punctation fine becoming dense laterally; female without foveae. Male genitalia not examined.

Material examined.—COLOMBIA: (5, BMNH); Bogotá (2, BMNH).

Diagnosis.—The presence of three distinct pronotal vittae (sometimes confluent basally) distinguishes *S. trilineatus* from all other *Semiotinus.*

Semiotinus virescens (Candèze), **n. comb.**
(Figs. 5, 17)

Semiotus virescens Candèze 1857: 331 (holotype, female: BMNH; type locality: Colombia); Candèze 1874: 185.

Description.—*Length* 13 mm (length/width ratio 3.9–4.0). *Head* fulvus to aurantiacus, front without spines; glabrous, nitidus with few erect setae over eyes and anterior margin, punctation deep and scattered throughout; ocular index 72.0–75.0. *Antenna* serrate, extending 1–2 segments beyond hind angle in male; segments 1 and 2 testaceus, segments 3–11 piceus. *Thorax* with pronotum 2–3 mm (length/width ratio 0.7–0.8), with sides nearly straight, hind angles divergent (Fig. 17), margin thin, faintly sulcate (especially posteriorly); fulvus with faint viridis sheen; glabrous, nitidus with fine punctation throughout. Scutellum fulvus, parallel-sided, anterior and posterior margins convex. Prosternum nearly straight in profile; fulvus to testaceus; glabrous with fine punctures medially, with fine erect setae and deep punctation laterally. Hypomeron fulvus to viridis; glabrous, nitidus with punctures becoming obsolete posteriorly. Mesosternum fulvus to testaceus, fossa glabrous and impunctate, lateral areas with dense setae and fine punctures. Mesepisternum fulvus to testaceus. Metasternum fulvus to testaceus; glabrous with very fine punctation medially, decumbent setae and denser setae anterolaterally. Femora fulvus to testaceus.

Elytron 10 mm (length/width ratio 3.0–3.1) subparallel on anterior half then narrowing to tip; fulvus to viridis; glabrous, nitidus, striae well marked medially, fainter laterally, strial punctures moderately deep; apex with apical spine and subapical tooth.

Abdomen aurantiacus to testaceus; glabrous with very fine punctation medially, decumbent setae and denser setae anterolaterally; female not seen. Male with parameres narrow medially, arcuate in profile, apical blades narrower than parameres at base, 21–23% length of parameres (Fig. 5).

Material examined.—COLOMBIA: (1, BMNH); nr. Saludito Valle, 6500 ft., 20-VII-1970, H. & A. Howden (1, CNCI).

Diagnosis.—The small size and immaculate pale fulvus to viridis dorsal coloration separate *S. virescens* from all other *Semiotinus*.

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A NEW SPECIES OF NORTH AMERICAN *PROTOCALLIPHORA* HOUGH (DIPTERA: CALLIPHORIDAE) FROM BIRD NESTS

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Abstract.—Adult and puparial characters of the bird nest blow fly, *Protocalliphora sialia* Shannon and Dobroscky (Diptera: Calliphoridae) are evaluated as to whether the eastern and western North American populations should be considered separate species. Based on an analysis of adult and puparial ratios and a variety of morphological features, the western North American populations are described as ***P. occidentalis,* new species**.

Key Words: bird, nest, blow fly, *Protocalliphora, sialia,* Diptera, Calliphoridae, North America, new species

Larvae of species of *Protocalliphora* Hough (bird blow flies) are obligate bloodsucking parasites of altricial nestling birds. Twenty-eight species of *Protocalliphora* have been described from North America, including two which are Holarctic, while 13 species have been described from the Palearctic Region. Sabrosky et al. (1989) redescribed 11 North American species and described 15 new species. Whitworth (2002) recently described two new species of *Protocalliphora* in North America.

Protocalliphora sialia Shannon and Dobroscky infests a broad range of hosts and is one of the most commonly collected bird blow flies in North America. It is found frequently in the cavity nests of bluebirds, tree swallows, and European starlings, as well as occasionally in the open nests of American robins, common ravens, and kingbirds. Bennett and Whitworth (1992) found *P. sialia* in 31% of 667 infested nests of 15 bird species in eastern North America and in 7.3% of 964 infested nests of 18 bird species nests in the West.

Protocalliphora sialia is one of several similar species where both sexes have the same color abdomens and white calypters, and males have digitate surstyli. This group includes *P. shannoni* Sabrosky et al., *P. hirundo* Shannon and Dobroscky, *P. bennetti* Whitworth, and *P. rugosa* Whitworth. A key to assist distinguishing these species was provided in Whitworth (2002).

Male *P. sialia* can be distinguished from similar species by their broad frons, with a frons to head ratio averaging 0.08–0.10, and a polished triangular preocellar area. *Protocalliphora sialia* puparia have a long prothoracic fringe with an average diameter of 500–600μ (compared to 350–400μ in most species), dorsal cuticle with moderate to pronounced ridges, and long hyperstigmatal spines, averaging 40–50μ.

Sabrosky et al. (1989) discussed the possibility that *P. sialia* was actually composed of two separate species. A comparison of adult male and female proportions revealed consistent, but overlapping differences between specimens from eastern and western North America divided roughly by the Great Plains. The most distinctive difference between adults is a polished preocellar area in eastern females, while western fe-

Fig. 1. Distribution of *Protocalliphora sialia* (●) and *P. occidentalis* (★) in North America.

males have a dull, microtomentose preocellar area. Only the eastern form of *P. sialia* puparia had been studied at that time and ultimately *P. sialia* was left as one species, pending future research. The purpose of this study is to determine the status of this diverse, widespread species.

METHODS AND MATERIALS

Protocalliphora are rarely found in nature, except in bird nests. Most of the nests for the current study have been collected since 1992, via Internet contacts with birders who collected them from bird nest boxes after nestlings fledged. Common bird names are from the "Checklist of North American Birds", 7th edition, American Ornithologists Union (2000). Most material from Utah was collected from 1969–1972. Methods used to sort adults and puparia from nests and to identify *Protocalliphora* species were detailed in Whitworth (2002). Taxonomic terms were defined and an explanation of how to determine ratios in

Table 1. Mean ratios and ranges comparing western, midwestern, and eastern adults of *Protocalliphora sialia* to data from Sabrosky et al. (1989).

	Adult Male		
	West	Sabrosky* West	Midwest
Frons Head	0.08 (0.07–0.09)	0.08 (0.07–0.09)	0.098 (0.09–0.11)
Frons Ocellar Span	1.18 (0.8–1.5)	1.10 (1–1.25)	1.27 (1.18–1.5)
Parafacial Frons	1.5 (1.25–2)	1.71 (1.5–1.87)	1.44 (1.16–1.75)
Parafacial Ocellar Span	1.75 (1.5–2.33)	1.88 (1.62–20.07)	1.83 (1.5–2.11)
Parafacial Vibrissal Interval	0.92 (0.75–1.18)	1.00 (0.84–1.18)	1.02 (.79–1.13)
Cheek Eye	0.42 (0.33–0.49)	0.40 (0.38–0.44)	0.43 (0.37–0.49)
Frons 3rd Antennal Segment	1.23 (.89–1.5)		1.23 (1.09–1.5)
Parafacial 3rd Antennal Segment	1.8 (1.5–2.13)		1.78 (1.36–2)

* Data from Sabrosky et al., 1989.

adults and puparia were discussed in Sabrosky et al. (1989). See Whitworth (2002) for further discussion of measuring prothoracic fringe and cuticular spines.

A preliminary comparison of puparia revealed that specimens from the northern midwest (Minnesota and Wisconsin) have some characters intermediate between the eastern and western forms. Therefore, an initial analysis of adult and puparial characters was conducted on three groups: Eastern, western, and midwestern. Twenty-five adults of each sex were measured from all three areas and those measurements are compared in Table 1, along with data from Sabrosky et al. (1989). Twenty-five puparia from each area were also measured and are compared in Table 2.

RESULTS

A total of 3,849 nests of 76 bird species were collected from 45 states in the contiguous U.S., Alaska and Canada. Of these nests, 39% (1,501) from 49 bird species were infested with 17 species of *Protocalliphora.* Over half of the infested nests (992) from 22 bird species were infested with "*P. sialia.*" Nests with this species were collected from 33 states in the contiguous U.S., Alaska, and Canada.

Measurements of adult males, females, and puparia suggest a close relationship between eastern and midwestern *P. sialia,* with western *P. sialia* often significantly different (Tables 1, 2). Because the midwestern and eastern forms are so similar, the two are combined in further discussion under the eastern form. The eastern form extends northwest from Georgia (recorded by Sabrosky et al. 1989) through Minnesota and Canada to Alaska, while the western form is found from Arizona and New Mexico to Prince George, British Columbia (Fig. 1). Sabrosky et al. (1989) recorded 3 male *P. sialia* from south central Mexico and, although we have not seen these specimens, it seems likely they are the western form, which extends south from New Mexico and Arizona.

Although the stigmatal regions of puparia often appeared quite different (Fig. 2), differences in measurements of the eastern and western forms were relatively small and ranges overlapped (Table 1, 2). Some midwestern puparia exhibited intermediate characters between the two forms, suggesting possible interbreeding, though the midwestern form was closer to the eastern form, indicating that two species were involved. This conclusion was further supported by the results of molecular analysis which revealed two well-separated groups, one composed of the eastern and midwestern forms and the other of western forms (E. Baudry, personal communication). Baudry and I are conducting a study of the taxonomic relationship between species of

Table 1. Extended.

Adult Male		Adult Female	
East	Sabrosky* East	West	Sabrosky* West
0.10 (0.09–0.12)	0.09 (0.08–0.11)	0.28 (0.27–0.31)	0.27 (0.25–0.30)
1.4 (1.2–1.75)	1.37 (1.13–1.67)	3.48 (3.08–4.10)	3.58 (3.06–4.00)
1.35 (1.2–1.67)	1.43 (1.20–1.62)	0.49 (0.43–0.56)	0.53 (0.48–0.60)
1.88 (1.46–2.22)	1.96 (1.69–2.18)	1.68 (1.45–2.11)	1.91 (1.73–2.29)
1.06 (.94–1.25)	1.04 (0.93–1.13)	1.06 (0.68–1.27)	1.03 (0.90–1.20)
0.44 (0.41–0.47)	0.42 (0.38–0.45)	0.48 (0.40–0.54)	0.43 (0.41–0.47)
1.26 (1–1.46)		3.93 (3.4–4.5)	
1.71 (1.33–2)		1.94 (1.67–2.25)	

Protocalliphora, based on molecular analysis, and plan a future publication.

Protocalliphora sialia was originally described as a new variety by Shannon and Dobroscky (1924), and no holotype was designated. Sabrosky et al. (1989) selected a lectotype and paralectotypes from Pennsylvania, so the eastern and midwestern populations are *P. sialia,* while the western populations are hereby named, *P. occidentalis.* I collected specimens of both species unless indicated otherwise. Most were taken from bird nests donated by birders who collected nests from nest boxes.

Protocalliphora (*P.*) *sialia* Shannon and Dobroscky (Figs. 2a, b, 3a,c)

Protocalliphora splendida var. *sialia* Shannon and Dobroscky 1924: 251.
Apaulina sialia: Hall 1948.
Protocalliphora sialia (eastern and western form): Sabrosky et al. 1989.

Diagnosis.—See Tables 1 and 2 for comparisons of ratios and measurements for adults and puparia. Male frons to head ratio averages 0.10 (0.09–0.12) vs. 0.08 (0.07–0.09) in *P. occidentalis.* Male polished preocellar area usually larger in *P. sialia* (Fig. 3a) vs. smaller in *P. occidentalis* (Fig. 3b). Female frons to head ratio relationship is opposite of the males. For *P. sialia* it is smaller averaging 0.25 (0.22–0.28) vs. 0.28 (0.27–0.31); preocellar area usually polished (Fig. 3c) vs. dull colored and microtomentose (Fig. 3d). Stigmatal region of puparia with pronounced folds (Fig. 2a) vs. folds faint to absent (Fig. 2c); ventral band ratio averages 0.83 (0.71–0.89) vs. 0.72 (0.57–0.85) (Table 2).

Material examined.—CANADA, ONTARIO: 2 nests Algonquin Park, Summer 1955, G.F. Bennett collector; 6 puparia, barn swallow nest #504; 6 puparia, nest #445, no host given. SASKATCHEWAN: 1 puparium, Saskatoon, kestrel nest #2548, Summer 1995.

UNITED STATES: ALASKA: Fairbanks, Creamer's Field, 2 tree swallow nests, July 1994, D.D. Roby collector; 12 puparia mixed with 27 puparia of *P. braueri* (Hendel) and 34 puparia of *P. bennetti* Whitworth, nest #41. 3 puparia mixed with 4 puparia of *P. bennetti,* and 10 puparia of *P. braueri,* nest #42. INDIANA: 55 adults, 60 puparia, Union Co., Brookville, eastern bluebird nest #4754, 5/24/01; 19 puparia, Terre Haute, eastern bluebird nest #3770, 6/29/00. KENTUCKY: 15 puparia mixed with 10 puparia of *P. deceptor* Sabrosky, Bennett, and Whitworth, Ashland, warbler species nest #3377, 6/10/00. MARYLAND: 10 puparia mixed with 8 puparia of *P. metallica* (Townsend), Cumberland Co., Allegany, mockingbird nest #3733, 7/12/00. MASSACHUSETTS: 9 puparia, Worchester Co., Worchester, eastern bluebird nest #4129, 7/16/00. MICHIGAN: 35 adults, 80 puparia, Hanover, eastern bluebird nest #4397, 8/10/00; 15 adults

Table 1. Extended.

	Adult Female		
	Midwest	East	Sabrosky* East
Frons Head	0.26 (0.23–0.28)	0.25 (0.22–0.28)	0.265 (0.24–0.29)
Frons Ocellar Span	2.97 (2.83–3.18)	3.13 (2.82–3.27)	3.31 (3.06–3.73)
Parafacial Frons	0.56 (0.51–0.63)	0.56 (0.5–0.61)	0.555 (0.52–0.62)
Parafacial Ocellar Span	1.67 (1.58–1.83)	1.73 (1.5–1.91)	1.84 (1.65–20.0)
Parafacial Vibrissal Interval	1.09 (1.05–1.25)	1.12 (0.9–1.24)	1.12 (1.0–1.32)
Cheek Eye	0.46 (0.42–0.5)	0.45 (0.39–0.49)	0.44 (0.42–0.46)
Frons 3rd Antennal Segment	3.12 (2.91–3.36)	3.18 (2.75–3.4)	
Parafacial 3rd Antennal Segment	1.74 (1.64–1.83)	1.77 (1.64–1.91)	

and 110 puparia, same location and host as above, nest #4399. MINNESOTA: Four eastern bluebird nests from St. Paul; 150 adults, 210 puparia, nest #3886, 7/15/00; 45 adults, 50 puparia, nest #4241, 8/7/00; 10 adults, 110 puparia, nest #4240, 8/6/00; 2 puparia, nest #4239, 8/6/00; 40 adults, 50 puparia, Sartell, eastern bluebird nest #5198, 7/21/01. NEW JERSEY: 7 adults, 6 puparia, Newtonville, house wren nest #3978, 6/30/00; 8 puparia, Medford, eastern bluebird nest #2717, 8/3/99. NEW YORK: 70 adults and 70 puparia, mixed with 5 *P. bennetti*, Cattaraugus Co., Franklinville, tree swallow nest #4073, 7/25/00; 110 puparia, same location as above, kestrel nest #4076, 7/25/00; 5 puparia, Gloversville, eastern bluebird nest #4465, 5/25/00. OHIO: 75 adults, 110 puparia, Richland Co., eastern bluebird nest #2713, 7/15/99; 19 puparia, Stark Co., Louisville, tree swallow nest #4385, 7/24/00. PENNSYLVANIA: 75 adults, 85 puparia, Harrisburg, tree swallow nest #2638, 6/28/99. RHODE ISLAND: 23 puparia, North Kingston, tree swallow nest #4896, 6/10/01. TENNESSEE: 32 puparia, Knoxville, eastern bluebird nest #5399, 8/4/01. VIRGINIA: 3 eastern bluebird nests from Roanoke Co., Roanoke: 35 adults, 40 puparia, nest #3338, 5/15/00; 50 puparia, nest #4146, 7/25/00; 160 puparia, nest #4147, 7/25/00. VERMONT: 9 adults, 55 puparia, Franklin, tree swallow nest #4350, 7/12/00. WEST VIRGINIA: 11 adults, 45 puparia, Marion Co., Fairview, eastern bluebird nest #3386, 6/10/00; 15 adults, 43 puparia, Lewisburg, tree swallow nest #3616, 6/15/00. WISCONSIN: 15 puparia, Dunn Co., Colfax, eastern bluebird nest #4942, 6/5/01; eight eastern bluebird nests, Dane Co., Black Earth: 35 adults, 39 puparia, nest #3295, 5/10/00; 3 adults, 15 puparia, nest #3296, 5/10/00; 45 adults, 50 puparia, nest #4279, 5/25/00; 15 adults, 28 puparia, nest #4282, 8/7/00; 2 adults, 25 puparia, nest #4290, 6/29/00; 45 adults, 56 puparia, nest #4302, 5/25/00; 25 adults, 35 puparia, nest #4320, 5/25/00; 30 adults, 40 puparia, nest #4326, 6/6/00.

Specimens examined.—847 adults, 1988 puparia.

Distribution.—Alaska, Connecticut, Illinois, Indiana, Iowa, Kentucky, Maine, Maryland, Massachusetts, Michigan, Minnesota, New Hampshire, New Jersey, New York, North Carolina, Ohio, Pennsylvania, Rhode Island, Tennessee, Virginia, Vermont, West Virginia, Wisconsin, Ontario and Saskatchewan, Canada (Fig. 1). These are the first records of this species from Indiana, Illinois, Kentucky, Minnesota, Rhode Island, Tennessee, and Wisconsin. Sabrosky et al. (1989) recorded this species from Delaware, New Brunswick, Northwest Territories, Ontario, South Dakota and Georgia.

Hosts.—Eastern bluebird, great-crested flycatcher, kestrel, purple martin, northern mockingbird, house sparrow, barn swallow,

Table 2. Mean ratios and ranges comparing western, midwestern, and eastern puparia of *Protocalliphora sialia.*

	West	Midwest	East	Sabrosky[*] East
# Puparia Measured	53	21	17	150
Ventral Band Ratio	0.72 (0.57–0.85)	0.79 (0.67–0.89)	0.83 (0.71–0.89)	0.89 (0.8–10.0)
Diameter Stigmatal Plates	175μ (143–210μ)	193μ (150–220μ)	191μ (168–215μ)	190μ (140–235μ)
Between Buttons	576μ (460–710μ)	520μ (420–660μ)	522μ (430–660μ)	450μ (235 690μ)
Across Plates	1176μ (980–1370μ)	1115μ (1010–1240μ)	1147μ (1020 1380μ)	1000μ (655–1390μ)
Stigmatal Ratio	0.48 (0.41 0.60)	0.46 (0.41–0.56)	0.46 (0.39–0.53)	0.46 (0.43–0.56)

[*] Data from Sabrosky et al. 1989.

tree swallow, tufted titmouse, house wren. The mockingbird and tufted titmouse hosts are new records for *P. sialia.*

Protocalliphora (*P.*) *occidentalis* Whitworth, new species

(Figs. 2c, d, 3b, d)

Protocalliphora (*P.*) *sialia*: Sabrosky et al. 1989 (in part).

Diagnosis.—*Protocalliphora occidentalis* adults are very similar to those of *P. sialia,* however male *P. occidentalis* have a narrower frons (0.08 vs. 0.10) (Table 1) and a smaller polished preocellar area (Fig. 3b vs. 3a); female *P. occidentalis* usually have a dull preocellar area (Fig. 3d) while *P. sialia* have a polished preocellar area (Fig. 3c). The stigmatal region of puparia in *P. occidentalis* usually has folds faint or absent (Fig. 2c) vs. distinct folds in *P. sialia* (Fig. 2a); ventral band ratios in *P. occidentalis* average 0.72 (0.57–0.85) vs. 0.83 (0.71–0.89) in *P. sialia* (Table 2).

Male.—Mean ratios for *P. occidentalis* compared to *P. sialia* given in Table 1. Frons usually narrower than *P. sialia,* preocellar area triangular, polished and 1–1.5 times depth of median ocellus compared to 2–2.5 times in *P. sialia.*

Female.—Mean ratios for head compared in Table 1. Preocellar area usually dull microtomentose, while in *P. sialia* usually large and polished (Figs. 3c, d).

Puparium.—Mean ratios for puparial characters compared in Table 2. Compared to *P. sialia, P. occidentalis* with smaller ventral band ratio, ridges in hyperstigmatal, mesostigmatal, and hypostigmatal areas faint or absent vs. moderate to prominent, mesostigmatal and hypostigmatal area spines sparse, short, and often reduced to tubercles vs. spines dense to 15μ long.

Types.—Holotype ♂, allotype and 42 paratypes (26 ♂ 16 ♀) with matched puparia from Washington State, Kittitas Co., Umtanum Ridge (road), 6/15/99, mountain bluebird nest #2612. Holotype and allotype in the National Museum of Natural History,

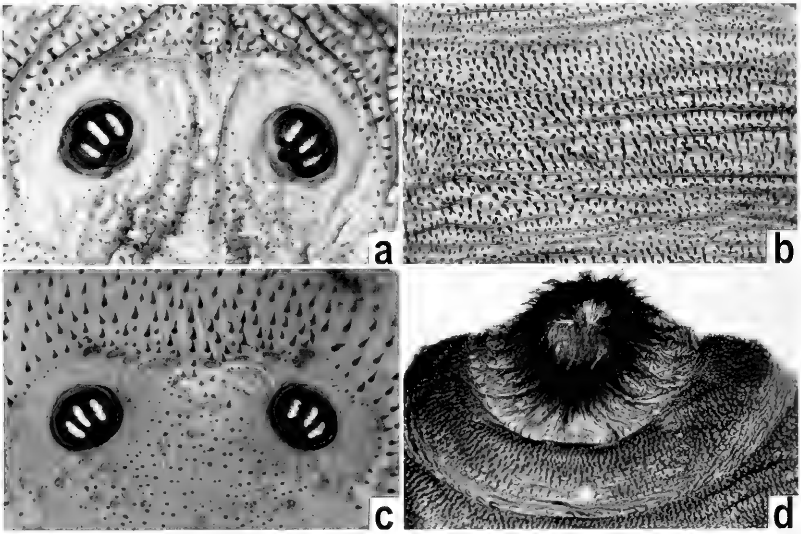

Fig. 2. Puparium of *Protocalliphora sialia*. a, Stigmatal view. b, Dorsum. Puparium of *P. occidentalis*. c, Stigmatal view. d, Prothoracic fringe.

Smithsonian Institution, Washington DC. Paratypes there and at Utah State University, Logan, Utah, and Washington State University, Pullman, Washington.

Additional paratypes.—CANADA, BRITISH COLUMBIA: 7 adults, 40 puparia, Osoyoos, western bluebird nest #3708, 7/1/00; 20 adults, 115 puparia, Osoyoos, tree swallow nest #3714, 7/1/00; 3 tree swallow nests, Dykes area 30km south of Prince George, Summer 2001, Russ Dawson collector: 7 puparia, with 9 *P. rugosa,* and 3 *P. bennetti,* nest #5793; 3 puparia with 28 *P. rugosa,* nest #5795; 10 puparia, nest #5807.

UNITED STATES: ARIZONA: Three western bluebird nests, Fredonia County, Mt. Trumbull: 10 adults, 110 puparia, nest #4015, 7/14/00; 35 adults, 115 puparia nest #4029, 6/10/00; 5 adults, 23 puparia, nest #4275, 8/7/00. CALIFORNIA: 11 puparia, El Dorado Co., Mt. Akum Road, western bluebird, nest #2815, 7/10/00; 10 puparia, Rescue, violet-green swallow nest #3690, 7/7/00; 110 puparia, Amador Co., Somerset, western bluebird nest #3849, 5/6/00. COLORADO: 130 adults, 175 puparia, Durango, ash-throated flycatcher nest #3620, 6/25/00; 2 adults, 35 puparia, Grand Junction, ash-throated flycatcher nest #3686, 7/4/00; 30 adults, 110 puparia, Durango, ash-throated flycatcher nest #4101, 7/15/00; 49 adults, 115 puparia, Durango, ash-throated flycatcher nest #4108, 5/13/00; 85 puparia, Lyons, tree swallow nest #4142, 7/25/00. IDAHO: 2 puparia, Bonner Co., Athol, tree swallow nest #4039, 7/5/00; 36 adults and over 150 puparia, Kootenai Co., Hoodoo Valley, tree swallow nest #4267, 7/25/00. MONTANA: 48 adults, 75 puparia, Granite Co., Philipsburg, mountain bluebird nest #3497, 6/18/00; 31 adults, 65 puparia, Granite Co., Philipsburg, mountain bluebird nest #3501, 6/16/00. NEW MEXICO: 9 adults, 92 puparia, Arroyo Seco, western bluebird nest #4392, 7/15/00; 9 adults, 12

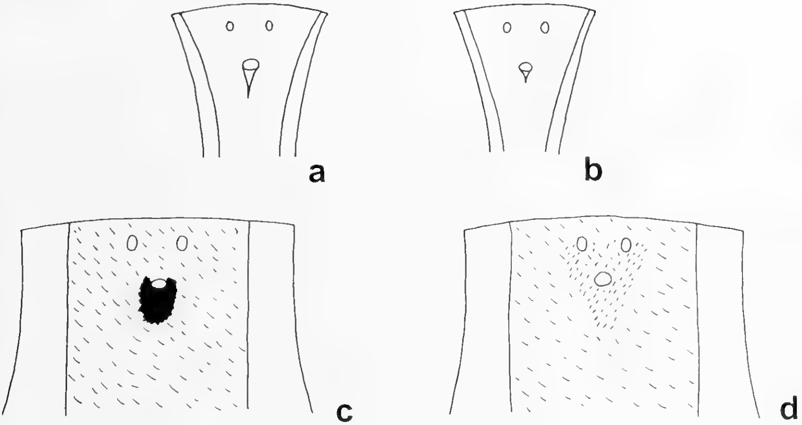

Fig. 3. Preocellar area of frons. a, Male *Protocalliphora sialia*. b, Male *Protocalliphora occidentalis*. c, Female *P. sialia*. d, Female *P. occidentalis*.

puparia, Arroyo Seco, violet-green swallow nest #4395, 7/29/00. OREGON: 3 nests from Springfield; 15 adults and 32 puparia, western bluebird nest #3739, 6/16/00; 1 adult, 9 puparia, tree swallow nest #3740, 7/2/00; 12 adults, 27 puparia, tree swallow nest #5550, 7/14/01. UTAH: 1 adult, 35 puparia, Cache Co., Franklin Basin, tree swallow nest #359, 7/18/70; 1 puparium mixed with 5 puparia of *P. hirundo,* Rich Co., Walton Canyon, cliff swallow nest #420, 7/22/70; 5 puparia mixed with 45 puparia of *P. parorum,* Box Elder Co., Mantua, house wren nest #569, 7/8/69; 15 puparia, Cache Co., Logan Canyon, house wren nest #1050, 7/5/71; 12 puparia, Cache Co., Logan, house sparrow nest #1302, 8/14/71; 2 *sialia* puparia mixed with 16 *P. rognesi* Thompson and Pont [*P. chrysorrhoea* (Meigen)] puparia, Cache Co., Wellsville, bank swallow nest #1906, 6/26/74; 22 adults, 115 puparia, Ogden, European starling nest #3764, 7/15/00. NEVADA: 6 puparia, Eureka, mountain bluebird nest #2926, 9/3/99; 2 puparia, Eureka, mountain bluebird nest #2927, 9/10/99. WASHINGTON: 34 adults with matched puparia, Kittitas Co., Umtanum Ridge, mountain bluebird nest #2611, 6/15/99; 20 adults with matched puparia, Kittitas Co., Umtanum Ridge, bluebird spp. (mountain or western bluebird) nest #2609, 6/15/99; 24 adults, 54 puparia, Kittitas Co., Umtanum Ridge, mountain bluebird nest #4226, 7/2/00; 22 adults, 35 puparia, Kittitas Co., Umtanum Ridge, western bluebird nest #4228, 7/10/00. Additional paratypes to the same locations as the type series, also to the Spencer Entomological Museum, University of British Columbia, University of California, Berkeley, California Academy of Science, and my personal collection.

Specimens examined.—533 adults, 1878 puparia.

Distribution.—Arizona, California, Colorado, Idaho, Montana, Nevada, New Mexico, Oregon, Utah, Washington, Wyoming, British Columbia, Canada and probably Mexico (Fig. 1). This is the first record of *P. occidentalis* from Nevada.

Hosts.—Mountain and western bluebird, mountain chickadee, ash-throated flycatcher, kestrel, pygmy nuthatch, red-breasted nuthatch, white-breasted nuthatch, house sparrow, European starling, barn swallow, tree swallow, violet-green swallow, oak titmouse, Bewick's wren, house wren. The red-breasted nuthatch and Bewick's wren hosts are new records for *P. occidentalis*, nests were contributed by Don Dahlsten, University of California, Berkeley.

Etymology.—The name is taken from the Latin, occidental or "western" which reflects the U.S. distribution of this species.

Discussion

Variation.—Individual adults of both species are difficult to distinguish from *P. bennetti*, *P. hirundo*, *P. rugosa*, and *P. shannoni*. See Whitworth (2002) for a key to these species. Lone females of *P. occidentalis* are virtually indistinguishable from female *P. rugosa*. Males of both species in good condition are usually distinctive, but dirty, teneral, or undersized specimens are a problem. The most distinctive feature of both species is the long prothoracic fringe in the puparia, which is usually 500μ in diameter or more. Only *P. parorum* Sabrosky et al. has a fringe that comes close, with some specimens to 450μ, and averaging 425μ. Occasionally specimens of *P. sialia* with undersized prothoracic fringe are found. The only Alaska specimens collected were puparia from two tree swallow nests in Fairbanks, and all had a smaller than usual prothoracic fringe ranging from 400–475μ. Based on the material available, I have concluded they are *P. sialia*, but characters are somewhat intermediate and until more material is examined, including adults, this is a tentative identification. The fringe of occasional specimens of *P. sialia* in the eastern U.S. were similarly reduced, but this was unusual. Some specimens of *P. occidentalis* from southern British Columbia, Washington, and Utah had an unusually long prothoracic fringe to 800μ. Sabrosky et al. (1989) noted apparent normal body length for *P. sialia* (which included the eastern and western forms) was 8.5–9.5 mm. However I reared many *P. sialia* that measured up to 10 mm, while *P. occidentalis* usually were 8.5–9.0 mm (rarely to 9.5 mm). This suggests that *P. sialia* tends to be longer, but size is not a good species character because nestlings often fledge before all larvae mature, producing some undersized adults.

The puparia of both species sometimes exhibit significant spine reduction in the mesostigmatal area. This is shared only with *P. parorum* among specimens with pronounced dorsal ridges. This character is common in *P. occidentalis* but also occasionally occurs in *P. sialia*. In *P. occidentalis* the stigmatal area of puparia usually has no folds, *P. sialia* usually has pronounced to moderate folds. Scattered specimens of *P. sialia* from Ohio, Wisconsin, and Virginia also had reduced folds.

Distribution.—The apparent wide separation of eastern and western populations by the Great Plains (Fig. 1) may prevent interbreeding and result in speciation. Specimens reared from nests in the extreme eastern or western U.S. are usually very different, but midwestern puparia often have some intermediate characters that suggest interbreeding is occurring. Few nests have been examined from the Great Plains so the absence of specimens from that area may be due in part to the lack of collection effort. However, *P. sialia* prefers the nests of birds in cavities and the lack of trees in the Great Plains could prevent populations from crossing the plains. With the expansion of farms and towns across the Great Plains in the past 150 years, the two populations of *P. sialia* recently may have had more opportunity for contact. Manmade structures often provide nest cavities and have shade trees or rows of trees for windbreaks, which also provide nest cavities. The introduction of the European starling, over 100 years ago, could have helped the two species meet across the Great Plains since it is a favored host of both species and often nests in and around manmade structures (Bennett and Whitworth 1992). More recently, many homeowners have begun installing nest boxes in places with few or no natural cavities to encourage bluebirds and other cavity-nesting birds, which may attract and disperse both species in areas without trees.

Some regions seemed to be totally devoid of both species, despite the fact that favored hosts like the eastern bluebird were abundant. The following nests and sites had neither species: sixty eastern bluebird nests in eastern Texas, 99 eastern bluebird nests in southeastern Oklahoma, 16 eastern bluebird nests in southeastern Nebraska, 24 eastern bluebird and purple martin nests in northern Missouri, 25 eastern bluebird nests in Arkansas, and 35 eastern bluebird and tree swallow nests in south central Iowa. *Protocalliphora sialia* or *P. occidentalis* has never been recorded from Arkansas, Missouri, Nebraska, Oklahoma, or Texas although *P. sialia* was found in northern Iowa. *Protocalliphora deceptor* was found in each of the above areas and occasionally infested nests which would usually be infested by *P. sialia.* With the absence of their usual parasite, eastern bluebird nests in these areas were rarely infested. In areas where these parasites were common, infestation rates in favored host nests often approached 100%. Neither species was found in North or South Dakota, or eastern Montana, but few nests were examined from those areas, so further study is needed before assuming they don't occur there. Sabrosky et al. (1989) recorded *P. sialia* from an unknown location in South Dakota. *Protocalliphora sialia* was never found in any of the southeastern states south of Tennessee including South Carolina, Georgia, Florida, Alabama, Mississippi, and Louisiana, although Sabrosky et al. (1989) recorded it from northern Georgia. In fact, *Protocalliphora* appears to be rare in much of the south, although I have recently examined a series of 8 nests (wrens, chickadees, and warblers) from Smith County, Texas, that were all infested with *P. deceptor,* several nests had over 100 puparia. This 100% infestation rate is in sharp contrast to infestation rates of 1%–5% by *P. deceptor* in over 200 nests examined from other areas of Texas.

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THE IDENTITY AND REINSTATEMENT OF *HOMALODISCA LITURATA* BALL AND *PHERA LACERTA* FOWLER (HEMIPTERA: CICADELLIDAE)

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Abstract.—*Phera lacerta* Fowler, **combination restored**, is transferred back to its original genus. *Homalodisca liturata* Ball, **validity restored**, is removed from synonymy with *P. lacerta*. Recent literature referring to *P. lacerta* as the smoke tree sharpshooter and a close relative of *Homalodisca coagulata* (Say), the glassy-winged sharpshooter, should actually be taken to refer to *H. liturata*.

Key Words: sharpshooter, Cicadellidae, *Homalodisca,* leafhopper

Phera lacerta Fowler, **combination restored**, was described in 1899 from Chilpancingo, Guerrero, in southwestern Mexico (Fowler 1899b). It was transferred to *Homalodisca* Stål by Young (1968) as a senior synonym of *Homalodisca liturata* Ball **validity restored**, which had been described from Phoenix, AZ, Yuma, CA, and Comundu, Baja California Sur, Mexico, in 1901. The synonymy was made without comment or explanation, although he had reviewed both *P. lacerta* (Young 1965) and *H. liturata* (Young 1958) previously in other studies. That synonymy is reversed here, as *P. lacerta* and *H. liturata* represent distinctly different entities belonging to different genera.

Homalodisca liturata (as *Homalodisca lacerta*) has been the subject of much discussion in recent literature (e.g., Nielson 1968, Powers 1973, Gill 1994, Sorensen and Gill 1996, Blua et al. 1999, Costa et al. 2000, Bethke et al. 2001, Rakitov and Dietrich 2001) as a close relative of the glassy-winged sharpshooter, *Homalodisca coagulata* (Say), a major pest of citrus, grapes, and ornamentals. Both *H. liturata* and *H. coagulata* are vectors of various strains of the phytopathogenic bacterium *Xylella fastidiosa,* which cause the diseases known as Pierce's disease in grapes, oleander leaf scorch, almond leaf scorch, phony peach disease, alfalfa dwarf, and citrus variegated chlorosis depending upon the crop species infected and bacterial strain involved (Blua et al. 1999). *Homalodisca coagulata,* a species from the eastern United States accidentally introduced to the western United States and northern Mexico, is the most important vector of this disease in North American agricultural systems at this time, but *H. liturata* is also of interest as a closely related vector apparently native to southwestern North America.

MATERIALS AND METHODS

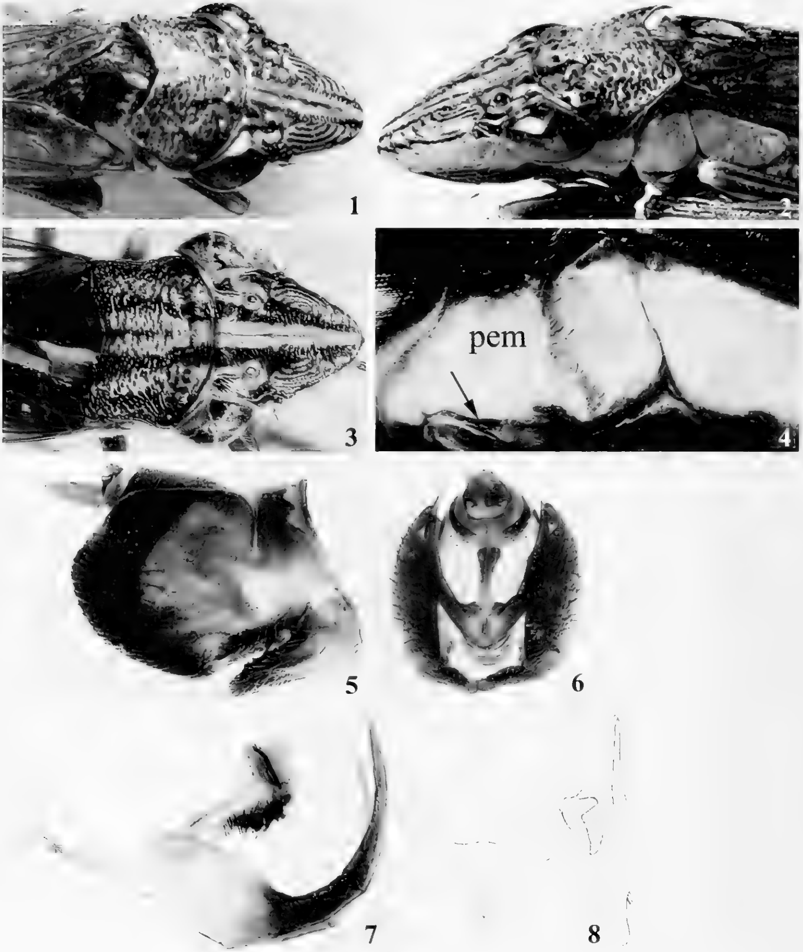
The type and other holdings of *Homalodisca liturata,* in the National Museum of Natural History, Smithsonian Institution (USNM), were examined, as well as numerous specimens (over 100) of that species at the University of California, Riverside, Entomology Research Museum (UCRC). Photographs (Figs. 1–2) of the lectotype (female) of *Phera lacerta* were obtained from The Natural History Museum (M. Webb, BMNH), which led to the location of an additional male at UCRC that we assign to *P. lacerta,* collected from Brazil (BRAZIL. São Paulo: Piracicaba, ESALQ, 5-IV-1996, Screen. sweep wooden area, J. Pinto). All other photographs are of UCRC specimens, taken using Auto-Montage software (version 4.00.0359 BETA, Synoptics, Ltd., UK 1997, 2001) through a 3-CCD digital videocamera attached to a stereoscope.

TAXONOMY

Phera lacerta is distinguishable from both *H. liturata* and *H. coagulata* by its longer, more robust proepimeron (Figs. 2, 4) with a flangelike ventral depressed margin, the yellow longitudinal band along the side of its head and thoracic pleuron, and its pronotum with a longitudinal pale band flanked by darker stripes. The linear markings on the vertex of *P. lacerta* (Figs. 1, 3) are also distinctive, but this character is widely variable (but not overlapping with *P. lacerta*) in *H. liturata* (Fig. 9), and we hesitate to treat it as a reliable character until more is known about its variation in *P. lacerta.* The yellow band along the thoracic pleuron (Figs. 2, 4) is an easily assessed character of the genus *Phera* Stål, but it is subject to variation in shape and color across several species, and may not be reliable as a generic character. Young (1968) used the proepimeral shape and form to distinguish *Phera* from *Homalodisca,* and this character is treated here to distinguish the two genera as it appears to be the most reliable and unambiguous morphological character known to date. The central area of the proepimeron is longer than tall in *Phera* (Figs. 2, 4), but not in *Homalodisca* (Fig. 10). *Phera* species also have a large, depressed, flangelike ventral proepimeral margin, but a minute, shorter flangelike margin is present anteriorly (normally hidden by the procoxa) in *Homalodisca.* Nevertheless, both proepimeral shape and the extent of its ventral depressed area appear to be reliable characters for distinguishing *Phera* from *Homalodisca,* except for *Homalodisca insolita* (Walker), which was regarded by Young (1968) as an unusual species of dubious generic placement. On strength of proepimeral shape and form, *P. lacerta* certainly belongs in *Phera,* and *H. liturata* in *Homalodisca.* The differences between *P. lacerta* and *H. liturata* are very striking and we are unable to explain why Young (1968) synonymized the two.

In addition to external differences, the genitalia of the male that we have identified as *P. lacerta* from Brazil (Figs. 5–8) differ substantially from those of *H. liturata,* which were accurately figured by Young (1958). The forms of the pygofers, aedeagus, connective, and styles of *P. lacerta* are very similar to those of *Phera carbonaria* (Melichar), as figured by Young (1968). In *P. lacerta* and *P. carbonaria,* the basal processes of the aedeagus are long and arching anteriad (Fig. 7), as opposed to those of *H. liturata,* which are always straight. Also, there is no projection from the atrium between the bases of the processes in *P. lacerta,* as there is in *H. liturata.* The pygofer of *P. lacerta* (Fig. 5) is also much longer than in *H. liturata,* greatly exceeding the length of the subgenital plates. Lastly, the subgenital plates of *P. lacerta* have lateral denticles not present in *H. liturata,* but which are found in several species of *Phera.*

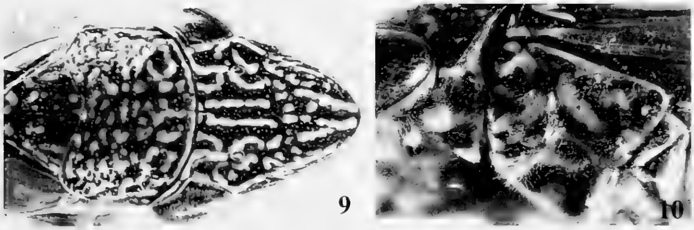
Ball (1901) was apparently already aware of Fowler's Central American and southern Mexican work at the time he described *H. liturata,* as he cited Fowler's discussion and figure of *H. insolita* in that publication. *Phera lacerta* was figured on the same plate as *H. insolita* (Fowler 1899a: plate XIV) and described only two months afterward (Fowler 1899b). Therefore, Ball was aware of at least the figure, and probably also the description, of *P. lacerta* at the time *H. liturata* was described, and probably was well aware that the two species were different. Melichar (1924) also correctly treated *H. liturata* and *P. lacerta* as two distinct species in his monograph of the Cicadelli-



Figs. 1–8. *Phera lacerta.* 1, Head and pronotum (dorsal view) of lectotype female. 2, Head and mesopleuron (lateral view) of lectotype female. 3, Head and pronotum (dorsal view) of male specimen. 4, Mesopleuron (lateral view) of male specimen. Arrow indicates ventral flange; pem = proepimeron. 5, Pygofer with subgenital plate. 6, Genitalia, posterior view. 7, Aedeagus, lateral view. 8, Connective and right style, dorsal view.

nae, although he treated *Homalodisca* and *Phera* as synonymous genera.

Literature records of *Homalodisca lacerta* from northern Mexico and the United States should be taken to refer to *H. liturata,* which remains distinguishable from the closely related *H. coagulata* using characters given by Young (1958). Aside from its



Figs. 9–10. *Homalodisca liturata*. 9, Head and pronotum (dorsal view). 10, Mesopleuron (lateral view, proleg removed).

original description, *P. lacerta* was correctly characterized only by Melichar (1924), and obviously remains very poorly known in terms of intraspecific variation.

Knowledge of the true identity of *H. liturata,* the probable sister species of *H. coagulata* (Rakitov and Dietrich 2001), is important in planning biological control efforts of *H. coagulata* and in studying the history of its distribution. *Phera lacerta* is apparently a tropical entity, known from southern Mexico to southern Brazil. Conversely, *H. liturata* is known from southwestern United States to central Mexico. The strategy of finding effective biological control agents in the home range of *H. coagulata* by studying the distribution of its apparent sister species needs to be adjusted in light of this new information.

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DASYMUTILLA JALISCO, A NEW SPECIES OF VELVET ANT (HYMENOPTERA: MUTILLIDAE) PLUS NEW SYNONYMY FOR *DASYMUTILLA CANINA* (SMITH)

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Abstract.—***Dasymutilla jalisco*, a new species** of velvet ant (Hymenoptera: Mutillidae) from Mexico, is described from both sexes. The female is similar in appearance to *Dasymutilla canina* (Smith), and the male is similar in appearance to *Dasymutilla intermixta* Mickel. A host for *D. jalisco* is the bee, *Diadasia knabiana* Cockerell (Hymenoptera: Apidae). *Sphaerophthalma philinna* Cameron and *Mutilla* (*Ephuta*) *variicolor* André are **new synonyms** of *D. canina* (Smith).

Key Words: *Dasymutilla jalisco,* Mutillidae, new species, *Dasymutilla canina,* new synonymy

A recognized problem in working with velvet ants (Hymenoptera: Mutillidae) is that strong sexual dimorphism makes sex associations extremely difficult. Color patterns and often overall body size of the two sexes can be quite different (Brothers 1989). Of more than 150 species of *Dasymutilla* Ashmead, only about one-third are known from both sexes (Krombein 1979, Nonveiller 1990).

Due to extreme sexual dimorphism, sex associations can be made only by catching pairs *in copula* (a very rare occurrence), through the use of caged females, or host data (Manley 1999). Although it is known that *Dasymutilla* species are parasitoids of other ground-nesting insects, primarily Hymenoptera, Mickel (1928) noted that host relationships are known for only a few species. The situation has not changed much since that time. This may be further complicated by the fact that mutillid males and females may develop on different hosts (Matthews 1997).

It is extremely rare to find evidence supporting both sex association and host relationship within the same specimens, as is the case here. The specimens described here include seven females and three males, as well as two host bees.

Materials and Methods

Specimens used in this study were included with material sent to me for identification by E. G. Riley from the Texas A & M University (TAMU) Insect Collection. All of these specimens were collected by William Godwin, and all were taken from cells of the same host in Jalisco, Mexico. The specimens have been compared with all known types of *Dasymutilla,* both males and females, and have been determined to be a new species. The two host bees were sent to Terry Griswold, Bee Biology and Systematics Laboratory, USDA, Utah State University, for identification.

***Dasymutilla jalisco* Manley, new species**
(Fig. 1A)

Diagnosis.—The female has the integument entirely black, with contrasting yel-

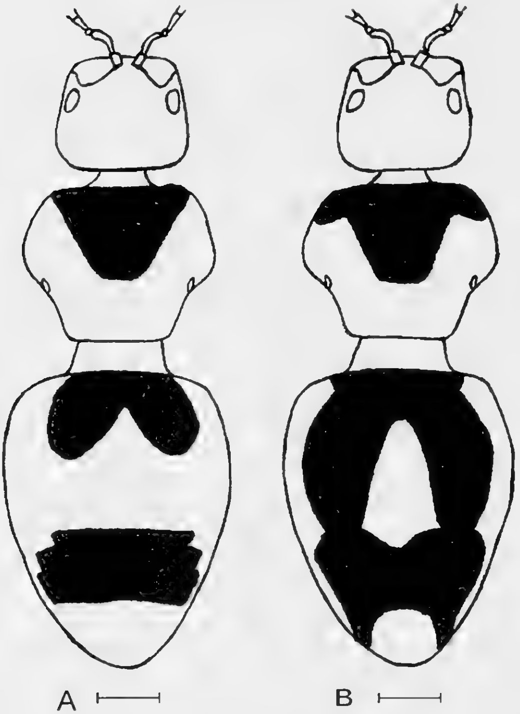

Fig. 1. Dorsum of females of *Dasymutilla jalisco* and *D. canina* showing patterns of black pubescence. A, *D. jalisco*. B, *D. canina*. [Scale lines = 0.8 mm.]

lowish/golden and black pubescence. The thorax is as broad or broader than long, and is lacking a scutellar scale. The antennal scrobes are distinctly, although feebly, carinate. A genal carina is lacking. The pygidium is rugose. The male has the integument of the head, thorax and legs entirely black. Integument of the abdomen is reddish except the terminal segment(s) black. Pubescence of the head and thorax is pale, contrasted with black. The abdominal tergites are clothed with brilliant red pubescence, except the terminal segment(s) with black. Sternite II has a small, oval pit filled with pale setae. The antennal scrobes are distinctly carinate. The last tergite lacks an apical fringe of setae.

Description.—*Female:* Length, 13.5–16 mm. Head black, vertex with dense, recumbent, yellowish/golden pubescence, remainder of head with paler pubescence; mandible acute at tip, each with conspicuous inner tooth about one-quarter distance from tip; clypeus truncate on anterior margin, but concealed by long, pale setae; scape weakly carinate, the carina concealed by short, appressed, pale pubescence; flagellomere I long, about as long as II and III united, remaining flagellomeres subequal in length to second; antennal scrobe distinctly, although feebly, carinate; front and vertex coarsely punctate, but with dense yellowish/golden pubescence concealing sculpture; gena not as coarsely punctate as front and vertex, lacking genal carina, covered with appressed pale pubescence; head almost as broad as thorax (3.3 mm × 3.5 mm).

Thorax black; dorsum of thorax approximately 1.1× as long as broad (~3.5 mm × 3.3 mm); scutellar scale absent; cephalic margin of pronotum evenly rounded, not emarginate medially; posterior face at sharp (~90°) angle to dorsal surface; dorsum of thorax with posterior V-shaped area of dense, appressed, yellowish/golden pubescence, concolorous with front and vertex, and anterior triangle of dense, appressed, black pubescence; posterior face of propodeum, pleura, and sternum with appressed, pale yellow pubescence.

Abdomen black; tergite I, including apical fringe, with appressed, pale yellow pubescence; tergite II with inverted V-shaped area of dense, appressed, black pubescence on anterior half; remainder of tergite II with dense, appressed, yellowish/golden pubescence, concolorous with front and vertex, except median half of apical fringe black; felt lines about 0.4× length of segment, consisting of appressed, pale yellow setae; tergites III–IV largely with dense, appressed, black pubescence, except lateral fringes of both tergites and apical fringe of tergite IV pale yellow; tergites V–VI entirely pale yellow pubescent; sternum, including apical fringes, pale yellow pubescent, except last sternite with long, black setae; sternite I with short, blunt carina, about 0.4× length of segment; pygidium coarsely rugose.

Legs black, clothed with dense, pale yellow setae.

All specimens (7) similar in size and coloration.

Male: Length, 13–14 mm. Head black, with long, appressed, white pubescence, dense on front and vertex, sparser elsewhere; mandible edentate, but each with strong dorsal carina ending about 0.1× length from tip; clypeus flat, bidentate medially on anterior margin; scape bicarinate beneath, lower carina stronger than the upper, thinly clothed with white pubescence; flagellomeres subequal in length; antennal scrobe conspicuously carinate; eye normal, distance behind eye about equal to its greatest diameter; ocelli small, ocellocular distance at least 3× greatest diameter of ocelli; head about as broad as thorax.

Thorax black, pronotum and scutellum clothed with dense, appressed, white pubescence, mesonotum with dense, appressed, black pubescence, remainder of thorax with long, sparse, erect, white setae; cephalic margin of pronotum not emarginate medially; tegula glabrous, impunctate, with sparse, appressed, black setae originating anteriorly.

Abdomen reddish dorsally, ferruginous ventrally, except first and last segments black; tergites II–VI with dense, appressed, red pubescence; first segment with long, sparse, white setae; last segment with long, sparse, black setae; felt line long, about 0.6× length of second segment, comprised of appressed, white setae; sternite I with median, longitudinal carina, not produced on either end into tooth; sternite II approximately 3 mm long, with small, round pit densely filled with appressed white setae, situated about one-third distance from anterior margin; sternites clothed with long, sparse, erect, white setae except as otherwise noted; pygidium finely rugose; pygidium lacking apical fringe of setae.

Legs black, with white setae; apices of middle and hind femora rounded, neither squarely truncate nor sulcate.

Apical half of forewing black, basal half infuscated but translucent; hindwing entirely translucent.

Holotype.—♀, MEXICO, Jalisco, Mpio. LaHuerta, Chamela Biol. Sta., VII-26-1996, Wm. Godwin, collector, deposited in the Texas A & M University (TAMU) Insect Collection.

Allotype.—♂, same data and deposition as holotype.

Paratypes.—6 ♀, 2 ♂, same data as holotype, 2 ♀ and 1 ♂ in the author's collection, remainder in TAMU collection.

Host.—*Diadasia knabiana* Cockerell (Apidae), same data as holotype, determined by Terry Griswold, Bee Biology and Systematics Laboratory, USDA, Utah State University, deposited in the TAMU collection.

Etymology.—Named for the Mexican state in which the specimens were collected.

DISCUSSION

Although no additional biological information is known, the fact that these 12 specimens (10 mutillids and two host bees) were all collected from the same host cell complex provides substantial evidence of both the conspecificity of the mutillids and the host relationship. *Diadasia* Patton is a known host for some species of *Dasymutilla* (Krombein 1979).

As is often the case with mutillids, the male and female differ in color pattern, although they are approximately the same size. The female goes to couplet 11 in Mickel's (1928, 1936) keys. It can be distinguished easily from all Nearctic *Dasymutilla* strictly by the color pattern.

The taxonomy of Neotropical *Dasymutilla* is clearly in a state of confusion. *Dasymutilla jalisco* is very similar both visually and morphologically to *D. canina* (Smith) (Fig. 1B). In *D. jalisco,* the black pubescent pattern of the thorax is more nearly triangular in shape, the inverted V-shaped black pattern on tergum II extends only to about the midline of the segment, and the pale pubescence of the abdominal tergum is yellowish/golden, concolorous with the pale pubescence of the head and thorax (Fig. 1A). In *D. canina,* the black pubescent pattern of the thorax extends anterolaterally to the humeral angles, thus giving more of a T-shaped appearance, the inverted V-shaped black pattern on tergum II extends past the midline, sometimes almost joining the black pubescence on the apical margin, and the pale pubescence of the abdominal tergum is almost white, much lighter than that of the head and thorax (Fig. 1B). Considering the within-species color variation in mutillids, it is possible that the females are color variants of the same species. However, there is no evidence to support that at this time.

Dasymutilla canina was described as *Mutilla canina* by Smith (1855) from the female only. The holotype is in The Natural History Museum (London). Saussure (1867) described both the male and female of *M. sumichrasti.* Mickel apparently could find neither in 1930–31 and designated a lectotype. The female lectotype designated by Mickel is in the Musée d'Histoire Naturelle (Genéve). Mickel synonymized the two (1964) without explanation. I have examined both female types and am in agreement with Mickel. No male type specimens were found by me in 1991.

Dasymutilla philinna (Cameron) was described in 1895 from the female only. The holotype is in The Natural History Museum (London). *Mutilla (Ephuta) variicolor* was described by André (1898) from the female only. The lectotype designated by Mickel in 1930–31 is in the Muséum National d'Histoire Naturelle (Paris). Mickel synonymized the two (1964), again without explanation. I have examined both of these types and again am in agreement with Mickel. Having examined all four female types, it is apparent that these are all the same species. New synonymy follows at the end of this paper.

I have examined male specimens identified as *D. sumichrasti.* I have not, however, come across any male types. Males of *D. sumichrasti* that I have examined are clearly (morphologically) different from the male of *D. jalisco. Dasymutilla sumichrasti,* as described by Saussure, appears to be a conglomerate of at least four different species, those being *D. personata* (Cameron), *D. terminata* (Smith), *D. deyrollesi* Mickel, and *D. thalia* (Cameron). It appears to be, in part, the male of *D. canina, D. person-*

ata, and *D. terminata*. *Dasymutilla thalia* is synonymous with *D. intermixta* Mickel, and is the male of *D. sicheliana* (Saussure) (Manley and Radke, 2002). *Dasymutilla deyrollesi* is clearly distinct.

Males of all of the above species, as well as *D. jalisco*, are very similar (almost identical) in appearance. They can, however, be distinguished morphologically. *Dasymutilla personata* can be distinguished easily from the others as it lacks a sternal pit filled with hairs. *Dasymutilla deyrollesi* can be distinguished from the remaining species by the presence of an apical fringe of setae on the last tergite. *Dasymutilla terminata* and *D. thalia* are the most difficult to distinguish. However, *D. terminata* has the sides of the propodeum smooth and polished, while in *D. thalia* the sides are punctate.

The male of *D. jalisco* keys to *D. intermixta* Mickel in Mickel's (1928, 1936) keys. It is distinguished easily from *D. intermixta* as well as the above species by its broad head, somewhat truncate on the posterior margin, by lacking an anterior emargination on the pronotum, by the anterior position of the pit on sternum II, and by the sculpture of the pygidium. *Dasymutilla intermixta* has the head narrowed posteriorly, has a median emargination on the pronotum, has the sternal pit more median in position, and has the pygidium glabrous and shining.

Although subsequent molecular and biological studies may change the taxonomic relationships of some (or all) of the species mentioned, it is clear that the specimens described herein represent male and female of the same species, and that the bee genus *Diadasia* serves as a host for this species.

Dasymutilla canina (Smith), **new combination**

Mutilla canina Smith 1855: 58. Holotype ♀ in The Natural History Museum (London).

Mutilla sumichrasti Saussure 1867: 357. Lectotype ♀ in the Musée d'Histoire Naturelle (Genève).

Mutilla (Sphaeropthalma) sumichrasti: Blake 1871: 236, ♀ (nec ♂).

Sphaerophthalma philinna Cameron 1895: 354. Holotype ♀ in The Natural History Museum (London). **New synonym.**

Sphaerophthalma sumichrasti: Cameron 1895: 359, ♀ (nec ♂).

Mutilla transmarina: Dalla Torre 1897: 92. ♀ (nec ♂).

Mutilla (Ephuta) variicolor André 1898: 56. Lectotype ♀ in The Museum National d'Histoire Naturelle (Paris). **New synonym.**

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FIVE NEW SPECIES OF *EUPARIXIA* BROWN (COLEOPTERA: APHODIIDAE: EUPARIINAE), WITH A REVISED KEY TO SPECIES

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Abstract.—Five previously undescribed species of *Euparixia* Brown, ***E. boliviana*** from Bolivia, ***E. campbelli*** from Costa Rica, ***E. isthmia*** and ***E. panamaensis*** from Panama, and ***E. mexicana*** from Mexico are described and integrated into the existing classification. A revised key to all known species is presented.

Key Words: taxonomy, new species, ant nests

Species of *Euparixia* Brown (1927) are highly modified, very distinctive beetles that have evolved for an existence in ant nests. Woodruff and Cartwright (1967) summarized the known biological information consisting of three documented host associations and several suspected associations. *Euparixia formica* Hinton, *E. bruneri* Chapin, and *E. moseri* Woodruff and Cartwright were collected in nests of leafcutting ants of the genus *Atta* Fabricius. *Euparixia campbelli,* n. sp., was taken from an *Atta* detritus cavity in Guatemala (J. M. Campbell, label data). Most specimens are found at lights; rarely is a species excavated from a host nest.

Discovery of a cryptic species closely similar to *E. duncani* Brown led to an investigation of the *Euparixia* holdings in the National Museum of Natural History, Washington, DC. This comparison of specimens revealed an additional three new species described here and still another undescribed species from Bolivia was discovered by Paul Skelley, Florida State Collection of Arthropods, Gainesville, FL.

Acronyms for collections mentioned in the text are as follows: (ASM) Scott McCleve, Douglas, AZ; (CNC) Canadian National Collection, Ottawa; (FSCA) Florida State Collection of Arthropods, Gainesville, FL; (MHN) Museo de Historia Natural "Noel Kempff Mercado," Santa Cruz, Bolivia; and (USNM) National Museum of Natural History, Smithsonian Institution, Washington, DC.

SYSTEMATICS

Genus *Euparixia* Brown

Euparixia Brown 1927: 288; Woodruff and Carwright 1967: 6. Type species: *Euparixia duncani* Brown. By monotypy.

Diagnosis.—Eupariini with inflexed clypeal margins; explanate pronotal margins; basally constricted pronotal sides; elytral intervals usually cariniform; epipleurae covering episternum, epimeron and apices of middle coxae; middle coxae widely separated; mesosternum separated from metasternum by transverse carina; middle and posterior tarsi long, slender.

Remarks.—Woodruff and Cartwright

(1967) reviewed the taxonomy of *Euparixia,* described one new species, and redescribed all known species. No subsequent studies have been published and Woodruff and Cartwright should be consulted for a summary of all previously known information concerning *Euparixia.*

Examination of all presently known species revealed a strong gradient of morphological adaptation from comparatively unmodified to highly modified pronota. *Euparixia panamaensis,* n. sp., and *E. costaricensis* Hinton possess almost rectangular pronota with only slight modifications of the lateral margin (Fig. 1). *Euparixia formica* Hinton and *E. isthmia,* n. sp., represent an intermediate stage in pronotal modification (Fig. 3), and the remaining species have highly modified pronota typified by an extreme constriction in the basal half (Figs. 5, 7, 9, 11) (Woodruff and Carwright 1967: 21, fig. 5).

REVISED KEY TO SPECIES OF *EUPARIXIA*

1\. Anterior clypeal apex with small tooth on each side (Figs. 1, 3) 2

– Anterior clypeal apex slightly angulate on each side (Figs. 5, 7, 9, 11) 3

2(1). Pronotum nearly rectangular, constricted in basal ⅙, lateral margin gradually, nearly evenly rounded anterior to constriction (Fig. 1) . . . . *panamaensis,* n. sp.

– Pronotum not rectangular, lateral margin more or less sinuate (Fig. 3) . . *isthmia,* n. sp.

3(1). Elytral intervals moderately convex, not cariniform, except *E. boliviana* with intervals 7–9 weakly carinate (Fig. 10) 4

– Elytral intervals distinctly cariniform (Figs. 6, 8, 12) 5

4(3). Pronotum narrowed only in basal ⅓ . . . . *costaricensis* Hinton

– Pronotum narrowed in basal ½ (Fig. 9) . . . . *boliviana,* n. sp.

5(3). Pronotum constricted only in basal ⅓, posterior angles prominent and acute (Figs. 1, 5, 7) 6

– Pronotum constricted in basal ½ or more (Fig. 11), posterior angles obsolete or nearly so (Fig. 11) 8

6(5). Pronotum narrowed only in basal ⅓, posterior angles prominent and acute (Figs. 5, 7) 7

– Pronotum narowed at middle, posterior angles weakly defined, rounded . . . . . . *formica* Hinton

7(6). Pronotal disc with deep punctures separated by thin, high "walls" presenting a honeycomb appearance (Fig. 7) . . . *duncani* Brown

– Pronotal disc with shallow punctures separated by flat pronotal surface (Fig. 5) . . . . *mexicana,* n. sp.

8(5). Basal ⅓ of pronotum with deep punctures narrowly separated by high "walls" presenting a honeycomb appearance (Fig. 11); metasternum densely, coarsely punctured . . . . *campbelli,* n. sp.

– Basal ⅓ of pronotum with punctures not deep, separated by low ridges or convex pronotal surface; metasternum essentially impunctate 9

9(8). Pronotum with lateral explanation nearly impunctate, lacking tubercles, pronotal surface slightly convex between punctures; (Louisiana and Cuba) . . . . *moseri* Woodruff and Cartwight

– Pronotum with lateral explanation weakly punctate, with some fine tubercles, pronotal surface with punctures separated by low ridges (Cuba) . . . . *bruneri* Chapin

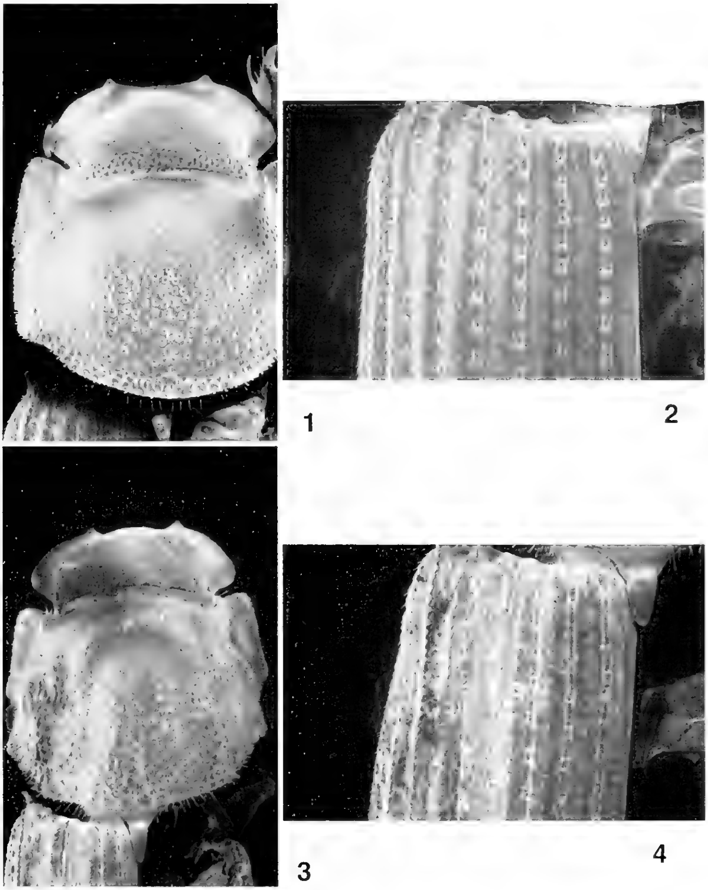
Euparixia panamaensis Gordon and McCleve, new species

(Figs. 1, 2)

Description.—Length 4.6 mm, width 2.1 m. Elongate, convex, shiny, dark red.

Head: Clypeus widely emarginate between toothed angles, sides arcuate to feeble genal sulcus. Margin not reflected dorsally at center, ventrally inflexed at center; genal angle obtuse. Surface with moderate, dense, nearly contiguous punctures across occiput; punctures smaller, sparser between eyes, becoming elongated anteriorly, progressively smaller, changing to minute punctures near anterior margin. Frontal suture not evident. Eye not visible in repose. Lateral margin of gena with narrow sulcus from margin to deep pore at anterior edge of eye, sulcus continued above eye, with short, sharp carina at margin adjacent to eye.

Pronotum: Broader than long (1.8 mm × 1.2 mm), moderately convex. Basal margin with single row of large, contiguous punctures; basal ½ of disc with few large, confused punctures anterior to basal row, then scattered, large punctures 1–2 diameters apart with tiny puncture or granule in



Figs. 1–4. Pronota and elytra. 1, *Euparixia panamaensis*, pronotum. 2, *E. panamaensis*, elytra. 3, *E. isthmia*, pronotum. 4, *E. isthmia*, elytra.

bottom of each, large punctures becoming smaller anteriorly. Scattered among large punctures are tiny punctures remaining unchanged to anterior margin where they become indistinguishable from reduced larger punctures. Sides explanate, weakly punctured, dull, with scattered small setae. Base with weak longitudinal groove in basal ½, larger punctures with small punctures in bottom often contiguous in and near groove. Oblique depressions moderately well defined, about 10 punctures long and 2–3 punctures wide. Anterior angles broadly rounded, sides slightly diverging, almost parallel for ⅖ of length of explanation to almost imperceptible angle, then slightly converging for remaining ⅗ of explanation; posterior angles obtuse, angles wider than elytra across base, basal constriction very short, only ⅕ of pronotum (Fig. 1).

Elytron: Elongate-oval (right elyron missing), widest at apical ⅓; intervals flat with scattered minute granules, each with an extremely minute seta, granules sometimes in single row, sometimes in weak, widely spaced, offset double rows. Striae with punctures moderately deep, small, sides of striae uneven and with indentation behind many punctures on outer side of stria, floor of stria with tiny transverse lip behind each puncture associated with each indentation of outer side of stria; mesal side of each stria nearly straight (Fig. 2). Scutellum with shallow, irregular, rugose, punctate depression at base.

Sternum: Prosternal process broadly arcuate at base, margins raised, shiny, thick at base, carinate laterally, disc depressed in a "V" with apex forward. Middle coxae separated by 1 ½ length of middle trochanter, middle depression clearly defined, depressed anteriorly, with 2 narrow isosceles triangular raised areas, 1 on each side, with base of each triangle near anterior margin of depression and apex pointing posteriorly; microsculpture of depression not evident at 50×. Meso- and metasterna separated by transverse carina with projections extending onto metasternum only, merging with shiny disc of metasternum. Center of metasternum with deep, longitudinal sulcus. Sulcus behind middle coxae deep anteriorly, moderately punctate, shallow, with large, confused punctures posteriorly. Disc of metasternum shiny with minute punctures, sides with few large punctures each with minute punctures in bottom. Depression behind middle coxa deep, sharply defined, shiny, rugulose, punctate in bottom. Side of metasternum laterally and anteriorly with small to moderate punctures.

Abdomen: First sternum with closely spaced, longitudinal carinae forming quadrate cells on posterior margin (fluting). Sterna 2–5 each depressed on anterior margin, depressions with closely spaced, long carinae forming quadrate cells, cells on second sternum about ⅙ length of sternum, ¼ length of sternum on third sternum, more than ½ length of sternum on fourth and fifth sterna at center. Posterior margin of sterna 2–3 with small ½ punctures, larger laterally, giving scalloped effect to margins. Posterior margin of fourth sternum with row of minute, light colored setae. Disc of sterna 2–3 shiny, with scattered, minute, setose punctures, punctures larger laterally. Sternum 4 with disc apparently impunctate at center, punctures evident laterally. Disc of fifth sternum shiny, with small setose punctures. Pygidum with disc somewhat shiny, with short, longitudinal carina at basal center and numerous, scattered, small tuberlces on each side. Basal ½ of pygidium with strong longitudinal sulcus at center.

Legs: Anterior tibia tridentate, middle tooth longest, apical tooth bent outward at obtuse, nearly right, angle. Apical spur elongate, narrow, slightly curved. Anterior trochanter prominent, shiny dorsally, dull ventrally, inner margin with few setae, crenulations vaguely evident. One long seta on femur near trochanter. Anterior femoral groove and about ½ of dorsal surface with appressed golden setae; ventral surface completely covered with moderate punctures separated by their own diameter. Middle femoral marginal groove complete from apex to near trochanter; posterior femoral marginal groove evident from apex to less than ½ distance to trochanter. Middle and posterior femora shiny, with minute punctures and associated setae, punctures separated by 1–3 a diameter. Posterior coxa between trochanters shiny with few moderate to large punctures on mesal ½.

Type material.—Holotype ♂: Panama, Canal Zone, Gamboa, 24-V-53 (USNM).

Distribution.—Known only from the type locality.

Material examined.—The holotype male.

Etymology.—The species is named for the country where the type specimen was collected.

Remarks.—The nearly rectangular outline of the pronotum with explanate margins continued almost to the base will serve to separate this species from those known. Other unique features include the large punctures with a tiny puncture in the bottom of each on the pronotum and metasternum, flat elytral carinae with scattered, minute granulations, scutellum with only a shallow, rugose depression at the base, and the unusual mesosternum with two triangular raised areas.

The holotype bears a handwritten label identical to that of two paratypes of *E. isthmia* except dates VI instead of V. Both species were likely collected from the same light trap, and this demonstrates for the first time that two species of *Euparixia* are sympatric. The holotype is missing the right elytron, right hind leg, and all, or parts of all, tarsi.

Euparixia isthmia Gordon and McCleve, new species

(Figs. 3, 4)

Description.—Length 4.4 mm, width 2.0 mm Elongate, convex, dull, dark brown.

Head: Clypeus broadly arcuate between toothed angles, sides arcuate to posterior margin without genal notch, anterior margin not reflected dorsally at center, ventrally feebly recurved at center; gena prominent, right angled. Surface densely, moderately punctate across base, punctures separated by less than a diameter, becoming much smaller and sparser anteriorly and laterally, changing to minute rounded denticles. Posterior margin of gena with narrow, shiny, impunctate sulcus extending almost to anterior pronotal margin, with small, deep pore above eye, and with short, sharp carina adjacent to eye. Frontal suture lacking.

Pronotum: Broader than long (2.0 mm × 1.2 mm), moderately convex (Fig. 3). Basal margin with single row of large, deep, contiguous punctures, punctures anterior to row confusedly placed and of various sizes, some contiguous or overlapping, others separated by a diameter, most smaller punctures bearing a short, light colored seta near anterior margin. Pronotum in basal ½ with deep, longitudinal, punctate groove 2 large punctures wide, and with deep, broad, oblique depression on each side of disc, depressions irregularly punctate with large punctures. Surface anterior to oblique depressions finely, regularly punctate, punctures becoming minute near anterior margin. Explanate sides dull, opaque, impunctate or with weak punctures or denticles and scattered short setae. Anterior angles shallowly, broadly rounded, forming nearly right angle with lateral margin. Explanate margins with angle at apical ⅓, constricted posterior to angle, then 2nd angle present at median ⅓ before basal constriction. Basal constriction short, basal margin about as wide as elytra at base (Fig. 3).

Elytron: Elongate oval, widest at apical ⅓, intervals on disc flat or only weakly carinate (Fig. 4), with single row of minute granules separated by about a diameter, each granule bearing a minute seta; intervals more carinate laterally, especially 9th interval, and apically. Each stria with row of indistinctly sculptured, elongate, shallow punctures separated by less than length of puncture. Scutellum narrow, shiny, without basal depression.

Sternum: Prosternal process broadly rounded at base, margins raised, slightly shiny, disc raised, irregularly, rugosely sculptured, with alutaceous sulcus on each side between disc and lateral margins. Mesosternum with coxae separated basally by 1½ length of middle trochanter; median depressed area clearly margined, depression deep, anterior ⅔ with sharp, central, longitudinal carina flanked on each side by deep groove, then series of 5–6 more or less parallel, anastamozing carinae; carinae and grooves between alutaceous, basal portion of mesosternum slightly shiny, with microreticulation barely evident at 50×. Meso- and metasterna separated by indistinct, transverse carina, longitudinal extension of carina onto meso- and metasterna lacking. Metasternum with center of disc depressed, with deep, coarse sulcus appearing to have tiny, longitudinal carina at bottom for nearly entire length; carina behind middle coxae strong, adjacent sulcus indistinct, weekly punctate; remainder of disc moderately shiny, minutely, moderately punctate, each puncture with minute, broad, whitish seta; depressed area in front of posterior coxa dull, deep; sides feebly shining, moderately, indistinctly punctate.

Abdomen: Basal sternum depressed along posterior margin, depression with longitudinal carinae forming rectangular cells. Second sternum with single row of short, weak, parallel, longitudinal carinae in anterior $\frac{1}{10}$, carinae not forming quadrate punctures; punctures on posterior margin enlarged, with posterior ½ of each effaced, forming scalloped margin; third sternum with single row of short, sharply distinct carinae about $\frac{1}{6}$ length of sternum, not forming quadrate cells along anterior margin, posterior margin with single row of enlarged ½ punctures forming scalloped margin; fourth sternum with anterior ½ depressed, depression with longitudinal carinae, forming quadrate cells, posterior margin weakly crenulate; fifth sternum with anterior ½ depressed, depression with closely spaced, longitudinal carinae forming cells about 4 times longer than wide; posterior ½ of sternum shiny; disc of sterna 2–5 weakly punctate, punctures small, moderately spaced, with tiny setae more evident than punctures. Pygidum with narrow, dull, apical margin; disc depressed, dull, with fine median carina at basal center and several small tubercles laterally. Basal ½ of pygidium alutaceous, with weak, longitudinal sulcus.

Legs: Anterior tibia tridentate, middle tooth longer than others, apical tooth obtuse, bent outward at less than right angle; apical spur slender, curved. Anterior trochanter large, inner margin with 3–4 setae in apparent punctures causing coarse, weak crenulation of margin, shiny and impunctate dorsally, ventrally dull, rugose, punctate. Anterior femur with single seta on each side near trochanter. Anterior femoral groove and about ⅓ of dorsal surface of femur covered with fine, sparse setae; posterior surface dull, with moderate punctures separated by about a diameter or less, some punctures indistinct. Middle femur with marginal groove strongly impressed from trochanter to apex. Posterior femur with marginal groove extending length of femur, except weak or absent near trochanter. Posterior coxa between trochanters alutaceous on mesal ½, shiny on lateral ½, without apparent punctures or setae.

Variation.—Length of male paratype 4.9 mm, and female paratype 4.5 mm. Both paratypes have either no setae or only 1 seta on anterior femur near trochanter. The female is lacking both elytra, one anterior leg, and all, or parts of all, tarsi except for one complete anterior tarsus.

Type material.—Holotype ♂: Panama, Canal Zone, Ft. Glick, Bldg. 708, 17 May '65, light (USNM). Paratypes, 2; 1 ♂, 1 ♀, Panama, Canal Zone, Gamboa, 24-VI-53. (USNM).

Distribution.—Known only from the Canal Zone, Panama.

Material examined.—The three type specimens.

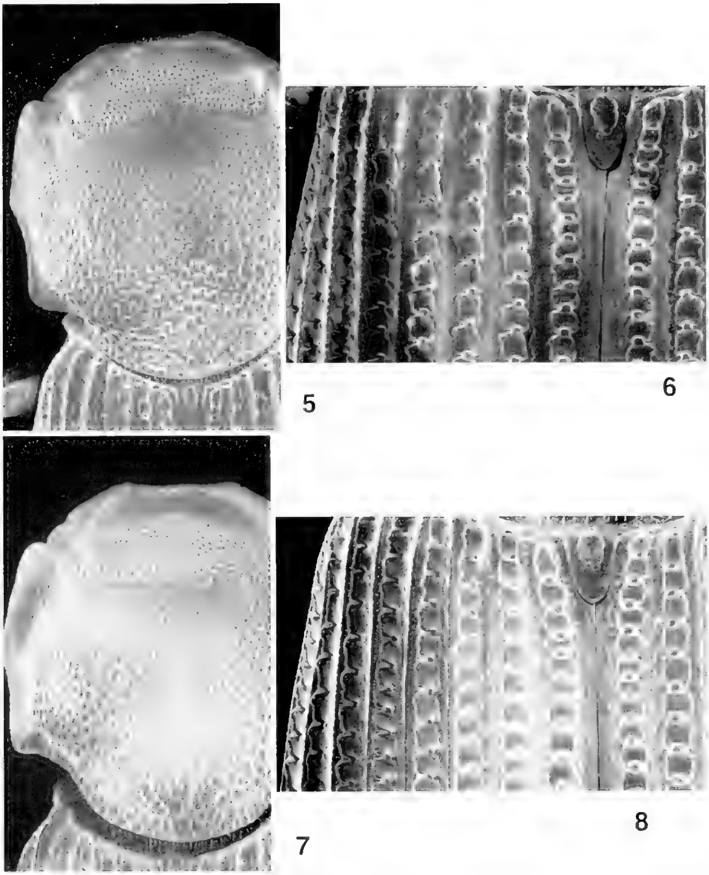
Etymology.—The specific epithet is from the Latin *isthmus,* meaning neck or narrow passage, and refers to the Isthmus of Panama.

Remarks.—This species has the intermediate type of pronotum (see generic discussion), a character shared only with *E. formica* Hinton. The mesosternal sculpture appears to be unique in the genus. The longitiudinal carinae are quite striking, somewhat like a portion of a woodcut as used in printing illustrations with the carinae and grooves seemingly carved into the surface. The lack of an anterior scutellar depression is also unusual.

Euparixia mexicana Gordon and McCleve, new species

(Figs. 5, 6)

Description.—Length 5.4 mm, width 2.4 mm Elongate, convex, feebly shiny, dark reddish brown.



Figs. 5–8. Pronota and elytra. 5, *Euparixia mexicana,* pronotum. 6, *E. mexicana,* elytra. 7, *E. duncani,* pronotum. 8, *E. duncani,* elytra.

Head: Clypeus widely truncate between weak angles, sides feebly arcuate to very slight genal notch, margin dorsally, feebly recurved at center and ventrally inflexed at center; genae prominent, right angled. Surface finely and densely punctate between eyes, punctures separated by a diameter or less, finer at sides and anteriorly, changing to minute granules in anterior ⅓, granules continuing to anterior margin. Frontal suture not visible. Eyes not visible when head in repose. Lateral margin of gena with a weak, punctate sulcus beginning near anterior margin and deepened gradually near eye into a deep pore, and with short carina at margin of gena adjacent to eye.

Pronotum: Broader than long (2.1 mm × 1.6 mm, very convex (Fig. 5). Basal margin with single distinct row of contiguous large punctures. Basal ½ of disc with large punctures a diameter or less apart, becoming abruptly smaller and sparser anteriorly; much smaller, shallow, punctures present between large punctures of basal ½ and continuing anteriorly, becoming denser as larger punctures disappear. Explanate sides impunctate or with indistinct small punctures. Oblique depressions on pronotum very weak, filled with about 20 large punctures in about 2 rows. Anterior angles broadly rounded. Posterior angles distinct, right angled. Explanate margins with an angle at anterior ⅓, then narrowed slightly to 2nd prominent angle at median ⅓, then narrowed sharply to short basal constriction. Pronotum at base much narrower than elytra at base.

Elytron: Elongate oval, widest at apical ⅓; intervals convex, weakly carinate (Fig. 6), each interval bears row of minute granules barely visible at 50×, separated by their own diameter. All 10 striae with series of deep punctures; superimposed above deep punctures is a chain of larger and shallower punctures (the stria itself) formed by toothlike points projecting from each side of each raised interval; points extend toward each other from each adjacent interval toward or partially over each deeper puncture, giving complex appearance. Scutellum narrow, with sharply defined depression at base.

Sternum: Prosternal process broadly rounded, almost truncate posteriorly, disc strongly margined at base, less so laterally. Mesosternum with coxae separated by 1 ½ length of middle trochanter; median depression clearly margined, depression in basal ⅔ somewhat shiny, microsculpture evident at 50×, anterior ⅓ of depression slightly raised nearly to level of margin and arcuately delimited behind on a line beginning opposite anterior ⅓ of middle coxa, curving anteriorly toward prosternal process and continued to middle of opposite coxa; raised anterior ⅓ of depression irregularly shiny, rugose, punctate. Meso- and metasterna divided by transverse carina with fine carina projecting both anteriorly into mesosternal depression and posteriorly onto metasternum. Latter carina gives way to long, coarse, deep median sulcus. Carina bordering posterior portion of middle coxa large, separated from disc of metasternum by deep, variably punctate sulcus, remainder of disc with fine to moderate punctures except for shiny impunctate area between posterior end of median sulcus and hind coxae; depressed area anterior to hind coxa deep, sharply bordered, confusedly rugulose, narrowly smooth and shiny adjacent to posterior coxa; anterior and lateral margins between middle coxa and epipleuron with punctures larger than on disc, surface shiny between punctures.

Abdomen: First sternum with irregularly spaced, longitudinal carinae on posterior margin forming quadrate cells open behind. Sterna 2–5 each depressed on anterior margin, depression with irregularly spaced, longitudinal carinae, depression longer on each successive sternum. Posterior ⅔ of sterna 2–3 with coarse punctures, larger laterally, followed by single row of larger punctures open behind, giving a scalloped effect to posterior margin. Sternum 4 with smaller punctures and with series of extremely minute, light colored setae at posterior margin. Fifth sternum impunctate at center of posterior margin. Pygidium with raised, shiny, apical margin thickened at middle; disc depressed, shiny, with short median carina at basal center and several small tubercles on each side near basal margin; Basal ½ of pygidium above ridge strongly alutaceous, with a strong, longitudinal sulcus.

Legs: Anterior tibia tridentate; apical tooth bent outward at nearly right angle. Apical spur elongate, narrow, slightly curved. Anterior trochanter prominent, shiny dorsally, rugose, punctate ventrally, inner margin with about 12 extremely short, light colored setae giving margin minute crenulations. Both anterior femora with 3 setae near trochanter. Anterior femoral groove and about ⅓ of dorsal surface covered with short golden setae. Middle femoral marginal groove complete from apex to apex of trochanter. Posterior femoral marginal groove extending from apex to apex of trochanter. Posterior femoral marginal groove extended from apex less than ½ distance to trochanter, feebly impressed. Middle and posterior femora with moderate punctures, each with short, conspicuous seta. Posterior coxa between trochanters punctate, punctures moderate, distinct, minutely setose.

Variation.—Length 4.8 to 5.7 mm. The single female from Tomatlan (4.9 mm) is essentially the same size as the male with same data (4.8 mm). Some specimens show a vague, short, longitudinal groove at the pronotal base. Some specimens bear minute setae on the pronotum, elytral intervals, and metasternum. One Ajijic specimen has the posterior angle of the pronotal explanation more developed than any other; the same specimen has the basal constriction of the pronotum longer than the others, although it also varies in length among the others. The number of setae near the trochanter varies considerably among specimens as follows, with the first number of each pair representing the left femur: 2–3, 5–2, 3–2, 3–4, 3–2, 3–3.

Type material.—Holotype ♂: Mexico, Sonora, 17 km sw Moctezuma, vii-21, 22–80, 944 m, at light, S. McCleve, P. Jump (FSCA). Paratypes, 6. 1 ♂, Mexico, JAL(Jalisco), 3 mi. N. Barra de Navidad, Bahia de Coastecomate, 17 August, 1964, WLNutting, lt. trap, thorn forest clearing; 2 ♂, Mexico, JAL., Ajijic, 21 June, 1964, 16 July, 1964, 5140′, WLNutting, UV. lt. trap; 1 ♂, 1 ♀, JA(Jalisco), hwy 200, 15 mi S Tomatlan, vii-11-84, UVL, S. McCleve, P. Jump; 1 ♂, Mexico, Sin(Sinaloa), Venodio(Venadillo?), C.17, Kusche '18, donor BP Clark (ASM, USNM).

Distribution.—Mexico (northern Sonora, Sinaloa, and Jalisco).

Material examined.—The seven type specimens.

Etymology.—The species name refers to the country where all type specimens were taken.

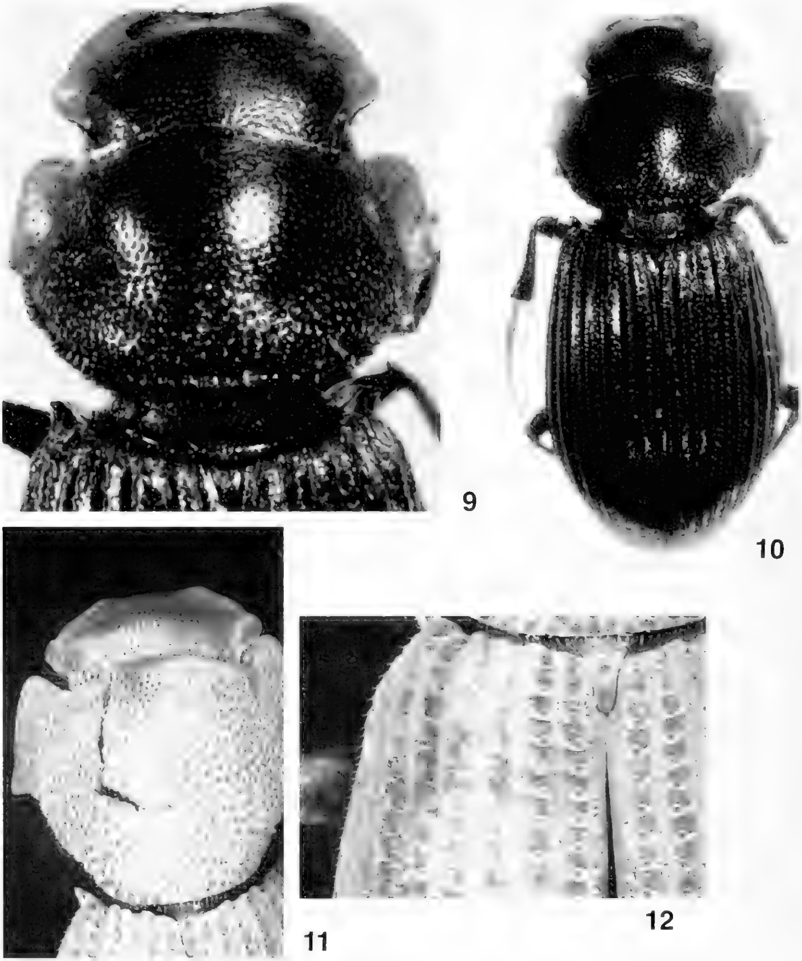
Remarks.—This species is most similar to *E. duncani* Brown. The pronotal outlines are very similar, but *E. mexicana* has narrower lateral explanations (Figs. 5, 7). The elytral intervals of *E. mexicana* are less carinate, bearing only a row of separate, minute granules, whereas in *E. duncani* the granules are crowded together onto the carinae (Figs. 6, 8). Both meso- and metasterna are sculpted differently in each species. Because of the similarity in appearance, this species has been misidentified as *E. duncani* Brown. The two Ajijic paratypes and the single Venodio, Jalisco, paratype were listed among specimens of *E. duncani* identified by Woodruff and Cartwright (1967). It is likely that other specimens of *E. mexicana* are confused with *E. duncani* in other collections. To our knowledge, no specimens of *E. duncani* have been collected in Mexico, although it almost certainly occurs at least in northern Sonora, having been collected at Douglas, Arizona, on the Mexican border. The host of *E. mexicana* is likely *Atta mexicana* (Smith) (which is common at the type locality in Sonora); therefore it also could occur in Arizona where *A. mexicana* exists in a small section of Organ Pipe National Monument.

Euparixia boliviana Gordon and McCleve, new species

(Figs. 9, 10)

Description.—Length 4.7 mm, width 2.1 mm. Elongate, convex, feebly shiny, dark reddish brown.

Head: Clypeus distinctly emarginate with angles rounded, sides straight to very slight genal notch, apical margin dorsally, feebly recurved at center and ventrally inflexed at center; genae feebly produced, rounded. Surface finely and densely punctate between eyes, punctures separated by a diameter or less, finer at sides and anteriorly, changing to minute granules in anterior ⅓, granules continuing to anterior mar-



Figs. 9–12. Pronota and elytra. 9, *Euparixia boliviana*, pronotum. 10, *E. boliviana*, elytra. 11, *E. campbelli*, pronotum. 12, *E. campbelli*, elytra.

gin. Frontal suture barely perceptible. Eyes not visible when head in repose. Lateral margin of gena with a weak, punctate sulcus beginning near anterior margin and deepened gradually near eye into a deep pore, and with short carina at margin of gena adjacent to eye.

Pronotum: Broader than long (1.8 × 1.2 mm), very convex (Fig. 9). Basal margin with single distinct row of contiguous large punctures. Basal ½ of disc with large, nearly contiguous punctures becoming gradually smaller and sparser anteriorly, small punctures absent. Explanate sides impunctate. Oblique depressions on pronotum distinct, filled with about 20 large punctures in about 2 rows. Anterior angle abruptly broadly rounded. Posterior angles obsolete. Explanate margins with angle at anterior ⅓, then strongly narrowed to base. Pronotum at base much narrower than elytral base.

Elytron: Elongate oval, widest at apical ⅓; intervals convex, not carinate except intervals 7–9 weakly carinate (Fig. 10), each interval with row of minute granules barely visible at 50×, separated by their own diameter. All 10 striae with series of deep punctures separated by less than diameter of a puncture. Scutellum narrow, with sharply defined depression at base.

Sternum: Prosternal process broadly rounded posteriorly, disc strongly margined at base, less so laterally. Mesosternum with coxae separated by 1 ½ length of middle trochanter; median depression clearly margined, with strong median carina, depression in basal ⅔ somewhat shiny, microsculpture evident at 50×, anterior ⅓ of depression slightly raised nearly to level of margin and arcuately delimited behind on a line beginning opposite anterior ⅓ of middle coxa, curving anteriorly toward prosternal process and continued to middle of opposite coxa; raised anterior ⅓ of depression irregularly shiny, rugose, punctate. Meso- and metasterna divided by transverse carina, carina smooth, without fine carinae. Latter carina gives way to long, coarse, deep median sulcus. Carina bordering posterior portion of middle coxae large, separated from disc of metasternum by deep, variably punctate sulcus, remainder of disc with fine to moderate punctures except for shiny impunctate area between posterior end of median sulcus and posterior coxae; depressed area anterior to posterior coxa deep, sharply bordered, confusedly rugulose, narrowly smooth and shiny adjacent to middle coxa; anterior and lateral margins between mesocoxa and epipleuron with punctures fine, surface shiny between punctures.

Abdomen: First sternum with irregularly spaced, longitudinal carinae on posterior margin forming very small quadrate cells open behind. Sterna 2–3 not depressed on anterior margin, with narrow row of fine, dense, nearly contiguous cells; sterna 4–5 with large, elongate, narrow cells on anterior margin separated by narrow, longitudinal carinae. Posterior margin of sterna 4 with row of small, irregular tubercles. Fifth sternum impunctate medially. Pygidium with raised, shiny, apical margin thickened at middle; disc depressed, shiny, with short median carina at basal center and several small tubercles on each side near basal margin; basal ½ of pygidium above ridge strongly alutaceous, with a strong, longitudinal sulcus.

Legs: Anterior tibia tridentate; apical tooth evenly curved outward. Apical spur elongate, narrow, slightly curved. Anterior trochanter prominent, shiny dorsally, rugose, punctate ventrally. Both anterior femora with 1 seta near trochanter. Anterior femoral groove and about ⅓ of dorsal surface covered with short golden setae. Middle femoral marginal groove complete from apex to apex of trochanter. Posterior femoral marginal groove extending from apex to apex of trochanter. Middle and posterior femora with small punctures throughout, punctures separated by less than to 3 times diameter of a puncture, each puncture with very short, stout seta. Posterior coxa between trochanters smooth with weak, sparse punctures.

Type material.—Holotype ♂: Bolivia, Santa Cruz, 3.7 km SSE. Buena Vista, Hotel Flora & Fauna, 430 m, 5–15-XI-2001, M.C. Thomas and B.K. Dozier, tropical transition forest, BLT. (MHN).

Distribution.—Known only from the type locality.

Material examined.—The holotype.

Etymology.—The species name refers to the country where the holotype specimen was collected.

Remarks.—This species is in the group with basally constricted pronota abruptly narrowed in the basal half, a group typified by *E. campbelli.* The noncarinate discal intervals are similar only to those of *E. costaricensis* which has a broad pronotum constricted only in the basal third.

***Euparixia campbelli* Gordon and McCleve, new species**

(Figs. 11, 12)

Description.—Length 5.2 mm, width 2.2 mm. Elongate, convex, dull, dark brown.

Head: Clypeus widely truncate between weak angles, sides obliquely truncate to weak genal notch, anterior margin barely reflected dorsally at center, inflexed ventrally at middle. Surface densely, deeply, coarsely and regularly punctate between eyes, some punctures elongate, punctures sharing margins in reticulate pattern becoming smaller in transverse, complete band between anterior margins of eyes, then larger again until gradually becoming smaller, giving way to minute granulations anteriorly on clypeus. Each puncture with short, minute, erect golden seta barely visible at 50×. Deep sulcus present along lateral margin of gena with deep pore at anterior inner corner of eye, continued weakly above eye with short, sharp carina adjacent to eye.

Pronotum: Broader than long (2.0 × 1.4 mm), very strongly convex. Almost entire dorsal surface covered with deep, coarse, regular, adjacent punctures much like a honeycomb, punctures becoming smaller and shallower near anterior margin, continuing to anterior margin. Minute, short, semierect, posteriorly projecting, golden seta present on anterior rim of each puncture. Punctures on lateral explanations becoming shallower but larger, then indistinct, giving way to irregular, minute granulations. Oblique depressions not evident except as a group of about 10 slightly shallower punctures where depressions should be; longitudinal groove at base lacking. Anterior angles narrowly rounded, acute. Explanate margins short, terminated with sharp right angle at anterior ⅓, followed by long basal constriction (Fig. 11); smooth, shiny sulcus present along lateral margin of basal constriction, merging with reticulate punctures near base.

Elytron: Elongate oval, widest at apical ⅓, intervals strongly carinate, at 50× showing single row of minute adjacent granules each with extremely minute seta visible in profile at 50×; sutural interval with prominent, distinct, single row of discrete punctures visible at 25×. Striae deep, punctures deep, small, sharply defined, a small, acute projection from carina on each side approaching each puncture; strial punctures separated by 1 to 2 their own diameter, area between shiny (Fig. 12). Scutellum narrow, elongate, with deep, porelike depression at base.

Sternum: Prosternal process broadly arcuate at base, all margins raised and shiny, disc depressed. Mesosternum with coxae separated basally by more than length of middle trochanter; median depressed area smooth, shiny, with microreticulation evident at 50×, becoming irregular, dull near prosternum. Meso- and metasterna separated by fine, transverse carina having short, longitudinal extensions; carina on metasternum succeeded by long, coarse, broad, deep sulcus irregularly and minutely rugose at bottom. Sulcus bordering middle coxa broad, deep, punctate at bottom. Remainder of disc shiny, covered with moderate to large punctures, most punctures except largest bearing 1 minute, light colored seta each; sides with punctures larger, less well defined than on disc; depressed area in front of posterior coxa weakly shiny, with shallow punctures.

Abdomen: First sternum with widely spaced, short carinae in posterior ½, not forming distinct quadrate cells. Sterna 2–5 depressed on anterior ½, depression with widely, irregularly spaced longitudinal ridges, depressed area more extensive on each subsequent sternum. Disc of sterna 2–3 with variably sized, moderate to large punctures; posterior margin of same sterna with moderate partial punctures giving margin scalloped effect.

Legs: Anterior tibia tridentate, apical tooth slender, longer than other 2, bent outward at right angle to tibia; apical spur elongate, slender; anterior trochanter large, prominent, shiny, impunctate dorsally, concave, rugose ventrally; inner margin with numerous minute setae, not clearly crenulate. Anterior femur with 3 setae near trochanter on left side, 2 on right side. Anterior femoral groove and about ⅓ dorsal surface of femur covered with fine, semiappressed golden setae; posterior surface of femur dull, covered with large, overlapping punctures. Middle femoral marginal groove complete from apex to near trochanter; posterior femur with marginal groove extended only ½ distance from apex to trochanter, strongly incised.

Variation.—The female paratype is 4.1 mm long and has 3 setae on each anterior femur near trochanter.

Type material.—Holotype ♂: Guatemala, Finca San Rafael Olimpo, Cuyatenango, Such.(Suchitepequez), I.21.1966, J. M. Campbell, ex. large detritus cavity of *Atta* sp., 6–8 ft. deep (CNC). Paratype, 1 ♀, same data as holotype (CNC).

Distribution.—Known only from the type locality.

Material examined.—The holotype and one paratype.

Etymology.—This species is named for the collector of the type series, J. M. Campbell, in recognition of his many contributions to the study of Coleoptera.

Remarks.—The shape of the pronotum, with only a single strong angle on the explanate margin, is similar to *Euparixia bruneri* and *E. moseri*. However *E. campbelli* lacks any indication of a weak angle behind the prominent angle of the lateral margin. The pronotal punctation of *E. campbelli* is also unique in being of uniform size and completely covering all but the explanate margins in a crowded honeycomb pattern.

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REVISION OF NORTH AMERICAN *ALEIODES* WESMAEL (PART 7): THE *COMPRESSOR* HERRICH-SCHAEFFER, *UFEI* (WALLEY), *GRESSITTI* (MUESEBECK) AND *PROCERUS* WESMAEL SPECIES-GROUPS (HYMENOPTERA: BRACONIDAE: ROGADINAE)

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Abstract.—Six North American species in four species-groups of the genus *Aleiodes* are treated. The *compressor* (Herrich-Schaeffer) species-group includes *A. palmatus* (Walley), **new combination** and ***A. palmatoides*, new species**; the *ufei* (Walley) species-group includes only *A. ufei* (Walley), **new combination**; the *gressitti* (Muesebeck) species-group includes ***A. lissos*, new species**; and the *procerus* species-group includes *A. granulatus* (DeGant), **new combination**, and ***A. angustipennis*, new species**. Other new combinations proposed are: *A. aligharensis* (Quadri), **new combination**; *A. compressor* (Herrich-Schaeffer), **new combination**; *A. gressitti* (Muesebeck), **new combination**; and *A. narangae* (Rohwer), **new combination**.

Key Words: Hymenoptera, Braconidae, parasitoids

The rogadine braconid genus *Aleiodes* Wesmael is worldwide in distribution but is particularly species-rich in the Holarctic Region. *Aleiodes* is well diversified in North America, with at least 90 species in the United States and Canada (S. Shaw et al. 1997). This study is the seventh paper in a series on *Aleiodes* species-groups, intended to provide a complete revision of the genus for North America (see S. Shaw et al. 1997, 1998a, 1998b; Marsh and S. Shaw 1998, 1999, 2001). The four groups covered here are small, with only 13 included Holarctic species, six of which occur in North America. This paper treats several minor and unrelated groups that are not frequently encountered, but nevertheless must be treated to complete our revision of North American species. For convenience, these are being consolidated into one paper. Because our intent is to provide a revision of the North American species, species treatments are limited to the Nearctic fauna.

Aleiodes species are koinobiont endoparasitoids of lepidopterous larvae, especially macrolepidoptera of the superfamilies Noctuoidea and Geometroidea, and to a lesser extent, Arctioidea, Sphingoidea, and Papilionoidea (S. Shaw et al. 1997). The method of parasitism, unique to the tribe Rogadini, is noteworthy: the *Aleiodes* larva completes its feeding and pupates within the shrunken and mummified remains of the host caterpillar. In all known cases, the form of the mummy caused by a particular *Aleiodes* species is characteristic for that host and parasitoid, so mummified remains are of considerable diagnostic value and should be retained with the parasitoid when reared. For a more complete discussion of *Aleiodes* biology, readers may refer to M. Shaw (1983, 1994), M. Shaw and Huddleston (1991), S. Shaw (1995) and S. Shaw et al. (1997). Very little is know about the biology of the species of the groups included in this paper, but the few records indicate parasitism of noctuid and arctiid larvae.

METHODS

Species covered in this paper can be identified as members of the subfamily Rogadinae using the keys of S. Shaw (1995), M. Shaw and Huddleston (1991), or Sharkey (1997). Our definition of *Aleiodes* follows that of S. Shaw (1993), S. Shaw et al. (1997) and van Achterberg (1991). Specimens can be determined as *Aleiodes* using the key of Shaw (1997). The species-groups of North American *Aleiodes* can be identified using the key provided in S. Shaw et al. (1997). Fortier (1997) and Fortier and Shaw (1999) provided a cladistic analysis of the *Aleiodes* species-groups.

Terminology follows that used for *Aleiodes* by S. Shaw et al. (1997), S. Shaw (1993), and Marsh (1989). Microsculpture terminology follows that of Harris (1979). Wing vein terminology agrees with the system adopted by Wharton et al. (1997). A labeled diagram of wing veins was provided by S. Shaw et al. (1997).

Acronyms for collections where type material is deposited are as follows: CNC (Canadian National Collection, Ottawa, Ontario, Canada), CUI (Cornell University, Ithaca, New York), FSCA (Florida State Collection of Arthropods, Gainesville, FL), MSU (Michigan State University, East Lansing, MI), NCDA (North Carolina Department of Agriculture, Raleigh, NC); RMSEL (Rocky Mountain Systematic Entomology Laboratory, University of Wyoming, Laramie, WY), UCD (University of California, Davis, CA), UCR (University of California, Riverside, CA), UK (University of Kansas, Lawrence, KS), USNM (National Museum of Natural History, Smithsonian Institution, Washington, DC).

ALEIODES COMPRESSOR SPECIES-GROUP

Included species.—*A. compressor* (Herrich-Schaeffer 1838), **new combination** (Europe); *A. aligharensi* (Quadri 1933), **new combination** (India, Spain); *A. palmatus* (Walley 1941), **new combination** (North America); *A. palmatoides*, new species.

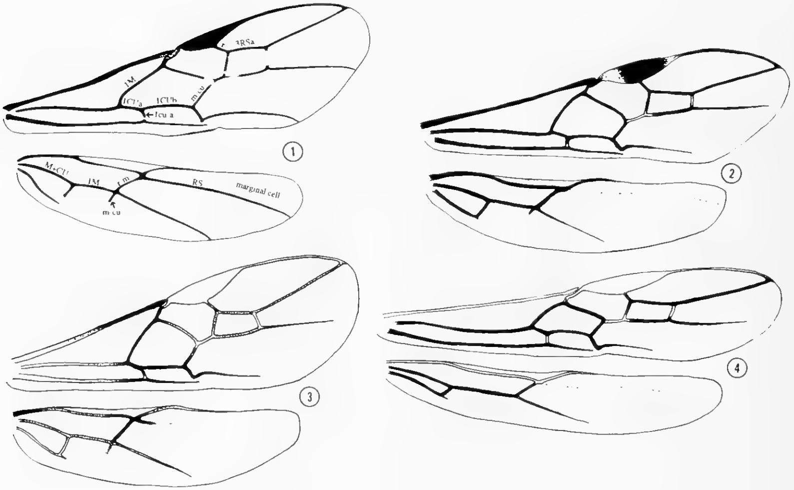
Diagnostic characters.—First metasomal tergum (petiole) parallel-sided (Fig. 8) or nearly so, apex of metasoma laterally compressed in some females (Fig. 6); hind wing vein RS sinuate, marginal cell narrowest in middle (Fig. 2).

Comments.—Species of this group are easily distinguished by the parallel-sided petiole, compressed metasoma, and form a monophyletic group within *Aleiodes* (Fortier and S. Shaw 1999). These species have been previously placed in the genus *Petalodes* Wesmael; however, van Achterberg (1991) synonymized this genus with *Aleiodes*. *Aleiodes ufei* (Wallley) was also included in *Petalodes* based upon the nearly parallel-sided petiole, but it has distinctly different venation in the hind wing and is placed in its own species-group (see Fortier and S. Shaw 1999).

M. Shaw (1994) stated that the European species, *A. compressor*, "has a blade-like gaster and parasitizes a common geometrid that lives concealed in spun leaves in its spring generation, and later in the summer a notodontid living in similar spun leaf packets." If the compressed metasoma (gaster) is a useful adaptation for getting at concealed hosts, then this may explain the convergent evolution of this feature in the *ufei* group.

KEY TO THE NORTH AMERICAN SPECIES OF THE *COMPRESSOR* SPECIES-GROUP

1. Apex of metasomal terga 3–6 brown; lateral mesonotal lobes usually brown . . . . *palmatoides*, new species



Figs. 1–4. Wings of *Aleiodes* species. 1, *A. ufei*. 2, *A. palmatoides*. 3, *A. lissos*. 4, *A. angustipennis*.

– Metasomal terga 3–6 entirely orange; lateral mesonotal lobes orange . . . . . *palmatus* (Walley)

Aleiodes palmatoides Marsh and Shaw, new species

(Fig. 2)

Female.—*Body color:* head including antenna and mouth parts honey yellow, ocellar triangle black; mesosoma honey yellow, with lateral mesonotal lobes and pronotum, mesopleuron and propodeum dorsally brown; metasoma honey yellow, first and second terga brown laterally, terga 3–5 brown apically, venter yellow; legs yellow, hind femur light brown apically; wings hyaline, veins brown, stigma bicolored brown with yellow at apex and base, tegula yellow. *Body length:* 4.0–5.5 mm; fore wing length, 3.0–3.5 mm. *Head:* eyes and ocelli large, 33–35 antennomeres, flagellomeres slightly longer than wide; malar space short, less than basal width of mandible and about ¼ eye height; temple narrow, about ⅓ eye width; occipital carina weak or absent on vertex, meeting hypostomal carina; oral space small and circular, diameter less than basal width of mandible and about ½ face height; clypeus weakly swollen; ocelli large, ocellocular distance about ¾ diameter of lateral ocellus; head entirely coriaceous; palpi not swollen; mandibles small, tips not crossing when closed. *Mesosoma:* pronotum rugulose laterally; mesonotum and scutellum coriaceous, notauli weakly scrobiculate, meeting in small triangular rugose area before scutellum; mesopleuron coriaceous, often weakly rugulose medially, subalar sulcus rugose, sternaulus absent; propodeum rugose coriaceous dorsally, coriaceous laterally, median carina complete. *Legs:* tarsal claws not pectinate; hind coxa finely coriaceous dorsally. *Wings* (Fig. 2): fore wing with vein r ⅓ length of 3RSa and ½ length of m-cu, vein 1cu-a beyond 1M by distance slightly greater than length of 1cu-a, vein 1CUa ⅓ length of 1CUb; hind wing with vein RS slightly sinuate, marginal cell narrowest in middle, vein r-m slightly shorter than 1M, vein 1M about ¾ length of M+CU, vein m-cu weakly indicated. *Metasoma:* first tergum costate, apical width only slightly greater than basal width, median carina complete; second tergum costate, apical width equal to or less than basal width, median carina complete; third tergum costate on basal ¾, smooth on apical ¼, median carina absent or weakly present on basal half; remainder of terga smooth, fourth tergum occasionally with few costae at base; ovipositor about ½ length of hind basitarsus.

Male.—Essentially as in female; 38–39 antennomeres, flagellomeres 3 times longer than wide; fourth metasomal tergum strongly costate.

Holotype.—Female: VIRGINIA, Louisa Co., 4 mi. S. Cuckoo, July 4–18, 1989, J. Kloke and D. R. Smith, Malaise trap. Deposited in USNM.

Paratypes.—VIRGINIA: 5 ♀, 3 ♂, same data as holotype, dates of July 4–October 6, 1989; 2 ♀, Essex Co., 1 mi. S.E. Dunnsville, September 17–October 10, 1991 and May 25–June 5, 1991, Malaise trap, D. R. Smith. NORTH CAROLINA: 3 ♀, Orange Co., Chapel Hill, September 9, 1975 and August 1, 1976, Malaise trap. Deposited in USNM, RMSEL, NCDA.

Distribution.—Known only from the type localities in Virginia and North Carolina.

Biology.—Unknown.

Comments.—This species differs from other North American species by the nearly parallel-sided first metasomal tergum, which is similar to *A. palmatus* from which is is distinguished by the brown markings on the mesonotum and metasomal terga.

Etymology.—The specific name refers to the similarity of this species to *A. palmatus.*

Aleiodes palmatus (Walley), **new combination**

(Figs. 6, 8)

Petalodes palmatus Walley 1941: 214.

Diagnosis.—Body unicolored honey yellow, stigma bicolored; body length, 6.0–7.0 mm; 33–35 antennomeres; malar space shorter than basal width of mandible; face rugo-coriaceous, frons, vertex and temple coriaceous; oral opening small and circular, diameter about equal to basal width of mandible; pronotum rugose; mesonotum and scutellum coriaceous, notauli weakly scrobiculate anteriorly, meeting in weak obscure rugulose area before scutellum; mesonotum coriaceous, subalar sulcus weakly rugulose, sternaulus absent; propodeum rugose coriaceous dorsally, coriaceous laterally, median carina complete; first metasomal tergum (Fig. 8) costate, basal width about equal to apical width, sides parallel, length nearly twice apical width, median carina complete although weak apically; second tergum costate, longer than wide, apical width slightly less than that of first tergum, median carina not complete; third tergum costate on basal half, coriaceous on apical half, median carina absent; remainder of terga coriaceous, laterally compressed from apical half of second tergum to tip of metasoma (Fig. 6); forewing with vein 1cu-a beyond vein 1M by distance greater than length of 1cu-a; hind wing with vein RS sinuate, marginal cell narrowest in middle, vein 1r-m about equal to 1M, vein m-cu weak, only short stub present; tarsal claws with 3–4 thin spines at base.

Type material examined.—*Petalodes palmatus* Walley, holotype female, BRITISH COLUMBIA, Canim Lake [CNC].

Distribution.—Ontario west to British Columbia, south to Wisconsin, Minnesota, Utah and California.

Biology.—Recorded as a solitary parasitoid of *Nycteola cinereana* Neumoegen and Dyar (Noctuidae). Also reared from an undetermined microlepidopteran on *Populus tremuloides* Michx.

Comments.—*Aleiodes palmatus* is distinguished from *A. palmatoides* by the honey yellow mesonotum and metasoma (in *A. palmatoides* the mesonotal lobes and apical borders of metasomal terga 3–6 are brown).

ALEIODES UFEI SPECIES-GROUP

Included species.—*A. ufei* (Walley) 1941, **new combination** (North America).

Diagnostic characters.—First metasomal tergum (petiole) parallel-sided, apex of metasoma laterally compressed in females; hind wing vein RS straight, marginal cell narrowest at base, widening gradually to apex (Fig. 1).

Comments.—Only one species is included in this species-group. It also has the nearly parallel-sided petiole as in the *compressor* species-group but is distinguished by the straight hind wing vein RS and the gradually widening marginal cell and by its bicolored black and orange body. Cladistic analysis by Fortier and S. Shaw (1999) indicated that this species is not closely related to members of the *compressor* group, despite superficial resemblance in the form of the metasoma.

Aleiodes ufei (Walley), **new combination**
(Fig. 1)

Petalodes ufei Walley 1941: 215.

Diagnosis.—Body bicolored black and orange, head, antenna and mesosoma black, first and second metasomal terga orange, remainder of terga black, third tergum occasionally orange on basal ⅓, legs orange, apex of hind tibia and tarsus black, wings hyaline, veins brown, tegula black; body length, 8.0–9.0 mm; 49–55 antennomeres; malar space longer than basal width of mandible; head entirely punctate and shining; ocellocular distance slightly longer than diameter of lateral ocellus; pronotum rugose, mesonotum and scutellum minutely punctate and shining, mesopleuron punctate and shining, subalar sulcus and sternaulus rugose; propodeum rugose dorsally, smooth laterally, median carina complete; first metasomal tergum parallel sided, apical width equal to basal width, first and second terga costate rugose, median carina complete, third tergum costate on basal ⅓, remainder of terga smooth, apical metasomal segments laterally compressed; vein 1cu-a of fore wing beyond 1M by distance slightly greater than length of 1cu-a; marginal cell of hind wing gradually widening to apex, vein RS straight, vein m-cu present (Fig. 1); tarsal claws not pectinate.

Type material examined.—*Petalodes ufei* Walley, holotype female, Lake Almanor, California [USNM].

Distribution.—Specimens have been examined from California, Nevada, and British Columbia.

Biology.—The type series was reared from *Ufeus plicatus* Grote (Noctuidae).

Comments.—This species is superficially similar in coloration to other bicolored black and orange species, such as *A. terminalis* Cresson and *A. abdominalis* Cresson, but is distinguished by the parallel-sided first metasomal segment and the laterally compressed apical metasomal segments.

ALEIODES GRESSITTI SPECIES-GROUP

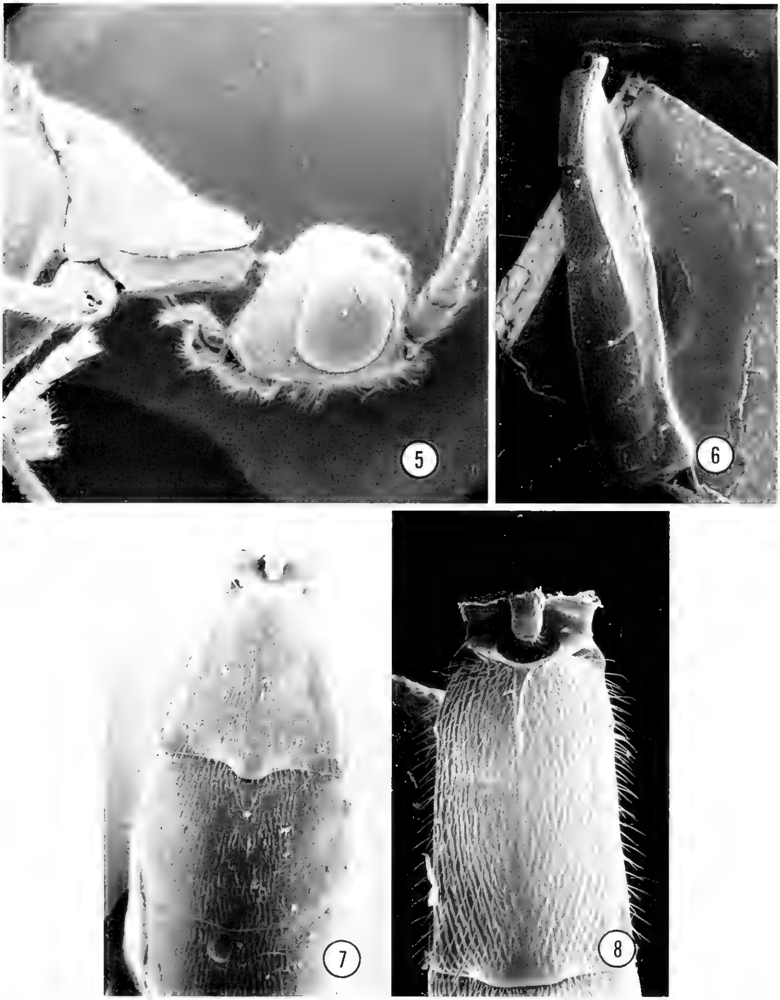
Included species.—*A. gressitti* (Muesebeck 1964), **new combination** (Campbell Islands); *A. lissos* new species.

Diagnostic characters.—Metasomal terga very finely coriaceous and shining, appearing smooth (Fig. 7); fore wing vein 1cu-a beyond 1M by 1.5 times length of 1cu-a; hind wing vein RS slightly sinuate, marginal cell narrowest in middle (Fig. 3).

Comments.—This is a monophyletic group (Fortier and Shaw 1999) of only two species at present which is defined by the nearly smooth and shining metasomal terga, which does not occur in any other species we have studied.

***Aleiodes lissos* Marsh and Shaw, new species**
(Figs. 3, 7)

Female.—*Body color:* entire body including legs honey yellow, flagellum gradually turning brown apically, wing veins light brown, stigma and vein C+Sc+R yellow. *Body length:* 5–6 mm; fore wing length, 5–6 mm. *Head:* 38 antennomeres, first flagellomere slightly longer than second, all flagellomeres longer than wide; malar space slightly longer than basal width of mandible and ⅓ eye height; temple ½ eye width; occipital carina meeting hypostomal



Figs. 5–8. Morphology of *Aleiodes* species. 5, Pronotum, lateral view, *A. angustipennis*. 6, Metasoma, lateral view, *A. palmatus*. 7, Metasoma, dorsal view, *A. lissos*. 8, First metasomal tergum, dorsal view, *A. palmatus*.

carina; oral space small and circular, width slightly less than malar space and about ½ face height; clypeus swollen; ocelli moderate size, ocellocular distance equal to diameter of lateral ocellus; face coriaceous with few rugae below antennae, median ridge between antennal sockets; frons coriaceous, rugose behind antennae; vertex and temples coriaceous; maxillary palpus not swollen; mandibles small. *Mesosoma:* pronotum coriaceous, weakly rugose medially; mesonotum and scutellum coriaceous; notauli scrobiculate, meeting in wide rugose area; prescutellar furrow wide, with one cross carina; mesopleuron finely coriaceous, subalar sulcus weakly rugose; sternaulus absent; propodeum coriaceous, with only short median carina at base. *Legs:* tarsal claws not pectinate but with 3–4 large spines at base; inner spur of hind tibia ⅓ length of hind basitarsus; hind coxa coriaceous dorsally. *Wings* (Fig. 3): fore wing with vein r ½ length of 3RSa and ⅔ length of m-cu, vein 1cu-a beyond 1M by 1.5 times length of 1cu-a, vein 1CUa slightly less than ½ 1CUb; hind wing with vein RS very slightly arched in middle, marginal cell narrowest in middle, vein M+CU slightly longer than 1M, vein m-cu weak. *Metasoma* (Fig. 7): all terga very finely coriaceous and shining; first tergum slightly wider at apex than length; median carina absent on all terga; ovipositor about ⅔ length of hind basitarsus.

Male.—Essentially as in female.

Holotype.—Female: CALIFORNIA, Monterey Co., Monterey Peninsula, August 9, 1978, C. P. Ohmart coll., reared from *Halisidota consobrina*? Deposited in USNM.

Paratypes.—CALIFORNIA: 1 ♀, 1 ♂, same data as holotype; 1 ♀, Berkeley, April 20, 1935; 1 ♂, Marin Co., parasitic on larva of *Halisidota harrisii* (label not clear on species name); 1 ♀, 4 mi. W. Stanton Ran. HQ, Sta. Cruz Is., September 14, 1964, M. Irwin; 1 ♂, Monterey, August 10, 1938, R. I. Sailer. COLORADO: 1 ♀, Davenport Camp, 36 mi. S. Florence, Custer Co., July 8, 1967, 8500 ft., F., P. & M. Rindge. NEW MEXICO: 1 ♀, 14 mi. N Silver City, Grant Co., July 8, 1961, G. C. Eickwort. ARIZONA: 1 ♀, Mt. Lemmon, 36 mi. N Tucson, 4300 ft., July 30, 1965, P. H. Freytag, L. P. Gibson collectors, blacklight trap. Deposited in USNM, RMSEL, MSU, CUI, UCR, UK.

Distribution.—Known only from California, Arizona, New Mexico, and Colorado.

Biology.—Three specimens of the type series are labeled as questionably reared from "*Halisidota consobrina*" and one from *Halysidota harrisii* Walsh (Arctiidae).

Comments.—This species is distinguished from all other North American species by the nearly smooth body, particularly the metasoma.

Etymology.—The specific name is from the Greek *lissos* meaning smooth in reference to the smooth metasomal terga.

ALEIODES PROCERUS SPECIES-GROUP

Included species.—*A. procerus* Wesmael, 1838 (Europe, Japan); *A. narangae* (Rohwer 1934), **new combination** (China); *A. granulatus* (De Gant 1936), **new combination** (North America); *A. crassipes* Telenga, 1969 (Mongolia); *A. angustipennis* new species.

Diagnostic characters.—Pronotum (Fig. 5) with median length greater than ocell-ocular distance; fore wings narrow, width about ⅕ length (Fig. 4); fourth metasomal tergum sculptured.

Comments.—The *procerus* species-group will run to the *dispar* species-group in the key to species-groups in S. Shaw et al. (1997). Subsequent to the publishing of that key, Fortier (1997) and Fortier and S. Shaw (1999) split the *procerus* group from the *dispar* group, and we have followed that system. The *procerus* species-group is distinguished by the long pronotum, the sculptured fourth metasomal tergum, and the narrow wings.

KEY TO THE NORTH AMERICAN SPECIES OF THE *PROCERUS* SPECIES-GROUP

1. Fore wing vein 1cu-a beyond 1M by distance less than length of 1cu-a, vein 1CUa shorter than 1cu-a; head, propleuron and apical metasomal terga black, rest of body usually orange . . . . *granulatus* (DeGant)

– Fore wing vein 1cu-a beyond 1M by distance equal to or greater than length of 1cu-a, vein 1CUa longer than 1cu-a; body entirely honey yellow . . . . *angustipennis*, new species

Aleiodes angustipennis Marsh and Shaw, new species

(Figs. 4, 5)

Female.—*Body color:* entirely honey yellow, coxae, trochanters and base of femora lighter yellow, apical ⅓ of flagellum brown; wings slightly fuscous, veins brown, stigma and vein C+Sc+R yellow. *Body length:* 7.0 mm; fore wing length, 4.5 mm. *Head:* eyes and ocelli small, not covering most of head; 49–50 antennomeres, all flagellomeres longer than wide; malar space long, longer than basal width of mandible and ⅔ eye height; temple broad, about ¾ eye width; occipital carina complete, meeting hypostomal carina; oral opening small and circular, diameter about equal to basal width of mandible and ⅖ face height; ocelli small, diameter of lateral ocellus 2/3 ocellocular distance; head entirely coriaceous; maxillary palpus not swollen; mandibles small, tips not crossing when closed. *Mesosoma:* pronotum (Fig. 5) distinctly lengthened, median length about twice ocellocular distance and length of first flagellomere, nearly on same plane as slightly declivous mesonotum, costate coriaceous; mesonotum and scutellum coriaceous, notauli weakly scrobiculate, meeting in shallow rugose area; mesopleuron coriaceous, subalar sulcus shallow and weakly costate, sternaulus weakly indicated by costate area; propodeum flat and not declivous apically, entirely costate coriaceous, median carina weak but complete. *Legs:* tarsal claws not pectinate; hind coxa coriaceous dorsally. *Wings* (Fig. 4): narrow, width of fore wing about ⅕ length; fore wing with vein r ⅓ length of 3RSa and ⅔ length of m-cu, vein 1cu-a beyond 1M by distance slight greater than length of 1cu-a, vein 1CUa ¼ length of 1CUb; hind wing with vein RS slightly sinuate, marginal cell narrowest in middle, vein 1r-m about ½ length of 1M, vein 1M ⅗ length of M+CU, vein m-cu absent. *Metasoma:* first tergum costate coriaceous, longer than apical width, median carina complete; terga 2–4 costate coriaceous, median carina complete on terga 2 and 3; remainder of terga finely coriaceous; ovipositor about ⅔ length of hind basitarsus.

Male.—Essentially as in female.

Holotype.—Female: FLORIDA, Marion Co., 9 mi SSW Ocala, Kings Land Country Estates, September 10–19, 1975, J. Wiley. Deposited in FSCA.

Paratypes.—FLORIDA: 1 ♀, Putnam Co., 2 mi NW Orange Springs, August 27–September 10, 1975, J. Wiley, Malaise trap; 1 ♀, Gainesville, Alachua Co., July 2, 1976, W. H. Pierce; 1 ♀, Highlands Co., Archbold Biol. Sta., April 4, 1979, H. V. Weems, Jr. and Sylvia Halkin, insect flight trap; 1 ♂, Suwannee Co., Houston, April 28, 1924, T. H. Hubbell. Deposited in RMSEL, UCD, FSCA, USNM.

Distribution.—Known only from the type localities in Florida.

Biology.—Unknown.

Comments.—This species looks somewhat similar to *A. aciculatus* Cresson (in the *coxalis* species-group) because of the costate metasoma and the lengthened pronotum, but it is distinct from *aciculatus* by its narrow wings, longer pronotum and entirely yellow stigma. It is distinguished from *granulatus* by fore wing vein 1cu-a being farther from vein 1M and by the entirely honey yellow body.

Etymology.—The specific name is from the Latin *angustus* meaning narrow and *penna* meaning wing in reference to the narrow wings.

Aleiodes granulatus (DeGant), **new combination**

Rogas granulata DeGant 1930: 163–164.

Diagnosis.—Body bicolored, head black, antenna and mouth parts yellow, mesosoma sometimes entirely black, pronotum and mesonotum always black, mesopleuron and propodeum sometimes orange, metasoma with first tergum orange or black, second and third terga orange, remainder of terga black, legs orange, apical half of hind femur and tibia black, wings hyaline, veins brown, stigma bicolored brown with yellow at apex and base; body length 4.5 mm; 45–50 antennomeres; malar space longer than basal width of mandible; head entirely coriaceous, face somewhat rugose; oral opening small and circular, diameter slightly less than basal width of mandible; ocelli small, diameter of lateral ocellus less than ocellocular distance; pronotum rugose coriaceous; mesonotum coriaceous; mesopleuron coriaceous, sternaulus absent; propodeum rugose coriaceous, median carina complete; metasomal terga 1–4 costate, median carina complete on terga 1–3; tarsal claws not pectinate; fore wing with vein 1cu-a beyond vein 1M by distance less than length of 1cu-a; hind wing with vein RS arcuate, marginal cell narrowest medially.

Type material examined.—*Rogas granulata* DeGant, holotype female, Cleveland, Ohio [USNM].

Distribution.—Michigan, Wisconsin, Ohio, Connecticut, New York, North Carolina, Ontario, New Brunswick.

Biology.—Associated with cabbage infested with "*Autographa brassicae*," (probably *Trichoplusia ni* (Hübner) (Noctuidae)).

Comments.—*Aleiodes granulatus* is not a particularly common species, considering that its presumed host is a pest of cabbages. This species is apparently closely related to *angustipennis* but differs by fore wing vein 1cu-a being closer to vein 1M and by the bicolored black and orange body.

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PODIOMITRA, A NEW GENUS OF HOMALOMITRINAE (DIPTERA: SPHAEROCERIDAE) FROM COSTA RICA

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Abstract.—***Podiomitra ostracotarsata*, new genus and species**, is described in the rare and poorly known subfamily Homalomitrinae (Sphaeroceridae). This fully-winged, but apparently flightless, species was collected in a Malaise trap in Costa Rica, probably in association with a winged army ant.

Key Words: Sphaeroceridae, Homalomitrinae, amy ants, *Podiomitra*

The subfamily Homalomitrinae was described by Roháček and Marshall (1998) for a group of five extremely rare, bizarre-looking species with reduced wing venation, an enlarged and flattened head, no ocelli, reduced chaetotaxy, and greatly enlarged legs with all tarsomeres swollen and with the apical tarsomere deeply excavated. We here report the discovery of yet another highly distinctive genus in this enigmatic, isolated subfamily.

Podiomitra Marshall and Roháček, new genus

Type species.—*Podiomitra ostracotarsata* Marshall and Roháček, new species.

Generic diagnosis.—The following characters distinguish *Podiomitra* from other homalomitrines: Antennae (Figs. 5, 6) distinctly separated, scape small, pedicel markedly tapered basally. Frons strongly differentiated into a prominent anterior portion and a medially flat upper portion (Fig. 5). Prosternum with setulae. Mesoscutum short, with only small setulae other than prescutellar dorsocentral setae; scutellum with 2 pairs of marginal scutellar setae (and a pair of minute setulae on disc), the apical pair long (Fig. 5). Anepisternum with only uniformly small setulae, katepisternal setae also reduced. Metapleuron with a single seta between base of halter and hind coxa (Fig. 1). Wings (Figs. 3, 4) with no venation beyond basal fifth; venation in basal fifth relatively complete but all veins very shortened (including C and R veins); cell br absent; M basally weakly sclerotized and fused to R4+5, apically tapered and reduced to fold beyond dm-cu; cell dm short, with rounded posterior apical corner; cross-vein r-m fused to basal part of M. Legs stout and long (Fig. 1), distal tarsomeres distally divided into anterior and posterior valves, claws arising in a dorsal position deep between the valves (Fig. 2). Abdomen with poorly sclerotized terga and sterna, and with very long and dense setae on terga, sterna and wrinkled pleural membrane (Figs. 8, 9). T7 expanded onto ventral side, posteriorly tapered, with a number of cup-like sensilla at anterior margin; S7 narrow; T8 and S8 short, the former transverse, the later posteromedially incised, both covered by micropubescence.

Etymology.—The generic name *Podiomitra* refers to the podium like frons.

Podiomitra ostracotarsata Marshall and Roháček, new species

(Figs. 1–9)

Species diagnosis.—Head brown, body otherwise pale yellow. Head as broad as thorax, lower frons strongly elevated and projecting anteriorly, upper frons depressed, broad and flat, ocellar triangle absent. Palpus barely visible in type, but apparently well developed and setose. Mesoscutum with uniformly small setulae except for a pair of posterior dorsocentral setae lying flat against upper surface of scutellum. Abdomen long-setose. Wing veins compressed into basal fifth of wing but relatively complete, R4+5 and costa forming a loop, r-m reduced, and dm-cu present. Costagial seta absent, but costa densely setose, distal setae conspicuously long.

Description.—*Holotype female:* Body length 1.6 mm. Body and legs pale, head brown. Head (Figs. 5, 6) as broad as thorax, frons and upper part of face strongly projecting anteriorly; eye restricted to posterior half of head, with relatively few (about 70), large facets, finely setulose. Gena broad, flat on lower half, with two, thin subequal setae on vibrissal angle. Postgena with expanded posteroventral corner (Fig. 1). Epistoma large but not depressed or delineated by a shelf. Antennae narrowly but distinctly separated, scape short but almost contiguous and apparently fused with intervening lunule (Fig. 6); pedicel very narrow basally; first flagellomere densely long setulose distally; arista long haired, white, slightly longer than head width. Frons (Fig. 5) with narrow, densely setulose orbital strips; a broad, flat upper frons surrounded by a silvery micropubescent stripe; and a prominent, shelflike lower frons with 6–7 small, inclinate interfrontal setae and a flat, densely microsetulose upper surface. Upper back of head setulose, outer vertical setae slightly longer than surrounding setulae, other setae indistinguishable. Ocelli and ocellar triangle absent.

Prosternum membranous, with four small setae. Mesoscutum (Fig. 5) with small setulae, uniformly distributed laterally and posteriorly, medially mainly restricted to 3 darker pigmented longitudinal stripes, and with a single pair of dorsocentral setae lying flat over the scutellum. Scutellum with large apical setae, minute lateral setae and a single pair of small discal setae. Anepisternum (Fig. 1) with only small setulae but densely setulose on anterior half; metapleuron with a single seta between base of halter and base of leg. Wing (Figs. 3, 4) with C restricted to basal fifth of wing. C (especially distally) and terminal portion of R1 with long setae. Sc almost invisible; R2+3 and R4+5 very short; R4+5 curved back to join costa in a continuous loop bisected by R2+3. Cell br absent (reduced because M is basally closely attached or fused to R4+5) and M apically tapered and reduced to foldlike structure beyond dm-cu; cell dm distinct though short, with rounded posterior outer corner; crossvein r-m attached to M, dm-cu and CuA1 distinct; A1 short, basally darkly pigmented, apically tapered. Anterior margin of wing beyond costa somewhat secondarily thickened and finely pubescent in contrast to posterior margin, which has a fringe of long hairs. Alula reduced, inconspicuous. Halter long, white; knob very large (collapsed and flat on type).

Legs (Fig. 1) long and thick, not flattened, uniformly covered with short setulae, only mid tibia with a small apicoventral bristle; all tarsomeres thickened, first, second and fifth tarsomeres of hind leg equal in length, third and fourth shorter and each with a small, dark microsetulose patch apicoventrally; apex of all tarsi valvelike, claws displaced to dorsal position and inserted between lateral valves, pulvulli facing each other within valvelike tarsal apex (Fig. 2).

Abdomen with very weakly sclerotized terga and sterna, all whitish yellow, densely and long setose, with longest setae inserted on darkened patches (Figs. 8, 9). T1+2 long but dorsomedially basally desclero-

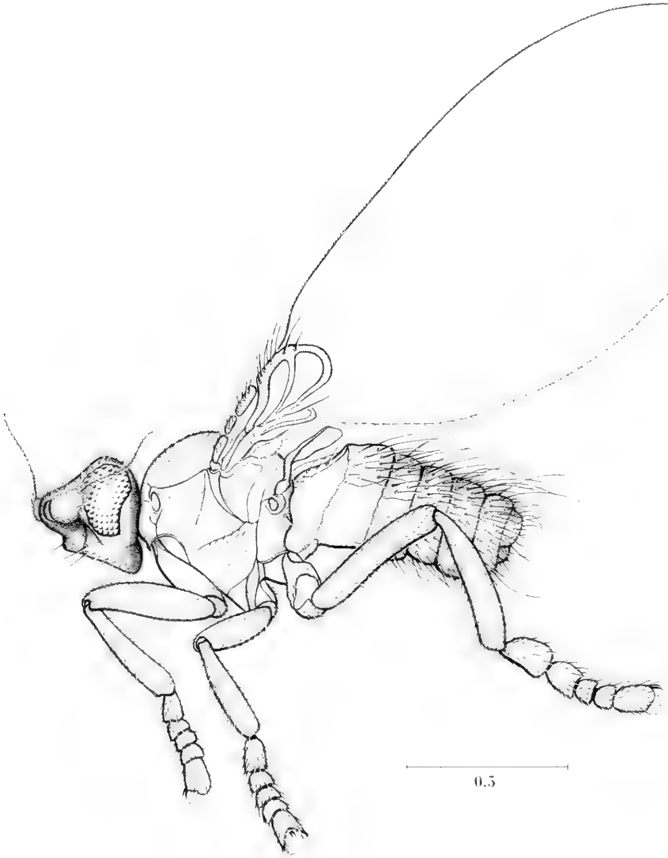
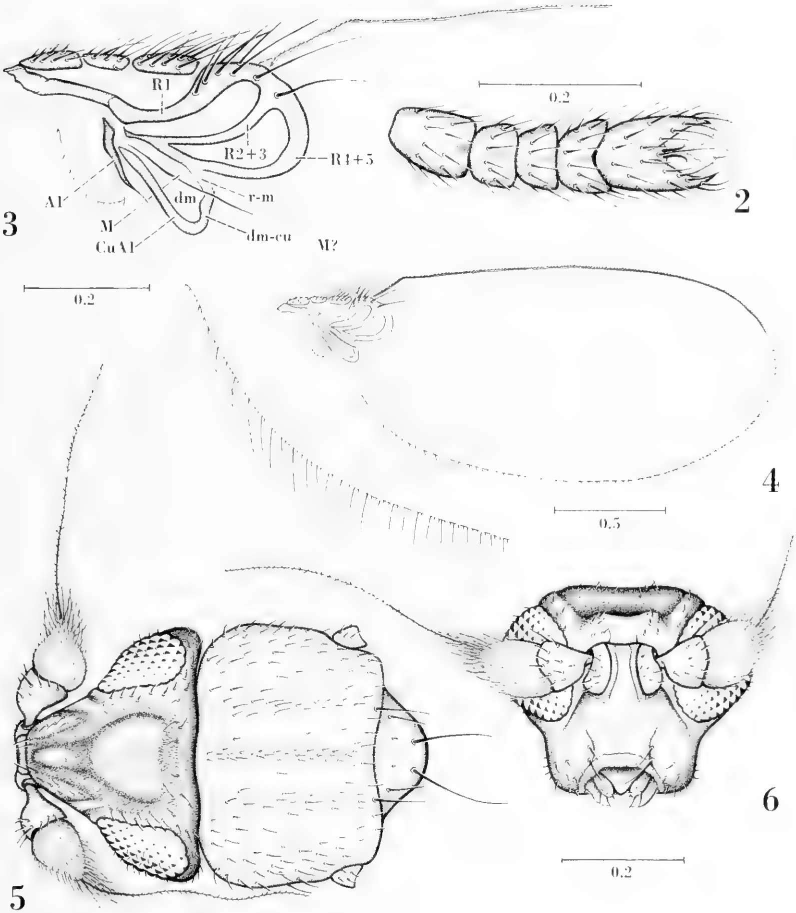


Fig. 1. *Podiomitra ostracotarsata*, female holotype. Wing reconstructed according to slide mounted right wing. Scale bar = 0.5 mm.

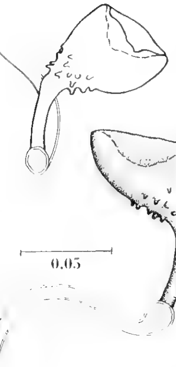
tized and with setae concentrated along posterior margin. T3–T6 slightly transverse, with very long setae, particularly at posterior margin; long dense setae also inserted on wrinkled dilatable pleural membrane. S2–S6 narrower than associated terga, about as long as broad, with long setae at lateral margins, medial setae short (Fig. 9).

Postabdomen (Figs 8, 9). T6 and S6 similar to those of preceding segment, including chaetotaxy. T7 dissimilar to all other homalomitrines, large, expanded lateroventrally forming an incomplete posteriorly conical ring, with long setae inserted in the middle of lateral margins and with peculiar dish-shaped sensilla clustered at anterior margin. S7 rounded trapezoidal, as broad as S6, with 2 pairs of long setae posteriorly.



Figs. 2–6. *Podiomitra ostracotarsata,* female holotype. 2, Mid tarsus dorsally. 3, Detail of wing venation. 4, Right wing. 5, Head and Mesoscutum dorsally. 6, Head frontally. Scale bars: Fig. 4 = 0.5 mm, others = 0.2 mm. Abbreviations: A1—anal vein, CuA1—cubitus, dm—discal medial cell, dm-cu—discal medial-cubital (= posterior) cross-vein, M—media, R1, R2+3, R4+5—1st, 2nd, 3rd branch of radius; r-m—radial-medial cross-vein.

T8 short, transverse, with small anteromedial incision and moderate setae at posterior margin; completely micropubescent as is posterior half of T7. S8 narrower than T8, with distinct posteromedial incision, hence posterior margin bilobate, all micropubescent, with fine setae posterolaterally. Spermathecae (Fig. 7) 1+1 blackish, with cup-



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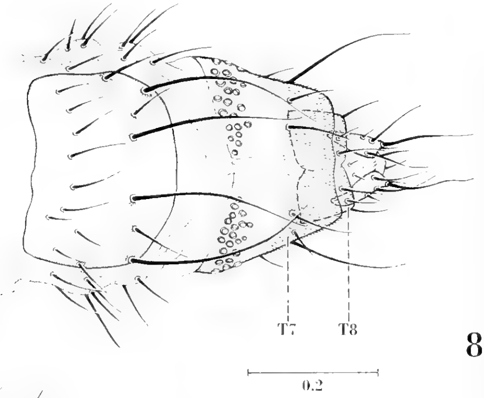

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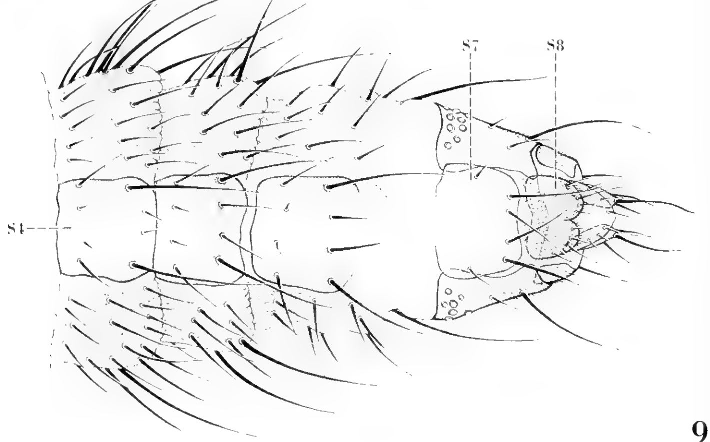

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Figs. 7–9. *Podiomitra ostracotarsata*, female holotype. 7, Spermathecae. 8, Postabdomen dorsally. 9, postabdomen (plus abdominal segments 4–5) ventrally. Scale bars: Fig. 7 = 0.05 mm, others = 0.2 mm. Abbreviations: T—tergum, S—sternum.

like body proximally covered by a number of tubercles and completely fused (no boundary visible) with sclerotized part of spermathecal duct (as in *Sphaeromitra*). T10 subtriangular, almost unpigmented, bare except for a pair of small medial setae. S10 larger than T10, subcircular, with short marginal setae, the posteromedial pair longest. Cercus (like T10 and S10) without micropubescence, with long, moderately sinuate apical, dorsopreapical and lateral preapical setae (Fig. 8).

Type material.—Holotype ♀: COSTA RICA, Prov. Cartago, La Represa, Torre del I.C.E., entre Porras y Villegas. [hydro-electric tower between Porras and Villegas] 1800m. ABR 1997. R. Delgado. Malaise L_N_186150_560100. INBio collection

#46783. Left wing with broken apical half, right (complete) wing removed and mounted on a microslide pinned below specimen. Abdomen detached, cleared and put in tube with glycerine also pinned below specimen. An unidentified mite is attached between the thorax and the ventral side of the abdomen.

Etymology.—The specific epithet *ostracotarsata* refers to the shell-like formation of the tarsal apex.

Relationships.—Although there is no doubt about the inclusion of *Podiomitra ostracotarsata* in the Homalomitrinae, it is not obviously more closely related to either one of the described genera in the subfamily, nor do the other two genera form a well-supported clade excluding *Podiomitra.*

Podiomitra ostracotarsata superficially resembles *Sphaeromitra* Roháček and Marshall in the size and shape of the eye, the short scape, and the extremely reduced wing venation, but only one of the eight putative synapomorphies listed by Roháček and Marshall (1998) for the genus *Sphaeromitra* (reduction of mesonotal chaetotaxy) could apply to *Podiomitra,* and this character differs in detail between the two genera. *Sphaeromitra* has only small setulae on both the scutum and scutellum; *Podiomitra* has distinct prescutellar dorsocentral setae and well-developed scutellar setae. Other possible synapomorphies of *Sphaeromitra* and *Podiomitra* include the postgena with expanded posteroventral corner, discal scutellar setulae (although there is only 1 pair in *Podiomitra*), shortened R2+3, and female abdominal sternite 7 smaller than tergite 7.

Podiomitra is superficially very different from *Homalomitra* Morgués-Schurter in wing development, head shape and chaetotaxy, but both genera share the plesiomorphic retention of crossvein dm-cu. Of the eight putative generic apomorphies listed by Roháček and Marshall (1998) for *Homalomitra,* two might be shared with *Podiomitra.* Both genera have a long fringe of fine setae along the posterior margin of the hind wing, and both genera have the antennae narrowly separated. The latter character, however, is more marked in *Homalomitra* and is accentuated by the greatly enlarged scape, as a result of which the *Homalomitra* looks very different from the other genera.

Possible synapomorphies linking the other homalomitrine genera (*Sphaeromitra* and *Homalomitra*) to the exclusion of *Podiomitra* include the strongly flattened legs and enlarged scape.

Although more putative synapomorphies (5) support a sister group relationship between *Sphaeromitra* and *Podiomitra* than other resolutions to this three taxon set (2 synapomorphies per alternative clade), some of the characters are of uncertain homology and polarity, and more material including male specimens is needed to resolve the generic relationships of the Homalomitrinae.

Discussion.—This remarkable subfamily is known from a very few specimens collected at scattered localities from throughout the Neotropical Region. Although most specimens are from Malaise traps, the modified legs, reduced thorax, and weakened wings of *Sphaeromitra* and *Homalomitra* led Roháček and Marshall (1998) to speculate that they might get around by phoresy rather than flight. Some specimens have been collected in association with ecitonine ants, so our best guess is that homalomitrines develop in ant kitchen middens, and move from nest to nest by phoresy. The discovery of the new species described here, in which the wing is reduced to a thin, veinless membrane over its distal ⅘, further suggests that these flies are phoretic. All homalomitrines have a pocket or cleft at the apex of the tarsus, but this feature is especially conspicuous in *Podiomitra ostracotarsata,* in which the apex of the tarsus is split into anterior and posterior halves, each half lined by a pulvillus that has rotated 90 degrees from its usual position, one facing forward and one facing backward. The claws are reduced and in a dorsal position deep in the cleft. The apical structure of each tarsomere is thus clearly modified for grasping something between its valvelike halves.

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PHYLOGENY, HISTORICAL BIOGEOGRAPHY, AND MACROEVOLUTION OF HOST USE AMONG *DIASTROPHUS* GALL WASPS (HYMENOPTERA: CYNIPIDAE)

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Abstract.—Phylogenetic relationships among 14 species of 3 Holarctic gall wasp genera, *Diastrophus* Hartig, *Gonaspis* Ashmead, and *Xestophanes* Förster (Hymenoptera: Cynipidae: Cynipinae: Aylacini), are inferred from 43 adult morphological characters. The incorporation of four characters associated with gall morphology is explored, although only a single parsimony-informative gall character is obtained. All analyses retrieve *Diastrophus* as paraphyletic with respect to the monotypic genus *Gonaspis*. These two genera share several morphological synapomorphies as well as related host plant associations. The genus *Gonaspis* is thus a **new junior synonym** of *Diastrophus*, and *Gonaspis potentillae* is herein transferred to *Diastrophus* as *D. potentillae* Bassett. In addition, *D. kincaidii* var. *austrior* Kinsey is formally elevated to specific status, as *Diastrophus austrior* Kinsey (**new status**). Association of *Diastrophus* species with *Rubus*, as well as with woody host plants, could have originated once, but the possibility of more than one origination cannot be excluded. In either case, at least two reversal events have contributed to the patterns of association of *Diastrophus* with *Potentilla*, and with herbaceous host plants. Reconstruction of the historical biogeography of the group using a dispersal and vicariance analysis model suggests that the ancestor of *Diastrophus* was either East Nearctic (EN) or Holarctic. The two West Palearctic (WP) species resulted from either two independent dispersals from EN followed by subsequent vicariance, or from a basal vicariance between WP and EN and a subsequent dispersal from EN to WP followed by a subsequent vicariance between the two regions. The West Nearctic species resulted from dispersals from EN and are relatively recent.

Key Words: biogeography, *Diastrophus*, *Gonaspis*, host shifting, host plant growth form, morphology, phylogeny

Extant gall-forming members of the family Cynipidae (Hymenoptera) comprise five of the six tribes in the subfamily Cynipinae, i.e., Aylacini, Cynipini, Eschatocerini, Pediaspidini, and Diplolepidini (Ronquist 1999). All the cynipid tribes except Aylacini are apparently monophyletic and appear to have relatively conserved host plant associations with host plants usually belonging to a single genus or a few closely related genera (Liljeblad and Ronquist 1998). In contrast, the tribe Aylacini, comprising 21 genera, is apparently an assemblage of paraphyletic and polyphyletic clades (Ronquist 1994, Liljeblad and Ronquist 1998, Ronquist 1999), and its members use a wide range of host plants belonging to Apiaceae, Asteraceae, Brassicaceae, Lamiaceae, Papaveraceae, Rosaceae, and Valerianaceae (Liljeblad and Ronquist 1998, Ronquist and Liljeblad 2001).

According to Liljeblad and Ronquist (1998), all cynipid wasps inducing galls on woody rosid plants form a monophyletic clade. These rosid gallers include the tribes of Diplolepidini inducing galls on *Rosa* (Rosaceae), Eschatocerini on *Acacia* and *Prosopis* (Fabaceae), Pediaspidini on *Acer* (Aceraceae), and the species-rich Cynipini primarily on *Quercus* (Liljeblad and Ronquist 1998, Ronquist 1999). Ronquist and Liljeblad (2001) explored various aspects of the host plant association of cynipid wasps on basis of the aforementioned phylogeny and concluded that cynipid gall wasps are 'extremely conservative' in their association with plant growth form. They further suggested that the gall wasp ancestor is likely to have been an herb galler, and colonization of woody hosts has occurred only three times, assuming that all the eight *Rubus*-galling species of *Diastrophus* Hartig form a monophyletic clade.

The genus *Diastrophus* is rather unusual among cynipid gall wasps in two aspects of their host plant associations. Firstly, *Diastrophus*, as well as *Gonaspis* Ashmead and *Xestophanes* Förster, is associated with rosaceous hosts of the genera *Rubus*, *Potentilla*, and *Fragaria* (with one species, *Diastrophus smilacis* Ashmead inducing galls on the monocotyledonous *Smilax* [Smilacaceae]), in contrast to the other Aylacini genera which induce galls on relatively advanced herbaceous host plants (Ronquist 1994). Secondly, host plants of the genus include both woody (*Rubus* and *Smilax*) and herbaceous (*Potentilla* and *Fragaria*) plants, a deviation from the generally very conservative pattern of association with plant growth form in Cynipidae. Therefore, the evolution of host plant associations in *Diastrophus* could shed light on the evolution of host use in Cynipidae in general.

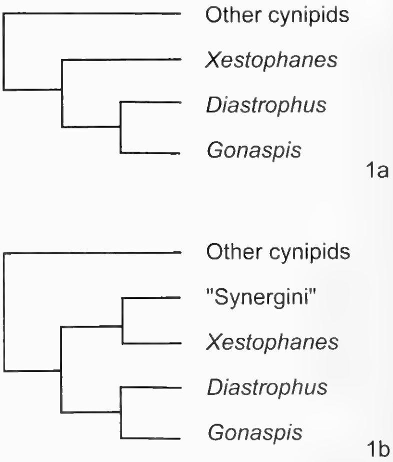

Fig. 1. Phylogenetic relationship among *Diastrophus*, *Gonaspis*, and *Xestophanes*, (a) as suggested by Nieves-Aldrey (1994), (b) as suggested by Liljeblad and Ronquist (1998).

Nieves-Aldrey (1994) suggested that *Diastrophus*, *Gonaspis*, and *Xestophanes* form a monophyletic clade (Fig. 1a) on the basis of their rosaceous host associations, and the presence of lobed claws and glabrous sculpture on the vertex and mesothorax (Figs. 2a–c). On the basis of phylogenetic analysis using morphological characters, Liljeblad and Ronquist (1998) partially supported this view, but suggested that *Xestophanes* and the inquilinous tribe Synergini form the sister clade of (*Diastrophus*+*Gonaspis*) (Fig. 1b). Recent molecular work (Liu et al. unpublished data) supports the view of Nieves-Aldrey (1994).

Diastrophus is morphologically distinct among Aylacini genera by the combination of strongly lobed claws, subcosta and radius reaching to anterior margin of wing; and completely free third and fourth abdominal terga in both sexes (Fig. 2d, cf. *Xestophanes potentillae* De Villers, Fig. 2e) (Nieves-

Aldrey 1994), and thus obviously monophyletic. It is not clear whether *Gonaspis*, which comprises only one known species, should be included within *Diastrophus* or is indeed a sister clade of *Diastrophus*. Ronquist (1994) and Liljeblad and Ronquist (1998) listed five synapomorphies for *Diastrophus+Gonaspis*. However, these studies, for their respective purposes, each included only one *Diastrophus* species and were not able to clarify the relationship among *Gonaspis* and *Diastrophus* species. In fact, only a single morphological feature separates the monotypic *Gonaspis* from *Diastrophus*: the scutellum of *Gonaspis* conspicuously projected posteriorly (Fig. 2f). This is an autapomorphic character, for which an intermediate form exists in *D. cuscutaeformis* Osten Sacken (not illustrated).

Biologically, the members of *Diastrophus*, as well as those of *Gonaspis* and *Xestophanes*, are univoltine and lack the alternation of generations (heterogony) found in the more derived oak-galling cynipids. Like galls induced by other wasps of the tribe Aylacini, their galls are mostly simple swellings on stems, leaves, and roots, and lack complicated secondary external structures. Cynipid wasps lumped in the tribe Aylacini invariably make galls not detachable from the host plant. This is also true for *Gonaspis*, *Xestophanes*, and most species of *Diastrophus*, regardless of host form, i.e., woody versus herbaceous. Only one species of *Diastrophus*, *D. cuscutaeformis*, makes detachable galls, as do some Cynipini gallers of woody plants. In addition, some members of *Diastrophus* associated with woody *Rubus* bushes are attacked by inquilines of the cynipid genus *Synophromorpha* Ashmead. Inquilines of cynipid gall wasps do not induce galls of their own, but instead live in and feed on galls induced by the other cynipid wasps. Only galls on woody host plants are known to be attacked by inquilines.

While *Gonaspis* is a monotypic genus endemic to the Nearctic and *Xestophanes* includes only two species from the West Palearctic, the genus *Diastrophus* (Hymenoptera: Cynipidae: Aylacini) comprises sixteen described species distributed throughout the Holarctic. Known species of *Diastrophus* include two from the West Palearctic (*D. mayri* Reinhard 1877 and *D. rubi* [Bouché 1834]) and one undescribed species from Japan in the East Palearctic identified on the basis of the presence of *Diastrophus* galls and rearing of the host-specific *Synophromorpha* Ashmead inquilines from these galls (Abe 1998, Abe personal communication); one described nominate subspecies (*D. k. kincaidii* Gillette 1893) and its heteronomic subspecies (*D. kincaidii austrior* Kinsey 1922) from the West Nearctic; and twelve East Nearctic species (*D. bassetti* Beutenmüller 1892, *D. cuscutaeformis* Osten Sacken 1863, *D. fragariae* Beutenmüller 1915, *D. fusiformans* Ashmead 1890, *D. minimus* Bassett 1900, *D. nebulosus* (Osten Sacken 1861), *D. niger* Bassett 1900, *D. piceus* Provancher 1886, *D. radicum* Bassett 1870, *D. smilacis* Ashmead 1896, *D. tumefactus* Kinsey 1920, and *D. turgidus* Bassett 1870). The two European species of *Diastrophus* Hartig 1840 (Hymenoptera: Cynipidae) were recently reviewed (Nieves-Aldrey 1994). However, there has been no revisionary study of the Nearctic species of this genus since Beuttenmueller (1909), although Burks (1979) compiled a list of all Nearctic species of the genus. Moreover, phylogenetic relationships among the *Diastrophus* species are not known and a phylogeny-based systematic revision has never been attempted.

Therefore, our goals of the present study are to reconstruct the phylogenetic relationships among *Diastrophus* species and *Gonaspis*, based on adult morphology, and use the resulting cladogram to examine (1) the macroevolution of associations between wasps and their host plants and test the hypothetical monophyletic shifting from herbaceous host plants to the woody *Rubus* host plants, (2) the historical biogeography of the genus, and (3) the phylogenetic position of *Gonaspis potentillae* in relation to

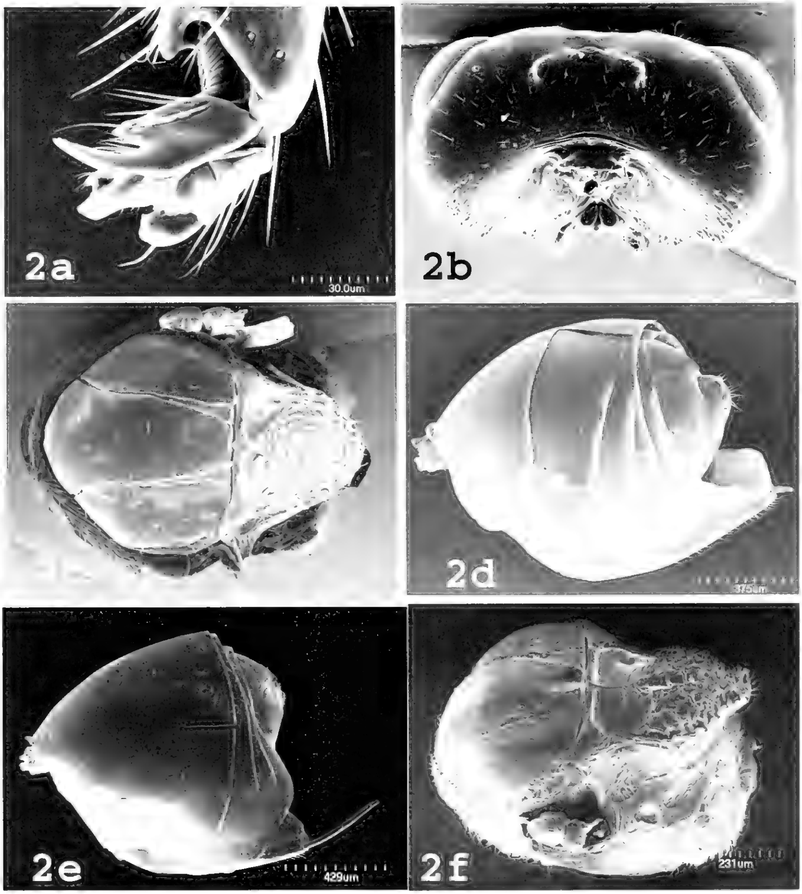

Fig. 2. *Diastrophus* and *Xestophanes* species. (a) hind claw of *D. nebulosus*; (b) head of *D. nebulosus*; (c) mesonotum of *D. nebulosus*; (d) metasoma of *D. nebulosus*; (e) metasoma of *X. potentillae*; (f) mesosoma of *D. potentillae*

Diastrophus species, testing the phylogenetic independence of the monotypic genus *Gonaspis*, as discussed by Liljeblad and Ronquist (1998).

Materials and Methods

Type specimens of 14 of the Nearctic species and the subspecies were examined, along with additional specimens compared to types for Nearctic and Palearctic species. The undescribed Japanese species is not included in the analysis because no specimens of this species were reared. *Diastrophus piceus* is also excluded from the study because the only reported material of this species is its type, which we were unable

Table 1. Taxa included in the study, their distribution and host plants. EN = East Nearctic, WN = West Nearctic, NA = Nearctic, and WP = West Palearctic. The undescribed species of *Diastrophus* from Japan, reported on basis of presence of galls, is not included in the analysis. The eastern Canadian species, *D. piceus* Provancher 1886, is not included in the study because we were unable to locate the type. References listed are in addition to original references to each species, of which all have been consulted.

Taxa	Distribution	Host Plant	References
Diastrophus austrior	WN	*Rubus*	Burks (1979)
D. bassetti	EN	*Rubus*	Burks (1979)
D. cuscutaeformis	EN	*Rubus*	Burks (1979)
D. frageriae	EN	*Fragaria virginiana*	Burks (1979)
D. fusiformans	NA	*Potentilla*	Burks (1979)
D. kincaidii	WN	*Rubus parsiflorus*	Burks (1979)
D. mayri	WP	*Potentilla argentea*	Nieves-Aldrey (1994)
D. minimus	EN	*Potentilla canadensis*	Burks (1979)
D. nebulosus	EN	*Rubus*	Burks (1979)
D. niger	EN	*Potentilla canadensis*	Burks (1979)
D. radicum	NA (mainly EN)	*Rubus occidentalis*	Burks (1979)
D. rubi	WP	*Rubus*	Nieves-Aldrey (1994)
D. smilacis	EN	*Smilax*	Burks (1979)
D. tumefactus	EN	*Potentilla*	Burks (1979)
D. turgidus	EN	*Rubus strigosus*	Burks (1979)
Gonaspis potentillae	EN	*Potentilla*	Weld (1950), Liu (field data)
Xestophanes potentillae	WP	*Potentilla*	Nieves-Aldrey (1994)

to examine. We also noted that Beutenmüller (1909) was unable to distinguish it from other *Diastrophus* species based on Provancher's original description and suggested that this might not be a valid species. The two subspecies of *D. kincaidii* were included as separate operational taxonomic unit. Loaned material included specimens from six institutions and three private collections. A total of 395 specimens were examined. Collections utilized for this study and the persons through whom the loans were kindly arranged are as follows:

AMNH	American Museum of Natural History, New York, NY, USA (J. Carpenter).
CASC	California Academy of Sciences, San Francisco, CA, USA (R. Zuparko).
CNCI	Canadian National Collection of Insects, Ottawa, ON, Canada (J. Huber).
EMEC	University of California, Berkeley, CA, USA (C. Barr).
FMNH	Field Museum of Natural History, Chicago, IL, USA (P. Goldstein).
MCZC	Museum of Comparative Zoology, Cambridge, MA, USA (P. Perkins).
UCDC	University of California, Davis, CA, USA (S. Heydon).
USNM	National Museum of Natural History, Smithsonian Institution, Washington, DC, USA (D. Smith).

Other specimen contributors are:

ZL	Zhiwei Liu
OP	Olivier Plantard
FR	Fredrik Ronquist.

Morphological characters for all species were examined and identified using a Leitz Wetzlar stereomicroscope. SEM images were obtained for *Gonaspis potentillae*, *Xestophanes potentillae*, and *Diastrophus nebulosus*, using Hitachi S4700 Field Emission Scanning Electron Microscope (FE-SEM) at the AMNH. Additional SEM images were also taken for *D. mayri*, *D. niger*, and *D. turgidus* using an Amray 1810 at the FMNH to assist character coding. Mounted specimens were first transferred to and kept in 70% ethanol for weeks, dissected in 70% ethanol, cleaned with kitchen ammonia, and washed in water and in a series of ethanol solutions of different concentration. Dissected body parts were then stored in 100% ethanol and air dried before being mounted to SEM stubs, and gold-coated.

Terminology for skeletal features follows Richards (1977), Ronquist and Nordlander (1989), and Ronquist (1995). Terminology describing surface sculptures follows Harris (1979). Phylogenetic relationships among the taxa were analyzed with gall morphology characters included and excluded, respectively, using parsimony algorithm as implemented in PAUP* version 4.0b8a (Swafford 2002). Heuristic search method was used with 5000 random addition sequence replicates, followed by tree bisection-reconnection branch swapping (other search options were default in PAUP). Calculations of Bremer support for each node (Bremer 1994) were programmed for batch processing using the same options as the tree searching procedure described above. All characters were unordered and unweighted.

Associations with host plant genera were investigated by optimization onto the resulting two best trees *a posteriori* using MacClade version 4.03 (Maddison and Maddison 2001). The number of host plant colonization events was evaluated assuming an ACCTRAN optimization. We evaluated the degree to which host associations were phylogenetically conserved by calculating their unit consistency indices.

Historical biogeography was reconstructed by using DIVA Version 1.2 (Ronquist 2001) according to the dispersal-vicariance optimization method proposed by Ronquist (1997). Dispersal-vicariance analysis reconstructs the ancestral distribution in a given phylogeny without any prior assumptions about the form of area relationships. Speciation is assumed to subdivide the ranges of widespread species into vicariant components; the optimal ancestral distributions are those that minimize the number of implied dispersal and extinction events (Ronquist 1997). The DIVA method differs from cladistic biogeography in that it allows nonhierarchical area relationships, and is therefore particularly useful when reconstructing the distribution history of groups occurring in areas that have a reticulate palaeogeographic history, such as the Northern Hemisphere (Nordlander et al. 1996 and references therein).

RESULTS

Character analysis.—We identified 43 morphological characters of adult wasps, and four characters of gall morphology (Appendix). Characters 8, 36, 42, and 45–47 were autapomorphic and thus parsimony-uninformative. They were excluded from analysis, but included in the matrix for reference purposes.

Cladistic analyses.—Parsimony analysis of all characters resulted in two equally most parsimonious trees (Length = 167; CI = 0.36; RI = 0.44; Figs. 3a, 3b). The strict consensus tree is shown in Fig. 4. Excluding the single parsimony-informative gall character resulted in the same two most parsimonious trees with no change in tree topologies, and only slight difference in tree statistics (Length = 165, CI = 0.36, RI = 0.44). Inclusion of gall morphology in analysis resulted in better, though slight, support for three internodes (noticeably two basal internodes) of the best trees (Fig. 4). The two most parsimonious trees differ only in the positions of *D. mayri* and *D. cuscutaeformis*.

As is shown in the strict consensus tree, the phylogenetic relationship among the *Diastrophus* species is mostly resolved. As we predicted, the monotypic genus *Gonaspis* is nested within *Diastrophus*. The relationship among *D. mayri, D. cuscutaeformis*, the clade (*D. rubi*, (*D. fragariae, D. tumefactus*)), and the rest of the genus at the base of the phylogenetic tree is not resolved. The two subspecies of *D. kincaidi*,

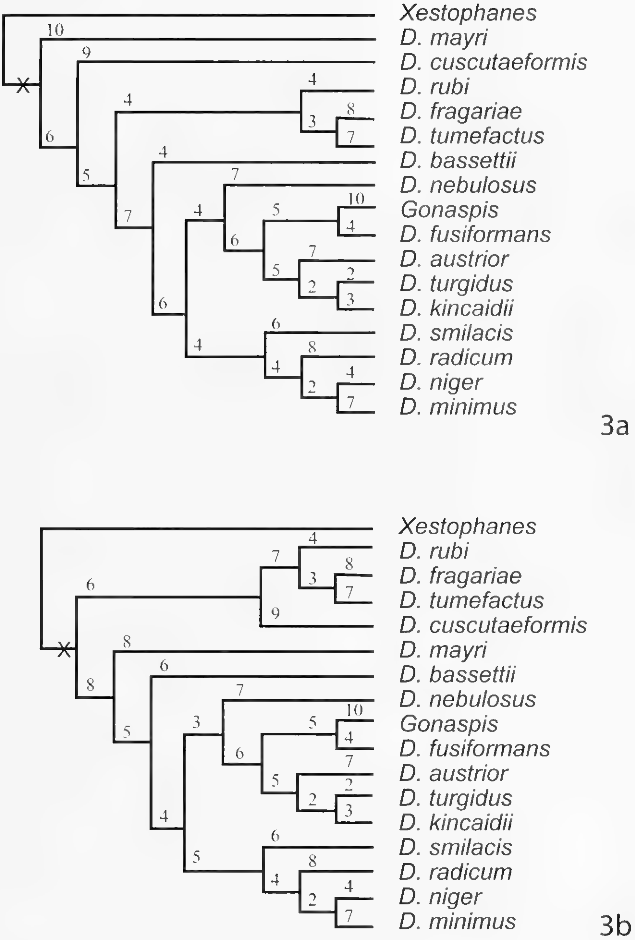

Fig. 3. Two equally most parsimonious trees for *Diastrophus*, *Gonaspis*, and *Xestophanes*, with the number of apomorphic character changes for each branch indicated (tree length = 167, CI = 0.36, RI = 0.44). Program for phylogenetic analysis was PAUP 4.0 (beta 10) (Swofford 2002). Six characters that are parsimony-uninformative were excluded from the analysis, but were included when calculating the number of apomorphic character changes on terminal internodes.

i.e., *D. k. kincaidi* and *D. k. austrior*, do not appear as sister species in the phylogeny, although they were shown to be closely related.

Optimization of host plant association onto tree #1 (Fig. 5a) requires 6 steps (CI = 0.50) to explain the current pattern. It suggests that the basal species of *Diastro-*

Table 2. Character matrix. Missing data and characters inapplicable to a particular taxon are represented by "-". Polymorphism is by letters "p" (=01), "q" (=02), and "x" (=12). Based on result of phylogenetic analysis, *Gonaspis* is treated in the present study as a synonym of *Diastrophus*, and thus *G. potentillae* = *D. potentillae*, *sensu lato*.

	Characters				
Taxa	1	10	21	31	41
Xestophanes	-011100001	0021110000	1-01211200	0101000011	1001001
'*Gonaspis*'	0001001111	1121021100	p111211211	2x01111121	0020000
D. austrior	1000120111	1111000100	01p1200000	100110x001	10x0001
D. bassettii	1001010110	0001010111	0101011111	0022102111	0021001
D. cuscutaeformis	0001110120	0011120000	00-2101121	11p110x000	0020011
D. frageriae	0110110100	0001020101	00-1000200	1p02101111	0010201
D. fusiformans	110pp11111	11010p0102	10-1011211	12p1101211	0020001
D. kincaidii	100p020111	1100100100	1q111pp000	1p0210x21p	0010001
D. mayri	0100020120	1000111110	1p01212q31	010110x011	p021001
D. minimus	1000110111	1100100110	0111011010	0000000100	0020001
D. nebulosus	1000010110	0010120111	1211201011	1100102211	0020001
D. niger	10011101x1	1010100100	1p02x11010	1000p02000	00x0001
D. radicum	1001111111	10p10q0112	1112x11010	1x22002x00	010p101
D. rubi	0001020120	0011011102	00-1111200	110x100111	0p10001
D. smilacis	100p010110	0001121110	1112100010	10q2000001	p020001
D. tumefactus	0101110100	0100011101	00-1111002	1100101211	p000001
D. turgidus	100p020111	11000p0100	110p21p030	1002102211	0010001

phus was associated with *Potentilla*, which appears to have been re-colonized twice by more derived species, and that colonization of *Rubus* has occurred once (having been reversed by the recolonizations of *Potentilla* and one shift each to *Fragaria* and *Smilax*). Optimization onto tree #2 (Fig. 5b) requires 7 changes (CI = 0.33) to explain the current pattern, an extra change over the previous scenario and suggests that the association with *Rubus* is less conserved. The associations with the plant genera *Fragaria*, and particularly that with *Smilax*, in both optimizations, are nested in the crown clade of each most parsimonious cladogram. Associations with both *Potentilla* and *Rubus* are slightly more conserved in tree #1 (Fig. 5a), in which the unit consistency indices of each association are 0.25 and 0.20, respectively, as compared with 0.20 and 0.17 in tree #2 (Fig. 5b).

Optimization of plant growth form associations onto tree #1 (Fig. 6a) requires four changes (CI = 0.25) and suggests that the basal species of *Diastrophus* was associated with herbaceous host plants and colonization of woody host plants occurred only once, followed by three subsequent reversals to herbaceous hosts. In contrast, optimization onto Tree #2 (Fig. 6b) requires five changes with lower consistency index (CI = 0.20), and is ambiguous about the ancestral state of plant growth form association.

DIVA analysis of the historical biogeography of *Diastrophus* based on the phylogenetic relationship among species depicted in Figs. 3a–b resulted in two equally optimal alternative reconstructions, each suggesting four dispersal events. Based on tree #1, the ancestor of *Diastrophus* was present in both West Palearctic and East Nearctic and a vicariance event split the West Palearctic *D. mayri* from the rest of the genus in East Nearctic (Fig. 7a). A clade later expanded its distribution to West Palearctic, followed by a vicariance event, which gave rise to *D. rubi* in West Palearctic and *D. fragariae* + *D. tumefactus* in East Nearctic. The West Nearctic species *D. austrior* and *D. kincaidii* resulted from independent dispersal events from East Ne-

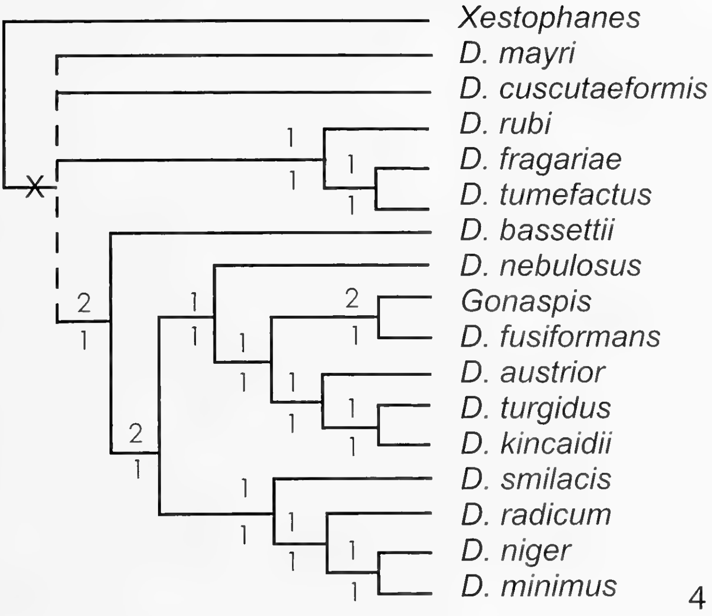

Fig. 4. Strict consensus tree of the two equally most parsimonious trees. Number above and below each branch are Bremer Support values resulting from constrained search with the single informative gall morphology character included and excluded.

arctic followed by subsequent vicariance. The occurrence of *D. fusiformans* is due to recent dispersal. Alternatively (Fig. 7b), the ancestor of *Diastrophus* was present in East Palearctic, and both West Palearctic species, i.e., *D. mayri* and *D. rubi*, are due to dispersal events to West Palearctic followed by a vicariance event. Otherwise the two reconstructions do not differ (Figs. 7a–b).

DISCUSSION

Phylogeny and systematics of *Diastrophus*.—The phylogenies should be viewed as working hypotheses about relationship of the group. Although resolved, the low consistency indices, retention indices, and Bremer values suggest that there is not enough character congruence in our data to render a robustly supported cladogram. External morphology in this group exhibits considerable homoplasy, possibly as a result of convergence associated with gall-forming life styles. An analysis based on molecular characters may be more informative. Nonetheless, our analysis does provide a provisional phylogeny and a preliminary basis for exploring the macroevolution of host plant associations and historical biogeography.

The phylogenetic position of the monotypic *Gonaspis* as nested within *Diastrophus* is confirmed by all analyses, thus the species *Gonaspis potentillae* (Bassett 1864) is hereby formally transferred to *Diastrophus*, where the species was originally placed. The genus *Gonaspis* was established by Ashmead (1897) based on *Diastrophus scutellaris* Gillette 1891, which

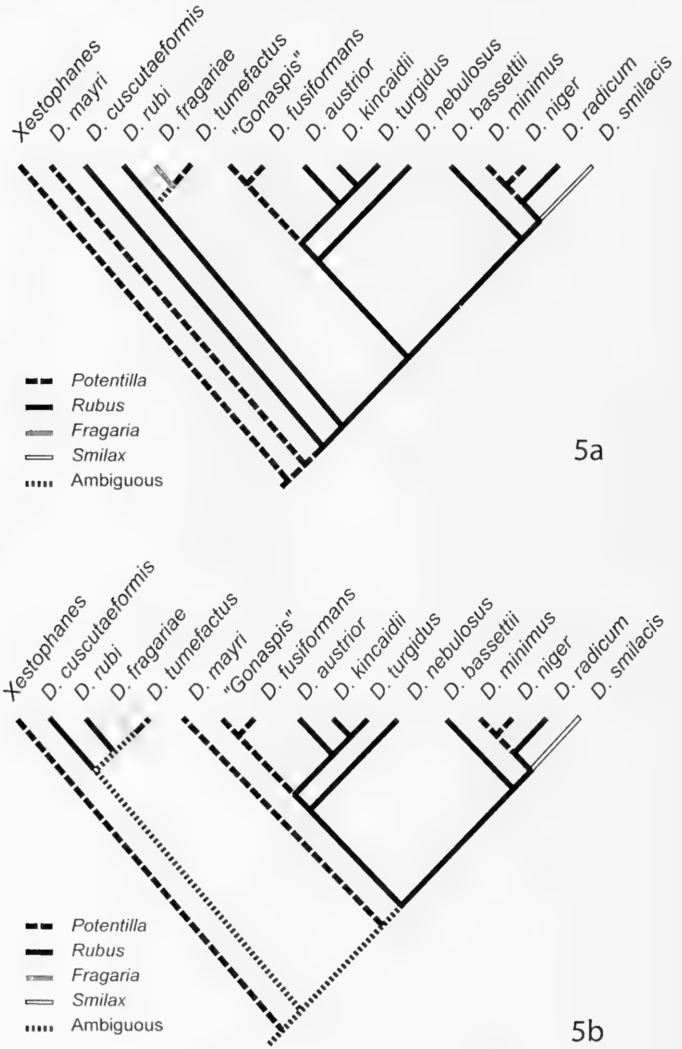

Fig. 5. Macroevolutionary pattern of host plant association in *Diastrophus*, *Gonaspis*, and *Xestophanes* as optimized using MaClade 4.0 onto best tree #1 and best tree #2, respectively.

was considered a junior synonym (Weld 1952), and listed as a variety of, *G. potentillae* by Weld (1959). Weld's first treatment has become accepted (Burks 1979). Therefore, the genus *Gonaspis* Ashmead 1897 is a **new junior synonym** of *Diastrophus* Hartig 1840.

Diastrophus kincaidii austrior, originally described by Kinsey (1922) as a variety of *D. kincaidii* Gillette, 1893, was later treated as a subspecies of the latter by Weld (1959). Burks (1979) listed it as a synonym of *D. kincaidii.* Since the two taxa do not appear as sister species in the cladogram, we thus establish *D. kincaidii* var. *austrior* Kinsey 1922 as a valid species, *Diastrophus austrior* Kinsey 1922. Both *D. kincaidii* and *D. austrior* induce galls on *Rubus parviflorus,* however, *D. kincaidii* is distributed in Washington and Oregon, and *D. austrior* is restricted to California based on known collection records.

Host plant associations and gall features.—Tree #1 suggests that an association with *Potentilla* was the ancestral condition with respect for *Diastrophus,* and was secondarily derived in *D. tumefactus,* and the respective common ancestors of the sister species [*D. minimus* + *D. niger*], and of [*D. potentillae* (= *Gonaspis potentillae*) + *D. fusiformans*]. The position of the species associated with *Smilax* and *Fragaria* suggests relatively recent and unique host shifts. In contrast, tree #2 offers an ambiguous scenario for ancestral host plant associations of *Diastrophus.* This is a result of the shifted position of *D. mayri.* Otherwise the two scenarios (Figs. 5a–b) are similar. In either case, association with *Potentilla* appears to have been labile, with at least three independent origins, whereas association with *Rubus* may be more conserved. In neither scenario did we find a perfectly conserved association with any host plant genus for which there exist more than one associated *Diastrophus* species (i.e., *Potentilla* and *Rubus*).

With regard to the macroevolutionary pattern of association with host plant growth form, tree #1 gives a more parsimonious and straightforward reconstruction compared with tree #2, which requires one more extra step, has lower consistency, and is uncertain about the ancestral state of host plant growth form association. The first scenario suggests a single event of host shifting from herbaceous to woody hosts. In contrast, the second scenario suggests this only as a possibility, but also suggests another possibility, i.e., colonization to woody hosts has occurred independently at least twice. In either case, reversal from woody hosts to herbaceous hosts has occurred at least twice, contrary to the general pattern in the clade of rosid gall makers, where colonization of woody hosts occurred only once and no reversal were observed (Ronquist and Liljeblad 2001). It is interesting to note the plasticity of the many aspects of *Diatrophus* biology. Most of *Diastrophus* (*sensu lato*) and *Xestophanes* are the only taxa that induce galls on rosaceous host plants among the 156 known species in the tribe Aylacini; all others are associated with advanced herbaceous hosts. *Diastrophus* is the only cynipid genus that has both members that are associated with herbaceous host plants and with woody hosts, contrary to the generally conservative association with plant growth forms in all other cynipid gall makers. As mentioned earlier, all basal cynipid genera are herb gallers, while the host plants of the rosid gallers are all woody. This conservative characteristic of association with plant growth form reaches its extreme in the rosid gallers comprising more than 1,000 species and with no single exception: Diplolepidini (63 species) are associated with *Rosa* (Rosaceae), Eschatocerini (3 species) with *Acacia* and *Prosopis* (Fabaceae), Pediaspidini (2 species) with *Acer* (Aceraceae), and Cynipini (ca 1,000 spp) with *Quercus* (Fagaceae, with a few exceptions associated with other genera of the same plant family; Ronquist 1994, Liljeblad and Ronquist 1998, Ronquist 1999).

According to phylogenetic study based on both morphology and molecular data,

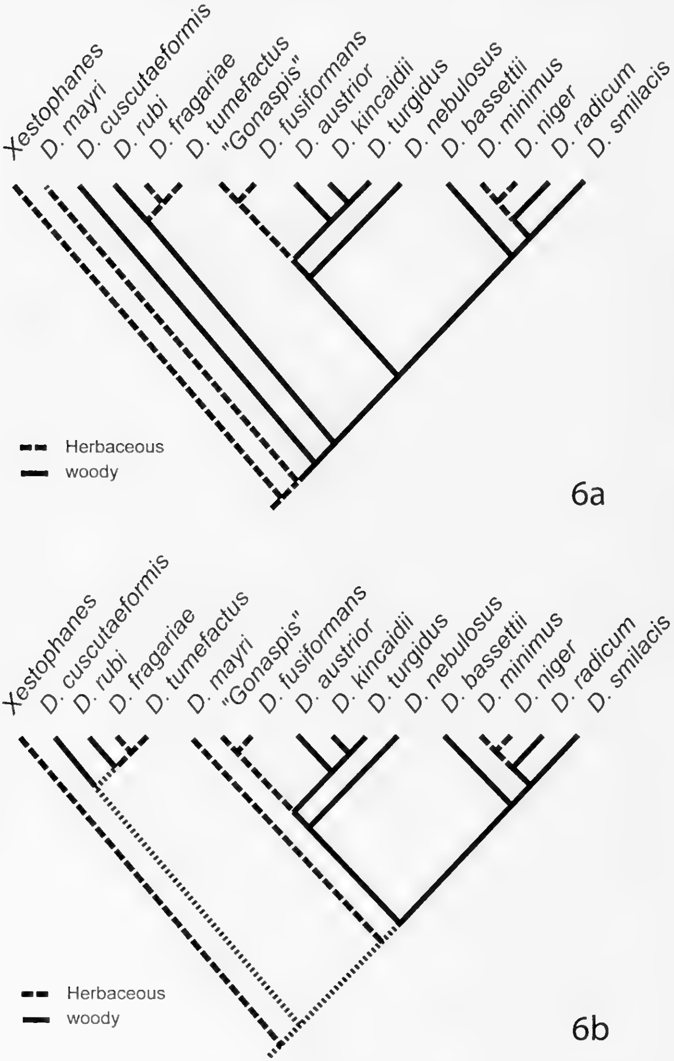

Fig. 6. Macroevolutionary pattern of association of host plant growth forms in *Diastrophus*, *Gonaspis*, and *Xestophanes* as optimized using MaClade 4.0 onto best tree #1 and best tree #2, respectively.

the plant genera *Fragaria, Potentilla,* and *Rubus,* associated with *Diastrophus* belong to a monophyletic clade with another genus *Rosa* in the plant family Rosaceae (Evans 1999). Therefore, species of *Diastrophus* are still conservative in their host plant association, with the exception of *D. smilacis.* Once the ancestral species of the genus colonized any of the genera *Fragaria, Potentilla,* or *Rubus,* it would have become less restrictive for subsequent colonization of other genera in the same clade, from herbaceous to woody host or vice versa, leading to repeated reversal events from woody hosts to herbaceous hosts (Figs. 6a–b) and thus the relatively high species diversity of the genus compared to most other herb-galling cynipid genera (cf., Ronquist and Liljeblad 2001).

Like all other herb gallers, *Diastrophus* species mostly induce simple swellings on stems with multi-chambers. However, several species show derivations; *D. cuscutaeformis* makes clusters of singular, detachable, and seed-like galls, *D. fragariae* makes galls on leaf petioles of strawberry (*Fragaria virginiana* Duch.), and *D. radicum* and *D. bassettii* make underground galls on the roots of *Rubus.* Indeed, the only parsimony-informative gall character we scored is the location of the galls, below or above ground, and that only by virtue of two species bearing one of two alternative states (underground gall-forming). However, this behavior appears convergent in each most parsimonious tree, considering that the galls of *D. bassettii* are stem galls and are not always below ground level (Beutenmueller 1909), and hence was coded as polymorphic in our analysis. Our phylogenetic analysis supported this by showing the *D. bassettii* and *D. radicum* are not sister species (Figs. 5a–b).

Biogeography.—The biogeographical reconstruction of speciation pattern based on tree #1 (Fig. 7a) suggested that the ancestral species of *Diastrophus* was distributed in both West Palearctic and East Nalearctic, with a basal vicariance event that separated *D. mayri* and the rest of the genus. In this scenerio, *D. rubi* originated from a vicariance event that followed dispersal of its common ancestral species with *D. fragariae* and *D. cuscutaeformis,* from East Nearctic to West Palearctic. Alternatively, reconstruction (Fig. 7b) based on the second best tree suggests that the common ancestor of *Xestophanes* and *Diastrophus* occurred in both West Palearctic and East Nearctic and had later become split through a vicariant event. Two subsequent dispersal events gave rise to the two West Palearctic *Diastrophus* species.

The two biogeographical reconstructions do not differ otherwise, and all other species involved have an East Nearctic distribution, except *D. austrior, D. kincaidii,* and *D. fusiformans. Diastrophus austrior* and *D. kincaidii* are only found in California, Oregon, and Washington, while *D. fusiformans* is also found in the East Nearctic. The host plant of the two species, *Rubus parviflorus* Nutt.), has a distribution in western North America and not beyond the Great Lake areas to the east. *Diastrophus fusiformans* makes galls on *Potentilla,* and its wider distribution may be attributable to the distribution of its host plant. The terminal position of this clade indicates that colonization of West Nearctic has been relatively recent event(s).

In a forthcoming study, Engel et al. (pers. comm.) suggested that *Aulacidea succinea,* a fossil species described from Baltic amber (Eocene, ca 45 MYA) by Kinsey (1937) and transferred therein to a newly erected genus, is closely related to the genera *Xestophanes* and *Diastrophus* (*sensu lato*). Therefore, the presence of *Diastrophus* possibly dates as far back as 45 million years ago in the Eocene. Since the oldest known cynipid fossils with putative associations with *Rosa* is from the Oligocene (33–23 MYA; Cockerell 1921, Ronquist 1999) and the oldest fossils that are definitely cynipine galls are on *Quercus* from Middle Miocene (ca. 15–12.5 MYA; Waggoner and Poteet 1996, Waggoner 1999), the species of *Dias-*

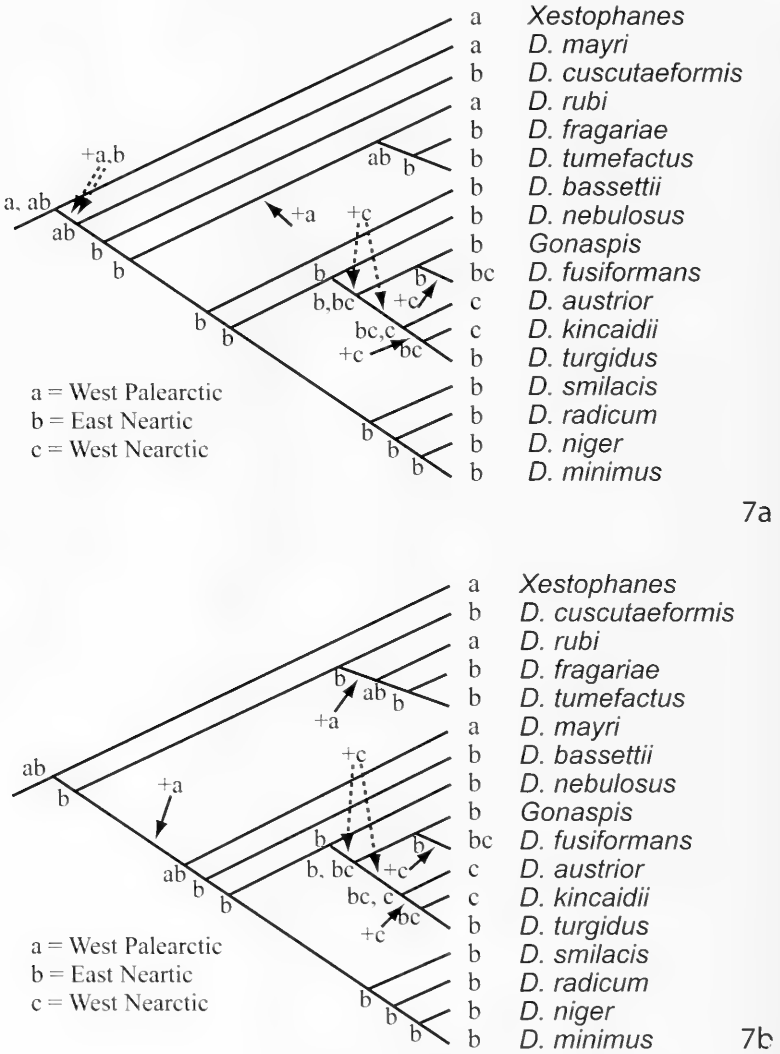

Fig. 7. DIVA reconstruction of historical biogeography for *Diastrophus* based on tree one and tree two, respectively. Search options were default in DIVA. Solid arrows are unambiguous dispersal events and dashed arrows indicate competing alternatives of dispersal events.

trophus associated with woody *Rubus* are likely to represent the first pioneers in Cynipidae in the woody world, although leading to a different clade from the by far more speciose clade comprising Diplolepidini, Eschatocerini, Pediaspidini, and Cynipini (Liljeblad and Ronquist 1998).

Definite evidence of the early appearance of Rosaceae in fossil records is not known before Middle Eocene (ca 42–50 MYA) (Stewart 1983), therefore the existence of the genus *Diastrophus* much earlier is unlikely. Land connections between North America and Europe probably existed until the Oligocene (37 Ma) (Hallam 1981). The presence in Beringia of temperate plants such as members of *Potentilla* was possible until the latest Tertiary or even Quaternary when glaciations cut off dispersal of temperate plants through the Bering land bridge (Tiffney 1985). Thus, it is difficult to speculate by which route, North America—Europe land connection or Beringia, earlier species of *Diastrophus* expanded their distribution. The collection of *Synophromorpha* from Japan as discussed earlier and from southern China (Liu, unpubl. data) indicates that *Diastrophus* is very likely to be present there as well. Inclusion of those species in future analysis certainly will present a clearer picture of the historical biogeography of the genus.

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APPENDIX

List of Characters

I. Structural characters

1. *Head width compared to mesosoma width:* (0) not or only slightly wider, (1) distinctly wider.
2. *Apparent number of female antennal segments:* (0) 13, (1) 14.
3. *Length of third antennal segment in relation to the fourth:* (0) distinctly longer, (1) subequal.
4. *Shape of face in frontal view:* (0) high, with height about four-fifths width of face, (1) transverse, with

height three quarters or less of width of face.

5. Shape of gena in frontal view below eye: (0) straight in upper three fourths and distinctly curved ventrally, (1) smoothly curved.
6. *Ventral projection of clypeus:* (0) not projected, (1) distinctly projected ventrally, forming broad emargination with ventral margin of malar space, (2) strongly projected ventrally, tonguelike.
7. *Height of pronotal plate:* (0) height about one-half width, (1) height at least two-thirds width.
8. Notauli: (0) incomplete; (1) complete.
9. *Width of notauli:* (0) narrow throughout, (1) conspicuously widened posteriorly, (2) wide throughout.
10. *Distance between notauli at the posterior margin of mesoscutum:* (0) ≥3 times width of notaulus at posterior margin, (1) not or slightly more than 2 times width of notaulus at posterior margin.
11. Distance between anterior ends of notauli or signal extensions of notauli relative to that between posterior ends of notauli: (0) about two times as wide anteriorly as posteriorly, (1) three to four times as wide anteriorly as posteriorly.
12. *Anterior extension of median mesoscutal impression:* (0) absent, (1) present.
13. *Parascutal carinae in dorsal view:* (0) smoothly curved, not raised lateroposteriorly, (1) expanded lateroposteriorly into a rounded angle, not raised posteriorly, (2) expanded lateroposteriorly into an acute, distinctly raised posterior angle.
14. *Parapsidal signa:* (0) absent, (1) present.
15. *Anteroadmedian signi on mesoscutum:* (0) present, (1) absent.
16. *Posterior projection of scutellum:* (0) absent, scutellum gradually sloped and rounded posteriorly, (1) scutellum distinctly projected posteriorly into an apical, broadly truncate process, (2) scutellum conspicuously projected posteriorly into an apical, narrowly truncate process (Fig. 2f).
17. *Slope of posterior projection of scutellum in lateral view:* (0) distinctly curving downward toward posterior apex, (1) almost flat.
18. *Extension of longitudinal linear carinae on dorsal surface of scutellum:* (0) absent completely or absent in posterior third of scutellum, (1) extending to end of dorsal surface.
19. *Anterior connection of longitudinal linear carinae on dorsal surface of scutellar disk:* (0) absent, (1) forming concentric semicircles at the anterior end of scutellar disk.
20. *Median depression of scutellum extending posteriorly from septum:* (0) absent, (1) only over anterior portion of scutellar disk, (2) throughout scutellar disk.
21. *Width of lateral bars:* (0) narrow (less than half length), (1) wide (greater than half length).
22. *Presence of areolet on forewing:* (0) absent, (1) present, but not defined by tubular vein(s), (2) present, defined by three distinct veins.
23. *Shape of areolet in forewing:* (0) present, less than 4 times width of anal vein, (1) present, equal to or wider than 4 times width of anal vein.
24. *Length of bulla in forewing:* (0) absent, (1) present, nearly as wide as vein width and less than two times vein width, (2) present, at least twice as wide as vein width.
25. *Size of abdominal tergum 3 in relation to post-petiolar metasoma in lateral view:* (0) more than half of metasoma, (1) about half the meta-

soma, (2) less than one-third metasomal area.

II. Surface sculpture

26. *Coarseness of radiating strigulation in malar space:* (0) coarsely substrigulate, (1) finely strigulate.
27. *Extension of strigulation from malar space upward to lower face:* (0) this pattern of strigulation not continued upward to lower face, (1) strigulation continued upward to bases of antennae, (2) pattern of strigulation is bent as it extends upward.
28. *Sculpture on elevated median quadrangular area between antennae and clypeus:* (0) mostly glabrous, (1) coriaceous, (2) mostly strigulate.
29. Sculpture on surface of clypeus: (0) glabrous, (1) strigulate near epistomal sulcus, (2) embossed, (3) with a spherical elevation.
30. *Sculpture of vertex and upper face:* (0) glabrous, (1) coriaceous to slightly strigulate.
31. *Sculpture of gena, especially posteriorly:* (0) glabrous, (1) strigulate, (2) coriaceous.
32. *Upper occiput:* (0) glabrous, (1) finely, transversely strigulate, (2) coriaceous.
33. *Surface sculpture of pronotal plate:* (0) mostly glabrous with sparse punctures, (1) strigulate with some punctures, (2) mostly punctate.
34. *Pubescence on pronotal plate:* (0) absent to sparse, (1) present in two dorso-lateral patches, (2) short setae evenly scattered.
35. *Degree and strength of diagonal carinae on lateral surface of pronotum:* (0) mostly glabrous, carinate only toward margins, (1) largely diagonally carinate.
36. *Surface sculpture of mesoscutum:* (0) glabrous, (1) coriaceous.
37. *Surface sculpture of mesopleuron:* (0) entirely glabrous, (1) mostly strigulate, (2) glabrous with a few central striae.
38. *Surface sculpture at bases of scutellar fovea:* (0) generally glabrous, (1) entirely strigulate-reticulate or rugulose, (2) some strigulation posteriorly.
39. *Sculpture on dorsal surface of axilla:* (0) glabrous except posteriorly, (1) rugulose, (2) coriaceous.

III. Body color and pubescence

40. *Color of head and mesosoma:* (0) brown to reddish brown entirely or in part, (1) deep dark brown to black.
41. *Color of metasoma:* (0) brown to reddish brown entirely or in part, (1) deep dark brown to black.
42. *Infuscation of membranous areas of forewings often appearing as a linear streak in Rs cell:* (0) absent or very faint, (1) present.
43. *Presence of infuscation of forewings near veins (especially R1 and 2r):* (0) absent, (1) present, but indistinct, infuscate area usually less than vein width, (2) infuscation dark and distinct, usually as wide as vein.

IV. Gall Features

44. *Position of gall growth:* (0) Above ground, (1) below ground.
45. *Plant tissues affected by gall growth:* (0) stem, (1) root, (2) leaf.
46. *Gall structure effects on plant surface:* (0) internal and integral, (1) external and detachable.
47. *Surface of gall indicating internal chambers:* (0) individual, (1) as single entire group, (2) multiple galls in close proximity.

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LARVAL DESCRIPTION OF A NEW WORLD GHOST MOTH, *PHASSUS* SP., AND THE EVOLUTIONARY BIOGEOGRAPHY OF WOOD-BORING HEPIALIDAE (LEPIDOPTERA: EXOPORIA: HEPIALOIDEA)

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Abstract.—We present a description of chaetotaxy and selected morphological features for an unidentified *Phassus* larva and examine the implications for hepialoid chaetotaxy and biogeography. The wood-boring genera *Phassus, Endoclita,* and *Aenetus* represent a monophyletic lineage in reference to the presence of a microtrichiated field enclosing SD1, SD2 and D2. Other larval characters that may support this clade include a longitudinal pit posteroventral to L1 on the meso and metathorax, and a medial triangular tooth on the labral margin. The wood-boring *Zelotypia* and *Cibyra* may represent more distant relatives within a monophyletic lineage of callus feeders and wood-borers within the Hepialidae sensu stricto. The spatial and nomenclatural problems in Lepidoptera chaetotaxy are reviewed with respect to *Phassus.* The term "microtrichiated pit" is distinguished from "microtrichiated field" referring to an extensive, concave or flat region that may enclose one or more setae. We argue that slight shifts in setal position and tonosensillar morphology for SD2 of the prothorax is more likely than convergent development of tonosensillar morphology in D2. A monophyletic relationship between *Phassus, Endoclita,* and *Aenetus* is biogeographically congruent with a Pacific basin origin rather than a typically 'Gondwanic' history. We suggest that much of the biogeography and evolution of the Hepialidae is closely associated with Pacific geology and tectonics and this would be consistent with what otherwise would be an "extraordinary and inexplicable" absence of Exoporia from parts of West Africa and Madagascar.

Key Words: Hepialidae, larva, chaetotaxy, biogeography, panbiogeography, *Phassus*

The Hepialidae (Lepidoptera: Suborder Exoporia) is almost global in distribution comprising 616 described species placed in 68 genera (Nielsen et al. 2000). Phylogenetic relationships within the Hepialidae are poorly understood with most studies focusing on the establishment and composition of genera and subgenera (e.g., Tindale 1932–1942, Viette 1946–1979, Nielsen and Robinson 1983, Dugdale 1994). The genera *Afrotheora* Nielsen and Scoble, *Antihepialus* Janse, *Fraus* Walker, and *Gazoryctra* Hübner lack derived features of other hepialids and comprise a basal group of uncertain monophyly (Nielsen and Kristensen 1989, Kristensen 1998). The remaining genera constitute the great majority of species and are believed to represent a monophyletic assemblage, the Hepialidae sensu stricto (Kristensen 1998).

Recent studies by Nielsen and Robinson (1983) and Nielsen and Kristensen (1989) attempted preliminary phylogenetic analysis of species relationships within selected genera, but intergeneric relationships remain generally uncertain. Wagner and Rosovsky (1991) examined the relationships of ten genera (nine restricted to North America and Eurasia) where male courtship behavior was known, and an unpublished revision by Wagner (1985) hypothesized a monophyletic status for *Phymatopus* from western North America and Eurasia. A morphological study by Brown et al. (2000) presented a cladistic phylogeny for the New Zealand Hepialidae, and Nielsen et al. (2000) catalogued the entire Hepialidae within an informal speculative phylogenetic arrangement.

Most hepialid larvae, including all the basal lineages, live in soil and feed on or within roots, or consume leaves and other herbaceous debris, including mosses and both monocotyledonous and dicotyledonous angiosperms. Host-plant relationships dissociated from soil microhabitats evolved in the genera *Aenetus* Herrich-Schäffer, *Cibyra* Walker (= *Aepytus* Herrich-Schäffer), *Endoclita* Felder, *Phassus* Walker, *Trichophassus* Le Cerf, and *Zelotypia* Scott where larvae enter the host-plant above ground level and tunnel into stems and branches. Larvae of *Endoclita, Trichophassus,* and *Zelotypia* are known to feed on callus tissues forming around the tunnel entrance (Rojas de Hernández and Chacón de Ulloa 1982, Grehan 1987, Grehan 1989). The primary food source for *Cibyra* remains unconfirmed (Rojas de Hernández and Chacón de Ulloa 1982, Hilje et al. 1992). Stem boring is documented for the monotypic genus *Leto* Hübner (Janse 1939, Duke and Taylor 1964) although whether larval activity originates within stems or is an extension of root-feeding is unknown. Fragments of the host-plant with tunnels (Peabody Museum of Natural History) do not show evidence of callus feeding.

By applying Hennig's vicariance criterion (Craw et al. 1999), Grehan (1987) predicted that the *Endoclita* lineage was most closely related to *Aenetus/Zelotypia* through vicariant differentiation of a widespread ancestor. Morphological characters subsequently identified in support of this lineage include the shared presence of sub-falcate forewings, reduced adult antennae, a weak truellum in the male genitalia, a small ventral spine crest on the seventh abdominal segment of pupae, and a prothoracic depression (or field) enclosing setae SD1, SD2, and D2 in larvae (Dugdale 1994). Absence of this trisetose feature in primitive *Fraus* and the hepialoid sister group Mnesarchaeidae led Nielsen and Kristensen (1989) to suggest it represented an apomorphy within Hepialidae.

Kristensen (1999) suggested male metatibial androconial scales may support a monophyletic lineage within Hepialidae sensu stricto (Table 1), including the callus-feeding genera *Aenetus, Endoclita,* and *Zelotypia.* These genera are exclusively wood-borers. Of the remaining androconial genera, only the Mexican-South American *Phassus* is known as a wood-borer (Grehan 1989). Root and stem boring is reported for the *Phymatopus*-clade of Wagner (1985), while larvae of *Sthenopus* Packard and related *Zenophassus* Tindale feed from roots into stems, although neither is reported feeding on callus (Grehan 1989). Larvae of *Oncopera* Walker feed on leaves of grasses and other herbaceous perennials (Grehan 1989), but the feeding biology of monotypic *Puermytrans* Viette is unknown (Nielsen and Robinson 1983).

The specialized trisetose prothoracic field represents a potential larval apomorphy for callus-feeding wood borers. Detailed larval descriptions of wood-boring larvae are limited to *Aenetus cohici* Viette (Boudinot 1991) *Aenetus virescens* (Herrich-Schäffer) (Grehan 1981, Dugdale 1994) and *Endoclita hosei* Tindale (Yasuda and Abe 1986). Larvae of other wood-boring genera are undescribed, or have received only generalized treatment. Larval descriptions of American wood-borers are limited to a general account of *Trichophassus giganteus* Le

Table 1. Feeding modes, geographical distributions, and important morphological features of ghost moth genera (Hepialidae). ? = character not recorded; * = inferred by probable relationship of *Zenophassus* with *Sthenopis*.

Genus	Feeding Mode	Geographic Range	Androconia Present	Androconia Red-Brown	Trisetose Thoracic Pit	Trilobate Labrum
Puermytrans	?	South America	yes	no	no	?
Oncopera	foliage	Australia	yes	no	no	no
Sthenopis	root/stem	America/Eurasia	yes	yes	no	yes
Zenophassus	root/stem	Europe	yes	yes	?*	?*
Phymatopus	root	Europe	yes	yes	yes	?
'*Phymatopus*'	root/stem	Northwestern North America	yes	yes	yes	yes
Schausiana	?	Mexico	yes	yes	?	?
Phassus	stem	America	yes	yes	yes	yes
Aenetus	stem	Southwest Pacific	yes	yes	yes	yes
Endoclita	stem	India/Asia	yes	yes	yes	yes
Zelotypia	stem	Australia	no	no	no	yes
Trichophassus	stem	Brazil	no	no	?	?
Cibyra (*Aepytus*)	stem	South America	no	no	no	?
Leto	stem	South Africa	no	no	no	yes

Cerf by Briquelot (1956) and brief notes on *Phassus triangularis* Henry Edwards (Schaus 1888, Dyar 1917). A color photograph of an unidentified *Phassus* larva from Ecuador by Gara and Onore (1989) indicates a shaded area corresponding to a prothoracic sensory field. In this paper we describe the larva of an undetermined species of *Phassus*, confirm the presence of a prothoracic field, and discuss phylogenetic and biogeographic implications of this character for the evolutionary history of wood-boring Hepialidae.

METHODS

Specimens examined.—One dried larva from Jalapa, Mexico (No. 15646, Collection of Henry Edwards, American Museum of Natural History (AMNH)), and four ethanol-preserved specimens (National Museum of Natural History, Smithsonian Institution (USNM)) found boring in living stems of *Lantana camara* Linnaeus by N. H. L. Kraus, as follows: one from Nogales, Veracruz, Mexico and one from Orizaba, Veracruz, Mexico, both during December, 1954; one from Orizaba, Veracruz, Mexico (Kraus 5053), and one from Cordoba, Veracruz, Mexico (Kraus 5055), both in November, 1954. The chaetotaxy of *Phassus* sp. was compared with specimens or descriptions of about 34 species of Hepialidae and one species of Mnesarchaeidae (Table 2).

The following description is based on study of the above larvae that did not differ significantly in morphology. Measurements are given only for the single, most intact larva (Orizaba, Mexico, December, 1954). All are ultimate or penultimate instars based on head width and body size.

Although the specimen from Jalapa (AMNH) and the two from December, 1954 (USNM) were determined as *Phassus argentiferus* Walker by the collectors, only the generic determination can be accepted with confidence. No reared adult material is associated with these larvae, but they are most likely *Phassus* as indicated by distribution and morphology. Three genera of Hepialidae are known as adults from Mexico (*Phassus* Walker with more than 8 species in Mexico, monotypic *Schausiana* Viette, and *Cibyra* Walker (sensu Nielsen et al. 2000), the latter containing a few Mexican species formerly placed in *Hampsoniella* Viette, *Pseudodalaca* Viette, and *Gymelloxes* Viette, all currently treated as subgenera of *Cibyra*. We expect larvae of the

Table 2. Taxa of Hepialidae and Mnesarchaeidae with larval material included in this study. Larval specimens were examined directly (with specimen depository) or cited from published descriptions (with reference citation).

Name	Location	Instar	Depository/Source
Abantiades latipennis Tindale, 1932	Australia: Tasmania	late-final	Forestry Tasmania, Department of Primary Industries
Aenetus cohici Viette, 1961	New Caledonia: Mt. Koeanonoa	late-final	John Grehan Collection
Aenetus dulcis (Swinhoe, 1892)	Australia: Western Australia	late-final	John Grehan Collection
Aenetus virescens (Doubleday, 1843)	New Zealand: North Island	late-final	John Grehan Collection
Aenetus cf. *scotti* (Scott, 1869)	Australia: Victoria	late-final	John Grehan Collection
Antihepialis sp.	South Africa: Storm River	post-first	John Grehan Collection
Aoraia insularis Dugdale, 1994	New Zealand: South Island	final	Dugdale (1994)
Cibyra serta (Schaus, 1894)	Colombia	post-first	Rojas de Hernandez and Chacón de Ulloa (1980)
Cladoxycanus minos (Hudson, 1905)	New Zealand	final	Dugdale (1994)
Dalaca sp.	Costa Rica: Santa Rosa	post-first	Illinois Natural History Survey
Dioxycanus fusca (Philpott, 1914)	New Zealand	final	Dugdale (1994)
Dumbletonius characterifer (Walker, 1865)	New Zealand	final	Dugdale (1994)
Dumbletonius unimaculata (Salmon, 1948)	New Zealand: Kapiti Island	final	John Grehan Collection
Elhamma sp.	Australia: Eastwood	late-final	Peabody Museum of Natural History
Endoclita excrescens (Butler, 1877)	Japan: Kyushu	late-final	Landcare, New Zealand
Endoclita sinensis (Moore, 1877)	Japan: Kyushu	late-final	Landcare, New Zealand
Fraus simulans Walker, 1856	Australia	late-final	Peabody Museum of Natural History
Hepialus humuli (Linnaeus, 1758)	England	final	Aitkenhead and Baker (1964)
Korscheltellus gracilis (Grote, [1865])	United States: Vermont	final	John Grehan Collection
Korscheltellus lupulina (Linnaeus, 1758)	England	final	Aitkenhead and Baker (1964)
Leto venus (Cramer, 1780)	South Africa: Plattenburg Bay	late-final	South African Museum, Cape Town
Mnesarchaea acuta Philpott, 1929	New Zealand: Wainuiomata	late-final	George W. Gibbs Collection
Oncopera fasciculatus (Walker, 1869)	Australia: Kalangadoo	late-final	Peabody Museum of Natural History
Oncopera intricata Walker, 1856	Australia: Tasmania	late-final	Peabody Museum of Natural History
Oncopera rufobrunnea Tindale, 1933	Australia: Tasmania	late-final	Peabody Museum of Natural History
Oxycanus antipoda (Herrich-Schaffer, [1853])	Australia: Tasmania	late-final	Peabody Museum of Natural History
Pharmacis aemilianus (Constantini, 1911)	Italy	final	Zilli (1998)
Pharmacis fusconebulosa (De Geer, 1778)	England	final	Aitkenhead and Baker (1964)
Phassus sp.	Mexico: Jalapa, Veracruz	late-final	Smithsonian Institution
Phymatopus californicus (Boisduval, 1868)	United States: California	late-final	John Grehan Collection
Phymatopus hecta (Linnaeus, 1758)	England	late-final	John Grehan Collection
Sthenopis argenteomaculatus (Harris, 1841)	United States: Vermont	late-final	John Grehan Collection
Sthenopis purpurascens (Packard, 1863)	Canada: Quebec	late-final	Canadian National Collection
Triodia sylvina (Linnaeus, 1761)	England	final	Aikenhead and Baker (1964)
Wiseana cervinata (Walker, 1865)	New Zealand	final	Dugdale (1994)
Zelotypia staceyi Scott, 1869	Australia: New South Wales	final	Peabody Museum of Natural History

Fig. 1. Photograph of preserved last larval instar of *Phassus*, unidentified species.

Cibyra alliance to lack a prothoracic microtrichiated field enclosing macrosetae SD1, SD2, and D2 based on the larval description of *Cibyra serta* (Schaus) (Rojas de Hernández and Chacón de Ulloa 1982).

Two larvae (from Nogales (USNM) and Jalapa (AMNH)) were macerated in warm 10% aqueous potassium hydroxide and soft tissues removed. The head capsule was removed by an incision along the posterior margin. The thoracic and abdominal cuticle was flattened under a glass slide for examination and subsequently stored in 70% ethanol.

Terminology.—At the present time the larval chaetotaxy of Hepialidae is a confusing patchwork of prior systems of nomenclature dating from Hinton (1946) and Gerasimov (1952). The terminology used in this paper follows in large part the general practice of recent authors (e.g., Nielsen and Kristensen 1989, Dugdale 1994, Zilli 1998) and makes no attempt to resolve homology issues with non-exoporian taxa. The chaetotaxy of the head capsule used here differs from that of Hinton (1946), following with few exceptions the nomenclature of Hasenfuss (1969) as a better-supported homology arrangement corresponding to ditrysian chaetotaxy (Leonard et al. 1992). Labeling of prothoracic setae SD1, SD2 and D2 follows Wagner (1987) and Wagner et al. (1989). For consistency, nomenclature of other setae and pores follow recent descriptive work on larval hepialids (Nielsen and Kristensen 1989) with any deviations noted in the text. Chaetotaxy is illustrated by a semischematic setal map for thoracic abdominal segments (T1–A2 and A6–A10, Fig. 4–5). Lengths of setae are given in general terms relative to a large, precisely measured seta on most segments.

DESCRIPTION

Last instar (Fig. 1).—Exoporian, hepialoid, hepialid (Nielsen and Kristensen 1989). Length, 56 mm; maximum head width, 5.84 mm; head length from epicranial notch to apex of frontoclypeus, 4.88 mm. Head weakly hypognathous, subspherical, maximum width slightly less than prothorax but greater than other segments. Body elongate, parallel-sided, narrowing from Ab8 to Ab10; Ab8 slightly gibbose dorsally, longer than other segments except Ab7; setae short, inconspicuous, set in large flattened pinacula or plates paler than adjacent cuticle; cuticle of body between sclerotized plates and pinacula densely shagreened with fine microtrichiae. Prolegs present on Ab3 to Ab6, subequal to each other, smaller than prolegs on Ab10.

Color: Head dark reddish brown, body paler grayish red brown except for pale yellow to brownish-yellow pinacula, these prominent as pale transverse dorsal folds on Ab1 to Ab8; prothoracic dorsal shield reddish brown, edged anteriorly and ventrally with brownish yellow; ventral areas concolorous with non-sclerotized areas on rest

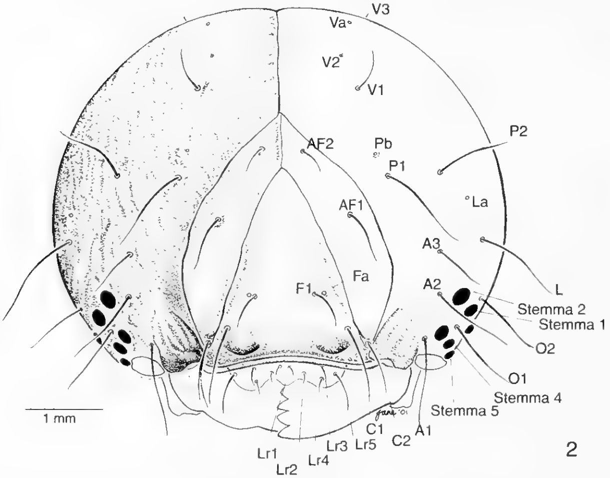

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Fig. 2. Chaetotaxy of head of last instar larva of *Phassus* sp., Veracruz, Mexico; dorsofrontal view of head capsule. Symbols used: A1–A3, anterior setae; Aa, anterior pore; AF1–AF2, adfrontal setae; C1–C2, clypeal setae; F1, frontal seta; Fa, frontal pore; L1, lateral seta; La, lateral pore; Lr1–Lr5, labral setae; V1–V3, vertexal setae; Va, vertexal pore; G1, genal seta; P1–P2, posterior setae; Pb, posterior pore; O1–O2, ocular or stemmatal setae; Sb, stemmatal pore; SO2–SO3, subocular or substemmatal setae.

of body; prolegs paler, contrasting with ventral abdominal coloration. Setae brown, spiracles black.

Head (Figs. 2–3): Epicranium subspherical, circular in dorsal view, smooth; postoccipital sclerites and sutures as in other Hepialidae; epicranial notch obscure; coronal suture (= epicranial suture from epicranial notch to ecdysial lines) about twice length of epicranial suture from ecdysial lines to dorsal apex of front. Front fused to clypeus with frontoclypeal suture obsolete, anterior clypeal region with a large, sclerotized protuberance on each side. Six stemmata on each side in two dorsoventral arcs, anterior arc of stemmata 3, 4, and 5 (dorsal to ventral), posterior arc of stemmata 2, 1, and 6 (dorsal to ventral); stemma 5 not displaced ventrally into paramaxillary region; distinct pore anteroventrad of stemma 4. Antennal fossa closed ventrally by pre-antennal bar that articulates with epicranium anterior to antenna and is posterior (not contiguous) to dorsal mandibular articulation. Antennal slit (sensu Dugdale 1994) a narrow strip of membranous cuticle continuous with that between antenna and base of mandible, extending posterodorsad and ending near two distinct pores just ventral to stemma 5. Antenna not studied.

Setation of head as for other Hepialidae (Nielsen and Kristensen 1989). Dugdale (1994) following nomenclature of Hasenfuss (1969) although homology of that system with ditrysian nomenclature (e.g., Stehr 1987) doubtful. Seta V1 macrosetose, setae V2 and V3 microsetose; pore present near seta P1 (termed Pb by Nielsen and Kristensen 1989); pore La present; pore medial to seta SO1 visible only in ventral view (perhaps homologous with pore SSa of ditrysian system); pores Sa (= Oa of Hasenfuss 1969), MGa, AFa, and Aa absent; two genal microsetae; seta SO3 minute, microsetose (not visible or depicted in Fig. 3).

Labrum with five pairs of setae; anterior margin with medial, broadly triangular tooth. Maxillolabial complex with basistipes and dististipes sclerotized. Maxillary palp three-segmented with distal segment subequal in size to large sensillum basiconicum as in other Hepialidae; lateral pore on basal segment of palp. Medial maxillary lobe laterally sclerotized with seven sensilla on distal surface: three large flattened sensilla dorsally, middle row of two apically rounded sensilla, lower row of two pointed sensilla with pitlike structure between them. Basistipes with two setae and a pore. Dististipes with single lateral seta. Labial palp minute with long apical seta, arising from lateral subapical plates of premental lobe (maxillary features similar to those illustrated for *Fraus* (Nielsen and Kristensen 1989)). Mandible with four triangular teeth on distal extremity; oral surface of mandible transversely rugulose without distinct molar area; mandible with two setae on aboral surface, basal seta M1, distal M2.

Prothorax (Fig. 4): Entire dorsal surface of prothorax sclerotized, anterior margin reflexed to join posterior margin of head capsule; prothoracic dorsal shield (sensu stricto) thicker and indistinctly delimited from sclerotized marginal regions, yellowish brown; sclerotization of dorsal shield includes L-group setae, narrowly separated from sclerotized region around spiracular peritreme.

Seta D1 strong, posterior to anterior margin of dorsal shield at a distance subequal to length of seta (0.76 mm); seta XD1 directly ventral to seta D1, more than twice as long. Seta XD2 slightly anterior to XD1, subequal in length to D1; seta D2 slightly ventral to level of XD2, slightly smaller than D1, approximately midway between SD1 and SD2. Three prothoracic pores (sensu Nielsen and Kristensen 1989): XDa directly ventral to D1, pigmented dark brown; XDb posterodorsal to XD1, pale; XDc posterodorsal to XD2, strongly pigmented; diameter of all pores slightly less than socket of associated setae.

Seta D2 ventral and slightly anterior to seta SD2, dorsal and slightly posterior to seta SD1; length of seta D2 0.59 mm; length of SD1 0.42 mm, equal to SD2. Both SD setae extremely slender, filiform, not attenuate, arising from bottom of distinct conical pits with strongly microtrichiated walls (similar to tonosensilla of ditrysian larvae); cuticular articulation of D2 unmodified with setal alveolus (socket) surrounding visible, pale setal membrane bearing base of seta. Seta D2, both SD setae, and associated pits included within broad region (field) depressed below surrounding cuticle (Fig. 6), continuously microtrichiated (shagreened) more densely than adjacent cuticle or elsewhere on body; basal pits of setae SD1 and SD2, and base of seta D2, darkly pigmented, contrasting with microtrichiated field; maximum dorsoventral dimension of microtrichiated field 1.45 mm, width 0.55 mm. Small unnamed pore on extreme dorsal edge of microtrichiated field dorsal to a line between setae D1 and SD2, diameter smaller than alveolus of seta D2, but greater than diameter of hyaline setal membrane at bases of SD1 and SD2.

Seta L1 near anterior edge of prothoracic shield directly anterior to middle of spiracle, subequal in length to seta XD1. Seta L2 anterodorsal to seta L1, approximately half the length of seta L1. Seta L3 directly anterior to middle of spiracle, displaced from anterior peritreme by less than horizontal diameter of spiracle, shortest seta on prothoracic shield (half the length of seta L2). Setae SV1 and SV2 below L-group setae on pinaculum narrowly separated from ventral edge of prothoracic shield; SV1 subequal in length to XD2 or D1, directly posterior to seta SV2 and twice its basal diameter; SV pinaculum yellowish tan, concolorous with ventral lobe of prothoracic shield.

Seta V1 subequal in size to seta L3, posterior to prothoraxic coxae on sclerotized mid-ventral plate. Seta MV3 macrosetose, subequal in size to seta L2, directly anterior to coxa; seta V1 on large plate which crosses ventral midline; seta MV2 macrosetose,

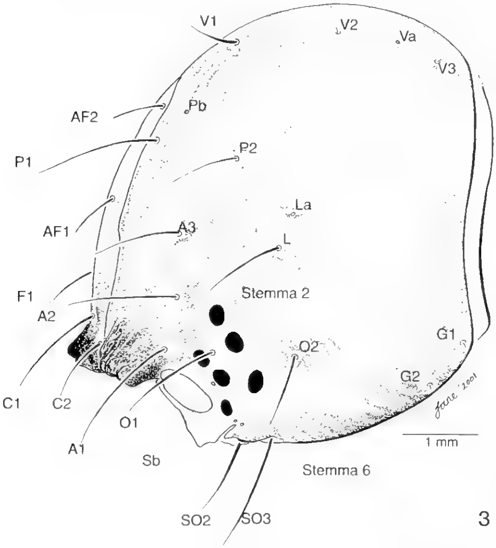


Fig. 3. Chaetotaxy of head of last instar larva of *Phassus* sp., Veracruz, Mexico; lateral view of head capsule. Symbols used as in Fig. 2.

subequal in size to seta V1, anterior to middle of prothoracic coxa on extreme anterior edge of cuticular fold such that seta is appressed to head capsule midway between cranial setae G1 and G2.

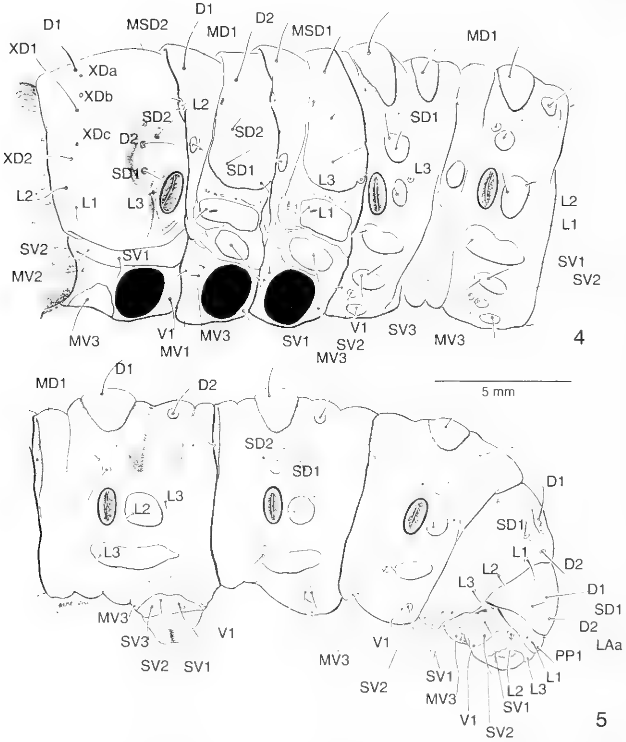
Spiracle vertically ovate, 0.89 mm high, 0.35 mm long; outer peritreme heavily sclerotized, darkly pigmented; inner (filter) recessed into atrium approximately 0.10 mm.

Prothoracic leg (Figs. 7–8): Prothoracic coxae proximate at base across ventral midline. Coxa with eight setae: anterodorsal pair (Cx1, Cx2) very small, subequal in size, near proximal edge of coxa with Cx1 dorsalmost; anteroventral setal pair (Cx3, Cx4) unequal in size with anterior Cx3 as small as Cx1 and posterior Cx4 longer and thicker; posteroventral setal pair (Cx5, Cx6) with Cx5 longest and most ventral; Cx6 near middle of posteroventral expanse of coxa, slightly shorter than Cx5; posterodorsal pair (Cx7, Cx8) subequal to Cx1; Cx7 near proximal edge of coxa and dorsalmost; Cx8 near upper middle of posterodorsal swelling of coxa. Trochanteral seta Tr1 microsetose, in extreme dorsal portion of trochanterofemoral membrane on anterior surface of leg; trochanteral pore Tra close by [second trochanteral pore Trb of Nielsen and Kristensen (1989) not evident]; trochanteral seta Tr2 microsetose, in trochanteral membrane at ventral (adaxial) edge of leg; trochanteral seta Tr3 microsetose, in extreme dorsal portion of trochanterofemoral membrane on posterior surface of leg. Femoral seta Fe1 the largest and longest seta on legs, midlength on ventral edge of femur; femoral seta Fe2 near distal posteroventral edge of femur. Six tibial setae [nomenclature as Nielsen and Kristensen (1989)], all in distal half of tibia; Ti1, Ti3, and Ti5 on anterior surface of tibia, dorsal, subventral, and ventral respectively; Ti2, Ti4, and Ti6 on posterior surface of tibia, dorsal, subventral, and ventral respectively; tibial pore Tia conspicuous, in posterodorsal surface of tibia near midlength. Four tarsal setae; dorsal pair near distal end of tarsus, Ta1 anterior, Ta2 posterior; ventral pair unmodified in shape, on ventral edge of tarsus, Ta3 at distal extremity, Ta4 directly basal to Ta3 near midlength of tarsus, shorter and thinner than Ta4. Tarsal claw smoothly tapered with slight ventral impression near base; without teeth or other modifications.

Mesothorax (Fig. 4): Two transverse dorsal shields continuously fused across dorsal midline; anterior mesothoracic shield bearing seta D1 (0.76 mm in length, subequal in size to D1 on prothorax), extending ventrad to level of seta XD2 on prothorax; D1 directly posterior to seta XD1 of prothorax. Posterior mesothoracic shield with seta D2 nearly twice the size of seta D1 (length 1.37 mm, subequal to seta D2 on prothorax), directly ventral to seta SD2, posterior to D1, and directly posterior to prothoracic seta SD1; posterior mesothoracic shield pale yellow with seta L3 in posteroventral corner; L3 very small, subequal to L3 on prothorax. Seta L1 on anterior end of distinct lateral shield; longitudinal pit posteroventral to L1, brown, sclerotized. Seta L2 subequal in size to L3, on fold directly below ventral extremity of anterior mesothoracic shield and directly anterior to SD1. Setae MD1, MSD1, and MSD2 located on surface of a single lateral fold which is occluded from view by posterior lobe of prothorax and bulging anterior shield of mesothorax (i.e., concealed in groove between prothoracic shield and mesothoracic shield). MD1 a microseta on outer edge of fold, directly anterior to seta SD2, with apex in space between thoracic shield and adjacent mesothoracic shield; seta MSD1 a microseta on anterior slope of fold, slightly ventrad of seta MD1, with apex in space between microsetal fold and prothoracic shield; seta MSD2 directly posterior to seta MD1 on posterior declivity of fold, with apex in space between microsetal fold and anterior mesothoracic shield. Setae MSD1 and MSD2 subequal in size, slightly smaller than seta MD1. Single SV seta in middle of large subventral, pale yellow shield; SV subequal or larger in size than setae D1 and SD2, but smaller than setae D2 and SV1. Two transverse plicae between mesothoracic coxae and posterior margin of prothorax; anterior plica very small, not visible in external ventral view, and bearing seta MV1 on its posterior face; posterior plica larger, visible in ventral view, bearing seta MV2 posterodorsal to seta MV3 on anterior declivity; MV2 directly opposite dorsal extremity of anterior margin of mesocoxa with apex extending forward and contacting posterior ventral region of prothorax. Setae MV1, MV2 and MD1 subequal in length; setae MSD1, MSD2, and MV3 subequal in length, slightly shorter than setae MV1, MV2, and MD1. Mesothoracic coxae separate at base. Subdorsal peg organ located in membrane on extreme anterior edge of posterior mesothoracic shield, opposite ventral posterior extremity of anterior mesothoracic shield, dorsoventrally midway between level of setae D2 and SD2. Mesothoracic leg as for prothorax, in general all setae slightly smaller, especially anterior coxal setae.

Metathorax (Fig. 4): As for mesothorax with the following differences; peg organ more exposed on leading edge of posterior metathoracic shield; anterior metathoracic shield slightly longer on midline than that shield on mesothorax; posterior metathoracic shield slightly shorter on midline than that shield on mesothorax; leg as on mesothorax.

Abdomen (Figs. 4–5): Generalized abdominal segment consisting of four annuli: first (anteriormost) annulus small, nearly hidden from view between second annulus and posterior edge of preceding segment, diminishing laterally to simple plica; second annulus largest, bearing seta D1; third annulus smaller than second, bearing seta



Figs. 4–5. Chaetotaxy of thoracic and abdominal segments of *Phassus* sp. (semischematic views). 4, Left side of thorax and first two abdominal segments. 5, Left side of abdominal segments 6–10. Symbols used: Ab1–2, Ab6–10, abdominal segments I, II, and VI through X; D1–D2, dorsal setae; L1–L3, lateral setae; LAa, lateral pore of Ab10; MD1, dorsal proprioceptor seta; MSD1–MSD2, subdorsal proprioceptor setae; MV1–MV3, ventral proprioceptor setae; PP1, paraproct seta; SD1–SD2, subdorsal setae; SV1–SV3, subventral setae; T1–T3, thoracic segments I to III; V1, ventral seta; XD1–XD2, anterior dorsal setae of T1; XDa–XDc, anterodorsal pores of T1.

D2; fourth annulus not sclerotized dorsally, subequal in size to third annulus.

Generalized setation of abdominal segments: Setae D1 and D2 subequal in size, similar in position to same setae on T3, D2 ventral to D1. Seta SD2 in center of large pale pinaculum, subequal in size to seta D1, about half size of seta SD1 on anterodorsal corner of same pinaculum. Peg organ conspicuous, dark, located in membrane midway between ventral side of plate D1 and dorsal side of plate bearing setae SD1 and SD2.

Spiracle on first abdominal segment (Ab1) largest, subequal to spiracle on T1 (height 0.92 mm, length 0.42 mm), that on Ab8 smaller (height 0.81 mm, length 0.42 mm), that on A2 smaller still (height 0.78 mm, length 0.42 mm) and those on A3–A7 subequal and smallest (height 0.69 mm, length 0.42 mm).

Abdominal segment 1: Seta MD1 ante-

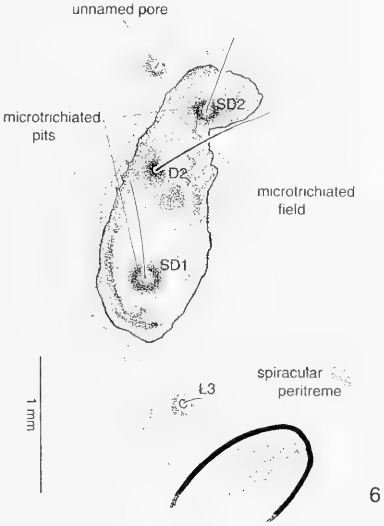


Fig. 6. Detail of microtrichiated field of larval prothorax, *Phassus* sp. Symbols used: D2, dorsal seta; L3, lateral seta; SD1–SD2, subdorsal setae.

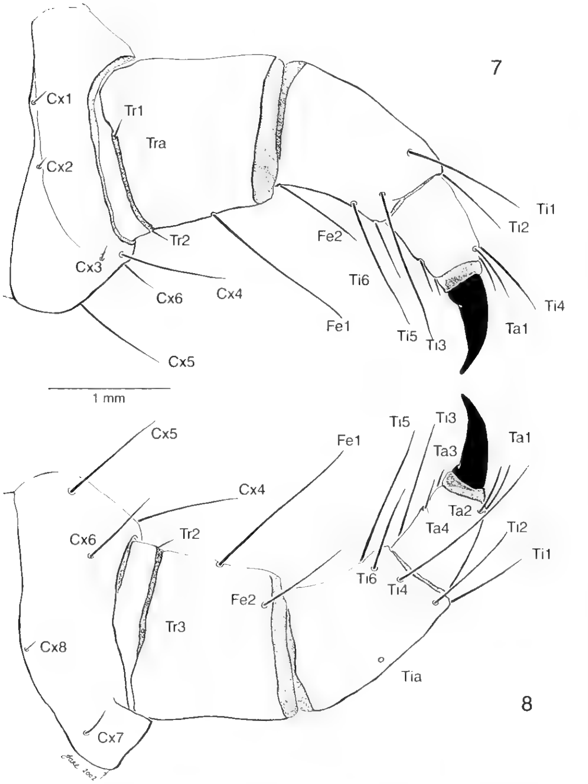
rior to peg organ, at bottom of groove between first and second annulus. Cuticle enfolded around seta MD1 forms open subspherical cavity, not collapsed by movement. Pinaculum of seta L2 directly posterior to spiracle; pinaculum of seta L1 dorsoposterior to pinaculum L2. Seta L3 slightly anterior to spiracle on extreme anterior edge of large longitudinal plate extending posterior to intersegmental groove. Setae SV1, SV3 located on dorsal half of same pale pinaculum.

Abdominal segment 2: As for Ab1 with following differences: Seta MD1 located near bottom of grove between annulus 1 of Ab2 and annulus 4 of segment Ab1; large oval plate without setae on annulus 1 at level of spiracle, subequal in size to spiracle; seta SD2 on small pinaculum approximate and dorsal to larger pinaculum bearing SD1; seta L1 located on extreme dorsoposterior edge of plate bearing L2, not on separate plate; seta MV relatively large, more than twice length of seta MV on segment Ab1.

Abdominals segments 3–6: As for segment Ab2 with following differences: seta SD2 on distinct pinaculum on segments Ab3–Ab4, that pinaculum reduced or absent on Ab5–Ab7; seta L1 on distinct small pinaculum posterodorsal to larger plate bearing seta L2; seta SV1 largest, most posterior, and dorsalmost of any SV seta; seta SV2 anteroventral to seta SV1 on same plate, half the length of SV1; seta SV3 anteroventral to SV2 on same plate, about half length of seta SV1; seta V1 directly between base of prolegs on same sclerotized plate encircling proleg and bearing all SV setae; seta MV3 directly anterior to proleg on extreme anterior edge of sclerite bearing setae V1 and SV1–SV3. Crochet conformation as uniordinal biserial ellipse, outer series with crochets greatly reduced in length.

Abdominal segment 7: As for segment Ab6 with following differences: setae SV1 and SV2 located on same plate, half the diameter of homologous plate on Ab2; seta SV3 absent; seta V1 directly ventral to seta SV2 on very small sclerotized plate; seta MV3 directly anterior of seta V1, subequal in size to seta MV3 on other abdominal segments.

Abdominal segment 8: As for segment Ab7 with following differences: spiracle subequal in size to that on segment Ab2; seta MD1 exposed in flat region anterior to annulus 1; seta SD1 on very small basal plate, SD2 anterodorsal to SD1, without sclerotized basal pinaculum; no prespiracular plate on annulus 1; seta L1 lacks pinaculum; plate around seta L2 smaller than adjacent spiracle; seta L3 located on small pinaculum anterior to and slightly separated from larger lateral plate without setae; setae SV1 and SV2 very close on shared basal pinaculum; seta V1 on small distinct plate; seta MV3 much smaller than same seta on segments Ab2–Ab7, near outer edge of intersegmental groove, halfway between SV1 and V1.



Figs. 7–8. Chaetotaxy of prothoracic leg of last instar larva of *Phassus* sp. 7, Anterior view of left prothoracic leg. 8, Posterior view of left prothoracic leg. Symbols used: Cx1–Cx8, coxal setae; FE1–FE2, femoral setae; MTRa, anterodorsal pore of trochanter; Ta1–Ta4, tarsal setae; Ti1–Ti6, tibial setae; Tia, posterodorsal pore of tibia; Tr1–Tr3, proprioceptor seta of trochanter.

Abdominal segment 9: As for segment Ab8 with following differences: only a single obvious annulus; all setae with reduced basal pinacula; D1 setae much closer to each other across midline than are setae D2 across midline; SD1 directly ventral to D1; seta SD2 missing; MD1 anterior to SD1, extending into intersegmental groove on anterior slope of segment; setaè L1, L2, and L3 in vertical row, equidistant, directly ventral to D2; setae SV1 and SV2 as on segment Ab8, directly ventral to L3 but not on shared basal pinaculum; seta V1 strong, near ventral midline; seta MV3 slightly ventral to SV2, enfolded within intersegmental groove.

Abdominal segment 10: Three setae (D1, D2, SD1) on dorsal anal shield; two setae (here interpreted as seta L1 (anterior) and paraproct seta PP1 (posterior)) and one pore (LAa) on posterior plate; two setae below anus and dorsal to proleg (interpreted as setae L2 (anterior) and L3 (posterior)); two lateral setae anterior to proleg (interpreted as setae SV1 (dorsal) and SV2 (ventral)); two ventral setae anterior to proleg (interpreted as seta V1 (posterior near edge of planta) and nearly macrosetose MV3 (near intersegmental groove with segment Ab9). Crochet conformation triserial, uniordinal, arranged as two semicircular loops on each anal proleg.

PROBLEMS WITH HOMOLOGY AND SETAL NOMENCLATURE

The multiplicity of chaetotaxic systems for lepidopterous larvae, and in particular for hepialids, makes it difficult to recognize and name setae that are homologous at the ordinal level. Resolution of this problem is not possible in this paper and awaits more extensive research on setation in Exoporia, other basal clades of Lepidoptera, and Ditrysia. As an initial set of concerns for future research in this area, we provide an annotated list of the setal groups found to be problematic in this study.

1. Thoracic and abdominal setae of the MV and V groups of Hinton (1946). Confusion arises from variation in stereographic position of setae and their relative size and structure.

2. Setae of the SV group, especially on the abdomen. This is a classic dilemma in many ditrysian superfamilies, especially for variation on the first two abdominal segments, and segments where prolegs may be reduced.

3. Setation of abdominal segment 10. This segment consists of problems of both number and position of setae on the anal shield (D and SD groups) and of presence and placement of setae on more ventral portions of the segment (L, SV, and V groups).

4. MD and MSD microsetae on thoracic segments. The problem here may be due to inadvertent but alternate nomenclature applied by Hardy (1973) and Yasuda and Abe (1986). We concur with Nielsen and Kristensen (1989).

5. Head setae. Many problems with almost every setal group on the head result from confusion about variable placement and size of setae. Although the chaetotaxy is not altered, a more thorough discussion of this problem is given below.

6. D, SD, and MXD group setae and associated pores on the prothorax. These are variable features unique to Exoporia. Prothoracic D and SD setae are discussed in detail below.

Setation of the head.—Investigators using setae in the comparative study of Lepidoptera larvae have usually followed prior convention in chaetotaxy. Students of hepialid larvae have revealed consistent differences in setal placement with ditrysian larvae, and these have resulted in a number of nomenclatural systems, each differing slightly from the others. This is especially true for setae of the head where a system dating from Heinrich (1916), Gerasimov (1935) and Hinton (1946) was modified by Hasenfuss (1969) for Hepialidae and by Stehr (1987) for Ditrysia, then variously modified again for Hepialidae by Wagner (1987), Wagner et al. (1989), Leonard et al. (1992), and Nielsen and Kristensen (1989). To avoid confusion other workers have wisely followed the nomenclature of recent authors when comparing setae within Hepialidae (Dugdale 1994, Zilli 1998). No worker since Hasenfuss has proposed and adequately defended a chaetotaxic system that seeks to recognize homology across the entire order, as such an undertaking would require detailed study of all world lineages.

For some groups of cranial setae there is no controversy among published descriptions in the last fifty years. All workers agree on the naming of setae on the frontal and adfrontal sclerites, and concur that pore AFa is absent in hepialids. They further agree that there are two mandibular setae, but do not distinguish between them (the basal seta is here named M1, the distal seta M2). All workers agree on the number and placement of L-group setae, and of SS-group setae (sometimes labeled SO1–SO3 (subocellar setae) as opposed to SS1–SS3 (substemmatal setae)).

For other groups of cranial setae there are major differences in opinion as to nomenclature. These differences may be clarified by noting how various authors have treated each major group of setae. Treatment of clypeal setae is divided into two groups: 1) those naming the lateral setae C1 (Hinton 1946, Hasenfuss 1969, Nielsen and Kristensen 1989, Dugdale 1994), and 2) those naming the medial setae C1 (Wagner 1987) as in Ditrysia (Stehr 1987).

Treatment of labral setae is ignored by all workers, but all concur in their drawings that hepialids have five pairs of externally visible labral setae. We here call these LR1–LR5 with a single pore, LRa, following the nomenclature of Rawlins (1992) as applied to ditrysian larvae. The homology of the lateral labral seta, LR5, with the ditrysian condition is uncertain as there are two lateral setae on each side in that lineage, LR5 and LR6.

Numbering of stemmata in hepialids is not provided by any of these workers. The system followed here is consistent with that used for Ditrysia, assigning numbers for the left side of the head from 1 to 6 in a counter-clockwise direction such that the most ventral stemma near the posterior edge of the antennal fossa is 5.

Treatment of S-group setae is divided into three groups: 1) those following the ditrysian system (Stehr 1987) and recognizing three S-group setae with S1 inside the stemmatal circle and S3 microsetose (Hasenfuss 1969), 2) those following the ditrysian system but considering S3 to be absent, replaced by seta G2 or MG2 (Nielsen and Kristensen 1989, Dugdale 1994), and 3) those adopting a system with S1 anterior to the stemmatal region and adjacent to the anterior mandibular condyle, S2 within the stemmatal field, and S3 immediately posterior to the stemmata (Hinton 1946, Wagner 1987).

Treatment of the genal setae may be divided into two groups: 1) those using the ditrysian system (Stehr 1987) with a single genal seta and pore, MG1 and MGa (Hasenfuss 1969), and 2) those recognizing two genal setae and a pore, G1, Ga, and G2 (or MG1, MGa, and MG2) (Hinton 1946, Wagner 1987, Nielsen and Kristensen 1989, Dugdale 1994).

Treatment of the dorsal setae is also divided into two groups: 1) as in Ditrysia (Stehr 1987) with three dorsal setae and a pore (MD1–MD3 and MDa, or V1–V3 and Va) of which MD1 or V1 is macrosetose (Hasenfuss 1969, Nielsen and Kristensen 1989, Dugdale 1994), and 2) those recognizing two dorsal setae and a pore, all microsetose (MD2–MD3 and MDa, or V2–V3 and Va) (Hinton 1946, Wagner 1987).

All workers agree on naming P1 setae, but treatment of P2 setae is divided into three groups: 1) the ditrysian condition with P2 posterodorsal to P1 and associated with pore Pb (Stehr 1987), 2) the ditrysian condition with P2 posterodorsal to P1 but not associated with a pore Pb (Hinton 1946, Wagner 1987), and 3) with P2 lateral or lateroventral to P1 and associated with a pore Pb (Hasenfuss 1969, Nielsen and Kristensen 1989, Dugdale 1994).

All past treatments agree on recognition of seta A2, and the absence of pores Aa and Pa. Treatment of other A-group setae is controversial and may be divided into two groups: 1) those naming the anteriormost seta near the anterior articulation of the mandible as A1 with seta A3 near stemma 2 (the ditrysian system (Stehr 1987) followed for Hepialidae (Hasenfuss 1969, Nielsen and Kristensen 1989, Dugdale 1994)), and 2) those naming the seta associated with stemma 2 as A1, and that associated with pore Pb as A3 (Hinton 1946, Wagner 1987).

Careful study of the bewildering situation above reveals that the fundamental conflict for determining setal homologies is between the size of setae (microsetose versus macrosetose) and their stereographic placement relative to each other and to pores. If the size of setae is ignored, then cranial setae of Ditrysia and Hepialidae are spatially and numerically consistent with one exception: seta P2 in hepialids is displaced ventrally and laterally from the expected position in Ditrysia. This arrangement requires recognizing the ventral genal microseta in hepialids (MG2 of authors) as homologous with the posterior macroseta S3 of Ditrysia and treating the posterior dorsal macroseta of hepialids as homologous with the anterior dorsal microseta of Ditrysia (MD1 of authors). Under this system there is no need to violate consistent spatial associations of A-group or S-group setae as proposed by Hinton (1946) and Wagner (1987).

If the microsetose or macrosetose condition of setae is hypothesized to be so important that setae of different sizes cannot be considered homologous, then a diversity of ad hoc hypotheses on setal homology are required to account for all setae. This requires switching the nomenclature of seta A1 and S1, thereby changing their stereographic placement on the head capsule relative to the mandible and stemmata, increasing the number of genal microsetae from 1 to 2, decreasing the number of dorsal microsetae from 3 to 2, hypothesizing the complete disappearance of macroseta S3, associating seta A3 with pore Pb, or removing seta P2 from association with that pore, and so on.

Given that both ditrysian and exoporian larvae possess the same number of primary cranial setae in very similar spatial relationship to each other and to cranial landmarks such as the antennal fossa, mandibular condyles, adfrontal sclerites, and stemmata, a parsimonious hypothesis of homology for these setae involves accepting major changes in setal size and a lateroventral shift in the position of seta P2. A chaetotaxic system corresponding to such homology requires application of names for macrosetae to microsetae (the hepialid seta MG2 becomes S3) or vice versa (the hepialid macroseta V1 become MD1). In retrospect it is unfortunate that a special nomenclature for microsetae arose following Hinton (1946) as this may have obscured major evolutionary shifts in setal size and function, and in any event has greatly complicated hypotheses of homology with an already abstruse chaetotaxy. This paper is not the place to present a testable, homologous system of nomenclature for setae on larval Lepidoptera or other holometabolous larvae, but the above discussion should underscore the need to do so in order to more clearly understand the evolution of setal size, placement, and function.

Microtrichiated pits and fields.—Previous authors have used a variety of terms to describe regions of microtrichiated cuticle surrounding the base of setae in larval Lepidoptera, including "pocket" (Rawlins 1984), "pigmented sensory pit" (Wagner 1987), "microtrichiated pit" (Nielsen and Kristensen 1989), "pigmented pit with microtrichiated walls" (Rawlins 1992), "microtrichial bed" (Leonard et al. 1992), and "felted pits" (Dugdale 1994). These terms confuse two different cuticular features, both distinguished by the presence of microtrichiae: 1) a relatively small, deeply impressed pit surrounding the base of a single seta, and 2) a more extensive, concave or flat region that may enclose one or more setae. We limit the expression "microtrichiated pit" to the former condition, almost always in association with filiform tonosensilla, and use the expression "microtrichiated field" to describe the latter. Microtrichiated pits and fields often occur independently, but pits can also be located within fields as in *Phassus,* and may be developmentally related, differing only in degree of expression.

Prothoracic setae.—A distinctive, and possibly apomorphic feature of some hepialid larvae is the presence of three setae (D2, SD1, and SD2) enclosed by a single continuously microtrichiated field, as opposed to having the field divided into two separate regions, each enclosing a seta. Because these setae are ventrally displaced from the position D2 occupies in Ditrysia, there has been confusion over their homology relative to other thoracic segments and prothoracic setae in other Lepidoptera. The problem is clarified but not resolved in the following paragraphs.

Criteria most often used to determine the homology of setae on a single larva may be broadly grouped into two categories: *Criterion 1,* stereographic position relative to other setae with respect to body axes (dorsal, ventral, anterior, posterior), and *Criterion 2,* morphological details of the seta itself (size, shape, color, surface microsculpture, and others) including region of articulation with adjacent cuticle. Analysis of homology for setae results from comparative study of their position and morphology between developmental instars and between larvae of different taxa. Ontogenetic comparisons are problematic, especially those involving first instars, as there is no a priori reason to believe that apomorphic features could not have evolved in the first instar. No first instar *Phassus* larvae were available for study.

To determine the homology of setae D2, SD1, and SD2 under the above criteria, we consider first the situation for each condition in Ditrysia.

Seta D2 Crierion 1: D2 dorsal and posterior to SD1 and SD2 (or at most with D2 directly dorsal to those setae).
Criterion 2: D2 variable in length, often shorter than SD2 and/or subequal in length to SD1; never positioned in a microtrichiated pit on any segment, and always a typical macroseta, never a filiform tonosensillum.

Seta SD1 Criterion 1: SD1 anterior and ventral to SD2, at most directly anterior or directly ventral to SD2 (never posterior or dorsal to SD2).
Criterion 2: SD1 shorter than SD2 in many lineages, but in some subequal or greater in length than SD2; positioned in a microtrichiated pit in some lineages; a filiform tonosensillum in some groups.

Seta SD2 Criterion 1: as above.
Criterion 2: as above, not associated with microtrichiated pit and not a filiform tonosensillum.

Contrast the above pattern to that observed in *Phassus* using the terminology of Wagner (1987):

Criterion 1.—D2 is ventral and anterior to SD2, dorsal and posterior to SD1. Conclusion: *Placement of both D2 and SD2 violates stereographic conditions both dorsal-ventral and anterior-posterior.* Seta SD1, however, is in accordance with Criterion 1 in the Ditrysia.

Criterion 2.—D2 slightly longer than SD1 and SD2 which are subequal in length; D2 a strong, typical tactile macroseta, but SD1 and SD2 are filiform tonosensilla positioned in microtrichiated pits; all three setae and pits within a microtrichiated field. Conclusion: D2 in accordance with Criterion 2 (large macroseta without a microtrichiated pit); SD1 in accordance (tonosensillum with a microtrichiated pit); *SD2 not in agreement with Criterion 2 being a tonosensillum in a microtrichiated pit.*

Switching names for setae D2 and SD2 conforms to the nomenclature of Nielsen and Kristensen (1989) produces the following situation under Criteria 1 and 2.

Criterion 1.—All setae are in accord with the condition in Ditrysia.

Criterion 2.—D2 subequal in length to SD1 and shorter than SD2; SD2 a strong, typical tactile macroseta, but SD1 and D2 are filiform tonosensilla positioned in microtrichiated pits; all three setae and pits within a microtrichiated field. Conclusion: SD2 and SD1 in accordance with Criterion 2, but *D2 not in agreement with Criterion 2 being a tonosensillum in a microtrichiated pit.*

The above analysis of setal condition in

Phassus reveals a conflict with both Criterion 1 and Criterion 2. Resolution requires weighting one over the other. In this case, weighting Criterion 2 over Criterion 1 requires hypothesizing convergent development of complex morphological features (tonosensillum in a microtrichiated pit) for either seta SD2 (Wagner 1987) or seta D2 (Nielsen and Kristensen 1989). Weighting Criterion 1 over Criterion 2 requires hypothesizing shifts in spatial placement for setae D2 and SD2 under Wagner's terminology, but not under that of Nielsen and Kristensen (1989). It is tempting to conclude that the most parsimonious solution would be the latter system, but this requires development of D2 as a tonosensillum in a microtrichiated pit, a situation not encountered elsewhere in Lepidoptera. The alternative system (Wagner 1987) requires relatively slight shifts in stereographic position for two setae and development of SD2 as a tonosensillum, a condition we feel more likely than for D2 insofar as tonosensilla are usually SD group setae in other Lepidoptera.

It is important to realize that a testable determination of which criterion to emphasize is not possible without further morphological and comparative study. For the time being we prefer to accept slight shifts in setal position and tonosensillar morphology for SD2 as more likely than convergent development of tonosensillar morphology in D2. Favoring a chaetotaxic system emphasizing the greatest likelihood of homology, we have used the terminology of Wagner (1987) in agreement with the logic of Dugdale (1994). Resolution of this problem may result from comprehensive study of tonosensilla for all larval instars across Lepidoptera.

IMPLICATIONS FOR PHYLOGENY AND BIOGEOGRAPHY

The inclusion of D2 with SD1 and SD2 within a common microtrichiated field in *Phassus* supports a monophyletic relationship with the Asian/Australasian stem-boring Hepialidae with the exception of *Zelotypia* that is characterized by two separate microtrichiated areas for SD1 and SD2. Dugdale's (1994) reference to all three setae being included in *Zelotypia* appears to be incorrect (Dugdale 1999, pers. comm.). A further larval character that may support a close affinity between *Aenetus* and *Phassus* is the elongate shape of the pit L3a on the mesothorax and metathorax. This pit is slightly elongate in *Zelotypia* and *Endoclita*. The pit is round in larvae of the root/stem boring *Phymatopus californicus* (Boisduval) of North America, and the detrital feeding *Dumbletonius unimaculata* (Salmon) (as *Trioxycanus enysii* of authors) in New Zealand (Grehan et al. 1983). The presence and shape of pits have been overlooked in many larval descriptions but may provide significant phylogenetic characters. The anterior margin of the labrum of *Aenetus*, *Phassus*, and *Endoclita* is trilobate, a feature also recorded from *Sthenopis*, *Phymatopus*, *Zelotypia*, and *Leto* (Table 1). The larval description of *Cibyra serta* (Schaus) by Rojas de Hernández and Chacón de Ulloa (1982) illustrates a prothoracic microtrichiated field common to SD1 and SD2 that excludes D2. Larval descriptions of the South American wood-borer *Trichophassus* are insufficient to confirm a trisetose setal pit, and the adult male of *Trichophassus giganteus* lacks metatibial androconia (Briquolet 1956). Kristensen (1998) notes that metatibial androconia have evolved several times in Lepidoptera. Androconia of *Oncopera* and *Peurmytrans* may have originated separately from those of the wood-borer lineages since the scales of *Aenetus*, *Endoclita* and *Phassus* are pale reddish brown or orange brown in contrast to the gray brown androconia of *Oncopera* and *Puermytrans* (Table 1). At least one species of *Aenetus* lacks metatibial androconia (Wagner and Rosovsky 1991).

Kristensen's (1998) suggestion for a close relationship between the monotypic wood-boring genus *Leto* of South Africa and the Australasian *Aenetus* was based on biogeographic speculations and is not otherwise substantiated (Kristensen pers. comm., 1999). Metatibial androconia are absent from *Leto venus* (Cramer) and larvae have no michrotrichiated fields at the base of SD1, SD2, or D2. Although larvae of *L. venus* are wood-borers, callus feeding is not recorded and pupae reside in a unique tubular silk/frass extension of the tunnel beyond the bark surface (Peabody Museum of Natural History specimens). We conclude the genera *Phassus, Endoclita,* and *Aenetus* represent a monophyletic lineage in reference to the trisetose pit, with the possibility that *Zelotypia* and *Cibyra* are more distantly related, and possibly comprising a monophyletic lineage of callus feeders and woodborers along with the *Phymatopus*-clade within the Hepialidae sensu stricto.

Exoporian and hepialid lineages are predicted by Nielsen et al. (2000: 832) to be 'very much' older than the fragmentation of Gondwana. The oldest fossil record for hepialoids are Paleocene Europe, mid-Miocene China (Kristensen and Skalski 1999) and Eocene New Zealand, the latter being fossil wing scales that may be referable to the extant genus *Wiseana* Viette (Evans 1931, Harris 1984). A purported Upper Cretaceous amber mnesarchaeid wing is considered by Kristensen and Skalski (1999) to be unsubstantiated in the absence of "strong family autapomorphies" in the specimen. In the absence of a well-endowed fossil record, Holloway and Nielsen (1999) regard the age of Mesozoic events influencing distribution patterns within Lepidoptera to be an open question. Grimaldi's (1999) interpretation of fossil evidence proposed an Upper Jurassic origin for tongued Lepidoptera (Glossata) and a Cretaceous origin for basal glossatan families (including Hepialidae). Grehan (1991) suggested the biogeographic patterns of Lepidoptera and Angiospermae support a pre-Cretaceous origin for lepidopteran lineages to family level. Lack of evidence for discrete continental monophyletic exoporian faunas is contrasted by Nielsen et al. (2000:832) with their "temptation" to view the Exoporia as relicts of Gondwanic fragmentation and resulting isolation and speciation.

Most Mesozoic models of evolution are linked to the geological fragmentation models of Pangaea or its Gondwanic and Laurasian fragments (Craw 1982). Distribution patterns congruent with this history are expected to exhibit distributional and phylogenetic links across the Atlantic and Indian Oceans resulting from the breakup of ancestral distributions on the supercontinents of Gondwana and Laurasia. This historical model is consistent with the distributions of primitive hepialid lineages (Fig. 9) comprising a biogeographic track connecting Australia, Africa, North America, and Eurasia (this connection does not assume a monophyletic status for these genera). In contrast, the *Endoclita/Aenetus/Phassus* clade is absent from Africa, although pres-

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Figs. 9–12. 9, Biogeography of 'primitive' Hepialidae. A minimal spanning link connects the generalized distributions of the African *Afrotheora* and *Antihepialus* with *Fraus* across the Indian Ocean basins (with baseline of track denoted by solid square) with an additional link to *Gazoryctra* between the African genera and the North American and Eurasian *Gazoryctra.* This pattern may be compatible with conventional 'Pangaean' origin although the genera are currently not known to be monophyletic (distribution data from Holloway and Nielsen 1999: Fig. 21–22). 10, Pacific biogeography of *Endoclita, Aenetus, and Phassus.* The nearest neighbor criterion links the distributions of *Aenetus* (Australasia) and *Endoclita* (India-eastern Asia) with the American *Phassus* across the Pacific (baseline as a solid square). This spatial homology suggests the evolution of this lineage is more closely linked to the geological history of the Pacific basin than with the Atlantic or Indian oceans of Gondwana (distribution data from Grehan 1987, Nielsen and Robinson 1983). 11, Pacific interpretation for the distribution of *Phymatopus*-clade. Although the North American '*Phymatopus*' is in closest geographic proximity to the related European *Phymatopus* directly across the Atlantic, the western distribution of '*Phymatopus*' may be the result of a former trans-Pacific connection through extinction of Asian representatives as indicated here

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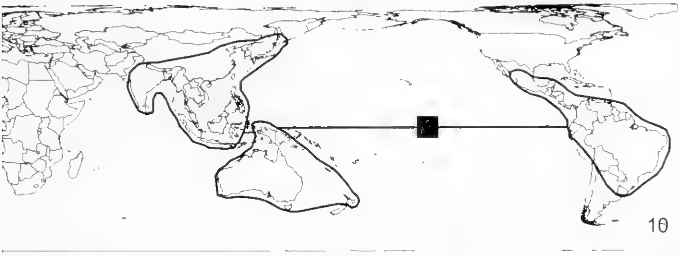

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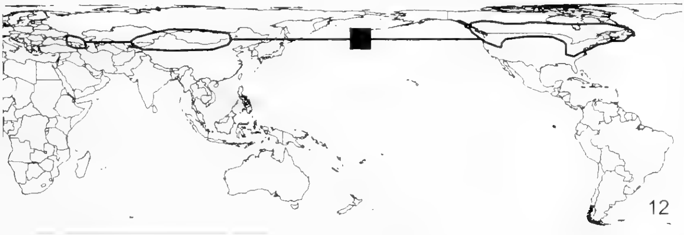

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by a north Pacific track and baseline (distribution data from Wagner 1985). 12, Pacific interpretation for the distribution of the *Sthenopis–Zenophassus* clade. As with the *Phymatopus* group, the Old World-New World disjunction between *Sthenopis* and *Zenophassus* may lie across the Pacific rather than Atlantic Ocean basins (distribution data from Tindale 1941—including Chinese records of '*Sthenopis*' aucttorum nec Packard [1865] of uncertain status (Nielsen et al. 2000)).

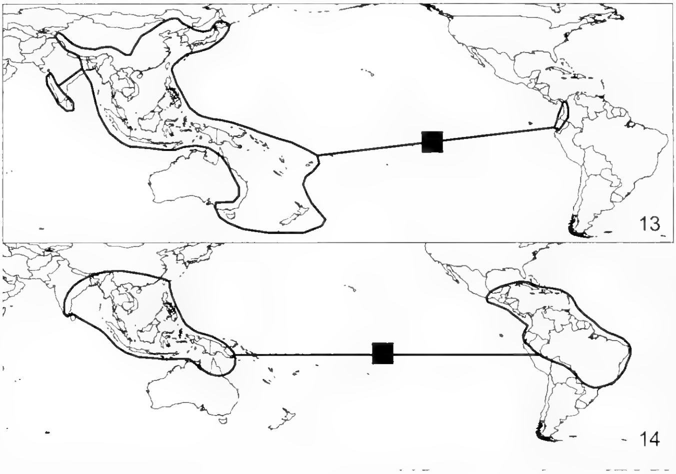

Fig. 13–14. Pacific spatial patterns. 13, Track for perichaetine earthworms (compiled from Easton 1987). 14, Track for the fabaceous genus *Ormosia* (from Croizat 1976, Fig. 1).

ent in the Gondwanic fragments of India, Australasia, and South America (Fig. 10).

A Gondwanic history for wood-boring Hepialidae may be supported by a close phylogenetic relationship being established with an African group such as *Leto* (Grehan 1984). Alternatively, the African gap may be accounted for by extinction of Gondwanic members or a biogeographic history for wood-boring and callus-feeding Hepialidae that bypasses Africa altogether. Gondwanic distributions bypassing Africa include tracks connecting Central and North America with the Mediterranean and Indian Ocean via the Tethyan geosyncline (Croizat 1964). Absence of wood-boring Hepialidae from North Africa and Europe does not support this biogeographic history. Distribution of the *Endoclita/Aenetus/Phassus* group is, however, consistent with Africa being 'bypassed' by a non-Gondwanic origin involving the Pacific Basin. This biogeographic connection may also be applicable to the *Phymatopus*-clade (Fig. 11) and to *Sthenopis/Zenophassus* (Fig. 12). There are also similarities in the geographic ranges of *Aenetus/Endoclita* with other Pacific groups such as the perichaetine earthworms (Fig. 13) in the Old World (Easton 1987) and the angiosperm genus *Ormosia* Jackson (Fig. 14) in both Old and New Worlds (Croizat 1976, fig. 1).

The geological evolution of the Pacific is a controversial biogeographic and geological subject. Geohistorical reconstructions treating the Pacific as a permanent oceanic basin are contradicted by the extensive documentation of allochthonous terranes around the Pacific Rim and Tethyan geosyncline. These terranes are widely interpreted as fragments of former Mesozoic and Tertiary island arcs or microcontinents of Pacific origin (Craw et al. 1999, Grehan 2001). Geological efforts to resolve the historical relationships between the circum-Pacific terranes include proposals for disruption of Mesozoic microcontinental fragments (e.g., Nur and Ben-Avraham 1977, 1989), fragmentation of oceanic superplume magmas (Kimura et al. 1994), and former island-arc bounded plates (Moores 1998). Pacific distributions comprise a biogeographic element distinct from Gondwanian or Laurasian distributions spanning the Indian Ocean and Pacific basins (Croizat 1958, 1976) and current biogeographic studies continue to verify a distinct Pacific pattern of biogeography for groups ranging from cycads and conifers (Contreras-Medina et al. 1999) to angiosperms (Heads 1999), dragonflies (De Marmels 2000), and dinosaurs (Rieppel 1999). A Pacific biogeographic homology for the origin of an *Endoclita/Aenetus/Phassus* lineage, possibly along with other Hepialidae, provides a historical solution to the absence of Exoporia from West Africa (except for the marginal presence of *Antihepialus* in western Congo/Zaire) and Madagascar described by Nielsen et al. (2000: 831) as "extraordinary and inexplicable." Absence of taxa from West Africa and Madagascar, far from extraordinary, is commonplace with many such groups being Pacific in origin whereas West Africa and Madagascar are regions central to the Atlantic and Indian Ocean biogeographic patterns of Gondwana (Croizat 1952, 1958, 1968a–b). The Pacific homology proposed here for wood-boring Hepialidae corroborates the caution expressed by Nielsen et al. (2000) against interpreting distribution of Exoporia as relicts of Gondwanic fragmentation. The lack of exoporian monophyly within continents (Nielsen et al. 2000) may be the result of ancestral differentiation predating geological dissolution of both Pacific and Gondwanic regions.

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DIVERSITY, ABUNDANCE, AND SEASONALITY OF ADULT AND LARVAL SYMPHYTA (HYMENOPTERA) IN THE GEORGE WASHINGTON NATIONAL FOREST, VIRGINIA, AND THE MONONGAHELA NATIONAL FOREST, WEST VIRGINIA

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Abstract.—Adult Symphyta richness and abundance were studied using data collected from 36 Malaise traps in the Monongahela National Forest, Pocahontas County, West Virginia, and in the George Washington National Forest, Augusta County, Virginia. A total of 8,884 adults representing 155 species in 49 genera and 8 families were collected. Diversity estimators suggest that approximately 81% of the actual species present on the two forests were sampled over five years (1995–1999). Fifty percent of all adults (4,481) were *Acordulecera dorsalis* Say (Pergidae). The next most abundant species were *Pristiphora banksi* Marlatt (Tenthredinidae) (12.8%), *Pachynematus corniger* (Norton) (Tenthredinidae) (4%), *Pracharactus rudis* (Norton) (Tenthredinidae) (3%), and *Taxonus pallipes* (Say) (Tenthredinidae) (2%). Larval symphytan richness and abundance were determined by foliage collections from *Quercus* spp., *Carya* spp., and *Acer* spp. Symphytan larvae from foliage numbered 11,621 specimens representing eight genera. Sixty-three percent of all larvae (7,373) were *Acordulecera* spp. The next most abundant genus was *Periclista* (2,328) which accounted for 20% of the total larvae. Differences in species richness and abundance of both adults and larvae occurred between forests and between years.

Key Words: Symphyta, richness, abundance, diversity, *Acordulecera dorsalis*

Symphyta are an important and abundant part of the insect fauna in hardwood forests. The adults are pollinators (Goulet 1996) and the larvae of at least two species have been responsible for heavy defoliation of oaks (Eidt and Nichols 1970, Matuzewski and Ward 1977, Hutchinson 1998). Much attention has been given to the conifer-feeding Symphyta; however, little is known about the richness or abundance of the Symphyta that feed on hardwoods and other Symphyta associated with forest ecosystems. Malaise traps commonly sample adult sawflies, but have seldom been used to assess sawfly community composition. Though Symphyta comprised the bulk of the Hymenoptera collected by Malaise traps in one New York survey (Matthews and Matthews 1970), the focus was not Symphyta, so the researchers gave no details about the species captured or their abundance. Similarly, a study comparing the ef-

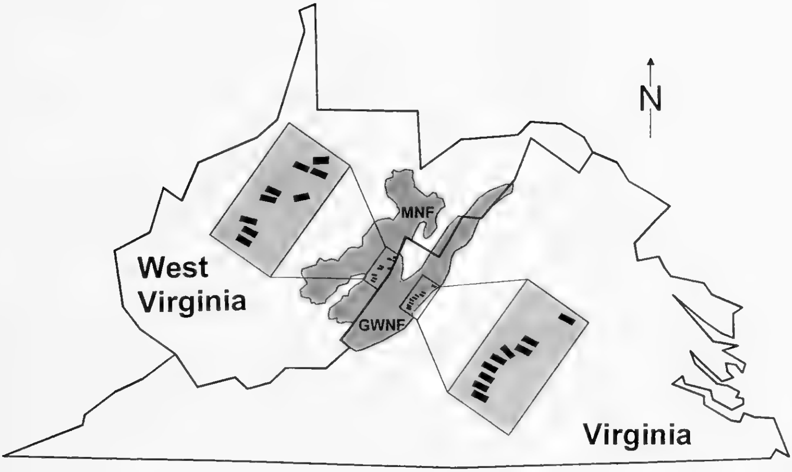


Fig. 1. Location of study plots in the George Washington National Forest and Monongahela National Forest.

fectiveness of different types of Malaise traps also mentioned Symphyta (Darling and Packer 1988), but they gave no information regarding richness or abundance in their predominantly oak setting. Other surveys have been conducted in urban environments (Smith and Barrows 1987) or have focused on a single genus (Smith 1991). The purposes of this study were to use Malaise traps for adults and foliage collections for larvae to determine which sawfly species are present in oak-dominated forests, measure their relative adult abundances, and document their adult seasonal occurrences.

MATERIALS AND METHODS

This study was part of a long-term analysis of nontarget effects of *Bacillus thuringiensis* variety *kurstaki* and Gypchek™ when used to suppress *Lymantria dispar* (L.) (Lymantriidae). Eighteen 200-ha study plots were established in gypsy moth susceptible, oak-dominated forests. Plots one through nine were located in the Deerfield Ranger District of the George Washington National Forest (GWNF), Augusta County, Virginia (Fig. 1). The GWNF plots range in elevation from 586 to 791 m and are located in a xeric forest of mixed oak and pine. Plots 10 through 18 were located in both the southern Greenbrier Ranger District and the Marlinton Ranger District of the Monongahela National Forest (MNF), Pocahontas County, West Virginia (Fig. 1). The MNF plots range in elevation from 860 to 1,070 m and are more mesic than the GWNF plots (Butler and Strazanac 2000). These forests were selected for study in 1994 because they contained a high percentage of gypsy moth-preferred hosts and were located ahead of the leading edge of gypsy most movement. Each 200-ha plot contained a 30-ha subplot within which were two sites, one located on a ridge and the other in a valley or near a stream.

Sampling adult Symphyta was done using Townes-style Malaise traps (Townes 1962). Each trap was designated by both plot number and lower or upper site. Two Malaise traps were operated per plot, one on each site for a total of 36 traps for the study. Each trap was oriented on the plot so that its spine ran east-west. Each Malaise head contained a jar with 175 ml of 70% ethanol and was collected on the same day each week and replaced with a fresh jar of ethanol. Sampling was for 15 weeks from early May through mid-August for five years. In the laboratory, sawflies were separated from other insects. Specimens were mounted and identified by DRS.

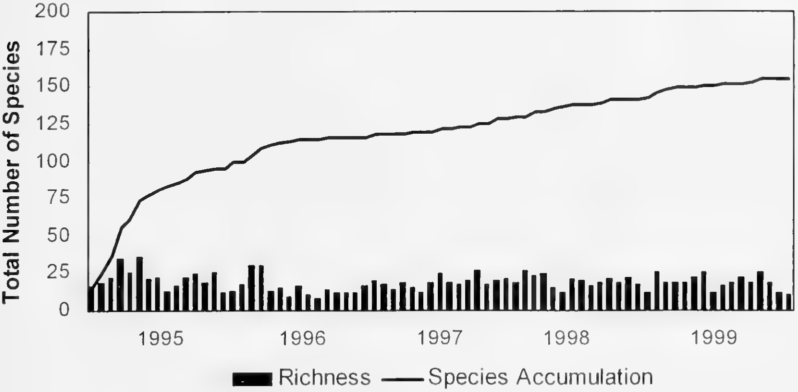
For larvae, five foliage samples per plot were taken each of 15 weeks from the lower and middle forest canopy using aluminum pruning poles with large plastic catch bags. Foliage samples were taken well within the boundaries of each plot, but just outside the bourdary of each subplot. One sample consisted of 21 branch-tip clippings from any species of maple (*Acer* spp.) except striped maple. The second sample consisted of 15 branch-tip clippings of any species of hickory (*Carya* spp.). The final three samples each consisted of 21 clippings of oak and contained either members of the red oak group [including scarlet oak (*Quercus coccinea* Muenchh.), black oak (*Q. velutina* Lam.), and red oak (*Q. rubra* L.)]; or the white oak group [chestnut oak (*Q. prinus* L.); or white oak (*Q. alba* L.)]. The foliage samples were taken to the laboratory and stored in a walk-in cooler until the arthropods could be removed from the foliage by hand during the following two days. All symphytan larvae were removed from the foliage and preserved in 70% alcohol for identification. Specimens were identified by DRS and RB.

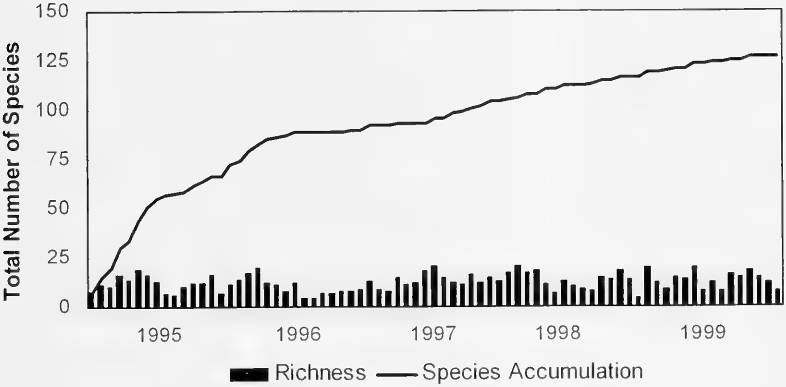
Voucher specimens of adults and larvae are deposited in the National Museum of Natural History, Smithsonian Institution, Washington, DC, and the West Virginia University Arthropod Collection, Morgantown, WV.

RESULTS

Malaise samples provided a wealth of information about adult symphytan richness, abundance, and seasonal occurrence in a hardwood forest. Data were analyzed using the EstimateS 5 program (Colwell 1997). Diversity estimators produced a fairly narrow range of species estimates for both forests combined and each forest individually. The bootstrap estimations were at the low end of the range for both forests combined and each forest separately. For example, bootstrap estimated that both forests combined may have 174 species. The high end of the range was determined by second order jackknife, which estimated 214 species for both forests (Table 1). The Chao 2 and ICE estimators produced moderate estimates (191 and 192, respectively) and may be more realistic for this data set. These two estimators suggest that approximately 81% of the actual species present on the two forests were sampled over five years. Species accumulation curves and weekly richness were plotted for the combined forests (Fig. 2), the GWNF (Fig. 3), and the MNF (Fig. 4).

The number of adult specimens captured over five years was 8,884 with 155 species identified: 104 from the GWNF and 127 from the MNF (Table 2). These adults represent eight families, with most species Tenthredinidae (121), followed by Pamphiliidae (14), Argidae (7), Pergidae (4), Cephidae (3), Xiphydriidae (3), and Xyelidae (2). Pergids were the most abundant with 4,529 individuals, 4,481 being *Acordulecera dorsalis* Say. Tenthredinid total abundance was 4,240, followed by Xyelidae (33), Argidae (31), Pamphiliidae (28), Xiphydriidae (15), Cephidae (7), and Diprionidae (1). Pergids made up 59% of the abundance in the GWNF, but only 4% of the species richness, In the MNF, pergids made up 38.6% of abundance and accounted for 3% of the richness. However, the tenthredinids collected in the GWNF comprised 76% of the richness and 39.9% of the abundance. MNF tenthredinids accounted for 81% of richness and 59.7% of abundance. The more abundant species following *A. dorsalis* were *Pristiphora banksi* Marlatt, *Pachynematus corniger* (Norton), *Paracharactus rudis* (Norton), *Taxonus*





Figs. 2–3. Species accumulation curves. 2 (Top), Combined George Washington and Monongahela national forests for 15 weeks each year from 1995–1999. 3 (Bottom), George Washington National Forest for 15 weeks each year from 1995–1999.

pallipes (Say), *Aneugmenus flavipes* (Norton), *Taxonus pallidicornis* (Norton), *Nematus radialis* Smith, *Taxonus rufocinctus* (Norton), and *Ametastegia pulchella* (Rohwer). All of these species were taken from both forests, though not in the same order of abundance (Table 3). Although species richness was high, as measured by the 155 species of Symphyta caught in the forests, 87 were represented by five or fewer specimens (Table 4).

Many species were collected from only one of the two forests. Twenty-eight species were found exclusively in the GWNF. Families which contained species unique to GWNF were Argidae (3), Cephidae (1), Diprionidae (1), Pamphiliidae (5), and Tenthredinidae (18). Fifty-one species were

Table 1. Species richness estimates using several diversity estimators for the George Washington National Forest (GWNF), Monongahela National Forest (MNF), and both combined.

Method	Both Forests	GWNF	MNF
Bootstrap	174	117	143
Chao2	191	144	157
ICE	192	139	157
2nd-order jackknife	214	156	177

found only in MNF, and these were in the families Cephidae (1), Pamphiliidae (6), Tenthredinidae (42), and Xiphydriidae (2). Sixty-one species were collected from both forests.

Trends in abundance for certain species were evident over the five years. *Acordulecera dorsalis* has a peak flight time at the end of May. Sampling after that yielded very few specimens. The flight time of *Pristiphora banksi* peaks during the second or third week in June.

Over the five years of sampling, adult Symphyta were collected from Malaise traps from the earliest date (6 May) through the latest (18 August) (Table 4). The ten more abundant species usually flew from early May until late August. While abundance peaked for these species at different times of the season, they were caught with some consistency during the entire three-month sampling period. The first five weeks of each sampling season were critical and accounted for 60% of 1995 adults, 82% of 1996 adults, 32% of 1997 adults, 47% of 1998 adults, and 66% of 1999 adults (Table 5).

Foliage samples produced 11,621 larval individuals from 1995 through 1999. Eight different genera were represented. *Acordulecera* comprised 63.5% of all symphytan larvae with 7,373 specimens, while *Periclista* (several species) comprised 20.0% with 2,328 specimens. Other larvae were Nematinae [probably mostly *P. chlorea* (Norton) and *Craterocercus* spp.] (1,220), *Caliroa* spp. (108), Pamphiliidae (31), *Arge* sp. (14), *Dimorphopteryx* sp. (14), and *Megaxyela* sp. (3).

The general trend for *Acordulecera* larvae was a sharp increase over the first few sampling weeks, peaking in late May, then sharply declining. *Periclista* larvae also declined sharply after their peak in early June.

DISCUSSION

While a high diversity of Symphyta occurred in our samples, there are a few factors that may have influenced sample content. First, sampling by Malaise traps captures only those species that fly at the level of the collecting net. Species that live primarily in forest canopy probably were not in the samples or occurred in small numbers. *Periclista,* for example, comprised 20% of the total larvae captured but only 0.01% of the adults. Second, Malaise traps

Table 2. Adult Symphyta species richness and abundance by family as sampled from 1995 through 1999 in the George Washington National Forest (GWNF) and Monongahela National Forest (MNF).

Family	Species Richness			Abundance		
	GWNF	MNF	Total	GWNF	MNF	Total
Argidae	7	4	7	18	13	31
Cephidae	2	2	3	5	2	7
Diprionidae	1	0	1	1	0	1
Pamphiliidae	8	9	14	12	16	28
Pergidae	4	4	4	3176	1353	4529
Tenthredinidae	79	103	121	2147	2093	4240
Xiphydriidae	1	3	3	8	7	15
Xyelidae	2	2	2	14	19	33
Total	104	127	155	5381	3503	8884

Table 3. The ten more abundant species of adult Symphyta sampled from 1995 through 1999 in the George Washington National Forest (GWNF) and Monongahela National Forest (MNF).

GWNF		MNF	
Species	Abundance (% Total)	Species	Abundance (% Total)
Acordulecera dorsalis Say	3,154 (58.6%)	*Acordulecera dorsalis* Say	1,327 (37.9%)
Pristiphora banksi Marlatt	1,083 (20.1%)	*Pachynematus corniger* (Norton)	419 (12.0%)
Aneugmenus flavipes (Norton)	158 (2.9%)	*Paracharactus rudis* (Norton)	256 (7.3%)
Taxonus pallidicornis (Norton)	100 (1.9%)	*Taxonus pallipes* (Say)	148 (4.2%)
Pristiphora cincta Newman	90.00 (1.7%)	*Pristiphora banksi* Marlatt	141 (4.0%)
Pachynematus corniger (Norton)	68.00 (1.3%)	*Nematus radialis* Smith	102 (2.9%)
Ametastegia pulchella (Rohwer)	53.00 (1.0%)	*Taxonus rufocinctus* (Norton)	97 (2.8%)
Taxonus pallipes (Say)	53 (1.0%)	*Empria multicolor* (Norton)	62 (1.8%)
Macrophya formosa (Klug)	50 (0.9%)	*Aglaostigma quattuordecimpunctatum* (Norton)	61 (1.7%)
Nematus ostryae (Marlatt)	44 (0.8%)	*Pristiphora chlorea* (Norton)	53 (1.5%)

were in use for only 15 weeks starting in early May. While traps were present during most species' peak fight times, some species which were more active either before or after traps were present may have been excluded entirely. The traps were placed in the same location each year, and some species may have avoided the traps. In most cases, the species that appeared in low numbers such as *Sphacophilus cellularis*

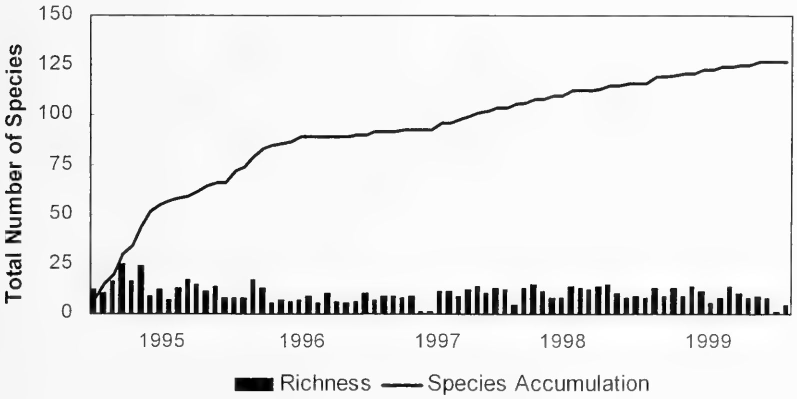


Fig. 4. Species accumulation curve for the Monongahela National Forest for 15 weeks each year from 1995–1999.

Table 4. Symphyta collected by Malaise traps from 1995 through 1999 in the George Washington National Forest (GWNF) and Monongahela National Forest (MNF).

	GWNF			MNF		
Family, Species	Flight Range	Total Count	Years Trapped	Flight Range	Total Count	Years Trapped
Argidae						
Arge macleayi (Leach)	25 May	1	1998	2 Aug–4 Aug	3	1997, 1999
Arge pectoralis (Leach)	24 Jul	1	1995	3 Aug	1	1998
Arge quidia Smith	20 Jul	2	1998	20 Jul	1	1998
Arge willi Smith	5 May–24 Jul	9	1995–1999	18 May–11 Aug	8	1996–1999
Schizocerella pilicornis (Holmgren)	4 Aug	1	1997			
Sphacophilus celluaris (Say)	10 Jul–26 Jul	3	1995, 1999			
Sterictiphora serotina Smith	15 May	1	1995			
Cephidae						
Janus abbreviatus (Say)				19 Jun	1	1995
Janus bimaculatus (Norton)	20 May–29 May	4	1995, 1996			
Janus integer (Norton)	29 May	1	1995	19 Jun	1	1995
Diprionidae						
Neodiprion sp. (male)	7 Jul	1	1997			
Pamphiliidae						
Acantholyda angulata (MacGillivray)				18 May	1	1998
Acantholyda luteomaculata (Cresson)				21 Jul	1	1997
Acantholyda zappei (Rohwer)	2 Jun	1	1997			
Neurotoma fasciata (Norton)	19 Jul	1	1999			
Onycholyda luteicornis (Norton)	19 May	1	1997	5 Jun	1	1995
Onycholyda quebecensis (Provancher)	8 May	1	1995			
Onycholyda rufofasciatus (Norton)				24 Jun	1	1996
Pamphilius middlekauffi Shinohara & Smith	25 May–8 Jun	2	1998			
Pamphilius ochreipes (Cresson)	10 May	1	1999			
Pamphilius pallimaculus (Norton)	12 Jun–24 Jul	4	1995, 1999	14 Jul–4 Aug	4	1997–1999
Pamphilius persicum MacGillivray				15 Jun–26 Jun	2	1995, 1998
Pamphilius phyllisae Middlekauff				25 May–12 Jul	4	1998, 1999
Pamphilius rileyi (Cresson)	8 May	1	1995	12 Jun	1	1995
Pamphilius semicinctus (Norton)				8 May	1	1995

Table 4. Continued.

Family Species	GWNF			MNF		
	Flight Range	Total Count	Years Trapped	Flight Range	Total Count	Years Trapped
Pergidae						
Acordulecera dorsalis Say	5 May–17 Aug	3,154	1995–1999	6 May–12 Aug	1,327	1995–1999
Acordulecera maculata MacGillivray	20 May–12 Jun	2	1995, 1996	26 May–26 Jul	3	1999
Acordulecera mellina MacGillivray	1 Jun–12 Aug	4	1995, 1996, 1998	19 Jul–21 Jul	2	1997, 1999
Acordulecera pellucida (Konow)	5 Jun–7 Aug	16	1995, 1996, 1999	20 May–11 Aug	21	1995–1999
Tenthredinidae						
Aglaostigma quattuordecimpunctatum (Norton)	17 May–31 May	2	1999	11 May–21 Jun	61	1995–1999
Aglaostigma semiluteum (Norton)				19 Jun–29 Jun	4	1995, 1996, 1998
Aglaostigma sp. #1				22 May	1	1995
Ametastegia aperta (Norton)	5 Jul–24 Jul	2	1995, 1999	12 Jun–24 Jul	5	1995, 1999
Ametastegia becra Smith	30 Jun–1 Jul	2	1996, 1997	28 Jul	1	1997
Ametastegia pallipes (Spinola)				18 May–28 Jul	11	1996–1999
Ametastegia pulchella (Rohwer)	5 May–14 Aug	53	1995–1999	24 May–14 Aug	48	1995–1999
Aneugmenus flavipes (Norton)	10 May–17 Aug	158	1995–1999	18 May–4 Aug	8	1996–1999
Caliroa lobata MacGillivray	15 Jul	1	1996			
Caliroa lunata MacGillivray	29 Jun–17 Jul	2	1995, 1998	21 Jul–7 Aug	2	1995, 1997
Caliroa obsoleta (Norton)				10 Jun–16 Aug	3	1996, 1999
Caliroa quercuscoccinea (Dyar)	5 Jun–17 Aug	11	1995–1999	26 Jun–14 Aug	5	1995, 1997, 1999
Caliroa spp. (males)	6 Jul–12 Aug	19	1996–1998, 1995	23 Jun–9 Aug	4	1997, 1999
Caulocampus acericaulis (Macgillivray)				10 May–29 May	4	1995, 1999
Craterocercus fraternalis (Norton)	5 May–12 May	7	1995–1997	6 May–31 May	28	1995–1999
Craterocercus obtusus (Klug)	6 May	1	1996	6 May–18 May	5	1996, 1998
Dimorphopteryx pinguis (Norton)	5 Jun–7 Aug	3	1995, 1996	5 Aug	1	1996
Dimorphopteryx virginicus (Rohwer)				26 Jul	1	1999
Dolerus hebes Goulet	17 May	1	1999			
Dolerus nortoni Ross				5 May–12 May	3	1996, 1997
Empria coryli (Dyar)				5 May–10 May	2	1997, 1999
Empria maculata (Norton)	20 May–13 Jul	9	1996, 1998, 1999	17 May–30 Jun	9	1995–1999
Empria multicolor (Norton)	25 May–12 Jun	6	1995, 1998, 1999	18 May–12 Jul	62	1995–1999
Erythraspides vitis (Harris)	7 Aug	1	1995			
Euparcophora parca (Cresson)				10 May–19 May	7	1996–1999
Eutomostethus ephippium (Panzer)	17 May–5 Jul	2	1999	10 May	1	1999
Fenusa ulmi Sundevall				19 May–27 May	2	1996, 1997

Table 4. Continued.

	GWNF			MNF		
Family, Species	Flight Range	Total Count	Years Trapped	Flight Range	Total Count	Years Trapped
Halidamia affinis (Fallen)				6 May–9 Jun	3	1996, 1997
Hemichroa militaris (Cresson)				27 May–12 Jun	7	1995, 1996, 1999
Hemitaxonus albidopictus (Norton)	25 May	1	1998	20 May–10 Aug	15	1995 1999
Hemitaxonus dubitatus (Norton)				10 May–22 May	2	1995, 1999
Hoplocampa halcyon (Norton)				5 May–13 May	20	1995–1997, 1999
Hoplocampa marlatti Rohwer	12 May	1	1997	5 May–20 May	8	1995–1999
Leucopelmonus annulicornis (Harrington)	11 May–5 Jun	11	1995, 1996, 1998, 1999	11 May–23 Jun	21	1995–1999
Macremphytus tarsatus (Say)	26 Jul	1	1999			
Macremphytus testaceus (Norton)	23 Jun–3 Jul	2	1995, 1997	26 Jul	1	1999
Macrophya cassandra Kirby	11 May–22 Jun	5	1995, 1996, 1998	20 May–17 Jun	1	1995, 1996, 1999
Macrophya flavicoxae (Norton)				7 Jun–22 Jun	7	1998, 1999
Macrophya flavolineata (Norton)				20 May–27 May	2	1996
Macrophya flicta MacGillivray	27 May–27 Jul	6	1995, 1996, 1998			
Macrophya formosa (Klug)	1 Jun–24 Jul	50	1995–1999	10 Jun–7 Jul	1	1995–1999
Macrophya goniphora (Say)	28 Jun	1	1999	12 Jul–9 Aug	17	1999
Macrophya lineata Norton				14 Jun	1	1998
Macrophya macgillivrayi Gibson				3 Jun–14 Jun	1	1996, 1999
Macrophya masoni Gibson	21 Jul–2 Aug	3	1997, 1999			
Macrophya mensa Gibson	18 May–10 Aug	5	1995, 1997–1999			
Macrophya nigra (Norton)	29 Jun–28 Jul	15	1995, 1997–1999	30 Jun–17 Aug	2	1995, 1997–1999
Macrophya pulchella (Klug)	20 May–26 Jul	11	1996, 1998, 1999	19 Jul–20 Jul	6	1998, 1999
Macrophya tibiator Norton	19 May–14 Jun	10	1995–1997, 1999	13 May–26 Jun	2	1995, 1996, 1998
Macrophya trisyllaba (Norton)				29 May–7 Aug	5	1995, 1997, 1999
Macrophya varia (Norton)	12 Jun–11 Aug	24	1995–1999			
Monophadnoides geniculatus (Hartig)	22 May–29 May	4	1995, 1999	24 May	1	1999
Monophadnoides pauper (Provancher)	24 May–31 May	3	1999	31 May	3	1999
Monophadnus aequalis Macgillivray	5 May	2	1997	8 May	1	1995
Monophadnus bakeri Smith				20 May	1	1996
Monophadnus conspiculatus MacGillivray	18 May–29 May	6	1995–1998			
Monophadnus pallescens (Gmelin)				5 May–6 May	1	1996, 1997
Monostegia abdominalis (F.)				28 Jun–28 Jun	5	1999
Nefusa ambigua (Norton)	18 May–12 Jun	16	1995, 1996, 1998, 1999	1 Jun–16 Aug	44	1995–1999

Table 4. Continued.

Family, Species	GWNF			MNF		
	Flight Range	Total Count	Years Trapped	Flight Range	Total Count	Years Trapped
Nematus #1	29 May	1	1995	19 Jun–12 Jul	4	1995, 1999
Nematus #2	6 Jul–12 Aug	27	1995–1999	27 Jul–17 Aug	11	1995–1999
Nematus #3				26 May–27 May	2	1996, 1997
Nematus #4	10 May–24 May	2	1999	5 May–14 Aug	35	1995–1999
Nematus abbotii (Kirby)	12 May–4 Aug	9	1995–1997	13 May–14 Jun	9	1995, 1996, 1998, 1999
Nematus carpini (Marlatt)				22 Jun	1	1998
Nematus coryli Cresson				3 Aug–4 Aug	2	1997, 1998
Nematus latifasciatus Cresson				8 Jun	1	1998
Nematus lipovskyi Smith	8 May–22 May	5	1995	5 May–24 May	6	1996–1999
Nematus near *atriceps* (Marlatt)	25 May–12 Aug	32	1995–1998	16 Jun–28 Jul	6	1997, 1999
Nematus ostryae (Marlatt)	19 May–17 Aug	44	1995–1999	5 Jun–14 Aug	11	1997–1999
Nematus radialis Smith	10 May–2 Jun	12	1995–1999	10 May–16 Jun	102	1995–1999
Nematus tibialis Newman	12 Jun–17 Aug	19	1995–1999	11 May–10 Aug	12	1995–1999
Neopareophora litura (Klug)	6 May–10 May	3	1995, 1996, 1999	5 May–12 May	13	1996, 1997, 1999
Pachynematus #1				29 May–5 Jun	3	1995, 1999
Pachynematus #2	27 May	1	1996			
Pachynematus corniger (Norton)	6 May–11 Aug	68	1995–1999	5 May–17 Aug	419	1995–1999
Pachynematus extensicornis (Norton)	20 Jul	1	1998			
Paracharactus rudis (Norton)	10 May–7 Jun	15	1996, 1998, 1999	6 May–17 Aug	256	1995–1999
Periclista albicollis (Norton)	10 May	3	1999	5 May–19 May	24	1997–1999
Periclista diluta (Cresson)	8 May	1	1995	10 May–2 Jun	7	1996–1999
Periclista inaequidens (Norton)				5 May–22 May	6	1995, 1997, 1998
Periclista marginicollis (Norton)	6 May–19 May	4	1995–1997, 1999	5 May–9 Jun	18	1995, 1997–1999
Periclista media (Norton)	8 May–12 May	6	1995, 1997, 1999	5 May–2 Jun	20	1995–1999
Periclista stannardi Smith				11 May–1 Jun	2	1998
Phymatocera fumipennis (Norton)				14 Jun	2	1999
Priophorus pallipes (Lepeletier)	29 May	1	1995	22 May–26 Jul	5	1995, 1999
Pristiphora banksi Marlatt	5 May–17 Aug	1,083	1995–1999	11 May–16 Aug	141	1995–1999
Pristiphora bivittata (Norton)	17 May	1	1999			
Pristiphora chlorea (Norton)	5 May–25 May	28	1995–1999	6 May–16 Jun	53	1996–1999
Pristiphora cincta Newman	8 May–7 Aug	90	1995–1999	20 May–17 Jul	2	1995, 1996
Pristiphora mollis (Hartig)				10 May	1	1999
Pristiphora rufipes Lepeletier				17 May–3 Aug	8	1997–1999
Pristiphora sp. #1				10 May	2	1999

Table 4. Continued.

	GWNF			MNF		
Family, Species	Flight Range	Total Count	Years Trapped	Flight Range	Total Count	Years Trapped
Pristiphora zella Rohwer	24 Jul	1	1995			
Profenusa alumna (MacGillivray)	17 Jun–16 Aug	2	1999	17 Jun–11 Aug	6	1996–1998
Pseudodineura parva (Norton)				25 May–1 Jun	5	1995, 1998
Strongylogaster impressata Provancher				27 May	1	1996
Strongylogaster multicincta Norton	10 May–22 May	2	1995, 1999			
Strongylogaster polita Cresson	12 Jun	1	1995			
Strongylogaster soriculatipes Cresson	10 May–20 May	3	1996, 1997, 1999			
Strongylogaster tacita (Norton)				25 May	1	1998
Taxonus borealis MacGillivray	15 Jun–28 Jun	3	1997–1999	1 Jun–12 Aug	52	1995–1999
Taxonus epicera (Say)	24 May–2 Jun	4	1996, 1997, 1999	25 May–16 Jun	7	1995–1999
Taxonus pallicoxus (Provancher)	27 May–31 Jul	18	1995, 1996	24 May–10 Aug	32	1995, 1998, 1999
Taxonus pallidicornis (Norton)	22 May–16 Aug	103	1995–1999	8 Jun–12 Aug	23	1995–1999
Taxonus pallipes (Say)	18 May–17 Aug	53	1995–1999	27 May–16 Aug	148	1995–1999
Taxonus proximus (Provancher)	21 Jul–14 Aug	3	1995, 1997	12 Jun–16 Aug	30	1995–1999
Taxonus rufocinctus (Norton)	29 May–10 Aug	14	1995–1999	24 May–16 Aug	97	1995–1999
Taxonus spiculatus (MacGillivray)	26 Jun–21 Jul	3	1995, 1997	19 Jun–31 Jul	4	1995, 1997
Taxonus terminalis (Say)	20 May–2 Aug	19	1995–1999	26 May–16 Aug	16	1995–1999
Tenthredo appalachia Goulet & Smith				10 Jun–10 Jul	2	1995, 1996
Tenthredo fernowi Goulet & Smith	12 Jun	1	1995			
Tenthredo grandis (Norton)				23 Jun	1	1997
Tenthredo lobata (Norton)	17 Aug	1	1998			
Tenthredo masneri Goulet & Smith				16 Jun–3 Aug	9	1995–1999
Tenthredo mellicoxa Provancher				23 Jun	1	1997
Tenthredo rufopecta (Norton)	14 Jun–10 Jul	2	1995, 1999	7 Jul–26 Jul	5	1997, 1999
Tenthredo sp. #1				3 Jun	1	1996
Tenthredo verticalis Say				24 Jun–31 Jul	2	1995, 1996
Tenthredo yuasi MacGillivray				14 Jun–15 Jun	3	1998, 1999
Xiphydriidae						
Xiphydria abdominalis Say				26 Jun–17 Jul	2	1995
Xiphydria maculata Say				8 Jun	1	1998
Xiphydria tibialis Say	22 Jun–7 Aug	8	1995–1999	12 Jun–30 Jun	4	1995, 1997, 1999
Xyelidae						
Xyela alpigena (Strobl.)	8 May–2 Jun	11	1995, 1997, 1999	8 May–16 Jun	11	1995, 1997
Xyela sp. (males)	8 May–26 May	3	1995, 1997	15 May–16 Jun	8	1995, 1997

(Say), *Sterictiphora serotina* Smith, and *Janus abbreviatus* (Say), have hosts such as morning glory, *Ipomoea purpurea* (L.) Roth, black cherry, *Prunus serotina* Ehrh., and *Salix* and white poplar, *Populus alba* L., respectively, which are uncommon in both forests. Alternatively, species such as *Acordulecera dorsalis*, whose hosts dominate the forest (*Quercus* spp. and *Carya* spp.), were found in greater abundance. However, some Symphyta did not fit this pattern. The host plant for *Pristiphora banksi*, *Vaccinium*, was not found in great abundance in the MNF and yet it was the second most abundant species of Symphyta.

A high diversity of symphytan larvae was collected even though only five host plant groups were sampled. These larvae as a group show considerable variability in their host plants and can feed on foliage of larger trees or small groundcover flora such as grasses, blueberries, ferns, and other plants. Another factor which limited our larval diversity is that only foliage from the middle to lower canopy was sampled. Symphytan larvae on other food plants in the forest or feeding on upper canopy foliage were not sampled using this method. The adult abundance and richness were affected by seasonal sampling time; the same is true of the larvae. Assessing population fluctuations and abundances is limited since our sampling period was only 15 weeks from early May through mid-August. Some symphytan larvae are present before, or after this period, or both. Seasonal population changes over the five-year period could be responsible for overestimated and underestimated abundances when comparing samples to predict species diversity. Larval feeding habits may have been a factor. For instance, *Acordulecera* larvae were especially problematic because they were in the only genus sampled that existed in large gregarious clusters. A single sample can contain hundreds of larvae.

Table 5. Weekly number of adult Symphyta collected by Malaise traps from 1995 through 1999 in both the George Washington National Forest and Monongahela National Forest.

	Year				
Week	1995	1996	1997	1998	1999
1	201	506	191	83	277
2	220	353	90	254	248
3	292	384	85	239	241
4	279	231	95	140	294
5	105	51	51	65	145
6	141	60	38	61	185
7	77	37	65	80	34
8	68	31	137	102	58
9	37	29	92	53	67
10	55	31	64	81	75
11	132	27	87	179	48
12	124	26	153	99	64
13	110	25	175	98	53
14	70	30	161	85	32
15	25	47	110	31	15

As with other species rich taxa, Symphyta diversity plays an important role in the forests. They are likely also important in forest food webs as herbivores preyed upon by numerous species of invertebrates and vertebrates. The eruciform larvae of Symphyta are similar to lepidopteran larvae which are recognized as having both high fat (Redford and Dorea 1984) and very low chitin content relative to other insects, thus making them especially valuable in the diets of songbirds (Sample et al. 1993). Some ornithologists collectively refer to larval sawflies and lepidopterans as caterpillars when recording dietary habits of songbirds (Rodenhouse and Holmes 1992). As abundance of spring defoliating lepidopterans may be reduced during *Btk* applications for gypsy moth suppression (Marshall et al. 2002), sawfly larvae may survive to be preyed upon by songbirds. Understanding the diversity, abundance, and seasonality of adult and larval Symphyta in a hardwood forest ecosystem may help make predictions about how certain chemical or biological controls effect Symphyta and the forest food web.

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FIRST REPORT OF *COENOSIA ATTENUATA* STEIN (DIPTERA: MUSCIDAE), AN OLD WORLD 'HUNTER FLY' IN NORTH AMERICA

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Abstract.—The Palearctic muscid *Coenosia attenuata* Stein is reported for the first time in North America based on collections from the U.S.A. and Canada. Adult flies were collected from commercial greenhouses in Erie, Monroe, Onondaga, Suffolk, Tompkins, and Wayne counties of New York State and Ontario Province, Canada, and from a Malaise trap in a suburban backyard of Los Angeles County, California. A diagnosis, redescription, and photographs of the adult are provided to help distinguish it from other North American Muscidae. Its biology and habits are summarized from the European literature, and its Old World distribution is reviewed.

Key Words: Diptera, Muscidae, *Coenosia attenuata*, North America, immigrant species, new record, New York, California, Ontario

In late August of 2002, several specimens of a small muscid fly, collected by EJS in a greenhouse in East Syracuse, New York, were submitted to ERH for identification. They proved to be *Coenosia attenuata* Stein, an obligatory predaceous fly indigenous to the Paleotropical Region and not known to occur in North America.

In this paper, we give the first North American records for *C. attenuata*, review the Old World literature treating this species, provide notes on its biology and habits, and redescribe and provide photographs of the adult to enable recognition of this species in the North American fauna.

Specimens of *C. attenuata* were first noticed in early October 1999 by Elise Schillo-Lobdell, an IPM scout, at a commercial greenhouse specializing in the large-scale production of poinsettias. It was at this same greenhouse where specimens were later collected by EJS on 28 August 2002 and identified by ERH.

Since this initial collection, numerous other specimens have been collected on yellow sticky card-traps set for monitoring pest populations (including shore flies and fungus gnats) in other greenhouses across New York as well as at a site in Ontario, Canada. Quite by accident and about the same time, the senior author also learned from Dr. Adrian Pont, a muscid fly specialist from Great Britain, that he had recently identified specimens of *C. attenuata* from California; these specimens were collected from a Malaise trap in a suburban backyard in Los Angeles County in mid-September of 2002 (Brian V. Brown, personal communication).

Coenosia attenuata Stein
(Figs. 1–4)
(Synonymy after Pont 1986)

Coenosia attenuata Stein *in* Becker 1903: 121.

Coenosia (*Caricea*) *flavicornis* Schnabl *in* Schnabl and Dziedzicki 1911: 80.

Coenosia confalonierii Séguy 1930: 86.

Coenosia (*Caricea*) *affinis* Santos Abreu 1976: 13.

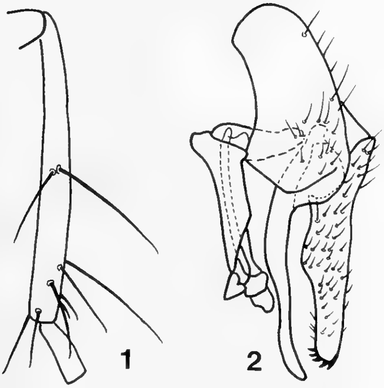
Coenosia (*Caricea*) *flavipes* Santos Abreu 1976: 13.

Diagnosis.—*Coenosia attenuata* is a member of the nominate subgenus *Coenosia* Meigen (*sensu* Huckett 1934) or the *tigrina*-group (*sensu* Hennig 1961), characterized by the hind tibia with two closely adjacent bristles at the middle, situated on the anterodorsal and anterior surfaces respectively (illustrated by Hennig 1961: 521, fig. 210B, and Fig. 1, herein). The Old World species *C. tigrina* F., *C. atra* Meigen, *C. humilis* Meigen, and *C. strigipes* Stein also belong to this *tigrina*-group, occasionally placed in its own genus *Caricea* Robineau-Desvoidy (Skidmore 1985); all are members of the greenhouse predator community (Kühne 2000), and are occasionally referred to by Old World workers as either "hunter flies" or "killer flies." *Coenosia tigrina* and *C. humilis* are recorded from North America (see remarks). From these two introduced species, *C. attenuata* can be easily differentiated by its smaller size (2.5–3.0 mm, male; 3.0–4.0 mm, female) (vs. 4.75–5.75 mm, male and 5.75–7.0 mm, female for *C. tigrina*; and 3.0–3.5 mm, male and 3.0–5.5 mm, female for *C. humilis*; measurements from d'Assis Fonseca 1968), legs of the male entirely pale yellow (vs. femora mostly black but broadly reddish yellow at apex in male of *C. tigrina*, and femora entirely black in male of *C. humilis*), and the distinctive male genitalia (Fig. 2).

Redescription [terminology for structures follows McAlpine (1981)]. Male and female habitus, Figs. 3–4. Redescribed from 29 specimens (East Syracuse, Onondaga Co., NY). Length: 2.5–3.0 mm, male (n = 20); 3.0–4.0 mm, female (n = 9).

Male.—*Head:* Parafacial, fronto-orbital plates, frontal vitta, and face silvery-white pruinose, with yellowish tinge; black ground color not visible under pruinosity except slightly on face. Pedicel silvery-white pruinose (with yellow tinge), black ground color visible at exteme base. Flagellomere 1 also silvery-white pruinose (with yellow tinge). Aristomere 1 very short; aristomere 2 not more than 2× as long as wide; aristomere 3 very long, evenly tapered to fine tip, with dense short hairs on basal half, longest of which equal basal diameter of aristomere 3. Orbital plate with 3 strong setae: lower and middle setae lateroclinate; upper seta reclinate. Ocellar and postocellar setae well developed. Inner vertical setae strong, parallel. Parafacial and facial ridge bare. Lower facial margin protruding slightly just below vibrissa when viewed in profile. Maxillary palpus yellow, slightly clavate apically, moderately haired.

Thorax: Black in ground color, except dorsum of scutum and scutellum light gray pruinose, with slight metallic blue tinge scarcely visible. In some specimens, 3 indistinct brownish lines or stripes visible on scutum. Acrostichal setae small to medium, arranged in roughly 2 irregular rows: approximately 4–6 presutural setae, and 6–8 postsutural setae. One strong presutural dorsocentral seta. Three strong postsutural dorsocentral setae. Two medium intra-alar setae. Two (one small, one strong) postalar setae. One strong supra-alar seta. Scutellum with one pair of strong crossed apical setae, one pair of strong subapical setae, and one pair of small basal setae. Dorsum of scutellum with several small discal setae. Anepisternum with at least 4–5 setae, 2 of these strong and extended to margin of lower calypter. Katepisternum with three strong setae. Wings with veins r_{4+5} and m parallel to margin. Halter yellow. Legs entirely yellow; tarsi appearing darker due to dense covering of numerous small black setulae.



Figs. 1–2. *Coenosia attenuata.* 1, Hind tibia. 2, Male genitalia (epandrium, cerci, and surstylus). Both figures redrawn from Hennig (1961: Textfig. 210B, p. 521 and Taf. XXVIII, fig. 533).

Hind tibiae with two closely adjacent bristles at middle, situated on anterodorsal and anterior surfaces respectively (Fig. 1).

Abdomen: Short, ovoid. T_{1+2} to T_5 dark gray pruinose, without dark maculations. All tergites with numerous small to medium discal and marginal setae. Epandrium of terminalia gray pruinose, cercus and surstylus yellow to orangish.

Male terminalia (Fig. 2): As illustrated by Hennig (1961: Taf. XXII, fig. 453; Taf. XXVIII, fig. 533) and Cui (1999: 929, fig. 2137).

Female.—Similar to male in most respects, except larger in size, and in coloration of head, antenna, and legs. Frontal vitta (not silvery-white pruinose as in male) generally dark with metallic blue-green pruinosity. Antenna darkened. Legs black (with gray pruinosity), except trochanters, extreme bases and apices of femora, tibiae, and tarsi yellowish.

Remarks.—Two other species of the *tigrina*-group are known from North America, both presumably introduced in the early to mid 1800s. *Coenosia tigrina* was first reported in North America by Walker (1849), who originally described it as a new species (*C. sexmaculata*), from Hudson Bay, Ontario (later synonymized with *C. tigrina* by Stein 1901). Its known geographic distribution is decidedly disjunct, occurring from British Columbia and Alberta to California in the west and from northwestern Ontario and Quebec to Michigan and Maine in the east (Huckett 1965). *Coenosia humilis* is widely distributed in North America, ranging from Washington to California and Colorado, and from Wisconsin and Illinois to Quebec and New Jersey (Huckett 1934, 1965). Huckett (1934) reported that the latter species occurs frequently in greenhouses.

Biology, habits, and immature stages.—In Europe, *Coenosia attenuata,* along with *C. atra, C. humilis, C. strigipes, C. tigrina,* and *C. testacea* Robineau-Desvoidy, are members of a greenhouse predator community (Kühne et al. 1994, Kühne 2000). These predaceous flies not only colonize greenhouses from the outside environment, but may also complete their development in greenhouse soil and become established there for long periods of time (Kühne 2000).

Both the larval and adult stages of *C. attenuata* are predaceous. Larvae have been mass reared on dipterous larvae of two taxa: *Bradysia difformis* Frey (= *paupera* Tuomikoski) (Sciaridae) (Kühne 2000) and *Scatopse transversalis* Loew (Scatopsidae) (Kühne 2000). The prey spectrum of adult *C. attenuata* in greenhouses in Baden-Württemberg, Germany, includes the greenhouse pests *Trialeurodes vaporariorum* Westwood and *Bemisia tabaci* (Gennadius) (Aleyrodidae), *Empoasca* sp. (Cicadellidae), and Sciaridae (Schrameyer 1991). Kühne et al. (1997) also recorded Psychodidae, Chironomidae, Ephydridae, and Drosophilidae as prey groups. In captivity, adult *C. attenuata* also consumed the leafminer *Liriomyza huidobrensis* Blanchard (Agromyzidae) (Schrameyer 1991), and the scavenger midge *S. tranversalis* (Kühne 2000).

Figs. 3–4. *Coenosia attenuata*, lateral aspect. 3, Male. 4, Female. Scale line, 1 mm.

According to Schrameyer (1991), adult *C. attenuata* employ a sit-and-wait strategy and pursue only prey that are in flight. Ambulatory prey are disregarded, even in extremely close proximity. The prey are pursued, caught, punctured with the proboscis, and the liquid body contents ingested. Manipulation of the food is accomplished by specialized mouthparts. A projection on the mid-labellum forms a daggerlike tooth to puncture prey, and 4–5 "teeth" and a raspy "tongue" structure tear the cuticle of the prey and mechanically grind it for ingestion (Kühne 2000). The daily capture of a single *C. attenuata* adult appears to be independent of its age. When food is in short supply, both adults and larvae may become cannibalistic (Kühne 2000).

In the laboratory, the adult reproductive behavior and duration of the developmental stages have been studied by Kühne et al. (1997) and Kühne (2000). The pre-oviposition period is approximately 4 days (Kühne et al. 1997), and most eggs are laid within a three week period at 25° C (Kühne 2000). The eggs of *C. attenuata* are of the *Phaonia*-type, *sensu* Ferrar (1987), and require a developmental period of 6.9 days at 21° C and 5.7 days at 25° C (Kühne et al. 1997). The number of larval instars has not been directly determined for *C. attenuata*. On the basis of morphological data, however, Kühne (2000) suggests that the larva emerges from the egg as a third instar. LeRoux and Perron (1960) found this phenomenon also to be true for *C. tigrina*; based on morphological evidence and the fact that larvae do not molt during larval life, they concluded that for this species the larvae emerge from the egg in the third instar. Complete larval development for *C. attenuata* requires 15.4 days at 21° C and 10.4 days at 25° C, while the pupal stage averaged a duration of 15.9 days at 21° C and 10.5 days at 25° C (Kühne et al. 1997). The maximum adult lifespan is as long as 7 weeks in captivity, but only ca. 50% of captive populations survive longer than 3 weeks (Kühne et al. 1997).

Distribution.—*Coenosia attenuata* is reported from southern Europe (Germany, France, Spain, Italy, Greece, Malta, Cyprus); Asia (Syria, Iraq, Israel, Tajikistan, Afghanistan); North Africa (Morocco, Algeria, Libya, Egypt); Madeira, Canary Islands; and the Oriental (widespread), Australasian (Papua New Guinea, Australia), and Afrotropical (Cape Verde Islands, Socotra, South Africa) regions (Pont 1986 and A. C. Pont, pers. comm.). Most recently, *C. attenuata* has been reported from South America (Ecuador, Peru) (Martínez-Sánchez et al. 2002).

New York, including at least six counties to date (Erie, Monroe, Onondaga, Suffolk, Tompkins, and Wayne), and California (Los Angeles Co.) in the United States, and Ontario, Canada are new records for North America.

Material examined.—All specimens deposited in the Cornell University Insect Collection, Ithaca, NY, except as noted. UNITED STATES: California: Los Angeles Co., Monrovia, 34.15°N, 117.99°W, 13–14 Sept. 2002, B. V. Brown, ex Malaise trap in suburban backyard (5 ♂, 2 ♀); same data, except 14–15 Sept. 2002 (1 ♂, 4 ♀) (California specimens in the collection of the Natural History Museum of Los Angeles County). New York: Erie Co., Eden, 24 Oct. 2002, E. J. Sensenbach, ex sticky trap (1 ♂). Monroe Co., Gates, 15 Oct. 2002, EJS (1 ♂, 2 ♀). Onondaga Co., East Syracuse, 28 August 2002, EJS and JPS (8 ♂, 7 ♀; of these, 3 ♂ and 3 ♀ in the collection of The Natural History Museum, London, UK); same data, except 12 Sept. 2002, ERH (20 ♂, 9 ♀); same data, except 12 Sept. 2002, EJS, ex sticky cards (2 ♂, 7 ♀). Suffolk Co., Mattituck, 29 Oct. 2002, M. Daughtrey, ex sticky cards (13 ♂, 2 ♀); Riverhead, 29 Oct. 2002, M. Daughtrey, ex sticky cards (2 ♂). Tompkins Co., Lansing, 30 Oct. 2002, W. Nelson, ex sticky cards (2 ♂). Wayne Co., Macedon, 15 Oct. 2002, EJS (1 ♂, 1 ♀); Newark, 15 Oct. 2002, EJS (1 ♂). CANADA: Ontario: Jordan Station, 17 Oct. 2002, G. Murphy, ex sticky cards

(9 ♂, 3 ♀); same data, except 25 Oct. 2002, T. Thiesen (1 ♂, 6 ♀). All specimens taken in New York and Ontario were from commercial production greenhouses.

Mode of introduction.—Because deliberate releases have only been reported in Germany (Kühne 2000), we doubt very strongly that *C. attenuata* was purposefully introduced into North America. According to Stefan Kühne (pers. comm. to EJS), in the last two years rearings of this predator fly have been initiated in Spain, Italy, and Portugal. Moreover, papers by Kühne, and especially K. Schrameyer, suggest these flies are being moved from place to place unintentionally with plant material, although there is no strong evidence to support this hypothesis. We would advocate that potting media are the most likely source for the accidental introduction of *C. attenuata* into North America.

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105(3), 2003, pp. 776–777

NOTE

A New Synonym of *Caudatella hystrix* (Traver) (Ephemeroptera: Ephemerellidae)

Caudatella Edmunds (Ephemeroptera: Ephemerellidae) was described as a Nearctic subgenus of *Ephemerella* Walsh (Edmunds 1959) for species included in McDunnough's (1935) *heterocaudata* species group. Allen (1980) later raised *Caudatella* to generic status. Allen and Edmunds (1961) constructed a *Caudatella* species key, in which specimens with well-defined ventral color patterns would "key with ease"; however, specimens with less distinct ventral markings would "key through a more difficult series of couplets."

Allen and Edmunds (1961) differentiated *C. cascadia* (Allen and Edmunds) and *C. hystrix* (Traver) (two species with overlapping geographic distribution) by ventral abdominal coloration, the respective presence or absence of occipital tubercles, and the relative development of abdominal tubercles. Examination of series of *C. hystrix* larvae, *C. cascadia* type material, and additional material from the *C. cascadia* type locale revealed that variability of occipital and abdominal tubercles development and ventral color pattern in *C. hystrix* encompasses the concept of *C. cascadia.* Some individuals from populations of *C. hystrix* have occipital tubercles such as described for *C. cascadia.* Additionally, we have found that the ventral color patterns associated with *C. cascadia* and *C. hystrix* are variable within single populations and have overlapping development. Therefore, we propose the following new subjective synonymy: *C. hystrix* (Traver) 1934 [= *C. cascadia* (Allen and Edmunds) 1961, **new synonym**]. Previously, Day (1954) recognized *Ephemerella spinosa* Mayo (nec *E. spinosa* Morgan, nec *E. spinosa* Ikonomov) as a synonym of *C. hystrix.*

All material examined is housed in the Purdue University Entomological Research Collection, West Lafayette, Indiana. George F. Edmunds, Jr. (Salt Lake City, Utah) and Bob Wissemann (Corvallis, Oregon) donated material for study. This study was funded in part by USEPA fellowship 91601701-0 to LMJ and NSF grant DEB-9901577 to WPM.

Material examined.—IDAHO: Lemhi Co., Opal Cr., 23-VII-1964, three larvae, one set larval exuviae. MONTANA: Judith Basin Co., Running Wolf Cr., 47°00′33″N, 110°22′18″W, 12-VI-2000, WP McCafferty et al., 25 larvae; Ravalli Co., Bitterroot R., N. of Sula on US93, AR Gaufin, 29-VI-1963, one larva; E. Fk. Bitterroot R., 10 mi. above jct. W. Fk. Bitterroot R., 24-VI-1965, JR Grierson, one larva. NEVADA: Washoe Co., Incline Cr., 2 mi. W. Mt. Rose Summit, GF Edmunds, Jr. & RK Allen, 21-IX-1957, six immature larvae. OREGON: Clackamas Co., Branch of Still Cr. on rd. to Timberline Lodge, Mt. Hood, 30-VIII-1958, GF Edmunds, Jr. & RK Allen, 18 larvae (*C. cascadia* holotype, paratopotype, and topotypes); Douglas Co., Jackson Cr. headwater trib., Umpqua NF, 43°03′N, 122°30′W, 14-VI-1990, RW Wissemann, four larvae; Klamath Co., Sun Cr., Crater Lake NP, 14/22-IX-1993, 10 larvae; Linn Co., Sweetwater Cr., Willamette NF, Rigdon Ranger District, IX-1997, three larvae. WYOMING: Park Co., Antelope Cr., Yellowstone NP, 17-VI-1949, GF Edmunds, Jr., one larva; Gibbon R. at Virginia Cascade, 12-VI-1963, ER Vincent, 15 larvae; Iron Cr., YNP, 21-VI-1949, GF Edmunds, Jr., one larva; Teton Co., Firehole R., Old Faithful, YNP, 6-VI-1942, GF Edmunds, Jr., one larva.

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NOTE

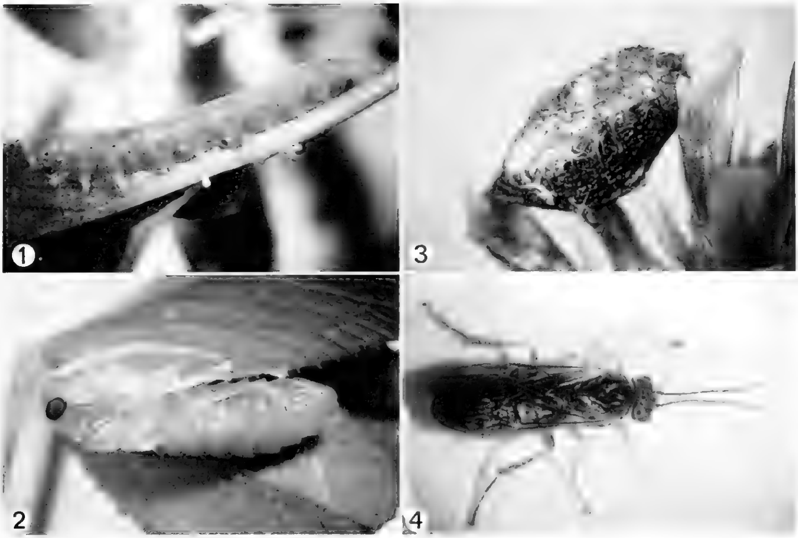
Food Plant, Life History Notes, and Distribution of *Nematus atriceps* (Marlatt) (Hymenoptera: Tenthredinidae)

Sawfly larvae were discovered feeding on *Trifolium wormskjolkii* Lenm. (Leguminosae) by GP at Seal Rock, Lincoln Co., Oregon, in the summer and fall of 2002. The reared adults were *Nematus atriceps* (Marlatt) (Nematinae) which occurs in the western United States and Canada. This is the first food plant record for this sawfly and the first record for any of the species placed in the *Nematus atriceps* group by Smith (1979). The food plant is unusual for *Nematus* in that most species feed on Salicaceae, Betulaceae, or other woody trees or shrubs. One Palearctic species, *Nematus myosotidis* (F.), is known to feed on *Trifolium* sp. (Taeger et al. 1998). *Nematus myosotidis* is very similar to *N. atriceps,* and could be placed in the same species group.

At Seal Rock, the clover plants were growing in a seepage area about 12 feet from the high tide level. *Nematus* larvae (Fig. 1) were first seen and collected while feeding on the flowers on July 12, 2002. Some lepidopteran larvae were found in other flower heads at the same site. On returning to the site on August 14, 2002, no insects were found on the same clover plants. However, on September 6, a number of small *Nematus* larvae were found eating clover leaves but leaving the midrib and larger veins. Three sawfly larvae were collected on September 23, 2002, from the leaves, and, on October 7, 2002, three additional small larvae were found on the leaves. After September, flowering drops off considerably, so the leaves are the major source of nourishment. Young larvae were reared in the laboratory on flowers and leaves of the same clover species. They would not eat white clover, *Trifolium repens* L. In rearing, they readily spun a tough, papery cocoon on the flowers (Fig. 3), or, if no flowers were present, under the filter pad in the petri dish. If the mature larvae are continually moved, they often did not form a cocoon and pupated naked (Fig. 2). Adults (Fig. 4) emerged in about 7 to 10 days. In the field, pupae were found only on flowers; however, they could have been in the duff even though it was quite wet under the plants.

The food plant is a native species commonly called marsh or spring bank clover. It is distributed from British Columbia to Mexico along the coast and also has inland populations in Idaho, New Mexico, and Colorado. It is a weak-stemmed perennial with large red, pink, or purple flowers. There is a mountain meadow race found along streams, as well as a coastal race found on beaches or edges of salt marshes. The coastal race is a rhizomed, matted form (Hickman 1996). Populations of the coastal race were examined by GP all along Oregon and into northern California (Lake Earl). The only locality where *Nematus* was found was at Seal Rock. The sawfly may have been missed at the other sites, although other insects were found in the flowers, such as larvae of *Hypera punctata* (F.), an Old World weevil.

Though *Nematus atriceps* feeds both on the leaves and inflorescence of *Trifolium wormskjoldii,* few other sawflies have been recorded feeding on inflorescences and *N. atriceps* provides one of the few examples. Other North American species include *Tenthredo* sp. on the flowers of *Ranunculus californicus* Benth. (Ranunculaceae) in California (Linsley and MacSwain 1959), and *Rhadinoceraea zigadenusae* Smith (Smith and McDearman 1990) and *R. sodsensis* Smith and Barrows (1995) on species of *Zigadenus* (Liliaceae) in southeastern U.S. and West Virginia.



Figs. 1–4. *Nematus atriceps*. 1, Mature larva feeding on a leaflet of *Trifolium*; length, 13 mm. 2, Pupa, without cocoon; length 8 mm. 3, Cocoon attached to florets of the clover flower; the larva developed on the petals; length, 11 mm. 4, Recently emerged adult, length, 12 mm.

The distribution of *Nematus atriceps* has not been recorded. It is found throughout western United States and in western Canada from the Rockies westward with several records east to Wisconsin and Manitoba. It generally overlaps the distribution of the food plant, but it is also possible *N. atriceps* feeds on other species of clover. Material examined by DRS is as follows: ALASKA: Nazan Bay, Atka, Aleutian Is., VII-27-1907, VIII-1-1907. ALBERTA: Beaverlodge, VI-7-1931; Wabamum, VII-31-1929. BRITISH COLUMBIA: "Vanc." CALIFORNIA: Smith River, VII-17; Rattlesnake Mdw., Siskiyou Co., 5800′, VIII-9-1970; Twin Lake, Siskiyou Co., VII-27-1971; Young's Valley, Siskiyou Co., 4600′, VII-4-1971; Swift Cr., Trinity Co., 5700′, VII-31-1973; Black Bsn, Trinity Co., 7100′, VII-29-1 972; Humboldt Co.: Mumford Bsn, Trinity Co, 6400′, VII-31-1972; 7 mi S Yellowjacket Camp, El Dorado Co., VI-29-1980; Cracker Mdws., Siskiyou Co., 5000′, VIII-16-1971; Cazadero, IV-12-1918; Oakland, Alameda Co., III-22-1952; Strawberry, Tuolumne Co., VI-21-1951; Tahquitz Mdw, San Jacinto Mts., VI-3-1940; Buck's Lake, Plumas Co., VII-1-1949; Muir Woods, V-19-1915; Cona Cr., Napa Co., IV-23-1949; 3 mi E. Mt. Lassen, VII-19-1953; Trinity Co., V-25-1934; Sagehen nr. Hobart Mills, VII-9-1954, VII-25-1954; Woodacre, III-28-1955; Pine Crest, Tuolumne Co., VII-1-1951; Kings Crk. Mdw., Shasta Co., VII-2-1947. COLORADO: "Colo."; 15 mi N Jct R. 14 & 40, VII-2-1962; Pitkin Co., Weller, 9360′, 8 rd. mi SE Aspen, VII-26-1977; Big Spring Ranch, Florissant, VII-18-1962. IDAHO: Lenore, V-7-1938; Weippe, 3006′, VII-5-1935; Vollmer, V-1930. MANITOBA: Aweme, VI-10-1928. MONTANA: Fairy Lakes, VIII-10-1968. NEVADA: "Nev." (holotype of *atriceps*); "Ormsby Co.," VII.

NEW MEXICO: Magdalena Mts., VIII-1894. NORTH DAKOTA: Bottineau Co., Malaise trap, VII-17-1972, VII-28-1974. OREGON: Seal Rock, Lincoln Co., 2002 (reared specimens); Cannon Beach, VIII-9-1940; Wheeler Co., road to Grant Spg., 500 yds SW Guard Station, VII-20-1962; Wallowa Co., 8 mi N Flora, VI-7-1963; Iron Mtn., 8 mi E Upper Soda, Linn Co., 5000′, VIII-11-1962; Kelsey Valley, Douglas Co., VI-26-1962; Horse Lake, High Cascade Mountains, Lane Co, VII-25–31-1909; Jackson Co., Squaw Lake, 7 mi E Copper, V-19-1962; Jackson Co., Dead Indian Soda Springs, 12 mi SE Lakecreek, 2500′, V-21-1964; Jackson Co., Pinehurst, 3375′, V-19-1960; Jackson Co., Buckhorn Mineral Spgs., 11 mi ESE Ashland, 2800′, Emigrant Cr., V-19-1960; Benton Co., Rock Creek, 4 mi S Philomath, IV-28-1963; Wasco Co., Bear Springs, 3180′, 25 mi W. Maupin, V-21-1959. WASHINGTON: Mt. Adams, VI-26-1931; Westport, VII-17-1949; Seattle, IX-17-1891. WISCONSIN: Polk Co., VII. UTAH: Bear R., n. sl. Uinta Mts., 8000′, VI-2-1919.

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NOTE

Notes on the Biology of *Synaxis formosa* (Hulst) (Lepidoptera: Geometridae) in South Central Washington State

Scoble (1999) recorded ten species of *Synaxis* Hulst from North America while McGuffin (1987) discussed four from Canada. McGuffin (1987) indicated that several of the species fly late in the season and probably overwinter in the egg stage; the larvae appear in the spring, feeding on conifers and hardwoods. For three of the Canadian species, he referenced significant host data along with flight periods. One species, *Synaxis formosa* (Hulst), had unknown immature stages and no host information. McGuffin indicated the flight period as October and recorded the species only from British Columbia. Hulst (1896) described the species from Colorado and southern California.

Since 1995, we have been conducting a survey of the biological diversity of select groups of arthropods on the Hanford Site located in south central Washington State. Consult Zack (1998) and Zack et al. (1998) for a description of the Hanford Site and the results of other aspects of the overall project. One of the groups of primary interest has been the moth fauna. Herein we report on the life history, host plant, and light trap captures of *S. formosa*.

Larvae of *S. formosa* were collected at the Chamna Natural Area (46°15.15′N 119°16.85′W) located south of Richland (Benton Co.) on 31 March 2001. This site is not within the Hanford Site but lies along the Yakima River just outside the boundaries of the Site. The habitat contains significant stands of big sagebrush (*Artemesia tridentata* Nuttall) bordering the riparian habitat along the river. Larvae were taken by beating big sagebrush plants and observing materials falling to sheets placed under the plants. Two geometrid larvae less than 1 cm in length (probably second instars) were collected; they appeared to be conspecific. Both larvae were placed on a potted sagebrush tubling and protected by placing a transparent plastic cover, with screened top, over the plant. The plant was kept outdoors, but out of direct sunlight to protect from overheating. One of the larvae died before attaining 1.5 cm, but the second survived, pupated, and emerged as an adult on 6 October 2001. The larva is a twig mimic as was noted by McGuffin (1987) for other species of *Synaxis*. The larva had pupated by mid-May and remained dormant throughout the summer. The pupal period was thus 130–140 days, much longer than the time period suggested by McGuffin (1987) for *Synaxis jubararia* Hulst (58–64 days). This longer pupal period may reflect the relatively long hot and dry summer period found in the south central Columbia Basin of eastern Washington where these observations were made. The reared adult was slightly smaller than wild caught individuals.

Adults were collected at several locations on the Hanford Site at 15-watt "black light" or 150-watt mercury vapor light. Collecting locations and dates are as follows: Benton Co. (all Hanford Site), SE base of Gable Mtn., 46°35.286′N 119°27.868′W, 15 Oct 1997 (5); Rattlesnake Spring, 46°30.447′N 119°41.887′W, 18 Oct 1996 (3) and 20 Oct 2001 (1); sand dunes, 46°31.369′N 119°21.192′W, 9 Oct 1996 (5) and 23 Oct 1996 (1). Grant Co. (all Hanford Reach National Monument—Saddle Mountain National Wildlife Refuge), 46°42.155′N 119°37.230′W, 18 Oct 2002 (3); 46°42.064′N 119°38.271′W, 18 Oct 2002 (3); 46°42.117′N 119°36.282′W, 18 Oct 2002 (1); 46°42.064′N 119°38.271′W, 5 Oct 2002 (14) and 25 Oct 2002 (1).

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NOTE

Confirmation of the Presence of *Amblyomma ovale* Koch 1844 and First Records of *Amblyomma scalpturatum* Neumann 1906 (Acari: Ixodida: Ixodidae) in the Amazonian Region of Ecuador

The senior author visited the Centro de Rescate Amazoonico (01°05′S, 77°32′W), Napo Province, in the Amazonian region of Ecuador in February, 2002. The following species of vertebrates were inspected repeatedly for ticks during that month: domestic dog (Carnivora: Canidae); *Nasua nasua* (L. 1766) (Carnivora: Procyonidae); *Tapirus terrestris* (L. 1758) (Perissodactyla: Tapiridae); monkeys (Primates: Cebidae), *Saimiri sciureus* (L. 1758), *Cebus capucinus* (L. 1758) and *Lagothrix lagotricha* (Humboldt 1812). Tick specimens obtained were preserved in 70% ethanol and deposited in the Tick Collection of Estación Experimental Agropecuaria Rafaela, Instituto Nacional de Tecnología Agropecuaria, Rafaela, Santa Fé, Argentina (INTA).

No ticks were found on monkeys. A nymph of *Amblyomma* spp. was found on a *N. nasua* (INTA N° 1727). *Amblyomma ovale* Koch 1844 was collected from dogs, tapirs and also a human, and *Amblyomma scalpturatum* Neumann 1906 was found on a tapir (Table 1). *Amblyomma ovale* was identified according to Aragão and Fonseca (1961b), and *A. scalpturatum* following Boero and Prosen (1960). One of us (JEK) searched the U. S. National Tick Collection for additional specimens of both tick species from Ecuador. The search yielded several records, all from the Amazonian region of Ecuador (Table 1).

Amblyomma ovale is widespread in the Neotropical Region, reaching the southern Nearctic (Guglielmone et al., in press). However, its presence in Ecuador has been documented only twice. Becklund (1968) found a specimen on an ocelot imported to U.S.A. from Ecuador, and Guglielmone et al. (in press) cites its presence in the country. Adults of this tick species primarily infest carnivores, but findings on tapir and man are not infrequent (Guglielmone et al., in press), as reflected in the records from Ecuador.

Amblyomma scalpturatum is usually found on tapirs and to a lesser extent on anteaters and dogs in Bolivia, Brazil, Colombia, French Guiana, Guyana, Peru and Venezuela (Jones et al. 1972). Evidentally, *A. scalpturatum* can occasionally parasitize humans (Aragão and Fonseca 1961a). These are the first records of *A. scalpturatum* from Ecuador, and expand the known distribution of this poorly known tick species.

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Table 1. *Amblyomma ovale* and *Amblyomma scalpturatum* from the Amazonian region of Ecuador at INTA Tick Collection (Rafaela, Argentina) and U. S. National Tick Collection (USNTC) (Statesboro, GA, U.S.A.).

Tick Sex	N	Host	Province	Locality	Coordinates	Date	Collector
				A. ovale INTA			
1♂ 1♀	1816	dog	Napo	CRA*	01°05′S 77°32′W	Feb 20, 2002	C. Zerpa
1♂	1817	dog	Napo	CRA	01°05′S 77°32′W	Feb 11, 2002	C. Zerpa
1♂	1819	dog	Napo	CRA	01°05′S 77°32′W	Feb 8, 2002	C. Zerpa
1♂	1820	dog	Napo	CRA	01°05′S 77°32′W	Feb 17, 2002	C. Zerpa
3♂ 1♀	1821	dog	Napo	CRA	01°05′S 77°32′W	Feb 2002	C. Zerpa
1♂	1822	dog	Napo	CRA	01°05′S 77°32′W	Feb 9, 2002	C. Zerpa
1♀	1823	*Tapirus terrestris*	Napo	CRA	01°05′S 77°32′W	Feb 2002	C. Zerpa
1♀	1825	*Tapirus terrestris*	Napo	CRA	01°05′S 77°32′W	Feb 12, 2002	C. Zerpa
1♀	1826	human	Napo	CRA	01°05′S 77°32′W	Feb 8, 2002	C. Zerpa
				A. ovale USNTC			
1♂ 1♀	RML64445	tapir	Sucumbíos	Tarapoa	00°07′S 76°25′W	May 25, 1974	D.J. Pletsch
1♂	RML65433	human	Sucumbíos	Lumbaqui	00°03′N 77°20′W	Feb 20, 1975	T. Monath
1♀	RML66535	tapir	Sucumbíos	Tarapoa	00°07′S 76°25′W	May 25, 1974	D.J. Pletsch
1♂	RML117072	dog	Napo	Zancudo	00°35′S 75°29′W	Oct 29, 1983	R.M. Timm
3♂ 1♀	RML117073	dog	Napo	San José de Payamino	00°30′S 77°19′W	Nov 21, 1983	R.M. Timm
2♂ 1♀	RML117074	dog	Napo	San José de Payamino	00°30′S 77°19′W	Nov 21, 1983	R.M. Timm
1♂	RML117075	human	Sucumbíos	Laguna Grande	00°00′ 76°11′W	Sept 30, 1983	R.M. Timm
1♂	RML117076	human	Napo	Zancudo	00°35′S 75°29′W	Oct 26, 1983	R.M. Timm
				A. scalpturatum INTA			
1♂	1824	*Tapirus terrestris*	Napo	CRA	01°05′S 77°32′W	Feb 2002	C. Zerpa
				A. scalpturatum USNTC			
8♂ 3♀	RML64445	tapir	Sucumbíos	Tarapoa	00°07′S 76°25′W	May 25, 1974	D.J. Pletsch
4♂ 4♀	RML66535	tapir	Sucumbíos	Tarapoa	00°07′S 76°25′W	May 25, 1974	D.J. Pletsch

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NOTE

Phylogenetics and the Reconfirmation of *Dentatella* Allen (Ephemeroptera: Ephemerellidae)

The history of Ephemeroptera taxonomy has involved instances of one species described as an adult and another species described as a larva proving to be the same species once rearing associations of the two stages have taken place. For some of the more recent examples establishing such associations, see Whiting and Lehmkuhl (1987), McCafferty and Provonsha (1988), McCafferty and Silldorff (1998), and Burian (2002). Lugo-Ortiz and McCafferty (1996a) argued that some such associations were inevitable but because of the present imperative to document the biodiversity of the world, the possibility of such eventual associations should not preclude the description of species based on either stage. In a recent instance (Burian 2002), adults of *Eurylophella coxalis* (McDunnough) (previously unknown as larvae) were shown to be associated with the known larvae of the genus *Dentatella* Allen, as both *D. bartoni* (Allen) and *D. danutae* McCafferty (previously unknown as adults). *Dentatella* and the more speciose genus *Eurylophella* Tiensuu had previously been shown to be sister branches within the Ephemerellidae subfamily Timpanoginae (McCafferty and Wang 1994, 2000). Burian's placement of the species in *Eurylophella* and dissolution of *Dentatella*, however, discounted compelling cladistic evidence (McCafferty 1977, 1978, 2000; McCafferty and Wang 1994, 2000) that, within a framework of strict phylogenetic hierarchical classification, allows this species to reside in a separate genus.

To support his position, Burian (2002) proposed an arbitrary rule that both adult and larval stages of lineages must possess defining morphological apomorphies in order to be recognized at the genus level. This effectively eliminated the genus *Dentatella* because its divergence with *Eurylophella* is based on larval apomorphies. We reject Burian's rule because it is both unrealistic and unnecessary to phylogenetic systematics, and would prove devastating to the higher classifications of metamorphic organisms. For example, we estimate that Burian's rule would eliminate well over half of the mayfly genera, by discounting genera that are now based on phenetic data and thus taken as hypothetical groupings yet to be tested with cladistics, and by discounting genera now unknown in one or the other stage, including nearly all extinct genera. A consideration of groups that have undergone cladistic analysis [for example, in the *Baetodes* complex (McCafferty and Baumgardner 2003), the *Bugilliesia* complex (Lugo-Ortiz and McCafferty 1996b), the *Hermanella* complex (Flowers and Domínguez 1991), the *Miroculus* complex (Savage and Peters 1982), Neoephemeridae (Bae and McCafferty 1998), Potamanthidae (Bae and McCafferty 1991), Teloganodidae (McCafferty and Wang 1997, McCafferty and Benstead 2002), and Timpanoginae (McCafferty and Wang 1994)] indicates that a combination of both adult and larval synapomorphies or autapomorphies does not exist at the point of generic branching in a large proportion of genera. Such does not even exist at more basal branchings involving several families and higher taxa of mayflies. For example, a single adult synapomorphy common to the Leptohyphidae is the basis of that taxon being recognized as a non-paraphyletic family separate from Coryphoridae (Molineri et al. 2001). Even if Burian intended to qualify his rule by limiting it only to monospecific genera [the largest category of genera in all biota (see e.g., Raup 1991)], his rule would still decimate higher classifications and undermine their potential applications.

Monophyly and branching sequence are the essential bases for phylogenetic higher classifications (e.g., Hennig 1966), with no specification of what life stage or multiple life stages of a lineage must contribute the apomorphies supporting hypotheses of monophyly and no specification of the degree of synapomorphy required at any branch for defining taxonomic categories. Because rates of morphological evolution vary considerably between larval and adult stages of mayflies (e.g., see McCafferty and Edmunds 1976, fig. 1) and other metamorphic organisms when different selection environments are involved, there is no logical reason to expect morphological apomorphies to be expressed in multiple life stages of every lineage and clade. These life stages are "character-bearing semaphoronts," the basic comparable elements of biology, in the terms of Hennig (1966), and any one semaphoront of an evolving lineage may sufficiently demonstrate morphological character evolution for the purposes of phylogenetics. Burian's rule, insisting on layered evidence from both adults and larvae for a particular taxonomic category is tantamount to an arbitrary gap criterion. McCafferty (1991) rejected the use of all gap criteria, following Wiley's (1981) admonition that phylogenetic classifiers must reject gaps and definitions of taxonomic categories based on such criteria. Finally and not in the least, imposition of Burian's rule and the resultant severe reduction of genera would significantly lessen the valuable indications of comparative biology (the "explanatory powers") that are inherent in the complex hierarchies of phylogenetic classifications (Ross 1974, Farris 1979, Wiley 1981, Ax 1987).

In keeping with a philosophy of providing strictly phylogenetic classifications of Ephemeroptera when possible, with a maximum of information content and unconstrained by gap or special criteria, or any selective use of such, we are regarding the above treated recently associated species as *Dentatella coxalis* (**new combination**), and thus continue to recognize the cladistic-founded genus *Dentatella*—a highly distinctive taxon in the larval stage and sister lineage to *Eurylophella*. These sister genera are phylogenetically distinct within the tribe Eurylophellini of the subfamily Timpanoginae. In the case of *Dentatella,* for example, the broadened larval femur is autapomorphic within the subfamily, and the relatively enlarged size of operculate gill 4, covering much of abdominal tergum 8 is autapomorphic within the order. For *Eurylophella,* the much elongated larval abdominal tergum 9 is a unique synapomorphy within the order. We know of no evidence, out-group or otherwise, that suggests alternative polarities with respect to these characters.

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NOTE

First Report of Nuptial Feeding in Sawflies, *Aneugmenus flavipes* (Norton) (Hymenoptera: Tenthredinidae)

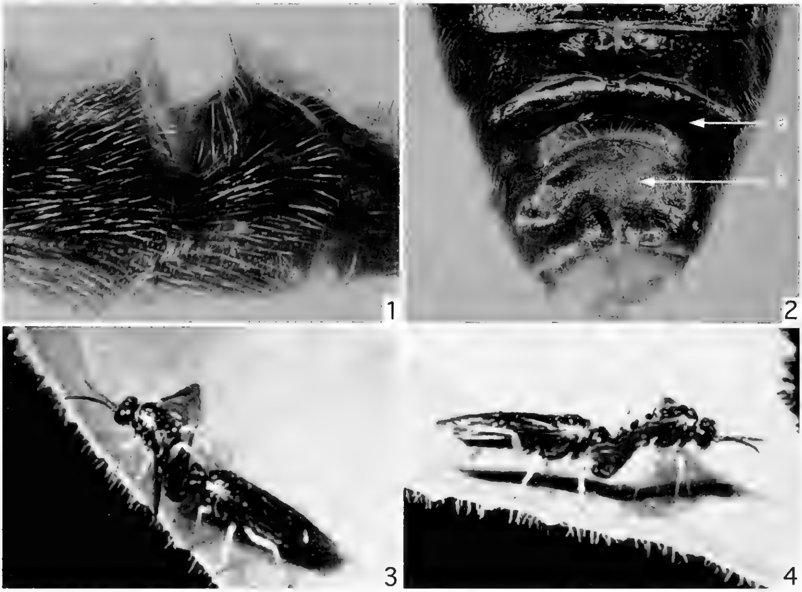
A deep, transverse concavity or depression is found on the seventh tergite in males of some sawflies of the subfamily Selandriinae (Tenthredinidae), most of which are fern feeders. This structure was first recognized by Malaise (1944: 28, 29, fig. 12) in some species of *Neostromboceros* Rohwer and in *Aneugmenus jacobsoni* (Enslin) from southeastern Asia. Malaise coined the term "*sinus sexualis*" "for this hitherto unnoticed secondary sexual organ of unknown purpose of certain species of the genus *Neostromboceros* Rhw." It is difficult to see the sinus sexualis in dried specimens because the abdomen is usually curved up with the anterior and posterior surfaces of the depression pressed together, thus hiding it. Modifications of the abdomen (Figs. 1–2) include the fifth and sixth tergites each divided into two halves by a medial suture and the hind margin of the sixth tergite carinate with two short apically projecting spines at the center; the seventh tergite deeply concave, cut deeply into the abdomen and posteriorly raised into a carinate posterior margin; and the eighth tergite with a large, central, oval, opaque or subopaque, shallowly depressed area. The functions of these modifications have not been documented.

This sexual modification also occurs in males of some New World and Palearctic species of *Aneugmenus* Hartig (DRS, personal observation), though it has not been recorded in the literature. It is present in males of *Aneugmenus floridella* Ross (southeastern U.S.), *A. scutellatus* Smith (southwestern U.S., northern Mexico), unidentified *Aneugmenus* species (Central and South America), *A. japonicus* Rohwer and *A. kiotonis* Takeuchi (Japan), and *A. coronatus* (Klug) and *A. fuerstenbergensis* (Konow) (Europe). We have not seen it in other genera except for *Neostromboceros*. We here report the occurrence of the sinus sexualis in *Aneugmenus flavipes* (Norton), a fern-feeding sawfly that occurs in the eastern United States and Canada and provide evidence that the structure serves to transfer glandular secretions from the male to the female.

A pair of *A. flavipes* (Figs. 3–4) were observed by SAM on low foliage in a mixed forest near Tobermory, Ontario, Canada. They were first noticed as they chased each other on the upper surface of a leaf, after which they took the position shown in Figs. 3–4, with the mouthparts of the female firmly affixed to the seventh tergite of the male. This position was held for about a minute, then broken, then reestablished after what appeared to be a brief attempt at copulation. It is not known whether copulation took place prior to the apparent transfer of glandular secretions from the male to the female *A. flavipes*.

We interpret this behavior in *A. flavipes* as the transfer of glandular secretions from male to female. Some other insects are known to transfer nutritional substances to the female both before and after mating. This behavior is well known in tree crickets (*Oecanthus* spp.), males of which produce glandular products in external notal glands. The time females spend feeding on the males' exudates is significantly correlated with egg production (Brown 1997). Some male cockroaches have tergal glands positioned similarly to those of *A. flavipes*, and the female feeds on the products of those glands in the same fashion (Brossut et al. 1975). Males of some soft-winged flower beetles, such as *Anthocomus bipunctatus* Harrer (Malichiidae), also have glandular areas in a conspicuous depression at the apex of the elytra (SAM, personal observation).

Most sawflies display little or no courtship behavior, as mentioned in some gen-



Figs. 1–4. *Aneugmenus flavipes.* 1, Lateral view of the "sinus sexualis." 2, Apex of abdomen, dorsal view; a = "sinus sexualis" of 7th tergite; b = central, opaque area of 8th tergite. 3–4, Nuptial feeding positions, male in front, female behind.

eral discussions (Benson 1950; Anderbrant 1993; Viitasaari 2002). At most, rapid wing vibration has been observed in some species such as *Hemitaxonus dubitatus* (Norton) (Tenthredinidae: Selandrdiinae) (Gordh 1975) and *Arge annulipes* (Klug) (Argidae) (Scott 1991). The observations reported here represent the first record of the possible function of the sinus sexualis in male Selandriinae and the first record of nuptial feeding in sawflies, and so far as we know, in Hymenoptera. We hope this will lead to further study of this unusual behavior in *Aneugmenus,* eventual determination of its purpose, and determination of the chemical substances involved.

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NOTE

New Nomenclatural Applications for Certain African Heptageniidae (Ephemeroptera)

Four species of African Heptageniidae have had a dubious history of generic placement. These species were originally described as *Adenophlebia bequaerti* Navás 1930; *A. sinuosa* Navás 1931; *A. tortinervis* Navás 1930; and *Afronurus njalensis* Kimmins 1937. All eventually were placed in the genus *Notonurus* Crass (1947) by Demoulin (1956, 1970). Gillies (1963) synonymized *Notonurus* with *Compsoneuriella* Ulmer, a genus originally described from southeastern Asia (Ulmer 1939). Gillies (1984) later elaborated his rationale but did not account for several other related Asian genera, and his synonymy was not universally accepted. Subsequently, Braasch and Soldán (1986) synonymized *Compsoneuriella* with *Compsoneuria* Eaton (1881). This synonymy was not followed, and current research shows that *Compsoneuriella* and *Compsoneuria* belong to different clades (McCafferty and Wang, in manuscript). In recent lists, these African species have continued to be considered in the genus *Compsoneuriella*; however, McCafferty and de Moor (1995) indicated that generic placement was tenuous.

Based on my studies of generic characterization and a broad spectrum of heptageniid materials from throughout the world, the four species are members of the genus *Thalerosphyrus* Eaton (1881). Three of the species are thus placed as *T. bequaerti*, **new combination**, *T. njalensis*, **new combination**, and *T. tortinervis*, **new combination**. Such a new combination of the fourth (*A. sinuosa*) species, however, creates a secondary homonym with respect to a different, Oriental species that has been known as *Thalerosphyrus sinuosus* (Navás) (originally *Ecdyonurus sinuosus*) based on Ulmer's (1939) recombination. The African species is therefore renamed ***Thalerosphyrus longinosi*** **McCafferty, new replacement name**, for *Adenophlebia sinuosus* Navás [= *T. sinuosus* (Navás) 1931, nec *T. sinuosus* (Navás) 1933]. The new epithet is after the Spanish Jesuit, Longinos Navás.

In addition to examining adults of *T. bequaerti* from the Democratic Republic of Congo and larvae and adults of *T. njalensis* from South Africa now held in the Purdue Entomological Research Collection, the descriptive literature associated with the species in question, for example, that brought together by Gillies (1984), has been sufficient for determining generic assignment. The fundamental characteristics associated with *Thalerosphyrus* include in the adults: mesothoracic sterna with a parallel-sided median depression, penes lacking dorsolateral spines, forelegs with a strongly elongated tarsal segment 1, and male hindtarsi about two-thirds or more the length of the hindtibiae; and in larvae: galealaciniae with scattered setae ventrally, mandibles with a single apical denticle, caudal filaments with whorls of spines well-developed, abdominal gills not strongly elongated, and meso- and metathoracic nota above the coxae produced as acute or subacute posterior projections.

The African species *T. ethiopicus* Soldán 1977 was correctly placed to genus when discovered, as was the Madagascar species *T. josettae* Sartori and Elouard 1996. Thus, among the Arctogaean family Heptageniidae, only *Thalerosphyrus* and the well-documented *Afronurus* Lestage (see e.g., Schoonbee 1968, Demoulin 1970, McCafferty 2003) can presently be documented from the Afrotropical Region.

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NOTE

Bdelloid Rotifers (Rotifera: Bdelloidea) Inhabiting Larval Black Flies (Diptera: Simuliidae) and Their Effect on Trichomycete (Zygomycota) Fungal Abundance

Black fly larvae (Diptera: Simuliidae) are restricted to lotic habitats where they anchor themselves with a silken pad spun onto solid substrates (e.g., rocks) and filter food from the water column (Adler and McCreadie 1997). Symbiotic relationships have evolved between black flies and other organisms, including, bacteria, fungi, nematodes, viruses, and protozoans (Crosskey 1990). During laboratory investigations of endosymbiotic trichomycete fungi of the genus *Smittium* (Zygomycota: Trichomycetes) and the larval black fly *Simulium vittatum* Zetterstedt cytospecies IS-7, we found bdelloid rotifers (Rotifera: Bdelloidea) in the simuliid larval midgut (Fig. 1). Here we report the first record of this association and provide evidence that the presence of rotifers in the larval midgut influences the ability of *Smittium* to establish in the hindgut.

Larvae of *Simulium vittatum* cytospecies IS-7 were reared from eggs obtained from a parasite-free colony housed at the University of Georgia (Athens, GA, U.S.A.). Approximately three weeks after submergence of eggs in 500 ml of aged tap water maintained at 22°C (Percival® incubator, Model: 1-36 VL), 40 larvae each were placed in 1-L polypropylene containers with 500 ml of aged tap water and moved to another incubator. All containers were aerated with aquarium pumps, and larvae were fed daily on a fish food slurry (McCreadie and Colbo 1991).

Fungi were reared on plates of 1/10 Brain Heart Infusion agar (Difco® 235–500: 0037-17) at room temperature (22–25°C) with sterile water overlays added to induce trichospore production. Trichospores are single sporangia, each housing a single sporangiospore and are the asexual infective stage of trichomycete fungi (Lichtwardt 1986). Once the trichospore enters the black fly larval hindgut, the sporangiospore extrudes, attaches to the cuticle, and produces a new thallus. In our experiments, a dosage of 4,000 trichospores/ml of rearing water was used.

To determine fungal abundance in hosts, larvae 4 days after inoculation were dissected in a drop of distilled water and the mid- and hindguts removed. Under phase-contrast microscopy, the hindgut was viewed at 400× through a 10 mm × 10 mm ocular grid. The number of grid squares that contained one or more hyphae were counted; relative abundance was expressed as the percentage of grid squares containing hyphae. During routine dissections in three experiments, four different treatment containers, out of 36, had larvae with active bdelloid rotifers in their midguts. In experiments 1 and 2, one out of 12 containers in each experiment had larvae with rotifers; in experiment 3, two out of 12 containers housed infected larvae. A total of 186 larvae were examined from these containers and 37 (19.9%) contained rotifers; abundance of bdelloids ranged from 0 to 24 individuals per larval host. Rotifers used a telescoping-type locomotion and fed on green algae in the simuliid midgut. Although the identity of the rotifers remains unknown, they possess characters consistent with the family Philodinidae (Wallace and Snell 2001). Whether the black fly larvae acquired bdelloids before or after trichospore inoculation, is unclear.

Bdelloid rotifers are free-living invertebrates that inhabit aquatic vegetation, sediment of lentic habitats, moist forest soils (Wallace and Snell 2001), and even the surface of freshwater insects and crustaceans

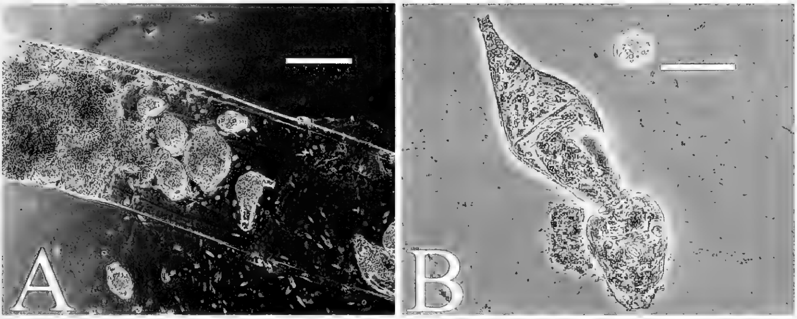

Fig. 1. A, Bdelloid rotifers inhabiting the peritrophic matrix of a larva of *Simulium vittatum* cytospecies IS-7. Bdelloids are located posterior to the food bolus on the left. Scale bar = 100 μm. B, A bdelloid rotifer with partial eversion of internal viscera. Scale bar = 25 μm.

(Pennak 1978). There are two dubious reports of bdelloid rotifers entozoic in larval *Culex* (Diptera: Culicidae) and *Chironomus* (Diptera: Chironomidae) (Marchoux 1898, Bartos 1951). Relationships between rotifers and trichomycete fungi are unknown, but some parasitic fungi, such as *Harposporium* (Deuteromycota: Moniliales), depend on rotifers for reproductive success (e.g., Baron 1980).

The source of the bdelloids in our material is unknown but might be related to the anhydrobiotic nature of these rotifers (Ricci 1987, 1998). The ability to survive dehydration (i.e., in a dessicated form) might indicate an airborne origin from within the laboratory or building. Stock cultures of larvae were always free of rotifers. Infections were not a result of epizoic rotifers since they were contained between food boluses in the black fly midgut in three different experiments conducted on different occasions. Thus, our reported occurrence of rotifers is not an isolated event. Bdelloid rotifers were noted in hindguts of several larvae, but none were alive. Also, dead bdelloid rotifers have been seen in hindguts of field collected *S. tuberosum* (Lundström) cytospecies F larvae from Mobile County, Alabama (Nelder, unpublished data).

During experiments in which rotifers

Table 1. Mean relative abundance of *Smittium megazygosporum*, *S.* near *typhellum*, and *S. morbosum* in the hindgut of larval *Simulium vittatum* cytospecies IS-7.

Trichomycete Species	Mean Relative Abundance % (n larvae examined)[a] Rotifers Absent in Container	Rotifers Present in Container
S. megazygosporum (experiment 1)[b]	19.2 (47)	0.6 (33)*
S. n. *typhellum* (experiment 2)	14.7 (20)	1.2 (10)*
S. n. *typhellum* (experiment 3)	8.4 (27)	0.0 (19)
S. morbosum (experiment 3)	26.8 (20)	9.9 (10)

[a] Relative abundance = percentage of ocular grid squares containing hyphae. For each experiment data were analyzed using a *t*-test on arcsine transformed percents; however, raw data are presented for comparative purposes. For each species, an asterisk indicates a significant difference ($p < 0.05$) in hyphal abundance. No test could be performed on *S.* n. *typhellum* from the second experiment.

[b] Each experiment had a total of 12 replications.

were found, black flies had been dosed with trichospores of either *Smittium megazygosporum* Manier and Coste, *S.* near *typhellum* Manier and Coste, or *S. morbosum* Sweeney. In black fly larvae taken from rotifer-infected containers, the relative abundance of both *S. megazygosporum* and *S.* near *typhellum* in the hindgut was significantly lower ($p < 0.05$) than in larvae taken from rotifer-free containers (Table 1). Trichospores of these fungi are well within the size range of particles fed on by bdelloids (i.e., 4–17 μm; Gilbert 1985). Accordingly, bdelloids might have reduced the number of trichospores passing to the hindgut, which in turn reduced the number of attached thalli.

We suspect the nature of the relationship between bdelloid rotifers and black fly larvae is one of accidental commensalism. Under this scenario, larval black flies are not effected by the rotifers; however, the rotifers use trichospores as a food source. Clearly, the exact nature of the relationship between black flies and rotifers warrants further investigation.

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NOTE

Depository of the Holotype of *Antonina nakaharai* Williams and Miller (Hemiptera: Pseudococcidae)

In a recent article we described and illustrated the three mealybug species of the *Antonina crawi* Cockerell complex (Williams and Miller 2002). In addition, we included a key to the species of *Antonina* that occur on bamboo and described and illustrated one additional species. Two new species were included: *A. maai* and *A. nakaharai*. In the "Type material" section of the description of *A. nakaharai* (page 903), we did not explicitly mention the depository of the holotype, but indicated in the "Specimens examined" section on page 906 that the series of specimens that included the holotype was deposited on BMNH and USNM. We did not indicate which of the two museums was the depository of the holotype, and it is possible (through somewhat unlikely) to assume that the holotype was not one of the specimens mentioned in the "Specimens examined" section. This omission was brought to our attention by F. Christian Thompson, who indicated that *A. nakaharai* should be considered as a *nomen nudum* until the description meets all criteria of Chapter 4 of the *International Code of Zoological Nomenclature* (2000); specifically, that we did not state where the holotype was deposited. Although broad interpretation of the description could suggest that the primary type was in one of the two museums, it is not clear if this information is specific enough to fit the criteria of Article 16.4.2 requiring "a statement indicating the name and location of that [the] collection" [where the holotype is deposited]. To be certain that there is no question of the validity of *A. nakaharai,* we here state that the holotype is deposited in the Coccoidea portion of the National Museum of Natural History Entomological Collection. Smithsonian Institution, Beltsville, Maryland.

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BOOK REVIEW

Scarab Beetles (Coleoptera: Scarabaeidae) of South Carolina. Biota of South Carolina Vol. 2. By Phillip J. Harpootlian. 2001. Clemson University, Clemson, S.C. ISBN 0-9712527-0-X. 157 pp. $37.50 (softcover). Available from Public Service Room, 96 Poole Agricultural Center, Clemson University, Clemson, South SC, 29634-0129 or purchase at http://cufan.clemson.edu/olos.

Identifying scarab beetles, especially for the generalist or serious hobbyist, is often quite challenging. The book by Arnett et al. (2002) has simplified generic level identifications but species level determinations remain problematic and require consultation of single species descriptions or revisions widely scattered in the scientific literature. For eastern United States, the regional works of Dillon and Dillon (1972) and Downey and Arnett (1996) provide the only comprehensive reviews of the region, but these works are incomplete and out of date. The works of Woodruff (1973), Woodruff and Beck (1989), and Ratcliffe (1991) are also useful for some groups. The book by Harpootlian, *Scarabs Beetles of South Carolina,* is extremely useful for identifying species from Virginia to Georgia. For example, of the 260 species and subspecies of scarabs that occur or are likely to occur in Virginia (Evans, in preparation), 225 also occur in South Carolina.

The foundation for the *Scarabs of South Carolina* is the species checklist gleaned from the papers of Cartwright (1934, 1939, 1950) and Kirk (1969, 1970). Literature records not verified by recent collections were also included, unless they could be shown to be in error. The checklist was supplemented with data from recent monographs. Additional data were gathered from university, museum, and private collections, as well as from the author's own field work.

The classification used by Harpootlian follows that of Downie and Arnett (1996), except that the tribe Pentodontini and subfamilies Trichiinae and Valginae are retained. Lawrence and Newton (1995) elevated several subfamilies within the Scarabaeidae to family rank (Geotrupidae, Ochodaeidae, Hybosoridae, Glaphyridae, Ceratocanthidae, Trogidae), a classification followed by Arnett et al. (2002). As is unfortunately customary among North American workers, the families Lucanidae (stag beetles) and Passalidae (bess beetles) are not included. Given the relatively small number of species in these two families represented in any region of United States, future authors would do well to consider launching more inclusive works aimed at completely characterizing the entire superfamily Scarabaeoidea of their region.

The keys of *Scarabs of South Carolina* are clear, concise, generally well illustrated and are easy to use, especially by those not intimately familiar with the group. This is due largely to the fact that the keys are designed primarily to identify taxa rather than reveal phylogenetic relationships. Sources for each key, when applicable, are cited beneath the heading. Couplets are numbered to allow the user to easily backtrack through the key. Keys are provided to distinguish subfamilies, tribes, genera, and species of South Carolina scarabs. Line drawings are used to illustrate characters used in the key. The male genitalia of many species are illustrated, particularly those of the genera *Phyllophaga* and *Serica.*

Each genus is followed by a list of its synonyms, type species, and a brief taxonomic review. Many genera are illustrated with habitus drawings that originally appeared in Woodruff (1973). Others are illustrated with reasonably clear black and white digital photographs or computer-assisted line drawings. The line drawings do not always accurately present the overall gestalt of the beetle, having rendered some of them shorter and wider than they appear in real life. An additional set of digital black and white habitus photos appears in an appendix at the back of the book. The overall utility of the book would have increased considerably had these images appeared in the appropriate places in the text.

The species information is easily accessible. The species are listed alphabetically within each genus rather than as they appear in the keys. This is an extremely useful feature, particularly for retrieving species data from larger genera such *Aphodius* and *Phyllophaga.* Each species is followed by its synonymy, a brief description, supplementary notes on taxonomy and biology, overall distribution, and South Carolina records. The South Carolina records are listed not by county, but rather alphabetically, a feature that does not easily facilitate atlasing efforts. Instead, the reader must refer to an appendix that provides an alphabetical listing of South Carolina localities, each followed by its county and ecoregion. Although this appendix eliminated much repetition throughout the text, the information would have been more user-friendly had it appeared with the species synopses.

A very useful three-page morphological glossary appears at the end of the work, clearly defining terms used in the keys, descriptions and text. The "Literature Cited" section appears complete for the taxa covered and includes publications up to the year 2000.

Harpootlian's taxonomic detective work is illuminating. He has clarified the authorship and dates for several taxa and presents a number of new synonyms. For example, the authorship of *Dynastes* is MacLeay, not Kirby and Ceratocanthinae is Martínez, not Cartwright and Gordon. *Osmoderma* Saint-Fargeau (usually cited as Le Peletier) and Serville was first proposed as a subgenus of *Trichius.* The authorship of *Ochodaeus, Popillia, Euparia,* and *Plectris* are Saint-Fargeau and Serville, 1828, not Serville, 1825 or 1828. The following synonyms are presented: *Copris fricator cartwrightii* Robinson = *C. fricator* (Fabricius); *Stephanuca thoracica* Casey = *S. areata* (Fabricius); *Euphoria appalachia* Casey = *E. scolopacea* Casey, and *E. oxysternum* Casey = *E. sepulchralis* (Fabricius) (see Hardy 2001); and *Geohowdenius* Zunino = *Geotrupes* Latreille.

New state records are clearly noted and include *Onthophagus gazella* (Fabricius), *Aphodius erraticus* (Linnaeus), *Martineziella dutertrei* (Chalumeau), *Platyomus notialis* (Cartwright), and *Serica loxia* Dawson. Two species removed from North American lists are noted because they still appear in the literature: *Dialytes umbratus* Balthasar (Aphodiinae) is restricted to Madagascar (an error traced to the 1964 Zoological Record, due to misspelling of the type locality "Kanada"), and *Epicometis vestita* (Say) (Cetoniinae) is known only from Eurasia.

Scarab systematists, collection managers, cataloguers, faunal surveyors, and hobbyists working with scarabs of eastern North America will find *Scarabs of South Carolina* an indispensable addition to their libraries. The author is to be congratulated on a well-done work that is sure to inspire others to create additional regional references.

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FIRST REPORT OF THE NEOTROPICAL DAMSEL BUG *ALLOEORHYNCHUS TRIMACULA* (STEIN) IN THE UNITED STATES, WITH NEW RECORDS FOR TWO OTHER NABID SPECIES IN FLORIDA (HETEROPTERA: NABIDAE: PROSTEMMATINAE)

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Abstract.—The first report of the prostemmatine nabid *Alloeorhynchus trimacula* (Stein) in the United States is given based on specimens collected in two counties of Florida. We diagnose the genus *Alloeorhynchus*, redescribe and provide photographs of the adult male and female of *A. trimacula*, and give other diagnostic information to help separate this newly discovered immigrant from other North American Nabidae. Also given are the first report of *Phorticus collaris* (Stål) in Florida and additional Florida records for *Pagasa confusa* Kerzhner.

Key Words: Insecta, Hemiptera, Nabidae, damsel bug, *Alloeorhynchus trimacula, Pagasa confusa, Phorticus collaris,* new records, United States, Florida

The family Nabidae is a relatively small group of predatory bugs, commonly referred to as damsel bugs; Kerzhner (1996) estimated 21 genera and 500 species worldwide. Harris' (1928) monograph of the North American fauna remains the most useful reference to identify members of this family, despite being more than 70 years old. More recently, Henry and Lattin (1988) summarized the literature in their catalog of the Nabidae of Canada and the United States, which included two subfamilies, four tribes, 10 genera, and 34 species. Since then, Asquith and Lattin (1991) established the new genus *Omanonabis* for the western U.S. species *O. lovettii* (Harris) and discussed the taxonomic position of *Nabis edax* Blatchley known from California. Kerzhner (1993) described the two new species *Lasiomerus andabata* and *Pagasa confusa* from Central America, Mexico, and the United States; resurrected *Hoplistoscelis pallescens* Reuter from synonymy under *H. sordida* Reuter and removed the latter and *H. dentipes* Harris from the U.S. list; gave species status to *Pagasa fusca* var. *nigripes*; and synonymized the subgenus *Parapagasa* Hussey under *Lampropagasa* Reuter. Kerzhner (1996) reduced *Omanonabis* to a subgenus of *Nabis* Latreille. Blinn (1996) reported *Phorticus collaris* Stål in North Carolina and Tennessee, a species previously known only from west of the Mississippi River, and Wheeler (2001) gave additional records and field notes for *Lasiomerus andabata* in Florida.

During ongoing faunal surveys in Florida, we have discovered specimens of three poorly known prostemmatine Nabidae. In this paper, we give the first records for *Alloeorhynchus trimacula* (Stein) in Florida and the United States, redescribe and provide photographs of the adult male and female, and furnish other diagnostic information to help separate this newly recognized immigrant from other North America Nabidae. Also given are the first report of *Phorticus collaris* in Florida and additional Florida records for *Pagasa confusa.*

Acronyms used for depositories cited in the paper are as follows: ABS (Archbold Biological Station, Lake Placid, Florida); FSCA (Florida State Collection of Arthropods, Gainesville, Florida); VGC (Vince Golia Collection, Boynton Beach, Florida); and USNM ([United States] National Collection and Natural History, Washington, D.C.).

Genus *Alloeorhynchus* Fieber 1860

Alloeorhychus Fieber 1860: 43 (n. gen.), 1861: 159 (first included species); Stål 1865 (3): 40 (descrip.), 1873: 107; Champion 1900: 300 (descrip.); Distant 1904: 393 (descrip.); Kerzhner 1981: 113 (descrip., genitalia); Henry and Lattin 1988: 518 (cat., distr.); Froeschner 1999: 141 (cat.). Type species: *Pirates flavipes* Fieber, 1836. Subsequent monotypy by Fieber 1861.

Alloeorrhynchus [*sic*] (*Alloeorrhynchus* [*sic*]): Reuter and Poppius 1909: 33 (descrip., key); Barber 1922: 103 (diag., key); Harris 1928: 12 (descrip., key).

Discussion.—The prostemmatine genera *Alloeorhynchus* Fieber, *Pagasa* Stål, and *Phorticus* Stål are known to occur in the United States (Harris 1928, Henry and Lattin 1988). The genus *Phorticus* may be recognized by the dull body texture, four-segmented antenna (supplementary segment II greatly reduced or absent), and the presence of a ventral median keel on the first visible abdominal segment. Both *Alloeorhynchus* and *Pagasa* can be distinguished from *Phorticus* by their overall shiny body texture, five-segmented antenna (presence of a distinct supplemental segment II), and the lack of a distinct median keel on the first abdominal segment. *Pagasa* is best recognized by the long supplementary antennal segment II (Fig. 1) that is half or more the length of antennal segment I, the relatively slender pro- and mesofemora (Figs. 2–3) that lack a stout tooth at the middle of each, and the overall uniformly shiny black body coloration. *Alloeorhynchus* is distinguished from *Pagasa* by the short supplementary antennal segment II (Fig. 4) that is much shorter than half the length of antennal segment III, the angularly widened pro- and mesofemora (Figs. 5–6) with each angle bearing a stout tooth, and the overall pale or multicolored body, often with yellow, orange, or red on the pronotum. Only the subgenera *Alloeorhychus* and *Psilistus* Stål are recognized in *Alloeorhynchus,* and only the former is known from the New World.

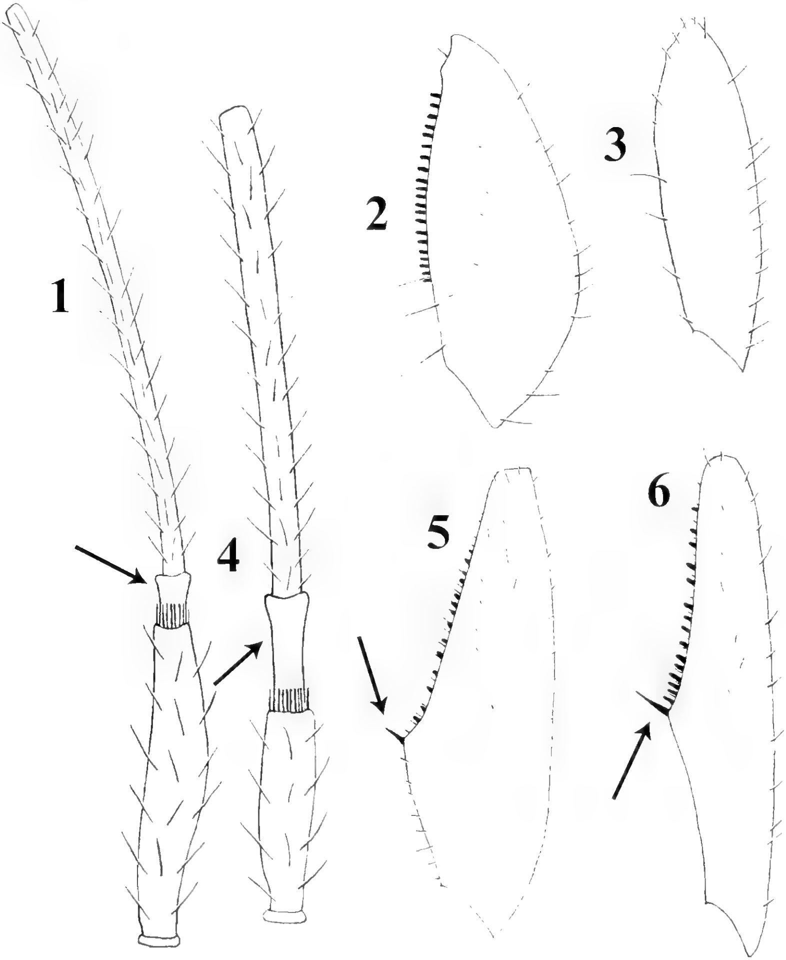
Alloeorhynchus trimacula (Stein) 1857
(Figs. 4–11)

Prostemma trimacula Stein 1857: 76 (n. sp.).

Alloeorhynchus trimacula: Stål 1873: 109 (distr.); Champion 1900: 300 (distr.); Froeschner 1999: 141 (cat.).

Alloeorrhynchus [*sic*] (*Alloeorrhynchus* [*sic*]) *trimacula*: Reuter and Poppius 1909: 40 (descrip., distr.); Barber 1922: 104 (diagnosis in key); Harris 1928: 16 (descrip., distr.); Blinn 1996: 216 (note).

Diagnosis.—This species (Figs. 7–11) can be recognized by the stout, shiny body having the head, three marks on posterior lobe of pronotum (one at each posterior angle and a triangular one at base of midline), scutellum, hemelytra, ventral area of thorax, lateral line on abdomen, and a spot on each of connexival segments 3–6 black; the bright reddish-orange pronotum, except for three black marks on posterior lobe; and the pale testaceous to pale brownish-white abdomen with the lateral line on each side and the genital segments black.



Figs. 1–6. Antennae and femora of *Pagasa* and *Alloeorhynchus* spp. 1–3, *Pagasa fusca* (♂). 1, Antennal segments I–III (arrow indicates long antennal segment II). 2, Profemur. 3, Mesofemur. 4–6, *Alloeorhynchus trimacula* (♂). 4, Antennal segments I–III (arrow indicates short antennal segment II). 5, Profemur (arrow indicates angulate area at middle bearing stout spine). 6, Mesofemur (arrow indicates angulate area at middle bearing stout spine).

Description.—Male (Figs. 9–10): Length 4.99 mm, width across widest area of hemelytra 1.44 mm, width across widest area of connexivum 1.90 mm. *Head:* Width 0.75 mm, vertex 0.31 mm; uniformly shiny black. *Rostrum:* Length 1.40 mm, extending to mesocoxae; fuscous. *Antenna:* Segment I, length 0.51 mm; II, 0.95 mm; III, 0.83 mm; IV, badly curled; segment I testaceous, becoming infuscated on apical half; segment II-IV brown to fuscous. *Pronotum:* Length 1.30 mm, basal width 1.54 mm; pronotum shiny red to reddish orange, except for black collar on anterior lobe and three black marks on posterior lobe, one at each posterior angle and along lateral edge and a triangular-shaped one at base of midline. *Scutellum:* Uniformly dull black, with three large, deep punctures; clothed with long, pilose setae about 2 × length of setae on hemelytra. *Hemelytron:* Macropterous; uniformly shiny black, including membrane; thickly clothed with erect, simple setae about half the length of setae on scutellum. *Ostiolar area:* Evaporative area dull black, becoming paler on lower half; auricle mostly shiny fuscous or black, elongate, horizontal, extending nearly to posterior edge of metapleuron. *Ventral surface:* Thorax uniformly dull black; abdomen pale testaceous or pale brownish white with lateral line, genital capsule and adjacent segments, and a spot on each of connexival segments 3–6 black. *Legs:* Overall pale testaceous, apex of procoxa becoming fuscous or black; pro- and mesofemora pale fuscous or black on apical halves, more so on outer face, metafemora fuscous or black on apical third; tibiae black at base and apex; tarsi and claws fuscous. Parameres symmetrical, reduced (see Harris 1928: 96, fig. 10).

Female (Figs. 7–8): Similar to male in coloration but larger in overall size; hemelytron sometimes submacropterous, not quite extending to apex of the abdomen. Length 5.95 mm, width across widest area of hemelytra 1.68 mm; width across widest area of connexivum 2.38 mm. *Head:* Width 0.78 mm, vertex 0.30 mm. *Rostrum:* Length 1.54 mm. *Antenna:* Segment I, length 0.58 mm; II, 1.14 mm; III, 1.00 mm; IV, ca. 1.16 mm (curled). *Pronotum:* Length 1.43 mm, basal width 1.76 mm.

Distribution.—Previously known from Brazil, Guatemala, Mexico, and Panama (Harris 1928). Florida represents the first record for the United States.

Specimens examined.—MEXICO: Tamaulipas: 1 ♀, Adolfo Lopez Mateos, El Chamalito camino al Paraiso, 30-III-2001, 400 m, L. Cervantes and N. Peñaloza (FSCA), on ground below *Ficus cotinifolia* H. B. & K. [Moraceae] (FSCA); Veracruz: 1 ♂, Lake Catemaco, 1–15 VII 1963, D. R. Whitehead (USNM); Veracruz: 1 ♂, 1 ♀, Actopan La Mancha, 26-XI-1998 & 19-VIII-2001, L. Cervantes, on the ground beneath *Ficus* sp. (USNM). UNITED STATES: Florida: 1 ♀, Alachua Co., Gainesville, NE 31 Ave. at 9th St., 10-VII-1995, J. Eric Cronin, on *Gaura angustifolia* Herb. Willd. Ex Steud. [Onagraceae] (FSCA); 1 ♀, Highlands Co., Archbold Biol. Sta., 1 Feb. 1999, Mark Deyrup, taken in yellow bowl trap on main grounds in disturbed oak hammock with ferns (ABS); 1 ♀, Highlands Co., Archbold Biological Station, 12-II-1999, L. Riopelle and Mark Deyrup, taken in yellow bowl trap on main grounds in disturbed hammock with ferns (ABS); 1 ♀, Highlands Co., Archbold Biol. Sta., 16 August 2000, Mark Deyrup, taken on walkway by main building (FSCA); 1 ♀, Highlands Co., Archbold Biol. Sta., 1 Feb. 2001, Mark Deyrup, taken in yellow bowl trap at bayhead by Lake Annie (USNM); 1 ♀, Palm Beach Co., Boca Raton, Route 441, 24 Aug. 1988, Vince Golia, at mercury vapor light (VGC); 2 ♂, St. Lucie Co., Ft. Pierce, City Park on Florida Avenue between SW 11 & 12 St., in leaf litter under *Ficus lutea* Vahl [Moraceae], 18-IX-2001, S. E. Halbert, G. B. Edwards, K. Hibbard, & J. Brambila (USNM); 1 ♀, St. Lucie Co., Ft. Pierce, City Park, 12-VII-2001, Ken Hibbard, Park, on soil below *Ficus lutea*, FSCA #E2001-2822 (USNM).

Discussion.—Only two species of *Al-*

Figs. 7–8. Photographs of *Alloeorhynchus trimacula*, adult ♂. 7, Dorsal aspect. 8, Lateral aspect.

loeorhynchus are known from the United States. In addition to *A. trimacula* reported from Florida in this paper, *A. nigrolobus* Barber is known from Arizona and Texas (Barber 1922). *Alloeorhynchus trimacula* can be separated from *A. nigrolobus* by the larger size (4.50–6.00 mm), the red to reddish-orange pronotum with three fuscous spots on the hind lobe (one at each posterior angle and one at base of middle), and the uniformly black hemelytra. *Alloeorhynchus nigrolobus* may be distinguished by the much smaller size (less than 4.00 mm), the bicolored pronotum with the anterior lobe pale brown and the posterior lobe black, and pale testaceous hemelytra.

Alloeorhynchus trimacula has been collected in several localities of Florida in leaf litter under *Ficus lutea* where lygaeoid nymphs occur. Only one specimen was taken on a plant, *Gaura angustifolia*. Luis Cervantes (personal communication) has observed this nabid feeding on lygaeoid nymphs in leaf litter under *Ficus* trees in Mexico. In Florida, two males were kept in captivity for 4 and 6 weeks, respectively, on a diet of rhyparochromid nymphs and water. When rhyparochromid nymphs were no longer available, one male survived for two weeks on laboratory-cultured, flightless *Drosophila*.

We consider *A. trimacula* a recent immigrant in Florida. Despite our searches through the Florida State Collection of Arthropods and the National Museum of Natural History, no material collected earlier than 1999 was found. Also, Florida is reasonably well collected, so if this species had


9


10

Figs. 9–10. Photographs of *Alloeorhynchus trimacula*, adult ♂. 9, Dorsal aspect. 10, Lateral aspect.


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Fig. 11. Photograph of adult *Alloeorhynchus trimacula* resting on dead leaf.

been present much earlier, it should have been found by other collectors. In addition, the distribution of *A. trimacula* in Florida is considerably disjunct from its previously known range, providing further evidence that it is adventive.

Phorticus collaris Stål 1873

Phorticus collaris Stål 1873: 109 (n. sp.); Champion 1899: 301 (distr.); Henry and Lattin 1988: 520 (cat.); Blinn 1996: 216 (descrip., distr.).

This species was described from Texas (Stål 1873) and later reported from Teapa, Mexico (Champion 1899). More recently, Blinn (1996) redescribed and illustrated *P. collaris* and gave new county records for Texas (Brazos and Hidalgo counties) and the first eastern U.S. records from North Carolina and Tennessee. *Phorticus collaris*, the only species of the genus known from the United States, can be distinguished from species of *Alloeorhynchus* and *Pagasa* by the dull body texture, four-segmented antenna, and presence of a median keel on the ventral surface of the first abdominal segment. The specimen recorded below represents a new state record for Florida.

Specimen examined.—UNITED STATES: Florida: 1 ♀, Leon Co., Tall Timbers Research Station, 23 June 1993, Vince Golia, at mercury vapor light (VGC).

Pagasa confusa Kerzhner 1993
(Figs. 1–3)

Pagasa confusa Kerzhner 1993: 43 (n. sp.).

This relatively newly recognized species, described from Costa Rica, Guatemala, Mexico, Panama, Puerto Rico, and the United States (Connecticut to Florida, and west to California), was long confused with *P. fusca,* from which it can be distinguished by the pale legs and greatly reduced male parameres (Kerzhner 1993, figs. 23–25). The genus *Pagasa* may be separated from *Alloeorhynchus* by the overall shiny black body, longer antennal segment II (Fig. 1), and the relatively slender pro- and mesofemora lacking a stout tooth (Figs. 2–3). From *Phorticus, Pagasa* may be separated by the shiny black body, five-segmented antenna, and absence of a median keel on the first abdominal segment. Though previously reported from Florida, the only recorded specimen was taken in 1911 from Newberry [Alachua Co.], Florida. Below we provide several new county records based on more recently collected material.

Specimens examined.—UNITED STATES: Florida: 2 ♂, Highlands Co., Archbold Biol. Stn., 27 May 1999, M. Deyrup, in yellow bowl trap near Lake Annie dock (FSCA, USNM); 1 ♂, Highlands Co., Archbold Biol. Stn., 28 Aug. 2000, M. Deyrup, in yellow bowl trap in marshy area near Lake Annie dock (ABS).

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THE UNUSUAL OCCURRENCE OF AQUATIC BEETLES IN AMBER, *COPELATUS APHRODITAE* BALKE, N. SP. AND *C. PREDAVETERUS* MILLER, N. SP., (COLEOPTERA: DYTISCIDAE: COPELATINAE)

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Abstract.—***Copelatus aphroditae* Balke, new species**, is described based on a single female from Baltic amber (Eocene), and ***C. predaveterus* Miller, new species**, is described from five specimens preserved in Dominican amber (late early Miocene to mid-Oligocene). The former does not fit into previously defined species groups and is assigned to the new *C. aphroditae*-group. *Copelatus predaveterus* is assigned to the *C. trilobatus*-group which currently contains at least 20 extant species and has, in aggregate, a Pantropical distribution. The discovery of these specimens is interesting since aquatic beetles are relatively rare in fossil tree resins. Also, they are very similar to derived extant *Copelatus*, suggesting relatively prolonged stasis in the morphology of this very speciose genus (>430 described species). Based on these specimens, *Copelatus* is at least 50 million years old and at least some of the species groups are perhaps 30 million years old.

Key Words: water beetle, Baltic and Dominican amber, phylogeny, fossil insects

Despite considerable interest in amber-preserved insect specimens, few diving beetles (Dytiscidae) have been reported from amber. This seems reasonable since aquatic beetles are seemingly unlikely candidates for preservation in tree resins. Nevertheless, the unusual occurrence of a few adult and even some larvae of aquatic adephagan beetles in amber has been mentioned including specimens of Gyrinidae (Hatch 1927; Helm 1896; Keilbach 1982; Menge 1856; Motschulsky 1856; Weitschat and Wichard 1998; Wichard and Weitschat 1996) and Dytiscidae (Berendt 1845; Helm 1896; Keilbach 1982; Poinar 1992; Poinar and Poinar 1999; Spahr 1981a, b; Weidner 1958; Weitschat and Wichard 1998; Wichard and Weitschat 1996; Wunderlich 1986), though many of these refer to the same specimens. The only species of Dytiscidae described from amber so far is *Glesseria rostrata* Koch and Berendt, 1845. This species is based on a single larva in Baltic amber and was originally assigned to Thysanura, not Coleoptera, albeit with some doubt (Handlirsch 1908; Koch and Berendt 1854).

Diving beetles are a comparatively well-studied family taxonomically, and the group is becoming better known phylogenetically (e.g., see Miller 2001). Despite this and despite the usefulness of fossils for providing unique character combinations and determining minimum ages of divergences, relatively little effort has been placed on the study of fossil dytiscids. Because diving beetles are aquatic, the chance of fossilization of specimens in sediments is probably higher than for many other insects. The literature does, in fact, contain many references to fossilized dytiscids (mainly impression fossils), but these are often described in only limited detail with very little evidence offered for their taxonomic placement. The numerous dytiscid (and other hydradephagan) fossils available in collections are a potentially large, untapped source of information about the evolution of the group. Though amber specimens of Hydradephaga are certainly much more rare than impression fossils, at least several comparatively well-preserved adult specimens of *Copelatus* Erichson are available for study and are described herein. These are the first species of Dytiscidae described from adult specimens in amber.

Copelatus is one of four genera of Copelatinae and is the most speciose genus of Dytiscidae (433 described species: Nilsson 2001) with most of its members occurring in the tropics. The genus has never been completely revised and is in need of a detailed cladistic analysis with broad taxon and character sampling in addition to considerable species-level monographic work. Extant species in the group are usually separable on the basis of male genital structure, as well as coloration and fine structural details of the cuticle, all of which are difficult or impossible to examine in amber preserved specimens. Nevertheless, the species described here appear to possess external character state combinations sufficient for diagnosing them from extant taxa. Here, we describe two new species which belong to the extant genus *Copelatus, C. aphroditae* Balke from Baltic amber, and *C. predaveterus* Miller from Dominican amber.

MATERIAL AND METHODS

Figures.—Line drawings of *C. predaveterus* and *C. aphroditae* were created with the aid of drawing tubes on a Wild M3C and a Leitz MZ12 dissecting microscope, respectively.

Preparation and condition of specimens.—Specimens of *C. predaveterus* were prepared with methods described by Grimaldi (1993). They were examined by placing the amber piece on a drop of glycerine on a microscope slide. A drop of glycerine was then placed on the dorsal surface of the amber piece and a coverslip placed over the drop. The entire piece containing *C. aphroditae* was placed in a small tray with glycerine and then examined.

Measurements.—Measurements of *C. predaveterus* and *C. aphroditae* were made using ocular scales in a Wild M3C and a Leitz MZ12 dissecting microscope, respectively. Some of the specimens are distorted by compression or stretching in the amber, but measurements do not correct for this in any way. For this reason, measurements are unavoidably inaccurate and give only a general idea of the actual dimensions of most of the specimens. Total length (TL) and greatest width (GW) are provided along with the ratio TL/GW to provide an indication of shape.

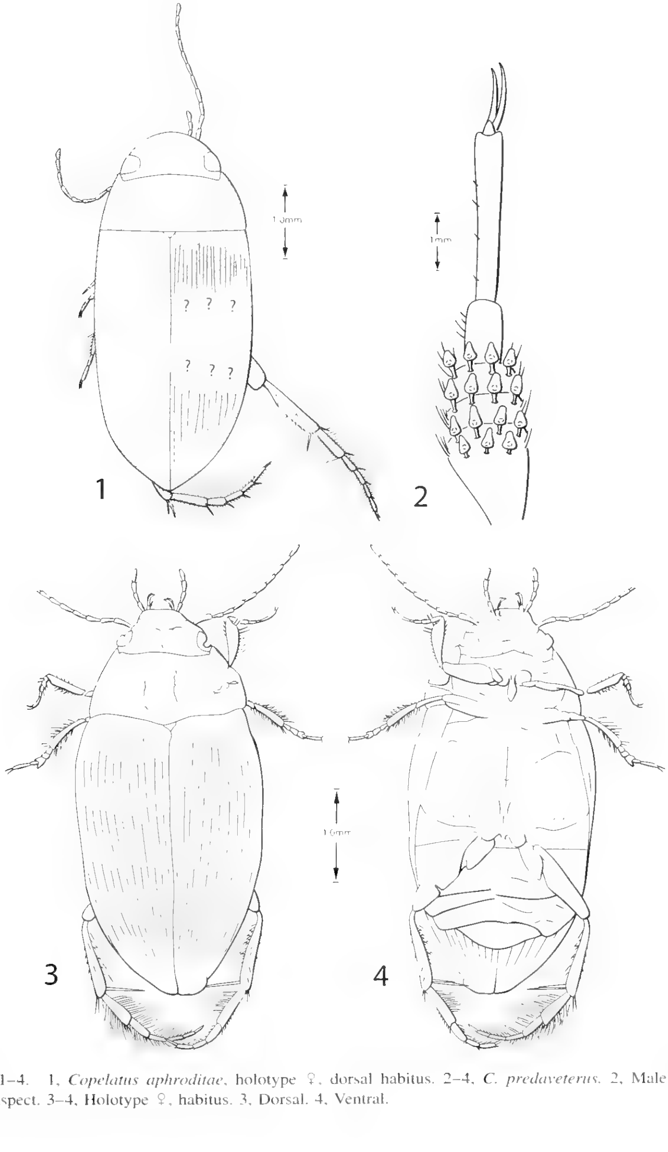
Copelatus aphroditae Balke, new species
(Fig. 1)

Holotype.—♀, in collection A. Herrling, Bramsche, Germany, labeled # 1153. The piece is clear, yellowish golden. The beetle is partly covered with a whitish film of air. Besides the beetle, there are two pieces of sclerotized, cuticular material in the amber, which could not be identified. Also, there are few "Sternhaare," which are thought to be minute parts of oak trees and which are characteristic of the Baltic Amber (Weitschat and Wichard 1998).

Diagnosis.—With 19 discal striae on elytron anteriorly; posteriorly with ten striae visible. Submarginal stria absent (Fig. 1); size small (total length 5.0 mm); body in dorsal view approximately parallel-sided (Fig. 1).

Description.—*Measurements:* TL = 5.0 mm; GW = 2.2 mm; TL/GW = 2.27.

Dorsal side (Fig. 1): Elongate, lateral margins continuously curved between pronotum and elytron. Body approximately parallel-sided in dorsal view. Head (partly



Figs. 1–4. 1, *Copelatus aphroditae*, holotype ♀, dorsal habitus. 2–4, *C. predaveterus*. 2, Male protibia, ventral aspect. 3–4, Holotype ♀, habitus. 3, Dorsal. 4, Ventral.

crushed) with distinct microreticulation (MR) of honeycomb-like cells; with few larger punctures, their diameters equal to that of meshes. Pronotum with MR of regular, slightly longitudinally-oriented cells, with few larger and smaller punctures; discally with short strioles which increase in length and depth laterally. Pronotum with lateral bead complete, extending nearly to anterior angle. Elytron with 19 longitudinal striae, with only 10 striae visible on posterior portion of elytron; without submarginal stria. With MR and relatively dense punctation between the striae.

Ventral side: Prosternal process moderately convex, apex narrowly rounded. Metasternum with MR of horizontally oriented cells; metacoxa with MR of cells in diagonal orientation, few larger punctures and with diagonal strioles. Metacoxal lines closely approximated posteriorly. Ventrites 1–5 chagreened and with few larger punctures; with oblique strioles on ventrite 1 becoming increasingly transverse posteriorly. Last visible sternite without lateral striae.

Etymology.—Named after Aphroditae, Greek god of love.

Occurence.—Baltic Amber, Eocene.

Comments.—This species does not fit well into other, currently-recognized species groups, and we assign it to a new *Copelatus aphroditae*-group based on the presence of nineteen discal impressed striae on the elytron and the lack of a submarginal elytral stria.

Copelatus predaveterus Miller, new species

(Figs. 2–4)

Type specimens.— Holotype, ♀, AMNH DR-14-615, labeled, "AMBER: Oligo-Miocene Dominican Republic AMNH no. DR-14-615 Locality:/Copelatus trilobatus-group Det AN Nilsson-96/*HOLOTYPE Copelatus predaveterus* Miller 2000."

Paratypes (4): 1 ♂, AMNH, same amber piece as holotype, same labels; 1 ♂, AMNH DR-14-974, labeled, "AMBER: Oligo-Miocene Dominican Republic AMNH no. DR-14-974 Locality:"; 1 ♀, AMNH DR-14-973, labeled, "AMBER: Oligo-Miocene Dominican Republic AMNH no. DR-14-973 Locality:/Amber: Oligo-Miocene Dominican Republic: mines at or near La Toca AMNH (no cat. no. yet)/ DYTISCIDAE COPELATUS SP. det. PJ Spangler"; 1 ♀, AMNH DR-14-616, labeled, "AMBER: Oligo-Miocene Dominican Republic AMNH no. DR-14-616 Locality:/Copelatus trilobatus-group Det AN Nilsson-96."

Although male specimens of Dytiscidae are generally selected as holotypes, a female specimen was selected since this individual is easily visible dorsally and ventrally, and the piece of amber in which it is included also contains a male specimen, which is currently less visible, but which, in the future, will be easily associated with the female holotype. The only other male specimen is the least distorted of the specimens and is also easily visible. However, it is on the extreme edge of the amber piece where this piece is broken, and some of the specimen is exposed to the air. Parts of the legs and antennae are in the piece that is broken off. Rather than selecting this specimen, which is in more tenuous condition, a specimen was chosen that is well within a relatively strong piece of amber and is entirely intact.

Diagnosis.—Eleven discal and one submarginal striae present on elytron, first stria not shortened, of similar length to others (Fig. 3); size small (total length 3.8–4.4 mm); male pro- and mesotarsal claws unmodified (Fig. 2); male without strioles on pronotum.

Description.—*Measurements:* TL = 3.82–4.40 mm; GW = 1.84–2.36 mm; TL/GW = 1.79–2.21.

Dorsal side: (Fig. 3). Elongate oval, lateral margins continuously curved between pronotum and elytron. Male apparently without distinct strioles on pronotum or elytra. Pronotum with lateral bead complete, extending nearly to anterior angle. Elytron with 11 discal and 1 submarginal striae; all discal striae elongate and distinct, not shortened (Fig. 3).

Ventral side: (Fig. 4). Prosternal process moderately convex, apex narrowly rounded (Fig. 4). Male pro- and mesotarsal claws not modified (Fig. 2). Male pro- and mesotarsomeres 1–3 moderately expanded, ventrally with 4 rows of adhesive setae (Fig. 2), 2 rows on tarsomere 1, 1 row on 2, and 1 row on 3, most proximal row with 3 adhesive setae, other rows with 4 adhesive setae. Male pro- and mesotibiae not modified.

Etymology.—This species is named *predaveterus* from the Latin *preda,* meaning "predator" and *veterus,* meaning "of a former time" in reference to the carnivorous habits and ancient existence of this species.

Occurrence.—Dominican amber, Oligocene-Miocene, Dominican Republic.

Comments.—This species is a member of the *Copelatus trilobatus*-group (*sensu* Guéorguiev (1968)) based on the presence of eleven discal and one submarginal impressed striae on the elytra. Within this group, it may be distinguished from most of the species by its smaller size. Other species in the group similar to *C. predaveterus* in size are *C. concolorans* Balfour-Browne, *C. gschwendtneri* Guiqnot, *C. perfectus* Sharp, *C. trilobatus,* Régimbart and *C. undecimstriatus* Aube, and members of most of these species are still generally larger than *C. predaveterus. Copelatus predaveterus* has unmodified male prostarsal claws, has the first elytral stria elongate (not shortened) and males apparently lack strioles on the pronotum, though fine details of cuticular surfaces are not easy to discern on these specimens. Based on these features, *C. predaveterus* may be most similar to the extant *C. perfectus.*

DISCUSSION

The very speciose genus *Copelatus* has been divided into informal species groups based on the number and type of longitudinal striae present on the elytron. These characters have yet to be adequately tested as synapomorphies, but given the extreme size of the genus and lack of a phylogenetic hypothesis it is convenient to recognize these informal groupings of species for ease of communication (Balfour-Browne 1939).

Based on the number of elytral striae, *Copelatus aphroditae* is rather isolated within *Copelatus.* The maximum number of elytral striae in *Copelatus* is typically 13 or less, with the extant South American *C. abonnenci* Guignot being the only known exception thus far. This species has 22 dorsal striae plus one submarginal stria (Guéorguiev 1968; Guignot 1939). It has been historically placed in a group of its own, the *C. abonnenci*-group, which was defined as having 14–23 striae (Guignot 1939). This is somewhat confusing since *C. abonnenci* is the only species of the group and it has 23 striae. Therefore, we redefine the *C. abonnenci*-group as those *Copelatus* with a total of 23 elytral striae. We assign *Copelatus aphroditae* to a new species group, the *C. aphroditae*-group, which is characterized by having 19 dorsal striae anteriorly on the elytron, and no obvious submarginal one.

Copelatus predaveterus belongs to the group with eleven sutural and one submarginal elytral striae (*Copelatus*-group 13 *sensu* Sharp (1882) and *trilobatus*-group *sensu* Guéorguiev (1968)). Other members of the *C. trilobatus*-group are tropical and occur in South America, Africa, southeast Asia and Australia. New World members occur primarily in northern South America and their habits are essentially unknown. However, other Copelatinae, such as *Aglymbus bromeliarum* Scott and *A. bimaculatus* Resende and Vanin, are known from Bromeliaceae (e.g. Resende and Vanin 1991). The unusual situation of having aquatic beetles entrapped in tree resin could be explained by their living in bromeliads, tree holes or other similar arboreal aquatic habitat. However, this is certainly speculative, and there are other possible explanations such as entrapment during dispersal or interrment in resins deposited in the water. The fact that the dytiscids from amber from very disparate localities and time periods are congeneric suggests that *Copelatus* may show a greater potential for becoming interred in amber, possibly because of specialized habitat preferences. Other inclusions in the Dominican amber pieces are terrestrial including several collembolans and a terrestrial hemipteran.

The age of Dominican amber has been controversial, but recent estimates place much of it at 15–20 million years (late Early to early Middle Miocene) (Iturralde-Vinent and MacPhee 1996) with others placing it at as much as 23–30 million years (Lower Miocene to mid Oligocene) (Grimaldi 1995). Baltic amber appears to be much older, and recent authors place it at some 40–55 million years (Eocene) (Michelsen 2000; Weitschat and Wichard 1998).

Little has been proposed regarding the phylogeny of Copelatinae. The striate *Copelatus* species appear to be monophyletic (Balke 2001), but relationships within this clade are not yet known. However, an upcoming molecular phylogenetic study of Copelatinae (Balke, Ribera & Vogler, in preparation) will likely help clarify the phylogeny of this diverse group. When attempting to propose potential historical explanations for diversity, it is crucial to reliably calibrate at least some nodes of cladograms used to infer divergences. Indirect, biogeographic evidence suggests a Gondwanian origin of Copelatinae, earlier than perhaps 120 mya (Balke 2001). Here, we present for the first time evidence for an origin of the more derived, striate forms of the genus predating perhaps 50 mya, a conclusion that will aid substantially any future studies of the evolution of this old and diverse group of beetles.

OTHER FOSSIL *COPELATUS*

Our new species are the first Copelatinae species described from amber and one, *C. aphroditae,* is the oldest fossil copelatine known. Three other fossil species in this genus have been described from well-preserved impression fossils from the middle Miocene (10–15 mya) in Northern Caucasian layers (Ríha 1974):

- *Copelatus stavropolitanus* Říha, 1974: eleven elytral striae (*C. nigrolineatus*-group).
- *Copelatus ponomarenkoi* Říha, 1974: six elytral striae plus one submarginal stria (*C. irinus* group).
- *Copelatus fossilis* Říha, 1974: ten elytral striae plus one submarginal stria (*C. erichsoni* group).

Copelatus species similar to these do not currently occur in this area. The closest extant relatives of these species are probably Afrotropical and/or Oriental.

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THE GENUS *MACROSTEMUM* KOLENATI (TRICHOPTERA: HYDROPSYCHIDAE) IN SRI LANKA

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Abstract.—Based on the study of types and, mostly, new material collected between 1970 and 1980, nine species of *Macrostemum* Kolenati are recognized on the island of Sri Lanka. The species *Macronema multifarium* (Walker), *M. nebulosum* (Hagen), and *M. sepultum* (Hagen) are redescribed based on the first material collected since the original types in the 1850s, and are formally transferred to *Macrostemum* (all **n. comb.**). *Macrostemum splendidum* (Hagen) and *M. pseudoneura* (Brauer) are redescribed, and *M. ethelda* (Banks) from southern India is reduced to a subspecies of the latter (**n. status**). *Macrostemum indistinctum* (Banks), a species widespread in southeastern Asia, is newly recorded from the island and *M. saowapa* Malicky is placed in its synonymy (**n. syn.**). ***Macrostemum barnardi*, *M. krombeini***, and ***M. malickyi*** are newly described. All species are described, the male genitalia figured (*M. krombeini* and *M. multifarium* are known only from females), and photos of the wing patterns presented. The species *Macronema obliquum* Hagen is transferred to the genus *Marilia* in the Odontoceridae (**n. comb.**).

Key Words: *Macrostemum,* Hydropsychidae, Sri Lanka, new species, descriptions, illustrations, wings

Sri Lanka (previously Ceylon) lies off the southeastern tip of India. Considering its proximity to India, it seems to have a surprising high level of endemism in its insect fauna. This level of endemism may be more due to the comparative lack of study of the south Indian fauna in comparison to the Sinhalese. Of the nine species treated here, only two are known from the continent, one of which is represented by different subspecies on the continent and the island, the other being found throughout southeastern Asia as far south as Sumatra.

The genus *Macrostemum* Kolenati, as presently recognized, is widespread over the World, being known from North and South America, Africa, and Asia. Most species presently placed in *Macrostemum* were originally described in *Macronema* Pictet. In 1982 Flint & Bueno divided *Macronema* into two generic entities, by resurrecting *Macrostemum. Macronema* is restricted to the Neotropical Realm. The Sinhalese species were mostly described in *Macronema,* and all were placed in this genus for most of the 20th century.

Walker (1852) described the first species now in this genus as *Hydropsyche multifaria,* and all subsequent mention of this species has been based on the type. Hagen in 1858 and 1859 described 7 species in *Macronema,* of which three, *M. splendidum, M. nebulosum,* and *M. sepultum* now lie in *Macrostemum. Macronema ceylanicum* has been transferred to *Pseudoleptonema* Mosely and *M. vitrina* to *Oestropsyche* Brauer, both in the Hydropsychidae; *M. annulicorne* was moved to *Anisocentropus* McLachlan in the Calamoceratidae; *M. obliquum* has remained in *Macrostemum* till now. I studied the holotype of the latter many years ago and realized that it was not a hydropsychid. During the preparation of this paper I restudied the holotype, including its cleared male genitalia. It is an Odontoceridae, and is here placed in the genus *Marilia* Müller (**n. comb.**), pending further revision of that genus and its possible dismemberment. I have not seen another example of this species in any material available to me. Brauer described *M. pseudoneura* from Sri Lanka in 1865, a species rediscovered and well characterized subsequently. In 1911 Banks described *M. indistinctum* from eastern India, it is here recorded from Sri Lanka and the recently described *M. saowapa*, is synonymized with it. Three new species have been discovered in the material collected under the auspices of the Smithsonian's "Ceylon Insect Project" directed by Dr. K. V. Krombein, and are described herein.

Several of the old localities and labels need some clarification. Hagen in his 1858 publication listed the types of *M. splendidum* and *M. nebulosum* as from Rainbodde. Further, on p. 487 he stated (translated) that the species labelled Rainbodde are all collected at this spot in the mountains, 3,500 to 4,000 feet above the sea. In his second paper (Hagen 1859) he corrected this spelling to Rambodde for the type of *M. sepultum*. This locality is now accepted as Ramboda and is at 7°04′N, 80°42′E in the District of Nuwara Eliya.

The paratype of *M. barnardi* in the Natural History Museum, London bears a handwritten label stating "Ceylon," but on the back a handwritten "N'pitia." This has been interpreted (Barnard 1980, p. 66) as Nawalapitiya, a town in the central highlands at 7°03′N, 80°32′E in the District of Kandy.

A series of *M. nebulosum* was collected at Kabaragala, Nillomalai, by S. & P. B. Karunaratne. Unfortunately there are two localities named Kabaragala, one a populated place at 6°03′N, 80°18′E, which would place it in the lowlands in the Galle District. The other an estate near Adam's Peak at 6°56′N, 80°26′E, which is about 6.5 km SSE of the Kitulgala Resthouse and right on the border between the Kandy and Kegalla Districts (it is labelled Kan. Dist.) at about 300 m. There is no Nillomalai in the gazetteer. Based on the other two collections of *M. nebulosum*, it seems that the lowland site is quite improbable for this species, and that the estate site is the one intended. Another P. B. Karunaratne site, Karambaketiya off Memure, Knuckles Range, is also problematic. I can not find Karambaketiya in the gazetteer, however, there is a Mimure (the label, handwritten, is Memure) about 7 km NNE of Corbets Gap and below Knuckles Peak at about 600 m. I place this locality for *M. splendidum* in the Kandy District in the vicinity of Mimure at 7°26′N, 80°50′E.

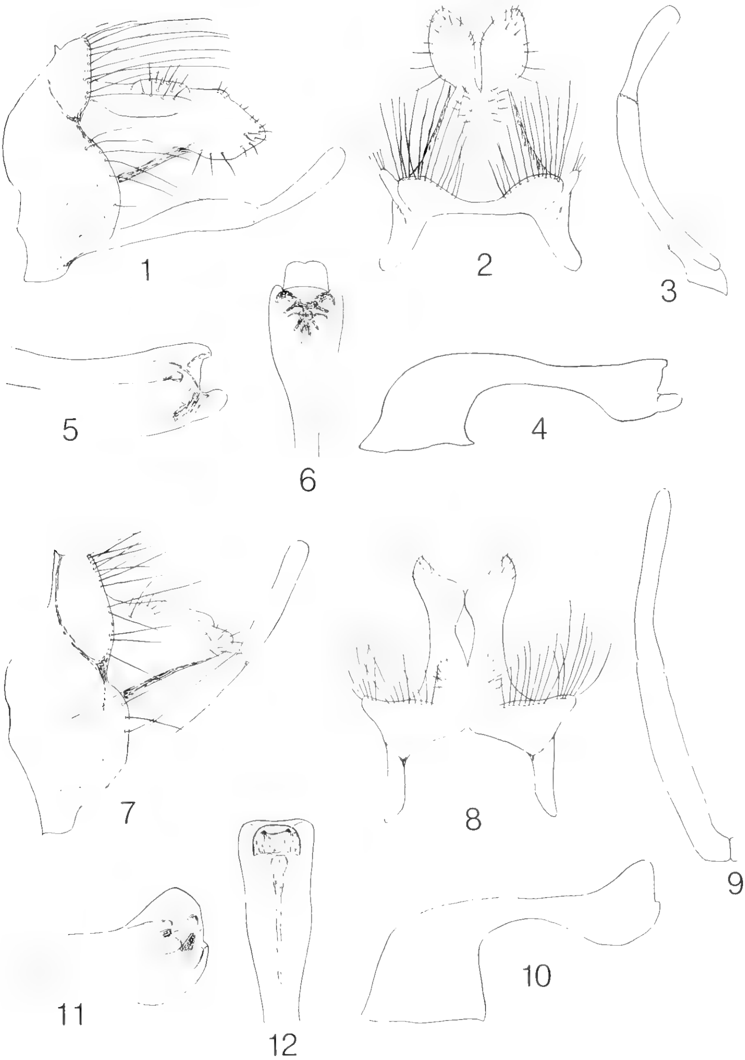
Fernand Schmid collected extensively on Sri Lanka (then Ceylon) in the first 4 months of 1954. The results of this field work were published in a large work in 1958. Many years later the Smithsonian purchased the vast majority of this collection, including the types. They are labelled Ceylan, a 2 or 3 letter initial for the province, locality, date and F. Schmid. However, in his work (1958) on pages 4–24 he also gave the name of the water course, elevation, and ecological setting at each of these localities. I have included, in brackets, these elevational and water course data for his localities whenever cited.

All descriptions are from adults, none having their immature stages positively associated. Acronyms used are given in Acknowledgments.

Macrostemum barnardi Flint, new species

(Figs. 1–6, 43)

This species is most similar to *M. pseudoneura* on the basis of coloration. The two



Figs. 1–12. Male genitalia. 1–6, *Macrostemum barnardi.* 1, Lateral. 2, Dorsal. 3, Inferior appendage, posteroventral. 4, Phallus, lateral. 5, Tip of phallus, lateral. 6, Same, ventral. 7–12, *M. indistinctum.* 7, Lateral. 8, Dorsal. 9, Inferior appendage, posteroventral. 10, Phallus, lateral. 11, Tip of phallus, lateral. 12, Same, ventral.

can be easily distinguished by the complete, transverse, pale band near the base of the forewing and the three, trianguloid, pale marks from the anterior margin beyond in *M. barnardi.* In contrast *M. pseudoneura* has a transverse, pale, band nearer the apex and this band is developed from the innermost of the three, pale, trianguloid marks. In addition there are many more smaller differences in maculation. The male genitalia suggest a closer relationship to *M. nebulosum* and *M. splendidum* based on the similarity in the structure of the tenth tergum and phallic apex. The basolateral ridge of the tenth tergum in *M. barnardi* is unique.

Male.—Length forewing 9–10 mm. Color fuscous, with cream-colored and clear marking. Head golden yellow, cuticle infuscate laterally between dorsal warts; maxillary palpus with 4 basal segments infuscate, apical segment golden; antenna with scape, pedicel and outer face of first flagellar segment, golden; following 3–4 segments fuscous, then stramineous, becoming infuscate apically. Cuticle of meso- and metanota and pleura, black. Legs golden yellow; tibia of foreleg darkened for apical half. Forewing (Fig. 43) with 3 pale-yellow marks from anterior margin, a series of small spots in costal cell basally, and a single, complete, transverse, pale-yellowish band at about ⅓ length of wing; apex with wash of golden setae anteriorly, posteriorly and apically with extensive pale yellowish or clear marks on a fuscous background; hindwing infuscate apically. Abdomen fuscous. Genitalia: Ninth segment with anterolateral margin broadly produced, rounded, posteroventral margin produced, rounded and shelflike above inferior appendage; posterior margin with scattered, elongate setae, becoming numerous dorsolaterally. Tenth tergum with dorsobasal setal wart, with distinct basolateral ridge, apex angulate; in dorsal aspect with apex produced laterad. Inferior appendage elongate, parallel-sided; in posteroventral aspect with apical segments not quite ⅓ of total length. Large basal section of phallus ⅓ of total length of phallus, curving sharply into stem; apex broadly rounded ventrally, dorsally barely elevated; apex nearly vertical with a small dorsal lobe and large ventral, liplike lobe.

Female.—Length forewing 8–9 mm. Coloration as in male. Mid tibia and tarsus flattened, broadened, concave on inner face.

Material examined.—Holotype, ♂: SRI LANKA, Ratnapura Dist., Weddagala, 8–13 Feb 1977, K.V. Krombein et al., collected at light [NMNH]. Paratypes: Same data, 2 ♂, 1 ♀; Gilimale, 17–18 Jun 1976, Krombein et al., light trap, 2 ♂; Gilimale, 17–18 May 1975, Wood & Petty, 1 ♂ (in alcohol); Gilimale, Induruwa Jungle, 5–7 Feb 1977, Krombein et al., blacklight trap, 1 ♀; 2 mi [ca. 3 km] S of Weddagala, Sinharaja Jungle, 8–12 Feb 1977, Krombein et al., 3 ♀. Galle Dist., Kanneliya Section, Sinharaja Jungle, 2–5 Oct 1980, Krombein et al., collected at blacklight, 1 ♂; Hiniduma, 22 Oct 1973, M. & B. Robinson, collected at black light, 1 ♀. Ceylon, N[awala]piti[y]a, McLachlan Coll BM 1938-674, 1 ♀ (BMNH).

Etymology.—I dedicate this species to Dr. Peter C. Barnard of The Natural History Museum, London in gratitude for all his help and friendship during my many visits to that Museum.

Macrostemum indistinctum (Banks)
(Figs. 7–12, 44)

Macronema indistincta Banks 1911:106 [forewing].

Macronema brisi Navás 1930:5 [forewing].—Fischer 1963:178 [catalogue].

Macronema fulvescens Martynov 1935:186 [♂, wings].—Fischer 1963:187 [catalogue].

Macronema indistinctum: Fischer 1963:189 [catalogue].

Macrostemum saowapa Chantaramongkol and Malicky 1986:528 [♂, wings, head].—Malicky 1998:777 [♂, wings]. **New synonym.**

Macrostemum indistinctum: Malicky 1998:

777 [♂, wings, synonymy of *M. brisi*, and *M. fulvescens*].

Malicky (1998) redescribed the species, placed *M. brisi* and *M. fulvescens* in synonymy, and extended its known distribution. I have studied a male paratype of *M. saowapa* from the Malicky collection, comparing its structures and genitalia with a male from Padukka, and the male type of *M. indistinctum* from Bengal, India. The male genitalia are in very close agreement, offering no notable differences. Unfortunately the wings of the *M. saowapa* paratype are now virtually decolored and offer no clues in terms of pattern; the pattern as originally reconstructed is compatible with *M. indistinctum* in spite of some differences. All the Sri Lankan material here recorded is quite uniform in coloration and agrees perfectly with the type of *M. indistinctum*. In all the material from Sri Lanka before me, there is no other species approaching *M. indistinctum* in structure or appearance; I, therefore, believe that *M. saowapa* is a synonym of it.

The species is known from India, China, Thailand, Laos, Malaysia, Sumatra, and now Sri Lanka (Malicky 1998). Our collection contains numerous captures of the species, but only one contains any males. Most captures were made at night at light traps; perhaps the males are generally active during the day with the females night active. This is a species of low elevations, most recorded elevations being 150 m or less, but one lot was taken at 900 m.

Male.—Length of forewing 11 mm. Color tawny, wings with clear markings. Color of head stramineous, browner dorsally; antenna stramineous. Thoracic cuticle brown; legs stramineous. Forewing (Fig. 44) basically tawny with clear marks, outlines rather indistinct; 3 clear marks from anterior margin, basalmost mark extending along anterior margin to wingbase; with membrane posteriad to clear marks darkened, with various, rather ill defined, pale marks apically and posteriorly. Hindwing clear with slight apical darkening. Genitalia: Ninth segment with anterolateral margin broadly produced, posteroventral margin produced, shelflike above inferior appendage; posterior margin with scattered, elongate setae, becoming numerous dorsolaterally. Tenth tergum with dorsobasal setal wart, apex rounded; in dorsal aspect with translucent, mesal lobe subapically. Inferior appendage elongate, parallel-sided; in posteroventral aspect with two segments of nearly equal length. Basal section of phallus relatively broad, about 45% of total length of phallus; apex broadly rounded ventrally, sharply, and obliquely elevated dorsally; apex nearly vertical with small indentation at midheight.

Female.—Length of forewing 8–11 mm. Coloration as in male. Midtibia and tarsus strongly flattened, broadened and concave on inner face.

Material examined.—Sri Lanka, ♂ paratype *M. saowapa* (HMPC). [India], Pusa, Bengal, Oct 07, A. Mujtaba, ♂ holotype 11765, *M. indistinctum* Banks (MCZ).

SRI LANKA: Colombo Dist., Labugama, 400 ft [ca. 120 m], 24 Aug 1973, G. Ekis, collected at blacklight, 9 ♀; Bayagama, sea level, 28–29 Aug 1973, G. Ekis, collected at black light, 2 ♀; Padukka, 6 Aug 1972, P. B. Karunaratne, at light, 3 ♂, 1 ♀. Galle Dist., Kanneliya Jungle, 11–16 Jan 1975, Krombein et al., blacklight, 11 ♀; Kanneliya, 22–24 May 1975, Wood & Petty, collected in Malaise trap, 2 ♀; Kanneliya, 6–15 Aug 1975, Panawatta, 11 ♀; Kanneliya, 500 ft [ca. 150 m], 21–22 Apr 1973, Baumann & Cross, at blacklight, 1 ♀; Kanneliya Jungle, Udugama, 400 ft [ca. 120 m], 6–12 Oct 1973, Krombein et al., at blacklight, 1 ♀; Kanneliya Jungle, 11 mi. [ca. 18 km] E. Udugama, 11 Oct 1973, Krombein et al., at blacklight, 4 ♀; Sinharaja Jungle, Kanneliya section, 13–16 Jul 1978, Krombein et al., blacklight trap, 1 ♀; Sinharaja, above Enselwatta, 3,000 ft [ca. 900 m], 20 Apr 1973, Baumann & Cross, 1 ♀; Hiniduma, 22 Oct 1973, M. & B. Robinson, collected at black light, 1 ♀. Hambantota Dist., Badagiria Tank, 6.5 mi [ca. 10.5 km] N Hambantota, 75 ft. (ca. 23 m), 27 Oct 1970, O. S. Flint, Jr., 1 ♀. Kalutara Dist., Agalawatta, 24 Jul 1975, Huang et al., light trap, 1 ♀. Kegalle Dist, Kelani Ganga, Kitulgala, 500 ft [ca. 150 m], 12 Mar 1973, Baumann & Cross, at blacklight, 5 ♀. Monaragala Dist., Menik Ganga, Sella Kataragama, 150 ft. (ca. 45 m), 24 Oct 1970, O. S. Flint, Jr., 1 ♀. Ratnapura Dist., Walawe Ganga, Embilipitya, 100 ft. (ca. 30 m), 21 Oct 1970, O. S. Flint, Jr., 2 ♀; dam site, Udawalawe, 250 ft. (ca. 75 m), 19 Oct 1970, O. S. Flint, Jr., 5 ♀; Gilimale, 17–18 Jun 1976, Krombein et al., light trap, 1 ♀; Gilimale, lumber mill, 115 ft [ca. 35 m], 20–25 Oct 1976, Hevel et al., blacklight, 1 ♀; Sinharaja Jungle, 2 mi. [ca. 3 km] S Weddagala, 8–12 Feb 1977, Krombein et al., 2 ♀.

Macrostemum krombeini Flint, new species

(Fig. 45)

The holotype of this species was first believed to be a variant of *M. sepultum,* but with the discovery of several new collections unquestionably *M. sepultum,* this now is untenable. The color pattern suggests a relationship to *M. sepultum,* but the pattern is reduced to only a single small spot on the anterior margin of the forewing and an elongate mark from the posterior margin. The apparent black stripes along the front and hind margins of the forewing, so apparent in Fig. 45, are an artifact of poor spreading; they are due to the wing being folded at these spots.

The specimen was collected by net in a heavily forested, bushy area by a very small streamlet. My field note indicates that a red-bodied macronematine was collected, the red now has faded to a tawny color.

Male.—Unknown.

Female.—Length of forewing 10 mm. Color generally fuscous with white marks. Head tawny frontally and dorsally, with frontal cuticle between eyes and central wart with bluish sheen; antenna with scape, pedicel, and first flagellar segment ventrally tawny, first flagellar segment dorsally and next 4 flagellar segments infuscate, remaining segments stramineous (missing beyond segment 15). Thoracic cuticle tawny; legs tawny, tarsi stramineous; midtibia slightly broadened and slightly concave mesally, tarsus unmodified. Forewing (Fig. 45) basically fuscous with creamy-white marks; 1 small spot at midlength from anterior margin, 1 elongate stripe from posterior margin at ⅔ length. Hindwing infuscate, a very small paler spot at stigma.

Material examined.—Holotype, female: SRI LANKA, Kandy Dist., Peradeniya [near top of hill behind University], 1,700 ft [ca. 520 m], 13 Nov [not Oct as labelled] 1970, O. S. Flint, Jr. (NMNH).

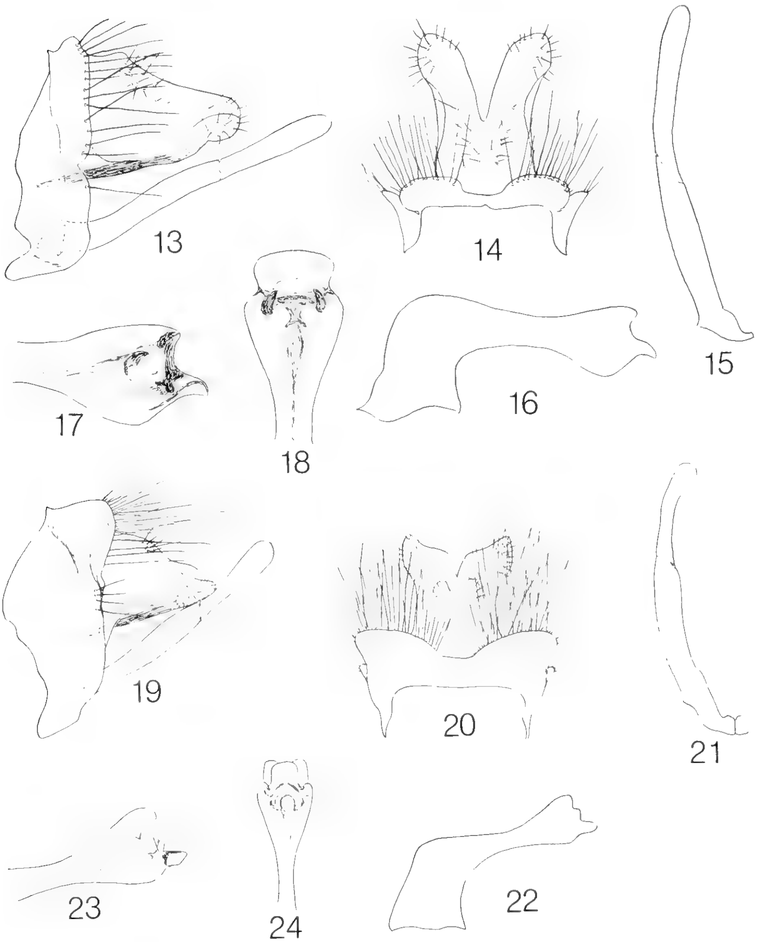
Etymology.—I dedicate this species to Dr. Karl V. Krombein of the National Museum of Natural History, Washington, in gratitude for all his efforts originating and directing the survey of the Sinhalese insect fauna.

Macrostemum malickyi Flint, new species

(Figs. 13–18, 46, 48)

This distinctive new species is, in maculation, most like *M. sepultum,* in that both have black wings, marked with a few, discrete, white spots. However, *M. malickyi* has four such spots, and *M. sepultum* has six. There are only two anterior marginal spots in *M. malickyi* and the outermost posterior mark extends from the wing margin anteriad into the gap between the two anterior marks, a pattern quite different from that of *M. sepultum.* The outline of the tip of the phallus in *M. malickyi* is also unique among the insular species.

Male.—Length of forewing 8.5 mm. Color fuscous with white marks. Head stramineous; frontal cuticle between eyes and central wart and posteriad on vertex, darkened; antenna with scape, pedicel and basal third of flagellum, stramineous, apical ½ of flagellum, infuscate. Thoracic cuticle shining fuscous; legs stramineous except meta-



Figs. 13–24. Male genitalia. 13–18, *Macrostemum malickyi*. 13, Lateral. 14, Dorsal. 15, Inferior appendage, posteroventral. 16, Phallus, lateral. 17, Tip of phallus, lateral. 18, Same, ventral. 19–24, *M. nebulosum*. 19, Lateral. 20, Dorsal. 21, Inferior appendage, posteroventral. 22, Phallus, lateral. 23, Tip of phallus, lateral. 24, Same, ventral.

tibia darkened. Forewing (Fig. 46) fuscous with 4 white spots, 2 of which extend posteriad from costal margin (posterior segment of outermost narrowly separated from main mark in holotype) and 2 extending anteriad from posterior margin with outermost extending between 2 anterior spots, other more basad. Hindwing infuscate with anterior margin and stigma white. Genitalia: Ninth segment with anterolateral margin irregularly produced with large, rounded anteroventral lobe, posteroventral margin nearly vertical; posterior margin with scattered, elongate setae, not much denser dorsolaterally. Tenth tergum with dorsobasal setal wart diffuse, apex rounded; in dorsal aspect with apex rounded, slightly curved laterad. Inferior appendage elongate, parallel-sided; in posteroventral aspect with two segments of nearly equal length. Basal section of phallus about ⅓ total length of phallus, relatively high and at right angle to stem of phallus; apex broadly bulging ventrally before apex, and slightly elevated dorsally; apex with large, lip-like process ventrally.

Female.—Length of forewing 7 mm. Coloration as in male, except posterobasal white mark of forewing much smaller (Fig. 48). Midtibia and tarsus unmodified.

Material examined.—Holotype, male: SRI LANKA, Galle Dist., Udugama, Kanneliya Jungle, 400 ft [ca. 120 m], 6–12 Oct 1973, K.V. Krombein et al., at black light (NMNH). Paratype: Same data, 1 ♀ (NMNH).

Etymology.—I dedicate this species to Dr. Hans Malicky, Lunz am See, Austria, in gratitude for his help with this project and to honor all his work on the Southeastern Asian fauna.

Macrostemum multifarium (Walker), **new combination**
(Fig. 47)

Hydropsyche multifaria Walker 1852:115.
Macronema multifarium: Ulmer 1907b:96 [wings in color].—Betten and Mosely 1940:202 [redescription, wings].—Fischer 1963:191 [catalogue].

This species, as well as several others of its congeners, has not been found since its original description. I have now seen four more examples, one of which has been compared directly with the holotype, and found identical in appearance. The holotype now lacks most of its abdomen, and mine are all females, thus the male genitalia are unknown. The midlegs of these females are not at all flattened, as in many other species.

The new sites are all in the wet, southwestern corner of the island, at elevations probably between 50 and 150 meters.

Male.—Unknown.

Female.—Length of forewing 10–11 mm. Color generally fuscous with cream colored marks. Head stramineous to tawny frontally, labrum fuscous, shining black dorsally between eyes; antenna with scape, pedicel, and first flagellar segment ventrally stramineous, first flagellar segment dorsally and next 10 flagellar segments infuscate, remaining segments tawny. Thoracic cuticle shining fuscous; legs stramineous; midtibia and tarsus unmodified. Forewing (Fig. 47) basically fuscous with cream-colored marks; 3 yellow marks from anterior margin, with various other pale marks apically and posteriorly. Hindwing infuscate with white stigma and basally directed streak in costal and subcostal cells. Abdomen apparently orangish dorsally.

Material examined.—Ceylon, William Templeton, holotype (BMNH).

SRI LANKA: Galle Dist., Sinharaja Jungle, Kanneliya section, 2–5 Oct 1980, Krombein et al., collected in Malaise trap, 2 ♀. Ratnapura Dist., Sinharaja Jungle, 8 Sep 1979, P. B. Karunaratne et al., in Malaise trap, 2 ♀.

Macrostemum nebulosum (Hagen), **new combination**
(Figs. 19–24, 49–50)

Macronema nebulosum Hagen 1858:485.—Ulmer 1907a:61 [redescription, wing tips, wings in color].—Ross 1952:34 [lectotype].—Fischer 1963:192 [catalogue].

This species is very poorly known, being recorded from only the original type series, a female paratype of which was figured in color by Ulmer (1907a). I here present photographs of the wings of the male lectotype and a female paralectotype from the MCZ, figure the male genitalia, and record several new collections. The species appears to be one limited to higher elevations and consequently to higher rainfall. The types from Ramboda were stated by Hagen (1859, p. 487) to be from 3,500 to 4,000 feet (1,065–1,220 m) above sea level, and the Adam's Peak collection was made at 6,000 ft. (1,825 m.).

Male.—Length of forewing 14–17 mm. Color pale brown with yellowish cast. Head flavescent with black mark between dorsal warts; antenna fuscous; maxillary palpus flavescent. Mesonotum flavescent with fuscous markings anteriorly and laterally, leaving rectangular flavescent area centrally; legs flavescent (Adam's Peak series with most of head dorsally fuscous with pale warts, thoracic notae with cuticle entirely fuscous). Forewing (Fig. 49) with pale spots poorly contrasting with ground color, only dark stigmal spot contrasting (even this spot in series from Adam's Peak is barely noticeable). Hindwing clear. Genitalia: Ninth segment with anterolateral margin produced and angulate, posterolateral margin nearly vertical; posterior margin with few setae laterally, with dense brush of long setae dorsolaterally. Tenth tergum with dorsobasal setal wart small, apex rounded in lateral view; in dorsal aspect with apex slightly flared laterad. Inferior appendage elongate, with each segment slightly constricted near base; in posteroventral aspect with basal segment nearly two-thirds of total length. Basal section of phallus relatively narrow, slightly more than one-third of total length of phallus; apex slightly rounded ventrally, and obliquely elevated dorsally; apex with distinct, lip-like projection.

Female.—Length of forewing 14 mm. Coloration either as in male, or forewing with darker ground color (Fig. 50). Midtibia and tarsus unmodified.

Material examined.—Ceylon, [Ramboda, Nuwara Eliya Dist.], Nietner, ♂ lectotype, ♀ paralectotype (MCZ).

SRI LANKA: Kandy Dist., Kabaragala, Nillomalai, 22–23 Mar 1975, S. & P. B. Karunaratne, 6 ♂. Nuwara Eliya Dist., Adam's Peak, 6 mi [ca. 9⅔ km] S Maskeliya, 6,000 ft [ca. 1,825 m], 17 Feb 1970, Davis & Rowe, 6 ♂, 1 ♀.

Macrostemum pseudoneura pseudoneura (Brauer)
(Figs. 25–30, 51)

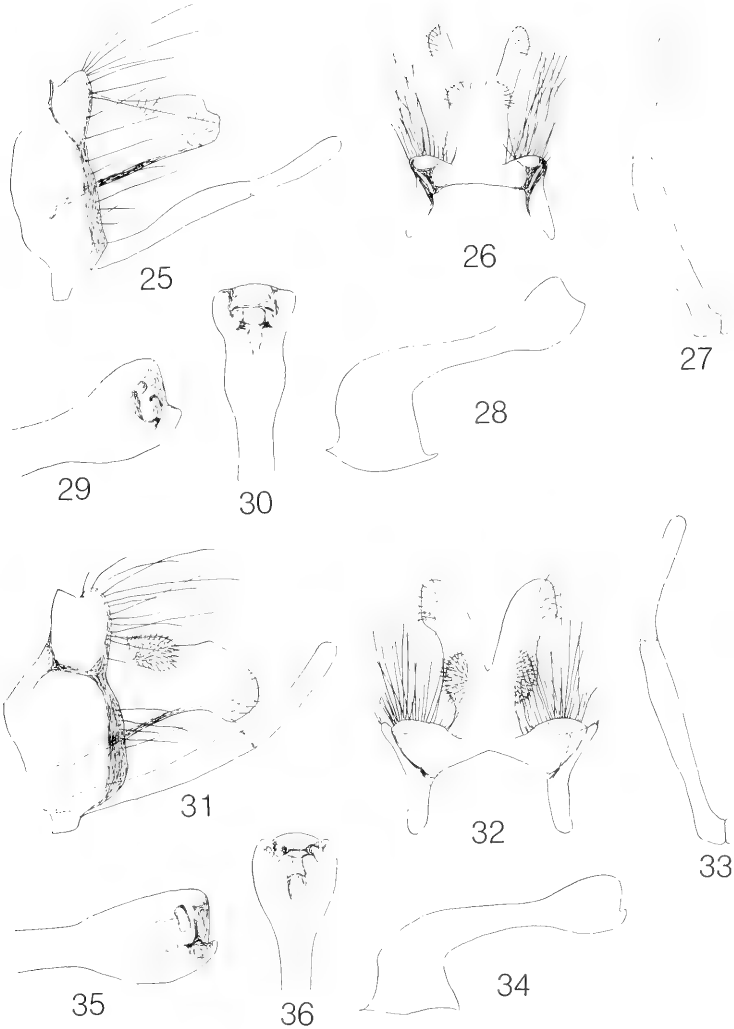
Macronema pseudoneura Brauer 1865: 420.—Ulmer 1907b:95 [redescription, forewing pattern].—Schmid 1958:108 [distribution].—Fischer 1963:194 [catalogue].

Macrostemum pseudoneura: Chantaramongkol and Malicky 1986:528 [♂, forewing pattern, head].—Malicky 1998:778 [♂, forewing pattern].

This has been the most frequently encountered species of the genus in Sri Lanka, and often comes to light in large numbers. The Sri Lankan specimens were captured at lower elevations, most recorded elevations being between 30 and 150 m, only one collection being made at 305 m and another 230 m.

Martynov (1935) recorded this species from Mysore State in southern India and presented a drawing (Fig. 93) of its wing pattern. This pattern agrees with the type of *Macronema ethelda* Banks, also described from Mysore State. I have studied the type of *M. ethelda* and compared it to the material available of *M. pseudoneura* from Sri Lanka. The continental example has a well-marked pale streak in the 2nd R_3 cell. This mark is lacking in the insular material, and in addition there are slight differences in their genitalia, especially the apex of the phallus. Considering the overall similarity in the color pattern between the two regions, it seems best to consider them subspecies, pending further study with more continental material. I therefore recognize *M. ethelda* as *Macrostemum pseudoneura ethelda* (Banks), **new status**.

Male.—Length of forewing 8–9 mm. Head stramineous, infuscate dorsally; frontal cuticle between eyes and central wart



Figs. 25–36. Male genitalia. 25–30, *Macrostemum pseudoneura.* 25, Lateral. 26, Dorsal. 27, Inferior appendage, posteroventral. 28, Phallus, lateral. 29, Tip of phallus, lateral. 30, Same, ventral. 31–36, *M. sepultum.* 31, Lateral. 32, Dorsal. 33, Inferior appendage, posteroventral. 34, Phallus, lateral. 35, Tip of phallus, lateral. 36, Same, ventral.

dark with bluish sheen; antenna and maxillary palpus stramineous. Pronotum stramineous; meso- and metanota and pleura, fuscous; legs stramineous. Forewing (fig. 51) with 3 white marks from anterior margin, innermost extending as oblique, transverse, white band completely across wing; series of smaller white marks apically and basally; wash of golden setae between most pale marks, leaving a narrow brown band surrounding most marks; hindwing infuscate apically. Abdomen fuscous. Genitalia: Ninth segment with anterolateral margin broadly produced, nearly vertical; posteroventral margin slightly produced and slightly oblique; posterior margin with scattered, elongate setae, becoming more numerous dorsolaterally. Tenth tergum with dorsobasal setal wart small, apex obtusely angulate in lateral view; in dorsal aspect with apex rounded, sides narrow, rodlike. Inferior appendage elongate, parallel-sided; in posteroventral aspect with apical segment only slightly shorter than basal. Basal section of phallus almost ⅓ of total length of phallus, relatively high and angled almost 90° to stem; apex broadly rounded ventrally, and obliquely elevated dorsally; apex oblique with small apicoventral, protruding angle.

Female.—Length of forewing 8 mm. Coloration as in male. Midtibia and tarsus, strongly flattened, broadened and concave on inner face.

Material examined.—SRI LANKA: Amparai Dist., Ekgal Aru tank, 100 ft [ca. 30 m], 19–23 Feb 1977, Krombein et al., blacklight, 2 ♀; Inginiyagala, 250 ft [ca. 75 m], 21–24 Nov 1976, Krombein et al., black light, 2 ♀. Anuradhapura Dist., Wildlife Society Bungalow, Hunuwilagama, Wilpattu, 200 ft [ca. 60 m], 10–19 Mar 1970, Davis & Rowe, 1 ♂, 8 ♀; Irrigation Bungalow, Padaviya, 180 ft [ca. 55 m], 27 Feb-9 Mar 1970, Davis & Rowe, 9 ♀; Padaviya, 180 ft [ca. 55 m], 2–8 Nov 1970, O. S. Flint, Jr, 11 ♂, 5 ♀; Padaviya, 180 ft [ca. 55 m], 19 May 1976, Krombein et al., blacklight trap, 1 ♀; Sluiceway, Padaviya, 170 ft [ca. 50 m], 3 Nov 1970, O. S. Flint, Jr, 17 ♂, 17 ♀; Balaya Wewa, nr. Padaviya, 150 ft [ca. 45 m], 4–5 Nov 1970, O. S. Flint, Jr, 2 ♀. Badulla Dist., 5 mi [ca. 8 km] E Mahiyangana, 1 Apr 1971, P. & P. Spangler, at black light, 2 ♀. [Batticaloa Dist.], Rukam Wewa, [90 ft, ca. 25 m], 14 Mar 1954, F. Schmid, [at light], 1 ♀. Colombo Dist., Gampaha Bot. Gardens, 16 Apr 1980, Mathis et al., 1 ♂; Labugama, 400 ft [ca. 120 m], 24 Aug 1973, G. Ekis, collected at black light, 1 ♂; [Wak Oya], Labugama, [173 ft, ca. 53 m], 7–9 Jan 1954, F. Schmid, [by net], 1 ♂. [Kelani Ganga], Kaduwela, [50 ft, ca. 15 m], 3 Apr 1954, F. Schmid, [at light], 4 ♀. Galle Dist., Kanneliya, 500 ft [ca. 150 m], 21–22 Apr 1973, Baumann & Cross, at blacklight, 24 ♂, 3 ♀; Kanneliya, 27 Apr 1980, Mathis et al., 3 ♂; Kanneliya, 6–15 Aug 1975, Panawatte, 2 ♀; Kanneliya, 22–24 May 1975, Wood & Petty, collected in blacklight trap, 4 ♂, 3 ♀; Kanneliya, 200 ft [ca. 60 m], 15–17 Oct 1976, Krombein et al., blacklight, 4 ♂, 4 ♀; Kanneliya Section, Sinharaja Jungle, 2–5 Oct 1980, Krombein et al., collected at blacklight, 8 ♂, 1 ♀; same, but 13–16 Jul 1978, blacklight trap, 1 ♂, 1 ♀; Kanneliya, Sinharaja Jungle, 9–10 Nov 1977, Krombein et al., collected in Malaise trap, 1 ♂; Kanneliya Jungle, 300 ft [ca. 90 m], 28 Jul 1973, G. Ekis, collected at blacklight, 8 ♂, 9 ♀; Kanneliya Jungle, 11–16 Jan 1975, Krombein et al., blacklight, 2 ♀; Udugama, Kanneliya Jungle, 400 ft [ca. 120 m], 6–12 Oct 1973, Krombein et al., at black light, 4 ♂, 7 ♀; same, but in Malaise trap, 1 ♀; 11 mi [ca. 18 km] E Udugama, Kanneliya Jungle, 11 Oct 1973, Krombein et al., at black light, 1 ♂, 5 ♀; Hiniduma, 22 Oct 1973, M. & B. Robinson, collected at black light, 1 ♀. Kandy Dist., Roseneath, Kandy, 25 Mar 1971, P. & P. Spangler, in Malaise trap, 10 ♂; Hasalaka, 16–19 Feb 1977, Krombein et al., blacklight trap, 2 ♂, 2 ♀; Aluthnuwara, Hasalaka, 19 Apr 1964, [collector unknown], at light, 1 ♀. Kegalle Dist, Lavant Estate, nr. Yatiyantota, 80 ft [ca. 25 m], 19 Nov 1970, O. S. Flint, Jr, 2 ♂; Kitulgala, 150 ft [ca. 45 m], 30 Sep 1970, O. S. Flint, Jr, 1 ♂, 2 ♀; Kitulgala, 31 May 1975, Wood & Petty, collected in blacklight trap, 12 ♂, 4 ♀; Kitulgala Resthouse, 150 ft [ca. 45 m], 3–5 Feb 1979, Krombein et al., blacklight trap, 26 ♂, 32 ♀; same, but 24–26 Oct 1977, 12 ♂, 5 ♀; same, but 10–12 Oct 1980, coll. in UV trap, 4 ♂, 8 ♀; Kelani Ganga, Kitulgala, 500 ft [ca. 150 m], 12 Mar 1973, Baumann & Cross, collected at black light, 1 ♂, 1 ♀. [Kelani Ganga], Kitulgala, [750 ft, ca. 230 m], 2 Mar 1954, F. Schmid, [at light], 1 ♀. [Monaragala Dist.], Bibile, 4 May 1974, Gans & Prasanna, 1 ♀. Ratnapura Dist., Panamure, 500 ft [ca. 150 m], 15–21 Oct 1970, O. S. Flint, Jr, 1 ♂; Uda Walawe, 300 ft [ca. 90 m], 1 Aug 1973, G. Ekis, collected at blacklight, 10 ♀; Gilimale, 17–18 Jun 1976, Krombein et al., light trap, 1 ♀; Gilimale, Induruwa Jungle, collected near Kaluganga, 5–7 Feb 1977, Krombein et al., blacklight trap, 2 ♀; Kalu Ganga, Induruwa Jungle, 1,000 ft [ca. 305 m], 23 Mar 1973, Baumann & Cross, 1 ♂. [tributary to Kalu Ganga, near Kiriella], Ratnapura, [80 ft, ca. 25 m], 3 Feb 1954, F. Schmid, [at light], 1 ♀. Vavuniya Dist., Irrigation canal, Parayanalankulam, 25 mi [ca. 40 km] NW Medawachchiya, 100 ft [ca. 30 m], 20–25 Mar 1970, Davis & Rowe, 1 ♀.

Macrostemum sepultum (Hagen), **new combination** (Figs. 31–36, 52)

Macronema sepultum Hagen 1859:209.—Ulmer 1907a:60 [redescription, wings, wings in color].—Ross 1952:35 [lectotype].—Fischer 1963:197 [catalogue].

As with *M. nebulosum*, this species has been known only from the original type series, a male paratype of which was figured in color by Ulmer (1907a). I here present photographs of the wings of a female paralectotype from the MCZ, figure the male genitalia, and record several new collections. The original series was from the wet, central highlands, at 1,065–1,220 m, the new material was found at elevations of around 150 m in the wet, southwestern corner of the island.

Male.—Length of forewing 8–8.5 mm. Color fuscous with white marks. Head stramineous frontally, shining black otherwise; frontal cuticle between eyes and central wart with bluish sheen; antenna with scape and pedicel tawny, first 3–5 flagellar segments slightly darkened, remaining segments stramineous. Thoracic cuticle shining fuscous; legs fuscous with tarsi stramineous. Forewing (Fig. 52) fuscous with 6 white spots, 3 lying on the costal margin, and 3 toward posterior margin. Hindwing infuscate with anterior margin and stigma white. Genitalia: Ninth segment with anterolateral margin produced and angulate, posteroventral margin produced, slightly oblique; posterior margin with few, elongate setae, becoming denser dorsolaterally. Tenth tergum with dorsobasal setal wart large with many short setae, apex rounded in lateral view; in dorsal aspect with apex produced laterad. Inferior appendage elongate, parallel-sided; in posteroventral aspect with apical segment only about ⅖ total length. Basal section of phallus relatively narrow, only ⅓ of total length of phallus; apex broadly rounded ventrally and dorsally; apex nearly vertical with a small lip-like lobe below midheight.

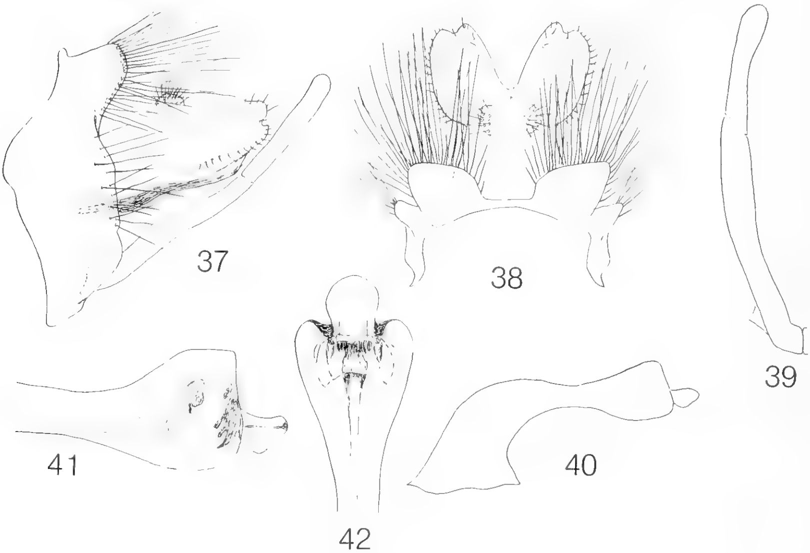
Female.—Length of forewing 8 mm. Coloration as in male. Midtibia and tarsus unmodified.

Material examined.—Ceylon, [Ramboda], Nietner, ♂ lectotype, ♀ paralectotype (MCZ).

SRI LANKA: Galle Dist., Kanneliya Jungle, Udugama, 400 ft [ca. 120 m], 6–12 Oct 1973, Krombein et al., at blacklight, 3 ♂, 2 ♀; Kanneliya, 22–24 May 1975, Wood & Petty, collected in Malaise trap, 1 ♂.

Macrostemum splendidum (Hagen) (Figs. 37–42, 53-54)

Macronema splendidum Hagen 1858: 484.—Ulmer 1907b:87 [redescription, forewing, wings in color].—Ross 1952: 35 [lectotype].—Schmid 1958:108 [dis-



Figs. 37–42. Male genitalia. *Macrostemum splendidum*. 37, Lateral. 38, Dorsal. 39, Inferior appendage, posteroventral. 40, Phallus, lateral. 41, Tip of phallus, lateral. 42, Same, ventral.

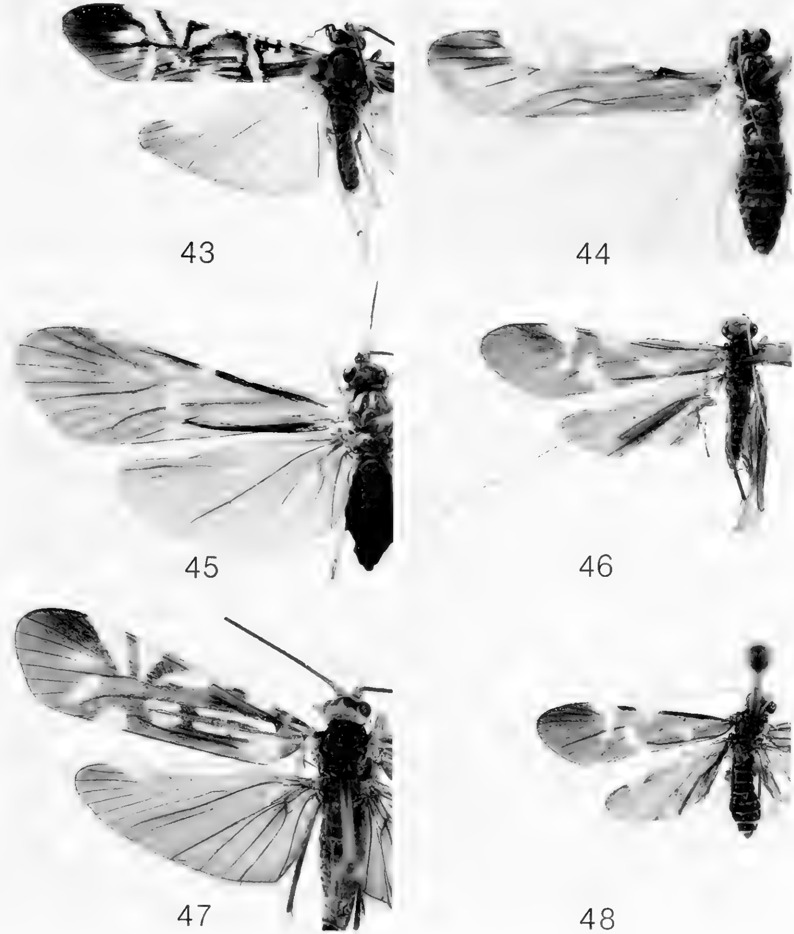
tribution, variation].—Fischer 1963:197 [catalogue].

Macrostemum splendidum: Malicky 1998: 778 [♂, wing pattern].

This species has been taken a number of times, but never in a large series. As remarked by Schmid (1958), the species is quite variable in color, no two of the specimens before me appearing exactly the same.

The species is known from the central highlands at elevations approaching 1,000 m, and in the southwestern quadrant of the island at elevations from almost 1,000 m down to 35 m. All of the known sites, however, are in high rainfall areas with precipitation averaging 100 inches (2,500 mm) per year or higher.

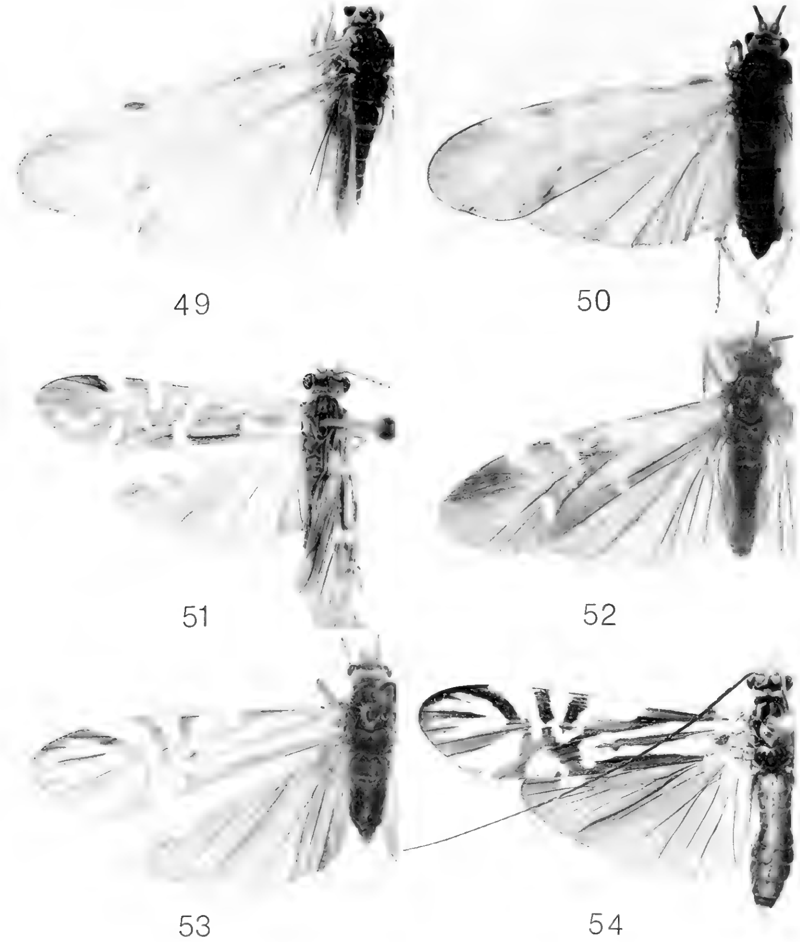
Male.—Length of forewing 11–15 mm. Color goldenyellow marked with fuscous. Head goldenyellow, cuticle black between dorsal warts; antenna with scape, pedicel and outer face of first flagellar segment, golden following ca. 12 segments fuscous, remaining segments pale. Cuticle of meso- and metanota and pleura black; mesoscutellum golden yellow. Legs goldenyellow. Forewing (Fig. 54) with 3 golden-yellow marks from anterior margin, posteriorly and apically with extensive golden-yellow marks on a fuscous background. Hindwing infuscate with white stigma and basally directed streak in costal and subcostal cells. Abdomen fuscous, with golden-yellow middorsal stripe. Genitalia: Ninth segment with anterolateral margin broadly produced, rounded, posteroventral margin produced ventrally, oblique; posterior margin with scattered, elongate setae, becoming very numerous dorsolaterally. Tenth tergum with dorsobasal setal wart small, apex with small excision at midheight; in dorsal aspect with apex shallowly emarginate, apicolateral margin produced and rounded. Inferior ap-



Figs. 43–48. Forewings. 43, *Macrostemum barnardi*, ♂, Kanneliya. 44, *M. indistinctum*, ♀, Udawalawe. 45, *M. krombeini*, ♀ holotype, Peradeniya. 46, *M. malickyi*, ♂ holotype, Udugama. 47, *M. multifarium*, ♀ compared with holotype, Sinharaja. 48, *M. malickyi*, ♂ paratype, Udugama.

pendage elongate, parallel-sided; in posteroventral aspect with apical segment ⅓ of total length. Basal section of phallus about ⅓ of total length of phallus; apex broadly rounded ventrally, and obliquely elevated dorsally; apex nearly vertical with large, ventral, lip-like projection.

Female.—Length of forewing 11–15



Figs. 49–54. Forewings. 49, *Macrostemum nebulosum,* ♂ lectotype, Ramboda. 50, *M. nebulosum,* ♀ paralectotype, Ramboda. 51, *M. pseudoneura,* ♂, Padaviya. 52, *M. sepultum,* ♀ paralectotype, Ramboda. 53, *M. splendidum,* ♀ paralectotype, Ramboda. 54, *M. splendidum,* ♂, Tunmodera.

mm. Coloration as in male (Fig. 54). Midtibia and tarsus flattened, broadened, concave on inner face.

Material examined.–Ceylon, [Ramboda], Nietner, ♂ lectotype, ♀ paralectotype (MCZ).

SRI LANKA: Colombo Dist., Tunmodera, 200 ft [ca. 60 m], 17 Nov 1970, O. S. Flint, Jr., 1 ♂, 2 ♀. Galle Dist., Kanneliya, 500 ft [ca. 150 m], 21–22 Apr 1973, Baumann & Cross, at blacklight, 1 ♂. [Kandy Dist.], Karambaketiya off Memure [Mimure], Knuckles Range, 8 Mar 1970, P. B. Karunaratne, at light, 2 ♂. Matale Dist., Hunas Falls, Elkaduwa, 3,000 ft [ca. 915 m], 5 Apr 1973, Baumann & Cross, 1 ♀. Matara Dist., Deniyaya, 1,000 ft [ca. 305 m], 20 Apr 1973, Baumann & Cross, at black light, 1 ♀. Ratnapura Dist., Gilimale, lumber mill, 115 ft [ca. 35 m], 20–25 Oct 1976, Hevel et al., blacklight, 1 ♂. Bultota Pass, 3,000 ft [ca. 915 m], 18–19 Apr 1973, Baumann & Cross, at black light, 1 ♂; [Kirinda Ela], Wattepanguwa, [1,500 ft, ca. 450 m], 18 Feb 1954, F. Schmid, [at light], 1 ♀.

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INVASIVE SOFT SCALES (HEMIPTERA: COCCIDAE) AND THEIR THREAT TO U.S. AGRICULTURE

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Abstract.—We provide a compilation of 147 species of soft scales that are considered either pests or represent a threat to United States agriculture. Included for each species, where applicable, is reference to origin and date of introduction if applicable, establishment in the United States, pest or threat status in the United States along with a validation citation, principal hosts, and biogeographical region of origin.

Key Words: Coccidae, soft scales, invasive species, biological control, quarantine, agriculture, forestry, horticulture, ornamentals, fruit trees

Invasive (non-native) species of insects represent an increasing concern to the United States. If non-native species become pests, the consequences include loss of production, diminished product quality, production cost increases, flexibility decreases in production/management decisions, increased risk of human disease, and damaging environmental and aesthetic effects (Huber et al. 2002). Various insects of agricultural concern have been identified as potentially damaging if introduced or reintroduced into the United States (Huber et al. 2002). Invasive species and potentially dangerous species of mealybugs (Pseudococcidae) have been recently examined as they pertain to agriculture in the United States (Miller et al. 2002). The Coccidae or soft scales, like all scale insects, are plant feeders. A few species of soft scales are valuable to man as biological control agents of noxious weeds, however, many are pests of economically important plants.

Because invasive species of insects represent a major concern to U.S. agriculture, we have investigated several parameters concerning invasive soft scales. Objectives of this paper are: 1) To develop a preliminary world list of the pest soft scales; 2) provide a list of pest soft scales introduced to the continental United States; 3) to determine which species in the previous two objectives are either introduced or native to the continental United States; 3) examine data provided by the United States Department of Agriculture, Animal and Plant Health Inspection Service—Plant Protection and Quarantine (USDA, APHIS-PPQ) concerning the most commonly intercepted soft scales at the United States ports-of-entry; and 5) using all of this information, try to predict which soft scales are the most likely candidates for future invasions into the continental United States.

MATERIALS AND METHODS

Executive Order 13112 established the National Invasive Species Council and provided a definition of an invasive species as "... a species that is 1) non-native (or alien) to the ecosystem under consideration and 2) whose introduction causes or is likely to cause economic or environmental harm or harm to human health." This definition not only includes species alien to the United States but also encompasses native species. The definition also has an economic or potentially economic component. By this definition, the tulip tree scale, *Toumeyella liriodendri* (Gmelin), would be an example of an invasive species in the United States even though it likely is native. Our definition is based on Miller et al. (2002) and is more simplistic. They considered invasive species to be those that are non-native [also introduced, nonidigenous, exotic, alien or invasive (Huber et al. 2002)] to the United States regardless of economic harm.

We have used a broad definition of the term "pest" to create a table of pest soft scales of the world (Table 1). If a soft scale is described in the literature as either a pest, causing damage, requiring control, or of economic importance, we have included it in the list. A pest species as defined by some authors (e.g., Ebeling 1959, Pfeiffer 1997) was regarded as any record of a soft scale on certain economic hosts. Ebeling's (1959) justification was based on his consideration that some species not of economic importance become major pests through adaptation or by being transferred to regions of lower environmental resistance. However, Pfeiffer's (1997) inclusion of *Eulecanium lespedezae* Danzig as a pest of deciduous fruit trees is probably an error because the only known host record of this species is *Lespedeza bicolor* Turcz. (Danzig 1986).

Our perspective for this paper has focused on the impact or potential impact of a pest soft scale on agriculture in the contiguous United States. For example, *Ceroplates psidii* (Chavannes) is known only from *Psidium* spp. Therefore, because guavas are not widely grown in the contiguous United States, it is considered to have relatively minor pest potential in the United States even though it may be far more important in areas of the world where guava is of greater economic importance. Conversely, *Ceroplastes japonicus* Green, occurs on many different agricultural plants that are economically important in the United States and it is therefore considered a major threat. The term "threat" is used for species that are considered pests but do not occur in the United States. Determination of the date of introduction in the U.S. was established either from literature records or from the oldest collection record in the National Entomological Collection of the National Museum of Natural History, in Beltsville, Maryland. In at least one case (e.g., *Eriopeltis festucae* Boyer de Fonscolombe), the first literature record in the U.S. is Patch (1905) but the oldest collection record is 1899. Obviously, these dates are estimates of the date when a species first invaded the United States.

It is difficult to determine the zoogeographic area of origin for some species. Some distributional records for *Ceroplastes* spp. are from Qin et al. (1998) and *Coccus* spp. are from Gill et al. (1977). It is not always clear whether an invasive species is from the Old or New World. In some cases, we have simply made a supposition based on the current distribution of the species, the distribution of what appears to be its closest relatives, and the natural distribution of its primary host plants. We have used the same criteria to determine if a particular species is native to the United States. Our use of the terms polyphagous, oligophagous, and monophagous has been slightly modified for the current paper and are hereby defined for those species that have greater than 10 host-plant families, 3–10 host-plant families, and 1–2 host-plant families respectfully.

RESULTS

Table 1 provides information on 147 species of soft scales. The table includes one species [*Prococcus acutissimus* (Green)] that has been introduced and established into the United States but is not considered

Table 1. Pest or threat soft scale species to United States agriculture. Abbreviations for origin are Afrotropical Region (AF), Australasian Region (AU), Nearctic (NE), Neotropical Region (NT), Oriental Region (OR), Palearctic Region (PA).

Pest or Threat Species	U.S. Origin and Date of Introduction	Established in U.S.	Pest or Threat Status in U.S.	Reference	Principal Hosts	Origin
Anapulvinaria pistaciae (Bodenheimer)		no	minor threat	Abu-Yaman 1970	monophagous, including pistachio	PA
Anthococcus keravatae Williams and Watson		no	minor threat	Gill and Kosztarab 1997	oligophagous, including tropical plants	AU
Ceroplastes actiniformis Green		no	threat	Swirski et al. 1997	polyphagous, including tropical fruits	OR
Ceroplastes bergi Cockerell		no	threat	Ebeling 1959	oligophagous, including citrus	NT
Ceroplastes brachyurus Cockerell	native?	yes	minor pest	Gimpel et al. 1974	oligophagous, including citrus and *Ilex*	NE(?)
Ceroplastes brevicauda Hall		no	threat	Murphy 1997	polyphagous, including coffee and citrus	AF
Ceroplastes ceriferus (Fabricius)	FL, 1908	yes	pest	Gimpel et al. 1974	polyphagous	NT
Ceroplastes cirripediformis Comstock	FL, 1881	yes	pest	Gimpel et al. 1974	polyphagous	NE
Ceroplastes cistudiformis Cockerell	native?	yes	minor pest	Gimpel et al. 1974	polyphagous, including citrus	NE(?)
Ceroplastes destructor Newstead		no	major threat	Sabine 1969	polyphagous, including citrus	AF
Ceroplastes dugesii Lichtenstein	FL, 1908	yes	pest	Hamon and Williams 1984	polyphagous	NT
Ceroplastes eugeniae Hall		no	minor threat	Pfeiffer 1997	oligophagous, including deciduous fruit trees	AF
Ceroplastes floridensis Comstock	FL, 1881	yes	pest	Gimpel et al. 1974	polyphagous, including citrus and ornamentals	NE
Ceroplastes flosculoides Matile-Ferrero		no	minor threat	Matile-Ferrero and Couturier 1993	monophagous, including *Myricaria dubia*	NT
Ceroplastes grandis Hempel		no	major threat	Gill and Kosztarab 1997	polyphagous, including ornamentals and fruit trees	NT
Ceroplastes japonicus Green		no	major threat	Pellizzari-Scaltriti and Antonucci 1982	polyphagous, including ornamentals	OR
Ceroplastes pseudoceriferus Green		no	major threat	Swirski et al. 1997	polyphagous, including tropical fruits and ornamentals	OR
Ceroplastes psidii (Chavannes)		no	minor threat	Hempel 1920	monophagous, including guava	NT
Ceroplastes quadrilineatus Newstead		no	minor threat	Pfeiffer 1997	oligophagous, including fruit trees	AF
Ceroplastes rubens Maskell	FL, 1955	yes	pest	Gimpel et al. 1974	polyphagous, including citrus and ornamentals	AF

Table 1. Continued.

Pest or Threat Species	U.S. Origin and Date of Introduction	Established in U.S.	Pest or Threat Status in U.S.	Reference	Principal Hosts	Origin
Ceroplastes rusci (Linnaeus)	FL, 1994	yes	pest	Ben-Dov 1988	polyphagous, including citrus and ornamentals	AF
Ceroplastes sinensis Del Guercio	NC, 1920	yes	pest	Gimpel et al. 1974	polyphagous, including citrus and ornamentals	NT
Ceroplastes sinoiae Hall		no	minor threat	Bedford 1968	oligophagous, including ornamentals	AF
Coccus africanus (Newstead)		no	minor threat	Ebeling 1959	oligophagous, including tropical fruits and coffee	AF
Coccus alpinus De Lotto		no	minor threat	Murphy 1997	oligophagous, including tropical fruits and coffee	AF
Coccus celatus De Lotto		no	minor threat	Murphy 1997	polyphagous, including tropical fruits and coffee	AF
Coccus capparidis (Green)	FL, 1975	yes	minor pest	Gill et al. 1977	polyphagous	OR
Coccus discrepans (Green)		no	threat	Ebeling 1959	polyphagous, including tropical fruits	OR
Coccus formicarii (Green)		no	minor threat	Pfeiffer 1997	polyphagous, including tropical fruits	OR
Coccus hesperidum Linnaeus	CA, 1880	yes	pest	Ebeling 1959	polyphagous	OR
Coccus longulus (Douglas)	NY, 1921	yes	major pest	Gill and Kosztarab 1997	polyphagous, including tropical fruits and ornamentals	OR(?)
Coccus pseudohesperidum (Cockerell)	DC, 1912	yes	major pest	Gill and Kosztarab 1997	monophagous, including orchids	NT
Coccus pseudomagnoliarum (Kuwana)	CA, 1910	yes	major pest	Ebeling 1959	oligophagous, including citrus	PA
Coccus viridis (Green)	FL, 1949	yes	major pest	Gill et al. 1977	polyphagous	AF
Coccus watti (Green)		no	threat	Ebeling 1959	monophagous, including citrus and camellia	OR
Cribrolecanium andersoni (Newstead)		no	threat	Brink and Bruwer 1989	oligophagous, including tropical fruits	AF
Crystallotesta fagi (Maskell)		no	threat	Hosking and Kershaw 1985	monophagous, including beech trees	AU
Didesmococcus koreanus Borchsenius		no	minor threat	Pfeiffer 1997	monophagous, including deciduous fruit trees	PA

Table 1. Continued.

Pest or Threat Species	U.S. Origin and Date of Introduction	Established in U.S.	Pest or Threat Status in U.S.	Reference	Principal Hosts	Origin
Didesmococcus unifasciatus (Archangelskaya)		no	threat	Gill and Kosztarab 1997	oligophagous, including deciduous fruit trees	OR
Drepanococcus chiton (Green)		no	threat	Campbell 1997	polyphagous, including tropical fruits	OR
Ericerus pela (Chavannes)		no	threat	Kosztarab 1997b	monophagous, including deciduous forest trees	PA
Eriopeltis festucae (Boyer de Fonscolombe)	NY, 1899	yes	minor pest	Williams and Kosztarab 1972	monophagous, including grasses	PA
Eucalymnatus tessellatus (Signoret)	CA, 1901	yes	major pest	Dekle 1973	polyphagous, greenhouse pest	NT
Eulecanium alnicola Chen		no	minor threat	Pfeiffer 1997	oligophagous, including deciduous fruit trees	PA
Eulecanium cerasorum (Cockerell)	CA, 1909	yes	major pest	Gill and Kosztarab 1997	oligophagous, including deciduous forest trees	PA
Eulecanium ciliatum (Douglas)		no	minor threat	Pfeiffer 1997	oligophagous, including deciduous forest and fruit trees	PA
Eulecanium douglasi (Šulc)		no	threat	Lagowska 1984	oligophagous, including deciduous forest and fruit trees	PA
Eulecanium kunoense (Kuwana)	CA, 1896	yes	major pest	McKenzie 1951	oligophagous, including deciduous fruit trees	PA
Eulecanium novicum Borchsenius		no	minor threat	Pfeiffer 1997	oligophagous, including deciduous fruit trees	PA
Eulecanium rugulosum (Archangelskaya)		no	minor threat	Pfeiffer 1997	oligophagous, including deciduous fruit trees	PA
Eulecanium sericeum (Lindinger)		no	threat	Kosztarab 1997a	monophagous, including conifers	PA
Eulecanium tiliae (Linnaeus)	CA, 1908	yes	major pest	Kosztarab 1996	polyphagous	PA
Eulecanium transcaucasicum Borchsenius		no	minor threat	Pfeiffer 1997	monophagous, including deciduous fruit trees	PA
Filippia follicularis (Targioni Tozzetti)		no	minor threat	Gill and Kosztarab 1997	oligophagous, including olive and pistachio	PA
Kilifia acuminata (Signoret)	MO, 1903	yes	pest	Nada et al. 1990	polyphagous	OR
Lichtensia viburni Signoret		no	threat	Gill and Kosztarab 1997	polyphagous, including ornamentals	PA

Table 1. Continued.

Pest or Threat Species	U.S. Origin and Date of Introduction	Established in U.S.	Pest or Threat Status in U.S.	Reference	Principal Hosts	Origin
Maacoccus bicruciatus (Green)		no	minor threat	Ebeling 1959	oligophagous, including citrus and mango	OR
Mallococcus vitecicola Young		no	minor threat	Wan et al. 1985	oligophagous, including ornamentals and medical herb	PA
Megapulvinaria maxima (Green)		no	threat	Chua 1997b	polyphagous, including tropical plants	OR
Mesolecanium deltae Lizer y Trelles		no	major threat	Teran and Guyot 1969	monophagous, including citrus	NT
Mesolecanium nigrofasciatum (Pergande)	native	yes	major pest	Kosztarab 1996	polyphagous, including fruit trees and ornamentals	NE
Milviscutulus mangiferae (Green)	FL, 1935	yes	major pest	Avidov and Harpaz 1969	polyphagous	OR
Milviscutulus pilosus Williams and Watson		no	minor threat	Chua 1997a	oligophagous, including coconut	AU
Neolecanium cornuparvum (Thro)	native	yes	minor pest	Williams and Kosztarab 1972	monophagous, including magnolia	NE
Neolecanium silveirai (Hempel)		no	major threat	Lepage and Piza 1941	monophagous, including grapes	NT
Neopulvinaria innumerabilis (Rathvon)	native	yes	major pest	Kosztarab 1997c	polyphagous	NE
Neosaissetia triangularum (Morrison)		no	minor threat	Chua 1997a	monophagous, including coconut	OR
Palaeolecanium bituberculatum (Signoret)		no	major threat	Lagowska 1984	oligophagous, including deciduous fruit trees	PA
Palaeolecanium kosswigi (Bodenheimer)		no	minor threat	Pfeiffer 1997	monophagous, including deciduous fruit trees	PA
Paralecanium cocophyllae Banks		no	minor threat	Chua 1997a	monophagous, including coconut	OR
Paralecanium milleri Takahashi		no	minor threat	Chua 1997a	oligophagous, including mango and coconut	OR
Parasaissetia nigra (Nietner)	AL, 1929	yes	major pest	Gill 1988	polyphagous	OR
Parthenolecanium corni (Bouché)	KS, 1874	yes	major pest	Hamon and Williams 1984	polyphagous	PA
Parthenolecanium fletcheri (Cockerell)	native	yes	pest	Kosztarab 1997a	monophagous, including conifers	NE
Parthenolecanium glandi (Kuwana)		no	minor threat	Pfeiffer 1997	oligophagous, including deciduous fruit trees	PA

Table 1. Continued.

Pest or Threat Species	U.S. Origin and Date of Introduction	Established in U.S.	Pest or Threat Status in U.S.	Reference	Principal Hosts	Origin
Parthenolecanium orientalis Borchsenius		no	minor threat	Pfeiffer 1997	oligophagous, including deciduous fruit trees	PA
Parthenolecanium persicae (Fabricius)	CA, 1897	yes	major pest	Williams and Kosztarab 1972	polyphagous	PA
Parthenolecanium pruinosum (Coquillett)	native	yes	major pest	Gill and Kosztarab 1997	oligophagous, including walnuts	NE
Parthenolecanium putnami (Phillips)		no	minor pest	Pfeiffer 1997	oligophagous, including deciduous forest and fruit trees	NE
Parthenolecanium quercifex (Fitch)	native	yes	major pest	Gill 1988	oligophagous, including oaks	NE
Parthenolecanium rufulum (Cockerell)		no	threat	Kosztarab 1997b	polyphagous, including deciduous forest trees	PA
Philephedra broadwayi (Cockerell)		no	threat	Nakahara and Gill 1985	oligophagous, including tropical fruits	NT
Philephedra tuberculosa Nakahara and Gill	native	yes	major pest	Gill and Kosztarab 1997	polyphagous	NE
Physokermes hemicryphus (Dalman)	CA, 1958	yes	pest	Santas 1988	monophagous, including conifers	PA
Physokermes insignicola (Craw)	native	yes	minor pest	Gill 1988	monophagous, including pines	NE
Physokermes piceae (Schrank)		no	threat	Santas 1988	monophagous, including spruce	PA
Physokermes taxifoliae Coleman	native	yes	pest	Kosztarab 1997a	monophagous, including fir	NE
Platinglisia noacki Cockerell		no	minor threat	Ebeling 1959	polyphagous, including avocado and ornamentals	NT
Platylecanium cocotis Laing		no	minor threat	Chua 1997a	monophagous, including coconut	AU
Prococcus acutissimus (Green)	FL, 1956	yes	not a pest	Gill et al. 1977	polyphagous	OR
Protopulvinaria longivalvata Green		no	threat	Ebeling 1959	polyphagous, including tropical fruits and ornamentals	OR
Protopulvinaria pyriformis (Cockerell)	FL, 1906	yes	major pest	Del Rivero 1966	polyphagous	NT
Pseudophilippia lanigera (Hempel)		no	minor threat	Ebeling 1959	oligophagous, including citrus	NT
Pseudophilippia quaintancii Cockerell	native	yes	pest	Ray and Williams 1980	monophagous, including pines	NE
Pulvinaria acericola (Walsh and Riley)	native	yes	pest	Kosztarab 1997b	oligophagous, including deciduous forest trees	NE
Pulvinaria amygdali Cockerell	native	yes	minor pest	Pfeiffer 1997	monophagous, including deciduous fruit trees	NE

Table 1. Continued.

Pest or Threat Species	U.S. Origin and Date of Introduction	Established in U.S.	Pest or Threat Status in U.S.	Reference	Principal Hosts	Origin
Pulvinaria aurantii Cockerell		no	threat	Gill 1997	polyphagous, including citrus	PA
Pulvinaria citricola Kuwana	MD, 1941	yes	major pest	Gill and Kosztarab 1997	oligophagous, including citrus and persimmon	PA
Pulvinaria decorata Borchsenius		no	minor threat	Ebeling 1959	monophagous, including citrus	AU
Pulvinaria delottoi Gill	CA, 1973	yes	major pest	Gill and Kosztarab 1997	monophagous, including iceplant	AF
Pulvinaria elongata Newstead	FL, 1927	yes	minor pest	Carnegie 1997	oligophagous, including sugarcane and grasses	NT(?)
Pulvinaria ericicola McConnell	native	yes	pest	Kosztarab 1997b	monophagous, including blueberries	NE
Pulvinaria ficus Hempel		no	threat	Ebeling 1959	polyphagous, including tropical fruits and ornamentals	NT
Pulvinaria flavescens Brethes		no	major threat	Kitayama 1993	oligophagous, including citrus	NT
Pulvinaria floccifera (Westwood)	GA, 1892	yes	pest	Gill and Kosztarab 1997	polyphagous, including citrus and ornamentals	PA(?)
Pulvinaria fujisana Kanda		no	minor threat	Pfeiffer 1997	monophagous, including deciduous fruit trees	PA
Pulvinaria horii Kuwana		no	minor threat	Pfeiffer 1997	oligophagous, including deciduous forest and fruit trees	PA
Pulvinaria hydrangeae Steinweden	native	yes	pest	Tondeur et al. 1990	polyphagous, including ornamentals	NE
Pulvinaria iceryi (Signoret)		no	minor threat	Carnegie 1997	monophagous, including grasses and sugarcane	AF
Pulvinaria kuwacola Kuwana		no	minor threat	Pfeiffer 1997	oligophagous, including deciduous fruit trees	PA
Pulvinaria mammeae Maskell		no	minor threat	Pfeiffer 1997	polyphagous, including tropical fruits	AU
Pulvinaria occidentalis Cockerell	native	yes	minor pest	Pfeiffer 1997	oligophagous, including deciduous fruit trees	NE
Pulvinaria okitsuensis Kuwana		no	minor threat	Ebeling 1959	oligophagous, including citrus and tea	PA
Pulvinaria peninsularis Ferris	native	yes	minor pest	Ebeling 1959	oligophagous, including citrus	NE
Pulvinaria peregrina (Borchsenius)		no	minor threat	Pfeiffer 1997	oligophagous, including deciduous fruit trees	PA

Table 1 Continued.

Pest or Threat Species	U.S. Origin and Date of Introduction	Established in U.S.	Pest or Threat Status in U.S.	Reference	Principal Hosts	Origin
Pulvinaria persicae Newstead		no	minor threat	Pfeiffer 1997	monophagous, including deciduous fruit trees	PA
Pulvinaria phaiae Lull	MA, 1897	yes	minor pest	Gill 1988	monophagous, including orchids	PA(?)
Pulvinaria polygonata Cockerell		no	threat	Gill 1997	oligophagous, including citrus and mango	OR
Pulvinaria pruni Hunter	native	yes	minor pest	Pfeiffer 1997	monophagous, including deciduous fruit trees	NE
Pulvinaria psidii Maskell	FL, 1909	yes	pest	Nada et al. 1990	polyphagous	OR(?)
Pulvinaria regalis Canard		no	major threat	Kozar et al. 1994	polyphagous, including ornamentals	PA
Pulvinaria rhois Ehrhorn	native	yes	minor pest	Pfeiffer 1997	oligophagous, including deciduous fruit trees	NE
Pulvinaria urbicola Cockerell	LA, 1925	yes	major pest	Gill and Kosztarab 1997	polyphagous	NT
Pulvinaria vitis (Linnaeus)	NY, 1880	yes	pest	Kosztarab and Kozar 1988	polyphagous	PA
Pulvinariella mesembryanthemi (Vallot)	CA, 1971	yes	pest	Donaldson et al. 1978	monophagous, including succulents	AF
Rhodococcus peronatus (Cockerell and Parrott)		no	minor threat	Ordogh 1995	monophagous, including roses	PA
Rhodococcus sariuoni Borchsenius		no	minor threat	Pfeiffer 1997	monophagous, including deciduous fruit trees	PA
Rhodococcus turanicus (Archangelskaya)		no	threat	Pfeiffer 1997	oligophagous, including deciduous fruit trees	PA
Saccharolecanium krugeri (Zehntner)		no	minor threat	Carnegie 1997	monophagous, including sugar cane	OR
Saissetia citricola (Kuwana)		no	minor threat	Pfeiffer 1997	oligophagous, including citrus and deciduous fruit trees	PA
Saissetia coffeae (Walker)	CA, 1914	yes	pest	Hamon and Williams 1984	polyphagous	NT
Saissetia miranda (Cockerell and Parrott)	FL, 1918	yes	pest	Stauffer and Rose 1997	polyphagous	NE
Saissetia neglecta De Lotto	FL, 1921	yes	pest	Stauffer and Rose 1997	polyphagous	NT
Saissetia oleae (Olivier)	KS, 1905	yes	pest	Bartlett 1978	polyphagous	PA(?)
Saissetia persimilis (Newstead)		no	threat	Pfeiffer 1997	polyphagous, including ornamentals and deciduous fruit trees	AF

Table 1. Continued.

Pest or Threat Species	U.S. Origin and Date of Introduction	Established in U.S.	Pest or Threat Status in U.S.	Reference	Principal Hosts	Origin
Saissetia socialis Hempel		no	minor threat	Pfeiffer 1997	monophagous, including deciduous fruit trees	NT
Saissetia subpatelliforme (Newstead)		no	minor threat	Ebeling 1959	oligophagous, including citrus	AF
Saissetia zanzibarensis Williams		no	minor threat	Chua 1997a	polyphagous, including tropical fruit trees	AF
Sphaerolecanium prunastri (Boyer de Fonscolombe)	PA, 1895	yes	major pest	Gill and Kosztarab 1997	oligophagous, including fruit trees	PA
Takahashia japonica Cockerell		no	minor threat	Pfeiffer 1997	oligophagous, including ornamentals and deciduous fruit trees	PA
Toumeyella cubensis Heidel and Köhler		no	threat	Gill 1997	monophagous, including citrus	NT
Toumeyella liriodendri (Gmelin)	native	yes	major pest	Burns and Donley 1970	oligophagous, including forest trees	NE
Toumeyella parvicornis (Cockerell)	native	yes	major pest	Rabkin and Lejeune 1955	monophagous, including pines	NE
Toumeyella pini King	native	yes	pest	Clarke et al. 1992	monophagous, including pines	NE
Toumeyella pinicola Ferris	native	yes	major pest	Gill and Kosztarab 1997	monophagous, including pines	NE
Toumeyella virginiana Williams and Kosztarab	native	yes	pest	Kosztarab 1997a	monophagous, including pines	NE
Vinsonia stellifera (Westwood)	FL, 1953	yes	pest	Dekle 1969	polyphagous	OR

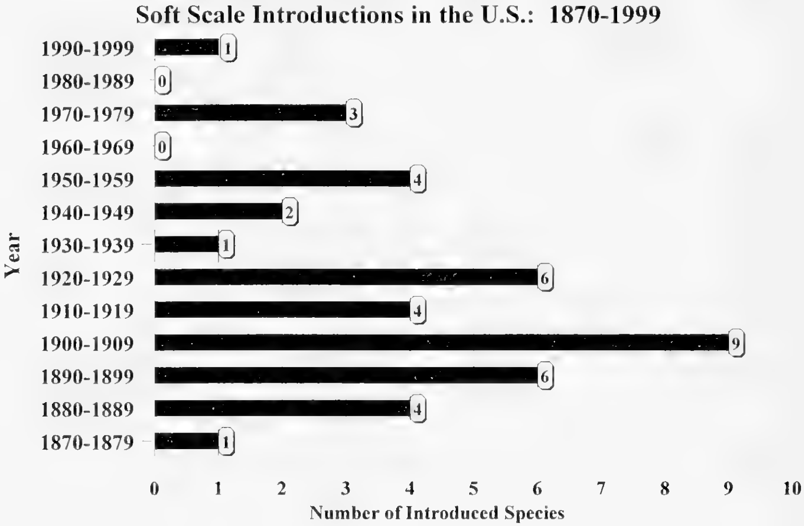

Fig. 1. Soft scale introductions in the United States from 1870–1999.

a pest. Therefore, we estimate that there are 146 species that are either pests or represent threats to U.S. agriculture. Of the 66 soft scales considered pests in the U.S., 25 are either native or possibly native species. Therefore, 41 of the soft-scale pests in the country are invasive. Based on Coccidae information presented in ScaleNet (Ben-Dov 2002), there are 105 species of soft scales in the United States; thus, the invasive component of the soft-scale fauna in the United States is approximately 39%. This percentage is much higher than the 13% of invasive species in the mealybug fauna of the U.S. (Miller et al. 2002). With the exception of the 1960's and the 1980's, at least one species of soft scale (Fig. 1) has been introduced every decade since the 1870's. The greatest number of introduced soft scales (nine species) occurred between 1900 and 1909. Two periods, the 1890's and the 1920's, witnessed the introduction of six species. More than 73% of the invasive soft scales were introduced in the first 69 years of record keeping (1870–1939).

A summary of the region of origin of all invasive soft scales in the U.S. is as follows: Palearctic Region, 13; Neotropical Region, 11; Oriental Region, 9; Afrotropical Region, 5; Nearctic Region outside of the U.S., 3; and Australasian Region, 0. Of all of these species in the U.S., only *Prococcus acutissimus* (Green) from the Oriental Region is not considered a pest.

Examination of the region of origin for pest soft scales worldwide provides the following results: Palearctic, 46; Nearctic, 29; Oriental, 25; Neotropical, 23; Afrotropical, 18; and Australasian, 6. Host characteristics of these pests include 38% polyphagous, 33% oligophagous, and 29% monophagous. Based on the characteristics of zoogeographic regional distributions of the highest number of soft-scale pests (Palearctic, Neotropical, and Oriental Regions, respectively), and greatest frequency of host plants (polyphagous and oligophagous), a list of the species most likely to invade the United States was determined. Those species likely to invade from the Palearctic Region include *Eulecanium douglasi* (Šulc), *Lichtensia viburni* Signoret, *Palaeolecanium bituberculatum* (Signoret), *Parthenolecanium rufulum* (Cockerell), *Pulvinaria aurantii* Cockerell, *Pulvinaria regalis* Canard, and *Rhodococcus turanicus* (Archangelskaya). Those species likely to invade from the Neotropical Region include *Ceroplastes bergi* Cockerell, *Ceroplastes grandis* Hempel, *Philephedra broadwayi* (Cockerell), *Pulvinaria ficus* Hempel, and *Pulvinaria flavescens* Brethes. Those species likely to invade from the Oriental Region include *Ceroplastes actiniformis* Green, *Ceroplastes japonicus* Green, *Ceroplastes pseudoceriferus* Green, *Coccus discrepans* (Green), *Didesmococcus unifasciatus* (Archangelskaya), *Drepanococcus chiton* (Green), *Megapulvinaria maxima* (Green), *Protopulvinaria longivalvata* Green, and *Pulvinaria polygonata* Cockerell.

USDA, APHIS-PPQ records from the past five years also were searched to determine which intercepted species of soft scales pose the greatest threat. A list of the top seven species most frequently intercepted at U.S. ports-of-entry are *Ceroplastes japonicus* Green, *Coccus moestus* De Lotto, *Philephedra broadwayi* (Cockerell), *Protopulvinaria longivalvata* Green, *Pulvinaria polygonata* Cockerell, *Tillancoccus mexicanus* Ben-Dov, and *Udinia catori* (Green). Comparison of the two lists reveals the following four species common to both: *Ceroplastes japonicus, Philephedra broadwayi, Protopulvinaria longivalvata,* and *Pulvinaria polygonata.* While the possibility exists that other soft scales could invade the U.S., we suggest that the four aforementioned species are the most plausible candidates as the next invasive soft scales into the United States.

DISCUSSION

Our data indicate that the decade starting in 1900 had the largest number of soft scale insect introductions into the U.S. Although Miller et al. (2002) speculated that high number of mealybug interceptions may be linked to detection strategies and procedures developed in conjuction with the Plant Quarantine Act in 1912, the number of soft scale introductions is not consistent with this hypothesis.

The introduction of even a single species is of concern to U.S. agriculture. Huber et al. (2002) hypothesized that if a pest can enter the United States, over time there is a strong likelihood for establishment. As a result, they believed more appropriate and cost-effective quarantine procedures must be developed. We think one step in this procedure is to identify those species of insects which pose the greatest threat.

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BIODIVERSITY AND ECOLOGY OF MYCOPHAGOUS DIPTERA IN NORTHEASTERN OHIO

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Abstract.—For this study, 134 species from 30 families of Basidiomycete fungi and 19 species from 11 families of Ascomycete fungi were collected from different sites in northeastern Ohio. Adult flies were reared from 87 separate fungal collections (basidiocarps or ascocarps = "mushrooms"). During this study, mycophagous species from a number of families were found (Tipulidae, Mycetophilidae, Sciaridae, Cecidomyiidae, Phoridae, Platypezidae, Chloropidae, Drosophilidae); the two most common fly species were *Drosophila falleni* Wheeler and *Leucophenga varia* Walker, both Drosophilidae. Less commonly found were *Drosophila tripunctata* Loew, *Drosophila putrida* Sturtevant, and *Mycodrosophila claytonae* Wheeler and Takada. Frequently, several species of Drosophilidae were found cohabiting the same mushroom. Unless factors are in operation to prevent competition (niche partitioning, predation, parasitism), mycophagous Diptera may pose a challenge to the Competitive Exclusion Principle. Preliminary evidence suggests parasitism and predation by other species of arthropods may play a role in reducing competition.

Key Words: Competitive Exclusion Principle, fungi-feeding flies, mushrooms

The sporophores of macrofungi (i.e., mushrooms of Basidiomycetes and Ascomycetes) are analogous to vascular plants in a number of ways: they are immobile, frequently contain chemical toxins, have few physical defenses, and have members that may be ephemeral or perennial in longevity (Hanski 1989). Fungi are found in virtually every ecological niche, and the sporophores of many groups of macrofungi serve as hosts of mycophagous Diptera. Despite the frequency and diversity of Diptera that inhabit mushrooms, few studies have been concerned with mycophagous species. Most such ecological studies were conducted several decades ago (Buxton 1960, Pielou 1966, Pielou and Mathewman 1966, Pielou and Verma 1968, Valley et al. 1969, Papp 1972, Shorrocks and Wood 1973) and often gave only anecdotal accounts of adult flies occurring on mushrooms (Patterson 1943, Valley et al. 1969, Graves and Graves 1985), not verifying true mycophagy. Still other studies have included flies as mycophages, where only one or two adults emerged from fungal material (Buxton 1960, Valley et al. 1969, Hackman and Meinander 1979, Graves and Graves 1985, Yakolev 1993), or had emerged solely from decaying mushrooms (thus, possibly only scavenging) (Frouz and Makarova 2001) and therefore did not establish a strong ecological association (i.e., food substrate, site of overwintering, etc.) with fungal sporocarps. Still other studies have focused on the evolution of tolerance of the amanitin toxin (present throughout the Basidiomycete genus *Amanita* Persoon) tolerance (Jaenike et al. 1983, Jaenike 1985) or mechanisms for aggregation of adult flies on mushrooms (Jaenike et al. 1992).

Overlooked by nearly all studies has been the ecology of mushroom-feeding species, and little is known about larval stages, feeding preferences, seasonality, or geographic range for numerous species (Buxton 1960; Graves and Graves 1985; Bunyard and Foote 1990a, b). The larval stages of many of the rarer species of mycophagous flies have never been described. Most mycophagous flies are probably generalists and not specific to any species of fungus, as fungal hosts are considered too patchy and/or ephemeral, or are scavengers, feeding on all sorts of decaying organic material (Jaenike 1978a, b). Oligophagous and specialist species are uncommon in nature and in the literature; many of the records reporting monophagy are likely artifacts of insufficient sampling (Hanski 1989). It has been postulated that mycophagous Diptera probably arose from ancestral detritivores (Bruns 1984). One of the largest groups of mycophagous Diptera, the family Drosophilidae, is considered to have evolved mycophagy more than once from a common ancestor that was a detritivore or fed on saprophytic yeasts (Courtney et al. 1990).

For this study I attempted to determine: a) the families of Diptera that are truly mycophagous, b) the existence of associations among families of Diptera with families of Basidiomycete host fungi, c) seasonality among mycophagous families of Diptera, and d) evidence of seasonality within a common mycophagous family, the Drosophilidae.

MATERIALS AND METHODS

Sites were selected to obtain a diversity of mushroom species, as well as biotic and abiotic conditions, and consisted of mature forest, mixed mesophytic forest, urban forest, and urban residential zones in northeastern Ohio (Cuyahoga, Geauga, and Portage counties). Two of the study sites have been described previously: Towner's Woods near Kent, Ohio (Portage Co.) (Bunyard and Foote 1990a) and The West Woods, near Newbury, Ohio (Geauga Co.) (Bunyard, in press).

Fungi were collected throughout the growing season from March to November, 2001. Many fungal species were collected more than once and/or on different dates or sites. Fungal material was placed in paper bags to prevent larvae of one sporophore from entering another sporophore. Different species were kept in separate bags; conspecifics from different sites also were kept separately. Fungal specimens were identified using keys in Lincoff 1984, Arora 1986, Phillips 1991, Smith and Weber 1996, Bessette et al. 1997. To avoid incidental occurrences of Diptera with the fungi (for example, resting or hiding in crevices) only adults which actually emerged from larvae occurring within the fungus were counted.

For rearing adult flies from fungal hosts, special rearing chambers were constructed as previously described (Bunyard and Foote 1990a) and consisted of the bottom of a petri dish (10 × 100 mm) to which had been added moistened vermiculite. The upper portion of the rearing chamber consisted of rigid clear plastic tubing (90 mm diameter) cut to various lengths. To the top end of each tube was glued a fine polyester mesh material. Fungal sporocarps were placed on the vermiculite substrate, and the upper portion of the chamber placed securely over the fungus, into the petri plate. The rearing chambers allowed the fungal specimens to remain in a somewhat natural condition. It was necessary to moisten the vermiculite substrate periodically to prevent desiccation of fungal material. As the sporocarps decayed, the substrate absorbed any excess moisture produced.

Following emergence, adult Diptera were kept alive for at least 24 hr to allow for exoskeleton hardening (to facilitate identification) and then killed in alcohol. Adult flies were dried and pinned for identification. Preserved specimens are in the Kent State University collection of Diptera.

RESULTS

During this study 134 species from 30 families of Basidiomycete fungi and 19 species from 11 families of Ascomycete fungi were collected from different sites in northeastern Ohio. Adult flies were reared from 87 separate fungal collections (Table 1). A few fungal species seemed to host only a single fly species per mushroom, but most were found to support more than one species of Diptera (Table 2). Five families of Diptera that include known or suspected mycophagous species (Tipulidae, Phoridae, Platypezidae, Chloropidae, Drosophilidae) were reared from fresh mushroom collections (Table 2), confirming mycophagy (as opposed to scavengening rotting material). Additionally, members of the Mycetophilidae, Sciaridae, and Cecidomyiidae also were seen (data not shown). Five other dipteran families that were reared from fungi (Psychodidae, Ceratopogonidae, Stratiomyiidae, Anthomyiidae, Sarcophagidae) likely are larval predators or scavengers occurring only in decaying mushrooms (Table 2). In some cases a single member of a dipteran family emerged from fungal material but was not counted, as it was unclear if any strong ecological association with fungi existed.

DISCUSSION

All Diptera reared in this study emerged only from Basidiomycete species (Table 1). No evidence for monophagy was seen by any of the dipteran taxa. In general, the larger the sporocarps, the greater the number of individuals, as well as diversity, of Diptera utilizing the mushroom host were seen, supporting previous studies (Bruns 1984, Hanski 1989). Previous demonstration of seasonality of mycophagous Diptera has been considered a function of seasonality of mushroom hosts (Hanski 1989) and was demonstrated here (Fig. 1). The highest number of emergences for all mycophagous taxa was seen in spring and fall; this correlated to the highest numbers of mushroom fruitings (Fig. 1).

More rearings of Drosophilidae were recorded than those of any other dipteran family (Fig. 1). The highest number of emergences for drosophilid species was seen in spring and fall. Thus, seasonality of mycophagous Drosophilidae likely is due to seasonality of hosts. Most species of Drosophilidae are considered yeast-feeders (Patterson 1943), with the food material serving as a culture medium for the yeast. It is thought that all extant species of this family came from a common ancestor that was detritivorous (Courtney et al. 1990) and became selective for rotting substrates supportive of yeast growth, especially fruits. Phylogenetic evidence suggests that mycophagy has arisen more than once within the family (Courtney et al. 1990). Today, most species of drosophilids feed on decaying fruit material, some are scavengers, and a few feed on fungi. All the species reared in this study (*Drosophila falleni* Wheeler, *D. putrida* Sturtevant, *D. tripunctata* Loew, *Mycodrosophila claytonae* Wheeler and Takada, *Leucophenga varia* Walker) are known to be mycophagous. During this study, the two most commonly reared species overall were *D. falleni* and *L. varia* (Fig. 2). These two species commonly coinhabited basidiocarps, occasionally with three other less common drosophilids: *D. tripunctata, D. putrida,* and/or *M. claytonae.* These findings support those of previous studies (Grimaldi and Jaenike 1984). Some drosophilid species have been shown to dominate (*D. tripunctata*) when competing with other species (*D. falleni* and *D. putrida*) (Worthen 1989), although this clearly was not seen here. Likewise, *Leucophenga* species may dominate in smaller species of mushrooms (Worthen et al. 1998). Several species of mycophagous species of Drosophilidae that were reared from fungi previously (Bunyard and Foote 1990a) were not obtained in this study, including *D. duncani* Sturtevant, *D. guttifera* Walker, *D. testacea* von Roser, and *M. dimidiata* Loew. Little is known about the life history of *D. duncani.* Likewise, *D. gutti-*

Table 1. Species of macrofungi, serving as hosts for mycophagous Diptera, arranged alphabetically by fungal family.

Family	Species	Diptera Species	Diptera Family
?	agaric sp.?	*Drosophila falleni*	Drosophilidae
Agaricaceae	*Agaricus arvensis* Schaeffer	*Tricimba lineella*	Chloropidae
		Drosophila falleni	Drosophilidae
			Phoridae
		Platypeza sp.	Platypezidae
			Sarcophagidae
	Agaricus augustus Fries	*Drosophila falleni*	Drosophilidae
		Leucophenga varia	Drosophilidae
			Phoridae
	Agaricus bitorquis Quelet	*Drosophila falleni*	Drosophilidae
		Drosophila putrida	Drosophilidae
			Phoridae
	Agaricus campestris Linnaeus	*Leucophenga varia*	Drosophilidae
			Phoridae
		Platypeza sp.	Platypezidae
			Sarcophagidae
	Agaricus sp.	*Drosophila falleni*	Drosophilidae
		Leucophenga varia	Drosophilidae
Amanitaceae	*Amanita flavorubescens* Atkinson	*Drosophila falleni*	Drosophilidae
		Leucophenga varia	Drosophilidae
			Phoridae
	Amanita muscaria Persoon	*Drosophila falleni*	Drosophilidae
		Drosophila putrida	Drosophilidae
	Amanita rubescens Persoon	*Drosophila falleni*	Drosophilidae
		Drosophila putrida	Drosophilidae
		Leucophenga varia	Drosophilidae
Bolbitiaceae	*Agrocybe praecox* Persoon	*Drosophila falleni*	Drosophilidae
		Leucophenga varia	Drosophilidae
			Phoridae
Boletaceae	*Boletus bicolor* Peck	*Drosophila falleni*	Drosophilidae
		Drosophila putrida	Drosophilidae
		Leucophenga varia	Drosophilidae
			Phoridae
	Boletus edulis Bulliard	*Drosophila falleni*	Drosophilidae
		Leucophenga varia	Drosophilidae
			Sarcophagidae
	Boletus sp.	sp. #1	Anthomyiidae
		Drosophila falleni	Drosophilidae
Cortinariaceae	*Cortinarius* sp.	*Drosophila falleni*	Drosophilidae
			Phoridae
	Galerina autumnalis Peck		Phoridae
Coprinaceae	*Psathyrella delineata* Peck	*Tricimba lineella*	Chloropidae
		Drosophila falleni	Drosophilidae
		Leucophenga varia	Drosophilidae
Hygrophoraceae	*Hygrophorus marginatus* Peck	*Leucophenga varia*	Drosophilidae
Pluteaceae	*Pluteus cervinus* Schaeffer	*Drosophila falleni*	Drosophilidae
			Phoridae
		Platypeza sp.	Platypezidae
			Sarcophagidae
Polyporaceae	*Bondarzewia berkeleyi* Fries	*Drosophila falleni*	Drosophilidae
		Mycodrosophila claytonae	Drosophilidae
			Phoridae
	Grifola frondosa Fries	*Drosophila falleni*	Drosophilidae

Table 1. Continued.

Family	Species	Diptera Species	Diptera Family
	Laetiporus sulfureus Fries	*Tricimba lineella*	Chloropidae
		Drosophila falleni	Drosophilidae
	Polyporus arcularius Bataille	*Drosophila falleni*	Drosophilidae
	Tyromyces chioneus Fries	*Limonia rara*	Tipulidae
Russulaceae	*Russula aeruginea* Lindblad	*Drosophila falleni*	Drosophilidae
	Russula brevipes Peck	*Drosophila putrida*	Drosophilidae
			Phoridae
		Ptecticus sp.	Stratiomyidae
		Limonia triocellata	Tipulidae
	Russula emetica Schaeffer	*Drosophila falleni*	Drosophilidae
		Ptecticus sp.	Stratiomyidae
	Russula mariae Peck	*Drosophila putrida*	Drosophilidae
		Leucophenga varia	Drosophilidae
	Russula ochroleucoides Kauffman	*Drosophila falleni*	Drosophilidae
		Leucophenga varia	Drosophilidae
			Phoridae
	Russula sp.	*Drosophila falleni*	Drosophilidae
		Leucophenga varia	Drosophilidae
			Phoridae
Strophariaceae	*Hypholoma fasciculare* Hudson	*Drosophila falleni*	Drosophilidae
	Pholiota malicola Kauffman	*Leucophenga varia*	Drosophilidae
	Pholiota sp.	*Limonia triocellata*	Tipulidae
	Pholiota sp.		Ceratopogonidae
		Drosophila falleni	Drosophilidae
			Psychodidae
Tricholomataceae	*Collybia acervata* Fries	*Drosophila falleni*	Drosophilidae
		Leucophenga sp.	Drosophilidae
	Mycena leaiana Berkeley	*Drosophila falleni*	Drosophilidae
		Leucophenga sp.	Drosophilidae
	Omphalotus olearius Schweinitz	*Drosophila putrida*	Drosophilidae
	Pleurotus dryinus Persoon		Phoridae
	Pleurotus ostreatus Jacquin	*Drosophila falleni*	Drosophilidae
		Drosophila tripunctata	Drosophilidae
		Leucophenga varia	Drosophilidae
		Mycodrosophila claytonae	Drosophilidae
			Phoridae
		Limonia triocellata	Tipulidae
	Tricholomopsis platyphylla Persoon	*Drosophila falleni*	Drosophilidae
		Leucophenga varia	Drosophilidae
			Phoridae
	Xerula furfuracea Peck	sp. #1	Anthomyiidae
		sp. #2	Anthomyiidae
		Drosophila falleni	Drosophilidae
		Limonia triocellata	Tipulidae

fera apparently is a rare mycophagous species known from only a few records (Patterson 1943). Bunyard and Foote (1990a) provided the only record for this species in Ohio. In a study of its life history, ovipositional preferences, and larval feeding habits it was found to be polyphagous for fruits and other vegetation, but with a strong preference for mushroom tissue (Bunyard and Foote 1990b).

Phoridae, a family of small flies, also is described as one of the most common inhabitants of fungal sporocarps (Hackman and Meinander 1979). Larvae are frequent-

Table 2. Species of mycophagous Diptera, arranged phylogenetically by family, reared from mushroom sporophores.

Family	Species	Fungus Family	Fungus Species
Tipulidae	*Limonia rara* Osten Sacken	Polyporaceae	*Tyromyces chioneus*
	Limonia triocellata Osten Sacken	Russulaceae	*Russula brevipes*
	Limonia triocellata Osten Sacken	Strophariaceae	*Pholiota* sp.
	Limonia triocellata Osten Sacken	Tricholomataceae	*Pleurotus ostreatus*
	Limonia triocellata Osten Sacken	Tricholomataceae	*Xerula furfuracea*
Psychodidae	Sp.?	Strophariaceae	*Pholiota* sp.
Ceratopogonidae	Sp.?	Strophariaceae	*Pholiota* sp.
Stratiomyidae	*Ptecticus* sp.	Russulaceae	*Russula brevipes*
	Ptecticus sp.	Russulaceae	*Russula emetica*
Phoridae		Agaricaceae	*Agaricus arvensis*
		Agaricaceae	*Agaricus augustus*
		Agaricaceae	*Agaricus bitorquis*
		Agaricaceae	*Agaricus campestris*
		Amanitaceae	*Amanita flavorubescens*
		Bolbitiaceae	*Agrocybe praecox*
		Boletaceae	*Boletus bicolor*
		Cortinariaceae	*Cortinarius* sp.
		Cortinariaceae	*Galerina autumnalis*
		Pluteaceae	*Pluteus cervinus*
		Pluteaceae	*Pluteus cervinus*
		Polyporaceae	*Bondarzewia berkeleyi*
		Polyporaceae	*Bondarzewia berkeleyi*
		Russulaceae	*Russula brevipes*
		Russulaceae	*Russula ochroleuca*
		Russulaceae	*Russula* sp.
		Tricholomataceae	*Pleurotus dryinus*
		Tricholomataceae	*Pleurotus ostreatus*
		Tricholomataceae	*Tricholomopsis platyphylla*
Platypezidae	*Platypeza* sp.	Agaricaceae	*Agaricus arvensis*
		Agaricaceae	*Agaricus campestris*
		Pluteaceae	*Pluteus cervinus*
Chloropidae	*Tricimba lineella* Fallén	Agaricaceae	*Agaricus arvensis*
	Tricimba lineella Fallén	Coprinaceae	*Psathyrella delineata*
		Polyporaceae	*Laetiporus sulfureus*
Drosophilidae	*Drosophila falleni* Wheeler	?	Agaric sp.?
		Agaricaceae	*Agaricus arvensis*
		Agaricaceae	*Agaricus augustus*
		Agaricaceae	*Agaricus bitorquis*
		Agaricaceae	*Agaricus* sp.
		Amanitaceae	*Amanita flavorubescens*
		Amanitaceae	*Amanita muscaria*
		Amanitaceae	*Amanita rubescens*
		Bolbitiaceae	*Agrocybe praecox*
		Boletaceae	*Boletus bicolor*
		Boletaceae	*Boletus edulis*
		Boletaceae	*Boletus* sp.
		Cortinariaceae	*Cortinarius* sp.
		Coprinaceae	*Psathyrella delineata*
		Pluteaceae	*Pluteus cervinus*
		Polyporaceae	*Bondarzewia berkeleyi*
		Polyporaceae	*Grifola frondosa*
		Polyporaceae	*Laetiporus sulfureus*
		Polyporaceae	*Polyporus arcularius*
		Russulaceae	*Russula aeruginea*

Table 2. Continued.

Family	Species	Fungus Family	Fungus Species
		Russulaceae	*Russula emetica*
		Russulaceae	*Russula ochroleuca*
		Russulaceae	*Russula* sp.
		Strophariaceae	*Hypholoma fasciculare*
		Strophariaceae	*Pholiota* sp. 1
		Tricholomataceae	*Collybia acervata*
		Tricholomataceae	*Mycena leaiana*
		Tricholomataceae	*Pleurotus ostreatus*
		Tricholomataceae	*Tricholomopsis platyphylla*
		Tricholomataceae	*Xerula furfuracea*
Drosophilidae	*Drosophila putrida* Sturtevant	Agaricaceae	*Agaricus bitorquis*
		Amanitaceae	*Amanita muscaria*
		Amanitaceae	*Amanita rubescens*
		Boletaceae	*Boletus bicolor*
		Russulaceae	*Russula brevipes*
		Russulaceae	*Russula mariae*
		Tricholomataceae	*Omphalotus olearius*
Drosophilidae	*Drosophila tripunctata* Loew	Tricholomataceae	*Pleurotus ostreatus*
Drosophilidae	*Leucophenga varia* Walker	Agaricaceae	*Agaricus augustus*
		Agaricaceae	*Agaricus campestris*
		Agaricaceae	*Agaricus* sp.
		Amanitaceae	*Amanita flavorubescens*
		Amanitaceae	*Amanita rubescens*
		Bolbitiaceae	*Agrocybe praecox*
		Boletaceae	*Boletus bicolor*
		Boletaceae	*Boletus edulis*
		Coprinaceae	*Psathyrella delineata*
		Hygrophoraceae	*Hygrophorus marginatus*
		Russulaceae	*Russula mariae*
		Russulaceae	*Russula ochroleuca*
		Russulaceae	*Russula* sp.
		Strophariaceae	*Pholiota malicola*
		Tricholomataceae	*Pleurotus ostreatus*
		Tricholomataceae	*Tricholomopsis platyphylla*
Drosophilidae	*Leucophenga* sp.	Tricholomataceae	*Collybia acervata*
		Tricholomataceae	*Mycena leaiana*
Drosophilidae	*Mycodrosophila claytonae* Wheeler and Takada	Polyporaceae	*Bondarzewia berkeleyi*
		Tricholomataceae	*Pleurotus ostreatus*
Anthomyiidae	Sp. #1	Boletaceae	*Boletus* sp.
	Sp. #1	Tricholomataceae	*Xerula furfuracea*
	Sp. #2	Tricholomataceae	*Xerula furfuracea*
Sarcophagidae	Sp.?	Agaricaceae	*Agaricus arvensis*
		Agaricaceae	*Agaricus campestris*
		Boletaceae	*Boletus edulis*
		Pluteaceae	*Pluteus cervinus*

ly found in decaying vegetation and fungi; some species (especially of the genus *Megaselia* Rondani) are serious pests of commercial mushroom farms; a few species are known to be parasitic on other insects. During this study, phorid flies emerged from more sporocarp collections than any other group except the Drosophilidae (Fig. 1).

Two species of Tipulidae, *Limonia rara* Osten Sacken and *L. triocellata* Osten

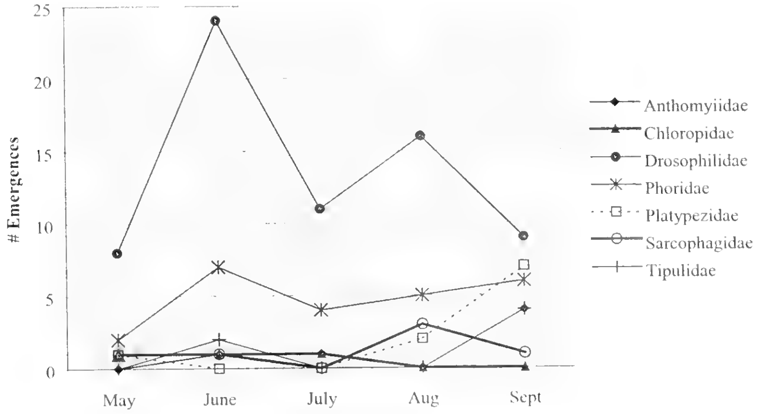

Fig. 1. Emergence numbers by month for families of Diptera.

Sacken, were reared in this study (Table 2). Most larvae of Tipulidae feed in decaying plant materials and frequently are aquatic or semi-aquatic, although several species are terrestrial. Tipulids have been reared from fungi previously (Alexander 1920, Bruns 1984). *Limonia triocellata* is a known consumer of decaying organic material (B. Foote, personal communication) and has been reared from senescent as well as fresh mushrooms (Bruns 1984). However, no information is available for the feeding substrate of larval *L. rara*. Several adults of *L. rara* were reared from sporocarps of the soft moist bracket fungus *Tyromyces chioneus* Fries. As the infested sporocarps

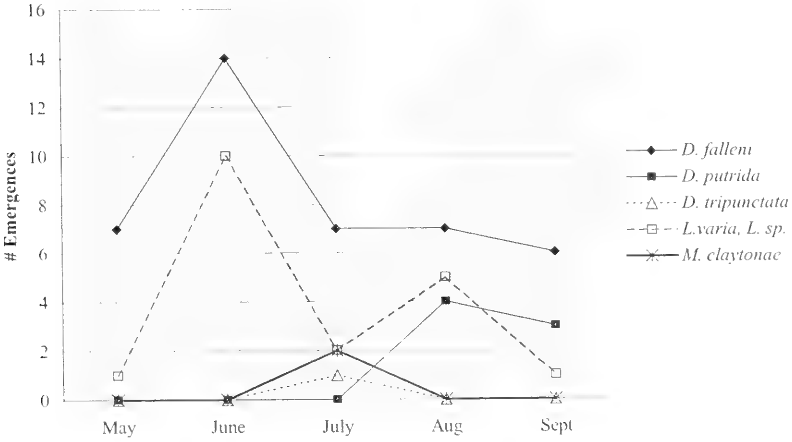

Fig. 2. Emergence numbers by month for species of Drosophilidae.

were newly emerged, this may indicate a strictly mycophagous (as opposed to scavenging on decaying fungal or other organic material) feeding habit for this species. No species of Tipulidae currently are considered to be strictly mycophagous.

Tricimba lineella Fallèn (Chloropidae) was reared on a number of occasions (Table 2). *Tricimba lineella* previously has been recorded from rotting plant material (Grimaldi and Jaenike 1983) and from macrofungi (Bunyard and Foote 1990a). One other species (*Gaurax atripalpus* Sabrosky) has been recorded from fungi, probably overwintering in polyporaceous species (Valley et al. 1969, Bunyard and Foote 1990a).

The family Platypezidae was reared from fresh sporocarps mostly towards the end of the growing season (Fig. 1). The association was especially significant between this family and the basidiomycete family Agaricaceae, as platypezids were reared almost exclusively from species of *Agaricus* (Table 2). Species of *Agaricus* produce some of the largest sporocarps and would seem an ideal host, but they seem to be rarely utilized by other mycophagous Diptera (Buxton 1960, Hackman and Meinander 1979). Members of the Platypezidae (the "flat-footed" or "smoke flies") comprise a small family (71 species in 18 genera in North America) of uncommon flies of wooded areas (Kessel 1987). Adult platypezids are noted by a fairly large head and characteristic flattened hind tarsi and tibiae. Although all platypezid species are thought to be mycophagous, the life cycles and larvae for many species remain unknown or have never been seen (Kessel 1987).

Unidentified adults from the families Anthomyiidae and Sarcophagidae were reared from a number of large, mostly decaying, Basidiomycete sporocarps (Fig. 1) suggesting scavenging behavior and not strict mycophagy. Both families are comprised of large bodied species that commonly are scavengers of decaying organic material.

Curiously, several species of mycophagous Diptera were conspicuously absent from this study. For example (besides those already mentioned above), *Leiomyza laevigata* Meigen (Asteiidae) is a rare species known from only a handful of studies (Sabrosky 1957, Papp 1972). Bunyard and Foote (1990a) confirmed its mycophagous habit.

Frequently, larvae of more than one family—often from several families—occupied the same sporocarp. Likewise, more than one species from a single family frequently emerged from the same sporocarp. Because fungal sporocarps are a limited and ephemeral food source, it would seem logical that inter- and intraspecific competition pressures should exist. The Competitive Exclusion Principle (Hardin 1960) states that two species cannot coexist in a single limiting resource. So, how can we explain so many closely related species occupying the same niche? Previously, a few studies have provided possible explanations as to how species of mycophagous Diptera avoid significant interspecies competition. In particular, most studies have focused on the commonly seen mycophagous species of Drosophilidae. Biotic pressures (predation, parasitism) may reduce competition and thus allow drosophilid species to cohabit (Worthen 1989, Worthen et al. 1995, Jaenike 1998). Predation by ants and beetles, and parasitism by nematodes were the focus. During this study, numerous predacious beetles frequently were seen feeding (presumably on fly larvae) on and within mushroom tissues, especially the larger Basidiomycete species that were associated with rearings of multiple species of drosophilids and other taxa. Adult parasitic Hymenoptera frequently emerged from the sporocarps. Presumably, parasitic wasps also could impinge upon the fly species to reduce their numbers, and thus lessen interspecific competition pressures.

Abiotic pressures also may reduce competition and allow different fly species to cohabit. Worthen and Haney (1999) found that when abiotic pressures (heat, desiccation) are strong, other dipterous species may dominate (e.g., *D. putrida* is more common in small mushrooms that are more subject to desiccation and was found to be more tolerant of chronic and acute bouts of drought or high temperatures). Our findings strongly support this; *D. putrida* was seen as a dominant species only in the months of August and September (Fig. 2).

Most of the attention of this paper—and the interrelationship between Diptera and fungal host—has been approached from the fly's point of view. It may be just as interesting to consider the host's (fungus) role in this symbiosis. Typical levels of mycophagy frequently resulted in the complete destruction of the sporocarp. One would think this to be detrimental to the host. If this is true, it is logical to expect the host to fight back (the "Red Queen" effect [Van Valen 1973]). Few studies have attempted to determine if any macrofungi are unsuitable to any groups of flies. Of course, by virtue of size alone, those fungi that form particularly small sporocarps will escape or have reduced mycophagy. Similarly, a few fungal species avoid damage by their physical makeup: many species of bracket fungi (mostly within the family Polyporaceae) have a hard, woody texture that is difficult for many arthropods to consume (Courtney et al. 1990). Basidiomycete and Ascomycete fungi produce a wide array of toxic metabolites, although the defensive properties of these have been poorly investigated. Insecticidal properties have been explored (Mier et al. 1996), although the authors carried out their study by feeding mushroom extracts to arthropods in a completely artificial fashion. Clearly, the ability to detoxify secondary metabolites of mushrooms is widespread throughout taxa of arthropods. This ability obviously has evolved more than once among families of Diptera. Furthermore, groups of basidiomycete taxa (e.g., *Amanita* spp., *Galerina* Earle spp.) considered deadly to most animals, including non-mycophagous Diptera, have no detrimental effect on mycophagous species (Jaenike et al. 1983, Jaenike 1985).

Mycophagous Diptera may be of some benefit to their fungal host. Stinkhorns (Phallales: Basidiomycotina) benefit from scavenging flies that disperse their basidiospores. Hodge et al. (1997) discussed the carriage of fungal material by adult *Drosophila*. Ascomycete fungi (including members of the genus *Balansia*) are known to benefit from symbiotic associations with insects. Recently, Diptera have been shown to disperse spermatia (a type of fungal spore) from one fungus to other individuals, thus facilitating fertilization (a sort of "pollination") (Bultman et al. 1998, 2000).

Clearly, this study indicates a great need for additional investigations into the interrelationships between fungal host and mycophagous Diptera. Likewise, there are many uncertainties regarding the life histories for many species of mycophagous flies, as well as the interrelationships among the mycophagous Diptera.

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ANNOTATED KEY TO THE ENSIGN WASP (HYMENOPTERA: EVANIIDAE) GENERA OF THE WORLD, WITH DESCRIPTIONS OF THREE NEW GENERA

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Abstract.—The genus-level taxonomic history of Evaniidae is discussed and three new genera are described: ***Vernevania* Huben and Deans** from the Indian subcontinent with ***V. urbanusorum* Deans, n. sp.**, ***Decevania* Huben** from Central and South America with *D. parva* (Enderlein), **n. comb.**, and *D. striatigena* (Kieffer), **n. comb.**, and ***Rothevania* Huben** from South America with *R. valdiviana* (Philippi), **n. comb**. The genus *Acanthinevania* Bradley is resurrected based on distinctive leg, mesosomal, and mouthpart morphology, raising the total number of valid genera to twenty. The following species are transferred from *Evania*: *Acanthinevania clavaticornis* (Kieffer 1911), **n. comb.**, *A. leucocras* (Kieffer 1911), **n. comb.**, *A. sericans* (Westwood 1851), **n. comb.**, and *A. szepligetiana* (Hedicke 1939) **n. comb.** Sixteen additional genera are also recognized as valid: *Afrevania* Benoit, *Brachevania* Turner, *Brachygaster* Leach, *Evania* Fabricius, *Evaniella* Bradley, *Evaniscus* Szepligeti, *Hyptia* Illiger, *Micrevania* Benoit, *Papatuka* Deans, *Parevania* Kieffer, *Prosevania* Kieffer, *Semaeomyia* Bradley, *Szepligetella* Bradley, *Thaumatevania* Ceballos, *Trissevania* Kieffer, *Zeuxevania* Kieffer. A key to the genera of the world is provided.

Key Words: ensign wasps, Evaniidae, *Acanthinevania, Vernevania, Rothevania, Decevania*

Despite the frequent collection and recognizable habitus of ensign wasps, there have been very few concentrated efforts directed at improving our understanding of them. The most obvious impediment to further research is the current state of evaniid classification. Since the early 1900's (the height of evaniid taxonomic activity) the amount of ensign wasp research has dwindled. Only one new extant genus has been described since 1953 (Deans 2002), and the last comprehensive taxonomic treatment was Hedicke's (1939) world catalog. However, this catalog does not include keys, and one must resort to Kieffer's (1912) outdated and inadequate monograph as the sole source for species or genus identification.

Several characteristics of evaniid biology make them an interesting group of insects for future research. All verifiable rearings indicate that evaniid larvae develop as solitary egg predators within cockroach oothecae (Roth and Willis 1960, Cameron 1957, Crosskey 1951). This represents a possible method of non-chemical control for pestiferous cockroaches (Thoms and Robinson 1987, Edmunds 1953), but few studies have tested the effectiveness of these wasps. Evaniids also form multifaceted mimicry complexes, particularly in South America, with distantly related species possessing the same possibly aposematic and/or disruptive color schemes of black, brown, orange, and red. No published research, however, has explored this phenomenon.

Several recent papers have contributed to our understanding of the evolutionary history of the Evaniidae. Basibuyuk et al. (2000a, b, 2001) describe extinct genera and how they shape our understanding of modern evaniids. Dowton and Austin (2001), Dowton et al. (1997), and Ronquist et al. (1999), among many others, discuss the yet unresolved relationship of Evaniidae to the rest of the Hymenoptera.

The purpose of this paper is to describe three new genera, two from South America (*Decevania* and *Rothevania*) and one from the Indian subcontinent (*Vernevania*), and to resurrect *Acanthinevania* Bradley. We also provide an illustrated key to the genera of the world. This is not meant to be a full revision but instead is intended as a starting point for researchers or budding evaniid taxonomists interested in determining specimens to genus as the genera are currently defined. Ongoing detailed morphological and molecular analyses by ARD into the generic limits, phylogenetic relationships of the genera, as well as how the Evaniidae relate to the rest of the Hymenoptera may improve our understanding of this enigmatic family.

TAXONOMIC HISTORY

The taxonomic instability within the Evaniidae has been well established, and most publications (1900–present) include one or two sentences bemoaning this fact. Frison (1922) divided the problems into several categories, which still apply today. First, nearly all species were described from only one or two specimens, allowing no discussion of variation. Color patterns can vary within a particular species, and it is possible that these color morphs have been described as separate species. Second, they are sexually dimorphic (usually in antennal morphology, body coloration, facial sculpture, and/or metasomal morphology) and difficult to associate; some described species may actually represent the opposite sex of other species. Third, most holotypes are difficult to find. Kieffer described most of the evaniid species but rarely designated holotypes or mentioned their depository. Compounding this problem is the fact that nearly all the original descriptions are vague and could actually apply to multiple closely related species. Frison (1922) also noted that the number and limits of the evaniid genera were disputed and difficult to rectify.

Table 1 summarizes the history of genus-level classification for the Evaniidae based on the largest, most complete monographs. Schletterer (1889a, b) provided the first comprehensive treatment of world species, collapsing the three known genera into a single genus, *Evania* Fabricius. Bradley (1908) added three new genera and reassigned species *non viso*. He based his taxonomic scheme on several wing venation and non-wing characters (e.g., metasoma shape, antenna, leg, tarsal claw, and mouthpart morphology, shape of the "furculum" between hind coxae). Kieffer (1912), in an unfortunate step backwards, reclassified the evaniids solely on wing venation characters. He synonymized *Acanthinevania, Evaniella,* and *Szepligetella* under *Evania,* and *Semaeomyia* under *Brachygaster*. Hedicke's (1939) world catalog largely followed Kieffer's (1912) classification but included all the genera and species described between 1912–1939.

Several synapomorphies define the Evaniidae. The most recognizable are the high insertion of the metasoma (Figs. 1–2) and the thin tubular shape of the petiole (Figs. 3–5) giving these wasps their characteristic habitus. Most species also have 11 flagellomeres (except *Decevania* spp. have 8; Fig. 1) and hind wings with greatly separated jugal lobes (Figs. 6–8) (except some *Evaniella* and *Prosevania* spp. <2.5 mm long). All evaniid rearings have been from

Table 1. Taxonomic history of the Evaniidae.

Genus (Year Described)	Schletterer (1889)	Bradley (1908)	Kieffer (1912)	Hedicke (1939)	Current (2003)
Evania (1775)	*Evania*	*Evania*	*Evania*	*Evania*	*Evania*
Hyptia (1807)	(syn. *Evania*)	*Hyptia*	*Hyptia*	*Hyptia*	*Hyptia*
Brachygaster (1817)	(syn. *Evania*)	*Brachygaster*[1]	*Brachygaster*	*Brachygaster*	*Brachygaster*
Zeuxevania (1902)		*Zeuxevania*	*Zeuxevania*	*Zeuxevania*	*Zeuxevania*
Evaniscus (1903)		*Evaniscus*	*Evaniscus*	*Evaniscus*	*Evaniscus*
Evaniellus (1905)		*Evaniellus*	*Evaniellus*	*Evaniellus*	(syn. *Hyptia*)[2]
Parevania (1907)		(sub.g. *Zeuxevania*)	*Parevania*	(sub.g. *Zeuxevania*)	*Parevania*[3]
Acanthinevania (1908)		*Acanthinevania*	(syn. *Evania*)	(syn. *Evania*)	*Acanthinevania*
Evaniella (1908)		*Evaniella*	(syn. *Evania*)	*Evaniella*	*Evaniella*
Semaeomyia (1908)		*Semaeomyia*	(syn. *Brachygaster*)	(sub.g. *Brachygaster*)	*Semaeomyia*[2]
Szepligetella (1908)		*Szepligetella*	(syn. *Evania*)	*Szepligetella*	*Szepligetella*
Chalcidopterella (1909)			*Chalcidopterella*	*Chalcidopterella*	(syn. *Hyptia*)[2]
Prosevania (1911)			*Prosevania*	(sub.g. *Evania*)	*Prosevania*[3]
Trissevania (1913)				*Trissevania*	*Trissevania*
Brachevania (1927)				*Brachevania*	*Brachevania*
Thaumatevania (1935)				*Thaumatevania*	*Thaumatevania*
Micrevania (1952)					*Micrevania*
Afrevania (1953)					*Afrevania*
Papatuka (2002)					*Papatuka*
Decevania (2003)					*Decevania*
Rothevania (2003)					*Rothevania*
Vernevania (2003)					*Vernevania*

[1] Bradley (1908) used the name *Semaedogaster* in place of *Brachygaster*.
[2] Huben (1995) synonymized *Evaniellus* and *Chalcidopterella* under *Hyptia* and raised *Semaoemyia* to genus level.
[3] Mani and Muzaffer (1943) raised to genus level.

cockroach egg cases, and it is assumed that this represents a synapomorphic lifestyle.

KEY TO WORLD GENERA OF EVANIIDAE

The Evaniidae would benefit enormously from a worldwide family-level revision. The limits between certain genera are not well defined, and we are aware of a few specimens that still do not key to the correct genus. These rare exceptions are discussed under each genus.

Wing venation varies greatly within the family and provides the most useful characteristics for distinguishing genera. Unfortunately, ensign wasps are prone to wing venation aberrations (usually missing or extra veins; see Mani and Muzaffer 1943) which may lead one to inappropriate couplets. Also helpful are head shape/sculpturing, tarsal claw morphology, metasoma shape, and female genitalia morphology. Qualifying terms are used to estimate the number of specimens displaying a particular character based on material examined (~7,000 specimens): sometimes (<50%), often (50–75%), or usually (75–99%). Wing veins disrupted by a fold (e.g., claval fold) are considered complete veins. The key is intended for both sexes, but some couplets contain additional information regarding female-specific characters. Morphological terminology used in the descriptions and keys follows that of Huber and Sharkey (1993), and wing venation terminology (Figs. 6–7) was adapted from Sharkey and Wharton (1997).

1. Wings absent or reduced, apex never reaching past petiole if present 2
– Wings present, extending past petiole 4
2. Brachypterous; wing with 7 complete cells, apex (portion without tubular veins) <33% of total wing (Fig. 10) . . . . . . *Brachevania* Turner [Ethiopia; 1 described species represented by 1 specimen; the only brachypterous evaniid.]
– Apterous 3
3. Antenna 10-segmented (Fig. 1); hind tarsomeres (at least) with extended apical projections (Fig. 1); total length <4 mm; New World . . . . *Decevania* Huben (in part) [At least one undescribed wingless species from Ecuador.]

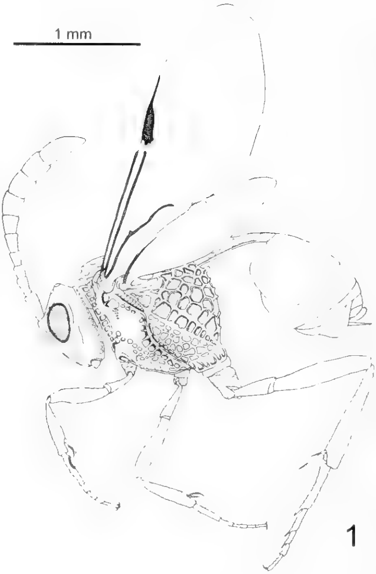


Fig. 1. *Decevania* sp., typical habitus.

– Antenna 13-segmented (as in Fig. 2); tarsomeres without extended projections; total length >5 mm; Old World . . . . *Papatuka* Deans [Kenya; currently 1 described species represented by 1 specimen; label suggests it was reared from a *Dasyproctus westermanni* (Dahlbom) (Sphecidae) nest (Deans 2002). At least one undescribed species exists from South Africa.]
4. Forewing with at least 6 cells enclosed by tubular or nebulous veins (Figs. 2, 6–8, 11–14) 5
– Forewing with 1–3 cells enclosed by tubular veins (Figs. 1, 9, 15–19) 15
5. Distance between mid- and hind coxa nearly equal to distance between fore- and midcoxa (Fig. 20), midcoxa never touching hind coxa when projected posteriorly; genae never uniformly strigate or costate 6
– Distance between mid- and hind coxa 0.6× or less the distance between fore- and midcoxae (Fig. 21), midcoxa often touching hind coxae when projecting posteriorly; genae variable 7
6. Forewing RS+M missing, fusing 1st submarginal and 1st subdiscal cells (Fig. 11); head in lateral view hemispherical (Fig. 22); anten-

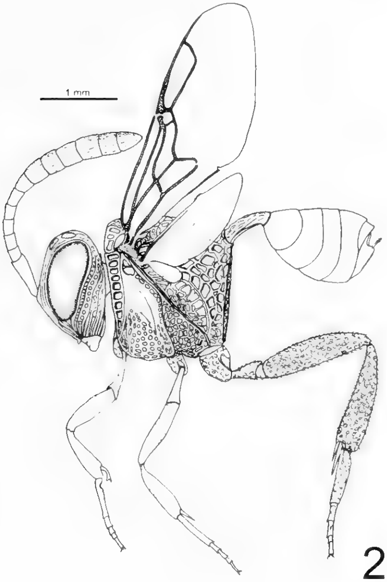


Fig. 2. *Vernevania urbanusorum*, habitus.

nae arising at midheight of head; ovipositor short, completely hidden within metasoma; female metasoma in lateral view circular or ovoid (Fig. 5); New World . . . . *Evaniscus* Szepligeti

[New World tropics; small genus of medium sized ensign wasps with 4 described and a few undescribed species; rarely collected.]

– Forewing RS+M present separating 1st submarginal and 1st subdiscal cells (near Fig. 8); head in lateral view slightly compressed (Fig. 23); antennae arising on upper third of head; ovipositor long, usually visible; female metasoma in lateral view triangular with metasomal tergite 8 expanded dorsally (Fig. 3); worldwide . . . . *Evania* Fabricius

[Worldwide; includes the cosmopolitan and frequently collected and studied *E. appendigaster* (L.) 1758; other species are found throughout the Old World and Central America; characterized by their long hind legs, widely separated coxae, somewhat flattened faces, and large size; nearly half of all evaniid species are currently assigned to this genus; further examination of types will likely result in reassignment for most of these species into *Evaniella, Parevania, Prosevania, Acanthinevania,* and *Szepligetella* (Townes 1949).]

7. Hind tibia and tarsus (at least) with evenly distributed long, prominent, erect spines, >2× the length of hind leg setae (Fig. 29); female metasomal tergite 8 usually expanded dorsally (near Fig. 3); ovipositor usually long, exposed; Pacific islands and Australasia 8

– Hind tibia and tarsus without prominent spines, or with spines <2× the length of hind leg setae distributed only on posterior portion of tibia (Figs. 30–31); metasoma (female) in lateral view often circular or ovoid (Figs. 4–5); ovipositor often short, concealed within metasoma; worldwide except Australia 9

8. Head never elongate (always semicircular in lateral view) (near Fig. 22); labial palp segment 3 swollen, semicircular to circular (Fig. 25); glossa usually hidden (depends on preservation); labium broad and flat or slightly folded anteriorly, never elongate; propodeal area ventral to petiole often concave . . . . *Szepligetella* Bradley

[Australasia, Pacific Islands; most species with concave depression posterior/ventral to the petiole; currently only 1 described species, with many incorrectly assigned to *Evania* or undescribed. All species from Australia currently belong in either *Szepligetella* or *Acanthinevania*.]

– Head usually elongate (Fig. 27); labial palp without swollen segments (Fig. 26); glossa exposed, semicircular, nearly bilobed (Figs. 26–27); labium folded strongly anteriorly, appearing long and narrow; propodeal area ventral to petiole flat or convex . . . . *Acanthinevania* Bradley

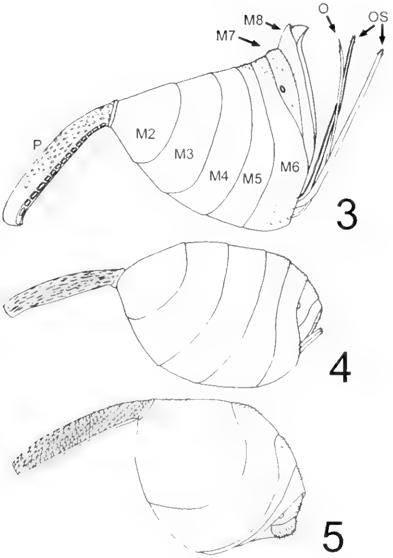
[Australia; erroneously synonymized with *Evania* by Kieffer (1912); differs from *Evania* by the mid- and hind coxae close together, the hind tibia (at least) with long, erect spines, and elongate mouthparts with an exposed glossa; currently 6 described species, with many incorrectly assigned to *Evania* or undescribed. All species from Australia currently belong in either *Szepligetella* or *Acanthinevania*.]

9. Forewing with 6 complete cells (Figs. 12–14) 10

– Forewing with 7 complete cells (Fig. 2, 6, 8) 12

10. Forewing 1RS missing, fusing basal and 1st submarginal cells (Fig. 12); head often appearing globular in lateral view (Fig. 24) . . . . *Zeuxevania* Kieffer

[Old World; 10 described species largely united by the characteristic wing venation; may



Figs. 3–5. Female metasomas. P = petiole, M2–8 = metasomal segments 2–8, O = ovipositor, OS = ovipositor sheath. 3, *Evania albofascialis* Cameron. 4, *Parevania atra* Kieffer. 5, *Evaniscus rufithorax* Enderlein.

be related to *Parevania* (Bradley 1908); in some species females have extended metasomas (posterior to the petiole), and both males and females possess a wide space between the hind coxae.]

– Forewing 1RS present, separating basal and 1st submarginal cells (Figs. 13–14); head usually appearing semicircular (near Fig. 22) or flattened in lateral view 11

11. Forewing 2cu-a absent, opening 1st subdiscal cell distally (Fig. 13); 4RS complete; stigma not enlarged; foreleg tarsomere 1 not expanded distally; costate sculpturing forming irregular circles around antennal sockets in some species (Fig. 34); Madagascar . . . . *Micrevania* Benoit

[Madagascar; 2 rarely collected described species; recognized by their small size (<2.5 mm), characteristic wing venation, and antero-posteriorly flattened heads. South American specimens keying here do not have circular sculpturing on the frons and currently belong in *Evaniella*.]

– Forewing 2cu-a present (1st subdiscal cell completely enclosed) (Fig. 14); 4RS incomplete; stigma enlarged; foreleg tarsomere 1 expanded distally into a long spine (Fig. 28); no costate sculpturing forming circles around antennal sockets; northern Africa and the Middle East . . . . *Thaumatevania* Ceballos

[Morocco and Israel; only 2 specimens known, both with characteristic wing venation, extended foreleg tarsomere 1, and enlarged stigma.]

12. Gena (at least) costate or strigate (Fig. 35), sometimes irregularly (may be difficult to see in specimens <2.5 mm) 13

– Gena nitid, setose, punctate, and/or foveolate 14

13. Legs relatively short, <3× as long as mesosoma height (Fig. 2); forewing 2M, 3M, 3CU missing or spectral, 1M clearly separated from Sc+R (Fig. 2); marginal cell elongate (~4× wider than high); Indian subcontinent . . . . *Vernevania* Huben and Deans

[Sri Lanka and India; 1 described species and at least 1 undescribed; compact habitus with short legs suggests a close relationship to *Brachygaster*.]

– Legs relatively long, >3× as long as mesosoma height; forewing 2M, 3M, 3CU usually present as nebulous veins, 1M often parallel and close to or convergent with Sc+R (Fig. 8); marginal cell not elongate (~2× wider than high); Old World . . . . . *Prosevania* Kieffer

[Old World; currently includes the cosmopolitan and frequently collected *Prosevania fuscipes* (Illiger) 1807, which probably does not belong in this genus; species recognized by the costate/strigate facial sculpturing and the metapleuron with a broad flat area extending dorsally to an elongate furrow immediately ventral to the wings (Fig. 38), and the somewhat elongate 1st discal cell which often runs parallel to the wing margin; some species with short spines posteriorly on hind legs; most Malagasy *Parevania* spp. have strigate facial sculpturing but not the other characteristics of *Prosevania*.]

14. Forewing 1RS usually attached to Sc+R basal to the stigma and curved slightly toward wing base (Fig. 6); hind wing M+CU often as long as hind jugal lobe; Old World . . . . *Parevania* Kieffer

[Old World; similar to *Evaniella*; Kieffer's (1912) description based solely on the inconsistent attachment of 1RS (often nebulous) to Sc+R basal to the stigma; Bradley (1908) treated as subgenus of *Zeuxevania*; 20 described species with several undescribed or assigned to *Evania*; most Malagasy species have strigate facial sculpturing but not the other characteristics of *Prosevania*; Australian species keying to this couplet probably belong to *Szepligetella*.]

Forewing 1RS attached to Sc+R at stigma, usually linear (Fig. 7); hind wing M+CU often shorter than hind jugal lobe; New World . . . . *Evaniella* Bradley
[New World; a frequently collected and extremely diverse genus with many undescribed species; at least 19 described species with many more still assigned to *Evania*; Australian species keying to this couplet probably belong to *Szepligetella*.]

15\. Forewing with 1 complete cell (Figs. 1, 17); New World 16

– Forewing with 2–3 complete cells (Figs. 9, 15–16, 18–19); worldwide 17

16\. Antenna 10-segmented (Fig. 1); notauli present (at least as row of depressions); hind tarsomeres 1–3 elongated posteriorly into spines (Fig. 1) . . . . *Decevania* Huben (in part)
[New World; characterized by small eyes (Fig. 36) and 8 flagellomeres (Fig. 1); collected throughout Central and Northern South America, often at high attitudes; 2 described and at least 6 undescribed species.]

– Antenna 13-segmented (as in Fig. 2); notauli absent in most specimens; hind tarsomeres not elongated into spines . . . . *Hyptia* Illiger
[New World; an extremely diverse genus with 49 described species and many more undescribed; wing venation extremely reduced (Fig. 17), resulting in a single complete cell; synonyms *Chalcidopterella* Enderlein and *Evaniellus* Enderlein were based on the variable forewing M+CU length.]

17\. Forewing 1st marginal cell complete (Fig. 19) . . . . *Trissevania* Kieffer
[Africa; rarely collected; 1 described species with distinct wing venation; wings often folded apically as in *Afrevania* (see next couplet).]

Forewing 1st marginal cell absent 18

18\. Forewing with 2 complete cells (costal and basal), 4RS present, tubular (Fig. 18); forewing long and floppy, folded back on itself apically (depending on preservation, may be expanded apically) . . . . *Afrevania* Benoit
[Africa; 1 rarely collected described species; characteristic floppy wings are usually folded apically; very similar morphologically to *Trissevania* (previous couplet) except wing venation.]

– Forewing with 3 complete cells (costal, basal, and subbasal), 4RS absent (Figs. 9, 15–16); forewing variable, but never naturally folded back on itself 19

19\. Forewing 4RS and r-m present as spectral veins (Fig. 15); legs relatively short, hind leg <2.5× mesosoma height; notauli often absent (may be present as thin furrow or slight depression in some species); entire body densely foveolate; Old World . . . . . *Brachygaster* Leach
[Old World and Australia; wing venation and compact habitus with short legs characteristic; a common European species, *B. minuta* (Olivier), has been studied extensively; at least 7 described with a few undescribed species; Bradley (1908) erroneously renamed this genus *Semaedogaster*.]

– Forewing 4RS, and r-m absent; legs relatively long, hind leg >2.5× mesosoma height; notauli present; body variously sculptured; New World 20

20\. Forewing 1CU+2CU vein ending before claval fold (Fig. 9); tarsal claws with apical tooth more prominent subapical tooth (Fig. 32) . . . . *Rothevania* Huben
[Chile and Argentina; similar to *Semaeomyia* and *Brachygaster*; 1 described and at least 3 undescribed species.]

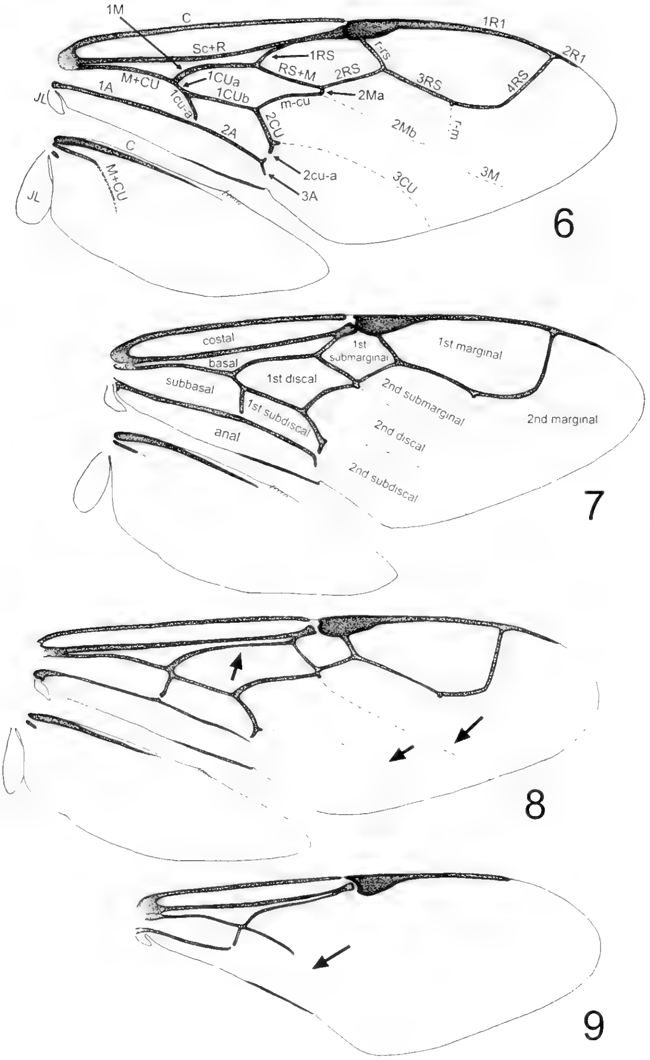
– Forewing 1CU+2CU vein reaching claval fold (Fig. 16); tarsal claws with sub-apical tooth more prominent than apical tooth (Fig. 33) . . . . *Semaeomyia* Bradley
[New World tropics; extremely diverse in morphology, size, and number of species; 38 described and many undescribed species.]

Chalcidopterella Enderlein, *Evaniellus* Enderlein

Huben (1995) included these two genera in *Hyptia*. They are morphologically identical to *Hyptia* except for the length of the forewing M+CU; *Chalcidopterella* has a short and nebulous or spectral M+CU, and in *Evaniellus* the M+CU is absent (Kieffer 1912). Wing venation within any genus of Evaniidae varies slightly, and the synonymy of these two genera with *Hyptia* is justified.

Semaeomyia Bradley

Semaeomyia was treated as a subgenus of *Brachygaster* (including all its New World species) by Hedicke and as a genus by Huben (1995). *Semaeomyia* differs from *Brachygaster* in at least the following characters: forewing venation never with spectral 4RS and r-m, tarsal claws with subapical tooth more prominent than apical tooth, and legs relatively long. This morphologically diverse taxon should be treated as a genus.



Figs. 6–9. Wings, arrows on 8–9 indicate diagnostic characters. 6, *Parevania* sp. with wing veins labeled. 7, *Evaniella* sp. with wing cells labeled. 8, *Prosevania* sp. 9, *Rothevania valdivianus* (Phillippi), forewing.

Acanthinevania Bradley
(Figs. 26–27, 29)

Type species.—*Evania princeps* Westwood 1841, original designation.

Diagnosis.—Medium to large with black or black and red color pattern. Head with elongate gena, mouthparts elongate and exposed (depends on preservation), palps without swollen segments, head deeply concave posteriorly, forewing veins enclosing 7 complete cells, hind tibia (at least) with long spines.

Description.—Length from head to metasoma varies between 4.0–14.0 mm. Color always black or a pattern of black and orange or red. Head appearing somewhat elongate with gena 0.5–1.0× as long as eye height. Face sculptured with elongate foveae (Fig. 27). Posterior portion of head concave, often greatly so. Mouthparts usually exposed revealing glossa and palps, appearing elongate (Fig. 26) due to long labium. Palps never with swollen segments. Maxillary palpus 5-segmented and labial palpus 4-segmented. Antenna 13-segmented. Mesosoma boxlike and usually densely foveolate except for small nitid area dorsally on mesopleuron and areolate or areolate-rugose metapleuron. Pronotum and mesoscutum square in dorsal view. Propodeal area ventral to insertion of petiole flat or very slightly concave. Metasternum expanded posteriorly into forked projection (furculum) with two short, slightly divergent tines. Legs relatively long, hind leg at least 2.5× longer than mesosoma height with at least hind tibia and tarsomere 1 spiny (Fig. 29). Leg spines at least 2.0× longer than tibial setae. Tarsal claws relatively elongate and straight with one subapical tooth medially (similar to Fig. 32). Wing venation similar to *Szepligetella* and *Evaniella* (Fig. 7). Apical edge of forewing with numerous wrinkles. Hind wing with 7–16 hamuli depending on body/wing size. Metasoma similar in shape to Fig. 3 with expanded apical segment. Ovipositor straight, as long as posterior edge of metasoma.

Biology.—Unknown, probably solitary egg predators within cockroach oothecae.

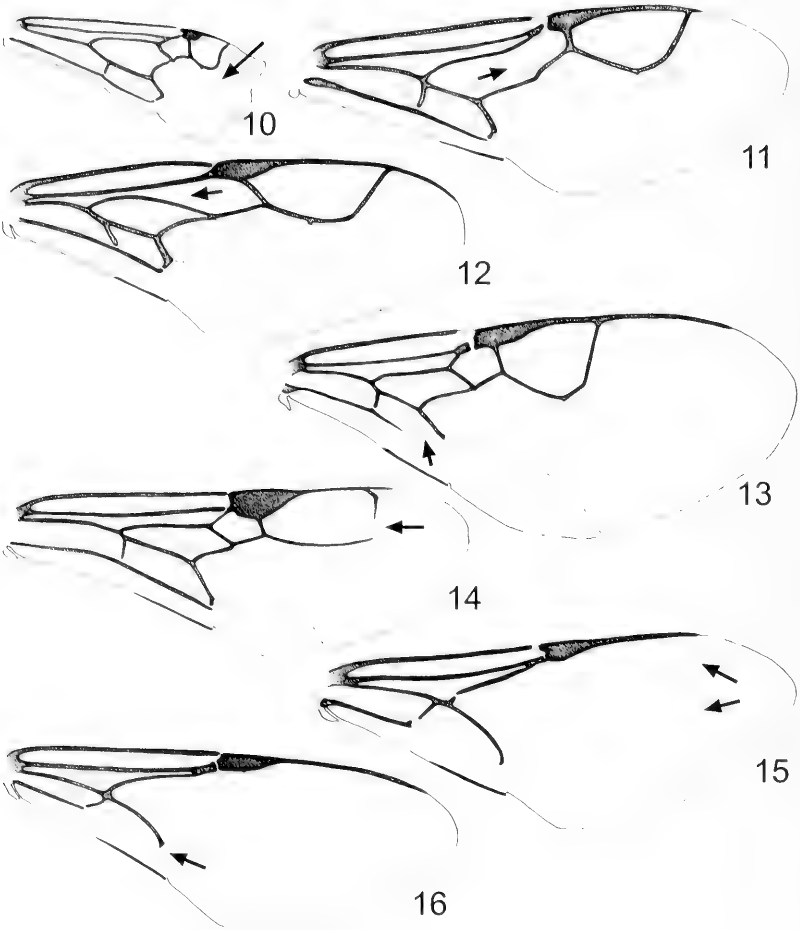
Comments.—Morphologically, *Acanthinevania* differs greatly from *Evania* and deserves to be reinstated as a genus. *Acanthinevania* possesses the following characters not present in *Evania*: head greatly concave posteriorly, mouthparts elongate with glossa exposed, palpi without swollen segments, mid- and hind coxae closer together than mid- and forecoxae, and hind tibia (at least) with long spines.

Based on our examination of holotypes deposited in The Natural History Museum in London we reassign the following species (**new combinations**, all originally described in *Evania*): *Acanthinevania clavaticornis* (Kieffer 1911), *A. leucocras* (Kieffer 1911), *A. rufiventris* (Kieffer 1911), *A. sericans* (Westwood 1851), and *A. szepligetiana* (Hedicke 1939) (deposited in the Cornell University Insect Collection, Ithaca, New York). The holotype for *Evania princeps* Westwood 1841 probably has been lost or destroyed. Our intepretation of this species is based on determined material from the Muséum National d'Histoire Naturelle, Paris, and the Cornell University Insect Collection; *A. princeps* is also the type species. Bradley (1908) assigned many species to this genus without examining the holotypes or properly determined material; many of these species belong to other genera. There are undoubtedly more described and undescribed species that belong in *Acanthinevania*, including one undescribed species from Chile.

***Decevania* Huben, new genus**
(Figs. 1, 36)

Type species.—*Hyptia striatigena* Kieffer 1910.

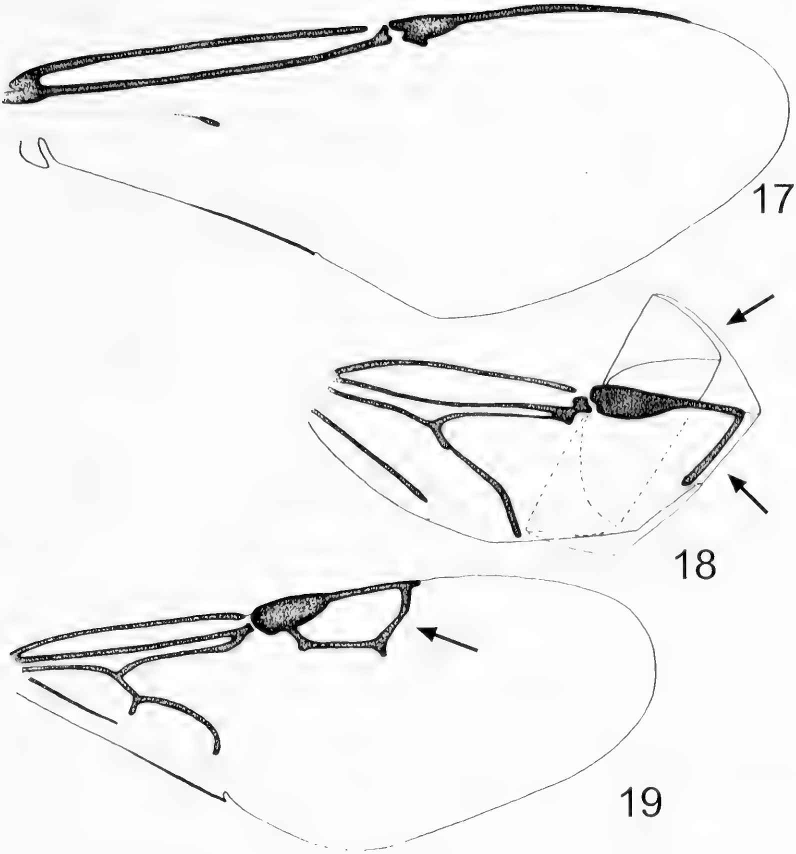
Diagnosis.—Small to minute and brown to dark brown. Head with relatively small eyes, antenna 10-segmented, wings long and floppy, forewing veins enclosing 1



Figs. 10–16. Forewings, arrows indicate diagnostic characters. 10, *Brachevania kristenseni* Turner. 11, *Evaniscus* sp. 12, *Zeuxevania* sp. 13, *Micrevania difficilis*. 14, *Thaumatevania* sp. 15, *Brachygaster* sp. 16, *Semaeomyia* sp.

complete cell, hind tarsomeres 1–3 (at least) projected apically into long spines.

Description.—Habitus antlike, minute (1.8–3.0 mm in length), dark brown. Sparse, long setae cover most of body and legs. Eye usually reduced to 0.5× or less head height. Face striated between eyes and mandibles. Gena with a carina extending from just outside eye to mandible. Postgenal area flat and nitid. Antenna 10 segmented, arising from just above the center of the face. Mandible with two teeth. Maxillary



Figs. 17–19 Forewings, arrows indicate diagnostic characters. 17, *Hyptia* sp. 18, *Afrevania* sp. 19, *Trissevania* sp.

palpus 4–5-segmented, labial palpus 3–4-segmented. Anterior surfaces of pronotum and mesonotum together flattened and nitid. Notauli distinct. Mesopleuron medially impunctate. Dorsal margin of mesopleuron with a sharply acute triangular areolate region bounded by a prominent ridge with a row of punctures on other side. Mesosoma otherwise coarsely punctured, areolate, or foveate everywhere except dorsomedially. Hindleg tarsomeres 1 to 3 (at least) each laterally compressed with a ventral carina and a distal spine. Rarely apterous. Wings delicate, sometimes with a large stigma, and often crumpled in dried specimens. Veins C, Sc+R, M+CU, 1CUa, 1CUb brown and tubular. Gaster nitid except for setae on genitalia. Ovipositor straight, short, usually partly concealed within gaster.

Etymology.—The genus name refers to

the 10-segmented antennae; gender, feminine.

Comments.—This new genus is described based on the following synapomorphies not present in *Hyptia*: 8-segmented flagellum, relatively reduced eyes, oversized, floppy wings, and posteriorly expanded hind tarsomeres 1–3. *Hyptia parva* Enderlein 1901 and *H. striatigena* Kieffer 1910 are reassigned: *Decevania parva* (Enderlein), **n. comb.**, and *D. striatigena* (Kieffer) **n. comb.** Holotypes for *D. striatigena* and *D. parva* were examined and are deposited in Museum für Naturkunde der Humboldt Universität, Berlin, Germany. *Decevania* is entirely Neotropical and is often collected at remarkably high altitudes (over 5,000 m) but can also be collected at sea level. Previously referred to as "Genus D" by Huben (1995).

Rothevania Huben, new genus

(Figs. 9, 32, 37)

Type species.—*Brachygaster valdiviana* Philippi 1871.

Diagnosis.—Small and black or black and orange. Forewings with 1CU+2CU vein ending before claval fold, forewing veins enclosing 3 complete cells, tarsal claws with apical tooth more prominent sub-apical tooth.

Description.—Length from head to metasoma 3.5–4.5 mm. Black to nearly entirely red. Head round in frontal view, ovoid in dorsal view. Frons and facial area surrounding antennae setose with crowded small punctures. Distinct lateral carinae on face extend from near eyes to above mandibles. Antenna with 13 segments, inserted centrally. Eye oval, slightly narrowed dorsally. Mandible setose, with 2 teeth. Anterior pronotum, mesonotum, and propleuron minutely punctate or ridged. Pronotum and mesonotum rounded anteriorly, without a sharp transverse ridge. Notauli present, distinct. Mesopleuron with an irregular band of transverse punctures or striae from anterior-dorsal corner medially to center. Apical tooth of tarsal claws more prominent than subapical tooth. Wings hyaline, setose. Veins C, Sc+R, M+CU, 1M, 1RS, 1CUa, 1CUb, 1A, 1cu-a, 2CU brown and tubular. 2CU much shortened, not reaching claval fold. Metasomal tergite 1 relatively long. Gaster circular in lateral view, concealing ovipositor in female. Ovipositor short, thin, straight.

Etymology.—This genus is named in honor of the late Dr. Louis M. Roth, a lifelong student of cockroaches; gender, feminine.

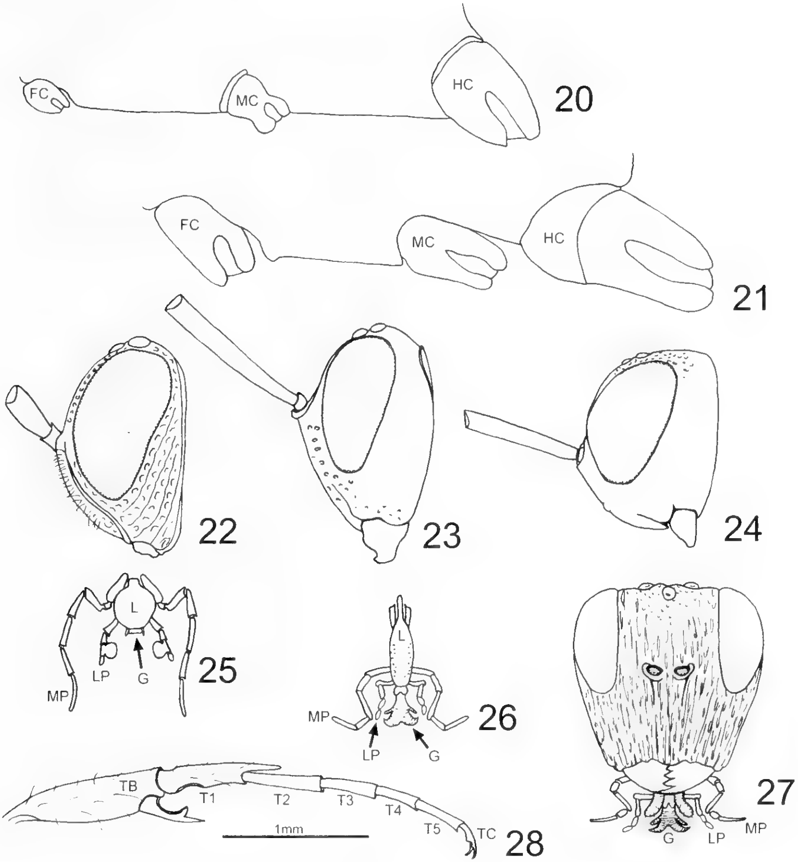
Comments.—*Rothevania* is separated from *Semaeomyia* by the unique wing venation and tarsal claw morphology. This genus is Valdivian in distribution, known only from Chile and Argentina. One specimen, labeled "Hardwar Gap, Jamaica," may represent another species and a curious range extension or a mislabeling. *Rothevania valdiviana* (Philippi) is a **new combination.** The holotype of *R. valdiviana* could not be located. The decision to describe a new genus for this species is based on the original description and examination of determined material at the American Entomological Institute (22 specimens), the California Academy of Sciences (16 specimens), and the Florida State Collection of Arthropods (119 specimens).

Vernevania Huben and Deans, new genus

Type species.—*Vernevania urbanusorum* Deans, new species.

Diagnosis.—Small and brown to dark brown. Head relatively large, with costate sculpturing dorsal to the eyes, mesosoma compact, forewing with elongate 1st discal and 1st marginal cells, forewing veins enclosing 7 complete cells.

Description.—Female: Length from head to metasoma 3.0–4.0 mm. Dark brown to black. Head circular in frontal view, semicircular in dorsal view. Frons and facial area surrounding antennae sparsely setose and densely foveolate. Clypeus forming a central projection extending over mandibles. Area surrounding



Figs. 20–28. Evaniid morphological characters. FC = forecoxa, MC = midcoxa, HC = hind coxa, L = labium, LP = labial palpus, MP = maxillary palpus, G = glossa, TB = tibia, T1-T5 = tarsomeres 1–5, TC = tarsal claw. 20, *Evaniscus* sp., coxal spacing. 21, *Parevania* sp., coxal spacing. 22, *Evaniscus rufithorax*, head. 23, *Evania dimidiata*, head. 24, *Zeuxevania* sp., head. 25, *Szepligetella* sp., mouthparts, posterior view. 26, *Acanthinevania* sp., mouthparts, posterior view. 27, *Acanthinevania* sp., head. 28, *Thaumatevania* sp., foreleg tibia and tarsomeres.

lower 0.5 of eyes costate. Gena striate ventrally, becoming costate-foveolate dorsally. Mandible slightly setose with 3 teeth. Maxillary palpus 5-segmented, elongate and thin. Labial palpus 4-segmented, segment 2 slightly swollen and semicircular. Antenna with 11 flagellomeres, swollen slightly after flagellomere 5, arising midway on face. Mesosoma compact, mostly foveolate. Notauli present as slight impressions (difficult to see). Metanotum forming thin irregularly scrobiculate band. Mesopleuron expanded, convex, nitid dorsally within leg groove. Propodeum areolate. Legs coarsely punctate, relatively short. Coxae coarsely foveolate. Tarsi strongly tapering with tarsomere 1 as long as tarsomeres 2–5 combined. Tarsal claws with two teeth of equal size. Wing venation characteristic (Fig. 2). Petiole (metasomal tergite 1) rugose-punctate dorsally, nitid ventrally. Metasomal tergites 2–8 forming ovoid gaster. Hypopygium extended with expandable pleats apically. Ovipositor short, partially concealed within gaster. Ovipositor sheath with small cluster of short, stiff setae apically.

Male: Similar to female except flagellomeres slightly elongate and never swollen.

Etymology.—This genus is named in honor of the late Verne Pechuman, Cornell University, mentor to MH; gender, feminine.

Comments.—*Vernevania* closely resembles *Brachygaster* in habitus, possessing a relatively large head, short legs, and coarse body sculpturing. However, *Vernevania* has a relatively full complement of wing veins arranged in a unique pattern with elongate 1st marginal and 1st discal cells.

Vernevania urbanusorum Deans, new species

(Fig. 2)

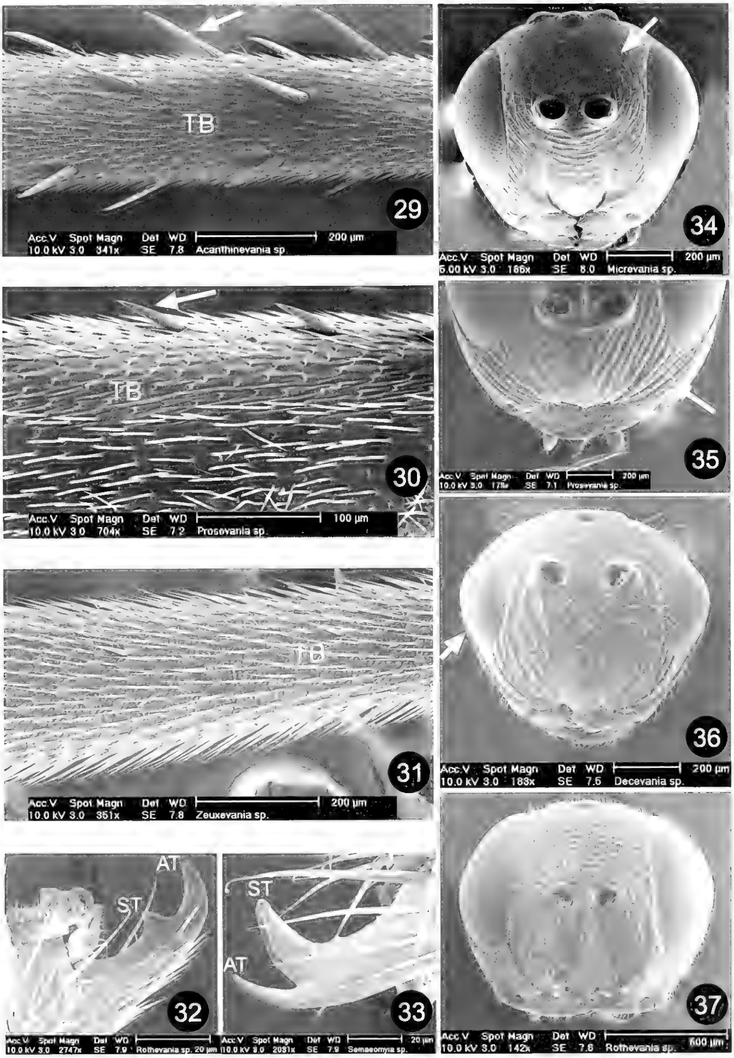
Description.—Female. *Head:* Equally high as wide, 0.5× as long as wide. Frons and facial area surrounding antennae sparsely setose and densely foveolate continuing ventrally with shallow foveae (~10) immediately beneath antennae. Clypeus and area immediately above clypeus without sculpturing. Widest distance between eyes 0.6× width of head. Postgenal area flat and nitid. Antenna arising midway on face; scape weakly punctate, setose dorsally, sparsely setose ventrally, 4.0× as long as pedicel; brown dorsally, light brown ventrally, with densely arranged placoid sensilla. Mandible brown to reddish brown. Eye silvery gray, widest dorsally, 2.2× higher than width at midheight. Ocelli clear yellow, nearly equal in size. Line between lateral ocelli 2.2× line between lateral ocellus and median ocellus.

Mesosoma: Dark brown to black, compact, broadly foveolate anteriorly becoming irregularly areolate posteriorly. Anterior pronotum and propleuron flat and nitid. Mesoscutum broadly foveolate, sparsely setose with yellow hairs, 2.3× wider than long. Tegula translucent light brown. Scutellum broadly foveolate, sparsely setose with yellow hairs, 3.0× wider than long. Metanotum 0.25× as long as scutellum. Lateral areas of metanotum and scutellum forming setose pits (at base of wings). Mesopleuron convex and coarsely foveolate ventrally, nitid dorsally within leg groove. Dorsal border of mesopleuron lined with broad foveae immediately ventral to mesopleural ridge. Ventral mesopleuron and metapleuron setose with silver hairs. Propodeum areolate, setose with silver hairs except bald in medial area where wings rest during expansion. Setae yellowish where petiole inserts into mesosoma. Legs brown, ~2.5× mesosoma height. Hind leg darker brown than mid and forelegs. Hind femur as long as hind tibia. Hind tibia as long as hind leg tarsomeres 1–5. Tibial spurs light brown, interior spur 1.3× as long as exterior spur. Each tarsomere with stiff spines apically. Tarsal claws 0.5× as long as tarsomere 5.

Wings: Hyaline, setose becoming more densely setose apically. Veins C, Sc+R, M+CU, 1M, 1RS, RS+M, 2RS, r, 3RS, 4RS, 1R1, 1CU-a, 1CU-b, m-cu, 1A, 1cu-a, 2A, 2CU, and 2cu-a brown, tubular. Veins 2M, 3M, r-m, and 3CU spectral. Hamuli consisting of 4 hooks (3 identical, fully curved hooks apically and 1 open hook basally). Jugal lobes present on both wings.

Metasoma: Petiole 3.0× longer than wide. Metasomal tergites 2–8 ovoid, brown, nitid.

Genitalia: Ovipositor short, at least 13× longer than wide, partially concealed within gaster. Ovipositor sheath with small cluster of short, stiff setae apically.



Figs. 29–37. SEM images of evaniid morphology, arrows indicate diagnostic characters. TB = tibia, AT = apical tooth, ST = subapical tooth. 29, *Acanthinevania* sp., hind tibia. 30, *Prosevania* sp., hind tibia. 31, *Zeuxevania* sp., hind tibia. 32, *Rothevania valdivianus*, tarsal claw. 33, *Semaeomyia* sp., tarsal claw. 34, *Micrevania difficilis*, head. 35, *Prosevania* sp., head. 36, *Decevania* sp., head. 37, *Rothevania valdivianus*, head.

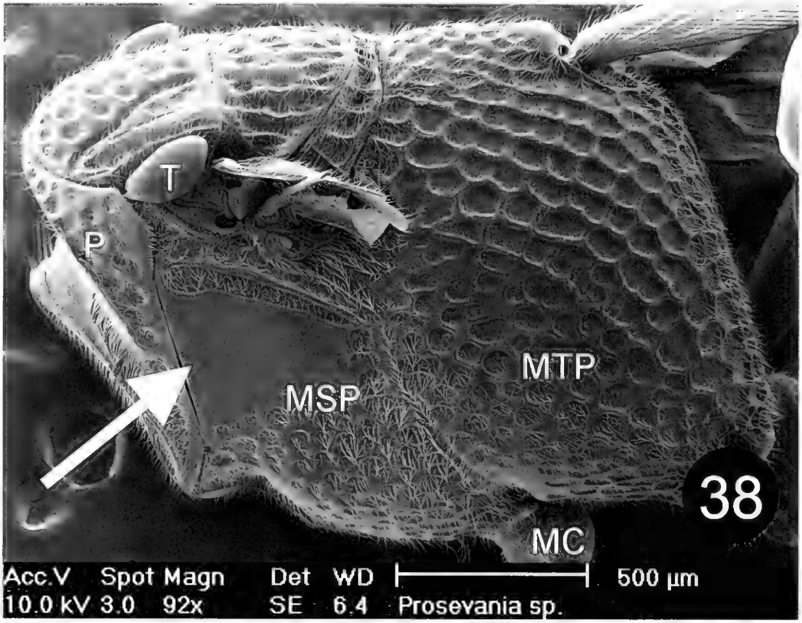


Fig. 38. SEM, *Prosevania* sp., mesopleuron. P = pronotum, MSP = mesopleuron, MTP = metapleuron, T = tegula, MC = midcoxa, arrow indicates flattened area.

Male.—Similar to female except flagellomeres slightly elongate and never swollen.

Biology.—Unknown.

Holotype.—Female, labeled "Sri Lanka: Mate. Dist.: Kibissa: 0.5 mi West of Sigiriya: jungle: Malaise trap [28-VI]-[4-VII]-1978, coll. K.V. Krombein, P. B. Karunaratne, T. Wijesinhe, V. Kulasekare." Deposited in the National Museum of Natural History, Washington DC.

Paratype.—Male labeled "Sri Lanka: Man. Dist.: Kokmotte Bungalow: 0.5 mi NE Wilpattu N.P.: voucher # 10777 C: 7-X-1977, coll. P. B. Karunaratne." Deposited with holotype.

Etymology.—The species is named as a tribute to Jeff and Amy Urbanus for their valued friendship and undying enthusiasm for the natural world.

Comments.—At least one other undescribed species exists from India. It is smaller (3.0–3.2 mm long) with slightly different propodeal sculpturing.

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We thank D. R. Smith of the Systematic Entomology Laboratory, USDA, at the Smithsonian Institution for allowing us to borrow much needed material and for help with publishing this manuscript. We very much appreciate the efforts and patience of the following individuals who also loaned us important specimens examined for this publication: R. Danielsson (Lund University), M. Elliott (Australian Museum), C. Favret (Illinois Natural History Survey), S. L. Heydon (R. M. Bohart Museum of Entomology), F. Koch (Museum für Naturkunde der Humboldt Universität), J. T. Longino (Evergreen

State College), M. O'Brien (University of Michigan Museum of Zoology), T. Osten (Staatliches Museum für Naturkunde Stuttgart), C. Schmid-Egger, M. Sharkey (University of Kentucky), D. Wahl (American Entomological Institute), R. Wharton and E. Riley (Texas A and M University), J. Wiley (Florida State Collection of Arthropods), D. Yanega (University of California at Riverside), and B. Zuparko (California Academy of Sciences and the Essig Museum of Entomology). Scott Robinson of the Beckman Institute's Imaging Technology Group helped tremendously with the SEM images. We also thank Jim Whitfield for providing useful comments regarding early drafts of this paper. This research was partially funded by a UIUC Campus Research Board Grant.

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A REVIEW OF THE NORTH AMERICAN FLEA GENUS *SPICATA* I. FOX, 1940 (SIPHONAPTERA: CERATOPHYLLIDAE)

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Abstract.—The species and subspecies of the genus *Spicata* are reviewed. *Dactylopsylla comis scapoosei* Hubbard, *D. c. tacomae* Hubbard, and *D. c. walkeri* Hubbard are **new synonyms** of *Spicata comis* (Jordan); *Dactylopsylla minidoka* Prince and Stark is a **new synonym** of *Spicata nuditenacula* (Prince), and *Dactylopsylla moorei moorei* Hubbard and *D. m. oregona* Hubbard are **new synonyms** of *Spicata pacifica* (Hubbard). A key to the remaining species is provided and their diagnostic characters are illustrated.

Key Words: *Spicata*, Ceratophyllidae, distribution, host/parasite, pocket gopher

There are three genera of fleas that are specific ectoparasites of North American geomyid rodents commonly known as pocket gophers. As might be expected they appear to be closely related, have a somewhat confusing nomenclatural history, and, in recent years, have been assigned to the subfamily Dactylopsyllinae. Members of the genus *Foxella* Wagner 1929 are distributed from western Indiana west to British Columbia and south to at least central Mexico. The other two genera, *Dactylopsylla* Jordan 1929 and *Spicata* I. Fox 1940 are much more poorly known and are restricted to western North America from Colorado and Wyoming, west to the coast, and south into Mexico.

Until now the genus *Spicata*, which was resurrected by Smit (1983), contained eight species, three of which contained named subspecies, for a total of twelve named taxa. Since the name was erected, ten of these names have been introduced into the literature with no apparent effort being directed toward exploring their validity. Indeed two of the species are still known only from females, certainly not the diagnostic sex in this order of insects. The following is an attempt to bring some order to the genus with an eye toward a taxonomic revision of the subfamily to which it belongs. Except for *S. comis* (Jordan) I have examined the primary types of all of the species and have concluded that there are only six valid species, at most. Following is a generic diagnosis, a key to the species and a brief resumé of what little is known of these taxa. Acronyms used are USNM = National Musuem of Natural History, Smithsonian Institution, Washington, DC; BMNH = The Natural History Museum, London.

Genus *Spicata* I. Fox 1940

Spicata I. Fox 1940: 272–276. Type species: *Dactylopsylla* (*Spicata*) *rara* I. Fox 1940. Original designation.

This genus contains species with the following diagnostic characters: *Head:* With a ventral seta between the lowest setae in the frontal and ocular rows. Eyes vestigial to absent, when present, unpigmented. Sensory pits on antennomeres 4–6, normal for the family. *Thorax:* First pair of lateral plantar setae on tarsomere V not displaced on to the plantar surface. *Abdomen:* Spicules on sternites very indistinct or absent.

Male modified segments: Tergum VIII without an area spiculosa on inner surface. Sternite VIII with at least a few long ventral setae. Posterior portion of distal arm of st IX with a patch of 3–25 setae which may be relatively long and straight or short and curly. Apical portion of this sternite forming a complete, elongated ellipsoid in lateral view. Two acetabular setae, at least the upper one arising remote from the margin of the fixed process. Movable process long and relatively straight, its apex sometimes inclined cephalad. Aedeagus without dorsoapical hooks or lobes. Female: Basal abdominal sternite with lateral setae. Base of bursa copulatrix darkly sclerotized. Bulga of spermatheca globular. Hilla with a large papilla. Anal stylet with two ventral and one dorsal subapical setae. Large fleas, 3.5–4.5 mm, in western North America.

The following key will separate the known species of the genus with the caveat that only four of the six species are known from the diagnostic sex and some are known from so little material that we have no knowledge of the range of intraspecific variation. Even with accompanying males the females remain extremely difficult to identify, at least until more material comes to hand.

KEY TO KNOWN SPECIES OF *SPICATA*

1. Male 2
– Female 5
2. Proximal lobe of distal arm of st IX with a dense submarginal patch of curly setae 3
– Proximal lobe of distal arm of st IX with a few long setae that are not curled 4
3. Fixed and movable processes long and narrow, the latter with almost parallel margins (Fig. 1); apex of st VIII clavate (Fig. 2); apical lobe of st IX long and narrow, its cephalic and caudal margins subparallel (Fig. 3) . . . . *comis*
– Fixed and movable processes broader mesally, their margins not parallel (Fig. 10); apex of st VIII not clavate, its margins almost parallel (Fig. 11); apical lobe of st IX shorter, oval, its margins not parallel (Fig. 12) . . . . *pacifica*
4. Movable process ~4× as long as wide at widest point (Fig. 7); apex of st VIII lacking pronounced apical extension and bearing long setae only along the caudal margin (Fig. 8); apical lobe of st IX long and narrow, acuminate ventrally (Fig. 9) . . . . *rara*
– Movable process ~6× as long as wide at widest point (Fig. 4); apex of st VIII with an apical extension and bearing long setae laterally as well as along the caudal margin (Fig. 5); apical lobe of st IX almost oval, its cephalic and caudal margins parallel (Fig. 6) . . . . . *nuditenacula*
5. Caudal margins of st VII with at least a shallow incision near the bottom of the segment (Fig. 18) . . . . *rara*
– Margin of this segment without an incision . . 6
6. Caudal margin of st VII essentially straight vertically for most of its length (Fig. 14) . . . . *comis*
Caudal margin of st VII projecting into a lobe of varying shape 7
7. Caudal lobe rounded 8
- Caudal lobe angled although its apex may be rounded 9
8. Caudal lobe smoothly rounded from venter (Fig. 15) . . . . *monticola*
– Caudal lobe less smoothly rounded, triangular in the middle (Fig. 13) . . . . *bottaceps*
9. Caudal lobe bluntly rounded, its ventral margin straight, or nearly so (Fig. 16) . . . . *nuditenacula*
– Caudal lobe more sharply rounded apically, its ventral margin slightly concave (Fig. 17) . . . . *pacifica*

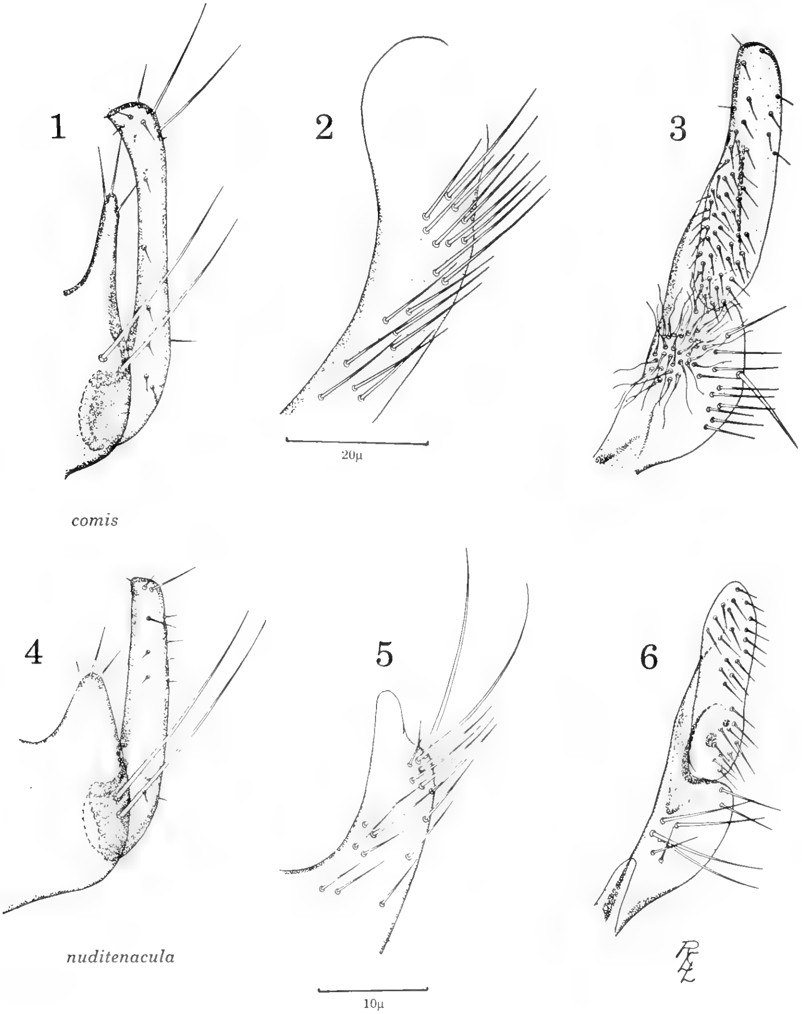
Spicata bottaceps (Hubbard 1943)
(Fig. 13)

Dactylopsylla (*Foxelloides*) *bottaceps* Hubbard 1943: 5, 1 unnumbered figure. USA, California, Del Norte County, school yard at Fort Dick, 41.54N 124.10W, from *Thomomys bottae*, 3.VII.1943, C. A. Hubbard leg. Holotype ♀, USNM No. 57084.

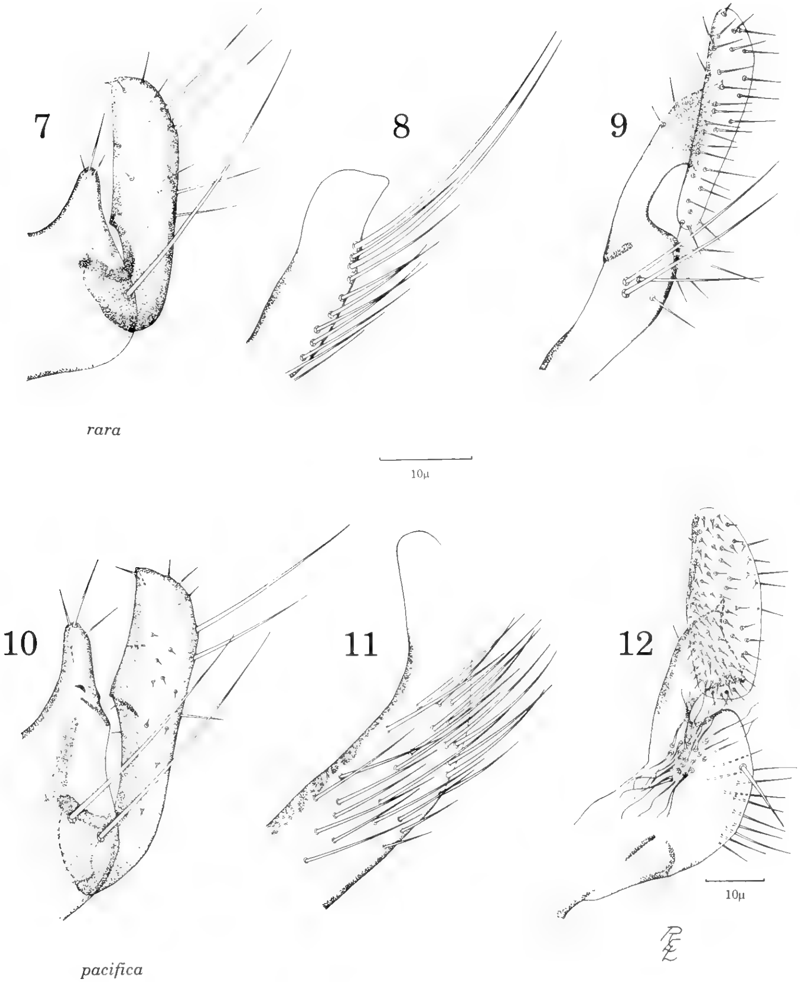
Nothing appears to have been added to our knowledge of this species since the original description. The spermatheca and contours of the caudal margin of st VII are reminiscent of *S. pacifica,* but in the absence of additional material, especially males, the species remains an enigma. Given the amount of individual variation in the species of the three genera in this subfamily, it is tempting to assign the two taxa to a single species.

Spicata comis (Jordan 1929)
(Figs. 1–3, 14)

Dactylopsylla comis Jordan 1929: 35: 38, pl. II, fig. 26. Canada, British Columbia,

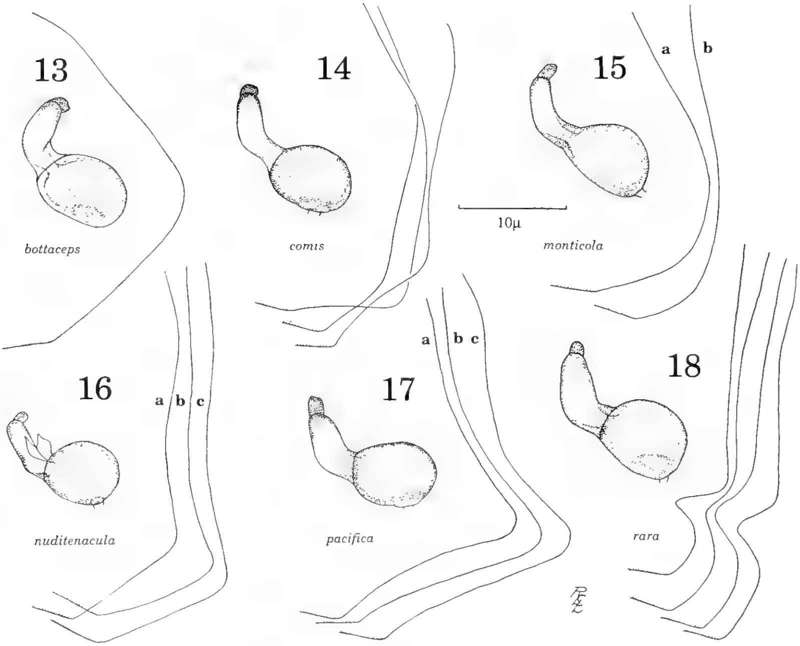


Figs. 1–6. 1–3, *Spicata comis*, not types. 1, Male clasper. 2, Apex of male st VIII. 3, Apex of male st IX. 4–6. *Spicata nuditenacula*, holotype. 4, Male clasper. 5, Apex of male st VIII. 6, Apex of male st IX.



Figs. 7–12. 7–9, *Spicata rara*, holotype. 7, Male clasper. 8, Apex of male st VIII. 9, Apex of male st IX. 10–12. *Spicata pacifica*, holotype. 10, Male clasper. 11, Apex of male st VIII. 12, Apex of male st IX.

Okanagan Landing, 50.12N 119.22W, from *Thomomys talpoides*, 2.V.1915, J. A. Munro leg. Holotype ♀, BMNH. Male described by Hubbard (1943) with the following data: USA, Oregon, Lane County, summit of McKenzie Pass, Frog Camp, ~44.15N 121.50W, from *Thomomys mazama*, 22.VII.1938, C. A. Hub-



Figs. 13–18. Spermatheca and caudal margin of female st VII. 13, *Spicata botticeps*, holotype. 14, *S. comis*, not types. 15, *S. monticola* (a) holotype, (b) paratype. 16, *S. nuditenacula* (a) allotype, (b) *S. minidoka*, allotype, (c) *S. minidoka*, paratype. 17, *S. pacifica*, (a) allotype, (b) *S. moorei moorei*, allotype, (c) *S. m. oregona*, allotype. 18, *S. rara*, not types.

bard leg, USNM No. 57086. The author erroneously referred to this specimen as the "allotype."

Dactylopsylla comis scapoosei Hubbard 1954: 169, figure unnumbered. USA, Oregon, Columbia County, Scapoose, 45.46N 122.54W, from *Thomomys talpoides*, 8.V.1951, C. A. Hubbard leg. Holotype ♂, allotype ♀, said to be in the USNM but not listed in the computerized type inventory and not located by Adams and Lewis (1995). **New synonym.**

Dactylopsylla comis tacomae Hubbard 1954: 170, figure unnumbered. USA, Washington, Pierce County, Tacoma, 47.16N 122.30W, from *Thomomys mazama*, 10.XI.1947, C. A. Hubbard leg. Holotype ♂, allotype ♀, USNM No. 104686. **New synonym.**

Dactylopsylla comis walkeri Hubbard 1954: 170, figure unnumbered. USA, Oregon, Curry County, Wedderburn, 42.27N 124.26W, from *Thomomys monticola*, 18.IX.1949, C. A. Hubbard leg. Holotype ♂, BMNH. **New synonym.**

Hubbard (1947) said that this species was so infrequently collected that he suspected it might be a nest flea or occur as adults only during the winter months. I have been able to examine eight pairs, and in addition to the localities cited in the synonymy, specimens came from Benton, Deschutes, Lane, Linn and Wasco counties in Oregon and Pend Oreille County in Washington. Hubbard (1947) also cited three females from Del Norte County in extreme northwestern California. In passing it should be noted that Fort Dick, California, the type locality of *S. bottaceps,* and Smith River, California, the collection site of Hubbard's females, are only slightly more than ten km apart, and both are situated on the coastal plain. Under the circumstance the identity of these specimens is subject to considerable question.

Spicata monticola (Prince 1945)
(Figs. 15)

Dactylopsylla monticola Prince 1945: 17, fig. 7. USA, Nevada, 21 km W Carson City, ~39.10N 119.55W, from *Thomomys monticola,* 19.VIII.1937, USPHS personnel leg. Holotype ♀, USNM No. 104652.

This species, described from two females, has evidently not been collected since and the male is unknown. Unlike females of so many taxa in this complex of genera, these females are unequivocally distinct. The caudal margin of st. VII is smoothly rounded and lacks a lobe or sinus. The spermatheca is elongated, its bulga and hilla are approximately equal in length and the latter bears a conspicuous apical papilla. Both the holotype and paratype are in the USNM.

The description places this species "13 miles west of Carson City, Ormsby County, Nevada." Carson City is evidently no longer associated with a county. There is no Ormsby County in Nevada or any of the contiguous states and thirteen miles west of Carson City places the locality approximately in the center of Lake Tahoe. Since the United States Public Health Service slides usually only indicate the county where the specimens were collected, the exact type locality can not be established with any degree of certainty. However, the host was the nominate subspecies of *T. monticola.* Although the range of this taxon does extend eastward to Carson City, the bulk of its range extends northward into central California, almost to the Oregon border. In the absence of documented males, the status of the species remains obscure, but the shape of the spermatheca and the contours of st VII are distinct from other females in the genus.

Spicata nuditenacula (Prince 1945)
(Figs. 4–6, 16)

Dactylopsylla (Foxelloides) nuditenacula Prince 1945: 17, figs. 3–4. USA, Montana, Gallatin County, 14.5 km NW West Yellowstone, ~44.40N 111.07W, from *Mustela frenata,* 24.V.1938, USPHS personnel leg. Holotype ♂, allotype ♀, USNM No. 104661.

Dactylopsylla minidoka Prince and Stark 1951: 136, figs. 11–15. USA, Utah, Box Elder County, Raft River Mts, Minidoka National Forest, 12 km SE Yost, 41.59N 113.32W, 1981 m, from *Thomomys talpoides,* 11.V.1947, K. R. Kelson leg. Holotype ♂, allotype ♀, USNM No. 104649. **New synonym.**

I have examined the types of *S. nuditenacula* and *S. minidoka,* as well as a pair of paratypes of the latter, and find them to be conspecific. Unfortunately, I have only been able to examine five males and seven females from rather widely separated localities. In addition to the type localities of the two species I have material from Deschutes, Harney, Jefferson, and Malheur counties. Based on this distribution it seems that the species is confined to the Great Basin.

Spicata pacifica (Hubbard 1943)
(Figs. 10–12, 17)

Dactylopsylla (Foxelloides) pacifica Hubbard 1943: 4, figure [unnumbered]. USA, Oregon, Lincoln County, Devil's Lake, ~44.57N 124.00W, from *Thomomys monticola,* 26.VI.1943, C. A. Hubbard leg. Holotype ♂, allotype ♀, USNM No. 57085.

Dactylopsylla moorei Hubbard 1949: 47, pl. 6. USA, Washington, Wahkiakum County, 19 km NE Cathlamet, 46.13N 123.22W, from *Thomomys talpoides*, 27.V.1949, A. W. Moore leg. Holotype ♂, Allotype ♀, USNM No. 104653. **New synonym.**

Dactylopsylla moorei oregona Hubbard 1954: 170, figs. unnumbered. USA, Oregon, Lincoln County, Devil's Lake, ~44.57N 124.00W, from *Thomomys monticola*, 8.IX.1949, C. A. Hubbard leg. Holotype ♂, allotype ♀, USNM No. 104665. **New synonym.**

I have been able to examine four males and five females of this species, including the holotype and allotype of *S. pacifica* and holotypes and allotypes of the two subspecies of *S. moorei*. While the nominate subspecies of the latter was described from the most southwestern county of Washington state, it should be noted that both *S. pacifica* and *S. moorei oregona* were described from the same locality and host species in adjacent Clatsop County, Oregon, about six years apart. All three taxa conform to the diagnostic characters of *S. pacifica* and the latter two are thus considered to be junior synonyms.

Spicata rara (I. Fox 1940)
(Figs. 7–9, 18)

Dactylopsylla (*Spicata*) *rara* I. Fox 1940: 275, figs. 5–6. USA, Colorado, Jackson County, *sine loco*, from *Thomomys fossor* [= *talpoides*], 13.VII.1926, S. C. McCampbell leg. Holotype ♂, USNM No. 54013.

In addition to the holotype of this species I have been able to examine five males and four females from Jackson and Montezuma counties, Colorado, and Big Horn County, Wyoming, from *Thomomys talpoides* and *T. bottae*. Most were collected in early May so this may be a "winter" species in the sense that adults are most common during the cooler months.

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A NEW GENUS, ONE NEW SPECIES, AND SYNONYMICAL NOTES ON THE TRIBE ACANTHOCERINI (HETEROPTERA: COREIDAE: COREINAE)

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Abstract.—***Rondoneva usta*, new genus** and **new species**, from Brazil are described, illustrated, and included in the tribe Acanthocerini (Coreidae). *Moreyacoris* Casini is reduced to a **new junior synonym** under *Beutelspacoris* Brailovsky, and *Moreyacoris dilatata* Casini is transferred to the genus *Beutelspacoris* (**n. comb.**).

Key Words: Hemiptera, Heteroptera, Coreidae, Acanthocerini, New Genus, New Species, Brazil, synonymical notes, taxonomy

The Acanthocerini is a New World tribe with is greatest diversity in the tropics. The tribe previous to this contribution contained 15 genera (Brailovsky 1987, 1988; Casini 1989; O'Shea 1980). Members of this tribe have the head subquadrate and strongly hypognathous anteriorly; the ocelli on prominent tubercles; a blunt tylus, slightly exceeding the juga; the hind femur armed; the hind tibiae sulcate, unarmed at apex, and lacking foliaceous dilations; the metathoracic peritreme with a single fused auricle; and the shape of spermatheca with the bulb elongate (Casini 1984, Packauskas 1994).

In this paper we add one new genus, and compare it with the genera *Euthochtha* Mayr, *Thlastocoris* Mayr, and *Zoreva* Amyot and Serville. *Moreyacoris* Casini is synonymyzed under *Beutelspacoris* Brailovsky.

The following abbreviations indicate institutions where specimens are deposited or which generously lent material: Colección Entomológica del Instituto de Biología, Universidad Nacional Autónoma de México (UNAM); National Museum of Natural History, Smithsonian Institution, Washington, D.C. (USNM).

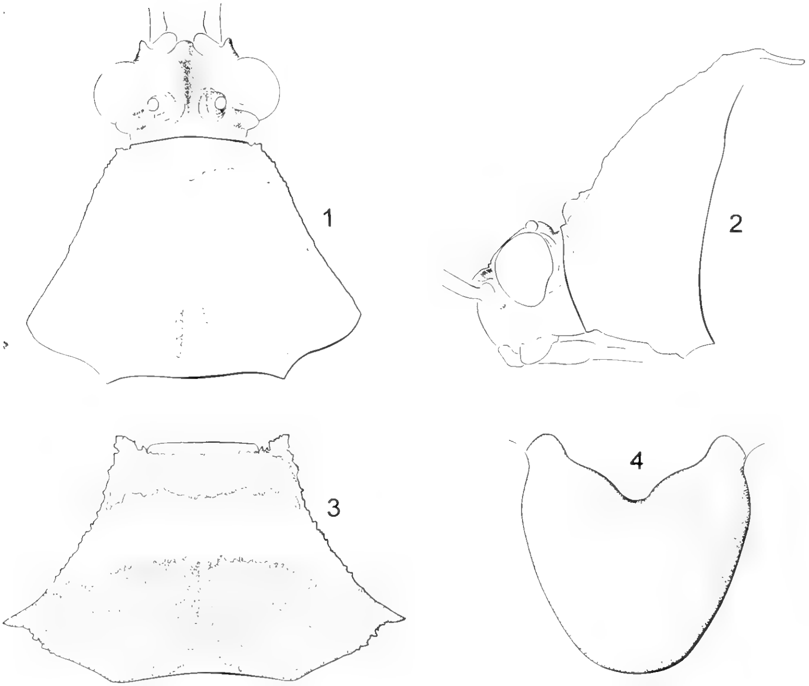
All measurements are given in millimeters.

Rondoneva Brailovsky and Barrera, new genus

Diagnosis.—This new genus is similar to *Euthochtha* Mayr and *Thlastocoris* Mayr in having the antenniferous tubercle armed laterally with a spine, the body length greater than 8 mm and less than 20 mm, and humeral angles of pronotum rounded.

The genus *Euthochtha* has the antennae long and slender; all femora ventrally armed; the hind femur incrassate and curved, especially in males; the hind tibiae flattened and armed with teeth along inner margin, especially in males; the pronotum steeply declivant; the mesosternum lacking a longitudinal median furrow; and the posterior lobe of male metapleuron bearing a large process that is absent in *Thlastocoris* and the new genus (Figs. 6, 10).

Thlastocoris has the antennae short and stout; the mesosternum with shallow longitudinal depression mesally; all femora at least slightly incrassate; the hind femur more incrassate, a little more in males than females; the hind femur ventrally armed;



Figs. 1–4. 1, Head and pronotum of *Rondoneva usta*, dorsal view. 2, Same, lateral view. 3, Pronotum, dorsal view, of *Zoreva dentipes* (F.). 4, Male genital capsule of *R. usta*, caudal view.

the fore and middle femora smooth or with short anteapical spine on ventral surface; the hind tibiae of females straight, slightly flattened, on males more flattened with widest part at midpoint, and armed with teeth along inner margin; and the pronotum shallowly declivant (Figs. 5, 11).

Rondoneva has the antennae long and slender; the mesosternum lacking a longitudinal median furrow; the fore and middle femora slender and unarmed; the hind femur slender and ventrally armed with short anteapical spines; the hind tibiae cylindrical, sulcate, slender and unarmed; and the pronotum shallowly declivant (Figs. 7, 9).

Zoreva Amyot and Serville, as well as *Rondoneva*, has the body relatively narrow and elongate, the antenniferous tubercle armed externally with a spine, the pronotum shallowly declivant, the fore and middle femora slender and cylindrical, the ocelli placed on prominent tubercles, and the antennae long and slender. In *Zoreva* the fore and middle femora are ventrally armed, the hind femur of male are curved, incrassate, and sometimes with sharp spine about ¼ from proximal end (hind femur of female relatively incrassate), the hind tibiae of male flattened, and armed with teeth along inner margin, and the humeral angles are produced laterally into narrow sharp spines (Figs. 3, 8).

Generic description.—Body medium sized, relatively narrow and elongate.

Head: Wider than long (across eyes), subquadrate, and strongly hypognathous anteriorly; tylus unarmed, apically globose, weakly raised, extending anteriorly to and laterally higher than juga; juga unarmed, laterally expanded and thickened; antenniferous tubercle broad, widely separated, and armed with distinct spine on external surface; antennal segment IV thickest, fusiform; segment I slender, cylindrical, slightly curved outward, and thicker than segments II and III which are cylindrical and slender; antennal segment II longest, III shortest, and I longer than IV; ocelli placed on prominent tubercles; eyes large sized, and fairly protuberant; postocular tubercle moderately protuberant; buccula rounded, short, raised, not projecting beyond antenniferous tubercle, without teeth, and closed posteriorly; rostrum reaching middle third of mesosternum; genae and mandibular plate unarmed.

Thorax: Pronotum wider than long, trapeziform, shallowly declivant; collar wide; frontal angles rounded or with blunt tubercle; anterolateral borders obliquely straight, and nodulose; humeral angles obtusely rounded; posterolateral borders sinuate, entire; posterior border straigth, entire; triangular process broad, apically subacute; calli transverse, and uniformly raised: Mesosternum lacking longitudinal furrow; anterior and posterior lobe of metathoracic peritreme equally prominent, resembling a single fused auricle (Figs 1–2).

Legs: Femora slender, at least slightly incrassate, and slightly broader than tibiae; fore and middle femora unarmed; hind femur ventrally armed with two rows of anteapical small teeth; tibiae unarmed, cylindrical, and sulcate; hind tibia slightly shorter than hind femur (Fig. 7).

Scutellum: Longer than wide, triangular, flat, with apex subacute.

Hemelytron: Macropterous, reaching or extending beyond apex of last abdominal segment; costal margin emarginate; apical margin almost obliquely straight.

Abdomen: Lateral margin parallel; posterior angle of connexivum unarmed, except for short and acute spine on connexival segment VI; abdominal spiracle rounded, close to anterior margin; abdominal sterna lacking medial furrow.

Integument: Body surface shining; pronotum, clavus, corium, propleuron, posterior margin of mesopleuron and metapleuron, and acetabula densely punctate; calli weakly and scattered punctate; head, connexivum, prosternum, mesosternum, metasternum, anterior third of mesopleuron and metapleuron, abdominal sterna, and male genital capsule impunctate; scutellum transversely striate and slightly punctate; dorsal surface glabrous; ventrally with few long bristlelike setae located on abdominal sterna; legs and antenna almost glabrous.

Male genitalia: Genital capsule broadly ovoid; posteroventral edge deeply concave, with lateral angles exposed and rounded (Fig. 4).

Female: Unknown.

Etymology.—Named for its occurrence in Rondônia, Brazil.

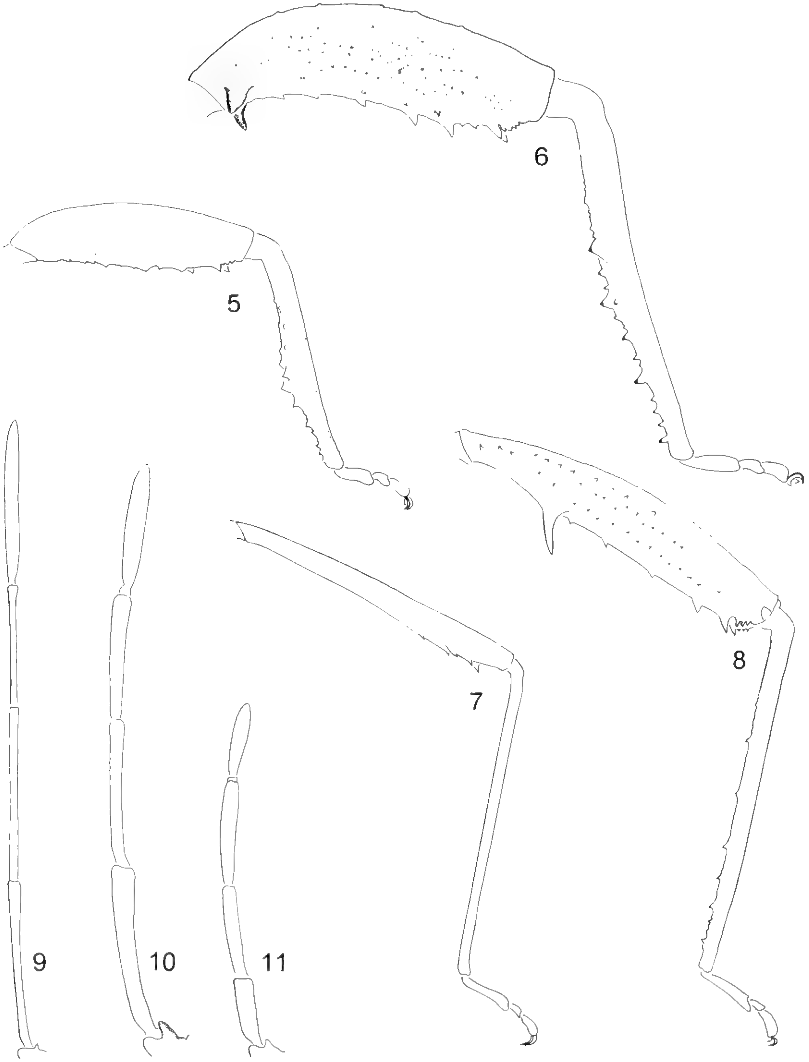
Type species.—*Rondoneva usta,* **new species.**

Rondoneva usta Brailovsky and Barrera, new species

(Figs. 1, 2, 4, 7, 9, 12)

Male.—*Measurements:* Head length 0.96; width across eyes 1.92; interocular space 0.93; interocellar space 0.45; length antennal segments: I, 2.84; II, 2.92; III, 2.12; IV, 2.72. Pronotum: Total length 2.88; width across frontal angles 1.76; width across humeral angles 3.56. Legs: Total length of hind femur 5.60; total length of hind tibia 5.30. Scutellar length 1.68; width 1.40. Total body length 13.85.

Dorsal coloration: Head pale chestnut orange; antennal segment I black with inner face yellow; segments II and III chestnut orange and IV reddish orange; pronotum chestnut orange with punctures reddish brown, and collar, calli, anterolateral and posterolateral margins and posterior margin



Figs. 5–11. 5–8, Hind legs. 5, *Thlastocoris laetus*. 6, *Euthochtha galeator*. 7, *Rondoneva usta*. 8, *Zoreva dentipes*. 9–11, Antennae. 9, *R. usta*. 10, *E. galeator*. 11, *T. laetus*.

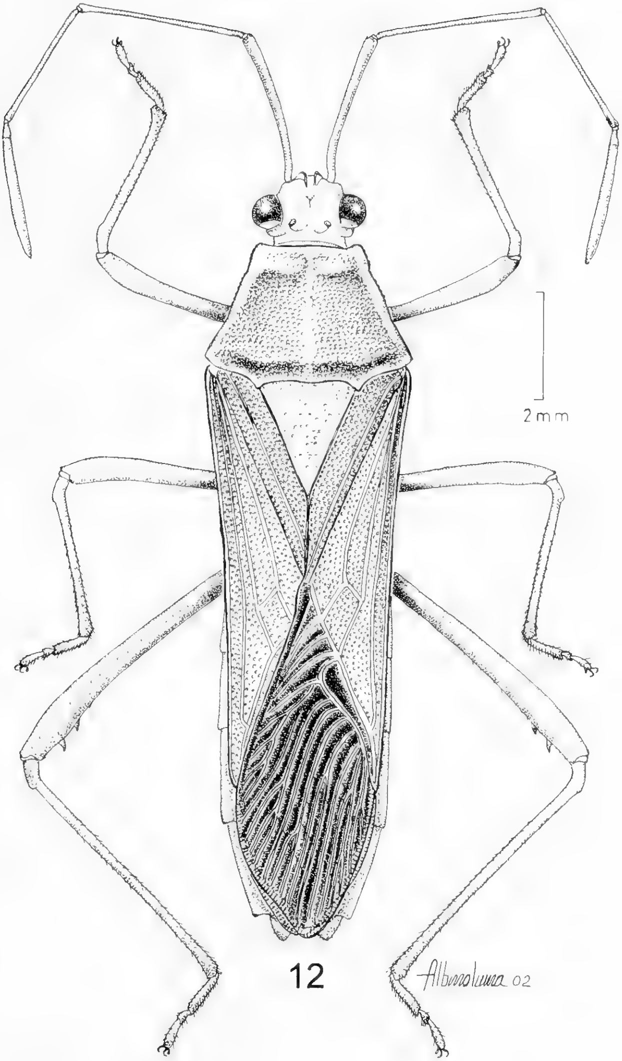


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Fig. 12. Dorsal view of *Rondoneva usta,* male.

dark yellow; pronotal disk with dark yellow longitudinal median stripe weakly visible; scutellum pale yellow; clavus and corium black to reddish brown with claval commissure, costal margin, apical margin, apical angle, and inner angle of endocorium close to claval commissure dark yellow; hemelytral membrane dark brown with basal angle black; connexival segments III to VI yellow, and VII orange to dark brown with posterior margin yellow; dorsal abdominal segments bright orange yellow with posterior third of segment VI and middle and posterior third of VII black. *Ventral coloration:* Included rostral segments (apex of IV black), metathoracic peritreme, coxae, trochanters and femora yellow; tibiae and tarsi bright orange yellow; genital capsule bright reddish orange; pleural margin of abdominal sterna III to VI with reddish orange longitudinal stripe located below the upper margin.

Female.—Unknown.

Type material.—Holotype: ♂, BRAZIL, Rondônia, 62 km SW Ariquemes, nr Fzda Rancho Grande, 3–15 December 1996, J. E. Eger (USNM). Paratypes: 2 ♂, BRAZIL, Rondônia, 62 km SW Ariquemes, nr Fzda Rancho Grande, 3–15 December 1996 J. E. Eger (UNAM, USNM).

Etymology.—The name is an arbitrary combination of letters and is to be treated as a noun.

Distribution.—Known only from the type locality in Brazil.

Beutelspacoris Brailovsky

Beutelspacoris Brailovsky 1987: 523–524.

Type species: *Beutelspacoris sanchezi* Brailovsky 1987. Orig. desig.

Moreyacoris Casini 1989: 25–26. **New synonym.**

Type species: *Moreyacoris dilatata* Casini 1989. Orig. Desig.

The genus *Beutelspacoris* was proposed by Brailovsky (1987) to include the species *B. sanchezi* collected in Santiago del Estero (Argentina). Later Casini (1989) described the genus *Moreyacoris* and included the species *M. dilatata* from Jujuy and La Rioja (Argentina). Examination of the type material of *Beutelspacoris* deposited in UNAM and the published drawings and description of *Moreyacoris* shows that both genera are the same and *Moreyacoris* is here synonymized under *Beutelspacoris*. We therefore offer the **new combination** *Beutelspacoris dilatata* (Casini).

ACKNOWLEDGMENTS

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VIBURNUM LEAF BEETLE, *PYRRHALTA VIBURNI* (PAYKULL) (COLEOPTERA: CHRYSOMELIDAE): DISPERSAL PATTERN OF A PALEARCTIC LANDSCAPE PEST IN NEW YORK AND ITS DISTRIBUTION STATUS IN THE NORTHEASTERN U.S. AND EASTERN CANADA

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Abstract.—Pyrrhalta viburni, a chrysomelid leaf beetle native to Eurasia, was first detected in central New York in 1996, and since has been spreading throughout the state. Distribution records are given and mapped for this *Viburnum*-feeding specialist in New York, Pennsylvania, Ohio, and Vermont. By summer of 2002, *P. viburni* had been recorded from 33 counties in New York, and its subsequent spread throughout a larger portion of the U.S. can be anticipated. In addition to feeding on several species of cultivated viburnums, the beetle also thrives on the native *Viburnum dentatum* var. *lucidum* (arrowwood), a widely occurring understory shrub in northeastern North America. The dispersal of *P. viburni* in New York has largely followed the distribution of its host plants, which leads us to predict that future spread will proceed most quickly through habitats contiguous with the current distribution of the pest and containing denser stands of *V. dentatum* var. *lucidum* or other native and cultivated viburnums that are suitable hosts for *P. viburni.* We also summarize the current distribution of *P. viburni* in neighboring states of the northeastern U.S. and in provinces of eastern Canada, based on personal communications with entomologists most acquainted with this ornamental and nursery pest.

Key Words: Coleoptera, Chrysomelidae, *Pyrrhalta viburni,* viburnum, invasive insects

Pyrrhalta viburni (Paykull), known commonly as the viburnum leaf beetle, is an urban landscape and nursery pest originally from Europe and Asia that is quickly spreading throughout the northeastern U.S. and eastern Canada. Although *P. viburni* was first detected in the Niagara Peninsula of Ontario (Fonthill) in 1947 (Sheppard 1955), established breeding populations were not documented until the late 1970's in the Ottawa-Hull regions of Ontario and Quebec, respectively (Becker 1979). In Canada, the beetle apparently spread slowly, reaching the Maritime Provinces by the early to mid 1990s (Wheeler and Hoebeke 1994) and in Maine by 1994 (Richard Dearborn, personal communication). It was recently detected in British Columbia (Anonymous 2001, Gillespie 2001) where viburnums in the Barnaby and Vancouver regions have been heavily infested (Robert Costello, personal communication). We report here the spread of *P. viburni* within New York following its initial detection in 1996, through 2002, when it had been recorded in 33 counties and had begun to expand its range to states bordering on the east and south.

The only known hosts for *P. viburni* are deciduous shrubs and small trees in the genus *Viburnum.* Viburnums are among our most important landscape shrubs because of their wide geographical adaptation, their versatility as functional landscape plants, and their visual qualities (Flint 1999). Approximately 150 species of *Viburnum* grow in the wild, most of them in temperate regions of Asia, Europe, and North America (Flint 1999). A number of native viburnums, such as *Viburnum dentatum* L. and its many varieties (arrowwood), *V. lentago* L. (nannyberry), *V. prunifolium* L. (northern black haw), *V. acerifolium* L. (maple-leaved viburnum), *V. rafinesquianum* Schultes (rafinesque or downy arrowwood), and *V. trilobum* Marsh. (American cranberrybush), and the introduced *V. opulus* L. (European cranberrybush) are favorite and highly susceptible hosts of *P. viburni* (Weston et al. 2000). Arrowwood (*V. dentatum*) is a variable species, growing wild over an immense range in eastern North America (Flint 1999); several natural varieties exist, differing in ultimate size and cold hardiness. In the northeastern U.S. and eastern Canada, *V. dentatum* L. var. *lucidum* Aiton (formerly known as *V. recognitum* Fernald, northern arrowwood) is the most northern of the "*dentatum* complex" populations, growing from New Brunswick, Canada, to Ohio and south to the mountains of northern Georgia (Flint 1999). It is this understory variety, occurring in low wet situations such as swampy woods and thickets (Soper and Heimburger 1982), that is so susceptible to attack and decimation by viburnum leaf beetle in the Northeast.

Adults and larvae of *P. viburni* can strip the leaves of viburnums in a relatively short period of time in outbreak situations. However, species of *Viburnum* differ greatly in their susceptibility to attack by *P. viburni*. Some species, notably arrowwood (*V. dentatum* var. *lucidum*) and the cranberrybush viburnums (*V. trilobum* and *V. opulus*), can be completely defoliated by the larvae and adults and killed after only a few years of repeated infestation, while others, especially leatherleaf (*V.* × *rhytidophylloides* J. Sur.) and Koreanspice viburnums (*V. carlesii* Hemsl.) and their relatives, are virtually immune (Weston et al. 2000, Weston and Desurmont 2002). Detailed information on the biology and seasonal history of *P. viburni* in North America is given by Becker (1979), while recognition features can be found in Wheeler and Hoebeke (1994).

One of us (ERH) has been conducting annual collecting survey trips to high-risk areas in the Northeast since the late 1970s with the intent to detect recently arrived exotic pests such as *P. viburni*. We are quite confident that the first breeding populations of the beetle were not present in New York much before 1996, if at all. We present here data regarding the spread of the beetle following its initial detection in New York State, offer an hypothesis to explain its dispersal in relation to native host plants, and make predictions concerning likely future range expansion.

DISPERSAL PATTERN

The initial detection of *P. viburni* in New York was in July of 1996 at Fair Haven Beach State Park, located in northern Cayuga County on the south shore of Lake Ontario (Fig. 1). Later that same summer, the beetle was found in Monroe, Niagara, Orleans, and St. Lawrence counties, and again at localities adjacent to the south shore of Lake Ontario and along the St. Lawrence Seaway (see distribution data below for details). Table 1 lists New York counties from which the beetle has been detected to date, and all collection sites are mapped in Fig. 1.

The most striking aspect of the invasion, or dispersal, sequence by *P. viburni* in New York is the bias for the beetle to be found in low-lying areas, especially near large bodies of fresh water. The initial detections in 1996 were sites in counties adjacent to the southern shore of Lake Ontario and the St. Lawrence Seaway. By 1998, the beetle was found in Wayne County, also bordering Lake Ontario. Also in the same year (1998), a number of the newly infested counties were confirmed, each bordering Lake Ontario, Lake Erie, or the St. Lawrence Sea-

Fig. 1. Map of New York showing current geographic range of *P. viburni* (open circles) as well as elevation contours. The northeast border of the state is almost entirely composed of major bodies of water including, from southwest to northeast, Lake Erie, Lake Ontario, and the St. Lawrence Seaway. Adjacent regions of Ohio, Pennsylvania, and Vermont are also included, with known collection sites for *P. viburni*. These images are from a CD-ROM collection of royalty-free maps by Map Resources Premier USA (http://www.mapresources.com).

Table 1. Detection of *Pyrrhalta viburni* in counties of New York following its initial detection in Cayuga County in 1996.

Year	County	Year	County
1996	Cayuga	1999 (cont'd)	Cortland
	Monroe		Essex
	Orleans		Madison
	Niagara		Oneida
	St. Lawrence		Onondaga
1998	Erie		Schuyler
	Franklin		Steuben
	Genesee		Tompkins
	Jefferson		Wyoming
	Livingston		Yates
	Ontario	2000	Tioga
	Oswego		Herkimer
	Seneca	2002	Allegany
	Wayne		Broome
1999	Chautauqua		Cattaraugus
	Clinton		Chemung
			Chenango

way, and a number of sightings were in counties bordering the previously infested counties, along larger inland bodies of water such as the Finger Lakes, or both (Fig. 1). This pattern of spread inland and along large bodies of water has continued during the period of 1999 to 2002; in 2000, the beetle was also discovered (by ERH) infesting native stands of *Viburnum* at Presque Isle State Park, Erie County, Pennsylvania (bordering Lake Erie and Chautauqua County, NY) and in Burlington, Chittenden County, Vermont (across Lake Champlain from Clinton and Essex Counties, NY). In late July 2002, ERH found a small population infesting native *V. dentatum* in Conneaut, Ohio (Ashtabula Co.), a lakefront community along the shore of Lake Erie in the very northern corner of the state adjacent to the Pennsylvania border. We believe this pattern is not merely coincidental, but instead can be largely attributed to the distribution of arrowwood (*V. dentatum* var. *lucidum*), a highly suitable, native host plant. This understory viburnum is found in a variety of habitats, but appears to prefer shaded, wetland areas along rivers and lakes. Comparing the distribution of freshwater wetlands with the recorded collections of *P. viburni,* one can see a fairly close correspondence between the two (Fig. 1). This leads us to predict that *P. viburni* will spread most quickly from its current distribution to adjacent areas that are favorable habitats for *V. dentatum* var. *lucidum.* In New York, this would include primarily the Mohawk River and Hudson River valleys. We would also expect the spread to continue fairly rapidly along the southern shore of Lake Erie into northern Ohio and Michigan. Ultimately, we might anticipate *P. viburni* to occupy most of the range of *V. dentatum* var. *lucidum* in the U.S. and Canada and perhaps beyond, but it is not clear if this landscape pest will be able to thrive in the hotter extremes of the range of *V. dentatum* var. *lucidum.* The distribution of this arrowwood variety will probably not be the major limiting factor in determining the eventual spread of *P. viburni* to more southern regions in the U.S.; the closely related *V. dentatum* L. var. *scabrellum* Torr. & Gray (rough arrowwood), distributed throughout the southeastern U.S. including Florida to Texas (cited as *V. dentatum* in Texas A&M Bioinformatics Working Group 1999), and *V. dentatum* var. *dentatum* Aiton (downy arrowwood), known from New Jersey to Florida and Texas, will, in all likelihood, serve as suitable hosts for *P. viburni.*

GEOGRAPHIC DISTRIBUTION

Here we provide distribution records of *P. viburni* from numerous New York localities (Fig. 1), based mainly on our collecting and observations, and those of a few others. At most sites, only adults were collected/beaten from viburnum foliage; however, at a few locations larvae also were observed and collected. Voucher specimens of adults and larvae have been deposited in the Cornell University Insect Collection, Ithaca, NY. Unless otherwise stated, most collections were made by the junior author (ERH); all collections made from *V. dentatum* actually refer to the var. *lucidum* (formerly known as *recognitum*).

NEW YORK: *Allegany Co.*, Alfred, Alfred State College, 30 May 2002, ex *V. dentatum.* Broome Co., Binghamton, Binghamton University, 13 June 2002, ex *V. dentatum* and *V. trilobum*; Vestal, Vestal Parkway West (Rt. 434), 13 June 2002, ex *V. dentatum*; Whitney Point, 13 June 2002, ex *V. trilobum.* Cattaraugus Co., Olean, St. Bonaventure University, 30 May 2002, ex *V. dentatum. Cayuga Co.*, Fair Haven, Fair Haven Beach St. Pk., 5 July 1996, 24 July 1996, ex *V. dentatum*; Auburn, 2 June 2000, ex *V. trilobum.* Chautauqua Co., southwest of Van Buren Point, Lake Erie St. Pk., 5 August 1999, ex *V. dentatum,* P. Weston and ERH; Fredonia, SUNY Fredonia, 5 August 1999, ex *V. dentatum,* P. Weston and ERH. Chemung Co., Newtown Battlefield, Rt. 17. 13 June 2002, ex *V. dentatum.* Chenango Co., Bainbridge, General Clinton Park, 13 June 2002, ex *V. dentatum.* Clinton Co., Plattsburgh, 27 May 1999, Amy D. Ivy, ex *V. opulus.* Cortland Co., Cortland, SUNY Cortland, 29 July 1999, ex *V. trilobum.* Erie Co., East Aurora, 21 August 1998, ex *V. dentatum*; Grand Island, 21 August 1998, ex *V. trilobum*; Wales Center, 21 August 1998, ex *V. trilobum.* Franklin Co., 1 mi. W. of Malone (First Natl. Bank), 20 August 1998, ex *V. trilobum*; Paul Smiths, 10 June 1999, Amy D. Ivy. Franklin/Essex Cos., Saranac Lake, 10 June 1999, Amy D. Ivy. Genesee Co., Alexander, 10 May 1998, ex *V. trilobum*; Pembroke Travel Plaza (Corfu), Rt. 90, 21 August 1998, ex *V. dentatum.* Herkimer Co., Indian Castle Travel Plaza (Little Falls), Rt. 90, 21 July 2000, ex *V. trilobum* Jefferson Co., Selkirk Shores St. Pk., 18 August 1998, ex *V. dentatum*; Southwick Beach St. Pk., 18 August 1998, ex *V. dentatum*; Westcott Beach St. Pk., 18 August

1998, ex *V. dentatum*; Burnham Point St. Pk., 18 August 1998, ex *V. trilobum*; Watertown, Rt. 11 nr. hospital, 20 August 1998, ex *V. dentatum*. Livingston Co., Geneseo, SUNY Geneseo campus, 21 August 1998, ex *V. trilobum*. Madison Co., Cazenovia, nr. lake park, 29 July 1999, ex *V. trilobum*; Hamilton, Colgate University campus, 29 July 1999, ex *V. trilobum*. Monroe Co., Hamlin, 6 July 1996, 12 July 1996, ex *V. dentatum*; east of Hamlin Beach St. Pk., along parkway, 12 July 1996, 28 August 1996, ex *V. dentatum*; Hamlin Beach St. Pk., 12 July 1996, ex *V. dentatum*; Lakeside Beach St. Pk., 12 July 1996, 28 August 1996, ex *V. dentatum*; Braddock Bay Park, 28 August 1996, ex *V. dentatum*; Scottsville, Scottsville Travel Plaza (Scottsville), Rt. 90, 21 August 1998, ex *V. trilobum*; Spencerport, 7 August 1999, ex *V. trilobum*; Webster, 14 July 1997, Cincy Kindle, ex. *V. dentatum*. Niagara Co., nr. Olcott, 28 August 1996, ex *V. dentatum*; Niagara Falls, 7 June 1997, 16 May 1998, ex *V. trilobum*. Oneida Co., Clinton, Hamilton College campus, 29 July 1999, ex *V. trilobum*; Oneida Travel Plaza (Westmoreland), Rt. 90, 21 July 2000, ex *V. trilobum*. Onondaga Co., Syracuse, Syracuse Univ. campus (Walnut Place at Waverly St.), 3 June 1999, ex *V. trilobum*; Marcellus, 4 June 2000, ex *V. trilobum*; Tully, 4 June 2000, ex *V. dentatum and V. trilobum*; Fayetteville, 17 June 2000, Howard Deutch, ex *V. trilobum*. Ontario Co., Clifton Springs Travel Plaza (Clifton Springs), Rt. 90, 21 August 1998, ex *V. dentatum*; West Bloomfield, 21 August 1998, ex *V. trilobum*; Canandaigua, Finger Lakes Community College campus, 21 August 1998, ex *V. dentatum*; Geneva, Hobart & Smith College, 30 May 1998, 18 August 1998, ex *V. dentatum*; Gorham, 29 May 1998, Brian Eshenaur, ex *V. dentatum*; Honeoye, 29 May 2000, ex *V. trilobum*. Orleans Co., Albion, 1 September 1996; Golden Hill St. Pk., 12 July 1996, 28 August 1996. Oswego Co., Oswego, SUNY Oswego campus, 30 May 1998, 18 August 1998, ex *V. trilobum* and *V. dentatum*; Oswego, Port of Oswego Authority, 18 August 1998, 6 June 2001, ex *V. trilobum*. Schuyler Co., Watkins Glen, Watkins Glen St. Pk., 26 August 1999, ex *V. trilobum*. Seneca Co., East Varick, Rt. 89 (Lakeshore Landscaping), 12 October 2000, ex *V. dentatum*; Geneva, Seneca Lake St. Pk., 21 August 1998, ex *V. trilobum* and *V. dentatum*; East of Seneca Falls, Cayuga Lake St. Pk., 21 August 1998, 25 August 1999, 6 June 2001, ex *V. trilobum*; Seneca Falls (Outlet Factory Mall), 29 May 2000, ex *V. trilobum*. St. Lawrence Co., Ogdensburg, public library, 11 August 1996, 31 May 1997, 19 August 1998; Canton, SUNY Canton, 11 August 1996, 31 May 1997, ex *V. dentatum*; Canton, St. Lawrence University campus, 20 August 1998, ex *V. dilatatum*?; Pottsdam, Clarkson Univ. campus, 11 August 1996, 20 August 1998, ex *V. dentatum*; Gouverneur, 12 August 1996, 31 May 1997, 20 August 1998, 3 June 2000, ex *V. dentatum* and *V. trilobum*; Massena, Robert Moses St. Pk., 20 August 1998, ex *V. trilobum;* Wanekena, SUNY Forestry School, 2 June 2000, ex *V. dentatum*. Steuben Co., Lawrenceville, 20 August 1998, ex *V. trilobum*; nr. Dansville, Stony Brook St. Pk., 5 August 1999, P. Weston and ERH, ex *V. trilobum*. Tioga Co., Owego, Tioga County Fairgrounds, 24 May 2000, ex *V. dentatum*. Tompkins Co., Ithaca, Buttermilk Falls St. Pk., 3 September 1999, ex *V. trilobum*; Trumansburg, nr. laudromat, 31 July 1999, 21 August 1999, 3 June 2001, ex *V. trilobum* and *V. dentatum*; Ithaca, Cornell University campus, 10 August 1999, ex *V. trilobum*; Varna, 31 May 2000, ex *V. trilobum*. Wayne Co., Clyde, 11 October 2000, ex *V. dentatum*; Wolcott, 30 May 1998, 18 August 1998, ex *V. trilobum*; East Bay Park, 29 May 1998, Dawn D. O'Brien, ex *V. dentatum*. Wyoming Co., Portageville, south end of Letchworth St. Pk., 5 August 1999, P. Weston and ERH, ex *V. trilobum*. Yates Co., Bellona Sta., 8 June 1999, ex *V. trilobum*, Gary Chicoine.

Status of *P. Viburni* in Other Eastern U.S. States and Eastern Provinces of Canada

Collections made by ERH during the period of 2000–2002 also confirmed the spread of *P. viburni* into Pennsylvania, Ohio, and Vermont, where viburnum leaf beetle was not known to occur previously. The new locality data for Ohio, Pennsylvania and Vermont are as follows: OHIO: Ashtabula Co., Conneaut, 19 July 2002, ex *V. dentatum*. PENNSYLVANIA: Bradford Co., Sayre, Gene Paluzzi Memorial Riverfront Park, 13 June 2002, ex *V. dentatum*. Erie Co., Erie, Presque Isle St. Pk., 24 August 2000, ex *V. dentatum*. McKean Co., Bradford, University of Pittsburgh-Bradford, 30 May 2002, ex *V. dentatum*; Smethport, McKean County Courthouse, 30 May 2002, ex *V. dentatum*. Potter Co., Denton Hill State Park, ski area, Rt. 6, 30 May 2002, ex *V. dentatum*. VERMONT: Chittenden Co., Burlington, Univ. of Vermont campus, 24 July 2000, ex *V. trilobum*; Burlington, Leddy Park, 24 July 2000, ex *V. trilobum*..

In the United States, *P. viburni* was first discovered in Maine as early as 1994; it was reported in a June 8, 1994 update on "Forest & Shade Tree Insect & Disease Conditions for Maine" that *P. viburni* was observed in the Portland area (Cumberland Co.), especially on maple-leaved viburnum (*V. acerifolium* L.). In this update on insect and disease conditions, populations of the beetle were reported to be "locally heavy," that "many shrubs had already been stripped," and that this was "at least the second year of such activity according to local reports." By July 24, 1994, viburnum leaf beetle was also reported from the Waterville area (Kennebec Co.). Presently, *P. viburni* is widely distributed in Maine, but is most abundant in areas south of a line drawn roughly through Rangeley (Franklin Co.), Greenville (Piscataquis Co.) and Millenocket (Penobscot Co.). It is also known as far north as Presque Isle on the east side of the state in Aroostock County (Richard Dearborn, personal communication). To date, *P. viburni* has not been reported from New Hampshire, although there is an unconfirmed sighting of damage several years ago (about 1997) on the eastern border with Maine at Eaton (= town name for Eaton Center) or Freedom (Carroll Co.) (Alan Eaton, personal communication). In spite of efforts by entomologists to locate *P. viburni* in Massachusetts, it is still unreported from that state (Craig Hollingsworth, personal communication). Since its discovery in Burlington, Vermont in the summer of 2000 (by ERH), *P. viburni* is now well established and causing significant damage to viburnums (*V. trilobum* and *V. dentatum* in particular), especially in the lake-bound areas of Grand Isle Co. (North Hero and other localities) and in at least six northern and central counties of Vermont (Margaret Skinner, personal communication); southern counties of the state have not been well surveyed for *P. viburni* and therefore, there are no records to date (Scott Pfister, Trish Hanson, personal communication). However, there is an unconfirmed sighting of foliage damage by *P. viburni* in Rutland County, across from Whitehall, New York (Washington Co.) (Scott Pfister, personal communication).

Pyrrhalta viburni has been expanding its range in the eastern Canadian provinces as well. Throughout most of southern Ontario, including the major population centers of Hamilton, Burlington, and Toronto, *P. viburni* has been considered a significant landscape pest of ornamental viburnums as well as of the native understory species (Steve Marshall, Christine Blaser, personal communication). Likewise, *P. viburni* is apparently widespread in southern Quebec, including the Montreal area (Terry Wheeler, personal communication). Based on several annual collecting surveys trips to the Canadian Maritime provinces made during the period 1993–2001 by ERH, *P. viburni* was found to be relatively common throughout the coastal area of New Brunswick between

Saint John and St. Stephen, as well as in Fredericton, and also in Halifax, Nova Scotia (Wheeler and Hoebeke 1994), and Charlottetown, Prince Edward Island (E. R. Hoebeke, unpublished data).

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Note added in proof.—Since preparing the original manuscript, *P. viburni* has been detected in two new counties in New York State (Albany and Rensselaer counties), apparently the result of transportation of infested nursery stock (Chuck Schmidt, Cornell Cooperative Extension, Albany, NY).

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A NEW SPECIES OF THE GENUS *ALLANTUS* PANZER (HYMENOPTERA: TENTHREDINIDAE) FEEDING ON *RHODODENDRON RETICULATUM* D. DON (ERICACEAE) IN JAPAN

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Abstract.—***Allantus rhododendri*, n. sp.**, from Japan is described and illustrated. It was reared from larvae feeding on *Rhododendron reticulatum* D. Don (Ericaceae). A key is provided for the eight Japanese species of *Allantus.*

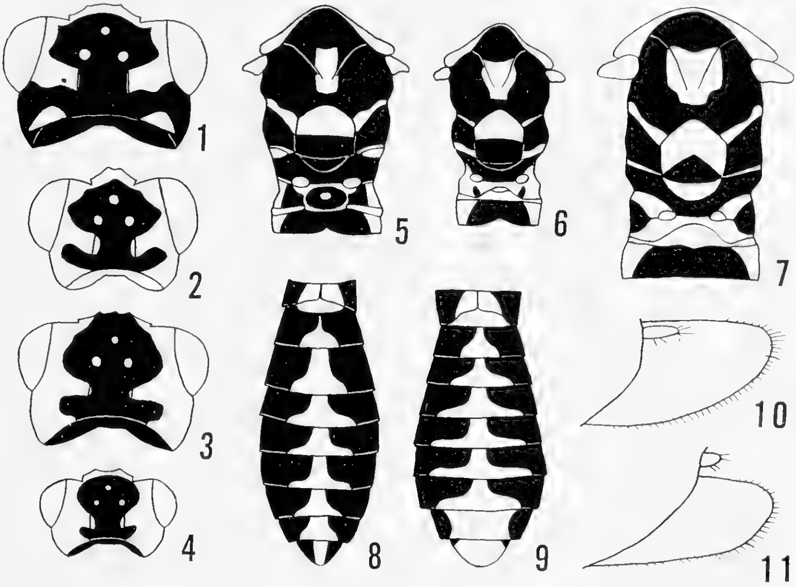
Key Words: Tenthredinidae, Allantinae, *Allantus,* new species, food plant, *Rhododendron reticulatum*

Allantus Panzer (Allantinae), is a Holarctic genus with about 35 species. Seven species are listed for Japan by Abe and Togashi (1989): *A. albicinctus* (Matsumura 1912), *A. basalis* (Klug 1814), *A. calliblepharus* (Konow 1900), *A. luctifer* (Smith 1874), *A. meridionalis* Takeuchi 1933, *A. nakabusensis* Takeuchi 1929, and *A. nigrocaeruleus* (Smith 1874). However, the genus has not been revised, and there is no key to Japanese species. The most common larval food plants are the Rosaceae, but Polygonaceae, Fagaceae, and Salicaceae also have been recorded. Okutani (1967) recorded the host plants for *A. albicinctus, A. meridionalis,* and *A. nakabusensis* as Rosaceae, and *A. luctifer* and *A. nigrocaeruleus* as Polygonaceae.

I had the opportunity to examine specimens of an *Allantus* which were reared from larvae feeding on the leaves of *Rhododendron reticulatum* D. Don (Ericaceae) from Kyoto Prefecture, through the courtesy of S. Sugiura. These specimens differed from the recorded Japanese species and the species recorded in the European and North American literature (e.g., Benson 1952, Smith 1979, Taeger 1986). They most resemble *A. nakabusensis* from Japan and *A. viennensis* (Schrank) from Europe and North America. Coloration and characters of the lancet, however, separate this species. Thus, I concluded that the specimens from *Rhododendron* represent a new species, and I describe it here and give a key to the Japanese species.

Key to Females of Japanese Species of *Allantus*

1. Nervulus interstitial with basalis in forewing (Fig. 22) 2
– Nervulus not interstitial with basalis in forewing (Fig. 23) 4
2. Wings infuscate or forewing with an infuscated spot below stigma 3
– Wings hyaline (lateroposterior corner of pronotum, lateral sides of coxae, lateroposterior corner of 5th and 6th abdominal tergites, central portion of 8th and 9th tergites and 4th to 7th sternites milky white) . . . . *nigrocaeruleus* (Smith)
3 Wings infuscate; labrum black; lateroposterior corner of 3rd to 5th abdominal tergites milky white . . . . *luctifer* (Smith)
– Wings hyaline with an infuscated spot below stigma (Fig. 26); labrum white; 1st abdominal tergite, posterior half of 5th abdominal tergite, and apical two abdominal tergites white . . . . *calliblepharus* (Konow)
4. Head mostly yellow with frontal area, postocellar area, and rather small macula on postocular area black; mesonotum with small yellow



Figs. 1–11. 1–4, Head, dorsal view. 1, *Allantus rhododendri,* female. 2, *A. rhododendri,* male. 3, *A. nakabusensis,* female. 4, *A. nakabusensis,* female. 5–7, Thorax. 5, *A. rhododendri,* female. 6, *A. rhododendri,* male. 7, *A. nakabusensis,* female. 8–9, Abdomen, dorsal view. 8, *A. rhododendri,* female. 9, *A. nakabusensis,* female. 10–11, Sawsheath, lateral view. 10, *A. rhododentri.* 11, *A. nakabusensis.*

macula; abdominal tergites with inverted T-shaped white maculae (Figs. 8–9) 5

– Head and mesonotum black; abdomen mostly black with white band or macula 6

5\. Mesoscutellum mostly yellow (Fig. 7); mesoscutellar appendage yellow (Fig. 7); lateral sides of 1st to 8th tergites yellow; 8th tergite with rectangular white macula (Fig. 9); 9th tergite mostly white (Fig. 9) . . . *nakabusensis* Takeuchi

– Anterior half of mesoscutellum yellow and posterior half black (Fig. 5); mesoscutellar appendage black (Fig. 5); lateral sides of 1st to 8th tergites black; 8th tergite with inverted T-shaped macula (Fig. 8); last tergite with median longitudinal yellow macula . . . . *rhododendri,* n. sp.

6\. Head in dorsal view dilated behind eyes; head black with small white spot on inner orbit, labrum brown; outer side of foretibia white; tegula white . . . . *basalis* (Klug)

Head in dorsal view parallel behind eyes; head black, labrum brown; inner surface of foretibia light brown; tegula black 7

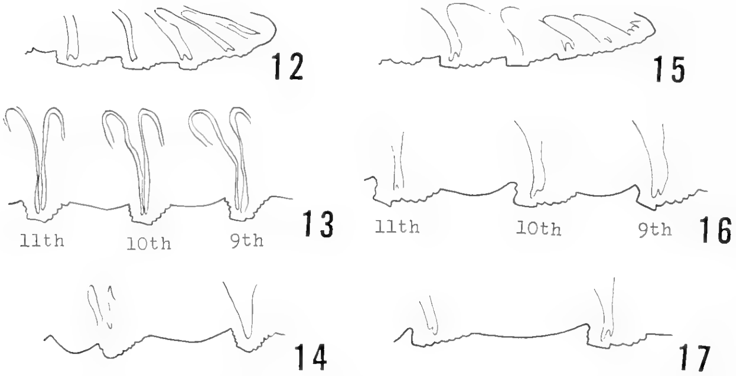
7\. Hind tibia entirely black; sawsheath more rounded in lateral view (Fig. 24) . . . . *albicinctus* (Matsumura)

– Basal portion of hind tibia white; sawsheath truncate at apex in lateral view (Fig. 25) . . . . *meridionalis* Takeuchi

Allantus rhododendri Togashi, new species

(Figs. 1–2, 5–6, 8, 10, 12–14, 18, 20)

Female.—Length, 7 mm. Head black with following yellow: labrum, clypeus, basal half of mandible, malar space, lower portion of gena, anterior margin of supraclypeal area, inner orbits, anterior third of postocular area, and triangular-like macula on posterior portion of postocular area (Fig. 1). Thorax black with following yellow: la-

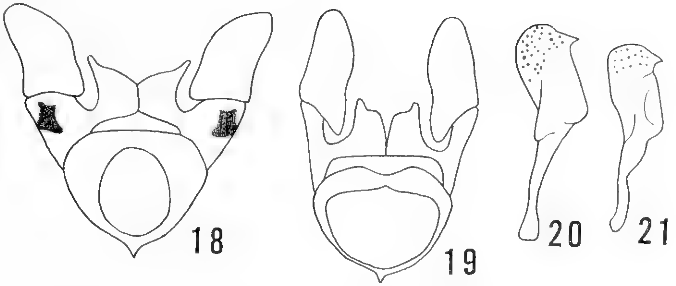


Figs. 12–17. Female lancet. 12–14, *Allantus rhododendri*. 12, Apical portion. 13, 9th to 11th serrulae. 14, basal 2 serrulae. 15–17, *A. nakabusensis*. 15, Apical portion. 16, 9th to 11th serrulae. 17, basal 2 serrulae.

teroposterior portion of pronotum, tegula, posterior portion of median lobe of mesoscutum, subquadrate macula on central portion and posterior side of lateral lobe of mesoscutum, anterior half of mesoscutellum, cenchrus, elliptic macula on metascutellum, lateroanterior corner of postnotum of mesothorax, lateral side of metascutum and postnotum of mesothorax (Fig. 5), and perapteron. Abdominal tergites black with following yellow: lateral side of 1st to 8th tergites, central portion of 1st and last tergites, inverted T-shaped maculae on 2nd to 8th tergites (Fig. 8), and cercus. Abdominal sternites yellow and basal plates mostly yellow. Antenna black with lateroventral side of basal two segments yellow. Wings hyaline; basal portion of stigma and apical portion of subcosta of forewing yellow, other veins dark brown to black. Legs yellow with following dark brown to black: forecoxa except for yellow inner side, apical half of outer side of fore- and midfemora, apical half of outer and inner sides of hind femur, apical ⅔ of tibiae, fore- and midtarsi, apical half of hind basitarsus, and apical hind tarsal segment.

Head from above transverse (Fig. 1); OOL:POL = 1.6:1.0; postocellar area pentagonal; circumocellar furrow distinct; interocellar furrow distinct and deep; postocellar and lateral furrows distinct; frontal area nearly flattened; median fovea deep and circular in outline; lateral fovea distinct and circular in outline, connected with antennal furrow; antenno-ocular distance slightly shorter than distance between antennal sockets; supraclypeal area slightly raised; clypeus moderately convex, anterior margin rather deeply emarginate, lateral lobe triangular; labrum nearly flattened, obtusely angled apically, malar space shorter than diameter of front ocellus; occipital carina defined. Antenna slightly longer than costa of forewing; relative lengths of segments about 1.9:1.0:3.8:3.2:2.8:1.8:1.4:1.4:1.4; pedicel length:width about 1.0:0.6; 3rd segment 1.2× length of 4th segment. Thorax with mesoscutellum nearly flattened; cenchrus small, distance between cenchri longer than width of one. Hind wing with petiole of anal cell shorter than nervulus; without middle cell. Legs with hind basitarsus nearly as long as following four segments combined. Sawsheath as in Fig. 10; lancet as in Figs. 12–14; serrulae of lancet trapezoidal (Fig. 13). Punctation: Head, thorax, and abdominal tergites covered with fine setigerous punctures, shining.

Male.—Length, 6 mm. Head yellow with



Figs. 18–21. Male genitalia. 18, *Allantus rhododendri*, genital capsule. 19, *A. nakabusensis*, genital capsule. 20, *A. rhododendri*, penis valve. 21, *A. nakabusensis*, penis valve.

following black: posterior half of frontal area, ocellar area, postocellar area, and rectangular spot on postocular area (Fig. 2); apical half of mandible black. Antenna with scape and basal 1/3 and ventral surface of pedicel yellow; dorsal surface of pedicel and 3rd to last segments dark brown to black; ventral surface of 3rd to last segments yellowish brown. Thorax black with following yellow: pronotum, tegula, posterior half of median lobe and V-shaped macula on central portion of lateral lobe of mesoscutum, posterior side of lateral lobe of mesoscutum, anterior half of mesoscutellum, mesoscutellar appendage, metascutum, metascutellum, lateral side of postnotum of metathorax. Abdominal tergites black with following yellow: lateral sides of all tergites, semicircular macula on 1st tergite, subrectangular macula on 2nd tergite, most of 3rd and 4th tergites, inverted T-shaped macula on 5th to last tergites; all sternites yellow.

Antennal, thoracic, and punctation structures similar to those of female except for sexual segments. Genitalia as in Fig. 18; penis valve as in Fig. 20.

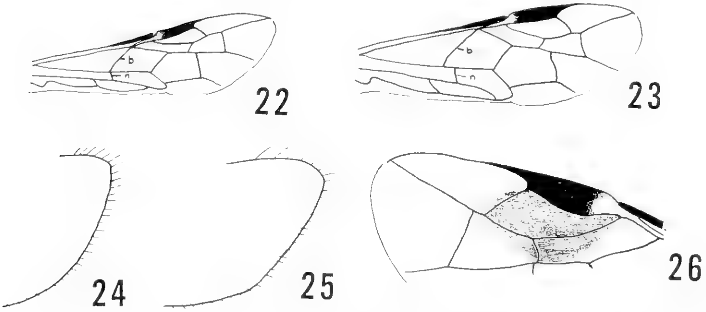
Distribution.—Japan (Honshu).

Food plant.—*Rhododendron reticulatum* D. Don (Ericaceae).

Holotype.—Female, emerged on 17.IX. 1999 from larva feeding on leaves of *Rhododendron reticulatum,* Kamigamo, Kyoto City, Kyoto Prefecture, S. Sugiura leg. Deposited in the National Science Museum (Natural History), Tokyo.

Paratypes.—Same data as holotype, except emerged 18.IX.1999 (1 ♀, 1♂), emerged 29.X-1999 (2 ♀). Deposited in the collection of the National Science Museum (Natural History), Tokyo (2 ♀, 1 ♂) and the National Museum of Natural History, Smithsonian Institution, Washington, DC (1 ♀).

Remarks.—This new species is separated from most Japanese species of *Allantus* by the nervulus not intersitial with the basalis in the forewing (Fig. 23), the mostly yellow head, and the abdominal tergites with inverted T-shaped white maculae. It appears most similar to *A. nakabusensis* and *A. viennensis.* The female is distinguished from *A. nakabusensis* by the black mesoscutellar appendage (yellow in *A. nakabusensis*), by the mostly black metascutellum (entirely yellow in *A. nakabusensis,* see Figs. 5, 7), by the yellow mesopleuron (black with the mesepimeron yellow in *A. nakabusensis*), by the shape of the sawsheath (see Figs. 10–11), and the structure of the lancet (see Figs. 12–17). The male of *A. rhododendri* is separated from that of *A. nakabusensis* by the coloration of the occiput and by the structure of the harpes, parapenis, and penis valve (see Figs. 18–21).



Figs. 22–26. 22–23, Forewing (b = basalis; n = nervulus). 22, *Allantus luctifer*. 23, *A. meridionalis*. 24–25, Female sawsheath. 24, *A. albicinctus*. 25, *A. meridionalis*. 26, Apical portion of forewing showing infuscate spot below stigma in *A. calliblepharus*.

From the female of *A. viennensis*, *A. rhododendri* is distinguished by the trapezoidal serrulae of the lancet (triangular in *A. viennensis*, see Smith 1979, fig. 225 and Fig. 13) and by the inverted T-shaped yellow macula on the 8th tergite (posterior margin of 8th tergite yellow in *A. viennensis*). The male of *A. rhododendri* is distinguished by the shape of the genitalia (see Smith 1979, figs. 231–232 and Figs. 18, 20).

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THE WINTER CRANE FLIES OF NORTH AMERICA NORTH OF MEXICO (DIPTERA: TRICHOCERIDAE)

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Abstract.—Twenty-eight species of winter crane flies in the family Trichoceridae are found in North America north of Mexico: *Diazosma pratti* Stary, *D. subsinuatum* Alexander, *Paracladura trichoptera* (Osten Sacken), *Trichocera* (*Metatrichocera*) *colei* Alexander, *T.* (*M.*) *garretti* Alenander, *T.* (*M.*) *lutea* Becher, *T.* (*M.*) *mackenzie* (Dahl), *T.* (*M.*) *salmani* Alexander, *T.* (*M.*) *tetonensis* Alexander, *T.* (*M.*) *ursamajor* Alexander, *Trichocera* (*Trichocera*) *annulata* Meigen, *T.* (*T.*) *arctica* Lundström, ***T.* (*T.*) *arnaudi* Pratt, n. sp.**, ***T.* (*T.*) *banffi* Pratt, n. sp.**, *T.* (*T.*) *bimacula* Walker, *T.* (*T.*) *bituberculata* Alexander, *T.* (*T.*) *borealis* Lackschewitz, *T.* (*T.*) *brevicornis* Alexander, *T.* (*T.*) *columbiana* Alexander, *T.* (*T.*) *excilis* Dahl, *T.* (*T.*) *fattigiana* Alexander, *T.* (*T.*) *gracilis* Walker, *T.* (*T.*) *hiemalis* (De Geer), ***T.* (*T.*) *idahoensis* Pratt, n. sp.**, *T.* (*T.*) *maculipennis* Meigen, *T.* (*T.*) *pallens* Alexander, *T.* (*T.*) *regelationis* (Linnaeus), and *T.* (*T.*) *setosivena* Alexander. *Trichocera longisetosa* Alexander is a **new synonym** of *Trichocera* (*Trichocera*) *setosivena* Alexander. Keys to genera and species, notes on distributions, and illustrations are provided.

Key Words: Diptera, Trichoceridae, winter crane flies, North America, taxonomy

Winter crane flies of the genus *Trichocera* Meigen are found on warm sunny afternoons in fall, winter, and spring in the contiguous United States, Canada, and Alaska. On the other hand, adults of the two species of *Diazosma* Bergroth are collected from June to September, the only trichocerids on wing in the summer in northern United States. Adults of *Paracladura trichoptera* (Osten Sacken) are found from August through the winter to spring in British Columbia, Washington, Oregon, and California. Swarms of *Trichocera* males are often seen dancing in the late afternoon sunlight, sometimes thousands of individuals in hundreds of swarms over many acres of lawns and open woodlands. Biologists also have noticed these coldhardy insects swarming above the snow, or specimens crawling on the snow when temperatures were between 0° and 10°C. Specimens in this study were collected by net, light trap, Malaise trap, and molasses trap.

The following acronyms indicate the location of types:

ANSP	Academy of Natural Sciences, Philadelphia, PA., USA.
BMNH	The Natural History Museum, London, UK.
CAS	California Academy of Sciences, San Francisco, CA, USA.
CNC	Canadian National Collection, Ottawa, ON, Canada.
LSI	Linnean Society of London, London, UK.
MCZ	Museum of Comparative Zoology, Harvard University, Cambridge, MA, USA.
MNHN	Muséum National d'Histoire Naturelle, Paris, France.
NMW	Naturhistorisches Museum, Wien, Austria.

USNM	National Museum of Natural History, Smithsonian Institution, Washington, DC, USA.
ZIL	Zoological Institute, Lund, Sweden.
ZISP	Zoological Institute, Academy of Sciences, St. Petersburg, Russia.

TAXONOMY

Alexander published two keys to the Trichoceridae found in the eastern United States (1919a, 1942) and one for the western United States (1967). He wrote a fine summary of the family Trichoceridae in the "Manual of Nearctic Diptera" in 1981. Dahl published many papers on winter crane flies. Dahl's 1966 publication on the Swedish Trichoceridae includes much information on several species found in North America, and her 1967 paper on arctic and subarctic Trichoceridae is the basic work on northern species. The world catalogue of Trichoceridae by Dahl and Alexander (1976) lists all the species known to 1976, references to the original descriptions, and known locations of types of most species. Pratt and Pratt (1984) published keys, illustrations and data on ten species of eastern North America. Pratt (1992) published a key to the Trichoceridae of North America.

Starý (1995) described *Diazosma pratti* and wrote that *Diazosma hirtipenne* (Siebke) is a European species and that North American records of this insect should be called *D. subsinuatum* (Alexander). Starý and Martinovsky (1996) wrote that *Trichocera japonica* Matsumura (1916) probably is not a North American species and that records of this species by Dahl and Alexander (1976) and Pratt (1992) should be called *Trichocera excilis* Dahl (1967). Krzeminska (2001) wrote that *Trichocera major* Edwards is a European species and that American records of this species should be called *Trichocera setosivena* Alexander.

Trichocera scutellata Say (1824) from Minnesota and *Trichocera brumalis* Fitch (1847) from New York are unrecognized because their types are lost. They are not treated further here. *Trichocera gracilis* Walker (1848) was described from a single female from York Factory, Manitoba, Canada. Byers (1976) published notes and figures of the terminal abdominal segments of the type. I know of no characters to separate this species from females of other species.

FAMILY CHARACTERISTICS OF THE TRICHOCERIDAE

Winter crane flies in the family Trichoceridae are small to medium sized (wing up to 12 mm in *Diazosma*) with slender long legs similar to the true crane flies in the family Tipulidae. Trichoceridae differ in having 3 ocelli, the V-shaped suture on the mesonotum incomplete in the middle, and long hairlike antennae. Tipulidae lack ocelli, have a complete V-shaped suture on the mesonotum separating the praescutum and scutum, and antennae usually short. True crane flies are often much larger than winter crane flies, with wings up to 25 mm or more.

Description.—Head with 3 ocelli. Antenna with 16 "segments," scape and pedicel enlarged, flagellomeeres 3–16 elongate and progressively more slender. Mouthparts reduced, mandibles absent, galea of maxilla well-preserved, palpus with 4 free segments, no trace of sensory pore (as in *Sylvicola* Harris and *Culicoides* Latreille). Thorax with V-shaped suture separating praescutun and scutum incomplete in middle, and no distict suture separating scutum and scutellum. Wing with Sc long joining C at midlength, 4 branches of R and 3 branches of M reaching wing margin, A_1 long, A_2 short and curved to wing margin in *Trichocera* and *Paracladura* Brunetti longer and subsinuous in *Diazosma.* Legs not markedly deciduous as in Tipulidae: Abdomen with 8 distinct pregenital segments, first segment short. Male genitalia with medio-basal projections of gonocoxites forming incomplete or complete bridge, gonostylus single, phallosome with aedeagus or sperm pump somewhat pearshaped and parameres joined medially by thin membrane. Female with ovipositor formed by sclerotized, elongate, downward curved cerci in *Trichocera* and *Paracladura* or short and fleshy in *Diazosma.*

KEY TO THE WINTER CRANE FLIES (TRICHOCERIDAE) OF NORTH AMERICA NORTH OF MEXICO

1. Tarsi with basitarsomere very short, about one-eighth as long as second tarsomere (Fig. 4); wing with m-cu crossvein present (Fig. 1); female with one spermatheca (Fig. 32) (*Paracladura*, one species, BC, WA, OR, CA) . . . . *Paracladura trichoptera* (Osten Sacken)

– Tarsi with basitarsomere longer than second (Fig. 5); wing with m-cu crossvein absent (Figs. 2–3); female with 3 spermathecae . . . 2

2. Wing with A_2 long, subsinuous, not curved evenly to wing margin (Fig. 2); tibial spurs absent (Fig. 4); ovipositor short, oval, fleshy (*Diazosma*) 29

Wing with A_2 vein short, curved evenly to wing margin (Fig. 3); tibial spurs present (Fig. 5); ovipositor short to long, tapering markedly to tip, curved downward (*Trichocera*) 3

3. Gonostylus with one or more lobes or swellings; gonocoxites frequently enlarged; bridge connecting gonocoxites complete, often with protuberance in middle (Figs. 9–15) (*Trichocera* (*Metatrichocera*)) 4

- Gonostylus simple, or with basal swelling or protuberance; gonocoxites not markedly enlarged; bridge connecting gonocoxites complete or incomplete, without protuberance in middle (Figs. 16–30) (*Trichocera* (*Trichocera*)) 10

4. Distal portion of gonostylus cylindrical, not enlarged or strongly expanded (Figs. 9–12) 5

Distal portion of gonostylus expanded, complex, often somewhat club-shaped (Figs. 13–15) 8

5. Lobe on basal portion of dististylus short, about as long as width of gonostylus at point of attachment (Figs. 9–10) 6

Lobe on basal portion of dististylus long, two or more times as long as width of gonostylus at point of attachment (Figs. 11–12) 7

6. Lobe on gonostylus with blunt tip, distal part of gonostylus beyond lobe with mesal face densely set with short dark setae; bridge connecting gonocoxites without pointed protuberance in middle (AK, BC, CA across northern U.S) (Fig. 9) . . . . *garretti* Alexander

– Lobe on gonostylus with pointed tip; distal portion of gonostylus byond lobe with sparse long setae; bridge connecting gonocoxites with pointed protuberance in middle (Fig. 10) (AK, OR, northwestern U.S.) (Fig. 10) . . . . *tetonensis* Alexander

7. Lobe of gonostylus at basal fourth of gonostylus; lateral lobes of ninth tergite with dense brush of long, reddish hairs 9th sternite flat (Fig. 11) (NH, MA, MD west to KS) . . . . *salmani* Alexander

– Lobe of gonostylus arising at base of gonostylus; later lobes of ninth tergite with a few sparse hairs; ninth sternite balloon-like with setose dorsal lobe (Fig. 12) (AK, northwestern Canada) . . . . *mackenzie* Dahl

8. Basal and distal portions of gonostylus with large irregular rounded lobe (Fig. 14) (Greenland) . . . . *lutea* Becher

– Base of gonostylus without large round lobe 9

9. Tip of gonostylus with large rounded lobe (Fig. 11) (AK, BC, WA, OR, CA) . . . . *colei* Alexander

Tip of gonostylus with very complex enlargement and conspicuous brush of setae (Fig. 15) (YT, NWT) . . . . *ursamajor* Alexander

10. Wing with a distinct dark spot in Cell R behomd origin of RS and a dark cloud over r-m crossvein (Fig. 3) 11

– Wing without a dark spot in Cell R, entirely clear or with a dark cloud over r-m crossvein 12

11. Gonostylus simple; 9th sternite deeply concave in middle of posterior margin and without setae in middle (Fig. 17) (eastern U.S. and Canada) . . . . *bimacula* Walker

– Gonostylus with small pointed tubercle; 9th sternite with two low bulges near middle of posterior margin and setae along posterior margin (Fig. 18) (BC to QC) . . . . *maculipennis* Meigen

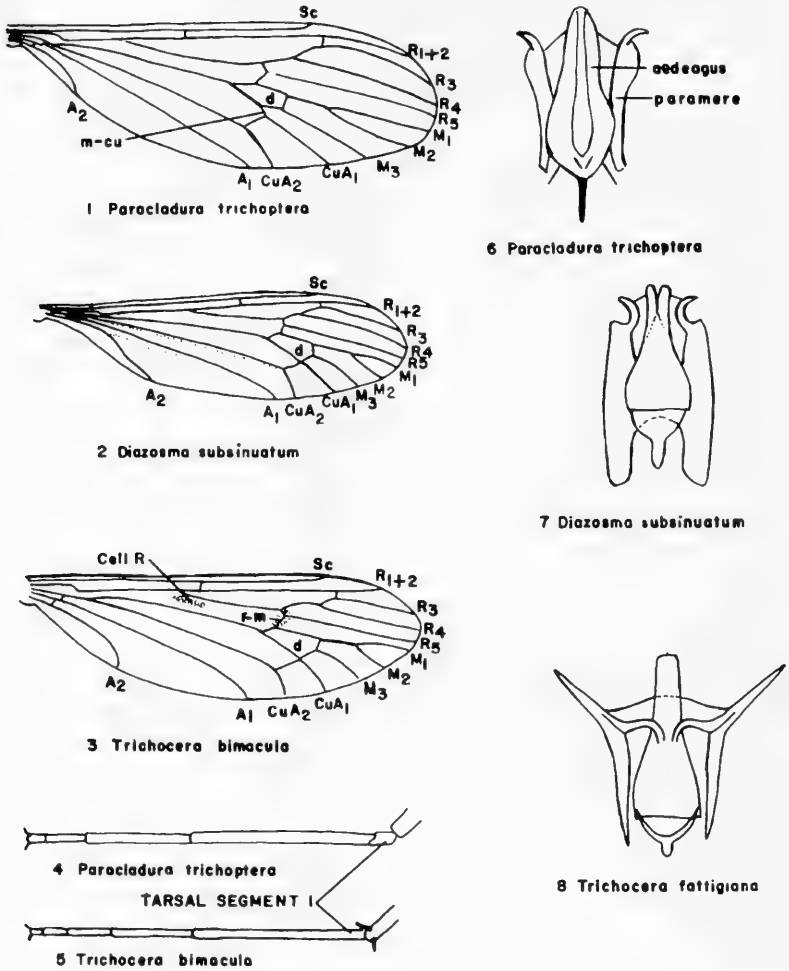
12. Abdomen distinctly annulate, tergites obscurely yellowish with posterior margins brownish (CA, OR, NFD, NY, CT, MD, VA) (Fig. 19) . . . . *annulata* Meigen

– Abdomen entirely dark, or dark above and pale beneath with two color meeting essentially in a straight line laterally 13

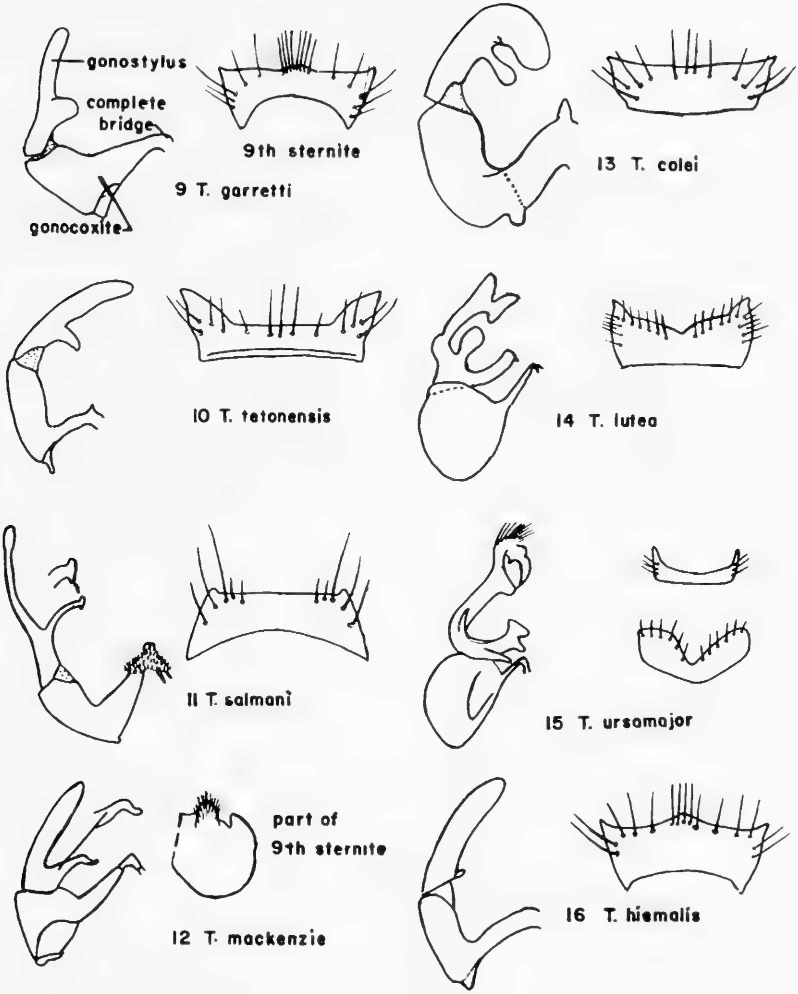
13. Wing with distinct cloud over r-m crossvein (eastern U.S. and Canada) (Fig. 20) . . . . *regelationis* (L.)

– Wing clear, sometimes with slight cloud in stigmal are, i.e., Cell R_1 14

14. Scape of antenna and thorax pale orange brown; abdomen with dorsum dark, venter pale, the two colors meeting laterally essentially in a straight line (CA, WA, BC) . . . . *arnaudi*, n. sp.



Figs. 1–8. 1, Wing, *Paracladura trichoptera,* San Francisco, CA. 2, Wing, *Diazosma subsinuatum,* Halifax Gorge, VT. 3, Wing, *Trichocera bimacula,* Atlanta, GA. 4, Tarsus, *P. trichoptera,* San Francisco, CA. 5, Tarsus, *T. bimacula,* Atlanta, GA. 6, Male genitalia, *P. trichoptera,* San Francisco, CA. 7, Male genitalia, *D. subsinuatum,* Halifax Gorge, VT. 8, Male genitalia, *T. fattigiana,* Atlanta, GA.



Figs. 9–16. Male genitalia details. 9, *Trichocera garretti,* Atlanta, GA. 10, *T. tetonensis,* Waterston National Park, AB, Canada. 11, *T. salmani,* Amherst, MA. 12, *T. mackenzie,* Masseure, Sweden. 13, *T. lutea,* Moravia. 15, *T. ursamajor,* redrawn from Dahl (1967). 18, *T. hiemalis,* Atlanta, GA.

Scape of antenna, thorax and abdomen dark 15

15. Male with complete bridge joining gonocoxites (Figs. 16, 21-23) 16

– Male with incomplete bridge joining gonocoxites (Figs. 24–27 19

16. Gonostylus simple (Fig. 21); wing with long trichia, those on distal portion of wing veins about as long as basal portion of R_2 . . . . *setosivena* Alexander

– Gonostylus with basal protuberance or tubercle (Figs. 16, 22–23) wing without trichia on wing veins 17

17. Male with 9th sternite usually with an obtuse point in middle of posterior margin (Fig. 16); first flagellar segment of antenna elongate, 3 to 4 times as long as basal width. . . . . *hiemalis* (De Geer)

Male 9th sternite without a point in middle of posterior margin; first flagellar segment of antenna about as long as following segments . . 18

18. Male 9th sternite with few setae near middle of posterior margin (AK, northern Canada) (Fig. 22) . . . . *arctica* Lundström

Male 9th sternite with many setae near middle of posterior margin (CA, OR) (Fig. 23) . . . . *pallens* Alexander

19. Halves of incomplete bridge slender, arising from mid-length of gonocoxites (Figs. 34–35); parameres about as long as aedeagus 20

– Halves of incomplete bridge broader, arising near base of gonocoxites (Figs. 24–27, 29–30); parameres longer than aedeagus 21

20. Gonostylus stout, tip rounded (Fig. 34); parameres with broad tip (ID) . . *idahoensis*, n. sp.

Gonostylus slender, tip pointed (Fig. 35); parameres with pointed tips (AB) . . . *banffi*, n. sp.

21. Gonostylus with 2 tubercles, one at base larger than one at basal third (Fig. 24) (AK, MA, NH) . . . . *bituberculata* Alexander

Gonostylus with one basal tubercle, a setigerous protuberance, or simple (Figs. 25–27, 29–30) 22

22. Gonostylus with basal tubercle (Fig. 25), parameres stongly angled, with spur beyond middle of aedeagus (Fig. 8); both sexes with last segment of palpus not constricted in middle (CT south to GA, west to MS) . . . . *fattigiana* Alexander

Gonostylus with basal setigerous protuberance or swelling, or simple (Figs. 26–27, 29–30); parameres gently curved, somewhat scimitar-shaped; last segment of palpus constricted in middle 23

23. Gonostylus with basal setigerous protuberance or swelling (Figs. 26–27) 24

Gonostylus simple (Figs. 29–30) 26

24. 9th sternite with posterior margin deeply scooped or concave, with 4 to 8 setae along posterior margin between postero-lateral corners (Fig. 26) (Canada, AK) . . . . . *excilis* Dahl

9th sternite with posterior margin slightly concave or straight usually with 10 or more setae between postero-lateral corners 25

25. Setae along posterior margin of 9th sternite almost all of same size (eastern U.S. and Canada) . . . . *regelationis* (L.)

– Setae along posterior margin of 9th sternite of more than one size (Fig. 27) (AK, northern Canada) . . . . *borealis* Lackschewitz

26. Male 9th sternite with posterior margin deeply concave, without setae in middle portion (Fig. 17) (eastern U.S. and Canada) . . . . *bimacula* Walker

Male 9th sternite shallowly concave or straight along posterior margin, with setae all along posterior margin between postero-lateral corners (Figs. 20, 29–30) 27

27. Male 9th sternite with 10 or more setae along posterior margin between postero-lateral corners (eastern U.S. and Canada) . . . . *regelationis* (L.)

Male 9th sternite with 6 to 8 setae along posterior margin between postero-lateral corners 28

28. Aedeagus with short basal apodeme and only slight trace of longitudinal groove (Fig. 29) (eastern U.S. and Canada) . . . . *brevicornis* Alexander

– Aedeagus with longer basal apodeme and longitudinal groove (Fig. 30) (western U.S. and Canada) . . . . *columbiana* Alexander

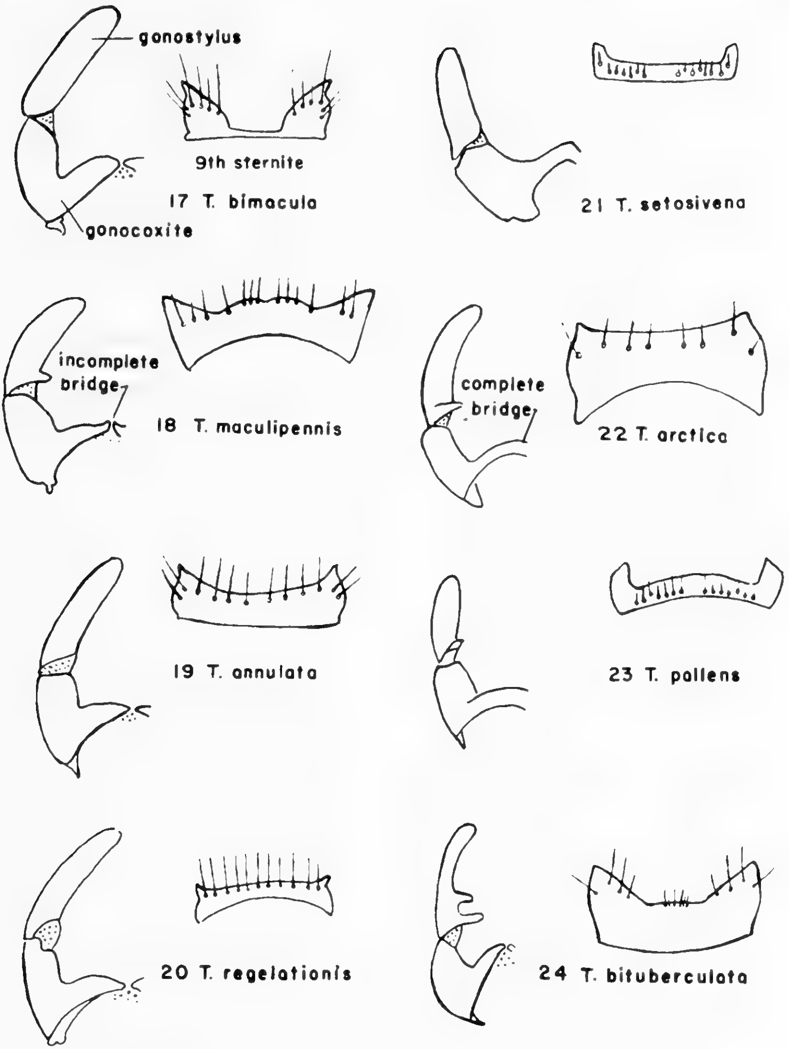
29. Male gonocoxites very stout, inflated with basal lobes forming distinct bridge; gonostylus slightly broadened distally, its tip rounded; female with tergite 10 subequal in length to cercus; spermatheca ovoid, with long sclerotized duct, subequal to spermathecal diameter (Fig. 31) (CO, ME, NH, VT, QC) . . . . *Diazosma subsinuatum* (Alexander)

– Male gonocoxites comparatively slender, without apparent bridge; gonostylus slender before apex into more or less obtuse tip; female with tergite 10 longer than cercus; spermatheca spherical with sclerotized duct less than half spermathecal diameter) (Fig. 36) (OR, UT) . . . . *Diazosma pratti* Starý

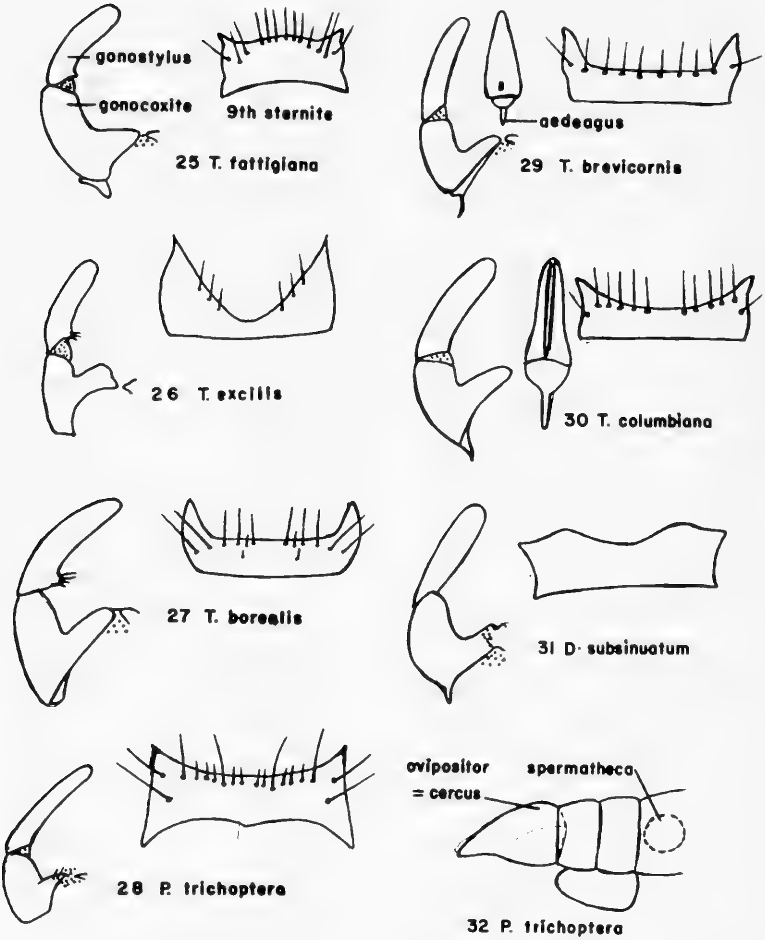
SPECIES

Diazosma Pratti Starý
(Fig. 36)

Diazosma pratti Starý 1995: 210–213, figs. 5–8. Holotype ♂, Cowly Canyon, Cache



Figs. 17–24. Male genitalia details. 17, *Trichocera bimacula,* Atlanta, GA. 18, *T. maculipennis* Bear Island. 19, *T. annulata,* Arlington, VA. 20, *T. regelationis,* Ithaca, NY. 21, *T setosivena,* Boyer, OR. 22, *T. arctica,* Banff, AB, Canada, 23, *T. pallens,* Santa Cruz Co., CA. 24, *T. bituberculata,* Amherst, MA.



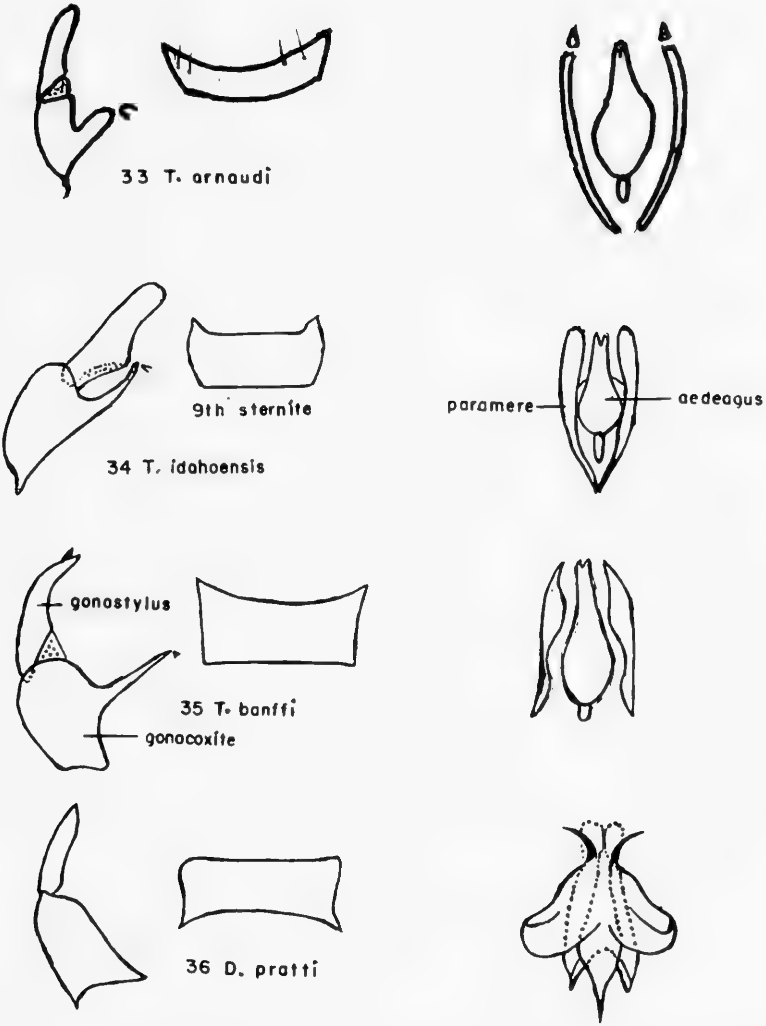
Figs. 25–32. 25–31, Male genitalia details. 25, *Trichocera fattigiana,* Atlanta, GA. 26, *T. excilis,* redrawn from Starý and Martinovsky (1996), Dawson, YT, Canada. 27, *T. borealis,* Aklavik, NT, Canada. 28, *Paracladura trichoptera,* San Francisco, CA. 29, *T. brevicornis,* Atlanta, GA. 30, *T. columbiana,* Pullman, WA. 31, *Diazosma subsinuatum,* Halifax Gorge, VT. 32, Female abdomen, *P. trichoptera,* Marin Co., CA.

Co., UT in collection J. Starý, Faculty of Science, Olomouc, Czech Reputblic.

Geographic range.—UT and OR (Starý 1995).

Diazosma subsinuatum Alexander
(Figs. 2, 7, 31)

Trichocera (*Diazosma*) *subsinuatum* Alexander 1916: 124–125, fig. 10. Holotype



Figs. 33–36. Details of male genitalis. 33, *Trichocera arnaudi*, Inverness, CA. 34, *T. idahoensis*, Moscow Mt., ID. 35, *T. banffi*, Banff, AB, Canada. 36, *Diazosma pratti*, Cache Co., UT.

♂, Hall Valley, Platte Canyon, CO. Carcass and slide in USNM.

Geographic range.—BC to CA across southern Canada and northern U.S. east to NY and VT (Alexander 1967, Pratt and Pratt 1984).

Paracladura trichoptera (Osten Sacken)
(Figs. 1, 6, 28, 32)

Trichocera trichoptera Osten Sacken 1877: 204. Holotype ♀, Lagunitas Creek, Marin Co., CA in MCZ

Geographic range.—BC, WA, OR, CA (Alexander 1967)

Trichocera (*Metatrichocera*) *colei* Alexander
(Fig. 13)

Trichocera colei Alexander 1919: 162. Holotype ♂, Forest Grove, OR, carcass and slide in USNM.

Geographic range.—AK, BC, WA, OR, CA (Alexander 1967).

Trichocera (*Metatrichocera*) *garretti* Alexander
(Fig. 9)

Trichocera garretti Alexander 1927: 71–72. Holotype ♂, Marysville, BC, Canada, slide only, no carcass in USNM

Trichocera alexanderi Dahl 1967:59, figs. 7–10. Holotype ♂, Mt. Robson, BC, Canada in CNC. Synonymy by Dahl and Alexander (1976).

Geographic range.—AK to CA east across southern Canada and northern U.S. to NH and GA (Pratt and Pratt 1984).

Trichocera (*Metatrichocera*) *lutea* Becher
(Fig. 14)

Trichocera lutea Becher 1886: 64. Holotype ♂, Jan Mayen in NMW.

Geographic range.—Jan Mayen, Spitzbergen, Bear Island, Greenland, Iceland, Fennoscandia, northwestern Russia, Alps (Dahl and Alexander 1976).

Trichocera (*Metatrichocera*) *mackenzie* (Dahl)
(Fig. 12)

Metatrichocera mackenzie Dahl 1967: 60–63, figs. 11–15, 56–60. Holotype ♂, Mackenzie Delta, NWT, Canada in CNC.

Geographic range.—AK, northern Canada, northern Sweden. (Dahl and Alexander 1976).

Trichocera (*Metatrichocera*) *salmani* Alexander
(Fig. 11)

Trichocera salmani Alexander 1927: 72. Holotype ♂, Amherst, MA, slide only, no carcass in USNM.

Geographic range.—MA, MD, KS, NH (Pratt and Pratt 1984).

Trichocera (*Metatrichocera*) *tetonensis* Alexander
(Fig. 10)

Trichocera tetonensis Alexander 1945: 398, figs. 1, 2. Holotype ♂, Hidden Falls, stn. 3 WY in USNM, carcass only, no slide.

Trichocera hyaloptera Alexander 1949: 274, fig. 3. Holotype ♂, Peavine Ridge, Yamhill Co., OR, carcass only, no slide in USNM. Synonymy by Dahl and Alexander (1976).

Geographic range.—AK, OR, northern Canada, northern U.S. (Dahl and Alexander 1976).

Trichocera (*Metatrichocera*) *ursamajor* Alexander
(Fig. 15)

Trichocera ursamajor Alexander 1959: 58. Holotype ♂, Bear Lake, NWT, Canada. slide only in USNM

Geographic range.—AK, northern Canada (Dahl and Alexander 1976).

Trichocera (*Trichocera*) *annulata* Meigen
(Fig. 19)

Trichocera annulata Meigen 1818:215. Holotype ♂, Austria in MNHN.

Geographic range.—Western Canada, Europe, Asia Minor, Ethiopia, southern Australia, New Zealand, CA, AK, BC, NY, NJ, VA. (Alexander 1967, Pratt and Pratt 1984).

Trichocera (Trichocera) arctica Lundström (Fig. 22)

Trichocera arctica Lundstrom 1915: 28, figs. 11, 41, 42. Holotype ♂, Russia in ZISP (*teste* Dahl and Alexander 1976).

Geographic range.—AK and northern coasts of Russia (Dahl and Alexander 1976).

Trichocera (Trichocera) bimacula Walker (Figs. 3, 5, 17)

Trichocera bimacula Walker 1848:84. Lectotype ♂ NS, Canada in BMNH. *Trichocera venosa* Dietz 1921: 236. Holotype ♀, Hazelton, PA in ANSP. *Trichocera fernaldi* Alexander 1927: 70. Holotype ♂, Amherst, MA, carcass and slide in USNM.

Geographic range.—NS, Canada, eastern and central U.S. (Pratt and Pratt 1984).

Trichocera (Trichocera) bituberculata Alexander (Fig. 24)

Trichocera bituberculata Alexander 1924: 81. Holotype ♂, Bethel, AK, carcass and slide in USNM.

Geographic range.—AK, MA, NH (Pratt and Pratt 1984).

Trichocera (Trichocera) borealis Lackschewitz (Fig. 27)

Trichocera borealis Lackschewitz 1934: 3, figs. 1a–c. Type ♂, Longyaarsbyen, Spitzbergen, probably in BMNH.

Geographic range.—AK, northern Canada, Greenland, Spitzbergen, northern Russia (Dahl and Alexander 1976).

Trichocera (Trichocera) brevicornis Alexander (Fig. 29)

Trichocera brevicornis Alexander 1952:89. Holotype ♂, Atlanta, GA, carcass and slide in USNM.

Geographic range.—Eastern U.S. VT to GA (Pratt and Pratt 1984).

Trichocera (Trichocera) columbiana Alexander (Fig. 30)

Trichocera columbiana Alexander 1927: 70. Holotype ♂, Prince Rupert BC, carcass and slide in USNM.

Geographic range.—AK, BC, WA, OR, CA (Alexander 1967).

Trichocera (Trichocera) excilis Dahl (Fig. 26)

Trichocera excilis Dahl 1967:71, figs. 43–45. Holotype ♂, Dawson, YT, Canada in CNC.

Geographic range.—AK, YT (Dahl 1967).

Trichocera (Trichocera) fattigiana Alexander (Figs. 8, 25)

Trichocera fattigiana Alexander 1952: 88. Holotype ♂, Atlanta, GA, carcass and slide in USNM.

Geographic range.—Eastern and central U.S. (Pratt and Pratt 1984).

Trichocera (Trichocera) hiemalis (De Geer) (Fig. 16)

Tipula hiemalis De Geer 1776:360, figs. XXI: 1–4. Neotype ♂, Lund, Sweden (Dahl 1966:101) in ZIL.

Geographic range.—Eastern Canada, eastern U.S., MA to GA, Europe (Pratt and Pratt 1984).

Trichocera (Trichocera) maculipennis Meigen
(Fig. 18)

Trichocera maculipennis Meigen 1818: 214. Type, Austria, non-existent (*teste* Dahl and Alexander 1976).

Geographic range.—European species found in southern Canada and Greenland (Alexander 1965).

Trichocera (Trichocera) pallens Alexander
(Fig. 23)

Trichocera pallens Alexander 1954: 25. Holotype ♂, Saddle Mountain, Boyer, OR, carcass in USNM, slide in CAS.

Geographic range.—CA, OR (Alexander 1967).

Trichocera (Trichocera) regelationis (Linnaeus)
(Fig. 20)

Tipula regelationis Linnaeus 1758: 587. Type, Sweden, in LSL, without abdomen according to Dahl and Alexander (1976).

Geographic range.—Europe; ON, Canada; eastern U.S. (Pratt and Pratt 1984).

Trichocera (Trichocera) setosivena Alexander

Trichocera (Trichocera) setosivena Alexander 1927: 68. Holotype ♂, Seward, AK, carcass and slide in USNM.

Trichocera longisetosa Alexander 1927: 69. Holotype ♂, Lake Cushman, WA, carcass and slide in USNM. **New synonymy**.

Geographic range.—AK, WA, OR, CA (Alexander 1967).

***Trichocera (Trichocera) arnaudi* Pratt, new species**
(Fig. 33)

Description.—Scape of antenna and thorax pale orange brown. Abdomen with dorsum dark and venter pale, two colors meeting somewhat in straight line laterally. Coxae, trochanters, and bases of femora pale orange brown, rest of femora, tibiae, and tarsi black. Wing 5 mm. Total length from head to tip of abdomen 5 mm.

Male terminalia (Fig. 33) with gonocoxites slender, shorter than gonostylus, with incomplete bridge and slender hook like basal apodeme; gonostylus somewhat parallel-sided, with rounded tip; aedeagus pear-shaped, with basal apodeme and long slender tip; parameres twisted in type slide, slightly longer than aedeagus, with pointed tips.

Types.—Holotype ♂ carcass and slide, California, Marin Co., Inverness, I-13-XII-1963, Paul H. Arnaud. In CAS. 6 paratypes in CAS from Inverness, CA; San Mateo County, CA; El Cerrito, CA; Fort Lewis, WA; and Pullman WA. Additional specimens in poor condition have been seen from several localities in California and British Columbia.

Etymology.—This species is named in honor of Paul H. Arnaud, Curator of Entomology at CAS, who collected the type specimens and provided many of the specimens on which this study is based.

Remarks.—This species may be confused with *Paracladura trichoptera* because generic distinctions are often difficult to see. Both have the scape and thorax pale orange brown. *Paracladura trichoptera* has the wing and wing margin with abundant fine setae, whereas *Trichocera arnaudi* has the wing clear without fine setae.

***Trichocera (Trichocera) banffi* Pratt, new species**
(Fig. 35)

Description.—Head, thorax, and abdomen black. Antenna missing. Wing clear, 5 mm. Length 4 mm.

Male terminalia (Fig. 35) with incomplete bridge arising from the middle of each gonocoxite, very slender and pointed; gonostylus slender, tapering to a point; parameres about as long as aedeagus, with pointed tips; aedeagus pear-shaped, with short basal apodeme and pointed, slender tip. 9th sternite transverse, without setae.

Type.—Holotype ♂ carcass and slide, Banff, Alberta, Canada, IX-20-1928, O. Bryant, at light, In CAS.

Etymology.—Named for Banff, the type locality.

Remarks.—*Trichocera banffi* and *Trichocera idahoensis* are very distinct from other *Trichocera* in having the incomplete, very slender, pointed bridge arising from the middle of the gonocoxites. *Trichocera banffi* is separated from *T. idahoensis* by the slender gonostylus with the tip pointed (Fig. 35) (stout with tip rounded in *T. idahoensis,* Fig. 34), and the pointed tips of the parameres (broad in *T. idahoensis*).

Trichocera (*Trichocera*) idahoensis Pratt, new species

(Fig. 34)

Description.—Male, head, thorax, and abdomen black. Wing clear, about about 7 mm. One fore leg without tarsi.

Male terminalia (Fig. 34) with gonocoxite stout, with rounded tip and triangular projectuon in middle; long, slender, incomplete bridge, each half arising from middle of respective gonocoxite. Aedeagus long and slender, tip notched, with long, darkened, basal apodeme, flanked by short parameres about as long as aedeagus, with blunt tips. 9th sternite with straight posterior margin and pointed postero-lateral cornersm apparently without setae.

Type.—Holotype ♂ carcass and slide, Moscow Mt., Idaho, 10 Sept., 1916, A. L. Melander. In ANSP.

Etymology.—This species is named for the type locality, Idaho.

Remarks.—The two new species, *Trichocera idahoensis* and *Trichocera banffi* differ from other *Trichocera* in having a very slender, long, incomplete bridge, each half arising from the middle of the gonocoxite, and by very short parameres, about as long as the aedeagus. See remarks under *T. banffi* and key.

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REVIEW OF THE GENUS *SAEMUNDSSONIA* TIMMERMANN (PHTHIRAPTERA: PHILOPTERIDAE) FROM THE ALCIDAE (AVES: CHARADRIIFORMES), INCLUDING A NEW SPECIES AND NEW HOST RECORDS

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Abstract.—We describe the new species ***Saemundssonia boschi*** recently collected from Least Auklets (*Aethia pusilla* (Pallas)) in Alaska and review the 11 names previously applied to *Saemundssonia* Timmermann species from alcids. *Saemundssonia procax* (Kellogg and Chapman) is relegated to a **new junior synonym** of *S. grylle* (O. Fabricius), along with the previously recognized junior synonym *S. megacephalus* (Denny). The nine previously described valid species are redescribed and illustrated and four new host records are documented from alcids. Finally, a key is provided for the identification of the ten recognized species of alcid *Saemundssonia.*

Key Words: chewing lice, *Saemundssonia*, Phthiraptera, Philopteridae, Alcidae

Recent fieldwork by DHC in Alaska yielded a series of lice from Least Auklets, *Aethia pusilla* (Pallas), and Crested Auklets, *A. cristatella* (Pallas). Examination of this material revealed a new species of *Saemundssonia* Timmermann from the Least Auklet. In describing this new species, we review the status of all 11 species-level names currently applied to the alcid lice of the genus *Saemundssonia.* We here redescribe the nine valid species, describe the new species, establish a new junior synonym and continue to recognize a previously established synonym, give four new host records, and provide a key for the identification of these ten species.

The material examined for this study is held in the following institutions: National Museum of Natural History, Smithsonian Institution, Washington, D.C. (USNM); Department of Biology, University of Utah, Salt Lake City (UU); University of Minnesota, St. Paul (UM); K. C. Emerson Museum, Oklahoma State University, Stillwater (OSU); Museum of New Zealand Te Papa Tongarewa, Wellington (MONZ); and Essig Museum of Entomology, University of California, Berkeley (UC).

Genus *Saemundssonia* Timmermann

Saemundssonia Timmermann 1936: 97. Type species: *Docophorus gonothorax* Giebel, by original designation.

This large genus contains over 100 recognized species and subspecies, primarily from hosts in the avian order Charadriiformes and, to a lesser extent, from the orders Procellariiformes, Gruiformes, Pelecaniformes, and Anseriformes. Typical species of this genus appear much as in Fig. 2, with a broad triangular head. The head bears a prominent dorsoanterior plate with a conspicuous darkly pigmented medioposterior process (Figs. 4–7). The abdomen is rounded, with at least tergites III–VIII divided at the midline. The abdominal sternum has only sparse chaetotaxy and lacks evident sclerites except for those associated with the terminalia. The male genitalia have a prominent pair of parameres, a large basal plate, and relatively complex mesosomal structures.

In our treatment of the ten species of alcid *Saemundssonia,* we divide the species into three species groups. This separation is based on the chaetotaxy of the metanotal margin and the divided or undivided state of male tergite IX.

In the following descriptions, all measurements are in millimeters. Abbreviations are DPL, dorsoanterior head plate length; TW, temple width; HL, head length at midline including the hyaline margin; PW, prothorax width; MW, metathorax width; AWV, abdomen width at segment V; TL, total length; GL, male genitalia length from start of basal apodeme to tip of parameres. Figures of similar structures are shown at the same magnification: whole drawings (Figs. 2–3, 13–14) at 75×, the dorsoanterior head plates (Figs. 4–7, 12, 15–17) at 125×, and the male genitalia (Figs. 1, 8–11, 18–20) at 180×. Host classification follows that of Sibley and Monroe (1990).

wumisuzume species group

The three species of this group are characterized by having the metanotal margin with 13–16 (usually 14) setae distributed across the segment (Figs. 2–3) and the male with undivided tergite IX.

Saemundssonia boschi **Price, Palma, and Clayton, new species**

(Figs. 1–4)

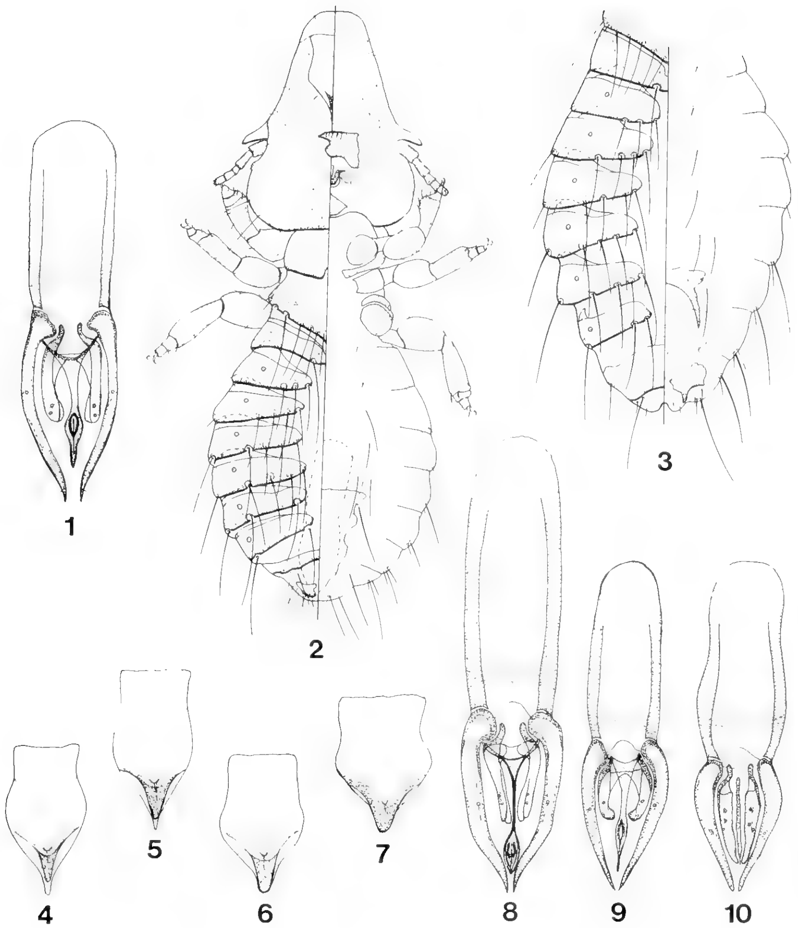
Type host.—*Aethia pusilla* (Pallas).

Male.—As in Fig. 2. Dorsoanterior head plate (Fig. 4) with posterior process seated within body of plate; DPL, 0.21–0.24. Abdomen (Fig. 2) with one or both sides with setae mediad of spiracle on tergite III, 3; IV–VI, 4; VII, 2; VIII, 1. Median sternal setae on each side of II–VII, respectively, short, short, long, long, 2 long, and long. Genitalia (Fig. 1) with slender, evenly curved parameres and mesosomal structures as shown. Dimensions: TW, 0.39–0.42; HL, 0.50–0.54; PW, 0.23–0.26; MW, 0.30–0.34; AWV, 0.46–0.58; TL, 1.34–1.44; GL, 0.34–0.38.

Female.—Similar to male. DPL, 0.24–0.28. Abdomen (Fig. 3) with setae mediad of spiracle on tergite VII, 3–4; VIII, 1–2. Dimensions: TW, 0.44–0.47; HL, 0.56–0.60; PW, 0.27–0.31; MW, 0.35–0.44; AWV, 0.61–0.85; TL, 1.70–1.93.

Type material.—Ex *A. pusilla,* the Least Auklet, holotype male in USNM, St. Lawrence Island, Alaska, 3–4 August 2001, LEAU 201, D. H. Clayton. Paratypes, all ex *A. pusilla*: 15 males, 9 females, same as holotype, but coded as LEAU 202, 203, 206, 207, 208, 210, 211, 212, 213, 216, 221, 222, and 224; 1 male, 1 female, St. Lawrence Island, Bering Sea, 2 June 1913, Brooks; 1 female, St. Paul Island, Alaska, 9 July 1964; 3 males, 3 females, Buldir Island, Aleutian Islands, Alaska, 12–15 July 1997, F. M. Hunter; 16 males, 8 females, same except August 1998; 7 males, 8 females, same except 20–30 July 2001, J. Hagelin; paratypes distributed among USNM, UU, UM, OSU, and MONZ.

Remarks.—This new species is distinguished from all other alcid *Saemundssonia* by the combination of its large number of marginal metanotal setae distributed across the segment, most abdominal tergites IV–VI each with 4 setae mediad of the spiracle, its consistently small dimensions, and the unique male genitalia. The morphologically closest species to *S. boschi* appears to be *S. merguli* (Denny), but the latter has fewer marginal metanotal setae, a smaller and different-shaped dorsoanterior head plate, and a similar type of male genitalia but with a distinct apical in-



Figs. 1–10. 1–3, *Saemundssonia boschi.* 1, Male genitalia. 2, Dorsoventral male. 3, Female metanotal margin and dorsoventral abdomen. 4–7, Male dorsoanterior head plate (note darkly pigmented medioposterior process). 4, *S. boschi.* 5, *S. wumisuzume.* 6, *S. merguli.* 7, *S. montereyi.* 8–10, Male genitalia. 8, *S. wumisuzume.* 9, *S. merguli.* 10, *S. montereyi.*

ward flexion of the lateral mesosomal sclerites (Fig. 9 vs. Fig. 1).

Bosch (1983:269) was the first to recognize that the *Saemundssonia* from *A. pusilla* represents a new species, but he reported his conclusion in abstract form only, without naming or describing the new louse. Our extensive search of the subsequent literature has revealed no formal description of that new species. Moreover, Bosch (personal communication, January 2002) informed us he has not published the description of the new species or any further paper on the alcid *Saemundssonia.*

Etymology.—This new species is named after Dr. H. Bosch, Stuttgart, Germany, in recognition of his early observations on relationships within the alcid *Saemundssonia.*

Saemundssonia wumisuzume (Uchida)
(Figs. 5, 8)

Philopterus wumisuzume Uchida 1949: 535. Type host: *Aethia cristatella* (Pallas).

Male.—Much as for *S. boschi,* except as follows. Dorsoanterior head plate as in Fig. 5; DPL, 0.21–0.27. Tergal setae mediad of spiracle on abdominal segment III, 3; IV–VI, 4 (rarely 5); VII, 2 (less often 3); VIII, 1. Genitalia (Fig. 8) with thickened parameres flexed near distal third and mesosomal structures as shown. Dimensions: TW, 0.43–0.47; HL, 0.52–0.58; PW, 0.27–0.31; MW, 0.35–0.41; AWV, 0.51–0.67; TL, 1.48–1.66; GL, 0.43–0.51.

Female.—Much as for *S. boschi,* except as follows. DPL, 0.23–0.29. Tergal setae mediad of spiracle on III, 3 (rarely 2 or 4); IV-VI, 4 (rarely 5); VII, 3–5; VIII, 1–2. Dimensions: TW, 0.48–0.52; HL, 0.58–0.64; PW, 0.30–0.33; MW, 0.40–0.46; AWV, 0.64–0.83; TL, 1.65–1.96.

Material.—Ex *A. cristatella,* the Crested Auklet, 63 males, 38 females, Alaska (25 host individuals). Ex *A. pygmaea* (Gmelin), the Whiskered Auklet, 57 males, 58 females, Alaska (50 host individuals).

Remarks.—This species is distinguished from other alcid *Saemundssonia,* except for *S. boschi,* by its metanotal and abdominal chaetotaxy. It is clearly separated from *S. boschi* by its unique male genitalia structure, including thicker flexed parameres and different shape of the median penis and lateral mesosomal sclerites, and by its much larger dimensions.

Our abdundant material from both the Crested Auklet and the Whiskered Auklet convinces us that the lice on these hosts are conspecific, and that they represent a species well apart from that found on the Least Auklet.

Saemundssonia insolita (Kellogg)

Docophorus insolitus Kellogg 1896: 94. Type host: *Ptychoramphus aleuticus* (Pallas).

Male.—Unavailable.

Female.—Similar to *S. boschi,* but with DPL, 0.20, and abdominal tergites III–VII each having only 3 setae mediad of spiracle.

Material.—Ex *P. aleuticus,* the Cassin's Auklet, 3 females (including syntype of *D. insolitus* in UC), California, British Columbia.

Remarks.—We were handicapped in fully determining the status of this species by the lack of male specimens. The females we examined had only 3 setae mediad of the spiracle on abdominal tergites III–VII, as illustrated by Kellogg (1896). We believe this difference, because it was consistent, is sufficient to justify continued recognition of *S. insolita* as a distinct species.

merguli species group

The four species of this group are characterized by having the metanotal margin with 10–12 (usually 12) setae distributed across the segment and the male with an undivided tergite IX.

Saemundssonia merguli (Denny)
(Figs. 6, 9)

Docophorus merguli Denny 1842: 42. Type host: *Alle alle* (L.).

Male.—Dorsoanterior head plate as in Fig. 6; DPL, 0.19–0.20. One or both sides with setae mediad of spiracle on abdominal tergite III, 3; IV–VI, 4; VII, 2; VIII, 1. Sternal setae as for *S. boschi.* Genitalia (Fig. 9) with slender evenly curved parameres and lateral sclerites of mesosome with apical portion distinctly flexed inwardly. Dimensions: TW, 0.41–0.43; HL, 0.49–0.53; PW, 0.26–0.28; MW, 0.31–0.35; AWV, 0.55–0.60; TL, 1.29–1.38; GL, 0.32–0.34.

Female.—Similar to male, except DPL, 0.20–0.22, and setae on each side of tergite VII, 3–4; VIII, 2 (rarely 1). Larger dimensions: TW, 0.45–0.48; HL, 0.53–0.59; PW, 0.29–0.31; MW, 0.37–0.41; AWV, 0.77–0.88; TL, 1.62–1.73.

Material.—Ex *A. alle*, the Dovekie, 6 males, 5 females, Faroe Islands, Newfoundland, Florida.

Remarks.—This is the first of four species that have only 12, less often 10 or 11, setae distributed across the metanotal margin, thereby differing from the preceding three species. While the male genitalia have similarities to both *S. boschi* and *S. wumisuzume*, additional differences associated with the dorsoanterior head plate and dimensions support these separations.

Saemundssonia montereyi (Kellogg)
(Figs. 7, 10)

Docophorus montereyi Kellogg 1896: 87. Type host: *Synthliboramphus antiquus* (Gmelin).

Male.—Much as for *S. merguli*. Dorsoanterior head plate as in Fig. 7; DPL, 0.18–0.21. Genitalia (Fig. 10) with evenly curved parameres but lacking protruding median penal structure. Larger dimensions: TW, 0.45–0.50; HL, 0.53–0.57; PW, 0.27–0.32; MW, 0.35–0.38; AWV, 0.58–0.64; TL, 1.38–1.52; GL, 0.32–0.37.

Female.—Much as for male. DPL, 0.20–0.22. Each side of tergite VII with only 3 (less often 2) setae mediad of spiracle. Large dimensions: TW, 0.50–0.56; HL, 0.57–0.62; PW, 0.30–0.33; MW, 0.40–0.43; AWV, 0.73–0.95; TL, 1.72–1.92.

Material.—Ex *S. antiquus*, the Ancient Murrelet, lectotype male, 19 male, 25 female paralectotypes of *D. montereyi* in UC, California; 1 female, Alaska. Ex *Brachyramphus marmoratus* (Gmelin), the Marbled Murrelet, 4 males, 5 females, Alaska, California.

Remarks.—The conspicuously unique mesosomal structures of the male genitalia and the large dimensions, especially the temple width, enable reliable separation of this species from *S. merguli*.

Saemundssonia fraterculae (Overgaard)
(Figs. 11–12)

Docophorus fraterculae Overgaard 1942: 10. Type host: *Fratercula arctica* (L.).

Male.—Dorsoanterior head plate as in Fig. 12; DPL, 0.21–0.25. Setae mediad of spiracle on abdominal tergite III, 2–3; IV, 4–5; V, 5–6; VI, 4–6; VII, 3–4; VIII, 1. Sternal setae close to those in Fig. 2, but with short seta on IV instead of long. Genitalia (Fig. 11) with stout evenly curved parameres and mesosomal details as shown. Dimensions: TW, 0.48–0.52; HL, 0.60–0.65; PW, 0.30–0.33; MW, 0.38–0.43; AWV, 0.66–0.71; TL, 1.61–1.77; GL, 0.40–0.45.

Female.—Similar to male. DPL, 0.20–0.23. Setae mediad of spiracle on abdominal tergite V–VI, 4–7; VIII, 1–2. Dimensions: TW, 0.53–0.57; HL, 0.61–0.66; PW, 0.34–0.37; MW, 0.43–0.45; AWV, 0.72–0.85; TL, 1.84–2.06.

Material.—Ex *F. arctica*, the Atlantic Puffin, 4 males, 4 females, Faroe Islands, Newfoundland. Ex *F. corniculata* (Naumann), the Horned Puffin, 1 female, Alaska. Ex *F. cirrhata* (Pallas), the Tufted Puffin, 1 male, 1 female, Alaska.

Remarks.—Overgaard (1942) provides such an excellent description of *S. fraterculae*, including the illustration of the male genitalia, that there is no doubt our material is representative of his species.

Saemundssonia acutipecta (Kellogg)

Docophorus acutipectus Kellogg 1896: 84. Type host: *Cerorhinca monocerata* (Pallas).

Male.—Unavailable.

Female.—Essentially as for *S. fraterculae,* except single short median sternal seta on each side of II–V and short+long pair on VI–VII (much as in Figs. 13–14).

Material.—Ex *C. monocerata,* the Rhinoceros Auklet, 3 females (including "Type" of *D. acutipectus* in UC), Oregon, California.

Remarks.—Bosch (1983:269) suggested placing *S. fraterculae* as a subspecies of *S. acutipecta.* The only differentiating feature we note between the females of these two species involves an often difficult-to-discern sternal chaetotaxy. In view of this, and with the absence of a male of *S. acutipecta,* it seems premature to endorse his action at this time.

grylle species group

The three species of this group are characterized by having the metanotal margin usually with 3 setae on each side (less often 4 on one side), with a wide central space without setae (Figs. 13–14), and the male with tergite IX medially divided.

Saemundssonia grylle (O. Fabricius)
(Figs. 13–15, 18)

Pediculus grylle O. Fabricius 1780: 218. Type host: *Cepphus grylle* (L.).
Docophorus megacephalus Denny 1842: 44. Type host: *Cepphus grylle* (L.).
Docophorus procax Kellogg and Chapman 1899: 54. Type host: *Cepphus columba* Pallas. **New synonymy**.

Male.—Dorsoanterior head plate (Fig. 15) unusually broad; DPL, 0.16–0.19. Abdomen as in Fig. 14. Setae mediad of spiracle on abdominal tergite III, 2; IV–VII, 3 (less often 4); VIII, 1. Single short median sternal seta on each side of II–V, median short+long setal pair on VI–VII. Genitalia (Fig. 18) with long curved parameres and median slender penis flanked by relatively short mesosomal sclerites each with 4 sensilla. Dimensions: TW, 0.47–0.50; HL, 0.51–0.53; PW, 0.29–0.30; MW, 0.36–0.40; AWV, 0.64–0.75; TL, 1.34–1.50; GL, 0.40–0.46.

Female.—Much as for male. Abdomen as in Fig. 13. Dimensions: TW, 0.51–0.57; HL, 0.54–0.59; PW, 0.31–0.34; MW, 0.41–0.46; AWV, 0.69–0.93; TL, 1.50–1.87.

Material.—Ex *C. grylle,* the Black Guillemot, 4 males, 6 females, Faroe Islands, Newfoundland, Labrador. Ex *C. columba,* the Pigeon Guillemot, 3 males, 16 females (including 5 female syntypes of *D. procax* in UC), Alaska, Oregon, California.

Remarks.—This species can be separated from the seven previously described species by its unique configuration of the metanotal marginal setae typical of this group. Each of the other two species of the *grylle* species group has a unique paramere and mesosomal genitalic structure, making them easy to distinguish from this species as well.

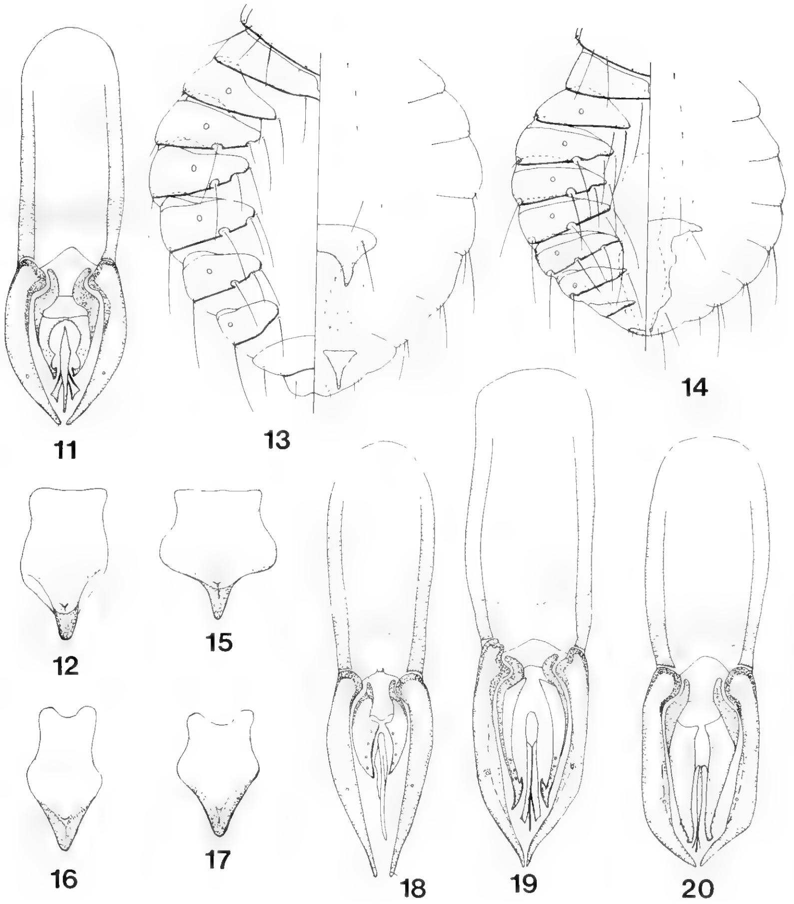
We concur with the earlier synonymy of *D. megacephalus* given by Hopkins and Clay (1952). Furthermore, our examination of *D. procax,* including syntype specimens, leaves us with no doubt that it, too, is a junior synonym of *S. grylle.* Bosch (1983) also concluded that *D. procax* was a junior synonym of *S. grylle.*

Saemundssonia celidoxa (Burmeister)
(Figs. 16, 19)

Docophorus celidoxus Burmeister 1838: 426. Type host: *Alca torda* L.

Male.—Near *S. grylle.* Dorsoanterior head plate long, narrow (Fig. 16); DPL, 0.18–0.21. Abdominal tergite on VII with 2–3 setae mediad of each spiracle. Sternum VI with medium+long setal pair, VII with only single long seta. Genitalia (Fig. 19) large, with parameres and associated mesosomal sclerites as shown. Dimensions: TW, 0.48–0.51; HL, 0.53–0.55; PW, 0.30–0.35; MW, 0.38–0.42; AWV, 0.64–0.78; TL, 1.50–1.62; GL, 0.48–0.51.

Female.—Head as for male, but slightly larger. Abdomen as for *S. grylle.* Dimen-



Figs. 11–20. 11, 12, *Saemundssonia fraterculae.* 11, Male genitalia. 12, Male dorsoanterior head plate. 13, 14, *S. grylle.* 13, Female metanotal margin and dorsoventral abdomen. 14, Male metanotal margin and dorsoventral abdomen. 15–17, Male dorsoanterior head plate. 15, *S. grylle.* 16, *S. celidoxa.* 17, *S. calva.* 18–20, Male genitalia. 18, *S. grylle.* 19, *S. celidoxa.* 20, *S. calva.*

sions: TW, 0.53; HL, 0.59; PW, 0.36; MW, 0.40; AWV, 0.92; TL, 1.77.

Material.—Ex *A. torda,* the Razorbill, 6 males, 1 female, England, Labrador.

Remarks.—Representing the second of three species with a similar marginal metanotal setal pattern, *S. celidoxa* is easily recognized by the shape of the dorsoanterior head plate and the unique genitalic details (Fig. 19 vs Figs. 18, 20).

Saemundssonia calva (Kellogg)
(Figs. 17, 20)

Docophorus calvus Kellogg 1896: 79. Type host: *Uria aalge californica* (H. Bryant).

Male.—Also near *S. grylle.* Dorsoanterior head plate as in Fig. 17; DPL, 0.15–0.19. Abdominal tergites on IV–VII usually with 3 (less often 2 on one side) setae mediad of spiracle. Sternal setae as for *S. celidoxa.* Genitalia (Fig. 20) with parameres sharply flexed at distal fourth and with slender median penis flanked by stout elongate mesosomal sclerites. Dimensions: TW, 0.49–0.53; HL, 0.49–0.56; PW, 0.29–0.32; MW, 0.37–0.40; AWV, 0.62–0.73; TL, 1.33–1.54; GL, 0.43–0.49.

Female.—Much as for male. Abdominal tergites on IV–VII usually with 3 (rarely 2 or 4 on one side) setae mediad of spiracle. Sternal setae as for *S. grylle.* Dimensions: TW, 0.53–0.60; HL, 0.51–0.59; PW, 0.32–0.35; MW, 0.38–0.46; AWV, 0.77–0.92; TL, 1.54–1.84.

Material.—Ex *U. aalge* (Pontoppidan), the Common Murre, 8 males, 9 females (including female type and female paralectotype of *D. calvus* in UC), California, Alaska, Newfoundland, Greenland. Ex *U. lomvia* (L.), the Thick-billed Murre, 7 males, 11 females, Alaska (11 host individuals), Maine, Faroe Islands, Newfoundland.

Remarks.—This is the last of the three species of the *grylle* species group. As stated earlier for each of the other two species of this group, the best distinguishing feature is the unique structure of the male genitalia.

KEY TO THE SPECIES OF *SAEMUNDSSONIA* FROM THE ALCIDAE

1\. Metanotal margin with only 6–7 setae, without any in median area (Figs. 13–14); *grylle* species group 2
– Metanotal margin with 10–16 setae, distributed across segment (Figs. 2–3) 4
2\. Dorsoanterior head plate broad (Fig. 15); male genitalia as in Fig. 18; ex *Cepphus* (guillemots) . . . . *grylle* (O. Fabricius)
– Dorsoanterior head plate narrow (Figs. 16–17); male genitalia as in Figs. 19 or 20 3
3\. Male genitalia as in Fig. 19, with slender curved parameres; ex *Alca* (Razorbill) . . . . *celidoxa* (Burmeister)
– Male genitalia as in Fig. 20, with broad, sharply flexed parameres; ex *Uria* (murres) . . . . *calva* (Kellogg)
4\. Usually with 12 marginal metanotal setae, less often 10 or 11; *merguli* species group 5
– Usually with 14 marginal metanotal setae, less often 13, 15 or 16; *wumisuzume* species group 8
5\. Female temple width <0.49; male temple width <0.44; male genitalia as in Fig. 9, with short, blunt, inwardly curved lateral mesosomal sclerites; ex *Alle* (Dovekie) . . . . *merguli* (Denny)
– Female temple width >0.49; male temple width >0.44; male genitalia as in Figs. 10 or 11, with longer different-shaped lateral mesosomal sclerites (male unavailable for *S. acutipecta*) 6
6\. Long median sternal setae on abdominal segments IV–V (as in Fig. 2); male genitalia as in Fig. 10; ex *Synthliboramphus* and *Brachyramphus* (murrelets) . . . . *montereyi* (Kellogg)
– Short median sternal setae on abdominal segments IV or IV–V (as in Fig. 14); male genitalia otherwise 7
7\. Long median sternal setae on segment V; male genitalia as in Fig. 11; ex *Fratercula* (puffins) . . . . *fraterculae* (Overgaard)
– Short median sternal setae on segment V; male unavailable; ex *Cerorhinca* (Rhinoceros Auklet) . . . . *acutipecta* (Kellogg)
8\. All abdominal tergites IV–VI each with 3 setae mediad of spiracle; male unavailable; ex *Ptychoramphus* (Cassin's Auklet) . . *insolita* (Kellogg)
– Most of abdominal tergites IV–VI each with 4–5 such setae 9
9\. Female temple width not >0.47; male temple width not >0.42; male genitalia (Fig. 1) <0.40 long, with slender evenly curved parameres; ex *Aethia pusilla* (Least Auklet) . . . . . *boschi* n. sp.
– Female temple width at least 0.48; male temple width at least 0.43; male genitalia (Fig. 8) >0.42 long, with broad, flexed parameres; ex *Aethia cristatella* (Crested Auklet) and *A. pygmaea* (Whiskered Auklet) . . . . . . *wumisuzume* (Uchida)

DISCUSSION

Table 1 shows the host list for the known alcid *Saemundssonia.* Using the host sequence given by Sibley and Monroe (1990), it is interesting that the three louse species of the *wumisuzume* species group cluster together, as do also the three species of the

Table 1. Host list for the alcid *Saemundssonia*.

Host Species(1)	Louse Species
Alle alle	*merguli*(a)
Alca torda	*celidoxa*(b)
Uria lomvia	*calva*(b)
Uria aalge	*calva*(b)
Cepphus grylle	*grylle*(b)
Cepphus columba	*grylle*(b)
(*)*Brachyramphus marmoratus*	*montereyi*(a)
Synthliboramphus antiquus	*montereyi*(a)
Ptychoramphus aleuticus	*insolita*(c)
Aethia cristatella	*wumisuzume*(c)
(*)*Aethia pygmaea*	*wumisuzume*(c)
Aethia pusilla	*boschi* n.sp.(c)
Cerorhinca monocerata	*acutipecta*(a)
Fratercula arctica	*fraterculae*(a)
(*)*Fratercula corniculata*	*fraterculae*(a)
(*)*Fratercula cirrhata*	*fraterculae*(a)

(1) Host names and sequence from Sibley and Monroe (1990).

(a) *merguli* species group.

(b) *grylle* species group.

(c) *wumisuzume* species group.

(*) New host records.

grylle species group. Principal discontinuities are shown only for the four species of the *merguli* species group, with one species appearing in the first position, one species in the middle, and two species in the last position.

The abstract provided by Bosch (1983) did not come to our attention until we had already finalized our taxonomic decisions for the alcid *Saemundssonia*. It is encouraging that our conclusions are, for the most part, consistent with what he found. Unfortunately, Bosch never published his work beyond this abstract and, therefore, none of his findings was formalized.

Waterston (1915) emphasized the significance of the louse male genitalia in species recognition by providing excellent illustrations for the genitalia of five species of auk *Saemundssonia*. Our illustrations are consistent with his.

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NOTES ON THE GENUS *LYCASTE* GISTL, AND RESURRECTION OF *CALLICOLASPIS* BECHYNÉ (COLEOPTERA: CHRYSOMELIDAE: EUMOLPINAE)

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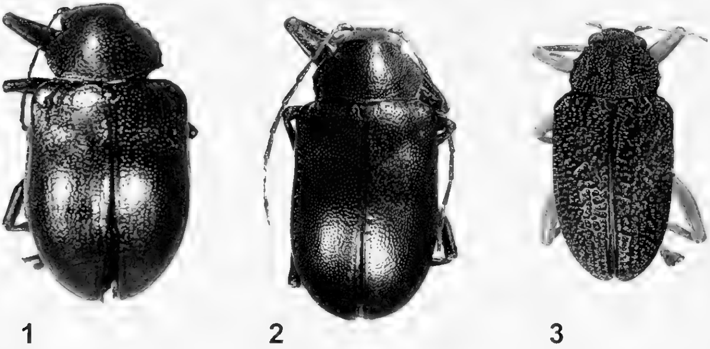
Abstract.—*Prionodera metallica* Jacoby is a **new synonym** of *Lycaste trichoa* Gistl. The genus *Lycaste* Gistl is redescribed and restricted to the species *L. trichoa* and *L. eumolpoides* (Lefèvre). The genus *Callicolaspis* Bechyné is resurrected for the remaining species formerly placed in *Lycaste*.

Key Words: Chrysomelidae, Eumolpinae, *Lycaste, Prionodera, Callicolaspis*

During a review of type specimens of the Eumolpinae genus *Prionodera* Chevrolat, I discovered that the holotype of *Prionodera metallica* Jacoby was not congeneric with either the type species of *Prionodera* (*P. bicolor* [Olivier]), or with any of the other known *Prionodera* species. The specimen, now in the Bowditch Collection at the Museum of Comparative Zoology, Harvard University, looks like a very large and brilliantly colored member of the widespread New World genus *Colaspis*. However, the specimen, a female, possesses a pair of long curved spines on the apical abdominal sternum which were unlike anything I had seen in any other Neotropical eumolpine genera. It was not until I visited the Frey Collection in the Naturhistorisches Museum in Basel—almost a decade after first studying the Jacoby type—that a second specimen of this species was seen and its identity established. It is *Lycaste trichoa* Gistl, identified and designated as the type species of *Lycaste* Gistl by Monrós and Bechyné (1956).

Bechyné (1950) erected the genus *Callicolaspis* for three large, showy South American species then placed in *Colaspis* Fabricius, two new species he described in that paper, and a sixth species described the following year (Bechyné 1951). The only unique character of the genus mentioned in the generic diagnosis was an unusually short apical tarsomere that scarcely surpassed the lobes of the third tarsomere. Later, in their review of genus names of the Chrysomelidae, Monrós and Bechyné (1956) synonymized *Callicolaspis* with *Lycaste,* designated Gistl's (1837) *L. trichoa* as the type species, and gave a brief description of *L. trichoa.* Upon further review of the species currently placed in *Lycaste,* I conclude that Monrós and Bechyné were partly right: *Lycaste trichoa* and *L.* (formerly *Callicolaspis*) *eumolpoides* (Lefèvre) are congeneric, but the remaining four species belong together in a different genus, for which *Callicolaspis* Bechyné is the available name.

Jacoby's (1884) original description and the notes in Monrós and Bechyné (1956) give an adequate description of the overall shape, color, and punctation of *Lycaste trichoa,* but they do not mention morphological characters that separate *Lycaste* species from other Neotropical Eumolpinae. In the descriptions given below, terminology of



Figs. 1–3. Dorsal views of *Lycaste* and *Callicolaspis*. 1, *L. trichoa*. 2, *L. eumolpoides*. 3. *C. heros*.

the genitalia follows Flowers (1995, 1999) and Askevold and Flowers (1994); terminology of the prothorax follows Selman (1963). Abbreviations for collections in which specimens are deposited are ENP, Escuela Nacional Politecnica, Quito, Ecuador; MCZ, Museum of Comparative Zoology, Harvard University, Cambridge, MA; NHMB, Naturhistorisches Museum, Basel, Switzerland; PUCE, Pontifica Universidad Catolica de Ecuador, Quito, Ecuador.

Lycaste Gistl 1837:404

Type species.—*Lycaste trichoa* Gistl 1837:404, designated by Monrós and Bechyné (1956)

Description.—Body elongate-oval, dorsally convex; length 11.5–13.4 mm; head, pronotum, elytra, underside, and legs dark blue, bright blue, or metallic green. *Head:* Clypeus coarsely punctate with sparse setae, punctures separated by distance less than the diameter of a puncture, surface between punctures smooth, apex of clypeus weakly emarginate. Frons finely to coarsely punctate; antennal calli smooth, swollen. Eyes oval, broadly emarginate at antennal insertion; ocular sulci weakly developed. *Antenna:* Scape elongate oval, pedicel subglobose, shorter than scape, distinctly shorter than flagellomere 1; flagellum filiform, each antennomere slightly wider at apex, elongate; antennomeres 3–6 with scattered appressed setae, antennomeres 7–11 densely pubescent, with whorl of long erect setae at apex of antennomeres 3–10; antennomere narrowly 11 spindle-shaped. *Mouthparts:* Labrum with apex strongly emarginate, with two dorsal setae and short row of lateral setae along outer margin. Mandible with outer margin with sharp bend, lateral surface smooth with scattered punctures and setae, apical teeth broad, pointed. Maxillary palpus with apical palpomere tapered or bluntly rounded. *Prothorax:* Distinctly wider than long; pronotum moderately convex, with posterior margin subequal to somewhat longer than anterior margin; basal marginal bead present, obsolete at middle; lateral margin narrowly undulate, forming three broad shallow teeth; with widest part of pronotum at or anterior to middle; disc coarsely regularly punctate. Undersurface of thorax smooth or alutaceous. Prosternum with long setae, weakly concave between fore coxae, expanded behind coxae; posterior margin of intercoxal process truncate, posterolateral angles weakly swollen. Lateral arms of prosternum with anterior margin straight, junction with prosternum continuous; surface densely setose, proepimeron weakly concave. *Mesosternum:* Subequal in width to prosternum, convex between coxae, flat on anterior face; surface punctate, with sparse short yellow setae. *Metasternum:* Convex, swollen anterior to hind coxae, weakly concave between coxae, transversely wrinkled, with sparse short yellow setae; metepisternum gradually narrowed posteriorly, with surface alutaceous. *Legs:* Sparsely covered with short prostrate setae; all surfaces alutaceous. Trochanters with strong seta on apical angle. Femora swollen in middle, tibiae multicarinate, slightly to moderately sulcate between carinae, with setae increasing in length toward apex of tibiae. Tarsi densely and uniformly pilose beneath; basal pro- and mesotarsomere distinctly longer than wide; second tarsomere broadly triangular, with acute apicolateral angles; third tarsomere longer than second, deeply bilobed; terminal tarsomere distinctly surpassing apex of third tarsomere; claws divergent, appendiculate. *Elytron:* Densely punctate; punctures confused or in irregular rows; humerus prominent, rounded; basal callus weakly to well developed; postbasal depression strong, deeper laterally. Sides subparallel or convex, convergent; apices conjointly rounded. Epipleuron narrow, acutely raised, slanted, tapering evenly from base to apex. *Scutellum:* U-shaped, with base shorter than length; surface smooth. *Abdomen:* with all segments subequal in length, surface of segments alutaceous. Sterna sparsely covered with short setae, setae longer laterally. Sternum VII of female with depressions along lateral margins and with apical margin bearing two submedian curved teeth and a median bidentate projection, and with long setae on apical margin. *Pygidium* (Figs. 8–9): Deep longitudinal groove on strongly raised central area; pygidial surface smooth, lateral margins smooth. *Female genitalia:* Segments VIII–XI forming elongate ovipositor (Fig. 14). Sternum VIII with long rod-like basal apodeme (Fig. 14, A8) and weak linear apicolateral arms (ALA) present or absent, with several setae, dorsal sclerites (DS) moderately sclerotized and widened apically with lateral branch at mid-length. Sternite IX with hemisternites (HS) with long basal rods, and paraprocts separated into a pair of long dorsal rods, apically forming hood-like projection above genital orifice (Fig. 15); baculum (B) distinct, subapical, subequal in length to gonocoxae (GC). Gonocoxae narrow, elongate, with long setae apically and laterally. Spermatheca (Figs. 17, 20) with receptacle wider than pump, duct sclerotized and forming convoluted mass at receptacle.

Remarks.—*Lycaste* can be distinguished from other Neotropical eumolpine genera by the following combination of characters: 1) Presence of curved spines on the female subgenital plate; 2) large size; 3) smooth elytra; and 4) appendiculate claws.

KEY TO SPECIES OF *LYCASTE*

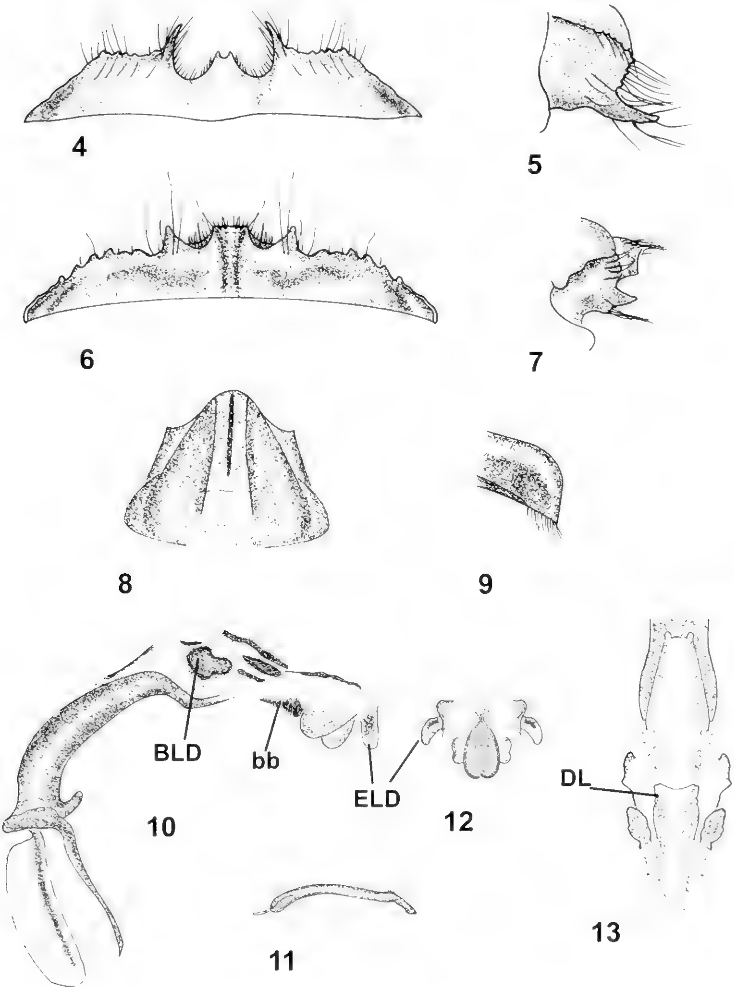
1. Elytra bright metallic green; elytral punctures striate at apex . . . . *trichoa* Gistl
– Elytra dark blue; densely punctate, non striate throughout . . . . *eumolpoides* (Lefèvre)

Lycaste trichoa Gistl
(Figs. 1, 4–5, 14–17)

Lycaste trichoa Gistl 1837:404

Prionodera metallica Jacoby 1884:128. **New synonymy**.

Female.—Body elongate-oval, dorsally convex; length 12.7 mm. Head and pronotum bright metallic blue-green, elytra metallic golden green; antenna reddish brown with green reflex. Underside and legs metallic green. Surface between punctures of head with clypeus smooth. Frons coarsely punctate, punctures separated by distance greater than the diameter of a puncture; surface between punctures smooth, shining; vertex with median impressed line. Prothorax distinctly wider than long, L/W = 0.58, pronotum moderately convex, with posterior margin somewhat broader than anterior margin; anterior angles acute, directed anterolaterally, posterior angles acute; widest part of pronotum at middle; disc coarsely, densely punctate, with punctures separated by a distance greater than their own diameters; surface between punctures smooth,



Figs. 4–13. Abdomenal and genitalic characters of *Lycaste*. 4–5, Sternum VII of *L. trichoa*. 4, Ventral view. 5, Lateral view. 6–7, Sternum VII of *L. eumolpoides*. 6, Ventral view. 7, Lateral view. 8–9, Pygidium of *L. eumolpoides*. 8, Dorsal view. 9, Lateral view. 10–13, Male genitalia of *L. eumolpoides*. 10, Median lobe and partly everted endophalus. 11, Apical sclerite. 12, Apical view of endophallic lateral digits. 13, Dorsal view of basal part of endophallus. Abbreviations: bb = basal setal field, BLD = basal lateral digit, DL = dorsal lobe, ELD = endophalic lateral digit.

shining, with numerous punctulae. Undersurface of pronotum alutaceous. Prosternum coarsely punctate. Lateral arms of prosternum with surface densely setose. Mesosternum with surface strongly punctate. Metasternum shallowly wrinkled. Femora moderately swollen in middle. Elytron finely punctate, with punctures tending to form irregular rows on disc and in apical fourth, punctures separated by distance greater than the diameter of a puncture. Surface between punctures smooth with numerous small punctulae; width across humeri 1.3 × width across pronotum, a pair of low basal costae between humerus and basal callus; basal callus well developed; postbasal depression strong, deeper laterally. Sides broadly rounded, convergent. Basal margin costate to scutellum. Abdomen with short appressed setae and surface of segments alutaceous. Sternum VII (Figs. 4–5) with a bidentate projection in center flanked by two slender incurving spines. Sternum VIII with basal apodeme elongate, rodlike, abruptly widened and weakened apically; apicolateral arms obsolete; two groups of setae apically; dorsal sclerites (Fig. 16) moderately developed, weaker and broader apically, with small recurved lateral branch at mid-length. Spermatheca (Fig. 17) with receptacle wider than pump; duct well sclerotized, contorted into a small, loose mass just beyond receptacle.

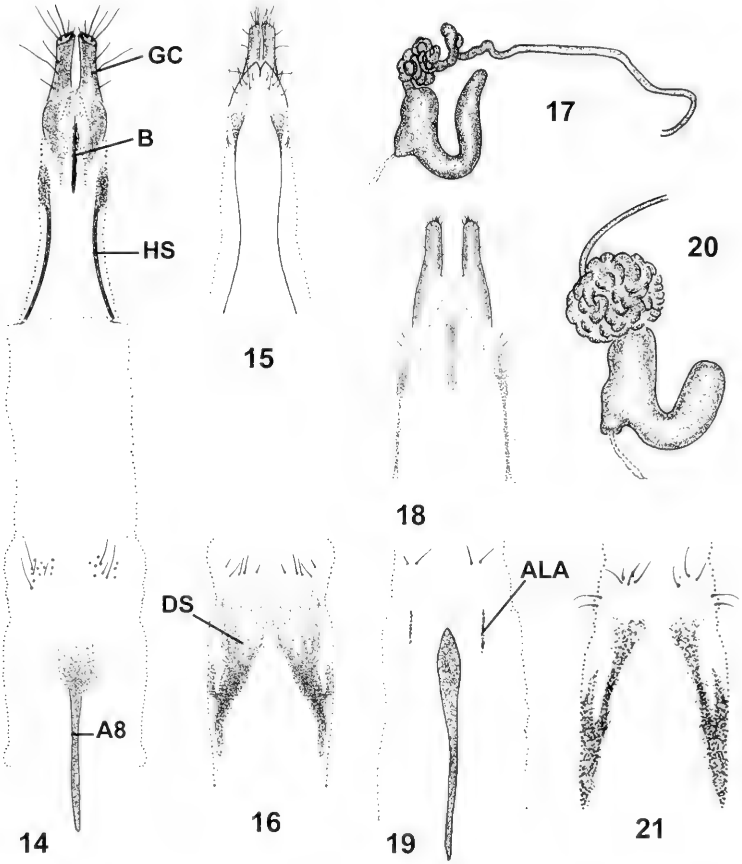
Male.—Unknown.

Specimens examined.—BRAZIL: 1 ♀ (NHMB), Brazil: Amazonas, Maués; 1 ♀ (MCZ), Amazonas/1st Jacoby Coll./Type/ (red MCZ type label) Type 9494.

Lycaste eumolpoides (Lefèvre)
(Figs. 2, 6–13, 18–21)

Colaspis eumolpoides Lefèvre 1877:136.
Callicolaspis eumolpoides: Bechyné 1950: 276.

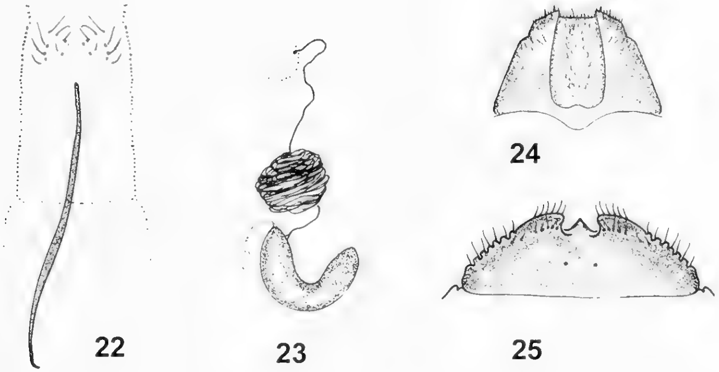
Male.—Length 11.5 mm. Head metallic green, pronotum and elytron dark blue; antenna with antennomeres 1–4 yellowish brown, washed with blue green dorsally, 5–11 piceous. Underside blue black, legs and tarsi piceous with shining blue reflex. Head with frons finely punctate, punctures separated by distance less than the diameter of a puncture; surface between punctures weakly granulate. Antenna with all segments slightly flattened. Mouthparts piceous; labrum yellowish brown. Prothorax distinctly wider than long, L/W = 0.6 ; anterior angles blunt, directed laterally, posterior angles obtuse; disc with punctures separated by a distance less than their own diameters; surface between punctures microreticulate, shining, with dense punctulae. Undersurface of thorax smooth. Ventral part of prosternum with evenly scattered large punctures, with surface wrinkled, shiny. Mesosternum with marginal beads along lateral edges, surface rugosely punctate, with sparse short yellow setae. Femora swollen in middle. Mesocoxa with a small right-angled tubercle near articulation point. Protibia flattened dorsally, evenly expanded to apex, apical margin rounded; middle and hind tibiae widened apically. Elytron densely punctate throughout, surface between punctures densely micropunctate; humeri prominent, rounded, width across humeri 1.3 × width across pronotum; basal calli weakly developed; postbasal depression shallow. Sides subparallel, convergent. Epipleuron tapering evenly from base to apical one-eighth. Abdomen with all segments subequal in length, each segment with long fine setae on apical half. Surface of segments alutaceous. Sternum VII with lateral margins smooth, a weak depression in center. Median lobe of aedeagus (Fig. 10) in lateral view curved; apex bent sharply; basal hood long, lightly sclerotized, with apodemes distinct at lateral margins of hood; subbasal fenestra present; basal spurs prominent; basal part of endophallus (Figs. 10, 12–13) with sclerotized basal (BLD) and endophallic lateral digits (ELD), additional dorsal and lateral sclerites, dorsal lobe (DL) elongate and truncate at apex, basal setal



Figs. 14–21. Female characters of *Lycaste*. 14–16, Ovipositor of *L. trichoa*. 14, Ventral view. 15, Dorsum IX. 16, Dorsum VIII. 17, 20, spermatheca. 17, *L. trichoa*. 20, *L. eumolpoides*. 18–19, 21, Ovipositor of *L. eumolpoides*. 18, Dorsum IX. 19, Sternum VIII. 21, Dorsum VIII. Abbreviations: A8 = apodeme of sternum VIII, ALA = apicolateral armos of sternum VIII, B = baculum, DS = dorsal sclerites of segment VIII, GC = gonocoxae, HS = hemisternites of segment IX.

field (bb) present; apical sclerite (Fig. 11) rodlike, well sclerotized.

Female.—Body oval; length 13.4 mm; head, pronotum, elytron and underside dark greenish, antenna and legs as in male. Prothorax distinctly wider than long, L/W = 0.67; pronotum with three broad low teeth on lateral margin. Width of intercoxal process 0.75 × diameter of procoxa, broadened behind coxa, posterior margin slightly concave. Mesosternum subequal in width to prosternum, flat, transversely wrinkled between coxae, otherwise similar to male. Legs with basal pro- and mesotarsomeres



Figs. 22–25. Female characters of *Callicolaspis heros*. 22, Sternum VIII. 23, Spermatheca. 24, Pygidium. 25, Sternum VII.

not expanded. Abdomen with all segments subequal in length. Sterna sparsely covered with short setae, setae longer laterally. Sternum VII (Figs. 6–7) with depressions along lateral margins and with apical margin bearing two submedian curved teeth and a median truncate projection, and with long setae on apical margin. Pygidium as in male. Sternum VIII (Fig. 19) with basal apodeme elongate, rodlike, slightly widened apically; apicolateral arms reduced to a pair of fine longitudinal sclerites; four setae apically; dorsal sclerites moderately developed (Fig. 21), weaker and broader apically, with apically directed lateral branch at mid-length; sternum (Fig. 18) and dorsum of segment IX as in *L. trichoa*. Spermatheca (Fig. 20) with duct well sclerotized, twisted into a round compact mass just before attachment to receptacle.

Specimens examined.—BOLIVIA: 1 ♂ (NHMB) (no other data); BRAZIL: 1 ♀ (NHMB) ob Jura, Amazon; ECUADOR: 1 ♂ (ENP) Napo, Sierra Azul (2,500 m), Oct. 95; Bosque de Aliso, Fo. Bersolsa, Col. 1 ♂ (PUCE) Yasuni 250 m, 5–6 Feb. 1997, X Cisneros, ♂ (ENP) Orellana, TBS Río Tiputini, 14–26 feb. 2001, 250 m. A. Lucky; colección manual, Bosque Húmedo Tropical. 1 ♀ Orellana, Yasuni, Onkonegare, fogging, 1996-05-(1-30), collect. P. Araujo et al. 1 ♂ same locality, Send. Murcielago 6-IV-2001 Mayer Rodríguez. 2 ♂ same locality, 1/2 km. S. orilla TBS, 07-II-02, Araujo, Ortega, Rosero. 1 ♀ Pastaza, Lorocachi, 220 m 76°09′W 01°39′S, 16–27 Feb. 1996, C. Carpio & M. Ayala.

Remarks.—*Lycaste eumolpoides* can be confused with members of the genus *Longeumolpus* Springlová. Females can be readily separated by the subgenital plate, which is spined in *Lycaste* but not in *Longeumolpus*. The only external difference in the males is the tarsal claws which are appendiculate in *Lycaste* and bifid in *Longeumolpus*.

Discussion

The remaining species considered by Bechyné to be in *Lycaste* do not share the characters of the genus and must be removed. Bechyné's original name for these species, *Callicolaspis* Bechyné, is available and is hereby resurrected, with *Colaspis heros* Lefèvre as the type species, designated by Bechyné (1950).

Callicolaspis Bechyné 1950: 275
cuneiformis Bechyné 1950: 277
guignoti Bechyné 1951: 301

heros (Lefèvre) 1877: 137
munifica (Erichson) 1847: 159
ornata (Jacoby) 1903: 183

Like *Lycaste*, *Callicolaspis* is rare in collections; outside of the Frey Collection, I have seen only a few specimens of *C. heros*. The known species of *Callicolaspis* all have a characteristic coarsely rugose metallic green pronotum and elytra, and contrasting bright orange-yellow legs. The body is elongate and somewhat tapered apically (Fig. 3), the female subgenital plate (Fig. 25) lacks the spines of *Lycaste*, and the pygidium does not have the groove on a raised area (Fig. 24). Internally, the spermatheca, spermathecal duct, and sclerites on segment VIII (Figs. 22–23) show significant differences from both species of *Lycaste*. In dorsal aspect, *Callicolaspis* resembles some of the members of the genus *Adorea* Lefèvre, specifically *A. splendida* (Jacoby), *A. chontalensis* (Jacoby) and *A. bifasciata* (Jacoby), all from Central America. Interestingly, these same *Adorea* species are the only Neotropical Eumolpinae that share with *Lycaste* the character of species specific spines on the female subgenital plate (Flowers, unpublished data).

Given the distinctive appearance of *Lycaste trichoa*, it is curious that Jacoby (1884) considered it a *Prionodera*, a genus that was (and still is) characterized by toothed anterior femora. It should also be noted that I have seen a genuine *Prionodera* species in several museums determined as *Prionodera metallica* by Bechyné. All these specimens are an undescribed species of *Prionodera* closely resembling *P. costata* Baly.

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TWO NEW SPECIES OF *PERLESTA* BANKS (PLECOPTERA: PERLIDAE) FROM EASTERN NORTH AMERICA

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Abstract.—Two new species in the Nearctic perlid stonefly genus *Perlesta* Banks are described from Virginia, USA. ***Perlesta roblei*, n. sp.**, is described from Middlesex and King and Queen counties, and ***P. puttmanni*, n. sp.**, is described from Hanover, Pittsylvania, and Prince William counties. The adult male, adult female, and egg are described and illustrated for both species.

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

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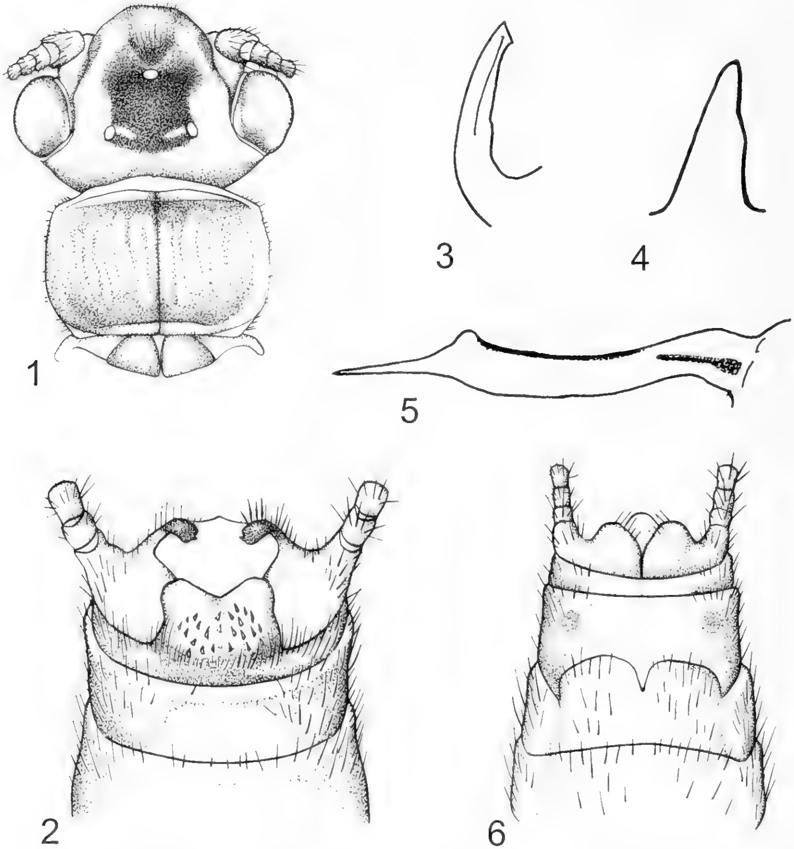
Remarkably, the Nearctic stonefly genus *Perlesta* Banks currently includes 19 species, whereas during most of the 20th century only a single widespread species was recognized (Stark 1989). Stark, in his 1989 revision, provided a firm taxonomic basis that has allowed an additional seven species to be described (Poulton and Stewart 1991, Stark and Rhodes 1997, Kirchner and Kondratieff 1997, DeWalt et al. 1998, Kondratieff and Baumann 1999, Kondratieff and Kirchner 2002, DeWalt 2002). Recently, DeWalt et al. (2001) provided a review of the genus in Illinois, recording eight species.

Kondratieff and Kirchner (1987) listed the stoneflies of Virginia. Subsequently, Stark (1989) and Kirchner and Kondratieff (1997) indicated that four species of *Perlesta* occurred in Virginia: *P. decipiens* (Walsh), *P. frisoni* Banks, *P. placida* (Hagen), and *P. teaysia* Kirchner and Kondratieff. Over the last several years Dr. Richard L. Hoffman, Virginia Museum of Natural History, submitted stonefly specimens to the authors for identification, among which were several new species of *Perlesta*. The authors collected additional adult material of two of these species, especially males with extruded penis tube + sac for comparative descriptions from several sites in the Piedmont and Coastal Plain physiographic regions of Virginia (Kondratieff and Kirchner 1987). These two species are described here. The terminology for the adults follows Stark (1989).

Perlesta roblei Kondratieff and Kirchner, new species
(Figs. 1–8)

Male.—Forewing length 8–9 mm. Head yellow with a large black to brown ocellar patch and large diffuse dark spot anterior to patch, prothorax black (Fig. 1). Forewing membrane and veins dark brown to black except for pale costal margin, pale areas proximal to arculus, along median vein anterior to cord, and in intercubital area. Femora yellow, distally and dorsally brown, tibiae brown with apices yellow. Abdominal terga black to brown posteriorly, yellowish anteriorly; sterna yellow. Cercus yellow ba-

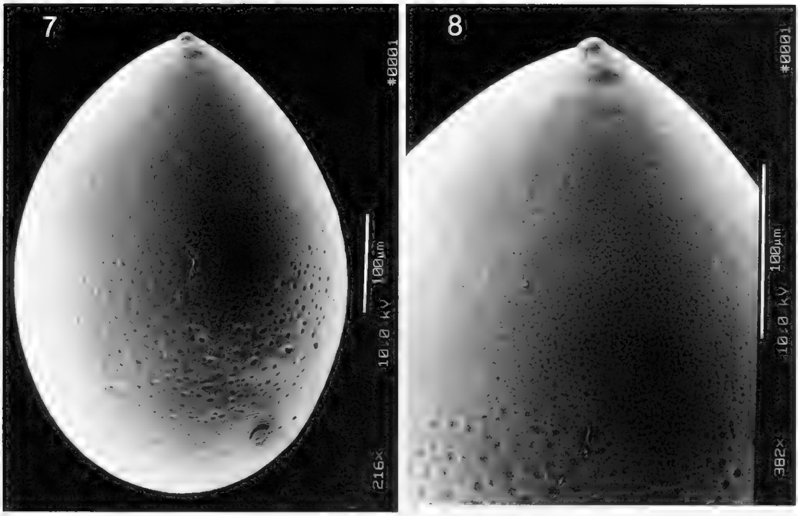


Figs. 1–6. *Perlesta roblei.* 1, Adult head and pronotum. 2, Male terminalia, dorsal. 3, Paraproct, lateral. 4, Paraproct, caudal. 5, Penis. 6, Female subgenital plate, ventral.

sally, each segment posteriorly brown, distal segments brown. Tergum 10 mesal sclerite brown, partially divided, sensilla basiconica distinct but small, not elevated into patches (Fig. 2). Paraproct in lateral view, long, slightly curved posteriad at apex, small anteapical tooth scarcely visible (Fig. 3) and not visible in caudal aspect (Fig. 4) [terminalia often need to be cleared to observe these characters]. Penis tube + sac long, caecum reduced (Fig. 5), dorsal patch narrow.

Female.—Forewing length 10–12 mm. Color pattern similar to male but paler. Subgenital plate lobes rounded to truncate and separated by a deep V-shaped notch (Fig. 6).

Egg.—Collar buttonlike (Figs. 7–8). Chorion surface with wide mesal band of shallow punctations. Eclosion line absent (Fig. 7).



Figs. 7–8. *Perlesta roblei.* Scanning electron photomicrograph of egg, 7, Entire egg, 216×. 8, Closeup of collar, 382×.

Nymph.—Not examined.

Material examined.—Holotype: ♂, VIRGINIA: Middlesex Co., Dragon Run, County Rte. 603, East Mascot, 37°38′0.9″N, 76°41′46.1″W, 22 May 2002, B. Kondratieff and R. Kirchner. Paratypes: Same as holotype, 27 ♂, 8 ♀; King and Queen County, Dragon Run, Big Island, 22 May 2002, Kondratieff, Kirchner, and Roble, 3 ♂, 4 ♀; Dragon Run Swamp, County Rte 603, NE Mascot, 19 May 2000, VDNH Survey, 2 ♂, 1 ♀.

The holotype is deposited at the National Museum of Natural History, Smithsonian Institution, Washington, D.C. Paratypes are deposited in the following museums and individual collections: Bill P. Stark, Clinton, Mississippi; C. P. Gillette Museum of Arthropod Diversity, Colorado State University; Illinois Natural History Survey, Urbana; Ralph F. Kirchner, Huntington, West Virginia; and the Virginia Museum of Natural History, Martinsville.

Etymology.—We honor Dr. Steven M. Roble, Virginia Department of Conservation and Recreation. His passion for the preservation of rare and imperiled insects of Virginia is exemplary.

Diagnosis.—*Perlesta roblei* is generally similar to at least eight species listed in Table 1. The male of *P. roblei* would key to couplet 6 in Stark (1989), including *P. adena* Stark and *P. cinctipes* (Banks), and is similar to both species, and *P. xube* Stark and Rhodes. However, the male of *P. roblei* differs in the structure of the paraprocts or aedeagus from both *P. adena* (see Stark 1989, figs. 71, 76), *P. cinctipes* (see Stark 1989, figs. 28, 32), and *P. xube* (see Stark and Rhodes1997, figs. 3–4, 6). The caecum of the aedeagus of *P. roblei* (Fig. 5) is reduced, distinguishing it from both *P. adena* and *P. xube.* In *P. roblei* the small anteapical tooth of the paraproct is scarcely visible in lateral view (Fig. 3), whereas in *P. cinctipes,* the mesoapical tooth of the paraproct is clearly visible in lateral view.

The egg of *P. roblei* is similar to *P. ad-*

Table 1. Comparison of the dark species of *Perlesta*.

Species	Tergum 10	Paraprocts in Lateral View	Caecum	Femora Pigmentation	Egg Collar	Geographic Range
adena	almost divided	long, slender mesoapical tooth	long/large	dorsal band	buttonlike	TN, OH
baumanni	entire	short, strongly curved apical tooth	unknown	distodorsal band	unknown	Quachita Mountains
browni	entire	long, slender mesoapical tooth	long	banded	short	Ozark-Quachita
cinctipes	partially divided	long, slender mesoapical tooth	long	banded	short, wide	midwestern to Ozarks
dakota	entire	long, slender subapical tooth indistinct	long	broad dorsal band	buttonlike to obscure	ND, SD
etnieri	entire	long, slender small mesoapical tooth	absent	dorsal band	obscure	TN
fusca	partially divided	short-triangular small apical tooth	reduced	distodorsal band	obscure	Ozarks
roblei	partially divided	long, slender mesoapical tooth	reduced	dorsal band	buttonlike	VA
xube	almost divided	long, slender, subapical tooth directed mesad	short	foreleg, dorsal band; mid/hind banded	obscure	NE to IL

ena, P. bolutka Stark, *P. dakota, P. fusca* Poulton and Stewart, *P. lagoi* Stark, *P. nitida* Banks, and *P. xube*. From the other known Virginia species, the small buttonlike collar distinguishes the egg of *P. roblei*.

Additionally, the darker coloration of the body and the deep V-shaped notch of the subgenital plate separate the female from all known sympatric species.

Remarks.—Dragon Run is a low gradient black-water stream that flows into the Piankatank River of the Chesapeake Bay. At the type locality, *Vallisneria americana* Michx. is common in the swifter zones of the stream, and the dominant riparian cover is *Taxodium distichum* (L.) Rich. The elevation at the site is 7.6 m and the stream gradient 0.5 m/km. Other adult stoneflies collected at the type locality were *Isoperla* nr. *davisi* James and another undescribed species of *Perlesta*.

Perlesta puttmanni Kondratieff and Kirchner, new species

(Figs. 9–15)

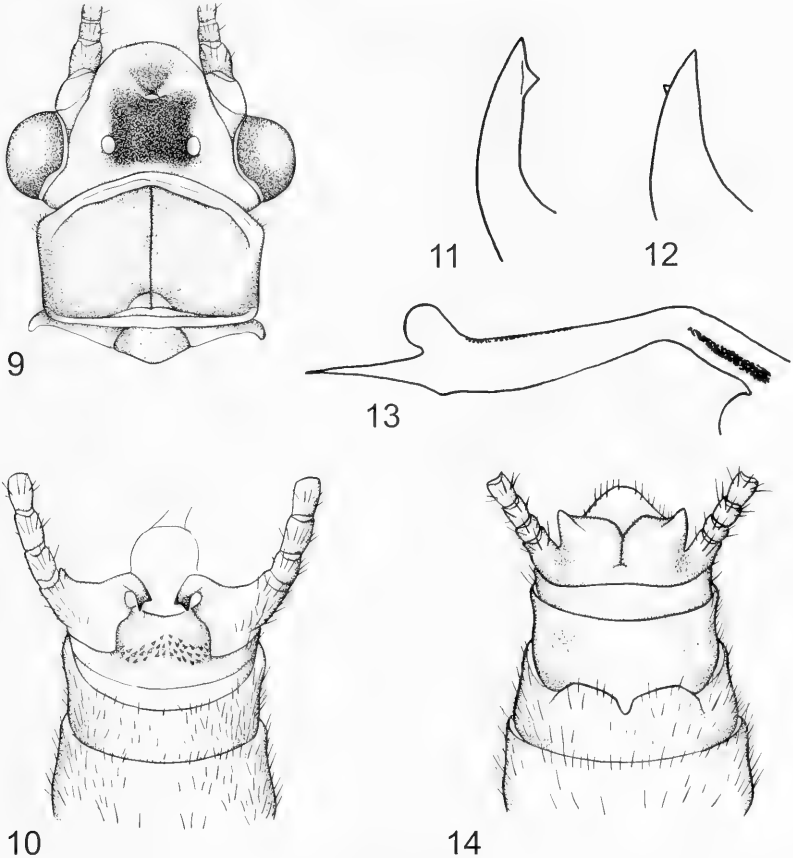
Male.—Forewing length 8–9 mm. General body color yellowbrown. Head yellow except for brown quadrangular area over ocelli, and small brown triangular area forward of median ocellus (Fig. 9). Wings yellow brown to amber. Femora with dusky brown dorsal band. Tergum 10 mesal sclerite light brown, not divided, sensilla basiconica distinct but small, not elevated into patches (Fig. 10). Paraproct short, stout, broad at base, with a prominent subapical mesad directed tooth (Fig. 11), visible in caudal view (Fig. 12). Penis tube + sac long, caecum prominent, long as wide, lateral sclerite prominent, dorsal patch narrow (Fig. 13).

Female.—Forewing length 9.5–10.5 mm. Subgenital plate with short broad lobes separated by shallow triangular notch (Fig. 14).

Egg.—Distinct collar short, anchor pedicel composed of many filaments (Fig. 15). Chorion finely punctate. Micropylar row set around anterior surface of eclosion line (Fig. 15).

Nymph.—Not examined.

Material examined.—Holotype: ♂, VIRGINIA: Hanover Co. South Anna River, Co. Rte. 657, 37°47′5.4″N 77°35′5.9″W, 23 May 2002, B. Kondratieff and R. Kirchner. Paratypes: Same data as holotype, 6 ♂, 2



Figs. 9–14. *Perlesta puttmanni.* 9, Adult head and pronotum. 10, Male terminalia, dorsal. 11, Paraproct, lateral. 12, Paraproct, caudal. 13, Penis. 14, Female subgenital plate, ventral.

♀; Pittsylvania Co., Banister River, Co. Rte. 640, 21 May 2002, B. C. Kondratieff and R. F. Kirchner, 2 ♂; Prince William Co., Cedar Run, 0.4 km S Camp Upshur, Quantico Marine Corps Base, 7 June 1999, A. C. Chazal, 13 ♂, 6♀; same but Copawamsic Creek, 9 June 1999, 3 ♂, 4 ♀.

The holotype is deposited at the National Museum of Natural History, Smithsonian Institution, Washington, D.C. Paratypes are deposited in the following museums and individual collections: Bill P. Stark, Clinton, Mississippi; C. P. Gillette Museum of Arthropod Diversity, Colorado State University; Illinois Natural History Survey, Urbana; Ralph F. Kirchner, Huntington, West Virginia; and the Virginia Museum of Natural History, Martinsville.

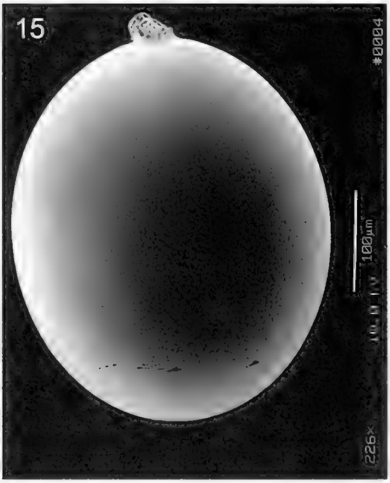


Fig. 15. *Perlesta puttmanni.* Scanning electron photomicrograph of egg, 216×.

Etymology.—We honor Steven J. Puttmann, Colorado Division of Wildlife, for his many contributions to the natural history of Colorado. His zeal to enhance the aquatic communities of Colorado is appreciated.

Diagnosis.—With the large prominent directed tooth of the paraproct (Fig. 11), the male of *P. puttmanni* could key to couplet 11 of Stark (1989), which includes *P. nitida* and *P. bolukta.* However, *P. puttmanni* is easily distinguished by the prominent mesoapical inwardly directed paraproctal tooth (Fig. 11), paraprocts curved in caudal view with point of tooth visible (Fig. 12), and the narrow spinule patch of the aedeagal tube (for *P. nitida,* see Grubbs and Stark 2001, fig. 1 and for *P. bolukta,* see Stark 1989, fig. 88). The general habitus of the male of *P. puttmanni* is similar to the sympatric *P. placida,* but the male of *P. placida* is readily characterized by the thin paraprocts usually lacking a tooth in lateral view (See Stark 1989, fig. 22). The subgenital plate of *P. puttmanni* (Fig. 14) is similar to *P. shubuta* Stark, but the anchor pedicel of the egg is composed of many filaments (Fig. 15).

Remarks.—Other stoneflies known from the South Anna River include *Allocapnia rickeri* Frison, *Amphinemura nigritta* (Provancher), *Taeniopteryx maura* (Pictet), *T. parvula* Banks, *Strophopteryx fasciata* (Burmeister), *Paragnetina fumosa* Banks, *Agnetina flavescens* (Walsh), *Acroneuria abnormis* (Newman), *Perlesta placida* (Hagen), *P. decipiens* (Walsh), *Suwallia marginata* (Banks), *Helopicus subvarians* (Banks), *Isoperla* spp., and *Pteronarcys dorsata* (Say). The ecology of several species of insects has been extensively studied from this river (Kondratieff and Voshell 1980, Parker and Voshell 1982). The South Anna River at the type locality is characterized by a long series of rifles, beds of *Justicia americana* (L.), and mats of *Podostemum ceratophyllum* Michaux on the rocks. The elevation at the site is 38 m and the gradient 3.4 m/km.

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We thank Bill P. Stark of Mississippi College for confirming the specific status of both species and the fine SEM photographs. Dr. Richard L. Hoffman is thanked for making material available and for guiding us to some of the collection sites. Steven M. Roble made arrangements for us to access the Dragon Run sites, and joined us in the field. The views of R. F. Kirchner do not purport to reflect the position of the Department of the Army or the Department of Defense.

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NOMENCLATURAL CHANGES IN THE DIASPIDIDAE (HEMIPTERA: COCCOIDEA)

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Abstract.—A database containing taxonomic information on two subfamilies of the diaspidid scale insects of the world is available on the World Wide Web. Several nomenclatural changes need to be validated including: *Diaspis amygdali rubra* (Maskell) new illustration and lectotype designation; *Diaspis barberi* Green **new junior synonym** of *D. amygdali rubra* and lectotype designation; *Pseudaulacaspis ernesti* Miller, Gimpel, and Williams a **new replacement name** for *Diaspis grandilobis* Green (junior, secondary homonym of *Diaspis grandilobis* (Maskell)) and new illustration; *Diaspis grandilobis* Green lectotype designation; *Lepidosaphes linearis* (Modeer) discussed as a species *incertae sedis*; *Pseudaulacaspis frutescens* (Hu) **new combination**; *Lepidosaphes meliae* (Tang) **new combination**; *Lepidosaphes lithocarpicola* (Tang) **new combination**, and *Lepidosaphes pseudogloverii* (Borchsenius), **new combination**. The correct spelling of an Asian armored scale should be *Chionaspis kinshinensis* Kuwana, not *C. kiushuensis*. Twenty-six changes of adjectival species epithets are necessary for gender agreement with the genus.

Key Words: armored scales, Coccoidea, Diaspididae, ScaleNet, catalog, new combinations, lectotype, internet

We recently completed a draft of a database on two subfamilies of the Diaspididae or armored scales (Diaspidinae and Leucaspidinae) of the world including about 1,500 valid species. This research is part of a larger project called "ScaleNet" (Ben-Dov et al. 2002) to develop a queriable systematic database of the Coccoidea of the world (see Ben-Dov et al. 1997, Miller et al. 2002, and Miller and Gimpel 1996). A controversial subject in synthesizing systematic data on diaspidids is to clarify the status of genera in the Lepidosaphini. Borchsenius (1966) recognized many genera that we considered to be synonyms of *Lepidosaphes* Shimer, such as *Mytilaspis* Targioni Tozzetti, *Cornuaspis* MacGillivray, *Scobinaspis* MacGillivray, *Insulaspis* Mamet, *Paralepidosaphes* Borchsenius, *Cornimytilus* Borchsenius, *Eucornuaspis* Borchsenius, *Parainsulaspis* Borchsenius, *Pinomytilus* Borchsenius, and *Pistaciaspis* Borchsenius. Other researchers such as Takagi (1970), Danzig (1993), Gill (1997), and Williams and Watson (1988) agreed that there were insufficient criteria for the separation of these genera. Unfortunately, synonymy of these genera causes several new combinations to be formed and they are given here.

A similar situation occurred with *Phenacaspis* Cooley and Cockerell which is widely considered to be a junior synonym of *Chionaspis* Signoret. In fact, Knipscher et al. (1976) demonstrated that *Phenacaspis nyssae* (Comstock) was the leaf form of *Chionaspis sylvatica* Sanders which occurs on the bark. Liu et al. (1989) provided information on other species with bark and leaf forms that previously were placed in *Chionaspis* and *Phenacaspis*. Others agreeing with the synonymy of *Chionaspis* and *Phenacaspis* include: Takahashi (1953), Takagi (1985), and Danzig and Pellizzari-Scaltriti (1998); those who considered them as distinct include: Borchsenius (1966), Yang, (1982), and Chen (1983). Species once included in *Phenacaspis* are now usually placed in *Chionaspis, Pseudaulacaspis* MacGillivray (Takagi 1985), or *Rutherfordia* MacGillivray (Takagi et al.1989).

DEPOSITORIES

Abbreviations given for type depositories are as follows: BMNH—The Natural History Museum, London, U.K.; NZAC—New Zealand Arthropod Collection, Landcare Research, Auckland, New Zealand; USNM—United States National Entomological Collection, National Museum of Natural History, Washington, D.C., U.S.A.

NEW COMBINATIONS

Pseudaulacaspis frutescens (Hu), **n. comb.**
Phenacaspis frutescens Hu 1986: 217

Lepidosaphes meliae (Tang), **n. comb.**
Paralepidosaphes meliae Tang 1986: 278

Lepidosaphes lithocarpicola (Tang), **n. comb.**
Cornimytilus lithocarpicola Tang 1986: 71

Lepidosaphes pseudogloverii (Borchsenius), **n. comb.**
Insulaspis pseudogloverii Borchsenius 1964: 160.

SPECIES INCERTAE SEDIS

Lepidosaphes linearis (Modeer), *incertae sedis*

Chermes arborum linearis Geoffroy 1762: 509
Coccus linearis Modeer 1778: 22
Mytilaspis linearis: Targioni Tozzetti 1868: 737
Lepidosaphes linearis: Lindinger 1936: 149

Remarks.—There has been much confusion about both the identity and authorship of *Coccus linearis*. It was originally described by Geoffroy (1762), but his description is invalid because he did not consistently use binominal nomenclature (Commission on Zoological Nomenclature Opinion 228). It was Modeer (1778) who gave the first valid description even though he was validating the work of Geoffroy. The author of the species has been given as several different individuals including: Targioni Tozzetti (Borchsenius 1966); Geoffroy (Signoret 1870); and Geoffroy and Modeer (Douglas 1886). *Lepidosaphes linearis* also has been considered a junior synonym of both *L. conchiformis* (Gmelin) (Gómez Menor Ortega 1937, 1956; Borchsenius 1966) and of *L. ulmi* (Linnaeus) (Lindinger 1911, 1931; Green 1928). Cockerell (1894) thought that it might be a senior synonym of *L. pomorum* Bouché (= *L. ulmi*). To further confuse matters, *Diaspis linearis* Costa is a junior synonym of *L. ulmi*. Because original material is apparently lost and we are unable to determine the true identity of this species, we consider it to be a species *incertae sedis*.

HOMONYMY, LECTOTYPE, AND REPLACEMENT NAME

Pseudaulacaspis ernesti Miller, Gimpel, and Williams, **new replacement name** (Fig. 1)

Diaspis grandilobis Green 1922: 1015
Pseudaulacaspis grandilobis: Lindinger 1935: 130
Chionaspis grandilobis: Takagi 1970: 52

Fig. 1. Adult female *Pseudaulacaspis ernesti*, Peradeniya, Sri Lanka, on *Diospyros thwaitesii*, E. E. Green.

Pseudaulacaspis grandilobis: Takagi 1975: 23

Remarks.—We concur with Lindinger's placement of *D. grandilobis* Green in *Pseudaulacaspis* as did Takagi (1975). Therefore, *Pseudaulacaspis grandilobis* Green (1922) became a junior, secondary homonym of *P. grandilobis* (Maskell 1894) when the latter species was moved into *Pseudaulacaspis* by Takagi (1985). Because no replacement name was given, we have selected the epithet "*ernesti*" in honor of Edward Ernest Green, the author of the species. A lectotype is here designated for *Diaspis grandilobis* Green to stabilize the nomenclatural status of this previously poorly known species. We have examined a single type slide which contains a series of syntypes as follows: a second instar, 4 complete adult females, 1 torn adult-female pygidium, and 1 prepygidium (probably from the same specimen). The slide is labeled as follows: right "Diaspis grandilobis/ ~~flacourtiae~~/ Green ~~Ruthfd.~~/ from Diospyros/ thwaitesii/ Ceylon." left label "TYPE." We have placed a label on the back of the slide that gives a map of the location of the lectotype. The lectotype is the smallest of the adult females and is located in the center of the cover slip. It is deposited in BMNH.

Because the identity of this species is not well known, we have included an illustration of the adult female (Fig. 1). In general appearance it resembles *Rutherfordia major* (Cockerell) by having an oval to turbinate body, large median lobes, and numerous macroducts. It possesses well-developed second and third lobes, however, and in *Rutherfordia*, these characters are rudimentary according to the concept of Takagi et al. (1989). Within *Pseudaulacaspis*, *P. ernesti* Miller, Gimpel, and Williams is most similar to *P. pentagona* (Targioni Tozzetti), *P. prunicola* (Maskell), and *P. manni* (Green). The former two species differ by lacking macroducts on the thorax. *Pseudaulacaspis manni* is more elongate and only the median and second lobes are well developed.

LECTOTYPE DESIGNATION

Pseudaulacaspis rubra (Maskell), **new status**

(Figs. 2–3)

Diaspis amygdali rubra Maskell 1898: 228
Diaspis barberi Green 1908: 35–36, **new synonymy**
Aulacaspis barberi: Rutherford 1915: 110
Pseudaulacaspis barberi: MacGillivray 1921: 316

Remarks.—Maskell (1898) included two species (from two locations) in the type series of *Diaspis amygdali rubra*. One species was from Japan on *Orixa japonica* Thunb. and was considered to be *Pseudaulacaspis prunicola* by Davidson et al. (1983). They treated *Diaspis amygdali rubra* as a junior subjective synonym of *P. prunicola* but did not designate a lectotype to formalize the action. The second part of the type series was from Sri Lanka (= Ceylon) on *Loranthus* sp. collected by Koebele (Koebele lot no. 1410; Maskell lot no. 565). (There is a note in the Maskell correspondence file at the USNM indicating that Koebele collected the specimens in Kandy, Ceylon). The second series of specimens is the same species as *Diaspis barberi* Green (1908). To clarify the identity of these species and to stabilize their nomenclatural status, we here designate lectotypes of *Diaspis amygdali rubra* and *Diaspis barberi*.

We have selected the lectotype of *D. amygdali rubra* from the series of specimens from Sri Lanka, thus making *Diaspis amygdali rubra* (= *Pseudaulacaspis rubra*) the valid name and *D. barberi* (= *Pseudaulacaspis barberi*) a junior synonym. This action will allow the primary type to be part of the Maskell collection in NZAC, and will include a series of paralectotype specimens in the USNM.

From the syntype series of slides we have selected as lectotype an adult female mounted alone which is labeled as follows:

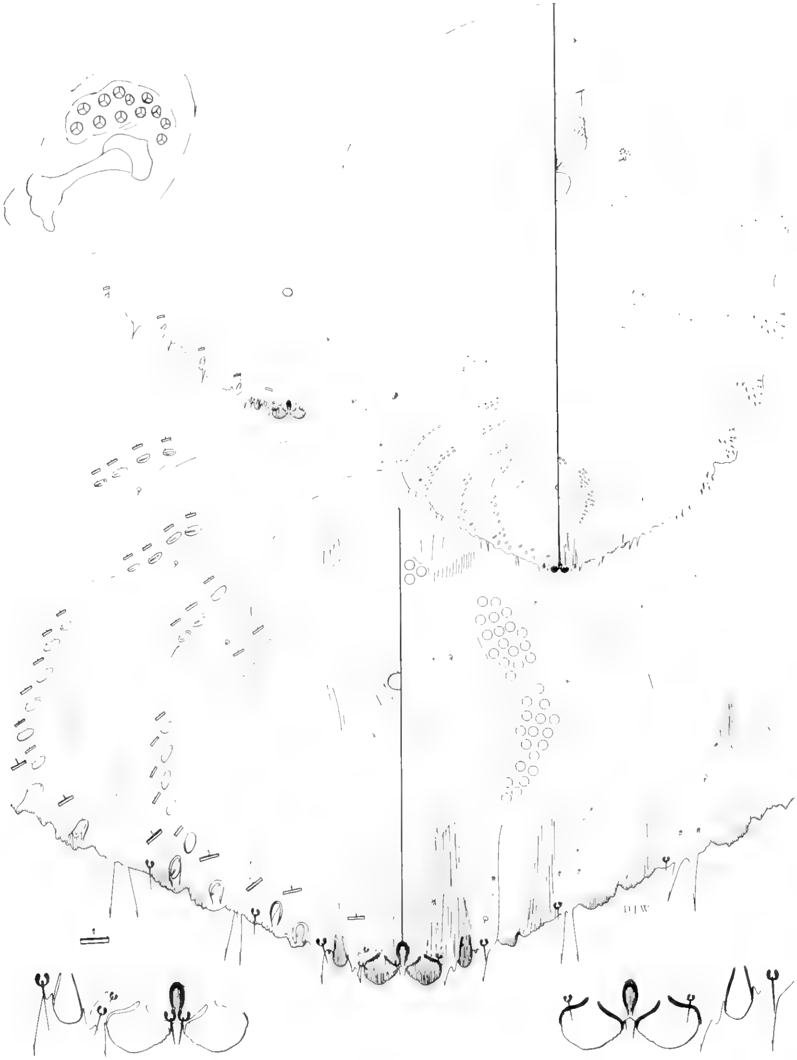

Fig. 2. Adult female *Pseudaulacaspis rubra*, Tanjore, India, on *Loranthus* sp., C. A. Barber. Showing round body form.

Fig. 3. Adult female *Pseudaulacaspis rubra,* Bangalore, India, on mango stems, VII-1973, Q. K. U. Kumar. Showing more elongate body form.

left "Diaspis/ amygdali/ var/ rubra/ adult female/ 1897 W. M. M./ Entomology Div., DSIR, NZ/ W.M. Maskell Collection." We have placed a label on the right side of the slide indicating that it is the lectotype. This is an original slide that was mounted by Maskell and is deposited in NZAC. In addition, there are 6 other slides in the USNM from the type series as follows: 1 slide with part of a cover; 1 with 2 adult females; 1 with 5 first instars; 1 with 1 first instar, 2 second instars, an immature soft scale, and a very poor prepupa; 1 with 3 adult females; and 1 with 3 adult female scale covers. These were mounted after the original description was published from dry type material and are paralectotypes with the exception of the soft scale.

The type series of *D. barberi* consists of 1 original slide that contains 6 second-instar females and 6 adult females. The slide is labeled as follows: right "Diaspis/ barberi, Green (~~type~~)/ From Loranthus/ Tanjore, India/ Coll. C. A. Barber" left label "TYPE." The lectotype is an adult female and is closest to the bottom of the cover slip. We have placed a label on the back of the slide that gives a map of the location of the lectotype. The lectotype slide is deposited in BMNH. There are 2 additional slides that were mounted from dry type material with the same data as the original slide. They each contain 2 adult females: 1 slide is in BMNH and 1 is in USNM.

Because the identity of this species is not well known, we have included two illustrations of the adult female. Fig. 2 shows a specimen with an oval body from *Loranthus,* and Fig. 3 shows a female with a more elongate body from mango. This species is most similar to *Pseudaulacaspis prunicola* by having: an oval body shape; simple pygidial gland spines; and 3 distinct pairs of lobes. *Pseudaulacaspis rubra* differs by having at least 2 submedial macroducts on each side of segment 6, whereas, these are absent from *P. prunicola.*

CHANGED SPECIES EPITHET ENDING

Under normal circumstances, changes in species epithet endings to agree with generic gender would not be worth mentioning in a nomenclatural paper, but in this instance it seemed best to provide a journal reference for these changes rather than a web page such as ScaleNet. Thus, we are including a series of species epithet ending changes.

Aulacaspis intermedia for *Aulacaspis intermedius* Chen, Wu, and Su, 1980: 290, 295. *Chionaspis discadenata* for *Chionaspis discadenatus* Danzig, 1976: 3.

Coccomytilus convexus for *Mytilaspis convexa* Maskell, 1894: 70.

Diaspis carmanica for *Diaspis carmanicus* Davatchi and Balachowsky, 1956: 106–109.

Diaspis cuneata for *Diaspis cuneatus* Vernalha, Rocha, Loyola, and Gabardo, 1965: 5–7. *Diaspis digna* for *Diaspis dignus* Hoke, 1928: 671–672.

Diaspis obliqua for *Diaspis obliquus* Costa, 1829: 21.

Diaspis uniglandulosa for *Diaspis uniglandulosus* Balachowsky and Ferrero, 1967a: 985–988.

Discodiaspis numidica for *Rugaspidiotus numidicus* Balachowsky, 1949: 107–108.

Ferreroaspis hungarica for *Acanthomytilus hungaricus* Vinis, 1981: 201–207.

Guizhoaspis subterranea for *Guizhoaspis subterraneus* Young, 1986: 205–206.

Heimaspis centrafricana for *Heimaspis centrafricanus* Balachowsky and Ferrero, 1967b: 40–42. *Kuwanaspis foliosa* for *Kuwanaspis foliosus* Wu, 1986: 306–307.

Kuwanaspis multipora for *Kuwanaspis multiporus* Tang, 1986: 95.

Lepidosaphes cornuta for *Lepidosaphes cornutus* Ramakrishna Ayyar, 1937: 147.

Lepidosaphes lobulata for *Mytilaspis lobulatus* Froggatt, 1914: 680.

Mohelnaspis toletana for *Berlesaspis toletanus* Gómez-Menor Ortega, 1927: 289–292.

Nimbaspis reticulata for *Nimbaspis reticulatus* Balachowsky, 1952: 129–132.

Nimbaspis squamosa for *Nimbaspis squamosus* Balachowsky and Ferrero, 1967c: 1021–1025. *Pinnaspis tuberculata* for *Pinnaspis tuberculatus* Tang, 1986: 297–298.

Protodiaspis parvula for *Protodiaspis parvulus* Cockerell, 1898: 428–429.

Protodiaspis vara for *Protodiaspis varus* Hoke, 1928:672–674.

Pseudaulacaspis sordida for *Pseudaulacaspis sordidus* Hempel, 1932: 333–334.

Sclopetaspis lanigera for *Chionaspis laniger* Newstead, 1920: 206–207.

Sclopetaspis malawica for *Sclopetaspis malawicus* Munting, 1970: 12–14.

Vinculaspis mamillata for *Vinculaspis mamillatus* Fonseca, 1973: 254–255.

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A REVISION OF *DARMISTUS* STÅL (HEMIPTERA: ALYDIDAE: MICRELYTRINAE)

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Abstract.—*Darmistus* Stål, a member of the micrelytrine tribe Micrelytrini, is revised and its three species keyed. These species are *D. subvittatus* Stål, *D. duncani* Van Duzee, and *D. crassicornis* Van Duzee. *Rimadarmistus* Bliven is synonymized with *Darmistus* (**new synonymy**), and *R. messor* and *R. deprecator* are both synonymized with *Darmistus subvittatus* (**new synonymy**). The genus is distributed from Washington State east into Kansas and Nebraska, and south into Costa Rica. The relationships of the genus are obscure; the similarity in its clypeal-paraclypeal relationship to that of *Protenor* Stål suggests a possible affinity. Members of the genus are probably grass-feeders, and males are attracted to carrion.

Key Words: Insecta, Hemiptera, Heteroptera, Alydidae, Micrelytrinae, *Darmistus, Rimadarmistus, Protenor,* grass-feeding, distribution

Darmistus Stål is a member of the micrelytrine tribe Micrelytrini. It has never been revised, and the keys to its species are either rather difficult to use (e.g., Van Duzee 1937, Torre Bueno 1941) or do not include all three species (Brailovsky and Flores 1979). The descriptions and redescriptions of the genus and of the species also are rather brief. Because representatives of the genus are common in collections from Mexico and the western United States, a revision of the genus is desirable.

The published range of the genus extends from California south into the American southwest, and thence south into Central America. Deay (1928) lists it from Kansas. In addition, I include here records of *D. subvittatus* from Washington State, Wyoming, and Nebraska.

Specimens were studied from the following institutions: California Academy of Sciences (CAS), Texas A&M University (TAMU), University of California at Berkeley (UCB), University of Connecticut (UCT), and the National Museum of Natural History, Smithsonian Institution (USNM).

Darmistus Stål 1860
(Figs. 1–2)

Darmistus Stål 1860: 469 (orig. descr.; type species: *Darmistus subvittatus* Stål, monotypy); Stål 1867: 543 (key); Stål 1873: 88 (key); Lethierry and Severin 1894: 100 (cat.); Fracker 1918: 258 (note); Deay 1928: 387 (key).

Rimadarmistus Bliven 1956: (orig. descr.; type species: *Rimadarmistus messor* Bliven, by designation); Froeschner 1988: 10 (cat. N. Amer.). **New synonomy**.

Description.—*Total length* (tip of abdomen): 8.5–11 mm. *General color:* Brown to yellow-brown, except following areas, where heavily punctate with dark punctations: much of medial area of head, prothorax, scutellum (except tip pale), corium (except anteriorly where lateral edges bear pale punctures, and tip sometimes pale). Venter pale yellow-brown, thorax with dark punctations laterally; usually with very small red punctations on abdominal venter. *Head:* About twice as long as wide (width behind eyes); parallel-sided behind antennae and behind eyes; paraclypei surpassing clypeus, meeting or nearly meeting in front of clypeus (Table 3, Fig. 1); ocelli small, on small dark brown ocellar tubercle, close to midline, distant from eyes; small brown or pale patch of micropunctations lateral to each ocellus (very indistinct when pale, as in *D. subvittatus*); distinct longitudinal midcephalic sulcus (groove) just anterior to level of anterior border of eye, about as long as width of an antennifer; medial half of head, and narrow band from antennifer to eye and from eye to head's base heavily beset with small dark punctations bearing small dark setae; these absent from lateral one-fourth of head (each side), from region around midcephalic sulcus, from paraclypei, and from antennifers, and sparse to absent medially from midocular level posteriorly to base of head; this absence continuing onto pronotum, giving appearance of a pale median line or stripe; bucculae small, pale, hemispherical, just reaching level of antennifers; underside of head glabrous. Antennal segments often darker than ground color; with setae longer than those on body; segment IV with many small setae; segment I stout, much surpassing head; other segments more slender; segment IV fusiform; measurements and ratios: Table 2. Rostrum reaching onto mesosternum; first rostral segment just reaching base of head; pale, except tip and ventral surface of segments II and III dark. *Thorax:* Pronotum nearly as long as wide, sides evenly and gradually tapering from posterior to anterior; with slight collar demarked posteriorly by low broad transverse ridge not reaching lateral edges; collar and ridge about the same width; posterior margin very slightly and broadly concave, sharply and narrowly declivent; humeral angles bluntly rounded, subterminally with low rounded callus; pronotum (except transverse ridge) heavily beset with dark punctations, these each bearing a very small dark seta; punctations fewer on transverse ridge (except submedially), becoming nearly absent laterally on pronotum; scutellum 1.5–2 times as long as wide, tip rounded, pale. Legs yellow brown, last tarsal segment and claws darker; setae on legs pale, longer than those on body, dark setiferous punctations making legs appear brown-spotted; each coxa with a small round dark spot laterally and another posterolaterally; fore- and midcoxae nearly touching, hind coxae further apart; hind femora not surpassing abdomen. Forewing as long as or just surpassing abdomen; corium not or somewhat extended posteriorly, lateral margin all or partly pale, apex sharp, color variable; clavus with 4–5 rows of punctures, the lateralmost row removed from others; membrane nearly clear to pale brown. Thoracic venter smooth medially, pleura with dark setiferous punctations dorsally (especially on propleuron); with dark mid-metasternal line. Metathoracic scent gland opening elongate, directed anterolaterally; peritreme slightly raised, evaporative area glabrous, rugose. *Abdomen:* Trichobothria only slighter longer than abdominal setae but less recumbent, their bases dark; spiracles pale. *Male genitalia:* Median extension of genital capsule's ventral rim sharp, prolonged, spinelike.

Type species.—*Darmistus subvittatus* Stål 1860. The date of this publication is often thought to be 1859 (see Froeschner 1988, Brailovsky and Flores 1979, inter al.). However, although Stål's paper is dated December, 1859, the journal itself reads "Stockholm, 1860."

Notes.—The generic description based on holotypes of *Darmistus duncani* Van Duzee and *D. crassicornis* Van Duzee, and on many specimens of *Darmistus subvittatus* Stål.

In 1956 Bliven described *Rimadarmistus.* I have examined type material of the two included species (*R. messor* Bliven and *R.*

deprecator Bliven), and other specimens identified by Bliven. Diagnosing his new genus, Bliven (1956) separated it from *Darmistus* by two characters: The clypeus is longer than the paraclypei (as in *Darmistus*), but "distinctly separated above its apex"; and "the posterior angles of the metapleura [I take these to be the dorsoposterior corners] are bluntly rounded or even truncate" (p. 7). However, the relationship between clypeus and paraclypei of Bliven's two *Rimadarmistus* species and of *D. duncani* seems to me to be identical. Also, the dorsoposterior corners of the metapleura are rounded in all species of both genera; those of *Rimadarmistus* are somewhat more elongate, but I do not consider this a specific difference, much less a generic one. The entire metapleura of both genera are very similar indeed. In addition, *Rimadarmistus* is smaller than *Darmistus*, judging at least by the type material (Table 1); but the sample size here is too small to draw conclusions as to generic distinctness.

Those being the only generic differences Bliven (1956) presents, and having found no others myself, I synonymize *Rimadarmistus* Bliven 1956 with *Darmistus* Stål 1860.

Breddin (1903) described a genus, *Eudarmistus* Breddin, with a single species, *E. bicolor* Breddin. I have not located any specimens of this species, and what follows is based on the original descriptions. Breddin (1903) wrote that *Eudarmistus* resembles *Darmistus,* and indeed there are many similarities. However, the two genera differ in several important respects: in *Eudarmistus* the distance between the ocelli ("Punktaugen") is equal to the distance from an ocellus to its ipsilateral eye (*Darmistus:* interocellar distance much less); in *Eudarmistus* the fourth antennal segment is the longest (not true of *Darmistus crassicornis* [Table 2]); in *E. bicolor* the rostrum reaches between the hind coxae (*Darmistus:* midcoxae); *E. bicolor* is 15 mm. long (the longest *Darmistus* is 11.8 mm. [Table 1]). Moreover, the ground color of *E. bicolor* is dark brown (*Darmistus:* brown to yellow brown); and the "Cicatricaltheil" (I confess I am not sure what this is) of the *E. bicolor* pronotum has "2 konischen Dornenspitzchen" (*Darmistus:* no spines, conical or not).

Another important difference of course is that *Eudarmistus bicolor* is described from the Bolivian Andes. *Darmistus* is known only from as far south as Costa Rica. It is possible that a population of *Darmistus* (presumably of *D. subvittatus,* the other species apparently not occurring in Central America) worked its way south, at high relatively cool elevations, and, becoming isolated, differentiated into *Eudarmistus bicolor.* But all of this remains highly speculative until specimens of Breddin's species are available.

Darmistus differs from other New World Micrelytrini in a combination of characters: The lack of scutellar or humeral spines, the extension of the paraclypei well beyond the clypeus, and the relatively small size (8.5–11.8 mm.); and in its somewhat northern distribution (western and southwestern United States, into Central America). Its range overlaps with those of *Cydamus* Stål, *Esperanza* Barber, and *Protenor* Stål, although the first of these genera has species extending much further south. (Note: Of the two North American *Protenor* species, *P. belfragei* Haglund is northern and *P. australis* Hussey is recorded only from Florida and Georgia [Hussey 1925]. However, there is a specimen of the latter species from Texas in the National Museum of Natural History [Schaefer unpublished]; and *P. tropicalis* Distant occurs in Guatemala [Distant 1881].) *Cydamus* and *Esperanza* both have scutellar spines (most *Cydamus* also have humeral ones) and neither has the paraclypeal extension. *Protenor*'s paraclypei also extend well beyond the clypeus and this is, indeed, the genus which in most keys shares a couplet with *Darmistus* (Fracker 1918; Stål 1867, 1873; Brailovsky and Flores 1979). However, although the adult *Protenor* lacks spines, as does *Darmistus,* the *Protenor* nymph has short humeral ones

(Schaefer unpublished). The fifth-instar *Esperanza texana* Barber does not have the scutellar spine of its adult (Wheeler and Henry 1984). Other, larger, New World Micrelytrini also have extended paraclypei (*Bactrophyamixia* Brailovsky, *Bactrophya* Breddin, and *Bactrocoris* Kormilev); none has spines as adults, but the nymphs of most are unknown, as is that of *Darmistus*. Similarly, the paraclypei meet in front of the clypeus in one of the two subtribes (Leptocorisidi) of the other micrelytrinae tribe, Leptocorisini (Ahmad 1965); neither humeral nor scutellar spines occur in any stage of the Leptocorisini (as far as is known).

Although genitalia of both sexes provide useful systematic characters in Leptocorisini (Ahmad 1965), only the genital capsule of the male has been studied in Micrelytrini (Schaefer 1980b). I have examined, and discuss below (Discussion), a few features of the capsules of the three *Darmistus* species. However, the determining of phylogenetic relationships of *Darmistus* and other micrelytrines, requires a more thorough study of the *Darmistus* capsule.

For now, one may suggest tentatively that *Darmistus* may be phylogenetically close to *Protenor*; but the qualifications in this statement attest to the fact that the evidence is weak.

Micrelytrini may be divided into two groups, each of which is represented in both the New and the Old Worlds. One group contains small, often ant-mimetic species, and the other contains more elongate species (see Schaefer 1996, 1999). *Darmistus* is a member of the latter group, which has the elongate paraclypei, like members of the leptocorisine subtribe, Leptocorisidi, whose members are also elongate (Ahmad 1965). The value of the extension of the paraclypei in working out phylogenetic relationships is therefore unclear. The only cladistic study of alydid genera (Li and Zheng 1993) did not include any New World Micrelytrinae.

Darmistus also belongs to what I have called "primitive grass-feeders," a category of Alydidae based on relative elongation of the body (total length relative to greatest width; indices 19–28; *Darmistus*' index is 22.7) (Schaefer 1972). *Esperanza, Darmistus,* and *Cydamus* are the New World members of this grade, to which I now add *Trachelium*. Despite my categorization of them, in 1972 I had no evidence that any of these genera did in fact feed on grasses. Since then, Wheeler and Henry (1984) have confirmed my prediction that *Esperanza texana* Barber is a grass-feeder, and a *Cydamus* species has been found to be a pest of range grasses in Colombia (D. Forrero, personal communication).

One specimen of *Darmistus subvittatus*, from San Pedro de Montes de Oca, Costa Rica, bears a label "on Pennisetum clandestinum Choiv." *Pennisetum clandestinum* is an east-African rangeland grass ("kikuyu") invasive in Central and North America; in the latter it is considered a pest (C. Schlichting, personal communication). Thus, there is now some evidence that a species of *Darmistus* too feeds on a grass.

In mid-May, 2002, 33 specimens of *D. duncani* and 6 specimens of *D. subvittatus* (all long-corium form) were collected in carrion-baited pitfall traps in the Davis Mountain Resort (Texas). All 39 specimens were male, which suggests carrion resembles the females' sex pheromone. Carrion is attractive to alydids (especially alydines), and it has been thought that the bugs are attracted to a source of soluble nitrogen (Schaefer 1980a). However, because the alydids thus attracted were not sexed, it is possible they were males drawn to carrion for sex, not food. In a review of heteropterans feeding on carrion and fecal matter, Adler and Wheeler (1984) found more records for Alydidae (all Alydinae, mostly *Alydus*) than for any other family, including families with more species (to these records may be added *Neomegalomus parvus* (Say) [Ventura et al. 2000]). Moreover, nearly all records were on carrion, a larger percentage than for any other family. Two references

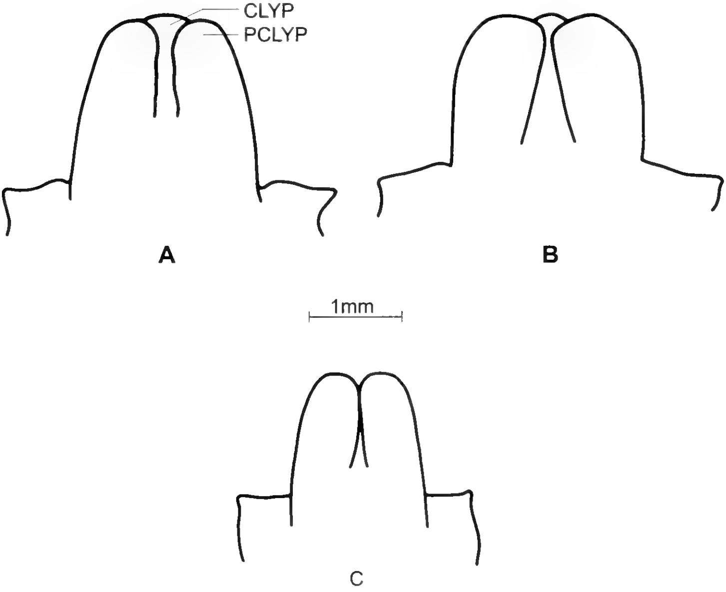

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Fig. 1. Anterior region of heads of *Darmistus* spp. (diagrammatic). A, *D. duncani.* B, *D. crassicornis.* C, *D. subvittatus.* CLYP = clypeus, PCLYP = paraclypeus.

mentioned mating pairs; and Adler and Wheeler (1984) suggest "perhaps some males [of heteropterans generally] are attracted directly or indirectly to carrion or excreta in search of females" (p. 22). The sex of the visiting bugs was not determined by the authors whose data were summarized by Adler and Wheeler (1984), nor by Ventura et al. (2000).

That these male *Darmistus* were drawn to the carrion for sex, not food, is indirectly supported by the facts that another *D. subvittatus* (short corium) collected in the Davis Mountains in a Malaise trap (1993), as well as another *D. duncani* from the Davis Mountains (collected 1992), are both female. And three of five other specimens from elsewhere in Jeff Davis County are female (two *D. duncani,* one *D. subvittatus* [short form]).

More direct evidence is the fact that some (all?) females of Alydinae produce as sex pheromones (and, less effectively, as attractant pheromones) the same butyrate esters as are produced spontaneously from the organic acids in vertebrate feces (Aldrich 1988, Aldrich et al. 2000) and, perhaps, carrion. However, the volatiles of no member of Micrelytrini have been analyzed.

KEY TO THE SPECIES OF *DARMISTUS*

1\. Antennal segment II longer than IV; antennal segment I thick, heavily setose . . . . *Darmistus crassicornis* Van Duzee

– Antennal segment II shorter than IV; I robust, not heavy, lightly setose 2

2\. Antennal segments I–III polished, dark; paraclypei not quite meeting in front of clypeus (Fig 1A) . . . . . . *Darmistus duncani* Van Duzee

– Antennal segments I–III not polished, pale to light brown; paraclypei meeting in front of clypeus (Fig. 1C) . . . . *Darmistus subvittatus* Stål

Darmistus subvittatus Stål 1860
(Figs. 1C, 2)

Darmistus subvittatus Stål 1860: 469 (orig. descr.); Distant 1881: 160, plate 15, fig. 10 (Mexico, color figure); Lethierry and Severin 1894: 100 (cat.); Gillette and Baker 1895: 19 (Colorado); Snow 1906: 151 (Texas); Banks 1910: 74 (cat.); Van Duzee 1916: 13 (list); Van Duzee 1917: 108 (cat.); Fracker 1918: 258 (redescr., U.S. distrib.); Deay 1928: 388 (distrib., transl. of orig. descr.); Blöte 1934: 271 (museum list); Froeschner 1988: 10 (U.S. distrib.).

Rimadarmistus messor Bliven 1956: 7 (orig. descr.), **new synonymy**.

Rimadarmistus deprecator Bliven 1956: 7 (orig. descr.), **new synonymy**.

Description.—*Total length* (end of abdomen): 9.25 mm. (male), 10.30 mm. (female). *Head:* Patch of micropunctures lateral to ocelli small, oval, punctations very small and difficult to see, some on pale and some on dark regions of head; band of dark punctations on either side of head extending a very short way onto genae; paraclypei meeting in front of clypeus (Fig. 1C); base of clypeus with a few to many dark punctations, apex with few; paraclypeus with many dark punctations medially and on sides, fewer in between, leaving pale "line" laterally; antennifers small, dirty yellow, without dark punctations; bottom of midcephalic sulcus dark brown; antennal segments I–III with a few long erect or suberect setae, more pale than IV, I often darker than II–III, II–III usually darker apically, IV with many small suberect setae; I and IV darker than II and III, II and III dark apically; I–III with brown spots; I more robust than IV, IV more robust than II and III; antennal measurements: Table 2; underside of head glabrous, with or without small red spots. *Thorax:* Pronotum densely punctate, sparsely setose with small recumbent setae; brown except lateral margins, medial "band," and a pair of poorly defined incomplete (posteriorly) "bands" yellow (= absence of dark punctations); pronotal transverse ridge poorly defined; propleuron heavily punctate dorsally, less so ventrally; not setose; meso- and metapleura less heavily punctate, dark punctations ending abruptly or not ventrally; dark line from midcoxa to anterior edge of mesosternum complete or interrupted; black medial line extending from base of rostrum to abdominal sternum 6, sometimes becoming obscure (or sometimes lacking) posteriorly; this band thickest on anterior abdominal sterna; scutellum heavily punctate, not pubescent, dark yellow brown, apex pale; clavus of hemelytron brown, with four longitudinal rows of punctations, these arranged somewhat irregularly longitudinally; corium brown, heavily punctate, lateral margin white or yellow to apex (rarely, brown), apex often white or yellow laterally and dark medially, extended (ending near level of posterior edge of abdominal sternum 6) or not (ending at level of anterior margin of sternum 6) (see Variation, below); membrane brown, clear. Legs yellow brown, with brown spots; tibiae lightly, femora more heavily setose with long erect setae; both coxal spots dark; third tarsal segment and claws dark. Peritreme of metathoracic scent gland apparatus raised, rounded, distinct, with medial groove. *Abdomen:* Setose with erect setae medially to sublaterally, pubescent medially to spiracular line; yellow; with a few small brown spots lateral to midsternal line, and with small red spots throughout (fewer on spiracular line). *Measurements:* Tables 1–2.

Material examined.—long-corium form (see Variation, below): UNITED STATES: *Arizona:* Huachuca Mts. [Cochise Co.], Ariz., 7-8-32 (2 specimens) (CWS); Huachuca Mts., Ariz., July 13 '05 (USNM); same, July 29 '05 (USNM); Huachuca Mts., Ar., VIII-19-50 (2 specimens) (USNM);

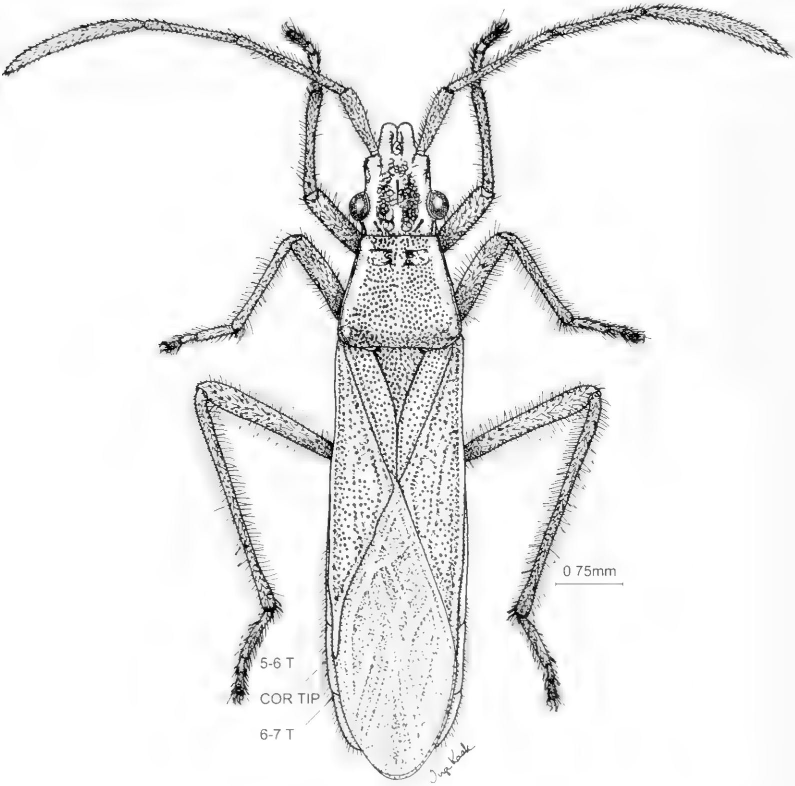

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Fig. 2. Dorsal view of *Darmistus subvittatus* (long-corium form). COR TIP = tip of corium, 5–6T = fifth-sixth abdominal segmental border, 6–7T = sixth-seventh abdominal segmental border.

Huach. Mts. [Cochise Co.], Ariz. [no date; additional label: Brooklyn Museum 1929] (USNM); Sunnyside Cn., W. side Huachuca Mts., Cochise Co., 6,000 ft., 4-VIII-52 (CAS); Douglas [Cochise Co.], Ar., 3/22/33 (UCB); Hereford, [Cochise Co.], Ariz., 10-9-27 (missing head) (UCB); Chiricahua Mts. [Cochise Co.], Ariz., June 9 1933; Nogales, St. Cruz Co., Ariz., VIII-31-06 (USNM); Patagonia [Santa Cruz Co.], Ariz., Aug 23, 1937 (3 specimens) (USNM); Patagonia [Santa Cruz Co.], Ar., 10-23-37 (USNM); Santa Cruz Co. nr. Tubac, VIII-11 1932 (USNM); ARIZSCruzR, near Tubac [Santa Cruz Co.], 10-23-37 (3 specimens) (USNM); ColCanyon [?], Ar., 12-7 (USNM). *California:* Eureka [Humboldt Co.], CA., Elk R., 24/X/1972 (CAS); Eureka, Cal., IX-15-59 (CAS); U.S.A., California, Humboldt County, Eureka, 14-II-1963 (CAS); same, 17-V-1957 (CAS); U.S.A., California, Humboldt County, Falk, 15-VI-1958 (CAS); same, 1-IX-1957 (CAS); same, 1-XI-1970 (CAS); Huntington Beach [Orange Co.], Cal., 3-30-

Table 1. Measurements (mm) of *Darmistus* species.

Species	Total Length to End of Wings (a)	Total Length to End of Abdomen (b)	Pronotal Width (Humeral Angles) (c)	Ratio (c/b)	Length Forewing (d)	Length Corium (e)	Ratio (d/e)
Rimadarmistus messor							
holotype ♂	9.10	8.71	1.67	0.19	5.98	4.42	1.35
R. messor allotype ♀	10.14	10.01	1.78	0.18	—	—	—
R. deprecator							
holotype ♂	9.10	8.45	1.65	0.20	5.98	4.42	1.35
R. deprecator							
allotype ♀	9.75	9.95	1.78	0.18	—	—	—
Darmistus crassicornis							
holotype ♂	11.38	10.92	2.15	0.20	7.15	4.68	1.52
D. duncani holotype ♀	11.83	10.92	2.35	0.22	7.80	5.07	1.54
D. subvittatus (2 ♀)*	10.40	10.30	2.02	0.20	7.15	5.20	1.38
D. subvittatus (3 ♂)*	9.86	9.25	1.89	0.20	6.63	3.70	1.38

From northern part of range.

45 (2 specimens) (USNM); Laguna Beach [Orange Co.], Calif. [no date] (CAS); Ft. Cronkite, Marin Co., Calif., IX-1-1957 (CWS); Rio Vista, Solano Co., Calif., iv-19-50 (CWS); *Colorado:* Boulder [Boulder Co.], March 18 (USNM); Boulder, Colo., March 20 (USNM); Boulder, Colo., March 22 (USNM); Delta [Delta Co.], June 25 1938 (USNM); Denver [Denver Co.], Colo., IV-22, 1961 (TAMU); same VIII-7, 1963 (TAMU); Ft. Collins [Larimer Co.], Colo., 9-15-28 (year obscure) (UCB); same 9-15-28 (USNM); same 9-11-28 (USNM); same 10/19/29 (2 specimens) (USNM); Clear Cr[eek] Can[yon], Col., 1926-27 (USNM); N.E. Col. [no further data] (USNM); Colo. [no further data] (2 specimens) (USNM). *Nebraska:* Glen Sioux Co., Neb., Aug 1903 (4 specimens) (USNM); Extreme nw. corner, Brown Co., Nebraska, June 10, 1950 (UCT). *New Mexico:* Albuquerque [Bernalillo Co.], N.M., 8.27-46 (USNM); Mesilla [Socorro Co.], Feb. 22 (USNM). *Texas:* Brownsville [Cameron Co.], Tex., 1/18/23 (USNM); Brownsville, Tex., V-8 33 (USNM); Brownsv[il]l[e], Tx., 1-4-32 (USNM); Jeff Davis Co., Davis Mts. Resort, upper Limpia Creek Cyn., 6,180 ft., IV-12-14-2002, carrion-baited pit-fall (6 specimens, all male) (TAMU). *Utah:* Zion Park [Washington Co.], Utah, 8/1/28 (USNM). *Washington:* Duckabush [Jefferson Co.], Wn., 7/31/47 (2 specimens) (UCT). *Wyoming:* Medicine Bow National Forest, Albany Co., Wyo., IX-4-1951 (UCT). MEXICO: *Chiapas:* 6 km n. San Cristobal, August 3, 1990 (2 specimens) (TAMU); 12 mi. east Huixtan, September 15, 1990 (TAMU); Mpio: San Cristobal San Felipe, 7,200′, August 5, 1990 (TAMU). *Chihuahua*(?): Mexico, El Paso [?Ciudad Juarez], 4-23-46 (USNM). *Colima:* 10 mi. ne. Comala, July 17–19, 1983 (TAMU). *Durango:* 19 mi. SE Durango, Dgo., VII-16–59 (TAMU). *Guadalajara:* [no further data] (13 specimens) (CAS). *Guanajuato:* 1 mi. n. Santa Rosa, April 8, 1990 (TAMU). *Jalisco:* 1 Sept. 1938 (CWS). *Guerrero:* 0.2 mi. w. Cacahuamilpa, July 6, 1974 (TAMU); 2.5 mi. ne. Cacahuamilpa, July 6, 1974 (TAMU); *Guerrero*(?): Mexico, Tasco [?Taxco de Alarcón], VIII 1955 (USNM); *Jalisco:* 20 mi. W. of Tecolotlan, 15 Sept. 1938 (3 specimens) (CWS); 10 mi. E. of unton de Tula, 16 Sept.. 1038 (CWS); 6 miles east of Lago de Moreno, July 29, 1978 (TAMU); Nevada de Colima road, 14 m. w. hwy. junct. (near Atenquilque), April 20, 1977 (2 specimens) (TAMU); 12 mi. w. Poncitlan, Jal., Mex., VII-24-66 (TAMU); 4 mi. sw. Tuxpan, Jal., Mex., VII-19-66 (TAMU); 1 mi. E. Jalisco, Nararit St. Line, Guadalajara, Hwy., Mex., VIII-21-1984

(TAMU); 32 miles southwest Guadalajara, Jal., VII-22-66 (TAMU); Chapala, Mex., Aug. 1949 (UCT). *México:* 4.3 mi. no. Ixtapan, July 6, 1974 (TAMU); Tejupilco [de Hildalgo], Mex., Temescaltepec, VII-1932 (2 specimens) (UCB); same data, VI-24-33 (UCB); Rio de Arriba, Temescaltepec, Mex., VI-9-33, Top of hill, alt. 5000 ft. (UCB) Ciudade, Méx., 8,100 ft., [no date] (USNM). *Miochoacán:* 6 mi. n. Cheran, July 6–7 1985 (TAMU); 6 mi. south Cheran, July 23 1983 (TAMU); 5 miles west Jacona, Mich., Mex., VII-18-66 (TAMU); 10 miles East of Tuxpan, Mich., Nov. 22, 1955. *Morelos:* Morelos, Mex., 7-14-36, 135 Kil. S. of Mexico City (CWS); Tepoztlan, Morelos, Mexico, 8-20-56 (2 specimens) (USNM); Cuernavaca, Morelos, June (USNM); Cuernavaca, Mor., Mexico, X-1944 (USNM); same, VI-45 (USNM); Mexico, Morelos, Cuernavaca, VIII-31-44 (USNM); Mexico: Mor. Cuernavaca, XI-1966 (USNM); Cuernavaca, Mex., Crawford [collector?] (CAS); Mexico, Cuernavaca, 27 July 1938 (CWS); 5.1 mi. E. Cuernavaca, 5,000 ft., 29 June 1973 (TAMU); 4.4 mi. e. Cuernavaca, July 6–7 1974 (TAMU). *Nuevo León:* 12.4 mi. northeast Doctor Arroyo, July 8, 1986 (TAMU). *Oaxaca:* Oaxaca, Crawford [collector?] (2 specimens) (CAS); Oaxaca, Oaxaca, Mex., VII-8-52 (CWS); 15 mi. SE Tamazulapan (USNM). *Puebla:* Xicotepec de Juarez, April 29, 1984 (TAMU); 3.7 mi. S Zacapoaxtla, 23-VII-1985 (TAMU). *Tabasco:* Jalapa, Crawford [collector?] 6 September 1972 (CAS). *Vera Cruz:* Cordoba, Mex., I-1-40, 3 mi. E. (CAS); Vera Cruz, Mex. [no further data] (USNM); 3 mi. NE Huatusco, July 23, 1984 (5 specimens) (TAMU); 3 miles n. Banderillo, April 17, 1979 ((TAMU); 34 km. n. Naolinco, Alt. 4,100′ April 20–21, 1978 (TAMU). NO LOCALITY: 9/4/35 (UCB).

Short-corium form: UNITED STATES: *Arizona:* Safford [Graham Co.], Ariz., July 20 1914 (2 specimens) (USNM); Huach[uca] {Cochise Co.], Ar., 6–15–30 (USNM). *California:* Santa Catalina Island [Los Angeles Co.], Cape Canyon, 850 feet, land [?], 3 July 1976 (USNM); Los Angeles Co., CAL., [no date] (USNM); Marin Co., CA [no date] (USNM); Eureka [Humboldt Co.], Elk R., 10.VI-1979 (CAS). *Colorado:* Fremont Co., 15 mi. N. of Canon City, 31 May 1987 (USNM); Semper [Jefferson Co.], COLO, May 25, 1919 (USNM); Boulder Co., VIII-10 1932 (USNM). *Nebraska:* Extreme nw. corner, Brown Co., Nebraska, June 10, 1950. *New Mexico:* Pecos [San Miguel Co.], N.M., July 8 [no year] (USNM). *Texas:* TEXAS: Jeff Davis Co., Davis Mts. resort, (D. Marqua residence), V-10-17-1993 (TAMU); [Jeff Davis Co.], Madera Canyon, west of Ft. Davis, Jeff Davis Co., Texas, August 9, 1969 (TAMU). *Wyoming:* Medicine Bow National Forest, Albany Co., Wyo., IX-4-1951 (2 specimens) (UCT). MEXICO: *Guadalajara:* [no further data] (5 specimens) (CAS); *México:* Tejupilco [de Hidalgo], Mex., Temescaltepec, VI-17-33 (4 specimens) (3 in UCB, 1 in CWS); same data, VI-16-33 (UCB); same data, VI-18-33 (UCB); Bejucos, Mex., Temescaltepec, VII-3-33 (UCB); Real de Arriba, Temescaltepec, VII-11-33, Mex. (UCB); same data, VII-8-33 (UCB); same data, V-28-29-'33 (UCB). *Morelos:* Morelos, Crawford [collector?] (CAS); *Oaxaca:* 4 mi. NE. Miltapec, 21-7-1984 (TAMU). Puebla: 4 mi. sw. Acatepec, July 11, 1973 (TAMU). GUATEMALA: Yepocapa, Guatemala, Aug 1948 (2 specimens) (USNM); same, June 1948 (USNM); Yepocapa, Guat., July 1949 (2 specimens) (USNM); Guatemala, Sololá, Panajachel, 28 Apr. 1956 (USNM). COSTA RICA: Costa Rica, 10 km N San José, July 71 (USNM); San Pedro de Montes de Oca CR [and] Barba, CR, Nov. 28, '35 [note label also gives host plant, "on Pennisetum clandestinum Choiv."] (USNM). Uncertain: "Mexiq" (USNM).

Other records (published).—UNITED STATES: *Colorado:* Fort Collins [Larimer Co.], June 25th; foot hills five miles west of Ft. Collins, March 12th to June 12th" (Gillette and Baker 1895, p. 19); Colorado Springs [El Paso Co.], 1934 (2 specimens)

Table 2. Lengths (mm) of antennal segments of *Darmistus* species (measurements from holotypes, except *Darmistus subvittatus*).

Species	Antennal Segments				Ratio 1/2
	I	II	III	IV	
Darmistus duncani	1.10	1.90	1.52	2.18	0.63
D. crassicornis	1.19	2.18	1.82	1.95	0.55
D. subvittatus	1.19	1.91	1.65	2.21	0.62
Rimadarmistus messor	1.04	1.57	1.35	1.82	0.66
R. deprecator	0.99	1.56	1.32	1.85	0.63

(Blöte 1934 1934, p. 271). MEXICO: "Mexico" [holotype, Stål 1860]. *Durango*; *Estado de México*; *Guerrero*; *Morelos*; *Nuevo León*; *Oaxaca*; *Puebla*; *Veracruz* (Brailovsky and Flores 1979, map 10); Jalapa [Tabasco], 1934 (4 specimens) (Blöte 1934, p. 271).

Distribution.—Coastal North America from Washington State and California, east into Kansas and Nebraska, south through Mexico into Guatemala and Costa Rica.

Variation.—In one specimen (from Tejupilco, México State), the paraclypei do not actually touch in front of the clypeus, but are nevertheless closer to one another than in either of the other two species; however, this specimen was collected with others in which the paraclypei do meet. Also in a few specimens, the pale midcephalic line is more diffuse than in most specimens; this is caused by a less sharp separation between the dark-punctated and nonpunctate (narrow medial) regions of the head's dorsal surface. The dark punctations on the meso- and metapleura end sharply sublaterally in some specimens, and end much more gradually in others; in the former case, the dark punctations appear as a dark band.

There appear to be two forms of *Darmistus subvittatus*, differing in the color and extension of the corium. In most specimens, the corium is extended well beyond the level of the anterior margin of the sixth abdominal sternum; in these specimens the corial tip is usually (but not always) white or pale yellow laterally, dark medially, and pale at the apex. However, in some specimens from central México (States of México, Morelos, and Michoacán) and south into Central America, and from the United States, the tip of the corium resembles that of *Darmistus crassicornis* and *D. duncani*, ending at the level of the anterior margin of the sixth abdominal sternum, and being (usually) uniformly brown. That these do not represent a new species is suggested by the presence among them of several individuals with the elongate pale-tipped corium (see also Discussion).

As Table 3 suggests, in nearly all *Darmistus subvittatus* the paraclypei meet in front of (and indeed slightly above) the clypeus, the corium is long (reaching beyond the level of the fifth-sixth abdominal suture), and the black midsternal line of the abdominal sternum is complete (onto the seventh sternum) or nearly so (onto the fifth sternum, indicated by "1/2" in Table 3). There seems to be no particular pattern or correlation among these character states, nor with any geographic locality.

Historical note.—The specimens from México State were collected in 1933 by two entomology students at The University of California, Berkeley. To earn money in the Great Depression, Robert L. Usinger and Howard Hinton hitchhiked and freight-hopped their way to central Mexico, there to collect insects and sell those they did not want. Their adventures on this collecting trip (protected in part by Hinton's experience as a college boxer) are recounted in Usinger's reminiscences (Usinger 1972). This account includes a map of the collecting areas, and a description of their headquarters, the village of Tejupilco.

Table 3. Character states of paraclypei, abdominal line, and corium in *Darmistus duncani* and *D. subvittatus.*

Specimen	Paraclypei Meeting in Front of Clypeus	Dark Abdominal Line	Corium (s = short, l = long)	Number Specimens
D. duncani (holotype)	0	0	s	1
D. subvittatus:				
Solano Co., Calif.	+	1/2	l	1
Eureka, Calif.	+	+	l	1
Eureka, Calif.	+	+	s	1
Humboldt Co., Calif.	+	+	l	2
Humboldt Co., Calif.	+	1/2	l	1
Laguna Beach, Calif.	+	+	l	1
El Paso, Tex.	+	+	l	1
Morelos, Mexico	+	0	s	1
Morelos, Mexico	+	+	l	1
Jalisco, Mexico	+	+	l	3
Oaxaca, Mexico	+	1/2	l	1
Cuernavaca, Mexico	+	+	l	1
Tejupilco, Mexico*	+	+	l	3
Tejupilco, Mexico*	+	1/2	s	4
Tejupilco, Mexico*	0	1/2	s	1
Bejucos, Mexico*	+	0	s	1
Real de Arriba, Mexico*	+	1/2	s	3
Real de Arriba, Mexico*	+	1/2	l	1
Guadalajara, Mexico	+	+	l	12
Guadalajara, Mexico	+	1/2	s	5

* Expedition of Usinger and Hinton (Usinger 1972).

Notes.—Bliven (1956) separated his two *Rimadarmistus* species in his description of *R. deprecator* as follows: "a little smaller, with head constricted behind the eyes, preocellar pits obsolescent, antennae slender, disc of pronotum depressed with calli distinct and underside extensively dotted with red" (pp. 7–8). I have examined the holotypes and allotypes of both species, and find hardly any of these differences. I did find the following differences, however: The band of dark punctures laterally on the head extends onto the genae in *R. deprecator* (and *D. crassicornis*), but not in *R. messor* (or the other *Darmistus* species). The posterior corners of the bucculae of *R. deprecator* are slightly more sharply rounded than in *R. messor* or the *Darmistus* species. The posterolateral spots on all coxae in *R. deprecator,* but only on the fore coxae of *R. messor,* are pale. The calli of *R. deprecator* are slightly more distinct than are those of *R. messor.* And the former has more red spotting on the venter of head and abdomen (the *R. messor* allotype has some spotting also, although the holotype does not). Red spotting, or an occasional suffusion of red, are not uncommon in pale coreoids (quite common in Rhopalinae). None of these differences is enough to distinguish species. In addition, in all respects, including the relative shape of the bucculae, the medial extension of the genital capsule, and the black medial abdominal stripe, the holotypes and the allotypes of both Bliven's species resemble *Darmistus subvittatus* Stål. I therefore synonymize *Rimadarmistus deprecator* Bliven 1956 and *Rimadarmistus messor* Bliven 1956 (which has priority, being printed first on p. 7) with *Darmistus subvittatus.*

Finally, both Bliven's species come from Humboldt County (including Eureka), California. In the CAS collection are many unidentified *Darmistus subvittatus* collected by Bliven himself in Eureka and elsewhere in the County, from 1957 to 1973. If Bliven had believed these specimens to be either of his two species, he would certainly have so labelled them. That he did not, suggests he had his doubts.

Darmistus crassicornis Van Duzee 1937
(Fig. 1B)

Darmistus crassicornis Van Duzee 1937: 28 (orig. descr.); Froeschner 1988: 10 (U.S. distrib.)

Description (based on holotype).—*Total length* (end of abdomen): 10.92 mm. *Head:* Patch of pale micropunctures lateral to ocelli small, oblique; band of dark punctations on each side of head extending anterior to antennifer onto genae; paraclypei not meeting in front of clypeus (Fig. 1B); bases of clypeus and paraclypei with some dark punctations, apex of clypeus with very few punctations; antennal tubercles well developed, yellowish, with many brown spots; bottom of midcephalic sulcus pale; antennal segments I–IV uniformly colored, I–III heavily setose, setae long, conspicuous; segment I robust, dilated, same color as head, with many dark spots; segments II and III yellow brown and cylindrical; segment IV somewhat robust, dark reddish brown, appearing smooth but with many very small setae; antennal measurements: Table 2; underside of head glabrous, with scattering of small red spots. *Thorax:* Pronotum heavily pubescent, densely punctose, yellow brown, except lateral margins and medial "band" pale yellow (absence of dark punctations); pronotal transverse ridge poorly defined; dark punctations on pronotum irregularly concentrated sublaterally, forming pair of poorly defined dark bands from posterior margin of pronotum to about midway anteriorly; propleuron heavily pubescent; prosternum less heavily pubescent; pleural margins of thorax pale yellow, sparsely punctate dorsally, punctations dwindling in number to none ventrally; dark interrupted line from mid coxae to anterior edge of mesosternum; black midmetasternal line continuing anteriorly along mesosternum and posteriorly on abdomen to sternum 7; scutellum pubescent, heavily punctate, yellow brown, apex pale yellow; clavus of hemelytron yellow brown, with 4 longitudinal lines of punctations, these regularly arranged longitudinally; corium yellowish, lateral margin pale for nearly its entire length, apex brown, not greatly extended (ending at level of anterior margin of abdominal sternum 6), densely punctate; membrane nearly colorless, clear. Legs heavily setose; both coxal spots dark; femora yellow anteriorly, medially, and posteriorly, with many spots (these fewer basally), and with well-defined hairs; tibiae pubescent, pale yellow, with dark spots; tarsi without spots. Peritreme of metathoracic scent gland round, indistinct, with medial groove. *Abdomen:* Sternum sparsely pubescent; pale yellow, with few punctations, with many small red spots like those on head's venter (these absent from spiracular line), and with black medial line running length of abdomen. *Measurements:* Tables 1–2.

Material studied.—UNITED STATES: *Texas:* Chisos Mts., Brewster Co., July 18 1921 (CAS) [holotype]. MEXICO: *México:* Tejupilco [de Hidalgo], Temescaltepec, VI-17-33 (UCB).

Other records (published).—UNITED STATES: *Texas:* 4 paratypes, same data as holotype; Sheffield, Pecos Co., July 24, [1921?] (Van Duzee 1937). MEXICO: *Guerrero:* Taxco (Brailovsky and Flores 1979).

Distribution.—Texas south into southern Mexico.

Darmistus duncani Van Duzee 1937
(Fig. 1A)

Darmistus duncani Van Duzee 1937: 29 (orig. descr.); Froeschner 1988: 10 (U.S. distrib.).

Description (based on holotype).—*Total length* (end of abdomen): 10.92 mm. *Head:* Patch of micropunctures lateral to ocelli rounded and extending as a thin line of punctures a little way anteriorly; band of dark punctations on each side of head extending anteriorly onto antennifer but not beyond; paraclypei not meeting in front of clypeus (Fig. 1A) and with thin dark line on inner (medial) border; base of clypeus with dark punctations, apex and paraclypei with none; antennifers well-developed, yellow, with a few dark brown spots below dark band; bottom of midcephalic sulcus light or dark brown; antennal segments 1–3 dark, 4 darker than ground color; 1–3 with a few long erect setae, 4 appearing smooth but with many recumbent small setae; 1 somewhat more robust than 2–4, 4 somewhat more robust than 2–3; antennal measurements: Table 2; underside of head glabrous with scattering of small red spots. *Thorax:* Pronotum not heavily pubescent but densely punctate, dark yellow brown except lateral margins and medial "band" yellow (absence of dark punctations); pronotal transverse ridge somewhat defined; dark punctations on pronotum evenly distributed; propleuron lightly pubescent; prosternum not pubescent; all pleural margins yellow, with dark punctations dorsally (especially on propleuron), these ending sharply on mid and hind pleura, ending more vaguely on propleuron; without dark line from mid coxae to mesosternum; without dark median line on pro- and mesosternum; black median metasternal line extending posteriorly as medial scattering of dark punctations on anterior abdominal sterna; scutellum not heavily punctate, pubescent, yellow brown, apex yellow; clavus of hemelytron yellow brown, with five rows of punctations, these arranged irregularly longitudinally; corium yellow brown, lateral margin pale for nearly its entire length, apex not greatly extended (ending at level of anterior margin of abdominal sternum 6), densely punctate, pale, sometimes darkening to light brown, sometimes brown; membrane pale brown, clear. Legs lightly setose, setae erect; both coxal spots dark; femora uniformly light yellow brown, with many small brown spots (fewer basally), without hairs; tibiae and tarsi light yellow brown, with very small brown spots; third tarsal segment and claws dark. Peritreme of metathoracic scent gland low, rounded, distinct, with medial groove. *Abdomen:* Nearly glabrous, sparsely beset with erect setae; pale yellow; with a few brown punctations sublaterally on anterior sterna, with red spots over surface (including spiracular line); midsternal line consisting of a medial scattering of dark spots on anterior sterna. *Measurements:* Tables 1–2.

Variation.—There is some variation in the degree of overall darkness, and in the amount of dark punctuation. The specimens from the Davis Mountains (Texas) have a thin dark line laterally (as well as medially) on each paraclypeus; the holotype has only the medial lines. In a few *D. duncani* from Texas, the first three antennal segments are red, not dark.

Material examined.—UNITED STATES: *Arizona:* base of Pinal Mts. [Gila Co.], Ariz., Jun[e] [no year] [holotype] (CAS); Pinery Canyon, Chiricahua Mts. [Cochise Co.], Ariz., alt. 4,800, VIII-8 1932 (USNM); Chiric[ahua] Mts. [Cochise Co.], Ar., 10-6-32 (USNM); Baboq[uivari] mts. [Pima Co.], Ar., 7-19-32 (USNM); Huachuca Mts. [Cochise Co.], Ariz. [no date] (USNM); S[anta] Rita Mts. [county?], Ar., 24.5 (USNM)); ARIZ., SW Res. Sta., 5 mi. sw., Portal [Cochise Co.], 5/25-IX-1965 (USNM); ARIZONA: Santa Cruz Co., 2.7 mi. n. junction FR 49 and FR 61 on FR 49, 5,260′, August 15, 1998 (TAMU). *Texas:* Salado, Bell Co., Tex., March 13, 1957 (TAMU); TEXAS; Brewster Co., 17 mi. east Alpine, August 15, 1992 (TAMU); [Brewster Co.] Green Gulch, Big Bend National Park, Texas, 5,700′, July 24, 1968 (2 specimens) (TAMU); TEXAS: Crockett Co., 16 mi.W. Ozona, rest stop, IV-19-1997 (2 specimens) (TAMU); Lange's Mill, Gillespie Co., Texas, Apr. 22, 1970 (TAMU); Gillespie Co., Tex., V-6-46 (USNM); 4 miles sw Doss, Gillespie Co., Texas, June 6, 1969 (TAMU); TEXAS: Jeff Davis Co., Davis Mts. Resort, Upper Limpia Creek Cyn., 6,180 ft., IV-12-14-2002, carrion-baited pit-fall (33 specimens, all male) (TAMU); TEXAS: Jeff Davis Co., 9.8 mi. s. Kent on 118, 16-18-VIII-82 (2 specimens) (TAMU); TEXAS: Jeff Davis Co., Davis Mts. St. Pk., VIII-7-1992 (TAMU); H.O. Canyon, w. of Ft. Davis, Jeff Davis Co., Texas, August 12, 1969 (2 specimens) (TAMU); TEXAS: Travis Co., vic. Long Hollow Cr., May 7, 1994 (TAMU). MEXICO: *Michoacán:* Pericutin, 28 Nov 1944 (USNM).

Other records (published).—UNITED STATES: *Arizona:* same data as holotype [allotype]; *Colorado*; *California* (Van Duzee 1937).

Distribution.—Southwestern United States into southern Mexico.

DISCUSSION

A significant difference between *Darmistus subvittatus* and the two other species is that in the first the paraclypei meet (or in a few specimens nearly meet) in front of the clypeus. In *D. crassicornis* they clearly do not, and in *D. duncani* they nearly meet and this species thus resembles a few specimens of *D. subvittatus* (see Fig. 1). As Stål (1860: 469) writes in his original generic description of *Darmistus,* "lateralibus [i.e., paraclypei] medio [i.e., clypeus] longioribus," which is true of *D. subvittatus,* the only species then in the genus; but he also writes "contiguis," which is not true of the two subsequently described species.

Van Duzee (1937) writes of his *Darmistus duncani* that "cheeks [= paraclypei] not exceeding the tylus [= clypeus]" (original description and key). However, paraclypei not only exceed the clypeus (although not by much), they nearly meet in front of it (Fig. 1A). Although the paraclypei do not meet in *D. crassicornis,* the difference between *D. duncani* and some *D. subvittatus* is more subtle than Van Duzee indicates (1937: 29). In both species the paraclypei extend beyond the clypeus; in most *D. subvittatus* they meet, but in some *D. subvittatus* and in *D. duncani* they do not. However, somewhat more of the paraclypei extend beyond the clypeus in *D. subvittatus* than in *D. duncani.*

The first three antennal segments of *Darmistus duncani* are darker and shinier than those of the other two species, as Van Duzee (1937) mentions. Another more subtle difference, as noted by Van Duzee (1937), is that *D. duncani* is somewhat larger (see Table 1) and darker than *D. subvittatus*; but this is not always so and, again, most clearly seen when specimens of both species are available. However, in the Davis Mountains (Texas), where the two species were collected together in pitfall traps at the same place and at the same time, the difference in size is considerable: *D. subvittatus* averaged 9.07 mm. long (N = 5) and *D. duncani* 11.65 mm. long (N = 5).

The clavus of *D. duncani* has five longitudinal rows of punctations, and those of the other two species have four. The punctations in *D. crassicornis* are arranged quite regularly; they are less regular in *D. subvittatus,* and even less regular in *D. duncani.* Another progression occurs in the peritreme of the metathoracic scent gland apparatus, which, although round and with a median groove in all species, is very low and indistinct in *D. crassicornis,* more raised and distinct in *D. duncani,* and higher and yet more distinct in *D. subvittatus.*

More obvious, and therefore better diagnostic, differences are these: Abdominal venter with black stripe along midline poorly developed in *D. duncani* and *D. crassicornis,* well developed (at least on sterna 3–5) in most *D. subvittatus* (reduced to a few black spots in one specimen from Morelos, Mexico); antennal segments 1–3 of *D. duncani* dark and polished (somewhat shiny); bucculae nearly round (slightly oval) in *D. subvittatus,* but much more oval (longer than deep) in *D. duncani* and *D. crassicornis.*

The forewing's corium extends further along the forewing in most *Darmistus subvittatus* (and both *Rimadarmistus* species) than it does in *D. crassicornis* or *D. duncani* (Table 1, where the smaller the ratio between forewing and corium lengths the longer the latter relative to the former); this is true of most *Darmistus subvittatus*, especially those found in its northern range where it overlaps with the other two species. The relative lengths of *D. crassicornis* and *D. duncani* are the same (Table 1). The tips of the coria also vary in color: usually dark in *D. crassicornis* and *D. duncani*, but usually pale (dark medially) on the extended tip of *D. subvittatus*.

The tip of the *Darmistus crassicornis* scutellum (holotype) is whitish or pale yellow, and that of *D. subvittatus* is paler than the yellow brown ("pardo amarillento") of the scutellum itself (Brailovsky and Flores 1979); the scutellar tips of both species thus contrast with the rest of the scutellum. The scutellar tip of *D. duncani* is only very slightly paler than the rest of the scutellum, except in darker specimens, where it is contrastingly pale.

I have compared the parameres, the genital capsule's ventral rim, and the capsule's composite cuplike sclerite-plus-median projection (see Schaefer 1980b), in males of these specimens: *Darmistus duncani*, holotype; *Darmistus subvittatus*, specimens from Temescaltepec (México State) (paraclypei not meeting, long corium, heavy complete abdominal line), same (paraclypei meeting, short corium, abdominal line extending only halfway), from Morelos (paraclypei meeting, short corium, without abdominal line), and from Solano County (California) (paraclypei meeting, long corium, abdominal line extending only halfway).

In all five specimens the parameres fit snugly between the midline extension of the ventral rim and the composite cuplike sclerite-plus-median projection; the parameres are separated only by a thin internal ridge on the ventral rim's extension. The four structures together form a single unit, visible externally, pointed apically (the ventral rim extension), and well-buttressed at the base by the other structures. Presumably, during copulation the parameres separate, to guide the aedeagus on either side as it is guided ventrally by the ventral rim's extension, and as it is supported basally by the extension's broadened base and the wider composite cuplike sclerite-plus-median projection.

This combination of parameres, ventral rim extension, and composite cuplike sclerite-plus-median projection occurs also in at least two other New World micrelytrine genera (*Cydamus*, *Trachelium* [Schaefer unpublished]), and perhaps in others as well, both New and Old World. The medial extension of the ventral rim is a feature of the family Alydidae, and is more pronounced, and the extension longer and more needlelike, in Micrelytrinae: Micrelytrini than in the other groups (Schaefer 1980b).

With one exception, my measurements (Table 1) of the *Rimadarmistus* types do not differ significantly from Bliven's (1956), if he measured from head to wing tip instead of to abdomen tip (a more accurate measure of length). His measurements (mm.) are: *R. messor* holotype, length 9.28, pronotal width 1.67; allotype, length 10.5, pronotal width 1.9; *R. deprecator* holotype, length 9.12, pronotal width 1.62; allotype, length 10.124, pronotal width 1.82 (Bliven 1956). I cannot explain the difference in body length of the *R. deprecator* allotype. Van Duzee (1937) writes that each of his species is 11 mm. long, very close my measurements, and suggesting he measured to the tip of the abdomen. In general, judging from these types, *Rimadarmistus* is small, another similarity between it and *D. subvittatus*.

The relative lengths of the antennal segments (Table 2) of *D. duncani*, *D. subvittatus*, *R. messor*, and *R. deprecator* are IV > II > III > I; those of *D. crassicornis* are II > IV > ~III > I, a sequence with which Brailovsky and Flores (1979) agree, although their specimen lacked the fourth segments. Fracker (1918) writes that the second and fourth antennal segments of *D. subvittatus* are subequal, and each is nearly twice as large as the first, which seems not to be so; Van Duzee (1937) writes that the first is two-thirds the length of the second, which is incorrect (Table 2); and Torre Bueno (1941) writes that the second and third are nearly equal (the third "*slightly* longer," emphasis in original), which again is not so; Torre Bueno also says the second segment of *D. duncani* is only three-fifths as long as the third, which is clearly wrong (Table 2). Moreover, Brailovsky and Flores' (1979) measurements of *D. subvittatus* indicate IV > II > I > III. It is clear the earlier literature is a bit unreliable.

In addition to the holotypes of the two Van Duzee species, I have seen only one other *Darmistus crassicornis* and about 50 other *D. duncani* specimens among the more than 130 specimens I studied. *D. crassicornis* occurs from Texas into México and Guerrero States; and *D. duncani* is also found in several U.S. states (Van Duzee 1937) and as far south as Michoacán. The scarcity and restricted distribution of specimens of these two species suggest they have more specialized habitats than does the ubiquitous *D. subvittatus.*

Finally, *D. subvittatus* occurs sympatrically with both other species. The México State specimen of *Darmistus crassicornis* was collected at the same place and on the same day as several specimens of *D. subvittatus* (Temescaltepec, June 17, 1933); and specimens of both short- and long-corium *D. subvittatus* were collected in the same week at this locality. Thirty-three specimens of *D. duncani* and six specimens of *D. subvittatus* (all male) were collected in pitfall traps on the same day and at the same place in the Davis Mountains of Texas. Here the *D. duncani* specimens were about the same length as the holotype (11.65 mm., N = 5), but the *D. subvittatus* were considerably smaller (9.07 mm., N = 5; cf. Table 1).

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A NEW SPECIES OF *DOLOPHILODES* (*SORTOSA*) NAVÁS (TRICHOPTERA: PHILOPOTAMIDAE) FROM BRAZIL

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Abstract.—**Dolophilodes (Sortosa) marinonii, n. sp.** (Trichoptera: Philopotamidae) is described and illustrated from the state of Paraná, southern Brazil. This is the second Brazilian species of the subgenus *Sortosa.*

Key Words: Trichoptera, Philopotamidae, *Dolophilodes, Sortosa,* Brazil, new species

The subgenus *Sortosa* Navás, 1918 of the genus *Dolophilodes* Ulmer, 1909 (Philopotamidae: Philopotaminae) occurs in widely separated regions of South America (Ross 1956, Flint 1983). Twenty species are known from the Chilean subregion, while only a single species, *Dolophilodes* (*Sortosa*) *sanctipauli* Flint 1971, is known from southeastern Brazil (Flint 1971, 1983, 1996; Flint et al. 1999). *Sortosa* is distinguished from the other subgenera by combining characters of wing venation and male genitalia (Ross 1956; Flint 1971, 1996).

In this paper, we describe the second Brazilian species in the subgenus, *Dolophilodes* (*Sortosa*) *marinonii,* collected during an entomological survey of eight localities in the state of Paraná conducted between 1986 and 1988 (Marinoni and Dutra 1993, Marinoni and Almeida 2000, Almeida and Marinoni 2000).

Dolophilodes (*Sortosa*) *marinonii* Almeida and Duarte, new species

(Fig. 1)

Diagnosis.—This species is related to the monotypic *sanctipauli* group of Flint (1983), with which it shares an elongate, straight apical segment of the inferior appendage. It also somewhat resembles *Dolophilodes* (*S.*) *spectabilis* Flint, 1983 in possessing a strong appendage arising between tergum X and the preanal appendage. However, the overall shape of the preanal appendage, enlarged basally and tapering apically, is very distinctive in the new species (*pr.,* Fig. 1).

Male.—Length of forewing 5.0–6.0 mm. Color in alcohol, pale brown. Venation typical for subgenus, as illustrated by Ross (1956: fig. 23). Genitalia as in Fig. 1. Sternum VII without mesal process. Tergum VIII with a pair of posterior setal warts. Sternum IX trapezoidal in lateral aspect, with anterior margin produced into rounded lobes separated by deep, V-shaped excision. Inferior appendages fused basally, in dorsal aspect inner margins delimiting a heart-shaped area from which arise a membranous sac; two-segmented; basal segment subquadrate, dorsal margin depressed anteriorly; apical segment three times longer than wide, apicomesal face densely covered with short, dark, peglike setae. Tergum X elongate, enlarged at base, narrow at distal

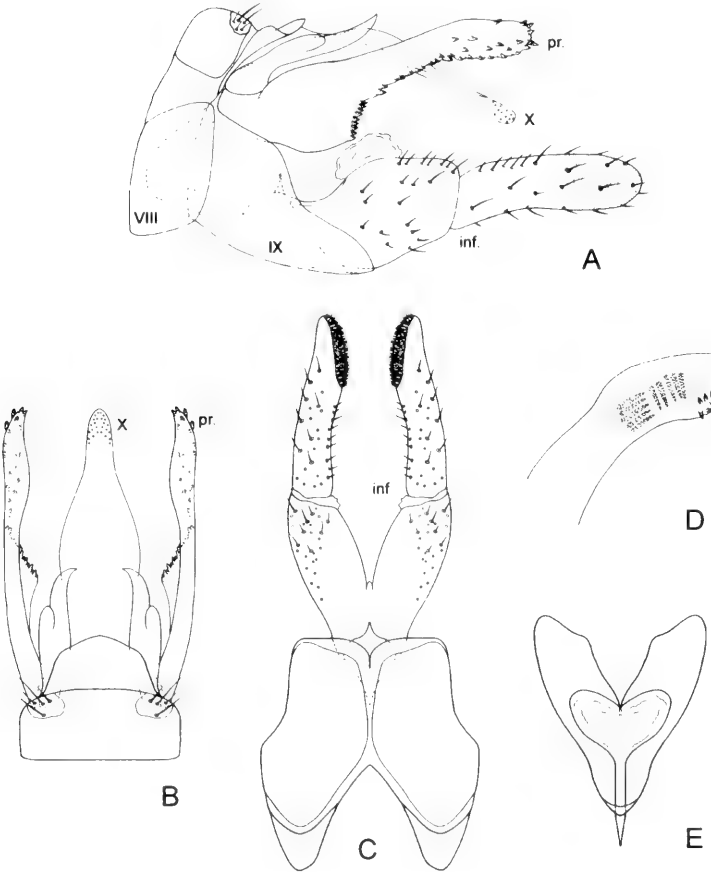

Fig. 1. *Dolophilodes* (*Sortosa*) *marinonii*, male genitalia. A, Lateral. B, Dorsal. C, Ventral. D, Phallus, lateral. E, Inferior appendages, basal segments, dorsal. Abbreviations: (inf.) inferior appendage; (pr.) preanal appendage.

end; apex bearing sensilla; a sclerotized, bipartite appendage arising basally on each side of tergum X, lateral branch rounded, distal branch acute. Preanal appendage as long as tergum X, enlarged basally, tapering apically; ventral margin and apex bearing short, stout spines. Phallus tubular, apex membranous with group of short, stout, black spines; internal fold with several spines about four times length of apical ones.

Female.—Unknown.

Type material.—Holotype, ♂. BRAZIL: Paraná: Antonina, Reserva de Sapitanduva, 25°28′S, 48°50′W, el. 60 m, 18.ii.1988, PROFAUPAR-lâmpada [light trap]. Paratypes: Same data as holotype, 28.v.1987, 1 ♂, 19.i.1988, 1 ♂, 17.iii.1988, 1 ♂. Deposited in the Coleção de Entomologia Padre Jesus Santiago Moure, Universidade Federal do Paraná, Curitiba, Brazil. The specimens are preserved in 70% ethanol.

Etymology.—This species is named in honor of Prof. Dr. Renato C. Marinoni, a coleopterist of the Departamento de Zoologia, Universidade Federal do Paraná, Brazil, who strongly supported the entomological survey called PROFAUPAR (Projeto de Levantamento da Fauna Entomológica no Estado do Paraná).

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AVIAN PREDATION ON IMMATURE STAGES OF THE LOCUST BORER, *MEGACYLLENE ROBINIAE* (FORSTER) (COLEOPTERA: CERAMBYCIDAE)

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Abstract.—Avian predation on the locust borer, *Megacyllene robiniae* (Forster), was studied in 15 black locust (*Robinia pseudoacacia* Linnaeus) stands in western Maryland during 1987–88. Only woodpeckers were observed in the act of predation, but other avian species could not be discounted in assessment of past predation. The overall predation rate was low, ranging from just 0–1.7%, except in one stand where birds depredated 20% of the borers over a 2-year period. Birds focused their attacks on late instar larvae and pupae, the largest life stages. There was no evidence of predation on the much smaller, overwintering first instar larvae. Intensity of predation was related directly to larval and, especially, pupal density. Predation was more common in relatively small, unhealthy trees and in small trunks and branches. Most predation was attributed to hairy woodpeckers (*Picoides villosus* Linnaeus), based in part on direct observations and excavation characteristics. The overall low predation was likely due to a complex of factors that limited numerical and functional predatory responses to locust borers, including predator territorial behavior and seasonal shifts in foraging patterns, relatively low borer density, and black locust tree characteristics that could impede foraging (e.g., large thorns).

Key Words: black locust, excavations, tunnels, woodpeckers

Woodpeckers have long been regarded as important predators of wood-borers (Beal 1911, Forbush 1927, Bent 1939), a complex of insects that tunnel in the sapwood and heartwood of live trees and account for substantial annual timber losses in the eastern United States (Donley and Worley 1976, Nielson 1981). Recent research has addressed biological aspects of potential wood-borer predators, particularly the red-cockaded woodpecker (*Picoides borealis* Vieillot), including foraging behavior (Engstrom and Sanders 1997, Doster and James 1998), competition (Knapps 1997, Saenz et al. 1998), habitat (Engstrom and Mikusinski 1998), and arthropod prey (Hanula and Fanzreb 1995). For pileated woodpeckers (*Dryocopus pileatus* Linnaeus), studies of habitat preferences have indicated importance of large trees and snags (Renken and Wiggers 1993), whereas others have dealt with interspecific competition in which pileated woodpeckers enlarged nesting cavities of red-cockaded woodpeckers (Saenz et al. 1998), and intra-specific competition between pileated woodpecker males (Oberman 1995). Although considerable research has been has been devoted to the role of birds in regulating insect populations (e.g., Knight 1958, Otvos 1965, Dickson et al. 1979, Cooper and Smith 1995), few studies have documented the impact of birds on populations of woodborers, or longhorned beetles, of the family Cerambycidae, and little information is available on factors that influence the rate of predation. In this paper, we describe avian predation, believed to be mostly by woodpeckers, on the locust borer, *Megacyllene robiniae* (Forster), a common woodborer invading the black locust tree *Robinia pseudoacacia* Linnaeus. In heavily-infested black locust stands in Ohio, Hall (1942) considered woodpeckers to be the most effective predator, but presented no data. Our objectives were to determine the rate and phenology of predation and examine possible relationships between the incidence of avian attacks and borer density, tree characteristics, and the within-tree location of borers.

The locust borer is a primary (i.e., invades only living trees), monophagous (consumes only one host species), univoltine (1 generation per year), wood-boring species that is native throughout much of the natural range of black locust (Hall 1942, Galford 1970). The egg, larval, and pupal stages reside in the live branches and trunks of black locust trees. Eggs are laid singly in bark crevices during August through early October. Hatching occurs from 8 through 10 days following oviposition. The first instars bore into the inner bark where they overwinter in small (4–5 mm diameter) oval galleries. Larval activity first becomes evident the following spring when they resume feeding, resulting in an accumulation of frass, wood dust, and sap along the bark surface just outside the excavation entrance. As the larval activity continues during early through mid-summer, their tunnels extend into the sapwood and heartwood. Tunnel access to the outside is maintained throughout this period, and scars with various configurations may form only after adult emergence (Harman and Dixon 1984). A completed borer mine ranges from 10–21 cm long, 5–8 mm in diameter and extends 1–6 cm deep into the wood. The mine typically resembles a twisted, inverted "J" and is occupied by a single larva. Cavities are usually excavated beneath the outer bark by the borer larvae in their early instars, as they begin feeding, prior to construction of tunnels. These vary in size to as deep as 1 cm, and as wide as 2 cm, and may harbor an array of inquiline invertebrate species (Larson and Harman 2003). When fully developed, larvae measure 20–30 mm long and 5–7 mm in diameter. Pupation occurs during mid-July through August and adults emerge in August through early September. Detailed accounts of the locust borer life cycle are provided by Hall (1942) and Galford (1970).

MATERIALS AND METHODS

This study was conducted in 15 black locust stands in western Maryland, near the Allegheny Ridge, in the central Appalachian Mountains. Stands were located at elevations ranging from 582 through 850 m, and all were of intermediate age (20–40 yrs). The landscape is dominated by oak, hickory, and northern hardwood forests interspersed with small farming communities and coal strip-mined areas.

To examine predation in a variety of habitats, we selected three stands in each of the following five site categories: (1) old field, (2) pasture, (3) forest opening, (4) roadside, and (5) reclaimed strip-mines. Each stand contained a natural (not planted or seeded) sere or progression of black locust growth that extended outward from mixed-species forest, 200 ha or larger, into an adjacent open area (e.g., an old field or reclaimed strip-mine). The seres comprised as many as five discrete, easily identifiable black locust successional stages: mixed forest, forest-clone edge, clonal black locust growth, clone-open edge, and open growth. Detailed descriptions of the vegetation in each successional stage are provided by McCann and Harman (1990) and McCann (1992). The above site categories were chosen because they were most representative of growth situations for black locust in the region.

Data collection.—During 1987, predation rate was estimated by determining the percentage of active borer mines that were depredated on the bottom 3 m of 10 randomly selected trees (herein referred to as sample trees) per successional stage per stand. Thus, as many as 50 sample trees per stand (total 489) were monitored for predation. In some stands, reduced sample sizes were necessary because certain successional stages were absent or fewer than 10 black locust trees per successional stage were present. Sample trees were selected using a modified point-quarter method (Cottam and Curtis 1956). This method involved establishing line transects at 8 m intervals perpendicular to the forest edge. At random points along the transects, the nearest black locust tree was chosen from a randomly selected 90° quadrant.

Active borer mines were tallied on the bottom 3 m of each sample tree during May. Larval tunneling was identified by presence of fresh sap, frass, and wood dust exhuding from entrance holes. Each mine was marked with crayon by placing a small dot on the bark within 3–6 cm of its entrance. Sample trees were then checked for predation once per month during May through Sept. A mine was considered probed by a predator if an excavation (e.g., a conical hole or chipped bark) was present within 5 cm of the mine entrance. Occasionally, identity of the prey item was uncertain and a knife was used to cut into the wood to verify the presence of an active locust borer mine.

Data collected for each sample tree included diameter at breast height (dbh), tree height, and crown class. Crown class designations were: dominant, codominant, intermediate, or suppressed (Smith 1962). Data collected for each active borer mine included height above ground, stem diameter, orientation of entrance (north vs. south), and branch versus main bole. In instances of predation, length, width and depth of the predatory excavation were measured. Also recorded was whether the predator entry was typical of a woodpecker species; remaining entries were considered birds of unknown species. To determine whether the borer evaded predation and survived to the adult stage, wire screen traps (3.1 × 3.1 mm mesh) were stapled over the emergence hole to capture any emerging adults. Traps were in place during during July through September, and were then checked for emerged adults every 7–10 days. In addition to the above, trunk surfaces of all trees in each stand were inspected for signs of predation to a height of 12 m, using 10 × 50 binoculars, an 8- m extension ladder or a modified rock-climbing method (Perry 1978). These surveys included counts of borer tunnels from previous as well as current year, and allowed us to (1) obtain additional information on predation characteristics, (2) qualitatively judge the validity of predation rate estimates, and (3) help determine if predation occurred during the overwintering stage (October through April). Complete stand surveys were conducted monthly during May through September and tri-monthly during October through April. During the winter surveys, any excavation found in trunks or branches was considered potential predation because young larvae show no external evidence of their presence until at least late April. If predation was suspected, the bark area surrounding the excavation was exposed with a knife to confirm the presence of a locust borer hibernaculum.

In one of the 15 stands (RD3) where the predation rate was relatively high, predation was monitored an additional year and predation characteristics were examined more closely. Here, current and previous year's borer attacks and predation rate were determined on the bottom 12 m of all trees, including sample trees. Trees were checked at least twice weekly during May through September of the additional year. Data collection proceeded as described above. Additionally, borer survival to the pupal stage was determined by checking for the presence of a well-defined adult emergence hole

Table 1. Summary of woodpecker predation rates on locust borers in 15 black locust stands in western Maryland during May through Sept. 1987. Presented are the number of black locust trees sampled, number of active borer mines on the lower 3 m of each sample tree, and number and percentage of depredated borers.

Site Type/Stand No.	Variable	Successional Stage					
		Mixed Forest	Forest-clone Edge	Clonal Growth	Clone-open Edge	Open Growth	Total
Old Field	No. Trees	24	30	20	20	20	134
	No. Borers	167	148	98	103	82	598
	No. Depredated	0	0	0	2	0	2
Pasture	No. Trees	20	20	30	28	16	114
	No. Borers	32	72	118	103	39	364
	No. Depredated	0	0	0	0	0	0
Opening	No. Trees	28	30	10	NP	NP	68
	No. Borers	124	148	81	NP	NP	353
	No. Depredated	0	1	0	NP	NP	1
Roadside	No. Trees	30	19	18	14	NP	81
	No. Borers	100	175	139	145	NP	559
	No. Depredated	8	6	1	0	NP	15
Strip mine	No. Trees	23	30	29	21	21	124
	No. Borers	119	260	328	239	211	1,157
	No. Depredated	0	0	0	3	8	11
Total	No. Trees	125	129	107	83	57	489
	No. Borers	542	803	764	590	332	2,679
	No. Depredated	8	7	7	6	8	30

> 4 mm in diameter in mid- through late July. A hole < 4 mm diameter indicated that a larva had died while small, probably prior to the pupal stage (McCann 1992).

Occasionally, predation on locust borers was directly observed. Data recorded during these incidental observations included the species, sex and, if possible, age (hatch year or after-hatch year) of the bird, and time required to extract the borer. Only hairy woodpeckers were observed in the act of predation.

Statistical analyses.—Using RD3 data, *t*-tests (for numeric variables) and chi-square tests (for categorical variables) were used to compare trees with versus without predation and depredated versus nondepredated mines (Sokal and Rohlf 1995). Relationships between incidence of predation, borer density, and tree characteristics were examined with Spearman's rank correlation test. Data were checked for normality and homoscedascity using a Kolmogorov-Smirnov test and Bartlett Box test, respectively. Means ± 1 standard deviation are reported. All statistical tests were considered significant if $P \leq 0.05$.

RESULTS

Overall predation rate.—A total of 2,629 active borer mines were monitored for bird predation. One or more mines were present on the bottom 3 m of 428 (87%) of 489 sample trees; no borers occurred in 61 trees (Table 1). The mean (±SD) number of mines per tree was 6.9 ± 8.4 (range, 0–64) and mines per stand ranged from 2.9 to 17.5.

Based on sample tree data, the overall predation rate in 1987 was only 1.01% (30 of 2,629 borers Table (1). No predation occurred in 9 stands. Among the other 6 stands, the predation rate ranged from 0.7 % (2 of 293 borers) through 1.7% (1 of 59 borers) except for one of the roadside stands (RD3), where 11.0% (14 of 127) of

Table 2. Summary of data on locust borer populations and woodpecker predation rate (bases on surveys of lower 12 m of all trees) in Roadside Stand no. 3 (RD3), western Maryland, during 1987 and 1988.

Variable	1987	1988	Both Years
No. active borer mines	627	397	1,024
No. depredated borers	108	94	202
Predation rate (%)	17.2	23.8	19.9
No. trees	46	32	78
No. trees with active borer mines	44	30	74
No. trees with depredated borers	26	20	46
Mean (±SD) no. active borer mines per tree	13.6 (8.7)	12.4 (11.0)	13.1 (9.6)
Mean (±SD) no. depredated borers per tree	2.5 (2.7)	3.0 (3.3)	2.7 (2.9)
Mean (±SD) percentage of borers depredated per tree	15.3 (16.8)	22.1 (23.4)	18.0 (19.8)
Mean (±SD) no. depredated borers per tree with ≥1 instance of predation	4.2 (2.4)	4.7 (2.9)	4.4 (2.6)

the borers in sample trees were depredated. There was little consistent variation in predation rate among site categories (range = 0–2.9%) although successional stages averaged higher due to one strip-mine stand (open growth, 12.8%) (range = 0.3–2.7%).

During complete stand surveys, we found a total of 304 instances of avian predation in 13 of the 15 stands. Approximately 36% (108 borers) of this predation occurred in RD3. Predation was not restricted to a particular habitat or successional stage. However, in a few stands and site types, the number of woodpecker attacks was relatively high in certain successional stages; e.g., 94.1% of the predation in strip mine sites occurred in either clone-open or open growth. One of the strip-mine stands, open growth stage, had 12.8% bird predation rate, the highest for any single stand. Strip mines had notably greater numbers of borers per tree than the other site types (9.3 versus 6.9 for roadsides and 4.4 for old fields); this feature has been confirmed in other regional investigations (Harman et al. 1985b, 1989)

Predation rate in RD3.—Stand RD3 contained a total of 1024 active mines and borers occurred in all but 2 trees during each year (Table 2). Borer density averaged 13.1 (± 9.6) active mines per tree (bottom 12 m) but varied considerably (range = 1.47). The borer infestation level in RD3 was moderate and not statistically different ($P \geq 0.1$) from that in other stands.The predation rate in RD3 during the first year was 19.9%, which, compared to other stands, was exceptionally high. A greater percentage ($X^2 = 6.05$, 1 *df*, $P = 0.014$) of borers was depredated during the second year than the first (23.8% versus 17.2%). However, there were no interyear differences in borer density ($t = 0.51$, 76 *df*, $P = 0.61$) or in the percentage of trees with active mines ($X^2 = 0.14$, 1 *df*, $P = 0.71$). The highest number of depredated borers found in a tree during a single year was 11 (of 15 borers) and the percentage of mines depredated per tree ranged from 5.6% (1 of 18 borers) to 75.0% (6 of 8 borers).

Predation phenology and success.—We found no evidence of predation during the egg, overwintering larval, or early spring larval stages. Most instances of predation occurred in July and August (29 versus 17%, respectively), when later-instar larvae and pupae were present. In RD3, where predation was monitored on a weekly basis during the second year, the number of avian attacks peaked during the third week of July, just before pupation when larvae attained maximum size and were most active. Predatory attempts per week for the six weeks from June 2–August 1, 1988, were 16, 21, 19, 27, 9, and 2.

Not all predatory entries into borer mines were successful, indicating that the borer larvae may have evaded the intrusion or the

Table 3. Comparison of black locust trees with and without woodpecker depredated locust borer mines in roadside stand no. 3 (RD3), western Maryland.

Variable	Year	Trees with Predation[a]			Trees without Predation[b]			P^c
		Mean	SD	Range	Mean	SD	Range	
Dbh (cm)	1987	11.9	2.3	7.6–18.3	14.5	3.7	6.1–19.7	0.013
	1988	12.2	2.6	8.6–18.3	15.3	2.4	12.7–18.8	0.003
	Both	12.0	2.4	8.6–18.3	14.8	3.3	6.1–19.7	<0.001
Tree height (m)	1987	10.1	2.1	7.9–18.0	12.5	32	7.7–18.6	<0.001
	1988	10.5	2.4	7.8–18.0	12.6	2.4	10.1–15.9	0.032
	Both	10.3	2.2	7.9–18.0	12.8	2.9	7.7–18.6	<0.001
No. larvae per tree	1987	18.0	8.3	4–32	8.9[d]	5.2	1–20	<0.001
	1988	17.5	10.8	4–47	4.7	3.9	1–11	<0.001
	Both	17.8	9.3	4–47	7.4	5.1	1–20	<0.001
No. pupae per tree	1988	6.5	4.3	1–19	1.1	1.0	1–3	<0.001
Larval survivorship to pupal stage (%)	1988	38.4	13.9	12.5–66.7	28.2	30.4	0–100	0.335

[a] Sample sizes were 26, 20, and 46 for 1987, 1988, and both years combined, respectively.
[b] Sample sizes were 18, 10, and 28 for 1987, 1988, and both years combined, respectively.
[c] *P*-values are based on *t*-tests.
[d] Means were different ($P \leq 0.05$) between years based on *t*-tests.

Table 4. Spearman's rank correlations[a] between black locust tree characteristics and the incidence of woodpecker predation on locust borers in roadside stand no. 3 (RD3), western Maryland.

Variable	Year	Depredated Borers/Tree	
		Number	Percent
Dbh	1987	−0.389	−0.457
	1988	−0.503	−0.662
	Both	−0.460	−0.587
Tree height	1987	−0.408	−0.482
	1988	−0.462	−0.582
	Both	−0.439	−0.482
Crown class	1987	−0.211	−0.226
	1988	−0.394	−0.657
	Both	−0.330	−0.226
No. larvae per tree	1987	0.841	0.318
	1988	0.748	0.379
	Both	0.663	0.318
No. pupae per tree	1988	0.849	0.374
Larval survivorship to pupal stage	1988	0.314	0.175

[a] Spearman's rank correlation coefficients are shown. Using a 2-tailed test of significance, * $P \leq 0.05$, ** P ~< 0.01. Sample sizes were: 1987 = 44, 1988 = 30, both years = 74.

predator may have missed its target. In RD3, borers survived to the adult stage in 8.4% of depredated mines (17 of 202), while in other stands the survival rate was significantly higher at 16.5% ($X^2 = 5.77$; 1 *df*; $P \leq 0.05$).

Some dimensional and vigor aspects of trees were associated with frequency of bird predation. In RD3, trees with predation were significantly smaller than trees without predation in terms of dbh, height, and of less thrifty crown class (Table 3). Correlation analyses revealed that both the number of depredated mines per tree and the percentage of borers depredated per tree were inversely related to dbh, tree height and crown class (Table 4). Predation was also also positively correlated with larval and pupal density. There were no significant correlations in RD3 between borer density, borer survivorship, tree size, or crown class.

Significant differences also existed between the characteristics of depredated and nondepredated borer mines. Depredated ones were at greater heights, relative heights (height above ground divided by

Table 5. Comparison of woodpecker depredated and nondepredated locust borer mines in roadside stand #3 (RD3), western Maryland.

		Depredated Mines[a]			Nondepredated Mines[b]			
Variable	Year	Mean	SD	Range	Mean	SD	Range	P
Height above ground (m)[c]	1987	4.3	2.3	0.6–11.1	3.1[d]	2.0	0.1–9.4	<0.001
	1988	4.6	2.5	0.4–10.6	3.5	2.3	0.1–10.1	<0.001
	Both	4.5	2.4	0.4–11.1	3.2	2.1	0.1–10.1	<0.001
Relative height above ground[c]	1987	0.44	0.22	0.06–0.98	0.29[d]	0.19	0.01–0.91	<0.001
	1988	0.47	0.24	0.04–0.92	0.32	0.21	0.01–0.89	<0.001
	Both	0.46	0.23	0.04–0.98	0.30	0.20	0.01–0.91	<0.001
Stem diameter (cm)[c]	1987	9.1	2.9	2.8–17.0	11.4	3.1	3.8–21.0	<0.001
	1988	8.9	3.2	2.5–16.0	11.3	3.1	3.8–21.0	<0.001
	Both	9.0	3.0	2.5–17.0	11.4	3.1	3.8–21.0	<0.001
% in branches (vs. main bole)[e]	1987	5.6			1.2			<0.001
	1988	7.5			0			<0.001
	Both	6.4			0.8			<0.001
% with north (vs. south) orientation[e]	1987	0.36			51.2			0.005
	1988	48.4			53.3			0.406
	Both	41.8			52.0			0.011

[a] Sample sizes were 26, 20, and 48 for 1987, 1988, and both years combined, respectively.

[b] Sample sizes were 18, 10, and 28 for 1987, 1988, and both years combined, respectively.

[c] P-values based on t-tests.

[d] Means were different ($P \leq 0.05$) between years.

[e] P-values are based on chi-square tests.

tree height), and in smaller diameter stems, as shown in (Table 5), which provides data from the RD3 stand only. These predation data were taken to a height of 12 m. In contrast, previous studies have shown lower borer density in higher tree portions (Harman and Harman 1990). Also, combining study years, more borers were depredated on the south than north-facing side of stems (Table 5). Only 19 (1.9%) of the 1,024 active borer mines in RD3 occurred in branches; however, few branches existed below 12 m in this stand due to heavy shading and natural pruning. Branch mines were depredated at a higher n rate (68.4%) than mines along the main bole (18.8%), perhaps again reflecting a tendency by the birds to attack mines at relatively greater heights and in small diameter stems.

In stands other than RD3, the low incidence of predation in sample trees precluded most meaningful statistical comparisons. However, data collected during the complete stand surveys suggest that predators foraged on trees with similar characteristics as in RD3. For example, trees with predatory attacks tended to be relatively small (9.0 ± 4.3 cm dbh, range = 2.0 to 21.3) and 7.8 ± 3.4 m tall (range = 2.0 to 18.0). Over 75% of the trees with predation were less than 11.7 cm dbh and 10.1 m tall, and most were in the intermediate and suppressed crown classes. Complete stand survey data also show that depredated mines were located in relatively small diameter stems (mean = 4.5 ± 2.8 cm) and over 95% of all woodpecker attacks were in stems less than 10.2 cm diameter. The smallest diameter stem with predation was 1.3 cm, corresponding with the minimum stem size in which locust borers reside. No predation was recorded in stems over 17.8 cm diameter although borers commonly tunnel in stems as large as 38 cm. The mean depredated mine height was 3.9 ± 2.2 m and, unlike RD3, most woodpecker attacks (67.3%) occurred in branches rather than in the main bole. Woodpecker excavations were usually conical shaped and oriented lengthwise along the branch or tree trunk. They measured, on average, 2.4 (± 0.9) cm long (range = 0.7–8.1) by 1.6 (± 0.6) cm wide (range = 0.5–3.6), and 1.6 (± 0.6) cm deep (range = 0.4–3.3). These dimensions were each correlated with stem diameter ($R \geq 0.67$, $P < 0.001$).

Direct observations.—Thirty-six instances of predation were directly observed. Adult hairy woodpeckers *P. vilosus* (26 ♂, 2 ♀) accounted for 28 instances, six were by adult downy woodpeckers (*P. pubescens*) (4 ♂, 2 ♀), and two were by adult pileated woodpeckers *D. pileatus* (1 ♂, 1 ♀). In RD3, all direct observations (n = 17) were of adult male hairy woodpeckers.

No predation was observed by northern flickers (*Colaptes auratus* Linnaeus) or red-bellied woodpeckers (*Melaneupes carolnus* Linnaeus), although both species nest throughout the study area. A number of other species, including white-breasted nuthatches *Sitta carolinensus* Latham, brown creepers (*Certhia familiaris* Bonaparte), and black-and white warblers (*Miniotilta varia* Linnaeus), have morphological and behavioral adaptations for tree-trunk foraging (Jackson 1979), and could be potential predators of borer larvae. Although our actual observations included only woodpeckers, these and other avian species should be included as possible foragers in some of the instances of past predation, which could not be definitely assigned to woodpeckers. Predation by hairy woodpeckers occurred in a variety of successional stages and site types, while pileated and downy woodpecker predation was observed only in mature forest and young open or clonal growth, respectively.

DISCUSSION

The scope of the sample for site type comparison was influenced by sampling on the bottom 3 m branches and stem portions, and numerical comparisons from these analyses apply to this lower portion rather than to the entire tree. Other parts of the study were not restricted to the bottom 3 m, and data were taken higher in the trees (i.e., 12 m for the roadside 3 stand, and unspecified height for direct observation with binoculars). The 3 m limit was necessary to facilitate the close viewing and evaluation of a large tree sample by an observor standing on the ground holding delicate equipment, and easily accessing all sides of the trees. Prior observations indicated that, in stands of this size, sufficient borer activity occurs below 3 m on trunks to allow valid comparisons. Sampling below 3 m, however, could cause data inferences to be influenced by such factors branch height, and/or comparative visibility of the features in question.

With a few exceptions, avian predation appeared to exert only minor mortality in this study. These findings concur with casual observations by other authors who reported little (3–7% larval mortality) or no avian predation on locust borers (Garman 1916, Van Tyne 1983, Bourne 1986). Hall (1942), however, believed that woodpeckers are capable of causing much greater mortality (30–40% of locust borer larvae) and, as in our study, described heavier predation usually occurring in small, localized areas. Hall's studies were conducted in Ohio, away from the optimal range for black locust, where black locust growth is less thrifty, and pressure from the locust borer more intense than in the Appalachian Plateau.

The response of a predator population to changes in prey abundance has been described as consisting of two components: a numerical and functional response (Holling 1959). We attribute the low incidence of avian attacks on locust borers to a variety of factors that limited both types of responses. Although birds, particularly woodpeckers, are capable of strong numerical responses to increases in prey density, especially through aggregation behavior, such as occurs during bark beetle (*Dendroctonus* sp.) outbreaks (Blackford 1955, Baldwin 1960, Koplin 1969), locust borer numbers are probably too low to elicit woodpecker aggregation behavior, even during severe infestations. Predation in our study occurred during or just after the nesting season for hairy, downy, and pileated woodpeckers (Stewart and Robbins 1958), when their concentrations are limited by territorial behavior. Hutchinson (1951) and Yeager (1955) observed woodpecker feeding aggregations in areas where bark beetle outbreaks exceeded 4 million larvae per ha and extended over thousands of hectares. Locust borers rarely reach even 1% of this density and the size of an infestation is ultimately limited by the availability of black locust trees, which typically are scattered or in small stands of less than 4 ha.

The overall predation rate appeared low compared to other wood-borer species, with similar-sized larvae, which have ranged from 9 to 39% for the red oak borer *Enaphalodes rufulus* Haldeman (Hay 1972, Petit et al. 1988, respectively), 67% for the oak branch borer *Goes debilis* LeConte (Solomon 1977), and as high as 81% for the ash borer *Podosesia syringae* (Harris) (Solomon 1975). However, there are major differences, such as the fact that these wood-borers have 2–4 year life cycles and overwinter as large, late-instar larvae and pupae with considerable energy value to predators. With these species, most bird predation occurs during fall and winter, and the predation rates reported were much higher than for locust borers (Solomon 1969, 1975, 1977; Hay 1972; Petit et al. 1988).

Predation may also be limited functionally by a combination of factors in addition to those named above. Downy, hairy and, to a lesser degree, pileated woodpeckers feed opportunistically on a variety of food resources, reducing the likelihood of concentrated foraging on a single prey species over an extended period of time (Beal 1911, Bent 1939, Lawrence 1966, Conner 1980). Each species also exhibits significant seasonal differences in diet and foraging behavior (Jackson 1970; Conner 1979, 1981). In late spring and summer, deep-wood insect prey such as wood-borers represent a relatively minor component of their diet. During fall and winter, the three species feed much more extensively on subcambial prey but locust borer larvae are extremely small at that time, measuring only about 2 mm long, and their oval galleries are only ~5 mm in diameter.

Habitat conditions in many sections of the stands also may have limited woodpecker predation. At least three (open, clone-open edge, and clonal) of the five black locust successional stages contained marginal or unsuitable foraging habitats for hairy and pileated woodpeckers, which prefer older forest conditions and larger diameter trees and branches as foraging substrates (Bent 1939, Hoyt 1957, Kisiel 1972, Conner and Crawford 1974, Conner 1980, Renken and Wiggers 1989). Although downy woodpeckers feed in a variety of forest successional stages and on relatively small diameter stems (Bent 1939, Jackson 1970, Kisiel 1972, Williams 1975, Conner 1980), subcambial prey represent a minor component of their diet, especially during spring and summer (Conner 1980, 1981). Downy woodpeckers are also physically less capable of excavating deep-wood prey due to their relatively small bill, short tongue, and less developed head and neck musculature (Selander 1966, Lawrence 1966). We attributed most predation to hairy woodpeckers based, in part, on direct observations and the size and shape of woodpecker excavations. This species accounted for over 75% of all direct observations of predation and all directly observed predation in RD3. Although hairy woodpeckers prefer more mature forest conditions and larger diameter stems, they frequently forage in sapling and pole stage forests (Kisiel 1972, Conner 1980). This species also is a more capable excavator than downy woodpeckers (Selander 1966, Lawrence 1966) and feeds more frequently on subcambial prey during spring and summer (Selander 1966, Lawrence 1966, Conner 1981).

Other factors act against avian predation of locust borers, such as the relatively short period of availability of late larval and pupal stages, and certain characteristics of black locust wood, which is among the hardest of any tree species in eastern North America (Roach 1958). Also present are thorns, especially on smaller diameter stems and tree trunks where locust borer densities also may be greatest (McCann 1992). The thorns may impede woodpecker movement along the bark surface and reduce overall use of black locust trees as foraging substrates. Bark features of other tree species (e.g., honeylocust, *Gleditsia triacanthos* Linnaeus), thorns, and bark shingles of shagbark hickory, *Carya ovata* (Mill.) K. Koch, can have a similar effect on woodpecker foraging (Jackson 1970, 1979). Locust borers in their late larval and pupal stages, when their size might justify a predatory attempt, are not near the stem surface, but often relatively deep beneath the surface.

Reasons for the relatively high predation rate (19.9%) in RD3 were not apparent, but this area appeared isolated and localized. Numerous factors could be involved, including woodpecker densities and habitat, fluctuations of alternate prey, and possible alterations in borer behavior. One such observation was reported by Hall (1942) during a drought year in Ohio, in which larvae tended to remain in subcortical cavities rather than exhibit the normal habit of constructing tunnels; this would place larger larvae and pupae nearer the surface and more vulnerable to predation.

Predation rate was correlated with crown class, and with compass direction, with higher instances of predation on south than north facing stem surfaces. Black locust is very shade-intolerant (Roach 1958) and increased shade is usually seen with downward progression from dominant to suppressed crown class, accompanied by increasing decline and greater susceptibility to insects and fungi. Locust borer attack rates have also been found to increase with increased percent of black locust in the stand (Harman et al. 1985a). Predation may respond due to increased borer infestation rates and aggregation of other invertebrates around wound entrances (McCann 1992).

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SPERMATOPHORE IN APHODIINAE (COLEOPTERA: SCARABAEIDAE)

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Abstract.—To study the spermatophore, females of three species, each of a different Aphodiini genus, and three species of one Eupariini genus we examined. All beetles were collected in the field throughout one reproductive cycle. In *Gonaphodiellus opisthius* (Bates) and *Planolinus vittatus* (Say) (Aphodiini), no spermatophore were found, probably because spermatozoa were freely transferred to the spermatheca in seminal fluid. In contrast, *Cephalocyclus hogei* (Bates) (Aphodiini), *Ataenius apicalis* Hinton, *Ataenius sculptor* Harold, and *Ataenius cribritorax* Bates (Eupariini) were found to form a spermatophore in transferring the spermatozoa. The spermatophore is formed by males during copulation. Its form and size are determined by the anatomy of the female genital chamber of each species. The spermatophore is a voluminous, vesicular structure, formed principally by a large quantity of secretions from the male accessory glands. Another small vesicle is found in the spermatophore's interior, containing secretions and the spermatozoa originating from the testes. The roles male secretions may play in female reproductive activity is discussed.

Key Words: spermatophore, Aphodiini, Eupariini

Limited studies have been done of reproductive anatomy, oviposition behavior, and reproductive cycles of Aphodiinae. These studies cover no more than 67 Aphodiini species and a few Eupariini and Psammodiini species (Martínez 2001, Martínez and Alvarado 2001, Martínez et al. 2001, Martínez and Cruz 2002, Cruz et al. 2002). Copulation has been observed superficially in four *Aphodius* species (Schmidt 1935, Landin 1961); in only one *Aphodius* species, *Aphodius distinctus*, has copulation been described in detail (Vitner 1995).

Neither the spermatophore nor functional aspects of the reproductive apparatus of either Aphodiinae sex is known. This paper provides the results of spermatophore studies in several species that belong to two tribes of this group, namely, Aphodiini y Eupariini. This classification is to be used in this paper, even there are differences of opinion and some researchers regard the Aphodines, Euparines and Psammodinaes as subfamilies of Aphodiidae (*sensu* Balthasar 1963).

MATERIALS AND METHODS

Females of three species of three different genera of Aphodiinae (*sensu* G. Dellacasa et al. 2001, 2002) were examined during the reproductive cycle: 98 females of *Gonaphodiellus opisthius* (Bates) and 126 females of *Planolinus vittatus* (Say) (collected monthly from October 2000 to December 2001 in Las Vigas, Veracruz); and 102 females of *Cephalocyclus hogei* (Bates) (50 collected in June and July 2000 in Cuiyachapa, Veracruz, and 52 collected in June

Table 1. State of ovarian maturity and presence of spermatophore in the genital chamber of females of some Aphodiini and Eupariini species (n, number of females with spermatophore).

Species	Total Number of Females Examined	State of Sexual Maturity, and Presence of Spermatophore (n)
Aphodiinae		
Cephalocyclus hogei	102	Maturing$^{(2)}$ Mature$^{(13)}$
Eupariinae		
Ataenius apicalis	130	Immature$^{(4)}$ Beginning maturation$^{(9)}$
Ataenius sculptor	57	Immature$^{(5)}$ Beginning maturation$^{(1)}$
Ataenius cribrithorax	30	Immature$^{(2)}$ Beginning maturation$^{(2)}$

and July of 2001 in San José Aguazuelas, Veracruz).

In the Eupariini studies, we examined females of three species from the same genus: 130 *Ataenius apicalis* Hinton females (collected monthly from June 1998 to June 1999 in Los Lirios, Actopan, Veracruz); 57 *Ataenius sculptor* Harold females (collected in July 2000 in La Estancia, Palma Sola, Veracruz); and 30 *Ataenius cribrithorax* Bates females (collected in February 1999 in Los Tuxtlas, Veracruz).

All insects were collected directly from dung pats in grasslands in the aforementioned localities.

Reproductive systems of all females were placed in Ringer solution and were extended, fixed in AFATD (96% ethanol-formaldehyde-trichloroacetic acid-dimethylsulfoxide), and stored in 96% ethanol. Spermatecae were spread over slides by crumbling, fixed in AFATD, and stained with the Feulgen green light technique to determine whether spermatozoa were present. After fixation, the genital chambers with spermatophore were imbedded in Histosec® and the histological sections of 7 μm were stained with Feulgen green light or hemotoxilin-eosin. After fixation, reproductive systems were drawn to scale using camera lucida to determine the state of sexual maturity of each female (Martínez 2002). Testicular follicle smears were made, fixed with methanol, and stained with Giemsa dye to observe the spermatozoa of each species.

RESULTS

Spermatophores were not often found in the species studied, even though we examined a large number of females of each species over their entire reproductive periods. Spermatophores were found in only about 15% of one of the dissected Aphodiini species, *Cephalocyclus hogei*, and at comparable levels (10%–13%) in the three Eupariini species, *Ataenius apicalis*, *A. sculptor*, and *A. cribrithorax* (Table 1).

No spermatophore was found in any of the 98 *Gonaphodiellus opisthius* females or the 126 *Planolinus vittatus* females, regardless of maturational state. Apparently, these species do not form a spermatophore as a differentiated structure.

In each of these species, when the spermatophore was present, it completely filled the genital chamber. When the spermatophore was examined during dissection before fixation, it appeared as a voluminous, dense, whitish, refracting structure that distended the genital chamber wall, taking the form of this anatomical region according to the species (Fig. 1).

In all species examined, the spermatophore is seen microscopically as a large vesicle, delimited by an amorphous wall, at

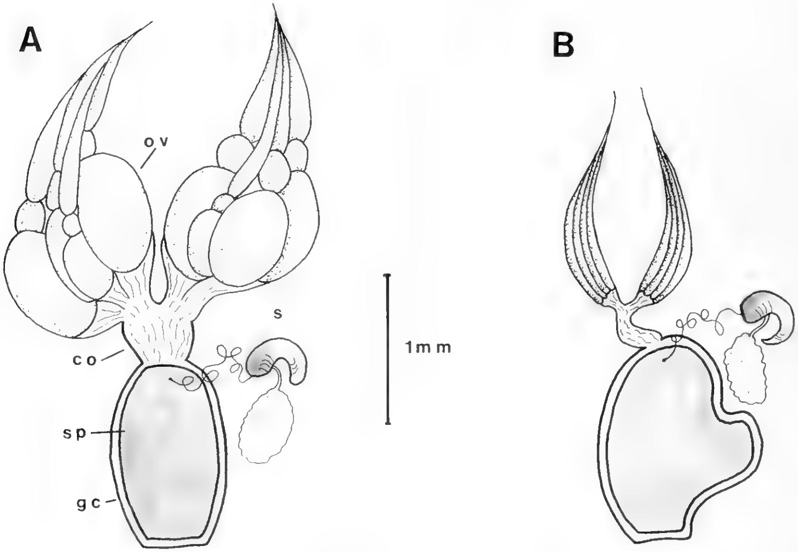

Fig. 1. Scheme of the spermatophore in the genital chambers. A, *Cephalocyclus hogei.* B, *Ataenius apicalis.* Abbreviations: co, common oviduct; gc, genital chamber; ov, ovary; s, spermatheca with its gland; sp, spermatophore.

times a very thick wall, depending on the species, which is contiguous with the epithelium of the genital chamber (Figs. 2A, B, C, D).

This vesicular structure holds a high concentration of secretions. Depending on the species, the secretions show greater affinities to different dyes, some to PAS +, others were acidophilic or basophilic. The secretions also show different forms: as larger or smaller platelets, or granular or amorphous structures, sometimes with vacuoles between them (Figs. 2A, B, C, D) . Another much smaller vesicle is seen among the mass of secretions toward the anterior part of the genital chamber and close to the exit of the spermathecal duct. Within this smaller vesicle are found a smaller quantity of secretions and the spermatozoa. This smaller vesicle is more apparent in *Ataenius* species (Figs. 2B, C, D).

The spermatophore is probably formed by the male during copulation, which in all the species studied takes place within a dung pat. Analysis of the glandular reservoirs of the males of the different species clearly shows morpho-functional modifications depending on state of sexual maturity, particularly relative to copulation. In immature males, the reservoirs are small and without secretions. In mature males before copulation, the reservoirs show their largest size and volume; and in males following copulation, the reservoirs decrease to roughly one-half (39%–67%) maximum volume, depending on the species (Fig. 3, Table 2).

During copulation, males liberate a large quantity of secretions from the accessory glands through the glandular ducts, secretions that have been stored in the glandular reservoirs. At the same time the males must liberate, through the vasa deferentia, the spermatozoa that come from the testicles.

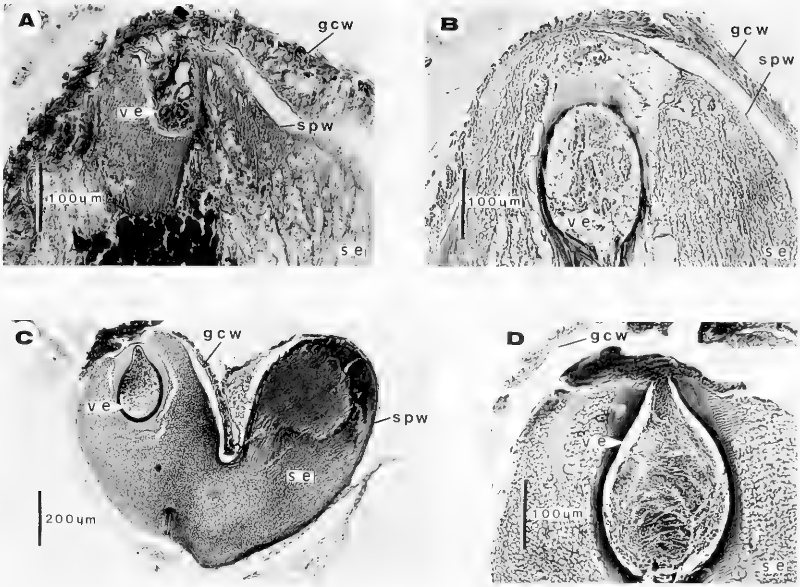

Fig. 2. Microphotographs of the spermatophore. A, *Cephalocyclus hogei*, partial view. B, *Ataenius apicalis*, partial view. C, *Ataenius cribritorax*, complete view. D, *Ataenius cribritorax*, partial view. Abbreviations: gcw, genital chamber wall; se, secretions; spw, spermatophore wall; ve, vesicle with secretions and spermatozoa.

Both the secretions and spermatozoa pass through the ejaculatory duct, found in the ejaculatory bulb, and from there through the internal sac of the aedeagus to be deposited in the female genital chamber as an elaborated spermatophore. In the six species examined, because the quantity of spermatozoa was low, morpho-functional changes in the testicles were not dramatic.

Spermatozoa size varied depending on the species. In Aphodiini, spermatozoa are long, though the length varies according to the species' follicle size. In *Gonaphodiellus opisthius*, males have seven follicles of the

Table 2. Variation in male glandular reservoir volume of some Aphodiini and Eupariini species in different states of sexual maturity (n, number of males examined).

State of Maturity	Glandular Reservoir Volume $(10^{-3}\ \text{mm}^3)$, $\bar{x} \pm$ SD, (n)		
	Cephalocyclus hogei	*Ataenius apicalis**	*Ataenius sculptor*
Immature	23.83 ± 14.11$^{(9)}$	1.03 ± 0.32$^{(5)}$	1.46 ± 1.08$^{(18)}$
Mature			
Before copulation	482.66 ± 71.04$^{(6)}$	46.50 ± 0.70$^{(6)}$	123.16 ± 5.0$^{(3)}$
After copulation	188.83 ± 49.38$^{(11)}$	22.64 ± 3.30$^{(15)}$	81.80 ± 6.0$^{(5)}$

* Because of the anatomy of *Ataenius* species, the volume calculated for these species was that of the sacs of the glandular reservoirs.

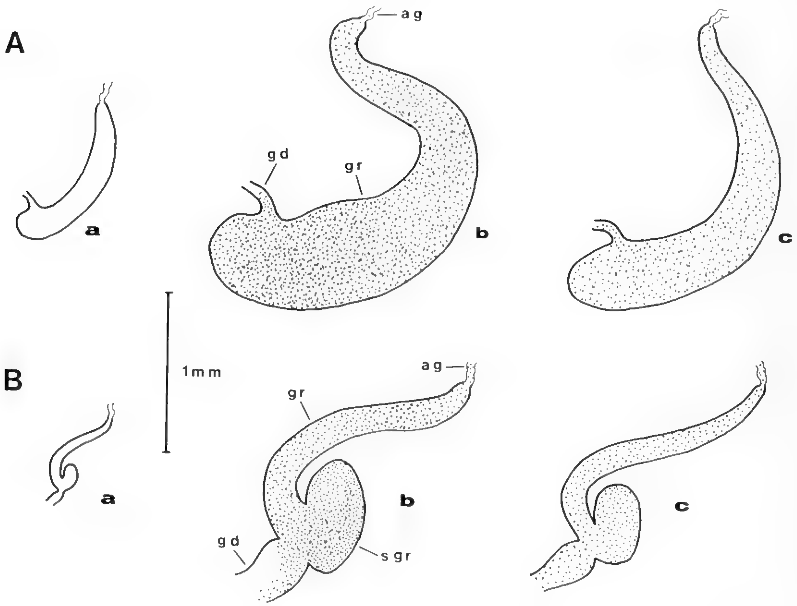

Fig. 3. Scheme of the male glandular reservoirs. A, *Cephalocyclus hogei.* B, *Ataenius apicalis.* a, immature; b, mature before copulation; c, mature after copulation. Abbreviations: ag, accessory gland termination; gd, beginning of the glandular duct; gr, glandular reservoir; se, secretions; sgr, sac of the glandular reservoir.

same size and the spermatozoa measure up to 2,000 μm. In contrast, *Planolinus vittatus* has six large follicles and two small ones, and two sizes of spermatozoa, 600 and 1,100 μm. *Cephalocyclus hogei* has three large follicles and two small ones, and two spermatozoa sizes, 800 and 1,500 μm. The three Eupariini species, *Ataenius apicalis, A. sculptor,* and *A. cribritorax,* each have just two testicular follicles of the same size per testis, and the size of their spermatozoa does not vary so much, from 100 to 160 μm, depending on the species.

The presence of a spermatophore and state of ovarial maturity differed among the species studied (Table 1). In *C. hogei,* the spermatophore was not present in any immature female, but it was found in maturing females with several oocytes per ovariole as well as in mature females before and after oviposition. In *A. apicalis, A. sculptor,* and *A. cribritorax,* the spermatophore was found in the genital chamber in immature females without oocytes and in females that had begun maturation (i.e., that presented a very small basal oocyte in each ovariole).

In all species studied, including *G. opisthius* and *P. vittatus,* the females toward the end of maturation or at maturity had spermatozoa in the spermatheca. This finding suggests that once immature or mature females have copulated, the spermatozoa pass to the spermatheca, while the secretions that form the spermatophore may be reabsorbed in the genital chamber. In *G. opisthius* and *P. vittatus,* in which spermatophores were never found, the spermatozoa must be freely transferred in the seminal fluid to the genital chambers of maturing females and from there to the spermatheca. In these species, it is very likely that the male secretions forming the seminal fluid are also reabsorbed in the genital chamber.

DISCUSSION

The form and size of spermatophore in *Cephalocyclus hogei, Ataenius apicalis, A. sculptor,* and *A. cribritorax* conforms to the genital chamber of each species, as in other Coleoptera species (Landa 1960, Cruz and Martínez 1992).

The spermatophore of these species is vesicular, as is also true for Coleoptera species belonging to other families (Fisher 1959, Gundevia and Ramamurty 1977, Obata 1987). In contrast, in the seven Scarabaeidae species that have been studied, this structure is more elaborate—a vesicular-filamentous structure with a very long filament (Heymons 1930, Halffter and López 1977, Halffter et al. 1980, Cruz and Martínez 1992).

In insects, particularly Coleoptera, the transfer of spermatozoa to the spermatheca is effected in two principal ways: through the initial formation of a spermatophore, which is transferred to the genital chamber, where it is reabsorbed, toward liberating the spermatozoa; or through the free transfer of spermatozoa in seminal fluid (Davey 1960, Mann 1984). *Cephalocyclus hogei, Ataenius apicalis, A. sculptor,* and *A. cribritorax* belong to the former group, and *Gonaphodiellus opisthius* and *Planolinus vittatus* to the latter.

The secretions that form the spermatophore in *C. hogei, A. apicalis, A. sculptor,* and *A. cribritorax* come from the accessory glands of the male, and the chemical nature of these secretions is unknown. The accessory glands of these species are very developed mesadenes, there are not ectadenes (Martínez et al. 2001). It has been widely observed that mesadenes in insects are the principal glands involved in spermatophore formation (Leopold 1976, Mann 1984).

The abundant secretions of the spermatophore of the species studied are no doubt involved in other reproductive processes. In insects, these secretions are responsible for inducing complex functions, such as intervening in the formation of the spermatophore, providing energy to maintain and transport spermatozoa in the female genital tract, inducing ovarian maturation and vitellogenesis, and even forming part of the oocyte yolk (Mann 1984, Huignard 1984, Martínez and Cruz 1999).

It is very likely that, in the species examined here, the secretions play an important role in ovarian maturation given that copulation is carried out with females that are immature or just beginning maturation, and not with those that are mature, as is the case for other species of insects (Raabe 1986), particularly some Scarabaeidae species (Martínez and Cruz 1990, Martínez et al. 1996). On the other hand, in *Cephalocyclus hogei,* copulation occurs when the females are mature. One possible explanation is that, because *C. hogei* has a very short reproductive cycle following a very long diapause (Cruz et al. 2002), the spermatophore secretions may terminate vitellogenesis such that oviposition may occur as quickly as possible. *Ataenius apicalis* and *A. sculptor,* in contrast, present longer reproductive cycles, particularly the first, which shows no diapause (Martínez and Cruz 2002). The cycle of *A. cribrithorax* has not yet been documented.

The fact that relatively few spermatozoa were seen in the spermatophore of the six Aphodiinae species studied is consistent with the studies of Virkki (1951, 1957). Virkki mentions that the number of spermatogonia in the germarium is low, with the result that fewer cysts are present during spermatogenesis and in turn fewer spermatozoa are seen at the end of the process.

The unusual spermatozoa size found in Aphodiini species has been observed in other Coleoptera species, including *Alogoasa bicolor* (L.) (Chrysomelidae) (Virkki and Bruck 1994), *Divalves bipustulatus* (F.) (Cleridae), and *Ptinella aptera* (Guerin)

(Ptiliidae) (Mazzini 1976, Taylor et al. 1982), and in some Diptera species, including *Drosophila littoralis* (Drosophilidae) Meigen (Bressac et al. 1991). What would be the advantage to Aphodiini species to have such a small number of long spermatozoa? Several other questions also arise about spermatozoa size: How do these spermatozoa pass from the testes to the spermatheca? And afterward, how are the spermatozoa released from the spermatheca to fertilize the oocyte?

This spermatozoa behavior during and after copulation is not known, nor is much else known about the reproductive strategies of dung beetles, in particular Aphodiinae species, which have been the least studied.

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SPHAERODERMA TESTACEUM (F.) (COLEOPTERA: CHRYSOMELIDAE), A PALEARCTIC FLEA BEETLE NEW TO NORTH AMERICA

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Abstract.—A common Palearctic flea beetle, *Sphaeroderma testaceum* (F.) is reported for the first time from North America. Adults were collected from Canada thistle (*Cirsium arvense*) in Canada (Bible Hill, Nova Scotia) on 3 August 2001. This apparently accidentally introduced species, a specialist on pest thistles and a promising biological control agent, is redescribed and habitus photographs that facilitate its identification are provided. Its Old World distribution, host plants, and natural history are summarized.

Key Words: Coleoptera, Chrysomelidae, *Sphaeroderma testaceum, Cirsium arvense,* Canada thistle, North America, distribution, natural history, biological control, immigrant species

Thistles include many species of composites in the subfamily Cynareae of the Asteraceae. Although most species in North America are native and beneficial to wildlife, several species that have been unintentionally introduced from Europe and North Africa have become serious weeds of crops and rangelands in North America. Invasive species that warrant control—chemical, cultural, or biological—include musk and Italian thistle [*Carduus thoermeri* (Weinmann) and *Carduus pycnocephalus* (L.)], Canada and bull thistle [*Cirsium arvense* (L.) Scopoli and *Cirsium vulgare* (Savi) Tenore], and milk thistle [*Silybum marianum* Gaertner].

The discovery and deployment of biological control agents to reduce populations of pest thistles below economic thresholds have been emphasized in North America, and several Old World insects have been released into the native landscape for thistle control or suppression. The most important of these species include three weevils [*Rhinocyllus conicus* (Froelich), *Trichosirocalus horridus* (Panzer), *and Hadroplontus litura* (F.); Curculionidae], two leaf beetles [*Altica carduorum* Guérin-Méneville and *Cassida rubiginosa* Muller; Chrysomelidae], and a stem-galling fly [*Urophora cardui* (L.); Tephritidae] (e.g., Harris 1984, Harris and Wilkinson 1984, Peschken 1984, McClay et al. 2002).

Canada thistle is considered one of the world's worst weeds (Holm et al. 1977, McClay et al. 2002) and the third most important weed in Europe (Schroeder et al. 1993). In Switzerland, *C. arvense* is regarded as the most troublesome weed in agricultural land and is equally problematic in adjacent fields (Bacher 1997). In North America, *C. arvense* is a noxious weed in 35 U.S. states and occurs throughout Canada, including the Atlantic Provinces (McClay et al. 2002).

On a recent collecting and survey trip to the Canadian Maritime Provinces, we observed numerous adults of *Sphaeroderma*

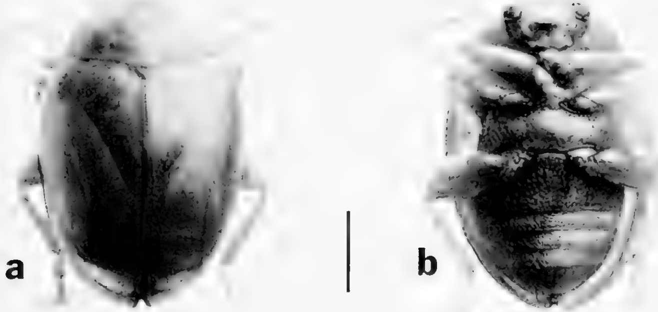

Fig. 1. *Sphaeroderma testaceum*, adult habitus. a, Dorsal aspect. b, Ventral aspect. Scale line, 1 mm.

testaceum (F.) at a site in Nova Scotia; on 3 August 2001, this widely distributed Palearctic flea beetle was beaten from the foliage of *C. arvense* growing (in edge areas) on the campus of the Nova Scotia Agricultural College at Bible Hill (Colchester Co.). We provide here a redescription and habitus photographs of *S. testaceum* to allow its recognition, and information on its Old World distribution, host plants, and natural history.

Sphaeroderma testaceum (F.)
(Fig. 1)
(synonymy after Heikertinger and Csiki 1940)

Altica testaceum Fabricius 1775: 114.
Haltica cardui Gyllenhal 1813: 551.
Sphaeroderma testaceum: Stephens 1831: 328.
Sphaeroderma centaureae Stephens 1831: 329.

Redescription (adapted from Konstantinov and Vandenberg 1996 and Savini and Furth 2001).—Body small, 3.0–4.5 mm, broadly spherical, coccinelliform, wide, strongly convex. Body, legs, and mouthparts orange yellow to reddish brown. Head with frontal sulcus horizontal from upper margin of compound eyes toward center of head. Supraantennal calli present, separated from each other, slightly raised and slightly separated from frontal ridge, and laterally strongly delineated from vertex by deep furrows. Compound eye small. Interantennal space wider than transverse diameter of antennal socket but narrower than transverse diameter of compound eye. Antenna 11-segmented, filiform. Pronotum convex, without prebasal transverse impression; anterior angles projected anteriorly, thickened, very blunt, not beveled. Anterior coxal cavities open behind. Metasternum longer than prosternal and mesosternal process together. Metafemur not greatly thickened, narrower than width of abdomen. Metatibia dorsally rounded, without excavation on outer edge and without preapical tooth. First metatarsomere triangularly enlarged and very thick. Elytral disc with very fine and confused punctation, with tendency to form striae. Epipleura totally visible laterally, very wide in anterior half and gradually tapering apically, almost reaching elytral apex.

Remarks.—Most species of *Sphaeroderma*, a genus of more than 150 species worldwide, are found in the Oriental and Afrotropical Regions; about 14 species also occur in the Palearctic Region (Konstantinov and Vandenberg 1996), with *S. rubidum* (Graells) and *S. testaceum* the most common. There are no native species of *Sphaeroderma* in the New World; two species (*optima* LeConte and *coerulea* Jacoby) previously included in the genus clearly belong to two different genera (Savini and Furth 2001). *Sphaeroderma optima*—recorded from Ohio, Maryland, North Carolina, Florida, and Texas (Wilcox 1975, Flowers et al. 1994)—belongs in the genus *Pseudodibolia* Jacoby, whereas *S. coerulea* (Panama) is now placed in the new genus *Neosphaeroderma* Savini and Furth. These genera, including *Sphaeroderma*, are diagnosed and separated in a key to genera by Savini and Furth (2001).

Distribution.—In the Palearctic Region, *S. testaceum* is widely distributed in Europe, ranging from Denmark and Scandinavia in the north, south to northern Spain, France, northern Italy, the Balkan states, Crimea, southern Russia, and the Caucasus (Heikertinger and Csiki 1940, Gruev and Tomov 1998).

Material examined.—Voucher specimens deposited in the Cornell University Insect Collection, Ithaca, NY. CANADA: NOVA SCOTIA: Colchester Co., Truro (Bible Hill) (45.24° N, 63.18° W), campus of Nova Scotia Agricultural College, 3 August 2001 (11 adults), beaten from Canada thistle (*C. arvense*).

Host plants and natural history.—In the field and in laboratory tests in Europe, adults of *S. testaceum* fed on the foliage of the composites *Carduus nutans* L., *C. crispus* L., *C. personatus* (L.) Jacq., *C. defloratus* L., and species of the genera *Cirsium, Carlina, Onopordum,* and *Silybum* (Batra et al. 1981). The larvae mine the leaves of their hosts, especially species of *Carduus* and *Cirsium,* feeding on the parenchyma. Their mines follow leaf edges, whereas those of *S. rubidum* follow the midrib and principal veins (Redfern 1983). In Bulgaria, *S. testaceum* is found from the seacoast up to 800 meters elevation; adults are present from May through September (Gruev and Tomov 1998).

In England, new-generation adults of *S. testaceum* probably appear from the beginning of April through July and survive until the end of October (Cox 1976). Oviposition extends from late June until the end of October. Egg hatch begins in early August and continues until early January. From early October until late March, fully grown third-instar larvae can be found in leaf mines of *Cirsium.* Fully grown larvae (third instars) apparently enter an obligatory diapause during winter, with pupation occurring from March until July (Cox 1976).

Discussion

Preliminary screening of the host range of *S. testaceum* in Europe suggested this chrysomelid's potential in North America as a biological control agent against invasive thistles of the genera *Carduus, Cirsium,* and *Silybum* (Batra et al. 1981). We were unaware of the beetle's actual release in North America, but our collection of *S. testaceum* on the campus of an agricultural college raised the possibility of an intentional introduction. This possibility seemed greater once we discovered that Glen Sampson, a faculty member at the Nova Scotia Agricultural College, is interested in weed management and has been involved with weed biocontrol projects in Nova Scotia. He is, however, unaware of any attempts to import, evaluate, and release *S. testaceum* in Canada (M.G. Sampson, personal communication). Moreover, this chrysomelid is not among insects known to have been released during 1969–1980 (Harris 1984, Peschken 1984, Harris and Wilkinson 1984) or 1981–2000 (McClay et al. 2002) to help suppress Canadian populations of *Carduus* or *Cirsium* thistles.

Sphaeroderma testaceum is a potentially useful biocontrol agent that apparently has been unintentionally introduced and has become established on Canada thistle in Nova Scotia. Several other Old World insects that feed on invasive thistles in North America, such as the weevils *Cleonus piger* (Scopoli) and *Larinus planus* (F.) and the leaf beetle *Cassida rubiginosa*, also are considered to have been accidentally introduced into North America (Wheeler and Whitehead 1985). *Larinus planus* subsequently has been released against Canada thistle in British Columbia and the Canadian Prairie Provinces (McClay et al. 2002). *Sphaeroderma testaceum* might also be considered for release against pest thistles in North America.

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Note added in proof.—In 2003, we recollected *S. testaceum* at Bible Hill on 29 July (13 adults) and found it at two additional localities in Nova Scotia: Antigonish Co., Antigonish, 30 July (6 adults), and Pictou Co., New Glasgow, 3 August (2 adults).

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A KEY TO THE PUPARIA OF 27 SPECIES OF NORTH AMERICAN *PROTOCALLIPHORA* HOUGH (DIPTERA: CALLIPHORIDAE) FROM BIRD NESTS AND TWO NEW PUPARIAL DESCRIPTIONS

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Abstract.—Keys are provided to the puparia of 27 species of North American *Protocalliphora* Hough (Diptera: Calliphoridae) (bird nest blow flies) for which puparia are known. Previously undescribed puparia are described for two species, *P. brunneisquama* Sabrosky, Bennett, and Whitworth and *P. hesperia* Shannon and Dobroscky, and the 25 remaining species are redescribed. Hosts, distribution, and habits are discussed for each. A table of bird hosts and associated bird blow fly parasite species is included.

Key Words: bird blow flies, bird hosts, bird parasites, Calliphoridae, keys, Diptera, North America, *Protocalliphora,* puparia

Species of the genus *Protocalliphora* Hough are obligate blood-sucking parasites of nestling birds. They are rarely collected using conventional insect collecting techniques, most are found only in bird nests. The taxonomy of this genus in North America was poorly understood until Sabrosky et al. (1989) redescribed the 11 known species and described 15 new species. Their work also included a detailed review of previous taxonomic and biological studies on *Protocalliphora.*

Bennett and Whitworth, co-authors with Sabrosky, subsequently published three articles which elaborated further on the life history, ecological relationships, and pathogenicity of *Protocalliphora* (Bennett and Whitworth 1991, 1992; Whitworth and Bennett 1992). Whitworth (2002, 2003) recently described three new species of *Protocalliphora,* bringing the total number of species known in North America to 29.

Sabrosky et al. (1989) also provided several keys, the most useful being based on reared material with matched males, females, and puparia. The key to single males is usually reliable for specimens in good condition, but the key to single females is reliable for only about 10 species. Keys to third instar larvae were provided for 16 species and to puparia for 22 species. Third instar larvae are not included in the present study, because, when larvae are available, they should be allowed to pupate and adults emerge. This provides both adults and puparia for identification. Some species are best identified by puparia, while others have distinctive adults. Nests collected more than 10 days or so after young fledge have only empty puparia and this is the form of *Protocalliphora* most frequently collected.

Bennett (1957) conducted pioneering research on the identification of *Protocalliphora* puparia. He identified numerous puparial features, which could be used to separate species, and developed techniques to prepare puparia for identification. His efforts were included in Sabrosky et al. (1989), but there was little opportunity to test his keys prior to publication. Subsequently, I have encountered a variety of problems with them. Although photos of each species were provided, many were of poor quality and of little value in support of the key. No other illustrations for immatures were included and, without them, interpretation of some of the terminology is confusing. The puparial key relies heavily on the length of prothoracic fringe spines, as measured in larvae. But this character is useless for puparia since the prothoracic region is inverted during pupation making the measurement of individual spines impossible. For this character to be used, third instar larvae would also be needed. Bennett's puparial key is fairly effective for specimens of the 10 or so species, which occur in southeastern Canada where his Ph.D. studies were conducted but I found the characters variable and unreliable for the same species in other areas. Descriptions of puparia for 13 species were based on specimens collected from only one geographic area and the 9 remaining puparial descriptions were based on specimens from only 2 or 3 areas. For many species, puparia were simply not available from other areas at the time keys were developed. When I began the current study, Bennett was deceased, thus making problems encountered in the keys more difficult to resolve. One complication was that Bennett did not clearly identify specimens of puparia used to write descriptions, so it was difficult to verify features. Ultimately, I obtained about 200 of his slides from the National Museum of Natural History, Smithsonian Institution, Washington, D.C. and about 100 slides from the Memorial University of Newfoundland. Most slides contained only fragmentary data, many were identified by species names that were never used and no synonymy was ever provided. Fortunately, I was able to reconstruct data for most of his slides and integrate his material with mine for this study. I determined his measurements and descriptions were accurate based on the material he had, thus I have let his puparial descriptions stand. Because *Protocalliphora* are readily collected as empty puparia, and the available puparial key is unreliable, the current study was initiated to develop a more effective key to the puparia of North American *Protocalliphora.*

MATERIALS AND METHODS

When I began studying this genus, I personally collected bird nests in Utah, Idaho, and Wyoming (Whitworth, 1977). Some were easily found, like the colonial nests of most swallow species, and the conspicuous nests of magpies and robins. For birds with nests that were difficult to locate, I enlisted the help of ornithologists who where studying birds such as raptors, chickadees, small sparrows, warblers, and vireos. More recently, I have been able to acquire many nests from nest boxes via Internet contacts with birders who send me nests once nestlings fledge. Most contributors were contacted with the help of the Cornell Birdhouse Network, which made it possible to obtain nests from throughout North America.

Nests were examined, puparia removed and counted, and if still viable, adults were reared. Unemerged puparia were either viable, parasitized or rarely dead. Dead puparia were lighter weight, adults emerged from viable puparia within about 10 days, while in parasitized puparia, wasps emerged from days to months later. Puparia were sometimes loosely scattered through nests (*P. braueri* (Hendel)), some were wrapped in dirt or hair cocoons (*P. sialia* Shannon and Dobroscky and *P. parorum* Sabrosky, Bennett, and Whitworth) or buried in dried mud (*P. hirundo* Shannon and Dobroscky). If viable puparia were available, some were sorted into individual vials so adults and puparia could be matched if mixed infestations or unusual species were suspected.

Many species were readily identified from empty puparia; some were so distinctive that they could be determined with a darkfield microscope (e.g., *P. sialia* and *P. braueri*). If identification could not be confirmed with this method, slides were made. If possible, only fully developed puparia were selected for slides, because characters in undersized puparia are usually distorted and they may not key properly. Infested nests usually included mature puparia, but if nestlings fledged or died before some third instar larvae matured, undersized specimens resulted. Slides were prepared by heating puparia for several minutes in 10% potassium hydroxide solution in a water bath to soften and clean them, then they were rinsed in distilled water. Specimens over-heated or left in solution too long were overcleared, and this destroyed spines making specimens difficult to key, especially those with slender spines. Optimum heating times varied with the thickness and sclerotization of the puparia. Softened puparia were sectioned with microscissors into dorsum, venter, stigmatal area, prothoracic fringe, and the cephalopharyngeal mechanism was removed and mounted. The sections were then cleared in specimen clearing fluid for 1–3 days, rinsed in 95% and then 100% ethanol, then dried and mounted in Euparal. Once slides were prepared, they were dried in a convection oven at 65°C for 10–14 days. Proper drying was important, because, if the medium was not dry, specimens tended to drift to the edges of slides in the thick medium. Slides of puparia were examined with a compound microscope at up to 400×. Measurements were made with a micrometer installed in the ocular lens, calibrated to microns.

Sabrosky et al. (1989) is cited regularly throughout this work and is the only Sabrosky reference cited. Hereafter any reference to Sabrosky refers to Sabrosky et al. (1989). References to Bennett are G. F. Bennett and references to Whitworth are the author.

Over 15,000 puparia from approximately 3,000 infested bird nests of 99 bird species were examined for this study. Material was studied from 46 of the 48 contiguous United States (*Protocalliphora* has not been found in Florida and Louisiana), Alaska, throughout Canada, and Greenland. About half of the material examined was from Bennett and Whitworth's early studies, as well as the collections of other researchers prior to 1992. Since 1992, a total of 4,077 nests of 79 bird species were examined by the author. Of these, 41% (1,691) from 52 bird species were infested with 20 species of *Protocalliphora* (Table 1).

Since this study began in 1992, no new material has been acquired for *P. avium* Shannon and Dobroscky, *P. bicolor* Sabrosky, Bennett, and Whitworth, *P. rognesi* Thompson and Pont (previously *P. chrysorrhoea* (Meigen)), *P. fallisi* Sabrosky, Bennett, Whitworth, *P. hesperioides* Sabrosky, Bennett, and Whitworth, *P. seminuda*, Sabrosky, Bennett, and Whitworth, or *P. tundrae* Sabrosky, Bennett, and Whitworth. Immatures for *P. beameri* Sabrosky, Bennett, and Whitworth and *P. sapphira* Hall, have never been collected. For *P. avium, P. bicolor, P. fallisi, P. hesperioides,* and *P. tundrae* I relied on Bennett's slides for key characters. I was also able to get a few puparial specimens of each of these species from series of adults in museums. I prepared slides of these puparia and verified that Bennett's slides matched the species, since many of his slides did not have correct species names. For *P. rognesi* and *P. seminuda* I was able to re-examine specimens retained from my study conducted between 1969–1975 (Whitworth 1977). A total of about 4,150 slides were prepared for all 27 species for which puparia were available.

Most puparial characters used here are defined in Sabrosky et al. (1989) where a glossary of terms is provided. Sketches of important characters are included here since they were lacking in Sabrosky. Puparia of *Protocalliphora* have a variety of characters which are useful for distinguishing species. The most important are found in the stigmatal area (Fig. 1) and on the venter (Figs. 8–9) and dorsum. The cuticle of most species is thickly covered with spines and often has folds or ridges.

Spines on puparia are extensions of the cuticle and most are reclinate, which appears to help larvae maintain their position in the

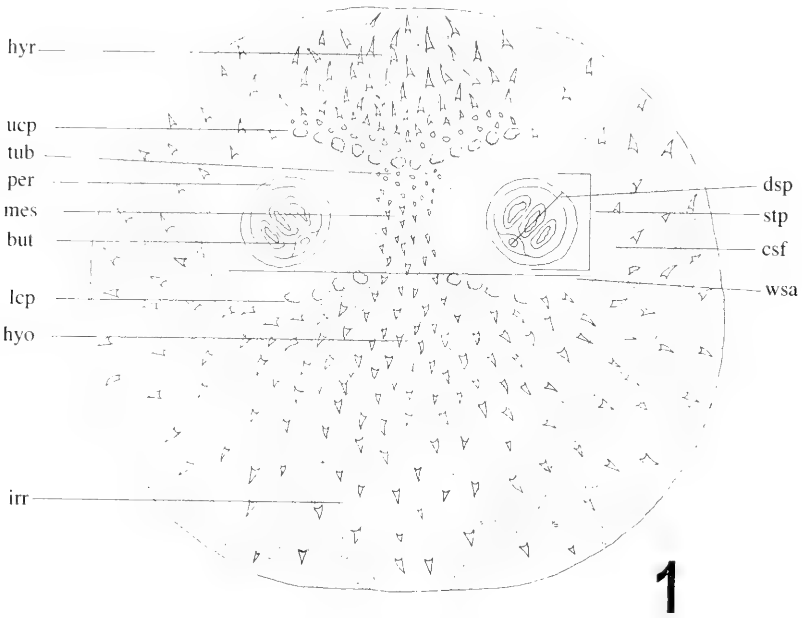
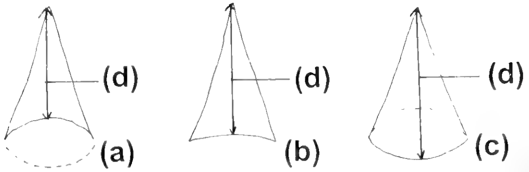


Fig. 1. Diagrammatic view of stigmatal area. but = button; csf = circumstigmatal folds; dsp = diameter of stigmatal plate; hyo = hypostigmatal region; hyr = hyperstigmatal region; irr = irregular folds; lcp = lower cuticular plaques; mes = mesostigmatal region; per = peritreme; stp = stigmatal plate; tub = tubercles; ucp = upper cuticular plaques; wsa = width of stigmatal area at level of the buttons (line is drawn below the buttons to reduce clutter).

nest, especially when feeding on nestlings (Fig. 2a). Some spines are upright and appear in profile (Fig. 2b), while some, especially in the stigmatal area, are proclinate (Fig. 2c). Most spines are translucent and appear 2-part, composed of a spine base and the spine, with spines in profile, the base is not visible. In most species, some spines are reduced to tubercles, which is the spine base with no spine projection (Fig. 7). Spine length is an important character (see Fig. 2 for how to measure; measurements vary with orientation of the spine). Spine lengths given in Sabrosky were averages of several spines in each area. I found averages tended to obscure differences between species, so in this work the longest spines in an area were measured. The longest spines on the dorsum are usually near the center of each segment. Exceptionally long, aberrant spines were not included. All spine measurements were made at 400× and spines were classified as long, medium, short, reduced to tubercles, or absent (Figs. 3–7). Spines also vary in thickness and are medium or slender (Figs. 4–5).

The stigmatal region is divided into the hyperstigmatal, mesostigmatal, hypostigmatal, and is bounded by circumstigmatal folds (Fig. 1). Spines in the lower hyperstigmatal area are shorter while those above are longer. Spines in the upper mesostigmatal area are often reduced to tubercles with longer spines below. Spines in the upper hypostigmatal area are shorter, while



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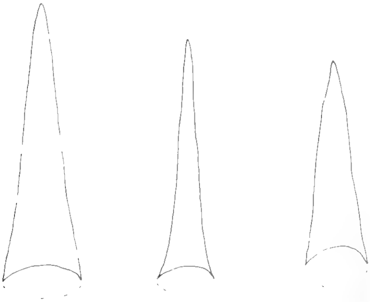

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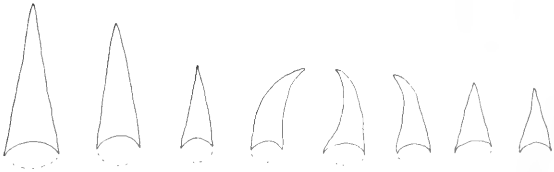

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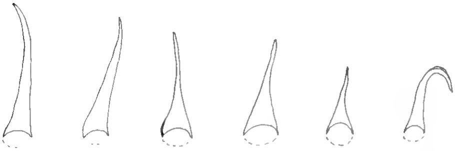

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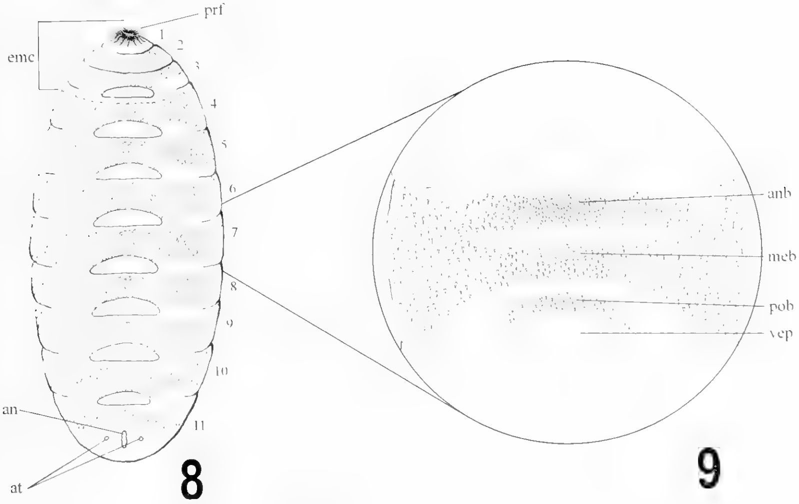
Figs. 2–7. Puparial spines. 2, How to measure: (a) reclinate; (b) profile; (c) proclinate; (d) measurement of spine length. 3, Long spines. 4, Medium spine width. 5, Slender spine width. 6, Short spines. 7, Tubercles. All examples of Figs. 3–7, 450×.

those below are longer. The stigmatal region may have pronounced folds (Fig. 21a, *P. aenea* Shannon and Dobroscky), moderate folds (Fig. 22a, *P. asiovora* Shannon and Dobroscky), faint folds (*P. halli* Sabrosky, Bennett, and Whitworth) or folds absent (Figs. 25a, 26a, *P. interrupta* Sabrosky, Bennett, and Whitworth, *P. metallica* Townsend). Bennett used the term folds for the stigmatal area and ridges for the venter and dorsum, folds were considered larger than ridges. This terminology is continued here for consistency, although some species have very large ridges and others have smaller folds.

Ridges of the dorsal and ventral cuticle may be pronounced (Fig. 21c, *P. aenea*), moderate (*P. parorum*), faint or absent (Fig. 25b, *P. interrupta*). This character is somewhat variable, but with practice can be useful for distinguishing some species. In some species with broad ridges (*P. hirundo, P. lata* Sabrosky, Bennett, and Whitworth), ridge width is a useful character. The venter normally has 3 distinct spine bands, the anterior, medial, and posterior bands on each segment, bounded by ventral pads (Figs. 8–9). On each segment the anterior band varies little between species, while the medial band may be regular (Fig. 10a, *P. sialia*), thinned in the center with opposing spines (Fig. 10b, *P. halli*), irregular and thinned in the center (Fig. 10c, *P. cuprina,* [Hall]), thinned in center not irregular (Fig. 10d, *P. bennetti* Whitworth) interrupted (Figs. 10e, 22b, *P. asiovora*), or center reduced to tubercles (Fig. 10f, *P. interrupta*). In species with reduction in the medial band, reduction usually progresses toward the rear. The posterior band is sometimes reduced or absent, especially to the rear (Figs. 14a, b, *P. halli*). This condition is also present in *P. aenea, P. fallisi,* and *P. tundrae*. Because of this reduction, ventral band ratio measurements will generally be lower to the rear in those species. In some species, the posterior band is reduced steadily to the rear, in others reduction does not occur until the last segment. This character is useful when present, but is variable within species. *Protocalliphora halli* exhibits the full range of variation from no reduction in the posterior band in some specimens, to extreme reduction in others. If in doubt, measure the ventral band ratio in an anterior and posterior segment to verify if reduction is occurring.

The ventral band ratio is an important species character but can be difficult to measure properly. This ratio is determined by measuring the sum of band widths of ventral bands and dividing it by the total distance between margins of ventral pads (Figs. 8–9, see Sabrosky, for details). Normally, bands should be measured in the center of each segment. In some species, the medial band is reduced or divided in the middle where band width is usually measured (Fig. 10e, 22b, *P. asiovora,* Fig. 10f, *P. interrupta*). When this condition was encountered, I measured band width to one side of the gap. When measuring band widths, I assumed there was no space between the rear of the posterior band and the adjacent ventral pad. Rarely, a distinct gap is present, if so, the actual band width is measured. Bands may be broad which produces a high ratio (Fig. 11, 29d, *P. spatulata* Sabrosky, Bennett, and Whitworth), to narrow with a low ratio (Fig. 12, *P. halli*). Bennett (in Sabrosky) advised ignoring small spines and tubercles when measuring bands, and I concur. However, some species like *P. parorum* (Fig. 13, 27b) and *P. bennetti* have medial and anterior bands with a broad row of tiny spines to the rear of the main band. When this condition was encountered, I included the small spines in the measurement. Finally, when puparia are heavily ridged as in *P. hirundo* and *P. rugosa* Whitworth, bands can be so distorted that they are very difficult to measure (Whitworth 2002). It may be necessary to measure several specimens to get an accurate measurement of ventral band ratio in these species.

The prothoracic fringe is a band of long spines on the anterior margin of the protho-



Figs. 8–9. 8, Diagrammatic view of venter. prf = prothoracic fringe; emc = emergence cap; an = anus; at = anal tubercle. 9, Expanded view of segment number 7. anb = anterior band; meb = medial band; pob = posterior band; vep = ventral pad.

racic segment of larvae and puparia. This character is unique to most of the genus *Protocalliphora* (Figs. 8, 15), although this character is absent in puparia of *P. braueri.* It is of minimal value for distinguishing puparia of most species, which have an average total diameter of about 350 μ, but it is useful for identifying *P. sialia* and *P. occidentalis,* which have exceptionally long fringe (500–800 μ) (Fig. 15b). *Protocalliphora interrupta* has an unusually short fringe, which averages 225 μ (200–250 μ), while *P. parorum* has a longer than average fringe of 425 μ (400–450 μ). Another character that was studied was the cephalopharyngeal mechanism. Unfortunately, it proved variable within species and was often distorted when mounted on a slide. If a better method can be found to prepare it for study, it may prove to have useful characters.

Problems were encountered calculating the distance across the stigmatal plates at the level of the buttons as explained in Sabrosky. After measuring numerous specimens, it was determined that when Bennett made this measurement he did not stop at the outer margins of the plates (as defined in the text), but extended it to the full width of the stigmatal area, roughly delineated by the circumstigmatal folds. Rather than remeasure everything to conform with the definition provided in Sabrosky, I have redefined this measurement as the width of the stigmatal area, at the level of the buttons (Fig. 1). Another problem was encountered measuring the diameter of the stigmatal plate. This measurement is defined in Sabrosky as extending from the top of the peritreme through the ventral slit to the bottom of the button (Fig. 1). However, McAlpine et al. (1981) define the stigmatal plate as bounded by the peritreme and technically the full diameter of the plate would extend past the button to the bottom of the peritreme. Again, rather than remeasure everything, the measurement, as defined in Sabrosky, is used for all measurements in this study.

Bennett included a variety of puparial measurements, such as the diameter of stigmatal plates, stigmatal ratio, distance between buttons, and width across stigmatal plates (Fig. 1). I have included these measurements in my descriptions, because they help characterize species. However, they have proven to be of little value in the keys and vary primarily with the size of the puparia.

RESULTS

I have identified 18 new bird hosts and 90 new host-parasite relationships since the publication of Sabrosky (Table 1). Thirty-six of the host-parasite relationships were from material I collected, the remaining 54 relationships were from other researcher's studies, and most were confirmed from material sent to me for identification.

To aid species identification, I have prepared a list of 160 infested bird species and the species of *Protocalliphora* known from their nests (Table 1). New relationships from other studies are identified by citation, if published, or if unpublished the researcher's name and affiliation are given. This table combines data from Sabrosky where bird hosts were listed by *Protocalliphora* species. When using puparial keys, it is important to check known host-parasite relationships, new relationships identified from puparia alone should be determined with caution. Puparia of similar species can be difficult to distinguish, but when hosts and species range are considered, distinctions may be made with confidence.

Most fly pupae found in bird nests in North America are *Protocalliphora*. Occasionally, sarcophagids or other genera of calliphorids are found in nests, usually associated with carrion. These latter taxa are more common in the nests of hawks and owls, which feed dead animals to nestlings. They also may be found in nests where nestlings have died. Sarcophagid puparia may be distinguished by having posterior spiracles in deep cavities and the dorsal cornu of the cephalopharyngeal mechanism deeply incised. Calliphorid puparia have posterior spiracles exposed at the apex of the terminal abdominal segment, and the dorsal cornu is not incised. Puparia of the subgenus *Protocalliphora* are distinguished by the presence of a prothoracic fringe and three distinct ventral spine bands (Figs. 8–9). Larvae of the subgenus *Trypocalliphora* lack a prothoracic fringe, the ventral medial band is absent, and the ventral anterior and posterior bands are weak or absent. Most scavenger calliphorid species have strong ventral anterior spine bands, or bands of spines associated with intersegmental areas.

The following key separates 27 species of *Protocalliphora* puparia. Some species are still poorly known, and key characters selected for them may be variable, making keying difficult. Species with puparia unknown and not included in the key are *P. beameri* Sabrosky, Bennett, and Whitworth and *P. sapphira* (Hall).

KEY TO PUPARIA OF NORTH AMERICAN *PROTOCALLIPHORA*

1\. Dorsal cuticular spines very sparse; ventral medial spine bands absent from all segments, anterior and posterior spine bands reduced or absent to rear; prothoracic fringe absent; spines in all regions less than 10 μ; obligatory subcutaneous nestling parasite. *Protocalliphora* (*Trypocalliphora*) (one species in this subgenus) . . . . braueri

– Dorsal cuticular spines numerous; three distinct ventral spine bands on, at least, anterior segments (Figs. 8–9); distinct fringe on the anterior end of the prothoracic segment (Figs. 8, 15a, b); puparia covered with spines, ranging from tubercles (Fig. 7) to short spines (Fig. 6), or long spines (Fig. 3), spines may be medium (Fig. 4), or slender (Fig. 5); not normally subcutaneous. *Protocalliphora* (*Protocalliphora*) (28 North American species in this subgenus, puparia known for 27 species) 2

2\. Center of medial spine band interrupted on at least some segments (Figs. 10e, 22b), interruption usually narrow and may be incomplete or with no interruption in a few specimens in a series; hyperstigmatal spines usually 25 μ or less, a few to 30 μ; mesostigmatal folds moderate; ridges of dorsum and venter faint to absent; ventral band ratio 0.63 (0.57–0.68/10) (usually in open nests of larger birds

Table 1. Bird species infested by species of *Protocalliphora.*

Bird Group	Infested Nests Examined in Current Study	Bird Species	*Protocalliphora* Species (Sum of species may exceed nests examined because of mixed infestations.)
Blackbirds	1	Brewer's—*Euphagus cyanocephalus*	*asiovora, braueri, interrupta, metallica* (1), *occidentalis, seminuda, sialia*
	1	red-winged—*Agelaius phoeniceus*	*fallisi, interrupta, metallica* (1), *shannoni*
	1	yellow-headed—*Xanthocephalus xanthocephalus*	*braueri, hirundo, interrupta, metallica* (W, 1)
Bluebirds	251	eastern—*Sialia sialis*	*asiovora* (1), *braueri* (W, 2), *deceptor* (W, 1), *hirundo, sialia* (247)
	73	mountain—*Sialia currucoides*	*occidentalis* (73)
	194	western—*Sialia mexicana*	*braueri* (W, 15), *parorum* (W, 1), *seminuda* (E, 1), *occidentalis* (178)
	37	mountain or western—*sialia* spp.	*occidentalis* (37)
Buntings		indigo—*Passerina cyanea*	*metallica*
		lazuli—*Passerina amoena*	*metallica*
		snow—*Plectrophenax nivalis*	*tundrae*
Bushtit		*Psaltriparus minimus*	*hesperioides*
Cardinal	1	northern—*Cardinalis cardinalis*	*deceptor* (1), *metallica*
Catbird	2	grey—*Dumetella carolinensis*	*avium, metallica* (2), *shannoni*
Chat	2	yellow-breasted—*Icteria virens*	*metallica, interrupta* (R 1, 1), *spenceri* (R 1, 1)
Chickadees	10	black-capped—*Poecile atricapillus*	**bennetti* (3), **braueri* (W, 1), **deceptor* (W, 3), *parorum* (3), *shannoni*
	7	*boreal—*Poecile hudsonicus*	**bennetti* (M)
	25	Carolina—*Poecile carolinensis*	**bennetti* (W, 3), *deceptor* (22)
	5	chestnut-backed—*Poecile rufescens*	*parorum* (5)
	71	mountain—*Poecile gambeli*	*braueri, occidentalis* (1), *parorum* (70), *sialia* (1)
	2	*Poecile* spp.	*braueri* (2)
Cowbird		brown-headed—*Molothrus ater*	*deceptor, shannoni*
Creeper		brown—*Certhia americana*	*parorum*
Crow		American—*Corvus brachyrhynchos*	*asiovora, avium, deceptor, occidentalis*
Cuckoo		black-billed—*Coccyzus erythropthalmus*	*metallica*
Dipper	2	American—*Cinclus mexicanus*	*aenea* (2), **braueri* (H)
Dove	1	mourning—*Zenaida macroura*	*asiovora, cuprina,* **metallica* (W, 1)

Table 1. Continued.

Bird Group	Infested Nests Examined in Current Study	Bird Species	*Protocalliphora* Species (Sum of species may exceed nests examined because of mixed infestations.)
Eagles		bald—*Haliaeetus leucocephalus*	*avium*
		golden—*Aquila chrysaetos*	*asiovora, braueri*
Falcons		gyrfalcon—*Falco rusticolus*	*avium*
		peregrine—*Falco peregrinus*	*avium*
		prairie—*Falco mexicanus*	(possible) *asiovora*
Finches		Cassin's—*Carpodacus cassinii*	*hesperia*
	1	house—*Carpodacus mexicanus*	*asiovora, braueri, cuprina, hesperia, hesperioides, *interrupta* (W, 1)
Flickers		northern (common)—*Colaptes auratus*	
	2	northern red shafted—*Colaptes auratus cafer*	*lata* (2)
		northern yellow shafted—*Colaptes auratus auratus*	*sialia*
Flycatchers		alder—*Empidonax alnorum*	*bicolor, braueri, metallica*
		*acadian—*Empidonax virescens*	**deceptor* (R)
	26	ash-throated—*Myiarchus cinerascens*	**parorum* (D, 4), *occidentalis* (22)
	1	dusky—*Empidonax oberholseri*	*cuprina* (1), *hesperioides*
	2	great-crested—*Myiarchus crinitus*	*braueri, deceptor, sialia* (2)
		pacific-slope (western)—*Empidonax difficilis*	*cuprina, hesperioides*
		willow—*Empidonax traillii*	*cuprina*
Goldfinches		American—*Carduelis tristis*	*bicolor, braueri, cuprina, metallica, shannoni*
		unidentified	*hesperioides*
Grackle	1	common—*Quiscalus quiscula*	*aenea, bicolor, braueri, deceptor, fallisi, hirundo, metallica, shannoni, sialia*
Grosbeaks		blackheaded—*Pheucticus melanocephalus*	*braueri*
		blue—*Guiraca caerulea*	*metallica*
		pine—*Pinicola enucleator*	**hesperia* *(W), **spenceri* (M)
Hawks		broad-winged—*Buteo platypterus*	*avium*
		Cooper's—*Accipiter cooperii*	*asiovora, avium*
		ferruginous—*Buteo regalis*	*asiovora*
		northern goshawk—*Accipiter gentilis*	*avium, lata, asiovora*
		northern harrier—*Circus cyaneus*	*avium*
		red-shouldered—*Buteo lineatus*	*avium*
		red-tailed—*Buteo jamaicensis*	*avium, lata, asiovora*
		Swainson's—*Buteo swainsoni*	*asiovora, avium*

Table 1 Continued

Bird Group	Infested Nests Examined in Current Study	Bird Species	*Protocalliphora* Species (Sum of species may exceed nests examined because of mixed infestations)
Jays		blue—*Cyanocitta cristata*	*shannoni*
		gray—*Perisoreus canadensis*	*hesperia, shannoni*
		pinyon—*Gymnorhinus cyanocephalus*	*asiovora*
	2	Stellar's *Cyanocitta stelleri*	*asiovora* (W, 2)
Juncos	1	dark-eyed—*Junco hyemalis*	**spatulata* (M), **occidentalis* (R-1, 1)
		oregon—*Junco hyemalis oreganus*	*braueri, parorum*
		slate colored—*Junco hyemalis hyemalis*	*metallica*
		unidentified	*braueri, shannoni*
Kestrel	8	American—*Falco sparvarius*	*asiovora,* **braueri* (W, 1), *lata, occidentalis* (5), *sialia* (2)
Kingbirds		eastern—*Tyrannus tyrannus*	*bicolor, cuprina, metallica, occidentalis, shannoni, sialia*
		western—*Tyrannus verticalis*	*braueri, cuprina, occidentalis*
Lark		horned—*Eremophila alpestris*	*braueri, seminuda, spatulata*
Magpie		black-billed—*Pica pica*	*asiovora, braueri*
Martin	19	purple—*Progne subis*	*hirundo, occidentalis,* **rugosa* (2), *sialia* (17)
Meadowlarks		eastern—*Sturnella magna*	*braueri*
		western—*Sturnella neglecta*	*braueri*
Mockingbird	3	northern—*Mimus polyglottos*	*deceptor,* **metallica* (W, 1), *sialia (W, 1)
Nuthatches		brown-headed—*Sitta pusilla*	possible *sialia*
	15	pygmy—*Sitta pygmaea*	**parorum* (D, 14), **occidentalis* (D, 1)
	5	red breasted—*Sitta canadensis*	*braueri* (W, 1), *parorum, occidentalis* (D, 5)
	14	white breasted—*Sitta carolinensis*	*braueri* (W, 1), *occidentalis, parorum* (D, 12), *sialia* (2)
Osprey		*Pandion haliaetus*	*avium*
Ovenbird		*Seiurus aurocapillus*	*braueri*
Owls		eastern-screech—*Otus asio*	*sialia*
	1	*ferruginous pygmy—*Glaucidium brasilianum*	**occidentalis* (P, 1)
		flamulated—*Otus flammeolus*	*occidentalis*
		great-horned—*Bubo virginianus*	*asiovora, avium, occidentalis*
		long-eared—*Asio otus*	*asiovora*
		western screech—*Otus kennicottii*	*occidentalis*

Table 1. Continued.

Bird Group	Infested Nests Examined in Current Study	Bird Species	*Protocalliphora* Species (Sum of species may exceed nests examined because of mixed infestations)
Phoebes		black—*Sayornis nigricans*	*halli*
	28	eastern—*Sayornis phoebe*	*aenea*, **bennetti* (RE, 1), *deceptor* (27), *hirundo*, *sialia*
	1	Say's—*Sayornis saya*	*aenea*, *halli* (1), *occidentalis*
Pipit		American—*Anthus rubescens*	*spatulata*
Raven		common—*Corvus corax*	*asiovora*, *occidentalis*, *sialia*
Redstart		American—*Setophaga ruticilla*	*bicolor*, *spenceri*
Robin	22	American—*Turdus migratorius*	*aenea*, *asiovora*, *avium*, *braueri* (1), *cuprina*, *hesperia* (10), *metallica*, *occidentalis* (1), *shannoni* (10), *sialia*
Shrike		loggerhead—*Lanius ludovicianus*	*asiovora*, *braueri*, *cuprina* (possible B)
Siskin		pine—*Carduelis pinus*	*braueri*
Solitaire		Townsend's—*Myadestes townsendi*	*braueri*
Sparrows		American tree—*Spizella arborea*	*braueri*
		*Bachman's—*Aimophila aestivalis*	**deceptor* (R)
		*Brewer's—*Spizella breweri*	**braueri* (HO)
	1	chipping—*Spizella passerina*	*braueri*, *brunneisquama*, *hesperia*, *metallica* (1)
		field—*Spizella pusilla*	*metallica*
		fox—*Passerella iliaca*	*metallica*, *interrupta*
		grasshopper—*Ammodramus savannarum*	*metallica*
	28	house—*Passer domesticus*	*braueri* (19), *chrysorrhoea*, *occidentalis* (2), **rugosa* (W, 1), *sialia* (7)
		savannah—*Passerculus sandwichensis*	*braueri*, *metallica*, **spatulata* (F&M)
	3	song—*Melospiza melodia*	*braueri*, *cuprina* (R-1, 1), *interrupta* (2), *metallica*, *shannoni*, *sialia*
	1	sparrow spp.	*metallica* (1)
		swamp—*Melospiza georgiana*	*fallisi*, *metallica*, **shannoni* (B)
		unidentified	*braueri*, *metallica*
		vesper—*Pooecetes gramineus*	*braueri*, *metallica*
	1	white-crowned—*Zonotrichia leucophrys*	*braueri*, **metallica* (W, 1), **spatulata* (F&M)
		white-throated—*Zonotrichia albicollis*	*fallisi*, *metallica*, *shannoni*
Starling	4	European—*Sturnus vulgaris*	*asiovora*, **bennetti* (W, 1), *bicolor*, *braueri* (2), *hirundo*, *occidentalis* (2), **rugosa* (W, 1), *sialia*

Table 1. Continued.

Bird Group	Infested Nests Examined in Current Study	Bird Species	*Protocalliphora* Species (Sum of species may exceed nests examined because of mixed infestations.)
Swallows		bank—*Riparia riparia*	*braueri, chrysorrhoea, hirundo, metallica, occidentalis,* **rugosa* (W, 1), *sialia*
	30	barn—*Hirundo rustica*	*aenea* (1), *asiovora* (1), *braueri* (4), *chrysorrhoea, cuprina* (1), **deceptor* (W, 2), *halli* (16), *hesperia, hirundo* (2), *occidentalis, parorum, rugosa* (W, 2), *seminuda, sialia* (3)
	3	cliff—*Hirundo pyrrhonota*	*asiovora, braueri, chrysorrhoea, hirundo* (3), *occidentalis,* **rugosa* (W), *sialia*
		northern rough-winged—*Stelgidopteryx serripennis*	*metallica, sialia*
	556	tree—*Tachycineta bicolor*	*bennetti* (W, 62), *bicolor, braueri* (54), *brunneisquama* (W, 1), **deceptor* (W, 4), *hirundo* (5), *metallica* (9), *occidentalis* (160), **parorum* (D, 1), **rugosa* (W, 70), *shannoni, sialia* (190)
		unidentified	*asiovora, avium, beameri, halli, hesperia*
	35	violet-green—*Tachycineta thalassina*	*braueri* (9), *chrysorrhoea, hirundo* (1), **rugosa* (W, 9), *occidentalis* (17)
Tanager		scarlet—*Piranga olivacea*	*metallica*
Thrashers	1	brown—*Toxostoma rufum*	*metallica* (1), *shannoni*
		sage—*Oreoscoptes montanus*	**braueri* (HO)
Thrushes	1	hermit—*Catharus guttatus*	**hesperia* (R-1, 2), *shannoni*
		Swainson's—*Catharus ustulatus*	*braueri,* **hesperia* (M), **shannoni* (M)
		veery—**Catharus fuscescens*	species unknown (R)
		varied—*Ixoreus naevius*	**hesperia* (M)
		wood—*Hylocichla mustelina*	*bicolor, deceptor, shannoni*
Titmouse	27	*oak—*Baeolophus inornatus*	**parorum* (D, 22), **occidentalis* (D, 5)
	14	*tufted—*Baeolophus bicolor*	**deceptor* (W, 13), **sialia* (W, 1)
Towhees		spotted—*Pipilo musculatus*	**brunneisquama* (B)
	1	eastern—*Pipilo erythrophthalmus*	**deceptor* (W, 1), *metallica*
Unknown	1	unknown	*shannoni*
Veery	3	*Catharus fuscescens*	**hesperia* (R-1, 2), **shannoni* (R-1, 1)

Table 1. Continued.

Bird Group	Infested Nests Examined in Current Study	Bird Species	*Protocalliphora* Species (Sum of species may exceed nests examined because of mixed infestations.)
Vireos	4	plumbeous—*Plumbeous plumbeous*	**cuprina* (W, 4)
		red-eyed—*Vireo olivaceus*	*bicolor*
	1	solitary (blue-headed)—*Vireo solitarius*	*bicolor*, **cuprina* (R-1, 1)
	1	warbling—*Vireo gilvus*	*spenceri*, **cuprina* (R-1, 1)
		*yellow-throated—*Vireo flavifrons*	**braueri* (R)
Warblers		*blackpoll—*Dendroica striata*	**spenceri* (M)
		black-throated blue—*Dendroica caerulescens*	*bicolor*
		*black & white—*Mniotilta varia*	**braueri* (R)
		Canada—*Wilsonia canadensis*	*braueri*
		chestnut-sided—*Dendroica pensylvanica*	*bicolor*
	3	*hooded—*Wilsonia citrina*	**deceptor* (W, 1, R), **braueri* (R-1, 2)
		*Kentucky—*Oporonis formosus*	**braueri* (R)
	1	*McGillivray's—*Oporonis tolmiei*	**metallica* (R), **interrupta* (R-1, 1)
		Nashville—*Vermivora ruficapilla*	*metallica*
		*orange-crowned—*Vermivora celata*	**braueri* (M)
		prairie—*Dendroica discolor*	*deceptor*
	40	prothonotary—*Protonotaria citrea*	**deceptor* (W, 10, R-1, 30)
	4	*Swainson's—*Limnothlypis swainsonii*	**braueri* (RE, 1), **deceptor* (R-1, 1)
		*Townsend—*Dendroica townsendi*	**braueri* (M), **shannoni* (M), **spenceri* (M)
		Wilson's—*Wilsonia pusilla*	*braueri*
		worm-eating—*Helmitheros vermivorus*	*deceptor*
	14	yellow—*Dendroica petechia*	*bicolor*, *braueri*, *cuprina* (12), **deceptor* (W, 1), *hesperioides*, *metallica*, *spenceri* (1)
	1	yellow-rumped—*Dendroica coronata*	*bicolor*, *braueri*, *cuprina*, **metallica* (M), *shannoni*, **spatulata* (M), **spenceri* (M)
Waterthrushes		Louisiana—*Seiurus motacilla*	*aenea*
		northern—*Seiurus noveboracensis*	*metallica*
Waxwing	1	cedar—*Bombycilla cedrorum*	**braueri* (W, 1), *shannoni*
Woodpecker		downy—*Picoides pubescens*	*fallisi*, *sialia*

Table 1. Continued.

Bird Group	Infested Nests Examined in Current Study	Bird Species	*Protocalliphora* Species (Sum of species may exceed nests examined because of mixed infestations)
Wood-pewee		western-wood—*Contopus sordidulus*	*cuprina*
Wrens	3	Bewick's—*Thryomanes bewickii*	**deceptor* (W, 2), **occidentalis* (D, 1), *parorum*
	7	Carolina—*Thryothorus ludovicianus*	*deceptor* (7)
	61	house—*Troglodytes aedon*	*aenea*, **bennetti* (W, 8), *braueri* (9), *deceptor* (6), *occidentalis* (6), *parorum* (22), *shannoni*, *sialia* (10)
	1	marsh—*Cistothorus palustris*	*braueri*, *interrupta* (1)
		unidentified	*metallica*
Yellowthroat		common—*Geothlypis trichas*	*fallisi*, *metallica*
Total examined = 1,691			

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* New host or new host-parasite associations determined since host list was published in Sabrosky et al. (1989). All identifications confirmed by Whitworth unless indicated otherwise. Species followed by (W) were collected by author in the current study. Some new relationships were determined from old Bennett slides, labeled (B). Other host-parasite associations were taken from material submitted for identification by other researchers, including Don Dahlsten (D), University of California, Berkeley, unpublished; Jeanne Fair (F), Los Alamos, NM, unpublished; Fair & Miller (F&M) 1995; Halstead (H) 1988; Howe (HO) 1991 (species confirmed by G. F. Bennett); Matsuoka et al. (M), 1997 & unpublished in part, Glenn Proudfoot (P), Texas A&M University, Department of Wildlife and Fisheries, unpublished; Will Reeves (RE), Clemson University, South Carolina, unpublished; Revels (R) 1996 (species confirmed by C. W. Sabrosky), Mia Revels (R-1), currently Northeastern State University, Talequah, OK, unpublished, confirmed by author.

[1] Sabrosky et al. (1989) listed pine grosbeak as a host for *P. halli* from my nest #414, a re-examination revealed it actually was *P. hesperia*.

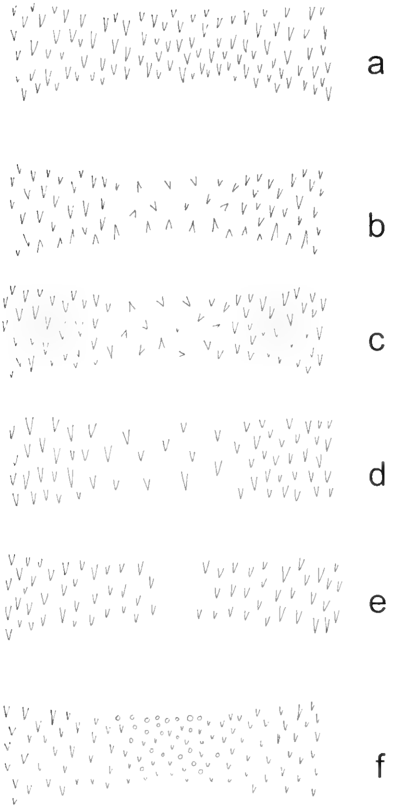

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Fig. 10. Puparia, ventral medial spine band condition: (a) regular, *Protocalliphora sialia*; (b) thinned in center, irregular with opposing spines to rear, *P. halli*; (c) thinned in center, irregular, few opposing spines, *P cuprina*; (d) thinned in center, regular, rarely opposing spines, *P. bennetti*; (e) interrupted, *P. asiovora*; (f) center reduced to tubercles, *P. interrupta*.

such as magpies, raptors, or crows; western only) . . . . *asiovora*

– Medial spine band complete, although sometimes narrowed on midline (Figs. 10a–d), or reduced to short spines or tubercles on some segments (Fig. 10f); hyperstigmatal spines, mesostigmatal folds, dorsal and ventral ridges, and ventral band ratios variable 3

3. Prothoracic fringe, when present, long, 500 μ or more in diameter, often with a large opening in center (Fig. 15b); dorsal cuticular ridges usually pronounced 4

– Prothoracic fringe 450 μ or less, central opening smaller (Fig. 15a); dorsal cuticle variable or fringe not present 5

4. Stigmatal region with numerous pronounced folds; lower portion of mesostigmatal area with distinct spines 10–20 μ (Whitworth 2003: Fig. 2a); ventral band ratio averages 0.81 (0.71–0.89); east of a line from Alaska to Kentucky . . . . *sialia* (in part)

– Stigmatal region with folds faint or absent; lower portion of mesostigmatal area with tubercles only, sometimes a few short spines (Whitworth 2003: Fig. 2c); ventral band ratio averages 0.72 (0.57–0.85); west of a line from Montana to New Mexico and probably into Mexico . . . . *occidentalis* (in part)

5. Hyperstigmatal, mesostigmatal, and hypostigmatal spines reduced to tubercles or short spines averaging 4–6 μ, at most 7.5 μ (Figs. 16–18, 25–26); center of medial band may be reduced to tubercles toward rear (Fig. 10f) 6

– Hyperstigmatal region with, at least, some distinct spines 10 μ or longer (Figs. 1, 19–20); center of medial band may be thinned or narrowed, but not reduced to tubercles toward rear 8

6. Posterior spine band on venter reduced or absent, especially to rear, medial spine band usually reduced to tubercles in middle, especially toward rear (Fig. 10f); mesostigmatal and hypostigmatal tubercles large (Figs. 17, 25a); prothoracic fringe short, 225 μ (200–250 μ); western only . . . . *interrupta*

– All 3 ventral spine bands about same size, spines of medial band distinct; mesostigmatal and hypostigmatal tubercles tiny; prothoracic fringe 300 μ or more 7

7. Hyperstigmatal tubercles with spine projections visible at 400×, usually 2.5–5 μ long, rarely to 7.5 μ, tubercles appearing larger than *P. metallica* (Fig. 16), at 400× "cell-wall," border usually lacking (Fig. 18); longest spines in center of anterior ventral band usually 12.5 μ or more; eastern and midwestern only, hosts include cardinal, chickadee, fly-

11

12

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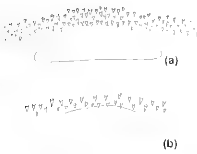

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Figs. 11–15. Puparia. 11, Venter segment 7, *Protocalliphora spatulata.* 12, Venter segment 7, *P. halli.* 13, Venter segment 7, *P. parorum.* 14, Posterior band reduced to rear, *P. halli, P shannoni*: (a) segment 4; (b) segment 10. 15, Prothoracic fringe: (a) *P. spatulata,* 300 μ; (b) *P. sialia,* 500 μ.

catcher, phoebe, warbler, and wren; adult male with broad surstyli, female with bluish abdomen . . . . . *deceptor*

– Hyperstigmatal tubercles without spines projections visible at 400×, individual tubercles usually bordered by circular "cell-wall," tubercles appearing as minute dots at 400× (Figs. 16, 26a); longest spines in center of anterior ventral band usually 10 μ or less; widespread, broad host range; adult male with slender surstyli, female with fifth tergite cupreous . . . . *metallica*

8. Hyperstigmatal spines usually short, longest spines 12.5 μ, rarely to 20 μ; mesostigmatal and hypostigmatal areas with tubercles and, at most, a few short spines (Fig. 19); posterior spine bands usually reduced to rear, sometimes only last segment reduced (Figs. 14a, b) . . . . *shannoni*

– Longest hyperstigmatal spines usually 20 μ or more; mesostigmatal and hypostigmatal areas usually with distinct spines; posterior spine bands variable 9

9. Dorsal cuticle with pronounced to moderate ridges (see Fig. 21c); most species with a high ventral band ratio of 0.65 or more; stigmatal region often with pronounced to moderate folds (absent in most *P. occidentalis*) 10

– Dorsal cuticle with ridges faint or absent (Fig. 23); ventral band ratio variable; stigmatal region usually with folds faint or absent . . . 18

10. Ventral band ratios average 0.58 (0.51–0.64) at the front, 0.48 (0.46–0.53) at the rear; posterior spine band reduced to rear (Fig. 21d); reduction may be slight, only last segment; mesostigmatal spines reduced to tubercles, or a few short spines at lower margin (Fig. 21a); known from dipper nests and 1 barn swallow nest in the west *aenea* (in part, western form)

– Ventral band ratios average 0.63 or more (aberrant individuals occasionally as low as 0.48); posterior spine band not reduced to rear; mesostigmatal spines usually not reduced 11

11. Dorsal cuticular ridges 50 μ or more wide, usually a few ridges 60–100 μ or more wide; dorsal ridges usually widely spaced (*P. hirundo,* Whitworth 2002: fig. 3a), closer together in undersized specimens 12

– Dorsal cuticular ridges usually average less than 50 μ in width; dorsal cuticular ridges more abundant and closer together (*P. rugosa,* Whitworth 2002: fig. 2c) 13

12. Mesostigmatal and upper hypostigmatal area bare, without tubercles or spines (Sabrosky: fig. 55); hyperstigmatal spines long 35–60 μ; fully developed puparia exceptionally large,

averaging 13 mm; known only in raptors and flickers in the west . . . . *lata*

– Mesostigmatal and upper hypostigmatal spines or tubercles present; hyperstigmatal spines shorter 25–35 μ; puparia 9 mm or less; primarily in cliff and bank swallows . . . *hirundo*

13. Longest hyperstigmatal spines usually less than 30 μ (25–35 μ); stigmatal area outlined in broad irregular folds 14

– Longest hyperstigmatal spines 35 μ (35–50 μ) or more; stigmatal area variable but folds, if present, narrower and more regular 15

14. Mesostigmatal area bare or with a few scattered spines; dorsum with short spines usually 25 μ or less (25–30 μ) (Sabrosky: fig. 44); known only in the east, midwest, and Alaska, primarily in crows and raptors . . . . *avium* (in part)

Mesostigmatal area with dense spines to 15 μ; dorsal spines long, usually 30 μ (30–50 μ) (Whitworth 2002: fig. 2); known only in northwestern United States and British Columbia, primarily in swallows . . . . *rugosa*

15. Almost exclusively in bank swallow nests; mesostigmatal spines distinct to 15 μ; prothoracic fringe 350–400 μ (Sabrosky: fig. 47) . . . . *rognesi*

Usually not in bank swallow nests; upper mesostigmatal area with tubercles, lower area with spines to 10 μ, sometimes longer; prothoracic fringe in *P. parorum* 350–450 μ, in *P. sialia* 500 μ or more 16

16. Dorsal cuticle with moderate ridges; venter with ridges usually faint or absent; anal tubercles pronounced and circular with no ridges (Figs. 20, 27a); several rows of small spines to rear of anterior and medial spine bands (Figs. 13, 27b); surstyli of adult male long and slender; primarily in nests of chickadees, wrens, and nuthatches . . . *parorum* (in part)

Dorsal cuticle with pronounced ridges; venter with ridges moderate to pronounced; anal tubercles indistinct, ridged with irregular cuticle; few small spines to rear of anterior and medial spine band; surstyli of adult male digitate; rarely in chickadees, but found in wrens and some nuthatches 17

17. Stigmatal region usually with distinct hyperstigmatal, mesostigmatal and hypostigmatal folds, outlined by pronounced circumstigmatal folds; lower portion of mesostigmatal area with distinct spines 10–20 μ (Whitworth 2003: Fig. 2a); ventral band ratio usually higher, average 0.81(0.71–0.89); east of line from Alaska to Kentucky . . . . . *sialia* (in part)

– Stigmatal region with few, if any, folds and no circumstigmatal folds; lower portion of mesostigmatal area only with tubercles, rarely a few short spines (Whitworth 2003: fig. 2C); ventral band ratio usually lower 0.72 (0.57–0.85); west of a line from British Columbia to eastern Colorado, south to New Mexico, and probably Mexico . . . *occidentalis* (in part)

18. Posterior spine band on venter significantly reduced or absent toward rear (Figs. 14a, b); medial band thinned and often irregular or with opposing spines (Figs. 10b–d) 19

Posterior spine band approximately equal in size on all segments, occasionally some reduction on last 2 or 3 segments to rear; medial band variable, primarily western, 2 eastern species 23

19. Hyperstigmatal spines broad at base but slender at tip (Fig. 5), longest spines 25–35 μ; ventral band ratio of last complete segment usually low, 0.37 (0.29–0.47) or less; known only from northern Canada and Greenland . . . . *tundrae*

– Hyperstigmatal spines medium (Fig. 4), length variable; ventral band ratio variable 20

20. Western only; in nests of barn swallows, phoebes, warblers, or flycatchers; posterior band with slight to extreme reduction to rear (Fig. 14); ventral spine band ratio at rear averages 0.46 (0.38–0.62) (Fig. 15) 21

Eastern only; posterior band usually extremely reduced to rear; ventral spine band ratio at posterior end averages 0.35 (0.29–0.47) . . 22

21. Medial spine band on last segment with spines irregular and opposing on rear edge (Fig. 10b); hyperstigmatal spines to 35 μ; usually in barn swallows or phoebes . . . . . *halli*

Medial spine band on last segment with only a few irregular spines, and at most, a few small opposing spines (Fig. 10c); hyperstigmatal spines usually less than 30 μ; usually in warblers, flycatchers, and occasionally barn swallows . . . . *cuprina*

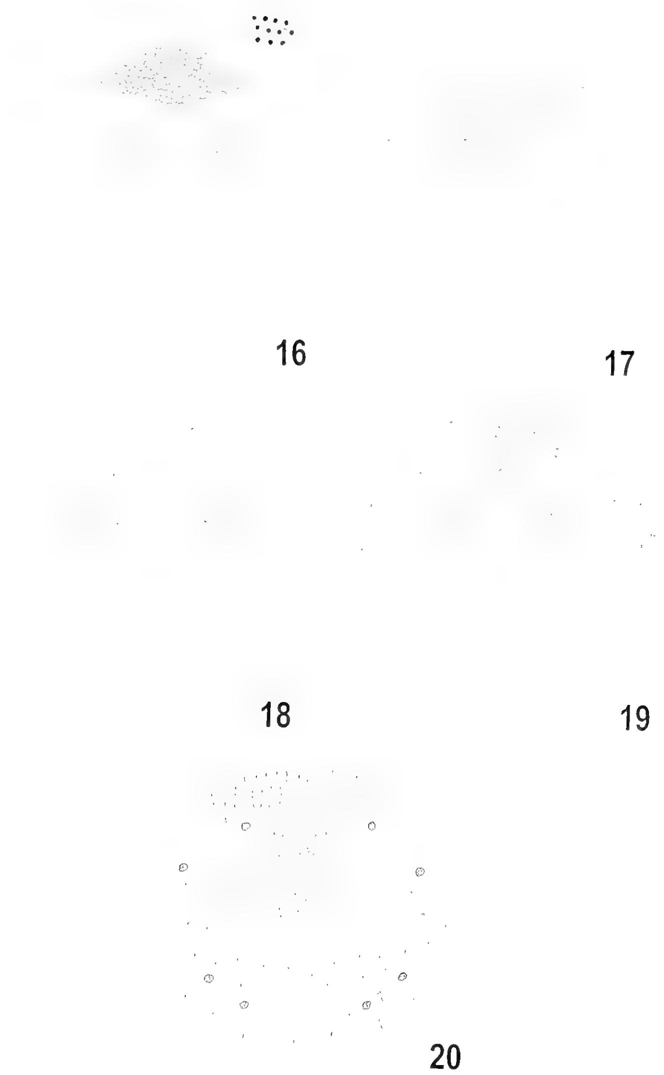
22. Posterior spine band reduced on all segments, extreme reduction or absent to rear; stigmatal spines sparse and short, most 25 μ or less; ventral band ratio to rear tends to be smaller 0.32 (0.29–0.36) (known from only two locations in Ontario) . . . . *fallisi*

Posterior spine band reduced or absent only toward rear; stigmatal spines closer together and longer, 25–30 μ (a few over 30 μ); ventral band ratio to rear tends to be larger 0.37 (0.31–0.47) . . . . . *aenea* (in part, eastern form)

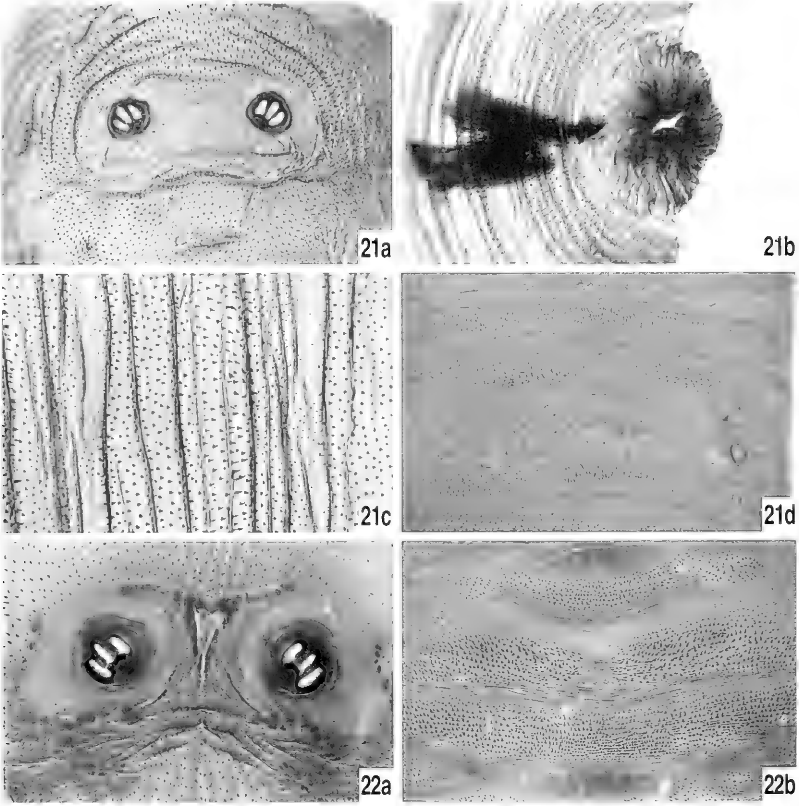
23. Hyperstigmatal spines exceptionally slender when viewed at 400× (Fig. 5); spine base may be broad, but upper half slender 24

– Hyperstigmatal spines usually medium (Fig. 4) 27

24. Known only from far eastern United States; ventral band ratio 0.63 (0.54–0.78); hyper-



Figs. 16–20. Puparia, stigmatal views. 16, *Protocalliphora metallica.* 17, *P. interrupta.* 18, *P. deceptor.* 19, *P. shannoni.* 20, *P. parorum.* Pattern of spines shown in the hyperstigmatal area of Fig. 16 occurs throughout the stigmatal area. Spines are denser than shown for Figs. 17–20.



Figs. 21–22. Puparia. 21, *Protocalliphora aenea* (top four figures): (a) stigmatal view; (b) prothoracic fringe; (c) dorsum; (d) venter. 22, *P. asiovora* (bottom two figures): (a) stigmatal view; (b) venter.

stigmatal area without folds; primarily in open nests of flycatchers and warblers ... *bicolor*

Known primarily from western United States or Alaska (one record of *P. spatulata* in Canada, northeast of Wisconsin); ventral band ratio averages 0.66–1.0; hyperstigmatal area variable, no folds in one species, folds in two species ... 25

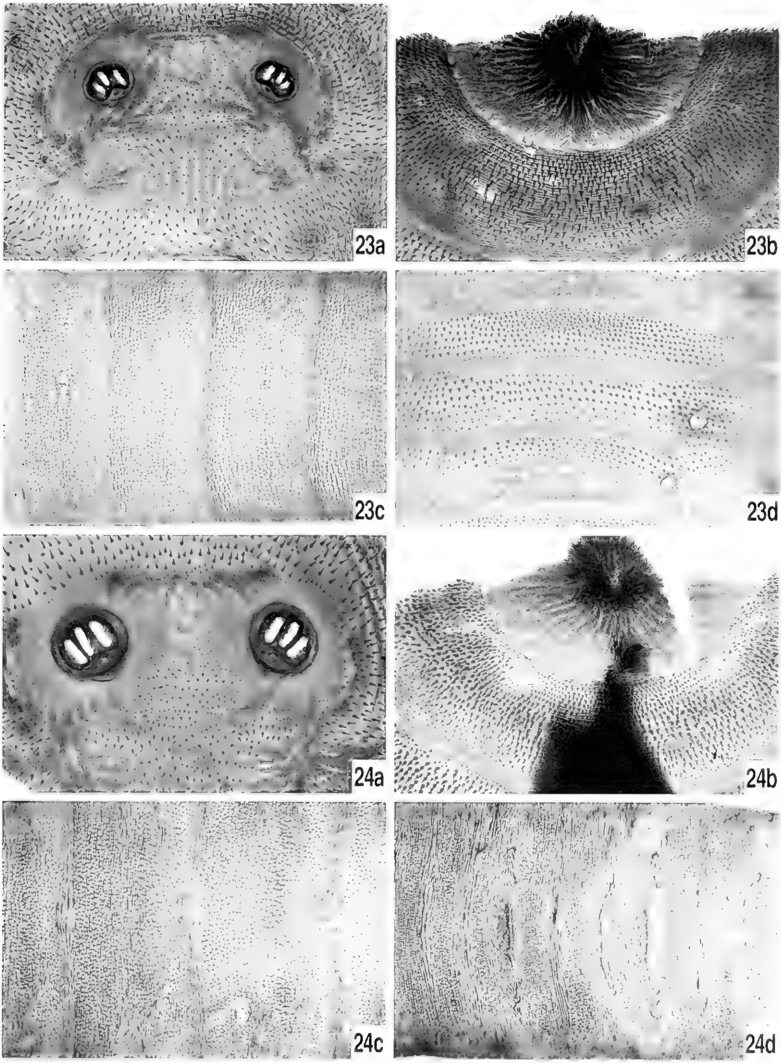
25. Mesostigmatal folds faint or absent (Fig. 30a); cuticle of hyperstigmatal area usually smooth; known primarily in warblers .... *spenceri*

Mesostigmatal folds pronounced; cuticle of hyperstigmatal area often very lumpy and uneven 26

26. Longest hyperstigmatal spines 25–30 μ; circumstigmatal folds faint to moderate; ventral band ratio averages 0.73 (0.67–0.84) (Fig. 28); known only from nests of horned lark, barn swallow, and bluebird, usually in desert habitats .... *seminuda*

Longest hyperstigmatal spines 30–50 μ; circumstigmatal folds pronounced (Fig. 29a); ventral band ratio averages 0.83 (0.72–1.0) (Fig. 11); known from nests of horned lark, rosy finch, several small sparrows, and water pipits; usually from high elevations or far north .... *spatulata*

27. Mesostigmatal and hypostigmatal regions



Figs. 23–24. Puparia. 23, *Protocalliphora brunneisquama* (top four figures): (a) stigmatal view; (b) prothoracic fringe; (c) dorsum; (d) venter. 24, *P. hesperia* (bottom four figures): (a) stigmatal view; (b) prothoracic fringe; (c) dorsum; (d) venter.

with tubercles and a few short spines, spines sometimes longer and more abundant; longest hyperstigmatal and dorsal spines usually 35–50 μ (Figs. 20, 27a); broad row of small spines to rear of medial band (Figs. 13, 27b); ventral band ratios usually greater than 0.70 (0.58–0.87); prothoracic fringe 350–450 μ found in nests of chickadees, titmice, and wrens; western only .... *parorum* (in part)

– Mesostigmatal and hypostigmatal regions with some distinct spines; longest hyperstigmatal spines 25–35 μ; ventral band ratios usually less than 0.70 (0.55–0.76); no small spines to rear of medial band or rows not as broad; prothoracic fringe 250–350 μ 28

28\. Longest hyperstigmatal spines 25 μ or less, a few to 30 μ 29

– Longest hyperstigmatal spines usually 30 μ or more 31

29\. Stigmatal folds broad, 0.30–0.50 μ wide, pronounced or moderate; mesostigmatal and hypostigmatal folds pronounced and irregular (Sabrosky, figs. 44a, b); ventral medial band not thinned in center; eastern or midwestern and north to Alaska; primarily in raptors and other large birds .... *avium*

– Stigmatal folds, if present, narrower and moderate, faint or absent; mesostigmatal and hypostigmatal folds absent or, if present, faint and regular; ventral medial band, thinned in center toward rear 30

30\. Spines of ventral medial band rarely irregular, never opposing on posterior segments (Fig. 10d); broad row of small spines to rear of medial band (Fig. 13, Whitworth 2002: fig. 1d); eastern United States, western Canada, and Alaska in cavity nests of chickadees, tree swallows, wrens, and starlings .... *bennetti*

– Spines of ventral medial band include some irregular and a few opposing on posterior segments (Fig 10c); only a few rows of small spines to rear of medial band; western only, known primarily from warbler and flycatcher nests .... *cuprina*

31\. Ventral bands narrow, especially to rear, ratio usually 0.60 μ or less (Utah front averages 0.55, rear 0.45, Washington front averages 0.62, rear 0.55); found primarily in nests of barn swallows and phoebes; in Utah, sometimes posterior band much reduced to rear .. .. *halli*

– Ventral bands wider, ratio usually 0.60 or more; found primarily in nests of robins, finches and chickadees 32

32\. Few or no small spines to rear of medial band; very rare, usual host unknown (recorded only from a chipping sparrow and tree swallow nest); adult male with exceptionally long, slender surstyli, calypters dark brown both sexes .... *brunneisquama*

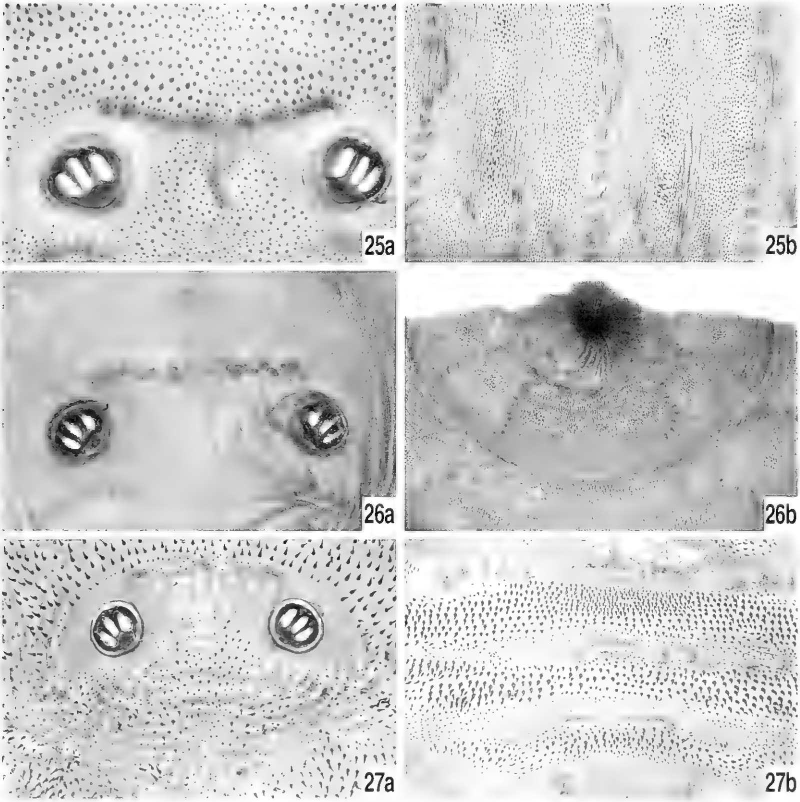
– Numerous small spines to rear of medial band 33

33\. Broad rows of small spines to rear of ventral medial spine bands on many segments (Figs. 13, 27b); found in nests of chickadees, titmice, and wrens .... *parorum* (in part)

– Some small spines to rear of ventral medial spine bands, rows not as broad; found in nests of robins and finches ..... *hesperia and hesperioides* (puparia currently indistinguishable)

DESCRIPTIONS

In the discussion that follows, diagnostic characters for puparia of each species are given, voucher slides are identified, characters to distinguish similar species are discussed, and new host-parasite relationships and range expansions are given. Host-parasite data and range data from Sabrosky are also listed to help characterize species (Table 1). New descriptions of puparia are provided for two species, *P. brunneisquama* Sabrosky, Bennett, and Whitworth and *P. hesperia* Shannon and Dobroscky, which have not been previously described. Although I accept Bennett's puparial descriptions, I have identified some additional key characters that help distinguish species and these are given in the diagnoses and key. Users of the key should refer to Sabrosky and Whitworth (2002, 2003) for additional information on puparia and some useful illustrations to help distinguish puparial characters. Since no specific puparia were associated with each species in Sabrosky, I have designated voucher slides listed under each species. Where possible, voucher slides were selected from specimens used in the original puparial description or from types or paratypes for that species. If the puparia of a species demonstrates extreme variation, examples of each extreme are selected. Most slides from the original descriptions were prepared in the 1950's and some are of poor quality. Newer, better quality slides were selected if no good quality original slide is available. All voucher slides will be deposited with the Sabrosky, Bennett, and Whitworth collection of *Pro-*



Figs. 25–27. Puparia. 25, *Protocalliphora interrupta* (top two figures): (a) stigmatal view; (b) dorsum. 26, *P. metallica* (middle two figures): (a) stigmatal view; (b) prothoracic fringe. 27, *P. parorum* (bottom two figures): (a) stigmatal view, (b) venter.

tocalliphora at the National Museum of Natural History, Smithsonian Institution. Common bird names follow the "*Checklist of North American Birds*," 7th edition, American Ornithologists Union, 1998, 2002. New hosts and range expansions are noted; if new records are part of a research project the collector is identified. For new range information, the nearest town or map feature is identified.

Protocalliphora (P.) aenea Shannon and Dobroscky
(Fig. 21)

Diagnosis.—Puparia usually with posterior spine band reduced to rear and a ventral band ratio of 0.50 or less. This species has an eastern (Sabrosky: fig. 42) and a western form (Fig. 21), and they come out separately in the key. The following is a comparison of distinctive characters with the eastern form first: dorsal cuticular ridges absent or faint vs. pronounced; mesostigmatal area with spines present vs. spines reduced to tubercles; ventral posterior spine band reduced or absent to rear vs. slight to moderate reduction to the rear; ventral band ratio averages 0.49/11 at front and 0.37/10 at rear vs. 0.58/8 at front and 0.48/8 at rear.

Voucher slides.—Eastern form: Barn swallow nest #48, Ontario, Canada, Algonquin Park, summer, 1955, Bennett. Western form: American dipper nest #4925-4, Cache County, Utah, Logan Canyon, summer 2001, Whitworth.

Similar species.—The eastern form is closest to *P. fallisi,* but *P. aenea* has less posterior band reduction and a larger ventral band ratio. The western form is similar to several species with pronounced dorsal ridges, but has a lower ventral band ratio and posterior ventral spine band reduced to rear. It is known almost exclusively from dipper nests in the west.

Hosts.—Western *P. aenea* were collected from nests of barn swallow, dipper, and Say's phoebe. Eastern *P. aenea* were collected from nests of common grackle, eastern phoebe, American robin, Louisiana water thrush, and house wren.

New range.—Collected near Kemmer, Wyoming. Sabrosky recorded western *P. aenea* from British Columbia, California, Colorado, Idaho, Oregon, Washington, and Utah; eastern *P. aenea* were recorded from Ontario, Quebec, Maine, New Hampshire, New York, Virginia, and West Virginia.

Discussion.—The eastern form of this species was never collected from eastern or midwestern United States during the current study despite the fact that six infested house wren nests and 30 infested eastern phoebe nests (known hosts) were examined within this species range. In 2001, it was found in two of three dipper nests under a bridge on Temple Fork Creek near Logan, Utah, where I had collected two nests infested with this species in 1971. It was also found in a barn swallow nest under a highway bridge near Kemmer, Wyoming. This is the first record of this species in a barn swallow nest in the west.

Sabrosky considered the possibility that the eastern and western forms of this species were separate species. They compared adult characters, found they overlapped, and concluded that the eastern and western forms represented a single species. I have compared puparia and found significant differences and, with apparent differences in host preference, I considered describing two separate species. However, I examined three *P. aenea* puparia collected by Halstead (1988) from dipper nests near Fresno, California, and they had only faint to moderate dorsal ridges and distinct spines in the mesostigmatal area unlike other western *P. aenea.* I believe it is prudent to wait until more specimens are collected in the west before determining the status of this species.

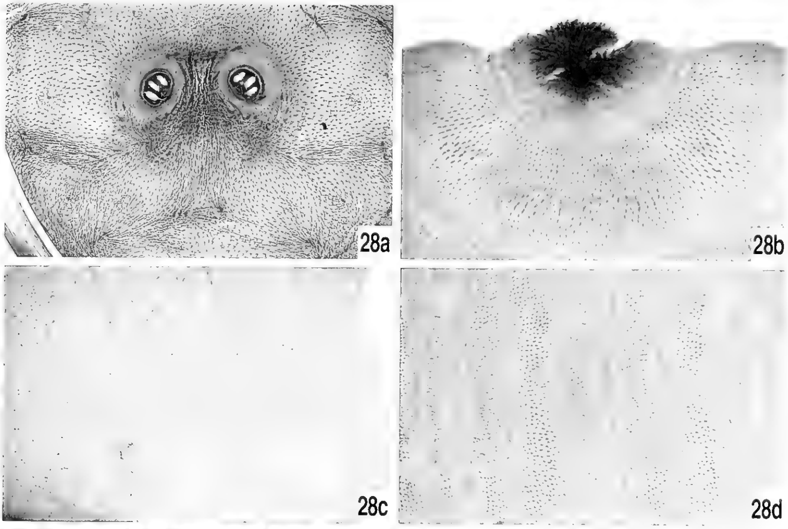
Protocalliphora (P.) asiovora Shannon and Dobroscky
(Figs. 10e, 22)

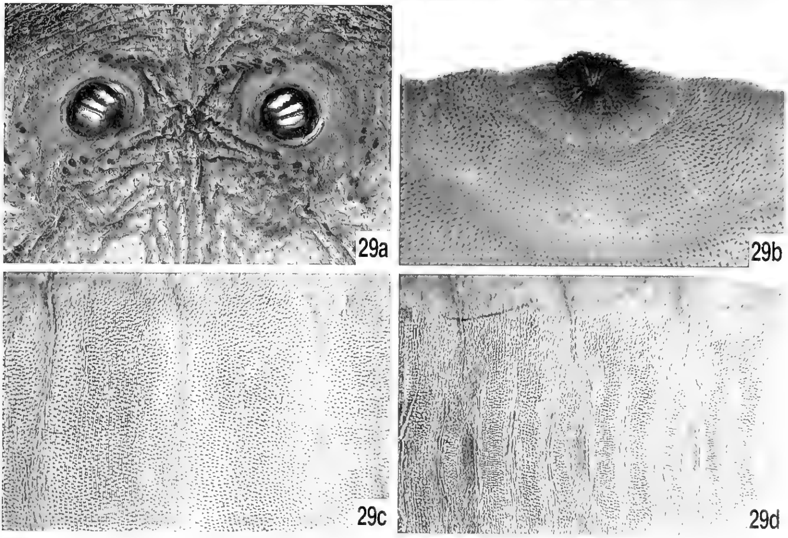
Diagnosis.—The pronounced interruption on the midline of the ventral medial spine band (Figs. 10e, 22b) will usually separate this species from all others. This feature may be present on only some segments and some individuals in a series may lack it completely. Mesostigmatal folds moderate, hyperstigmatal spines dense, slender, and short, usually 25 µ or less (Fig. 22a). Dorsal and ventral ridges faint to absent.

Voucher slide.—Black-billed magpie nest, Okanogan County, Washington, June 6, 1939, W.L. Jellison, from puparial description.

Similar species.—*Protocalliphora interrupta* may have the midline of the ventral medial spine band reduced to tubercles (Fig. 10f), but in the stigmatal area all spines are reduced to tubercles (Fig. 25a). Slender hyperstigmatal spines would place with species at couplet 23 if interruption of medial spine band is missed.

New hosts.—Stellar's Jay, Tacoma, Washington. I also collected this species from a small hanging nest (bird species un-





Figs. 28–29. Puparia. 28. *Protocalliphora seminuda* (top four figures). (a) stigmatal view; (b) prothoracic fringe; (c) dorsum; (d) venter. 29. *P. spatulata* (bottom four figures): (a) stigmatal view, (b) prothoracic fringe, (c) dorsum; (d) venter.

known) high in a tree, in the Clarkston, Washington, area, this seems to be a very unusual host for this species.

Other hosts.—Sabrosky listed the species from many corvids, raptors and a variety of smaller passerines, including Brewer's blackbird, Amercian crow, mourning dove, golden eagle, house finch, northern goshawk, Cooper's, ferruginous, red-tailed and Swainson's hawks, pinyon jay, black-billed magpie, great horned and long-eared owls, common raven, American robin, loggerhead shrike, European starling, barn and cliff swallow.

Range.—Collected only in Washington in this study, Sabrosky listed it from most western states.

Discussion.—A Stellar's Jay nesting near Tacoma, Washington, had a clutch of 3 nestlings, and, about a week before they were old enough to fledge, a nestling was observed on the ground under the nest. I captured it and noticed it showed abundant scabs on its abdomen, possibly from feeding by *Protocalliphora* larvae. When I attempted to replace it in the nest, I found its two siblings had very recently died. The nestling refused to stay in the nest and ultimately disappeared. When the nest was examined, 60 mature third instar larvae were found in the nest. With the death of its siblings, larval feeding focused on the survivor and I suspect caused its premature fledging. Previous studies suggest populations of over 10 larvae per nestling make nestlings anemic (Whitworth and Bennett 1992).

Protocalliphora (P.) avium Shannon and Dobroscky

Diagnosis.—Broad, pronounced stigmatal and circumstigmatal folds, pronounced ridges on dorsum and venter (Sabrosky: fig. 44). Dorsal and ventral ridges occasionally faint, thus this species keys to two places in the key.

Voucher slide.—American crow nest #12, Algonquin Park, Ontario, Canada, summer 1951, Bennett.

Similar species.—Puparia are closest to *P. rugosa,* known only from the northwestern United States and British Columbia. The ranges of these two species do not overlap. *Protocalliphora hirundo* and *P. lata* are also similar, the former is primarily in swallow nests, the latter is found only in northwestern North America.

Hosts.—Not found in this study. Nests of favored hosts, raptors and corvids in its range, were not examined.

Range.—Eastern and midwestern United States, Canada and Alaska.

Discussion.—Sabrosky debated whether this species is distinct from its sister species *P. asiovora,* based on adult features. Puparia of *P. asiovora* are very different, leaving little doubt they are distinct species (Fig. 22).

All characters were described from Bennett's slides, some have dorsum and venter with ridges faint to absent. These slides are 50 years old, and it is uncertain if this condition actually exists, is a processing anomaly, or an effect of age.

Protocalliphora (P.) bennetti Whitworth (Fig. 10d)

Diagnosis.—Dorsal ridges faint to absent, ventral spine bands usually regular though the medial band may be thinned and irregular (Fig. 10d) and has several rows of small spines to the rear similar to *P. parorum* (Fig. 13). This species is one of several remaining after puparia of species with distinct characters have been keyed. Puparia are illustrated and described by Whitworth (2002).

Voucher slide.—Carolina chickadee nest #3351-4, Roanoke, Virginia, May, 2000, Whitworth, from type series.

Similar species.—*Protocalliphora cuprina* puparia are closest to this species, their ranges overlap in the northwestern United States and Canada. The medial band of *P. cuprina* is usually thinned with some spines irregular, but rarely opposing (Fig. 10c). Other similar species include *P. halli, P. brunneisquama, P. parorum, P. hesperia,*

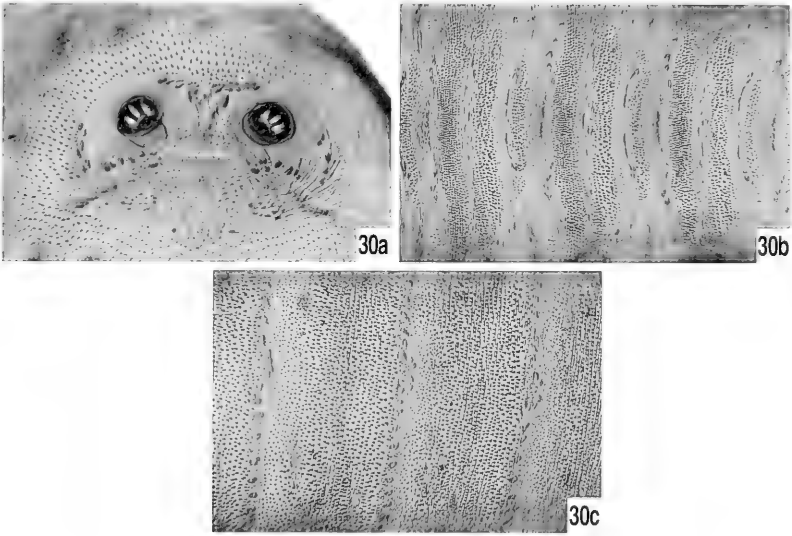


Fig. 30. Puparia. *Protocalliphora spenceri*: (a) stigmatal view; (b) venter; (c) dorsum.

and *P. hesperioides*. Adults are intermediate between *P. shannoni* and *P. sialia* and are difficult to distinguish. This species is known primarily from chickadee, tree swallow, and house wren nests, which will help distinguish it from similar species.

Hosts.—New host found in an eastern phoebe nest from Sevier County, Tennessee, submitted by Will Reeves, Clemson University. Also found in nests of boreal, black-capped, and Carolina chickadee, European starling, tree swallow, and house wren. Eastern bluebird, listed as a host in Whitworth (2002), was an error.

Range.—Sevier County, Tennessee. Whitworth (2002) also listed Alaska, Maine, Massachusetts, Minnesota, New York, Virginia, West Virginia, British Columbia, Ontario, and Saskatchewan.

Discussion.—This species was discovered while analyzing data for this study (Whitworth 2002).

Protocalliphora (P.) bicolor Sabrosky, Bennett, and Whitworth

Diagnosis.—Slender hyperstigmatal spines (Fig. 5), no posterior spine band reduction, known only from the northeastern United States, primarily in warbler and vireo nests.

Voucher slide.—American redstart nest, Holderness, Hew Hampshire, August 10, 1930, Mrs. Harding, from puparial description.

Similar species.—*Protocalliphora tundrae* has slender hyperstigmatal spines, but the posterior spine band is reduced to the rear. This species has been found only in northern Canada and Greenland. Other species with slender hyperstigmatal spines are found only in the west.

Hosts.—Sabrosky listed this species from nests of flycatchers, warblers, vireos, and American Goldfinch.

Range.—New York, New Hampshire, Wisconsin, Ontario.

Discussion.—This species was not collected during this study, though many nests were examined from its known range. Nests of favored host species were rarely collected, and most nests examined were from nest boxes. Most specimens examined were old slides from Bennett's collection. This species may be the ecological counterpart of *P. cuprina* which has similar hosts in the west.

Protocalliphora (Trypocalliphora) braueri (Hendel)

Diagnosis.—Sparse dorsal cuticular spines, ventral medial spine band absent, prothoracic fringe absent. Stigmatal folds weak in eastern material, often pronounced in the west (Sabrosky: figs. 46a, b). Larvae are obligate subcutaneous parasites.

Voucher slide.—Eastern form: House wren nest #2804-4, Hiwassee, Virginia, June 24, 1999, Whitworth. Western form: Tree swallow nest #4213-1, Umtanum Ridge, Kittitas County, Washington, July, 2000, Whitworth.

Similar species.—Most likely to be confused with sparsely spined puparia of sarcophagids or other genera of calliphorids which may be found in nests with dead nestlings. Sarcophagids have their posterior spiracles in a deep cavity, whereas spiracles in calliphorids are flush with the surrounding cuticle. Other genera of calliphorids usually have spine bands limited to the intersegmental area.

New hosts.—Black-capped chickadee, Tacoma, Washington; cedar waxwing, Eatonville, Washington; American kestrel, Saskatoon, Saskatchewan. Revels (1996) recorded it from black and white warbler, Kentucky warbler, and yellow-throated vireo. I have examined additional material from Revels, Northeastern State University, Talequah, Oklahoma, and found this species from hooded and Swainson's warbler nests collected near Idaho Falls, Idaho. Also collected from nests of American robin and European starling. Sabrosky listed numerous additional hosts.

New range.—Black Earth and Sheldon, Wisconsin. Revels (1996) recorded Arkansas. This species is widespread throughout North America, though it was considered rare in the east by Sabrosky.

Discussion.—Many Europeans place this species in the genus *Trypocalliphora* (Rognes 1985), while North Americans consider it only a subgenus of *Protocalliphora* (Sabrosky). I have followed the usage in Sabrosky for consistency, but suspect it deserves full genus status. Bennett (in Sabrosky) described larvae of this species as having a short prothoracic fringe averaging 7 μ (3–10 μ), but larvae I examined had no discernable fringe. Cais (1965) compared the larvae of three species of European *Protocalliphora*. His illustrations show no prothoracic fringe in *P. hirundo* (= *P. braueri*) while showing a prominent fringe in the other two species. Larvae of this species are obligate subcutaneous parasites while species of the subgenus *Protocalliphora* are occasionally found in ears and nares, they are almost never subcutaneous. When these immature characters are considered with the distinctive aedeagus in the male and the lack of reclinate upper orbital bristles in the female, a strong case can be made that *Trypocalliphora* deserves full genus status.

This species was common in western Oregon, western Washington, and western British Columbia, where other species of *Protocalliphora* were often uncommon. In one group of 90 infested nest boxes examined near Tacoma, Washington, 63 (70%) were infested by this species (Bennett and Whitworth 1991). This species was uncommon in the rest of the west and occasionally found throughout most of North America.

Protocalliphora (P.) brunneisquama Sabrosky, Bennett, and Whitworth (Fig. 23)

Diagnosis.—Hyperstigmatal spines to 33 μ, mesostigmatal spines 10–15 μ, ventral band ratio anterior end 0.76, posterior end 0.67.

Voucher slide.—Tree swallow nest #4864-2, see data below.

Similar species.—Puparia of this species have no distinctive characters, they key near *P. parorum, P. hesperia,* and *P. hesperioides.*

Range.—Sabrosky listed it from California, Colorado, Idaho, Montana, New Mexico, Utah, and Washington.

New hosts.—Five adults were reared from 15 puparia found in a tree swallow nest from Corona, California. I previously found this species in a chipping sparrow nest in Utah, but puparia were undersized and not suitable for use in a description (Sabrosky). I have concluded the listing of brown towhee as a host for *P. lata* in Sabrosky was a misidentification and, in fact, the specimens were *P. brunneisquama.* See comments under *P. lata.*

Discussion.—Thirty-one other infested tree swallow nests were examined in California and this species was not found again. It also was not found in several hundred other tree swallow nests throughout its range, so its favored host is not likely tree swallows. Puparia of this species were not described in Sabrosky, a description follows: Length 7.2 mm (7–8 mm)/9; breadth 3.5 mm (3–4 mm)/9; posterior region (Fig. 23a): Stigmatal plates 181 μ (175–198 μ)/4; distance between buttons 580 μ (540–630 μ)/4; and width of stigmatal area across stigmatal plates 1,144 μ (1,100–1,200 μ)/4; stigmatal ratio 0.51(0.49–0.53)/4. Upper mesostigmatal area tubercles or short spines, lower area spines to 15 μ, folds absent; hyperstigmatal spines numerous, longest spines to 33 μ (25–33 μ); hypostigmatal area spines to 25 μ (15–25 μ); circumstigmatal folds faint. Dorsal cuticle (Fig. 23c): Spines to 37.5 μ (35–37.5 μ), ridges faint. Ventral cuticle (Fig. 23d): Ventral band ratio, anterior end 0.76(0.73–0.80)/4, posterior end 0.67 (0.61–0.73)/4. Diameter of prothoracic fringe 300 μ (250–350 μ)/4 (Fig. 23b).

Basis for description.—5 adults, 15 puparia, Corona, California, tree swallow nest #4864, May 29, 2001.

Protocalliphora (P.) cuprina (Hall)
(Fig. 10c)

Diagnosis.—Posterior, ventral spine band may or may not be reduced to the rear, medial band thinned on the midline toward rear, usually some irregular spines and a few opposing (Fig. 10c); longest hyperstigmatal spines to 25 μ (Sabrosky: fig. 48). Keys to two places because characters are variable. Narrow host preferences, primarily in warbler and flycatcher nests, western only.

Voucher slide.—Western wood pewee nest #1255, Franklin Basin, Cache County, Utah, August 10, 1971, Whitworth, from puparial description.

Similar species.—*Protocalliphora halli,* see discussion below.

New hosts.—Plumbeous vireo, Mt. Trumbull, Arizona; song sparrow, blue headed and warbling vireo, submitted by Revels, from Idaho Falls area, Idaho; also found in barn swallow and yellow warbler. I have examined a puparial slide prepared by Bennett labeled USNM X-20 which lists collector as Neff in California (loggerhead) shrike as host. Bennett had not written species identification on the slide, but Sabrosky listed this host for *P. asiovora* from Neff in California. I have keyed this specimen to *P. cuprina,* which would be an unusual host. It is possible Bennett misidentified this slide and if so, the listing for *P. asiovora* should be changed to *P. cuprina.* Sabrosky listed it from finches, kingbirds, wood peewees, and warblers.

New range.—Mt. Trumbull, Arizona; also found in British Columbia, Oregon, and Washington in this study. Sabrosky listed it from California, Idaho, Montana, Utah, and Wyoming.

Discussion.—Puparia of this species can be difficult to separate from numerous others, but its narrow host preferences eliminate most similar species, except *P. halli.*

This species has been found in mixed infestations with *P. halli* in barn swallow nests in Washington and Oregon. Both species have ventral medial band thinned, differences include *P. cuprina* rarely has opposing spines on medial band (Fig. 10c) vs. *P. halli* often has opposing spines on the rear margin and toward the rear (Fig. 10b); *P. cuprina* usually has shorter hyperstigmatal spines, 25 μ or less vs. 30 μ or more in *P. halli*; ventral posterior band usually with only small reductions to rear vs. some specimens with extreme reduction to the rear in *P. halli.*

Protocalliphora (P.) deceptor Sabrosky, Bennett, and Whitworth
(Fig. 18)

Diagnosis.—Hyperstigmatal spines reduced to small tubercles with tiny spine projections when viewed at 450× (Fig. 18).

Voucher slide.—Eastern phoebe nest USNM 556-236, Shenandoah, Virginia, July 21, 1956, A. Wetmore.

Similar species.—*Protocalliphora interrupta* is similar but has larger round hyperstigmatal tubercles (Figs. 17, 25a), ventral posterior spine band reduced to rear, ventral medial spine band reduced to tubercles on midline (Fig. 10f). *Protocalliphora metallica* is similar, but hyperstigmatal tubercles are usually smaller, surrounded by cell-like borders (Figs. 16, 26a), and the tubercles do not have spine projections. Occasional *P. deceptor* have hyperstigmatal tubercles with cell-like borders and no spine projections, very similar to *P. metallica.* However, *P. deceptor* tubercles are larger, and spines of anterior spine band are longer. Occasionally *P. shannoni* have short hyperstigmatal spines (2.5–7.5 μ) or tubercles and will key to *P. deceptor.* Mesostigmatal spines and tubercles in *P. shannoni* are usually very sparse, those in *P. deceptor* are usually dense. *Protocalliphora shannoni* favors robins and thrushes throughout North America, while *P. deceptor* favors chickadees, warblers, and wrens, only in eastern Northern America.

New hosts.—Eastern bluebird, Mt. Pleasant, Texas; black-capped chickadee, Coweta, Oklahoma; barn swallow, Paris, Texas; eastern towhee, Charleston, South Carolina; hooded and prothonotary warblers, Richmond, Virginia; Swainson's warbler, Ozark National Forest, Arkansas, Mia Revels; Bewick's wren, Norman, Oklahoma. Also recorded by Revels (1996) from nests of acadian flycatcher and Bachman's sparrow. Other hosts found in this study include Carolina chickadee, northern cardinal, common grackle, eastern phoebe, tree swallow, tufted titmouse, yellow warbler, Carolina wren, and house wren. Sabrosky also listed it from brown-headed cowbird, American crow, great-crested flycatcher, northern mockingbird, wood thrush, and prairie and worm-eating warblers.

New range.—Arkansas, Fayetteville; Palatine, Illinois; Ashland, Kentucky; Peru, Nebraska; Newtonville, New Jersey; Mt. Morris, New York; Ada, Oklahoma; Lebanon, Pennsylvania; Mt. Pleasant, Texas; Beaver Dam, Wisconsin; other states are Delaware, Georgia, Indiana, Missouri, North Carolina, Ohio, South Carolina, Tennessee, Virginia. Sabrosky listed it throughout the eastern United States, west to Missouri and south to Mississippi.

Discussion.—This species sometimes infests nests favored by *P. sialia* in the southeastern and lower midwestern United States where *P. sialia* was not collected (Whitworth 2003).

Protocalliphora (P.) fallisi Sabrosky, Bennett, and Whitworth

Diagnosis.—Extreme ventral posterior spine band reduction, short hyperstigmatal spines (25 μ or less), ventral band ratio at rear averages 0.32 (Sabrosky: fig. 50). Known only from Ontario.

Voucher slide.—Host not identified, nest #54-568-5, Ontario, possibly Algonquin Park, summer 1954, Bennett. The only puparia found for this species were 11 slides prepared by Bennett, most were in poor condition.

Similar species.—*Protocalliphora aenea* occurs in the same area, but has less reduction of the posterior ventral spine band and longer hyperstigmatal spines.

Hosts.—Sabrosky listed red-winged blackbird, common grackle, swamp and white-throated sparrows, rough-winged swallow, and downy woodpecker.

Range.—Known only from two locations in Ontario.

Discussion.—Key characters for this species were taken from a few poor quality slides in the Bennett collection and Bennett's description in Sabrosky. This species was not collected during this study.

Protocalliphora (P.) halli Sabrosky, Bennett, and Whitworth
(Figs. 10b, 12, 14)

Diagnosis.—Posterior spine band on venter often reduced to rear. Medial spine band on venter thinned in middle, often with opposing spines on rear edge (Fig. 10b). Opposing spines are usually most evident on the last three segments, and may just involve a few spines. Posterior band variable from significant reduction to none, longest hyperstigmatal spines 30 μ or more, low ventral spine band ratios.

Voucher slides.—Three voucher slides are designated because of extreme variations in puparia of this species. Barn swallow nest #245 (TW4-4), Logan, Utah July 9, 1970, Whitworth, used by Bennett to describe puparia of this species, exhibits extreme reduction of ventral posterior band to rear. Barn swallow nest 1155-4, Logan, Utah, July 11, 1971, Whitworth from holotype series, not used by Bennett for puparial description, only slight reduction of posterior band to rear. Barn swallow nest 5186-1, Bellingham, Washington, summer 2001, Whitworth, posterior band not reduced to rear.

Similar species.—Very close to *P. cuprina* and sometimes found in mixed infestations with it. *Protocalliphora cuprina* usually has shorter hyperstigmatal spines, to 25 μ, and few opposing spines on the rear margin of the ventral medial band (Fig. 10c).

Hosts.—Known primarily from barn swallows, also black and Say's phoebes, (Sabrosky).

New range.—Scappoose, Oregon; Bellingham and Tacoma, Washington; Grants, New Mexico. Sabrosky also listed California, Utah, Wyoming, and British Columbia.

Discussion.—Puparia from Washington and Oregon did not show the extreme reduction of the ventral posterior band as described in Sabrosky. I re-evaluated all Utah material, including lot #1155, which was the basis for the puparial description, and it was accurate. However this lot was nontypical and puparia from an additional 140 *P. halli* infested nests from Utah and Wyoming rarely had such extreme reduction. I originally thought this variation represented a separate species, but all adults were similar and some posterior band reduction to the rear was observed from a variety of series throughout *P. halli's* range.

Sabrosky listed pine grosbeak as a new host for this species from my nest #414 near Logan, Utah, collected July 22, 1970. A re-examination of the material, including three puparial slides, revealed they are actually *P. hesperia*.

Protocalliphora (P.) hesperia Shannon and Dobroscky
(Fig. 24)

Diagnosis.—Hyperstigmatal spines to 30 μ (rarely to 35 μ), folds faint or absent, dorsal spines to 40 μ, dorsal ridges faint to absent, ventral band ratio averages 0.65 (0.55–0.76)/25 (Figs. 24a–d).

Voucher slide.—Barn swallow nest, Gold #1, Adin Bridge, Modoc County, California, August 6, 1978, C.S. Gold, from paratypes, see description below.

Similar species.—Puparia of *P. hesperioides* are very similar, and *P. parorum* puparia with spines in mesostigmatal area are also similar, but this species has a broad row of small spines to the rear of the posterior spine band.

New hosts.—Pine grosbeak, parasite misidentified in Sabrosky as *P. halli,* see note under that species. Swainson's and varied thrush, from Steve Matsuoka, United States Geological Survey, Anchorage, Alaska; veery, from Mia Revels, Idaho Falls area, Idaho and hermit thrush, Mogollon Rim, Arizona. Sabrosky listed other hosts including American robin, house finch, and barn swallows.

Range.—Idaho Falls, Idaho; Mogollon River, Arizona, Sabrosky also listed Alaska, British Columbia, California, Oregon, Washington, and Utah.

Discussion.—Hyperstigmatal spine length was variable throughout this species range, some specimens longest spines were only 25 μ. Bennett did not describe puparia of this species in Sabrosky, therefore a description follows: Length 7.5 mm (7.1–7.7)/8; breadth 3.3 mm(3.0–3.5)/8. Posterior region: Stigmatal plates 164 μ (145–198 μ)/27 in diameter; distance between buttons 514 μ (440–650 μ)/27; and across the stigmatal plates 1,074 μ (820–1,300 μ)/27; stigmatal ratio 0.48(0.44–0.50)/27; mesostigmatal spines short to 15 μ, folds faint to absent, a few moderate; hyperstigmatal spines to 35 μ, folds faint to absent; hypostigmatal spines to 15 μ, folds moderate to absent (Fig. 24a). Dorsal cuticle: Spines to 40 μ, ridges faint to absent, rarely moderate (Fig. 24c). Ventral cuticle: Ventral band ratio 0.65(0.55–0.76)/25; ridges faint to absent (Fig. 24d). Diameter of prothoracic fringe 300 μ (275–325 μ)/10 (Fig. 24b).

Basis for description.—Alaska: 6 slides, Kenai, gray jay or thrush, June 10, 1978, G.E. Haas; 4 slides, Anchorage, varied thrush nest #KMB012, June 26, 1998, Steve Matsuoka, United States Geological Survey. California: 3 slides, Modoc County, Adin Bridge, barn swallow, August 6, 1978. Utah: Logan, 3 slides, American robin nest #350, July 17, 1970; 3 slides, Pine grosbeak nest #414, July 22, 1970; 1 slide, Cassin's finch nest #499, August 7, 1970; 8 slides, American robin nest #534, June 22, 1980; 2 slides, American robin nest #927, June 25, 1971.

Protocalliphora (P.) hesperioides Sabrosky, Bennett, and Whitworth

Diagnosis.—Puparia currently indistinguishable from *P. hesperia.* See discussion.

Voucher slide.—House finch nest, Anaheim, California, July, 1936, A.J. Basinger, from paratypes.

Similar species.—Currently puparia of this species are indistinguishable from *P. hesperia. Protocalliphora hesperioides* can be confused with *P. brunneisquama, P. cuprina, P. halli,* and *P. parorum.*

Hosts.—Sabrosky listed bushtit, house finch, goldfinch species, dusky and western flycatcher, and yellow warbler.

Range.—California, Washington, and British Columbia.

Discussion.—This species was not collected during this study, and only 10 puparia were available for study. Bennett described this species as having pronounced stigmatal folds (Sabrosky: fig. 52), but in all the material I examined (including 5 of Bennett's slides) stigmatal folds ranged only from faint to moderate. As more material becomes available, distinctive characters may be found.

Protocalliphora (P.) hirundo Shannon and Dobroscky

Diagnosis.—Broad pronounced dorsal cuticular ridges, stigmatal area with a few pronounced folds, mesostigmatal and hypostigmatal area with distinct spines (Whitworth 2002: figs. 3a, b).

Voucher slide.—Swallow species (probable cliff swallow), Ventura, California, June 23, 1949, J.N. Belkin, from puparial description.

Similar species.—*Protocalliphora lata* also has broad dorsal cuticular ridges, but the mesostigmatal and hypostigmatal areas are usually bare. *Protocalliphora rugosa* has pronounced ridges and folds, but they are more abundant and closer together than in *P. hirundo.*

Hosts.—During this study *P. hirundo* was found in nests of cliff, tree, barn and bank swallows. Sabrosky also listed the species from yellow-headed blackbirds, eastern bluebirds, common grackles, eastern phoebes, and European starlings. Sabrosky also listed it from nests of purple martins and violet-green swallows, but most of these hosts in the west were actually infested by *P. rugosa.*

Range.—During this study, *P. hirundo* was found in Washington and Oregon; Sabrosky listed it from Maine to Washington, south to southern California and north to Alaska.

Discussion.—I recently described a new species, *P. rugosa,* which Sabrosky did not distinguish from *P. hirundo* (Whitworth 2002). As adult and puparial descriptions found in Sabrosky were based on *P. hirundo,* there is no need to redescribe this species.

Bennett (in Sabrosky) described ventral band ratio averaging 0.53 (0.40–0.74); however, I measured 36 specimens from many different areas and my specimens averaged 0.65 with a range of 0.48–0.79. Occasional aberrant specimens had very low ratios, ventral band ratios were sometime difficult to measure in these heavily ridged puparia.

Protocalliphora (P.) interrupta Sabrosky, Bennett, and Whitworth
(Figs. 10f, 17, 25)

Diagnosis.—Hyperstigmatal spines reduced to tubercles and short spines (Figs. 17, 25a). Posterior band on venter reduced to rear, medial band reduced to tubercles on midline (Fig. 10f). Prothoracic fringe exceptionally short, averaging 225 μ (200–250 μ).

Voucher slide.—Yellow-headed blackbird nest #104-1, Mendon, Cache County, Utah, June 18, 1970, Whitworth, from puparial description.

Similar species.—Other species with hyperstigmatal spines reduced include *P. deceptor* (Fig. 18), and *P. metallica* (Fig. 16).

New hosts.—House finch, Tacoma, Washington; yellow-breasted chat, and McGillivray's warbler, Idaho Falls, Idaho, Mia Revels. Other hosts found during this study are long-billed marsh wrens and Brewer's blackbirds. Sabrosky also listed yellow-headed, and red-winged blackbirds and song sparrow.

New range.—Idaho Falls, Idaho; Tacoma, Washington, Sabrosky also listed Utah, California, and British Columbia.

Discussion.—A long series of *P. interrupta* reared from a brewer's blackbird nest in Washington included aeneous adult females that would key to *P. aenea* in couplet 3 of the adult key in Sabrosky. I initially suspected this was a new species, but after analyzing adults and puparia of Washington and Utah material I found puparia were essentially the same. Some aeneous adult females were also found in the Utah material and this appears to be a genetic variation which is often scattered through specimens in a reared series, this condition was not noted in the original description. If males and puparia are available, these two species are readily distinguished since *P. aenea* surstyli are digitate while *P. interrupta* surstyli are slender and curved; also in puparia, the hyperstigmatal area has distinct spines vs. spines reduced to tubercles in *P. interrupta* (Fig. 17).

Protocalliphora (P.) lata Sabrosky, Bennett, and Whitworth

Diagnosis.—Broad, pronounced dorsal cuticular ridges, mesostigmatal and hypostigmatal areas few or no spines, puparia to 13 mm; the largest known species of *Protocalliphora* (Sabrosky: fig. 55).

Voucher slide.—American kestrel nest #380-1, Mendon, Cache County, Utah, July 20, 1970, Whitworth, from puparial description and type series.

Similar species.—*Protocalliphora hirundo* is similar, but the mesostigmatal and hypostigmatal areas have abundant spines and puparia are, at most, 9 mm in length.

Hosts.—Found in northern flicker. Sabrosky also listed red-tailed hawk, northern goshawk, American kestrel, and brown towhee. The identification of *P. lata* in towhees appears to be an error. Sabrosky mentioned the larval description for *P. lata* was based on 3 specimens from Anaheim, California. I have found 3 Bennett slides (2 larvae and 1 puparium) from Anaheim, California that list "towhee" as host. The specimens are clearly not *P. lata* and key to *P. brunneisquama.* I have concluded this was a misidentification. I dropped towhee as a host for *P. lata* and have listed it under *P. brunneisquama.*

Range.—British Columbia, California, Idaho, Oregon, Idaho, and Utah.

Discussion.—Karen Weibe, University of Saskatchewan, Saskatoon sent specimens from two northern flicker nests that I confirmed were *P. lata.* She reported seeing some large larvae (almost certainly *P. lata*) attached to flicker nestlings each year near Riske Creek, British Columbia. I also found this species in flicker nests in Utah and Idaho, but the nests were so fouled with nestling excrement that the larvae usually died before maturing (Bennett and Whitworth 1992). Karen noted that her flicker nests were sometimes not so foul and I suspect flickers are a common host for this species.

Protocalliphora (P.) metallica (Townsend)
(Figs. 16, 26)

Diagnosis.—Stigmatal area covered with tiny tubercles surrounded by cell-like walls (Figs. 16, 26a). Walls occasionally not visible so only tiny tubercles are present. These features are minute and best seen at 450× in a slide mount.

Voucher slide.—Common grackle nest #144, Algonquin Park, Ontario, Canada, Summer 1955, Bennett, from puparial description.

Similar species.—*Protocalliphora deceptor* has stigmatal spines reduced, but with short spine projections (Fig. 18), *P. interrupta* has larger stigmatal tubercles (Fig. 17) and posterior spine bands reduced to the rear.

New hosts.—Northern mockingbird, Gilford, New Hampshire; mourning dove, Hanover, Michigan; white-crowned sparrow, Tacoma, Washington; yellow-rumped warbler, Anchorage, Alaska. Revels (1996) recorded it from MacGillivray's warbler. Other hosts found during this study include Brewer's blackbird, red-winged blackbird, gray catbird, sparrow sp., and tree swallow. Sabrosky listed it from many hosts.

New range.—Anchorage, Alaska and Lenoir City, Tennessee; also collected from Iowa, Illinois, Massachusetts, Maryland, Michigan, Minnesota, New Hampshire, New York, Virginia. Sabrosky found it widespread in the United States and in British Columbia.

Protocalliphora (P.) occidentalis
Whitworth

Diagnosis.—Prothoracic fringe 500 μ in diameter or longer. Dorsal cuticular ridges pronounced. Stigmatal area with folds faint or absent; mesostigmatal area with spines reduced to tubercles; ventral band ratio averages 0.72; western North America. Puparial characters are illustrated in Whitworth (2003).

Voucher slides.—Mountain bluebird nest 2926-2, Eureka, Nevada, September 13, 1999, Whitworth.

Similar species.—*Protocalliphora parorum* with diameter of prothoracic fringe 450 μ or less. *Protocalliphora sialia* is very similar and was, until recently, considered the same species. See Whitworth (2003) for a detailed discussion.

New hosts.—From nests contributed by Don Dahlsten, University of California, Berkeley, red-breasted nuthatch, pygmy nuthatch, and Bewick's wren, all nests from central California, dark-eyed Junco from Idaho Falls area, Mia Revels.

New range.—Eureka, Nevada. Also collected from Arizona, California, Colorado, Idaho, Montana, New Mexico, Oregon, Utah, Washington, Wyoming, and British Columbia.

Protocalliphora (P.) parorum Sabrosky, Bennett, and Whitworth

(Figs. 13, 20, 27)

Diagnosis.—Dorsal cuticular ridges usually moderate, occasionally faint or absent. Usually a broad row of small spines to the rear of the anterior and medial ventral spine bands (Figs. 13, 27b); mesostigmatal area often with spines reduced to tubercles (Figs. 20, 27a). Prothoracic fringe long, to a diameter of 450 μ. Narrow host range, primarily in chickadees, nuthatches, titmice, and wrens.

Voucher slide.—Mountain chickadee nest A2840, Modoc County, California, early 1980's, C.S. Gold, from puparial description.

Similar species.—Close to *P. occidentalis,* but the difference in prothoracic fringe diameter usually separates them (500 μ or more in *P. occidentalis* vs. 450 μ or less in *P. parorum*). *Protocalliphora parorum* tends to have distinct circular anal tubercles (Fig. 20) while *P. occidentalis* tends to have less distinct, more irregular tubercles. Dorsal cuticular ridges are usually moderate in *P. parorum* and pronounced in *P. occidentalis.* Adult males are readily distinguished: *P. parorum* surstyli are long and slender, *P. occidentalis* surstyli are digitate.

New hosts.—Western bluebirds and white-breasted nuthatch, Flagstaff, Arizona. Additional new hosts from material contributed by Don Dahlsten, University of California, Berkley, included ash-throated flycatcher, pygmy nuthatch, tree swallow, and oak titmouse. Other hosts found in this study include black-capped, mountain, and chestnut-backed chickadee, house and Bewick's wren. Sabrosky also listed brown creeper, red-breasted nuthatch, barn swallow, and Oregon (dark-eyed) junco.

New range.—Arizona, Colorado, Idaho, New Mexico, Oregon, Washington, and British Columbia, Canada. Sabrosky also listed California and Utah.

Discussion.—This species often has most mesostigmatal spines reduced to tubercles, like *P. occidentalis.* Specimens usually have a few short spines, some have no spines, and a few have abundant spines. When many distinct spines are present in the mesostigmatal area, this species is difficult to distinguish from *P. brunneisquama* and *P. hesperia.* Puparia of this species are variable throughout its range, thus it appears three times in the key.

Protocalliphora (P.) rognesi Thompson and Pont

Protocalliphora chrysorrhoea: Sabrosky et al. 1989; Bennett and Whitworth 1991, 1992; Whitworth and Bennett 1992; Koslov and Whitworth 2002.

Diagnosis.—Pronounced dorsal ridges, long hyperstigmatal spines, to 50 μ, prothoracic fringe 350–400 μ, almost exclusively in bank swallows (Sabrosky: fig. 47).

Voucher slide.—Bank swallow nest, Tok, Alaska, July 14, 1948, R. Sailer, from puparial description.

Similar species.—*Protocalliphora parorum, P. occidentalis,* and *P. sialia* are similar, but the former has only tubercles or short spines in the mesostigmatal area, and a broad row of short spines to the rear of the ventral medial spine band. The latter two have a longer prothoracic fringe over 500 μ in diameter.

Hosts.—Known almost exclusively from bank swallow nests; also recorded from house sparrow, barn swallow, and violet-green swallow.

Range.—Sabrosky recorded this species from across the northern United States, Ontario, and Alaska.

Discussion.—Thompson and Pont (1993) proposed the replacement name *P. rognesi* for the preoccupied *P. chrysorrhoea* (Meigen). While identifying samples of blow flies collected from the Kola Peninsula in Russia, I found two adult female *P. rognesi* in samples taken from flytraps (Koslov and Whitworth 2002).

Protocalliphora (P.) rugosa Whitworth

Diagnosis.—Pronounced, dense dorsal cuticular ridges, pronounced irregular folds in the hypostigmatal area, short hyperstigmatal spines (30 μ or less), mesostigmatal area with dense spines (Whitworth 2002: fig. 2a).

Voucher slide.—Tree swallow nest 1198-2, Logan Canyon, Cache County, Utah, July 17, 1971, Whitworth, from puparial description.

Similar species.—*Protocalliphora avium* is similar but has very sparse or no spines in the mesostigmatal area and a limited range which does not overlap with *P. rugosa* which is known only from the northwestern United States and British Columbia.

Hosts.—Purple martin, house sparrow, European starling, bank, barn, cliff, tree, and violet-green swallow.

Range.—Idaho, Montana, Oregon, Utah, Washington, Wyoming, and British Columbia.

Discussion.—This species was separated from *P. hirundo,* see discussion under that species. It was discovered while analyzing data for this study (Whitworth 2002).

Protocalliphora (P.) seminuda Sabrosky, Bennett, and Whitworth
(Fig. 28)

Diagnosis.—Slender hyperstigmatal spines, 30 μ or less, mesostigmatal folds moderate to pronounced (Figs. 28a–d). Ventral band ratio 0.73 (0.67–0.84).

Voucher slide.—Brewer's blackbird nest #244-6, Pocatello Valley, Oneida County, Idaho, July 5, 1970, Whitworth, from puparial description.

Similar species.—Similar to *P. spatulata,* see differences discussed under that species. *Protocalliphora spatulata* tends to favor higher elevations or occur farther north, while *P. seminuda* is often associated with desert habitat.

New hosts.—Western bluebird, Los Alamos, New Mexico, collected by J.M. Fair, Los Alamos Labs, adults only, no puparia. Sabrosky listed it from Brewer's blackbird, horned lark, and barn swallow.

Range.—Sabrosky listed the species from California, Idaho, New Mexico, Utah and Wyoming.

Protocalliphora (P.) shannoni Sabrosky, Bennett, and Whitworth
(Figs. 14, 19)

Diagnosis.—Short hyperstigmatal spines to about 12.5 μ (rarely to 20 μ), mesostigmatal and hypostigmatal spines reduced to tubercles (Fig. 19). Ventral posterior spine bands reduced to rear, sometimes only last one or two segments reduced, rarely little or no reduction.

Voucher slide.—Robin nest #190, Algonquin Park, Ontario, summer 1955, Bennett, from puparial description.

Similar species.—*Protocalliphora deceptor* has shorter hyperstigmatal spines and no reduction to the ventral posterior spine band. Occasionally *P. shannoni* has short spines or tubercles in the hyperstigmatal area and would key to *P. deceptor,* see comments under *P. deceptor.*

New hosts.—Townsend's warbler and Swainson's thrush nests contributed by Steve Matsuoka, United States Geological Survey, Anchorage, Alaska; veery, Idaho Falls area, Mia Revels. Nine puparial slides prepared by Bennett, labeled 55-147, which would be summer 1955, Algonquin Park Ontario, listed swamp sparrow as host but included no species identification. Six slides were *P. metallica,* two were *P. fallisi* and one was *P. shannoni,* which would be a new host-parasite relationship. Matsuoka also collected it from American robin and yellow-rumped warbler (under myrtle warbler in Sabrosky). Sabrosky listed *P. shannoni* from a variety of hosts.

New range.—Idaho Falls, Idaho, Waldo, Maine, and Anchorage, Alaska, also collected from New Hampshire and New York. Sabrosky found this species primarily in the northeastern and northwestern United States and Canada.

Discussion.—Sabrosky stated that eastern forms of this species have pronounced cuticular ridges while western forms have weak cuticular ridges. I found cuticular ridges weak in most specimens and occasionally moderate to pronounced in specimens from both the east and west. Hyperstigmatal spine length can be quite variable, from tubercles to 20 μ. Patches of longer spines may be found throughout the hyperstigmatal region, especially near the upper portion. Puparia of this species are somewhat variable, but a comparison of adults and puparia from Maine to Washington, and north from British Columbia to Anchorage, Alaska, revealed many shared features and *P. shannoni* appears to be a widespread, variable species. One adult character not mentioned in Sabrosky is the thorax of many adult females which have aeneous highlights.

Protocalliphora (P.) sialia Shannon and Dobroscky
(Figs. 10a, 15b)

Diagnosis.—Prothoracic fringe usually 500 μ in diameter or longer. Dorsal cuticular ridges pronounced. Stigmatal area with pronounced folds; mesostigmatal area with distinct spines; ventral band ratio averages 0.81. Puparial characters are illustrated in Whitworth 2003.

Voucher slide.—*P. sialia*: Barn swallow nest #64, Ontario, Algonquin Park, Summer 1952, Bennett.

Similar species.—*Protocalliphora occidentalis* is very similar, see comments under that species.

New hosts.—Northern mockingbird, Allegany, Maryland and tufted titmouse, Gorton, Massachusetts.

New range.—Indiana, Illinois, Kentucky, Minnesota, Nevada, Rhode Island, Tennessee, and Saskatchewan. Also collected from Alaska, Iowa, Maine, Maryland, Massachusetts, Michigan, New York, Ohio, Pennsylvania, Vermont, Virginia, West Virginia, and Ontario. Sabrosky listed New Brunswick, Northwest Territories, Quebec, Delaware, Georgia, and South Dakota.

Protocalliphora (P.) spatulata Sabrosky, Bennett, and Whitworth
(Figs. 11, 15a, 29)

Diagnosis.—Hyperstigmatal spines slender and long (up to 50 μ, Fig. 5). High ventral band ratio averaging 0.83 (0.72–0.92) (Fig. 11), circumstigmatal folds pronounced (Fig. 29a).

Voucher slide.—Horned lark nest #XII, Beartooth Pass, Park County, Wyoming, August 20, 1964, N.A.M. Verbeek, from puparial description.

Similar species.—*Protocalliphora seminuda* is similar, but has shorter hyperstigmatal spines (30 μ or less), lower ventral band ratio averaging 0.73, and circumstigmatal folds faint to moderate.

New hosts.—Savannah and white-crowned sparrows, 150 km east of Delta Junction, Alaska, Fair and Miller (1995); yellow-rumped warblers and dark-eyed juncos from Steve Matsuoka, vicinity of Anchorage, Alaska. Sabrosky listed it from horned lark and water pipit and an undetermined species of rosy finch.

Range.—Sabrosky reported this species in Alaska, California, Colorado, Montana, New Mexico, Wyoming, Northwest Territories, Ontario, and Yukon Territory.

Discussion.—Fair and Miller (1995) reported subcutaneous *P. spatulata* larvae in sparrow nestlings. However, I examined the reared series from their study, and it contained a mix of *P. braueri* and *P. spatulata*. It is likely *P. braueri* was the subcutaneous species observed (J.M. Fair, pers. comm.).

Protocalliphora (P.) spenceri Sabrosky, Bennett, and Whitworth
(Fig. 30)

Diagnosis.—Slender hyperstigmatal spines, mesostigmatal folds faint or absent, ventral band ratio averages 0.71 (0.55–0.95) (Figs. 30a–c).

Voucher slide.—Warbling vireo nest #1237-3, Franklin Basin, Cache County, Utah, July 21, 1971, Whitworth, from puparial description.

Similar species.—*Protocalliphora seminuda* and *P. spatulata* are similar but have pronounced mesostigmatal folds.

New hosts.—Blackpoll, Townsend's, yellow-rumped warblers, pine grosbeak, from Steve Matsuoka, Anchorage, Alaska, yellow-breasted chat, Idaho Falls area, Mia Revels. Sabrosky listed American redstart, warbling vireo, yellow warbler and slate-colored (dark-eyed) junco.

New range.—Anchorage, Alaska. Sabrosky recorded it from British Columbia, Manitoba, Idaho, and Utah.

Discussion.—The only puparia of this species available for study were from Utah, Idaho, and Alaska. Ten puparia from Alaska had ventral band ratios averaging 0.64, while four puparia from Utah averaged 0.73 and five puparia from Idaho averaged 0.92. Bennett measured ventral band ratios in 15 specimens, including 5 from Utah, which I have, plus 10 from British Columbia, which I have not seen. His ratios averaged 0.70 (0.40–0.80) which suggests Alaska specimens have lower ratios than Utah and British Columbia specimens. The hyperstigmatal spines of Alaska specimens were broader at the base, with only tips slender, while Utah and Idaho specimens had spines uniformly slender.

Protocalliphora (P.) tundrae Sabrosky, Bennett, and Whitworth

Diagnosis.—Posterior spine band reduced to rear, hyperstigmatal spines with slender tips, ventral band ratios usually low, averaging 0.52 (0.43–0.58) to front and 0.37 (0.29–0.47) to rear (Sabrosky: fig. 64).

Voucher slide.—Snow bunting nest, Nedre midsommer Sö, Pearyland, Greenland, July 10, 1966, J.E.H. Martin, from paratypes.

Similar species.—*Protocalliphora aenea* and *P. fallisi* are similar and their ranges overlap. The slender hyperstigmatal spines should separate *P. tundrae,* but it is known from only a few specimens, and it is not certain how constant the character is.

Hosts.—Known only from the nests of snow buntings and savannah sparrows.

Range.—Known only from far northern Canada and Greenland.

Discussion.—Few samples of puparia were available, most specimens were slides from the Bennett collection.

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STUDIES ON NEW GUINEA MOTHS. 1. INTRODUCTION (LEPIDOPTERA)

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Abstract.—This is the first in a series of papers providing taxonomic data in support of ecological and biogeographic studies of moths in New Guinea. The primary study is an extensive inventory of the caterpillar fauna of a lowland rainforest site near Madang, Papua New Guinea, from 1994–2001. The inventory focused on the Lepidoptera community on 71 woody plant species representing 45 genera and 23 families. During the study, 46,457 caterpillars representing 585 species were sampled, with 19,660 caterpillars representing 441 species reared to adults. This introductory contribution is intended to provide background on the project, including descriptions of the study site, sampling methods, and taxonomic methods.

Key Words: Malesia, Papua New Guinea, Lepidoptera, biodiversity, rearing, community ecology

A very large portion of tropical biodiversity consists of herbivorous insects, and among them, Lepidoptera are among the most amenable to study. To better understand the structure and maintenance of tropical biodiversity, we undertook a series of related inventories of Lepidoptera in New Guinea. Our most extensive data set is an inventory of the caterpillar fauna of lowland rainforests near Madang, Papua New Guinea, from 1994–2001. Our ecological analyses focus on the Lepidoptera community on 71 woody plant species representing 45 genera and 23 families near Madang. Of these species, 69 are native, while 2 species of *Piper* are not native. But for taxonomic purposes we have evaluated specimens accumulated more broadly, including the material resulting from a study focused on 10 woody plant species conducted near Wau, Papua New Guinea, in 1992 and 1993 (Basset 1996, Basset et al. 1996). This paper represents the first in a series of papers providing taxonomic documentation in support of the broader studies, and is intended to provide general background, including descriptions of the study site, sampling methods, and taxonomic methods.

During 2002, we sampled an additional 19 woody plant species near Madang, bringing the total sampling universe to 90 species representing 58 genera and 32 families. The sampling effort per plant was reduced according to the guidelines in Novotny et al. (2002c). The insects from these surveys are still being analyzed. At the time of this writing, the Madang study is being expanded to include montane sites and a series of lowland sites, and material from these studies will be discussed and described in later papers in this series. Sampling began at our first montane site in June 2001 in primary and secondary forests and partially deforested landscape around Mu Village near Kundiawa town in Chimbu Province (145°02′E, 6°05′S, 1,800 m).

MATERIALS AND METHODS

Madang Study Area

The study area is situated in Madang Province, Papua New Guinea, extending from the coast to the slopes of the Adelbert Mountains. Average annual rainfall in this area is 3,558 mm, with a moderate dry season from July to September; mean air temperature is 26.5 °C (McAlpine et al. 1983). The area is covered with species-rich evergreen rainforest (152 species of woody plants with diameter at breast height ≥5 cm per hectare; Laidlaw et al., in press). Fieldwork was concentrated in primary and secondary lowland forests near Baitabag, Ohu, and Mis villages, and in a coastal area near Riwo Village (145°41–8′E, 5°08–14′S, ca. 0–200 m). Specific localities are Baitabag (145°47′E, 5°08′S, ca. 100 m), Ohu (145°41′E, 5°14′S, ca. 200 m), Mis (145°47′E, 5°11′S, ca. 50 m), Riwo Village (145°48′E, 5°09′S, 0 m).

Madang Plant Sampling

Seventy-one species of trees and shrubs from 45 genera and 23 families (see appendix), including 15 species of *Ficus* and 1 species of *Artocarpus* (Moraceae), 6 species of *Macaranga* and 9 species representing 9 other genera of Euphorbiaceae, 4 species of *Psychotria* and 12 species representing 12 other genera of Rubiaceae, 3 species of *Syzigium* (Myrtaceae), 3 species of *Piper* (Piperaceae) and 18 species representing 18 other families of flowering plants, were selected for the study of their associated caterpillars. Moraceae, Euphorbiaceae, and Rubiaceae, which were studied in detail, are important components of lowland rainforest flora in the Madang area and elsewhere in New Guinea (Oatham and Beehler 1998). The five genera represented by multiple species are among the most important ones in local rainforests, with combined diversity of 579 species in New Guinea (Höft 1992). This selection of families includes all main lineages of flowering plants, viz. gymnosperms, monocotyledons, basal eudicots, euasterids and eurosids (APG 1998). Further, locally common plants from all main habitats within the study area, including early and late stages of forest succession as well as riverine and seashore habitats, were represented (Leps et al. 2001).

Plants were identified by Wayne Takeuchi at Lae Herbarium and many of them were subsequently verified by the best available international specialists. Plant vouchers are deposited in Bishop Museum (BISH), Rijksherbarium (L), Lae Herbarium (LAE) and Smithsonian Institution (US) (herbarium acronyms follow Holmgren et al. 1990).

Madang Insect Sampling and Rearing

All externally feeding caterpillars (Lepidoptera), including leafrollers and leaftiers, were collected by hand from foliage. During each sampling occasion, a collector spent one day walking throughout the study area searching the foliage of the target tree species for caterpillars. The sampling included only more accessible branches, i.e., those which could be reached easily by climbing or reached from the ground. Numerous trees from various parts of the study area were sampled during each sampling occasion. The number of tree inspections, that is, a particular tree sampled at a particular time, was recorded, as well as the approximate area of the foliage sampled. Each tree species was sampled continuously for the period of at least one year between July 1994 and December 2001. Sampling effort was equal for all plant species and amounted to 1,500 m^2 of foliage area examined per species, while the number of tree inspections exceeded 1,000 per plant species. This sampling effort represented approximately 2,000 person-days of fieldwork. In the laboratory, each caterpillar was provided with fresh leaves of the plant species from which it was collected, and was reared to an adult whenever possible. Only the specimens that fed were considered in the analyses. Caterpillars and adults were assigned to morphospecies. Morphospecies were assigned seven character codes as permanent identifiers—four letters representing the family and three digits—which remain unchanged even if the field identification of the family was incorrect.

Our sampling of the 71 plant species produced 46,457 caterpillars representing 585 species, with 19,660 caterpillars representing 441 species reared to adults. Most of the field activities were carried out by parataxonomists, as described in Basset et al. (2000). The numbers reported in our analytical papers are often lower, because various analyses included only a subset of the plant species or were adjusted to equalize sample size per host plant.

In addition to the basic locality data and adult morphospecies code, standard labels including caterpillar morphospecies, host plant name, host plant abbreviation, and specimen number, were affixed to each specimen. The caterpillar morphospecies code begins with "CAT" and is used on specimens after 1995. The original host plant identification on the label sometimes has changed with further study, so should be used with care. For this reason, beginning in 1996, the labels include a three letter host plant abbreviation that does not change with subsequent identifications. Individual specimen numbers are assigned to all specimens reared to adults. Early specimens bear numbers in Bishop Museum database series, while later specimens bear numbers in Smithsonian database series—the use of Bishop Museum and Smithsonian on the labels provides a unique specimen number and does not in itself identify ownership of the specimen (e.g., Thompson 1994).

All data regarding specimens, their rearing status, morphospecies numbers, and identifications, along with images of insects and hosts, are recorded in a custom Access database, described in Basset et al. (2000). Background data and images are available at www.nmnh.si.edu/new_guinea.

Our taxonomic studies also incorporate material reared near Wau, Papua New Guinea by Yves Basset and assistants during the precursor to the Madang project in 1992–1993 (Basset et al. 1996). Morphospecies numbers for these specimens are distinguished by beginning with "LE." The plants from that study were identified by Robert Höft and vouchers are deposited at LAE and L.

Insect Identification

In the laboratory, the morphospecies concepts were confirmed by disection of genitalia (Clarke 1941, Robinson 1976) and examination of other characters. Identifications were made using relevant literature, but especially by comparison to the collections of Smithsonian National Museum of Natural History, Washington (USNM), Bishop Museum, Honolulu (BPBM), and especially the rich historic collections of The Natural History Museum, London (BMNH), as well as less frequent comparisons to collections of Australian National Insect Collection, Canberra (ANIC) and Nationaal Natuurhistorisch Museum, Leiden (RMNH), and types in other collections. Because most of the types of New Guinea moths are at BMNH, it has been the critical resource, and we are especially indebted to their staff, as well as research associates J.D. Holloway and M. Shaffer, for unlimited access.

General taxonomic context is provided by Holloway et al. (2001), although we follow Kristensen (1998) in recognizing Crambidae as a family. For macrolepidoptera, the ongoing series "Moths of Borneo" (Holloway 1984–present) provides a vital foundation. For pyraloids and microlepidoptera, Robinson et al. (1994) and Diakonoff (1952–1955) provide a general context. Nielsen et al. (1996) provide a taxonomic framework for the Australian fauna that has been very helpful. Gressitt and Szent-Ivany (1968) provide a bibliography of Lepidoptera systematics literature for New Guinea, now updated by us and available online at www.nmnh.si.edu/new_guinea.

Taxonomic characters, and definitions of genera and species, follow those in general use in Lepidoptera (e.g., Miller 1994), as well as specialist literature as available. The reviews of many families in "Moths of Borneo" have been especially important in guiding generic and specific concepts. Because our immediate need is identification of the reared species, we often verified identifications by dissection of type specimens, but have not reviewed the variability across the entire geographical range of the species. Cytochrome oxidase I (COI) sequences, DNA barcodes of Hebert et al. (2003), follow the protocols outlined in Hebert et al. (2003). The primary set of Lepidoptera vouchers are deposited in USNM, with representatives in the National Agricultural Research Institute (Port Moresby), BPBM, and other collections as appropriate.

Other Material

The historic collections of USNM, BPBM, and especially BMNH (Frodin and Gressitt 1982) provided the context for the Madang collections. USNM collections include material collected in Irian Jaya by Syuti Issiki May–August 1936, and in Papua New Guinea by Gary Hevel in December 1976, Scott Miller and Pamela Miller in July–August 1983, and Vitor Becker in September–October 1992. The BMNH collection is especially rich because of a series of excellent collectors sent to New Guinea by Walter Rothschild for the Tring Museum (Rothschild 1983), and also includes many vouchers from agricultural and forestry projects (e.g., Bigger 1988).

In addition to the general collections at BPBM (Frodin and Gressitt 1982) and material collected by Larry Orsak around Wau and Madang in the early 1990s, there is an important collection of Geometroidea assembled by the late J. J. H. Szent-Ivany. From 1968 to 1971, and again in 1974, Szent-Ivany collected Geometroidea at light and by rearing around Wau Ecology Institute, Papua New Guinea. He assembled a collection of some 300 species (listed in Gressitt and Nadkarni 1978: 83–88) which is now at BPBM. Szent-Ivany identified these during an extended visit to BMNH. Unfortunately, little of his rearing data have been published, and many of the reared specimens remain cryptically labelled.

DISCUSSION

A prerequisite to investigation of the ecology of species-rich insect taxa in diverse habitats such as lowland tropical rain forests is a large sample size. Our sampling generated data on a scale that has rarely been achieved in the tropics (see Janzen 1988, Janzen and Gauld 1997, Janzen 2003 for a similar exercise in Costa Rica). Our data are now being used for a series of taxonomic (e.g., Holloway and Miller 2003) and ecological analyses (e.g., Novotny et al. 2002a, b, c). Some of the ecological conclusions are reviewed below.

Individual host-plant species sustained from 9 to 75 (median 25) species of caterpillars. Caterpillar communities were strongly dominated by a single or few species. The single most common species typically represented 52% of individuals and 50% of biomass while the five most common species represented >80% of individuals and biomass in the entire community (Novotny et al. 2002c). In addition to these dominants, each community included a large number of very rare species (Novotny and Basset 2000). Despite significant sampling effort, the species accumulation curves for individual host plant species did not approach an asymptote which suggests that the total species richness of caterpillar communities was not sampled (Novotny et al. 2002c).

Caterpillars were mostly specialized to a single plant family, and within families to a single genus, while capable of feeding on multiple congeneric hosts (Novotny et al. 2002b). Only 15% of the caterpillar species feeding on *Ficus, Macaranga,* and *Psychotria* strongly preferred a single host species (Novotny et al. 2002a), but even among these species, none was strictly monophagous. Thus, it is conceivable that no, or very few, genuinely monophagous caterpillars feed on speciose plant genera in rain forests. A large overlap among caterpillar communities on congeneric plants means that the total number of species feeding on speciose plant genera is relatively small, in comparison with their size. These differences, in combination with low host specificity of herbivores with respect to congeneric plants, suggest that the average overlap among herbivore communities on tropical trees may be higher than on temperate trees (Novotny et al. 2002a).

Caterpillar communities were not seasonal, and the majority of species were present almost continuously throughout the year (Novotny et al. 2002c). Community composition was also constant spatially over distances <20 km (Novotny et al. 2002c). The dominance of caterpillar communities by a small number of species, which also exhibited low spatial and temporal variability, permitted robust and reliable estimates of community composition and between-community similarity from small samples, typically <300 individuals per host plant. In contrast, even considerably larger samples were not sufficient for estimates of community species richness (Novotny et al. 2002c).

The analyses produced from these data show the importance of large samples collected over multiple years in understanding the structure of tropical insect communities. These large samples have only been logistically feasible with a team approach, utilizing the skills of parataxonomists, ecologists, and systematists.

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APPENDIX

Full list of the 90 species of plants sampled near Madang, alphabetically by family. The three letter code is used on insect specimen labels and allows positive association with the correct name in case the plant identification has changed from the original identification. Novotny et al. (2002b) provided a phylogeny for 45 of these species.

Family	Name	Abr
Agavaceae	*Cordyline terminalis* P. Beauv.	COR
Agavaceae	*Dracaena angustifolia* Roxb.	DRA
Apocynaceae	*Tabernaemontana aurantica* Gaud.	TAB
Araliaceae	*Osmoxylon sessiliflorum* (Lauterb.) W.R. Philipson	OSM
Arecaceae	*Hydriastele microspadix* (Becc.) Burret	ARE
Bignoniaceae	*Spathodea campanulata* (L.) Kunth.	SPA
Caesalpiniaceae	*Maniltoa* cf. *plurijuga* Merrill & Perry	MAN
Euphorbiaceae	*Breynia cernua* (Poir.) Muell. Arg.	BRE
Euphorbiaceae	*Codiaeum ludovicianum* Airy Shaw	COD
Euphorbiaceae	*Endospermum labios* Schodde	END
Euphorbiaceae	*Excoecaria agallocha* L.	EXC
Euphorbiaceae	*Homalanthus novoguineensis* (Warb.) K. Schum.	HOM
Euphorbiaceae	*Macaranga aleuritoides* F. Muell.	MAA
Euphorbiaceae	*Macaranga bifoveata* J.J. Smith	MAP
Euphorbiaceae	*Macaranga brachytricha* Airy Shaw	MAF
Euphorbiaceae	*Macaranga densiflora* Warb.	MAD
Euphorbiaceae	*Macaranga novoguineensis* J.J. Smith	MAU
Euphorbiaceae	*Macaranga quadriglandulosa* Warb.	MAQ
Euphorbiaceae	*Mallotus mollissimus* (Geisel.) Airy Shaw	MAL
Euphorbiaceae	*Melanolepis multiglandulosa* (Reinw. ex Bl.) Reichb.f. & Zoll.	MEL
Euphorbiaceae	*Phyllanthus lamprophyllus* Muell. Arg.	PHY
Euphorbiaceae	*Pimelodendron amboinicum* Hassk.	PIM
Euphorbiaceae	*Eupomatia laurina* R. Br.	EUP
Fabaceae	*Pterocarpus indicus* Willd.	PTE
Flacourtiaceae	*Casearia erythrocarpa* Sleum.	CAS
Gnetaceae	*Gnetum gnemon* L.	GNE
Heliconiaceae	*Heliconia papuana* W.J. Kress	HEL
Lecythidaceae	*Barringtonia* sp.	BAR
Leeaceae	*Leea indica* Merrill	LEE
Loganiaceae	*Neuburgia corynocarpa* (A.Gray) Leenh.	NEU
Malvaceae	*Hibiscus tiliaceus* L.	HIB
Malvaceae	*Sterculia schumanniana* (Lauterb.) Mildbr.	STR
Malvaceae	*Trichospermum pleiostigma* (F. Muell.) Kostermans	TRI
Meliaceae	*Aglaia* cf. *cucullata* (Roxb.) Pellegr.	AGL
Monimiaceae	*Kibara* cf. *coriacea* Hook.f. & Thoms.	STG
Moraceae	*Artocarpus communis* J.R. et G. Forst.	ART
Moraceae	*Ficus bernaysii* King	BER
Moraceae	*Ficus botryocarpa* Miq.	BOT
Moraceae	*Ficus conocephalifolia* Ridley	CON
Moraceae	*Ficus copiosa* Steud.	COP
Moraceae	*Ficus dammaropsis* Diels	DAM
Moraceae	*Ficus erythrosperma* Miq.	ERY
Moraceae	*Ficus gul* K. Schum. & Laut.	GUL
Moraceae	*Ficus hispidioides* S. Moore	HIS
Moraceae	*Ficus microcarpa* L.	MIC
Moraceae	*Ficus mollior* F. Meull. ex Benth.	MOL
Moraceae	*Ficus nodosa* Teysm. & Binn.	NOD
Moraceae	*Ficus pachyrrhachis* K. Schum. & Laut.	PAR
Moraceae	*Ficus phaeosyce* Laut. & K. Schum.	PHA

APPENDIX

Continued.

Family	Name	Abr
Moraceae	*Ficus pungens* Reinw. ex Blume	PUN
Moraceae	*Ficus septica* Burm.	SEP
Moraceae	*Ficus subtrinervia* Laut. & K. Schum. (= *F. pachystemon* Warb.)	PAS
Moraceae	*Ficus ternatana* Miq.	TER
Moraceae	*Ficus tinctoria* Forst.	TIN
Moraceae	*Ficus trachypison* K. Schum.	TRA
Moraceae	*Ficus variegata* Blume	VAR
Moraceae	*Ficus wassa* Roxb.	WAS
Myristicaceae	*Myristica* cf. *sepicana* D.B. Foreman	MYL
Myrtaceae	*Syzigium longipes* (Warb.) Merrill & Perry	SSW
Myrtaceae	*Syzygium* sp. 1	SRS
Myrtaceae	*Syzygium* sp. 2	SRB
Piperaceae	*Piper aduncum* L.	PAD
Piperaceae	*Piper macropiper* Pennant	PMV
Piperaceae	*Piper umbellatum* L.	PUB
Rubiaceae	*Amaracarpus nymanii* Valeton	AMA
Rubiaceae	*Dolicholobium oxylobum* K. Schum.	DOL
Rubiaceae	*Gardenia hansemannii* K. Schum.	GAR
Rubiaceae	*Morinda bracteata* Roxb.	MOR
Rubiaceae	*Mussaenda scratchleyi* Wernh.	MUS
Rubiaceae	*Nauclea orientalis* (L.) L.	SAR
Rubiaceae	*Neonaclea clemensii* Merrill & Perry	NEO
Rubiaceae	*Pavetta platyclada* Lauterb. & K. Schum.	PAV
Rubiaceae	*Psychotria leptothyrsa* Miquel	PSF
Rubiaceae	*Psychotria micralabastra* (Laut. & K. Schum.) Val.	PSM
Rubiaceae	*Psychotria micrococca* (Laut. & K. Schum.) Val.	PSS
Rubiaceae	*Psychotria ramuensis* Sohmer	PSL
Rubiaceae	*Randia schumanniana* Merrill & Perry	MEN
Rubiaceae	*Tarenna buruensis* (Miq.) Val.	TAR
Rubiaceae	*Timonius timon* (Spreng.) Merrill	TIT
Rubiaceae	*Versteegia cauliflora* (K. Schum. & Laut.)	VER
Rutaceae	*Lunasia amara* Blanco	LUN
Sapindaceae	*Pometia pinnata* Forster	POM
Sapotaceae	*Pouteria* sp.	POU
Sterculiaceae	*Kleinhovia hospita* L.	KLE
Ulmaceae	*Celtis philippensis* Blanco	CEL
Urticaceae	*Leucosyke capitellata* (Poir.) Wedd.	LEU
Verbenaceae	*Geunsia farinosa* Blume	GEU
Verbenaceae	*Premna obtusifolia* R.Br.	PRE
Verbenaceae	*Teijsmanniodendron* sp.	TEI
Zingiberaceae	*Hornstedtia scottiana* (F. Muell.) K. Schum.	HOR

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STUDIES ON NEW GUINEA MOTHS. 2. DESCRIPTION OF A NEW SPECIES OF *XENOTHICTIS* MEYRICK (LEPIDOPTERA: TORTRICIDAE: ARCHIPINI)

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Abstract.—***Xenothictis gnetivora*, new species,** from Papua New Guinea, is described and illustrated based on morphological characters and DNA barcode. The type series consists of 124 specimens reared from leaf-rolling larvae primarily on *Gnetum gnemon* L. (Gnetaceae), but also on *Celtis philippensis* Blanco (Celtidaceae), *Sterculia schumanniana* (Laut.) Mildbr. (Sterculiaceae), and other plants during a multi-year rearing project (1995–2001). The five previously described species of *Xenothictis* are from Australia and Melanesia.

Key Words: Malesia, Melanesia, Papua New Guinea, genitalia, pupa, *Gnetum gnemon, Celtis philippensis, Sterculia schumanniana*

The archipine genus *Xenothictis* Meyrick includes five previously described species distributed from Australia north and east to New Caledonia, Lifou (northeast of New Hebrides), Vanuatu (New Hebrides), and Fiji (see Appendix). Beyond brief original descriptions of the species, little has been published on the genus. Clarke (1958) illustrated the adult and male genitalia of *X. atriflora* Meyrick and its synonym, *X. melananchis* (Meyrick). Diakonoff (1961) illustrated the adult and male genitalia of *X. noctiflua* Diakonoff, presented brief comments on Meyrick's (1910) description of the genus, and commented on the relationship with his new genus *Xeneda* Diakonoff. Horak et al. (1996) transferred *Barnardiella sciaphila* Turner to *Xenothictis* and synonymized *Barnardiella* Turner with the latter.

Holloway (1979: 225) provided the following comment: "There is one group [of Tortricinae] that appears to have radiated within New Caledonia and spread to other areas of the Pacific. The species are assigned at present to the closely related genera *Xenothictis* and *Xeneda* and are being studied by Mr. K. Tuck [The Natural History Museum, London] . . . who has suggested they might be congeneric. The two genera together contain at least six species in New Caledonia, two in the Loyalties and one in each of the New Hebrides and Fiji." In addition, there are several undescribed species from New Caledonia in the collection of the National Museum of Natural History, Smithsonian Institution.

During a recent (1995–2001) insect ecology project in Papua New Guinea (Basset et al. 2000; Novotny et al. 2002a, b, c), a large series of an undescribed species of *Xenothictis* was reared from several plants. The purposes of this paper are to name the

Figs. 1–2. Male and female of *Xenothictis gnetivora*. 1, Male. 2, Female.

new species, provide descriptions and illustrations of adult facies, male and female genitalia, and immatures, and to present a list of the described species of the genus. Although considerable material, including other new species, has accumulated in major museums worldwide, it is not within the purview of this paper to review this information or describe additional new species. We have not seen any other species of *Xenothictis* from New Guinea.

Materials and Methods

General field and laboratory methods for the project are described in Miller et al. (2003) and Novtony et al. (2002a, b, c). We examined 124 pinned specimens of the new species, all of which were obtained during the rearing project in Papua New Guinea. Text descriptions are composite, based on all available specimens. Forewing measurements were made with an ocular micrometer under low power of a Leica MZ12© dissecting microscope. Terminology for genitalia structures follows Horak (1984). Cytochrome oxidase I (COI) sequences, DNA barcodes of Hebert et al. (2003), follow the protocols in Hebert et al. (2003).

Systematics

Xenothictis gnetivora Brown, Miller, and Horak, new species

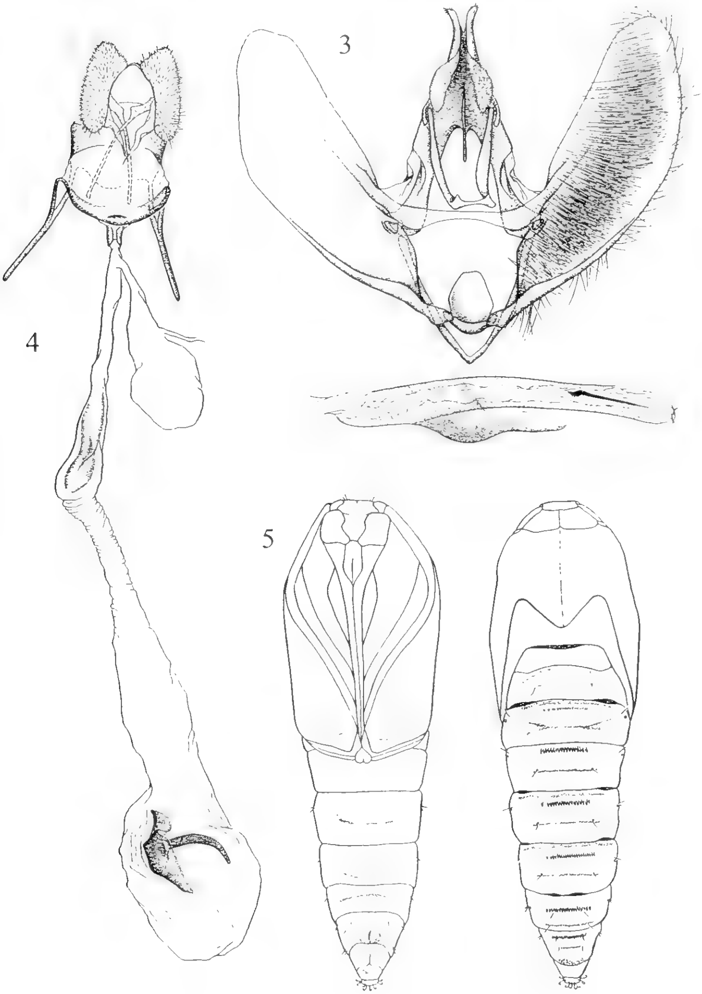
(Figs. 1–9)

Diagnosis.—Superficially, adults of *X. gnetivora* are characterized by a grayish brown forewing, finely and faintly reticulated with pale reddish brown throughout. Males have a bold, contrasting, blackish brown, short, slightly curved fascia originating near mid-dorsum, terminating near the middle of the discal cell; females lack the fascia. The male genitalia of *X. gnetivora* are distinguished by the narrow tegumen, simple, obovate valva with costa and ventral margin subparallel and with extremely slender sacculus not separated by a shallow emargination from rest of valva, slender gnathos arms with cross-bar close to tips, a narrowly ovate juxta, and a long, slender aedeagus with 1–2 cornuti. Among the tortricids reared by the project team near Madang, it is distinguished by the differential coloration of the fore- and hindwings, maculation of the forewing, and the large, shiny scales on the abdomen in both sexes.

Description.—Male. *Head:* Lower frons pale tan to buff; upper frons slightly darker; vertex with overhanging tuft of scales short. Labial palpus short, ca. 1.0 times horizontal diameter of compound eye, robust, third segment very short; pale tan to buff mesally, pale reddish brown laterally. Antenna with two rows of dorsal scales per flagellomere, tan; cilia long, ca. 1.2–1.5 times width of flagellomere. Chaetosema well developed. Ocellus moderately large. Proboscis present, presumably functional. *Thorax:* Buff; tegula large, pale grayish brown. Forewing (Fig. 1) length 6.5–8.1 mm (0 = 7.7 mm; n = 10). Ground color grayish brown, finely and faintly reticulated with pale reddish brown throughout; a bold, short, slightly curved, blackish brown fascia originating near mid-dorsum, terminating near middle of discal cell; 4–5 extremely short costal strigulae from base to mid-costa; a small brown spot near mid-costa, an additional ill-defined costal spot ca. ¾ distance from base to apex; costal fold absent; without modified scales on underside. Fringe concolorous with ground color. Hindwing uniformly gray brown, without modified scales. *Abdomen:* Pale gray brown. Genitalia (Fig. 3; drawn from USNM slide 92771; 4 preparations examined) with tegumen narrow; a long, narrow, medial spine extending anterad from dorsal fusion of lateral halves of posterior portion of tegumen. Uncus moderately slender, bifurcate from base. Socius short, ca. ½ length of uncus, pendant, weakly setose. Gnathos slender, arms long, weakly undulate, arising relatively close because of narrow tegumen; slightly and gradually convergent distally; slightly upturned and joined subdistally by transverse bar, free points short. Transtilla slender, extremely weak. Valva moderately long, obovate with costa and ventral margin roughly parallel, attenuate distally, with fine hairs throughout middle portion; sacculus simple, narrow, confined to ventral edge, extending ca. ½ length of valva. Juxta a narrowly ovate plate. Aedeagus slender, ca. 9/10 length of valva, weakly curved, attenuate in distal 1/10; vesica with one or two long, slender cornuti.

Female. *Head:* Essentially as described for male, except antennal cilia short, unmodified. *Thorax:* Buff; tegula large, pale grayish brown. Forewing (Fig. 2) length 7.9–9.6 mm ($\bar{x}$ = 8.7 mm; n = 10). Ground color grayish brown, finely and faintly reticulated with pale reddish brown throughout; 4–5 extremely short costal strigulae in basal ½; a small brown spot near mid-costa, an additional ill-defined spot ca. ¾ distance from base to apex. Fringe concolorous with ground color. *Abdomen:* Genitalia (Fig. 4; drawn from USNM slide 82244; 6 preparations examined). Papillae anales simple, slender slipper-shaped, unmodified. Sterigma an extremely slender, broadly U-shaped band, sometimes with patch of sclerotization immediately posterad of ostium. Ductus bursae extremely long, narrow, gradually widening into corpus bursae; colliculum present immediate anterad of ostium; an irregularly-shaped sclerotized patch ca. ⅓ distance from ostium to junction of ductus bursae and corpus bursae, at which point the ductus bursae is curved or weakly bent. Corpus bursae simple, ovoid, non-spiculate, with signum typically archipine with a long, strong, internal curved spine from large, strongly sclerotized, elongate diamond-shaped process on the surface of the corpus bursae.

Pupa (Fig. 5). Typically tortricine without modified head (Sohn 2002); no conspicuous sculpturing; abdomen with one



Figs. 3–5. Genitalia and pupa of *Xenothictis gnetivora*. 3, Male genitalia, with valva spread and aedeagus removed (below genitalia capsule). 4, Female genitalia. 5, Pupa, venter on left, dorsum on right.

row of spines dorsally on A3 and two rows on A4–8 in both sexes, posterior row conspicuously weaker, extremely weak on A4; spines on A9 as a small irregular patch at posterior edge of segment; cremaster well developed with lateroposterior horns; 4 pairs of long, hooked bristles, two laterally and two mesally.

Gene sequence.—A male and a female, specimens 109973 and 120720, possessed identical COI-5′ sequences (DNA barcodes), which have been deposited in GenBank under the accession numbers AY313945 and AY313944, respectively.

Type material.—Holotype, ♂, Papua New Guinea, Madang Province, Ohu Village, 5 July 1999, reared from *Gnetum gnemon*, by the project team (Novotny, Basset, Cizek, Auga, Boer, Dal, Hiuk, Isua, Kasbal, Kutil, Manumbar & Molem). Deposited in National Museum of Natural History, Washington, D.C. Project specimen 107091.

Paratypes, 51 ♂, 72 ♀. Papua New Guinea, Madang Province, Mis, Baitabag, and Ohu Villages, reared during 1995 to 2001 by the project team. All labeled with project morphospecies TORT039 (or one of the synonyms, TORT101 and TORT119), and including the following project specimens: 64808, 86216, 86817, 88484, 88170, 87565, 87554, 87700, 87545, 87719, 87631, 87695, 87672, 87285, 87480, 87292, 87454, 109523, 109529, 109527, 109538, 109521, 109542, 109130, 109317, 107600, 107359, 107596, 107461, 107454, 107370, 107419, 107598, 107323, 107364, 107365, 107470, 108953, 108955, 108867, 108915, 108857, 107931, 107987, 107870, 107864, 108796, 107829, 108918, 107849, 106999, 106960, 106990, 106973, 107037, 106938, 106834, 108459, 108262, 108482, 109973, 108367, 109995, 108585, 108579, 108454, 108945, 121278, 121049, 120702, 121101, 120737, 120577, 120995, 121425, 120977, 120869, 122699, 122951, 122449, 122346, 121662, 122474, 122587, 122485, 122383, 122080, 122591, 122058, 122477, 121602, 122081, 122400, 122374, 121579, 122578, 122762, 122024, 122023, 122430, 121603, 122510, 121606, 125410, 125185, 124501, 125172, 125182, 124979, 124887, 124820, 124880, 124597, 124648, 125489, 124661, 125116, 124757, 125024, 127025, 126975, 195727, and 195728. Project specimens 86216 and 86817 are in the PNG reference collection in the laboratory in Madang, and 195727 and 195728 are in the Australian National Insect Collection, CSIRO, Canberra. Paratypes will be deposited in the following institutions: Bishop P. Berenice Museum, Honolulu, Hawaii, U.S.A.; The Natural History Museum, London, England; Australian National Insect Collection, CSIRO, Canberra; Nationaal Natuurhistorisch Museum, Leiden, The Netherlands; National Agriculture Research Institute, Port Moresby, Papua New Guinea; Museum Zoologi Bogor, Cibinong, Indonesia; and National Museum of Natural History, Smithsonian Institution, Washington, D.C., U.S.A.

Distribution and biology.—All specimens are from a 25 km^2 area, including the villages of Mis, Baitabag, and Ohu, near Madang in Madang Province, Papua New Guinea. Our project encountered 224 larvae and successfully reared 124 adults (see Miller et al. 2003 and Novotny et al. 2002a for methods). The species feeds primarily on *Gnetum gnemon* (n = 188) (Figs. 6–7), *Sterculia schumanniana* (Laut.) Mildbr. (Stericuliaceae) (n = 25), and *Celtis philippensis* Blanco (Celtidaceae) (n = 5). We also reared adults twice from *Ficus nodosa* Teysm. & Binn (Moraceae) and once each from *Ficus variegata* Blanco, *Artocarpus communis* J. R. Forst. & G. Forst. (Moraceae), *Psychotria micralabastra* (Laut. & Schum.) Val. (Rubiaceae), and *Leucosyke capitellata* (Poir.) Wedd. (Urticaceae). Because of the low occurrence of larvae compared to the density of sampling, we do not consider the last five "normal" hosts (see Novotny et al. 2002a for discussion). Larvae were collected year-round.

Etymology.—The species name is a noun in apposition, derived from the genus of the most common larval host (*Gnetum*) and the Latin "to eat" (*vorare*).

Discussion.—*Xenothictis* are characterized by slight to moderate sexual dimorphism in forewing pattern and length; a venation with all veins separate and chorda present or at least indicated in forewing, in hindwing Rs an M1 closely approximated

Figs. 6–7. Live larvae of *Xenothictis gnetivora* on *Gnetum gnemon*. 6, On leaf surface. 7, In leaf roll.

to connate, M2 somewhat distant from connate M3 and CuA1; a very long labial palpus with a greatly enlarged, triangular third segment (not so in *X. gnetivora*); a ciliate antenna in male; a bifurcate uncus; and long, subparallel gnathos arms joined by a cross-bar. While the male genitalia of *Xenothictis* are moderately plesiomorphic, with the valva, transtilla, and aedeagus little modified, the well developed signum of the female genitalia unambiguously associates the genus with Archipini. The absence of the second row of spines on the dorsum of abdominal segment 3 of the pupa has not previously been reported in Tortricidae and may represent a synapomorphy for the genus.

Xenothictis gnetivora differs from all congeners by its short, unmodified labial palpus in both sexes. However, wing venation, wing pattern, and genitalia of both sexes leave no doubt that *X. gnetivora* forms a monophyletic group with all other *Xenothictis* species. Its simple valva is more plesiomorphic than that of its three congeners with known males (*X. atriflora, X. noctiflua,* and *X. sciaphila*) and is nearly identical to that of the Australian genus *Thrincophora* Meyrick. Further apomorphies linking *Xenothictis* to *Thrincophora* and its sister genus *Acropolitis* Meyrick are overall very similar female genitalia and the same tegumen, juxta, aedeagus, and transtilla structure, although the latter is dentate in *Thrincophora* and *Acropolitis.* The short labial palpus of *X. gnetivora* is similar to that of *Thrincophora* and *Acropolitis,* suggesting that it represents the plesiomorphic character state for the group as a whole. Given the combination of morphological characters present in *X. gnetivora,* it is even more doubtful that *Xeneda,* with its modified, elongate labial palpus, should be treated as a separate genus simply on the strength of the two patches of bristles on its uncus base, leaving *Xenothictis* parapyletic and without a generic synapomorphy. It is more likely that the patches of bristles represent a species-level autapomorphy.

The rearing data on the leaf roller *X. gnetivora* are the first comprehensive biological information for the genus *Xenothictis.* There is only one host record in the Australian National Insect Collection for the Australian *X. sciaphila,* with its larva found in or on the fruit of *Musa sapientum* at Montville and Eumundi, Queensland, June 1962 and August–September 1963 by D. A. Ironside.

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Our colleagues Yves Basset, Vojtech Novotny, and George Weiblen collaborated at all stages of the project. Kevin Tuck assisted in identifying this species and commented on an early draft of the manuscript. Illustrations were skillfully prepared by Karolyn Darrow, Department of Systematic Biology, National Museum of Natural History, Washington, D.C. Parataxonomists John Auga, Willian Boen, Chris Dal, Samuel Hiuk, Brus Isua, Martin Kasbal, Richard Kutil, Markus Manumbor, and Kenneth Molem assisted with most aspects of the project in PNG. Numerous collectors, acknowledged elsewhere, assisted with insect sampling. The landowners Kiatik Batet, Hais Wasel, and Sam Guru kindly allowed us to collect on their lands. Plant taxonomists are acknowledged in Miller et al. (2003). DNA barcodes were provided by Paul Hebert and Erin Penton, University of Guelph. The following provided helpful reviews of the manuscript: F. Christian Thompson and David Smith, Systematic Entomology Laboratory, USDA, National Museum of Natural History, Washington, D.C., U.S.A; and Kevin Tuck, The Natural History Museum, London, England. The project has been funded by U.S. National Science Foundation (DEB-94-07297, 96-28840, 97-07928, 02-11591), National Geographic Society, Czech Academy of Sciences (GAAV 651106), Czech Ministry of Education (ES 041), Czech Grant Agency (653112), International Centre of Insect Physiology and Ecology (Nairobi), and Otto Kinne Foundation. The Smithsonian Institution, Bishop Museum, and The Natural History Museum (London) provided critical facilities for the taxonomic work.

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APPENDIX

Xenothictis Meyrick

Xenothictis Meyrick 1910, Proc. Linnean Soc. N. S. Wales 35: 279. Type species: *Xenothictis paragona* Meyrick 1910, by original designation.

Barnardiella Turner 1925, Trans. Roy. Soc. South Austral. 49: 49. Type species: *Barnardiella sciaphila* Turner, 1925, by original designation.

atriflora Meyrick 1930 (*Xenothictis*), Exotic Microlepid. 3: 609. TL: Fiji (Vunidawa). HT (male): The Natural History Museum, London.

melananchis Meyrick 1933 (*Xenothictis*), Exotic Microlepid. 4: 424. TL: Fiji (Vunidawa). HT (male): The Natural History Museum, London.

noctiflua Diakonoff 1961 (*Xenothictis*), Ann. Soc. Entomol. France 130: 66. TL: New Hebrides (Vanuatu). HT (male): Muséum National d'Historie Naturelle, Paris.

paragona Meyrick 1910 (*Xenothictis*), Proc. Linnean Soc. N. S. Wales 35: 280. TL: Lifu. HT (female): The Natural History Museum, London.

sciaphila (Turner 1925) (*Barnardiella*), Trans. Roy. Soc. South Austral. 49: 50. TL: Australia (Queensland, Toowoomba). HT (male): Australian National Insect Collection, Canberra, Australia.

semiota Meyrick 1910 (*Xenothictis*), Proc. Linnean Soc. N. S. Wales 35: 280. TL: Lifu. HT (female): The Natural History Museum, London.

Xeneda Diakonoff

Xeneda Diakonoff 1961, Ann. Soc. Entomol. Fr. 130: 62. Type species: *Xeneda coena* Diakonoff, 1961, by original designation.

coena Diakonoff 1961 (*Xeneda*), Ann. Soc. Entomol. Fr. 130: 64. TL: New Caledonia (environs of Noumea). HT (male): Muséum National d'Historie Naturelle, Paris.

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NOTE

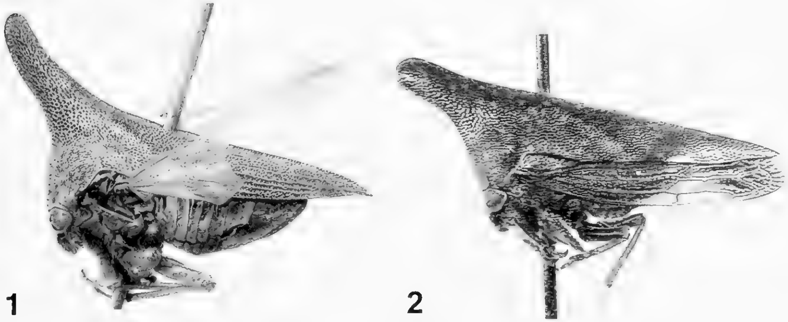
Aconophora lineosa Walker 1858, New Junior Synonym of *Thelia bimaculata* (Fabricius 1794) (Hemiptera: Membracidae)

Aconophora lineosa Walker 1858 is here considered a junior synonym of *Thelia bimaculata* (Fabricius 1794), **new synonymy**. In July 2001, MSW and LLD examined the holotype of *Aconophora lineosa* Walker 1858: 134 (see Walker's "Introduction," page not numbered, for an explanation on the number of specimens he examined) at The Natural History Museum, London (see also Broomfield 1971: 359), and concluded it is a female of *T. bimaculata* (Fig. 1). Thus, *A. lineosa* Walker 1858 is a junior synonym of *T. bimaculata* (Fabricius 1794), not a junior synonym of *Platycotis vittata* (Fabricius 1803), as currently placed (McKamey 1998). The holotype was nevertheless correctly placed under *T. bimaculata* at The Natural History Museum (see key below), but with no indication of who first noted the apparent synonymy. Van Duzee (1908: 124) doubtfully placed the species within *Platycotis* Stål 1869 as "? *lineosa* Walker [sic: for (Walker)]." Later Funkhouser (1923: 110) placed the species as a synonym of *P. vittata* (Fabricius), but noted that the type could not be located in the British Museum collection. Based on Funkhouser's placement, this species was not examined during Dietrich and Deitz's (1991) revision of the Neotropical tribe Aconophorini (Membracinae). Although often similar to *Thelia* Amyot and Serville 1843 in pronotal shape, members of the genus *Platycotis* have distinctive club-shaped hind tibiae.

Thelia is a Nearctic genus of the tribe Smiliini (Smiliinae). It includes only two species (see key), both known from Canada and the United States (Kopp and Yonke 1974 [U.S. distribution maps], McKamey 1998, Maw et al. 2000, Wallace et al. 2003).

KEY TO SPECIES OF *THELIA*

1. Pronotum (Fig. 1) distinctly striate posterolaterally, its median horn directed anterodorsally at slight angle from pronotum (degree of angle varies); pronotal color of female mostly grayish (Fig. 1), of male dark brown to black with



Figs. 1–2. *Thelia*. 1, Female of *T. bimaculata* [photograph of the holotype of *Aconophora lineosa* Walker 1858 from "North America," © 2003, The Natural History Museum, London]. 2, Female of *T. uhleri* (North Carolina State University Insect Collection, Raleigh).

bright yellow stripe on each side (Wallace et al. 2003: fig. 6); on *Robinia pseudoacacia* L. (black locust) . . . . *T. bimaculata* (Fabricius)

– Pronotum (Fig. 2) not striate posterolaterally, its median horn directed anteriorly (dorsal pronotal margin straight); pronotal color (both sexes) dark without yellow stripes; on *Malus* (apple) and *Prunus americana* Marshall (wild plum) . . . . *T. uhleri* Stål

We thank M. D. Webb for providing Fig. 1 and for his hospitality during our visit to The Natural History Museum, London. This work was supported by the National Science Foundation under Grant Nos. DEB-9815867 and DEB-9978026 and by the North Carolina Agricultural Research Service.

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NOTE

First Report of *Amblyomma pseudoconcolor* Aragão (Acari: Ixodida: Ixodidae) from Bolivia, with a New Record of this Tick from the Grey Brocket Deer, *Mazama gouazoupira* (G. Fischer) (Mammalia: Artiodactyla: Cervidae)

Most of the 57 generally recognized species of *Amblyomma* known from the Neotropical Zoogeographic Region occur in humid lowlands, where they and their hosts are accessible to collectors, with the result that only seven new species in this tick genus have been described from the Neotropics during the last half century (Guglielmone et al., in press). But while the job of inventorying the Neotropical amblyommine fauna may be virtually complete, there still are large gaps in our knowledge of the biology and distribution of many species, especially those that seldom parasitize humans or domesticated animals. *Amblyomma pseudoconcolor* Aragão is representative of this problem: its preimaginal stages remain undescribed, its principal hosts are armadillos (Xenarthra: Dasypodidae), and its recorded range—Argentina, Brazil, French Guiana, Paraguay, Surinam, and Uruguay—is disjunct, an artifact of incomplete collecting (Buitendijk 1945, Boero 1957, Floch and Fauran 1958, Aragão and Fonseca 1961, Venzal et al. 2002). Contrary to most of its Neotropical congeners, *A. pseudoconcolor* is also small (male body length ≈ 3 mm) and indistinctly ornate, so that even investigators who regularly examine armadillos are likely to overlook this tick. Between 1999 and 2001, two of us (SLD and AJN) were able to collect modest numbers of *A. pseudoconcolor* (Table 1) from three species of armadillo (*Dasypus novemcinctus* L., *Euphractus sexcinctus* (L.), and *Tolypeutes matacus* (Desmarest)) examined in the vicinity of the Cerro Cortado field camp, on the boundary between the Izoceño-Guaraní (Isoso) indigenous territory and the vast Kaa-Iya del Gran Chaco National Park (Parque Nacional y Área Natural de Manejo Integrado Kaa-Iya del Gran Chaco), about 300 km southeast of the city of Santa Cruz and 25 km east of the nearest Izoceño-Guaraní community (19.31.36S, 62.18.36W). We believe that these are the first collections of *A. pseudoconcolor* ever reported from Bolivia. In addition, on 10 July 1999, SLD removed a single male of *A. pseudoconcolor* while conducting a postmortem examination of a female grey (also known as brown) brocket deer, *Mazama gouazoupira* (G. Fischer). Because armadillos and brocket deer are ecological associates in the Gran Chaco, this new host record is less surprising than it might otherwise seem.

The Chaco ecosystem surrounding Cerro Cortado field camp chiefly consists of short, dense thorn forest (3–5 m canopy, with emergents 8–15 m tall). Annual precipitation averages just 550 mm, and the dry season can last from May to December. Similar conditions prevail (though precipitation rises to 800 mm in the east) throughout the neighboring national park, which comprises 3,441,115 ha of largely virgin dry forest, and whose creation was proposed by the Izoceño-Guaraní people, with assistance from the Wildlife Conservation Society. Originally, South America's Chaco dry forest extended over 1 million km^2 of eastern Bolivia, northern Argentina, and Paraguay. This habitat type shelters a conspicuously endangered mammal fauna, including the Chacoan peccary, *Catagonus wagneri* (Rusconi), tapir, *Tapirus terrestris* (L.), Chacoan guanaco, *Lama guanicoe voglii* (Krumbiegel), jaguar, *Panthera onca* (L.), maned wolf, *Chrysocyon brachyurus* (Illiger), salt-desert cavy, *Dolichotis salinicola* Burmeister, and the armadillos *Cabassous*

Table 1. Collections of *Amblyomma pseudoconcolor* from the vicinity of Cerro Cortado field camp, near Kaa-Iya del Gran Chaco National Park, Bolivia.

MEDARKS No.*	Ticks	Host	Date	Collector
1999–0176	6 ♂	*Tolypeutes matacus* ♀	18 March 1999	S. L. Deem
1999–0175	1 ♂	*Euphractus sexcinctus* sex?	17 May 1999	S. L. Deem
1999–0010	1 ♂	*Mazama gouazoupira* ♀	10 July 1999	S. L. Deem
2000–0049	1 ♂	*Dasypus novemcinctus* ♀	18 July 2000	S. L. Deem
2001–0012	2 ♂	*Tolypeutes matacus* ♀	26 March 2001	S. L. Deem
2001–0113	1 ♀	*Dasypus novemcinctus* ♂	6 November 2001	A. J. Noss
2001–0012 (recapture)	1 ♂	*Tolypeutes matacus* ♀	9 November 2001	A. J. Noss
2001–0118	2 ♂, 2 ♀	*Tolypeutes matacus* ♀	9 November 2001	A. J. Noss
2001–0117	1 ♂	*Tolypeutes matacus* ♀	10 November 2001	A. J. Noss
2001–0116	4 ♂, 1 ♀	*Tolypeutes matacus* ♀	10 November 2001	A. J. Noss
2001–0121	6 ♂	*Tolypeutes matacus* ♂	11 November 2001	A. J. Noss
2001–0120	2 ♂	*Tolypeutes matacus* ♂	11 November 2001	A. J. Noss
2001–0115	2 ♂	*Tolypeutes matacus* ♂	24 November 2001	A. J. Noss
2001–0114	1 ♂	*Tolypeutes matacus* ♀	25 November 2001	A. J. Noss

* Medical Archives, Field Veterinary Program, Wildlife Conservation Society.

chacoensis Wetzel, *Chlamyphorus retusus* Burmeister, and *Priodontes maximus* (Kerr) (Taber et al. 1997, Noss et al. 2002).

We have no explanation for the scarcity of female *A. pseudoconcolor* on the three species of armadillo that we examined, but so little is known about the biology of this tick that no statement can safely be made concerning the prevalence or intensity of parasitization by either sex. Significantly, our collections of *A. pseudoconcolor* from armadillos were often accompanied by equal or larger numbers of *A. parvum* Aragão, a common Central and South American tick that has been reported from a wide variety of mammals (Fairchild et al. 1966) and that superficially resembles *A. pseudoconcolor* (Jones et al. 1972). Thus, while our 12 armadillos (including one recaptured animal) yielded a total of 33 specimens of *A. pseudoconcolor,* the total number of *A. parvum* removed from these hosts was 65. If *A. parvum* is usually more numerous than *A. pseudoconcolor* on Bolivian xenarthrans, then the two tick species might easily be confused and lumped as "*A. parvum,*" which could account for the absence until now of *A. pseudoconcolor* in published Bolivian tick collections.

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NOTE

First Records of Hymenopterous Larval-Pupal Parasitoids of *Anastrepha fraterculus* (Wiedemann) (Diptera: Tephritidae) in the Northwestern Province of Catamarca, Argentina

In the northwestern provinces of Catamarca, Tucumán, Salta, and Jujuy (Argentina) there are important citrus-growing areas where the native *Anastrepha fraterculus* (Wiedemann) and the exotic *Ceratitis capitata* (Wiedemann) coexist in wild and commercially grown, native and exotic fruit. However, most previous fruit fly parasitoid surveys were focused largely in citrus orchard areas of Tucumán (Hayward 1940, Fernández de Araoz and Nasca 1984, Ovruski 1995). No published reports exist on the fruit fly parasitoid fauna of Catamarca. Only a small amount of information on fruit flies has been published, mainly based on specimens caught in traps in several Departamentos of Catamarca Province (Rosillo 1953, Vattuone et al. 1999).

Based on the above, the aim of this study was to survey exotic host plant species commonly infested by both *A. fraterculus* and *C. capitata,* and to identify all larval-pupal parasitoids associated with these tephritid species in the southeastern region of Catamarca Province, as well as to determine the infestation levels in each fruit species sampled.

From November 1994 to April 1995 (rainy summer season), fruit samples from seven exotic plant species of four families were collected in family orchards and in patches of disturbed wild vegetation adjacent to citrus groves throughout the localities of La Viña (28°01′S, 65°34′W, 590 m altitude) and Sumampa (28°03′S, 65°31′W, 550 m), southeastern Catamarca. The climate of these counties is defined as temperate-humid, with a dry winter. Native vegetation is a subtropical mountain rainforest locally known as "Yungas forest" which is distributed throughout NW Argentina.

The fruit samples consisted only of fallen ripe fruit, and ranged in number from 20 to 150 fruit, depending on fruit availability. In the laboratory, each fruit was counted and weighed, then placed in closed styrofoam boxes with damp sand in the bottom as a pupation substrate. All formed pupae were removed weekly and the *A. fraterculus* and *C. capitata* pupae were separated using external pupal characters (White and Elson-Harris 1992). These pupae were transferred to plastic trays containing sterilized humid sand. Each tray was then placed inside a sealed wooden box and kept inside a room at 25 ± 1°C and 75 ± 5% relative humidity for four months. S. Ovruski identified all emerged flies and parasitoids. Voucher specimens are placed in the insect collection of the Fundación Miguel Lillo in San Miguel de Tucumán. All parasitization rates and fruit infestation levels reported here are based on the number of emerged adult flies and parasitoids, and on the number of fruit fly pupae per kg of fruit, respectively.

A total of 129 (12.8 kg) sweet oranges (*Citrus sinensis* (L.) Osbeck), 93 (11.5 kg) sour oranges (*Citrus aurantium* L.), 56 (12.7 kg) grapefruit (*Citrus paradisi* Macfadyn) (all Rutaceae), 345 (13.4 kg) peaches (*Prunus persica* (L.) Batsch), 118 (5.2 kg) plums (*Prunus domestica* L) (both Rosaceae), 231 (5.3 kg) figs (*Ficus carica* L., Moraceae), and 278 (12.2 kg) guavas (*Psidium guajava* L., Myrtaceae) were sampled. Of these fruit samples, 998 and 892 pupae of *A. fraterculus* and *C. capitata* were recovered, respectively. All the *Citrus* species and *F. carica* were only infested by *C. capitata,* whereas the *Prunus* species and *Psidium guajava* were simultaneously infested by both *A. fraterculus* and *C. capitata.* The lowest infestation rates were recorded in *C. sinensis, C. paradisi,* and *C. aurantium* (8.9, 3.7, and 2.6 pupae/kg of fruit, respectively), the largest fruit species sampled, while the highest infestation level by *C. capitata* (43.4 pupae/kg of fruit) was found in fig, the smallest fruit species sampled. In the case of the *Prunus* species, *P. persica* was mainly infested by *C. capitata* (21.8 *C. capitata* pupae/kg fruit vs 12.0 *A. fraterculus* pupae/kg fruit), whereas *P. domestica* was infested largely by *A. fraterculus* (38.5 *A. fraterculus* pupae/kg fruit vs 12.7 *C. capitata* pupae/kg fruit). The highest infestation rate by *A. fraterculus* was recorded in guava (55.3 pupae/kg fruit). In this fruit species, the infestation level by *C. capitata* was low (8.3 pupae/kg fruit). These data on fruit infestation rates add further evidence about the predominance of *C. capitata* in *Citrus* species and fig, and about the importance of *P. guajava* as principal host of *A. fraterculus* in the southeastern part of Catamarca, where the climate is warm and humid. Similar observations were made in citrus orchard areas of the northwestern province of Tucumán, where guavas are abundant in patches of wild vegetation adjacent to crops (Ovruski, Schliserman and Aluja, unpublished data).

From *C. capitata* pupae, 485 adult flies were recovered, and from *A. fraterculus* pupae, 561 adult flies and 68 hymenopterous parasitoids were obtained. The following parasitoid species were reared in association with *A. fraterculus*: *Doryctobracon areolatus* (Szépligeti), *D. brasiliensis* (Szépligeti), and *Utetes anastrephae* (Viereck) (all Braconidae, Opiinae), and *Aganaspis pelleranoi* (Brèthes) (Figitidae, Eucoilinae). Table 1 summarizes parasitoid species abundance, and parasitization rates of *A. fraterculus* based on fruit species. The three braconid species are specialized, solitary, koinobiont endoparasitoids of *Anastrepha* larvae, which are attacked inside host fruit. *Doryctobracon areolatus* and *U. anastrephae* are widely distributed in the Neotropical Region ranging from the southern United States to Argentina, whereas *D. brasiliensis* is known only from southern Brazil and Argentina (Ovruski et al. 2000). The eucoiline *A. pelleranoi* is another larval-pupal endoparasitoid of *Anastrepha* and *C. capitata* larvae, which occurs naturally from central Mexico to northern Argentina (Ovruski et al. 2000). All native parasitoid species recovered during this study are new records for Catamarca. These four species have also been collected in the Yungas forest areas of neighboring Tucumán province (Fernández de Araoz and Nasca 1984, Ovruski 1995). Thus, the data presented here show that all these parasitoid species appear to be common and abundant at least in the southern portion of the Yungas forest. However, these records do not represent the southernmost natural distribution range in the Americas for these four parasitoid species. The authors of this note have recently collected close to 400, *A. fraterculus* puparia from several Myrtaceae species in Santa Lucía, located at 29°S, 59°W in the northeastern Province of Corrientes. From these puparia, we have been able to obtain specimens of the four parasitoid species cit-

Table 1. Parasitization rates, number and relative abundance of parasitoids reared from *Anastrepha fraterculus* pupae in three host plant species sampled in La Viña and Sumampa localities, southeastern Catamarca, between November 1994 and April 1995.

Host Plant	Total of recovered parasitoids (and % parasitism)	Parasitoid species, number of specimens and relative abundance (%) in the fruit samples			
		D. areolatus	*D. brasiliensis*	*U. anastrephae*	*A. pelleranoi*
Guava	42 (10.5)	19 (45.2)	7 (16.7)	3 (7.1)	13 (31.0)
Peach	15 (13.2)	3 (20.0)	5 (33.3)	0	7 (46.7)
Plum	11 (9.6)	4 (36.4)	2 (18.2)	1 (9.0)	4 (36.4)
Total:	68 (10.8)	26 (38.2)	14 (20.6)	4 (5.9)	24 (35.3)

ed here (Ovruski and Schliserman, unpublished data). Both *A. pelleranoi* and *D. areolatus* were also recorded from rainforest areas in Misiones (northern part of northeastern Argentina) (Ogloblin 1937) and from irrigated fruit producing valleys in desert areas in La Rioja (southern part of northwestern Argentina), but the presence of these two parasitoid species in this last region was probably via their introduction in fruit infested with *A. fraterculus* or *C. capitata* larvae parasitized by either the opiine or the eucoiline parasitoid transported from northern Argentina (Ovruski 2002).

Doryctobracon areolatus is often the most abundant species of *Anastrepha*-parasitoid guilds throughout its distribution range in the Neotropics (Sivinski et al. 2000). Interestingly, *A. pelleranoi* was as adundant as *D. areolatus* in this study. This relative abundance of *A. pelleranoi* has been observed only from fruit samples collected from the ground in a recent fruit fly parasitoid survey carried out in Tucumán (Ovruski, Schliserman, and Aluja, unpublished data). As noted by Ovruski (1994) and Aluja et al. (2001), *A. pelleranoi* prefers to search for host larvae in ripe fruit that has fallen from the tree, and it reaches its hosts by entering wounds in fruit.

No parasitoids from *C. capitata* pupae were recovered in this study. This information coincides with the data obtained from the fruit fly parasitoid surveys in Salta and the northeastern Province of Corrientes (Ovruski, unpublished data). However, few *A. pelleranoi* specimens have been obtain from *C. capitata* puparia in Tucumán (Ovruski 1995). This eucoiline species have a broad host preference, including *C. capitata* (Wharton et al. 1998). Other parasitoids species, such as the braconids *D. areolatus* (Fernández de Araoz and Nasca 1984) and *U. anastrephae* (Nasca 1973), have been supposedly reared from *C. capitata* puparia, but these records need verification.

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NOTE

Archasia pallida (Fairmaire) (Hemiptera: Membracidae) in North Carolina

The acquisition of baseline distributional information for our native insect species is imperative as habitats are increasingly threatened by development, environmental degradation, and the introduction of invasive species. The treehoppers of North Carolina are relatively well documented (Dietrich et al. 1999, Wallace et al. 2003), based on specimens collected statewide over more than a century. Nevertheless, records from other states suggest that further species likely occur in this region (Dietrich et al. 1999, Wallace et al. 2003), but have yet to be collected in North Carolina. The Nearctic genus *Archasia* Stål 1867 includes only three species: *A. auriculata* (Fitch 1851), *A. belfragei* Stål 1869, and *A. pallida* (Fairmaire 1846) (see keys to genera of "Telamonini" and species of *Archasia* by Kopp and Yonke 1974: 81–82). *Archasia auriculata* and *A. belfragei* were both previously reported from North Carolina (Dietrich et al. 1999), and Wallace et al. (2003: fig. 5) provided a photograph of *A. belfragei.* We here present North Carolina's first records of *A. pallida* (Fig. 1) NEW STATE RECORD: USA: NC: Mecklenburg Co., Charlotte, 35°11.5′N, 80°50.5′W, 12-V-2000, Henry P. Stockwell, at black light (1 ♂: Schiele Museum, Gastonia, NC); Wake Co., Raleigh, Mission Valley Shopping Center, Avent Ferry Road, 35°46.7′N, 78°40.5′W, 21-V-2002, Geoffrey R. Balme, on *Quercus phellos* L. (willow oak) (1 ♀: NCSU Insect Collection, Raleigh). The record on willow oak is the first specific host association for *A. pallida.* The only prior host data was: "from oaks at Sanford, Florida" (Ball 1931, Kopp and Yonke 1974). Previously, *A. pallida* was reported from Arizona, Florida, Mississippi, Missouri, New Jersey, Ohio, Oklahoma, and Pennsylvania (Ball 1931, Metcalf and Wade 1965, Kopp and Yonke 1974). The discovery of this rare insect in North Carolina brings the number of described treehopper species in this state to at least 90 (see Dietrich et al. 1999 regarding records of the *Enchenopa binotata* species complex).

Fig. 1. *Archasia pallida* ♀, Raleigh, Wake Co., NC.

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NOTE

New Nearctic Record for *Epitranus clavatus* F. (Hymenoptera: Chalcididae)

Grissell and Smith (2003) recently documented the first known record of *Epitranus clavatus* F. and its inclusive subfamily Epitraninae (Chalcididae) in the Nearctic Region, based on a single female specimen collected from a Malaise trap in West Virginia in 2002.

Epitranus clavatus was originally described from Guyana and subsequently recorded from St. Vincent, Brazil, and Hawaii (see Grissell and Smith 2003 for details). Bouček (1982), who also recorded *E. clavatus* from India, Malaysia, Taiwan, and the Seycehelles, suggested that this parasitoid was likely introduced into tropical America on multiple occasions before effective quarantine measures were enacted. Prior to Grissell and Smith's (2003) reporting of *E. clavatus* in WV in 2002, all previously collected specimens in the New World were found before 1901 (Bouček 1992), a span of over one hundred years.

As a result of a 1997 multi-state arthropod survey supporting house fly integrated pest management programs in caged-layer poultry systems (conducted by PEK under a subcontract to IPM Laboratories, Inc., Locke, NY) and the subsequent identification of parasitoids and predators (by ERH) taken in poultry manure pits at multiple locations in North Carolina, Georgia, California, Alabama, and New York, we report here only the second known collection of *E. clavatus* from the Nearctic Region. Two female specimens were collected in a Hister House on 8 October 1997 in a high-rise caged-layer poultry house in Monroe, North Carolina (Union Co.). Hister Houses are commercial, disposable (mesh-bottomed) traps that are placed on poultry manure to attract and capture the histerid beetle *Carcinops pumilio* (Erichson), an important predator of house fly eggs and larvae in poultry facilities (patent number 5,930,945, IPM Laboratories, Inc.).

Because *E. clavatus* has been reared from the pupa of a case-bearing cotton moth in India and from *Tinea palaechrysis* Meyrick or *Crypsithyris* sp. in Malaysia (Boucek 1982), and that pyralids and tineids have a wide range of hosts including stored cotton and fabrics, Grissell and Smith (2003) suggested that *E. clavatus* was likely transported into North America via its moth host in "shipping bags, clothing, and carpeting all made from natural fibers."

Some larvae of Tineidae and Pyralidae also are documented as scavengers in bird nests and in poultry manure. Larvae of the Palearctic moth *Niditinea fuscella* (L.) (synonym: *fuscipuntella* Haworth), known as the brown-dotted clothes moth or the poultry-house moth, are frequently observed in nests of birds, mammals, or Hymenoptera (Emmet 1988); breeding in the trash of pigeons' nests and similar refuse (Forbes 1923); often found abundantly in poultry houses (Legner and Eastwood 1973, Legner et al. 1975); and indoors feeding on refuse and on stored products of plant and animal origin (Emmet 1988). *Niditinea fuscella* is also widely distributed in North America. The moths *Pyralis manihotalis* Guenée and *P. farinalis* L. (Pyralidae) and an unidentified species of *Monopsis* (Tineidae) were inventoried among the many arthropods associated with poultry manure samples from three farms in the Western Cape Province of South Africa (Matanmi and Giliomee 2002). In their study, Matanmi and Giliomee (2002) also reported the emergence of an *Epitranis* sp. from a moth, a *Pyralis* sp. (presumably a larva), in the manure at each of these poultry farms.

Although no moths (adults or larvae) were collected at the Monroe, NC, poultry facility, we hypothesize that larvae of a pyralid or tineid moth (and possibly *N. fuscella*) may have served as the host for *E. clavatus.* The two parasitoid specimens are deposited in the Cornell University Insect Collection, Ithaca, NY. To see a habitus photograph and to review a diagnosis of this chalcid, the reader is referred to Grissell and Smith (2003).

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NOTE

The Status of *Darmistidus* Uhler (Hemiptera: Rhopalidae)

In 1893 Uhler described *Darmistidus maculatus* new genus and species, for four specimens (one headless) from St. Vincent in the West Indies; these four are syntypes. Writing "[c]losely related to *Stachyocnemus,*" and perhaps influenced by the reduced metathoracic scent gland apparatus of both genera, Uhler (1893: 707) placed *Darmistidus* in the alydid subfamily Alydinae. There it rested until Barber (1926), studying the headless syntype in the National Museum of Natural History (Washington, D.C.), synonymized it with *Xenogenus* Berg, a genus in the Rhopalidae (Rhopalinae: Chorosomatini); Rhopalidae is a family characterized (in part) by a reduced metathoracic scent gland apparatus. Barber (1926) also synonymized the species (*maculatus*) with *X. extensum* Distant. Torre-Bueno (1941) in his synopsis, followed Barber. Göllner-Scheiding, who also saw, and dissected, a syntype, agreed with this generic synonymy in her revision of *Xenogenus* (1980), and again in her catalog of the Rhopalidae (1983). She further synonymized *X. extensum* with *Xenogenus picturatum* Berg (Göllner-Scheiding 1980). Thus, both *Darmistidus maculatus* Uhler and *Xenogenus extensum* Distant are now junior synonyms of *Xenogenus picturatum* Berg. However, none of these authors commented on how Uhler's *Darmistidus* differs from Alydidae, or indeed from *Stachyocnemus.*

Several syntypes of *D. maculatus* are in The Natural History Museum (London), and the headless syntype is in the National Museum of Natural History (Washington, D.C.). One of the London syntypes has been dissected, presumably by Göllner-Scheiding.

As a brief exercise in the clearing away of taxonomic underbrush, I have examined an undissected male syntype (from The Natural History Museum, London) of *Darmistidus maculatus.* Here I agree, and explain why, that the species is not related to the alydine *Stachyocnemus,* that it is indeed a rhopalid, and that it belongs in *Xenogenus.*

Darmistidus maculatus Uhler not an alydine

1) Although the head is somewhat elongate, as in many rhopalids, it is not nearly so elongate as are the heads of alydines; that is, the length-to-width ratio is greater in alydines than it is in rhopalids and than it is here in *Darmistidus maculatus.*
2) The hind femora are only very slightly incrassate. The hind femora of Alydinae are much more incrassate.
3) The trichobothria of the sixth abdominal sternum are arranged in a horizontal line (a rhopalid characteristic) rather than in a triangle as in Alydidae (see Schaefer 1975).
4) *Darmistidus maculatus* is small for an alydine. At 6.76 mm., it is much smaller than even *Tollius* spp., which are certainly the slightest (narrowest and shortest) of the New World Alydinae, and I believe of all Alydinae.

Darmistidus maculatus not closely related to *Stachyocnemus*

1) *Stachyocnemus* contains a single species (see Schaefer and Schaffner 1997). The genus is distinguished from all other New World alydines by the two rows of spines on the hind femora (Schaffner 1965, Schaefer, in press). *Darmistidus* lacks these spines, although if closely related the genus might be expected to have them.
2) *Stachyocnemus apicalis* is a more robust species than *Darmistidus maculatus,* and

Alydinae is a subfamily the species in whose genera do not vary in robustness. Again, a genus closely related to *Stachyocnemus* might perhaps be closer in overall form and size. (Length/width: *Stachyocnemus* = 3.26 [n = 4], *Darmistidus* = 3.75 [n = 1].)

3) The humeral angles of *Stachyocnemus* are sharp (but not extended), whereas those of *Darmistidus* are rounded.
4) *Stachyocnemus* is essentially a Nearctic genus, although it occurs in Mexico (Froeschner 1988) and Cuba (Schaefer and Schaffner 1997). It is unlikely, although not impossible, that a species "[c]losely related to *Stachyocnemus*" (Uhler 1893: 707) would be found in St. Vincent, so far from any recorded locale of *Stachyocnemus*.

Note: The evidence that *Darmistidus* is not an alydine is stronger than the evidence that it is not a *Stachyocnemus*. This is to be expected, because Uhler described his *Darmistidus* as a separate genus, and therefore one not identical—but merely closely related—to *Stachyocnemus*. Demonstrating differences between the two therefore proves at best only that they may not be closely related. However, the fact that *Darmistidus* does not belong to the same subfamily as *Stachyocnemus*, renders the former argument moot.

Darmistidus maculatus a rhopalid

1) The genital capsule of the male is retracted into the seventh segment, whose external (posterior) opening is triangular. Although not a universal characteristic of rhopalids, this occurs often in this family and rarely in other coreoid families (Schaefer, unpublished).
2) The lateral rims of the genital capsule have the paralateral lobes considered to be characteristic of the Rhopalidae (Chopra 1967, Schaefer 1978).
3) There is some red mottling, and some red blotching, of the specimen. This occurs in other families, but is particularly common in Rhopalidae: Rhopalinae.
4) The metepimeron and metepisternum are fused and enlarged, forming a flange which extends somewhat back over the abdomen. This too occurs in most rhopalids.

Note: In most Alydinae the metathoracic scent gland opening and peritreme are prominent. In most Rhopalidae they are much reduced or apparently absent. They are apparently absent in *Xenogenus* and—unlike the situation in other alydines—in *Stachyocnemus* also. This similarity may have influenced Uhler's placing of his new genus near *Stachyocnemus*, although he does not mention this in his description.

Darmistidus maculatus is a true species of *Xenogenus*

The male syntype before me keys to *Xenogenus* in Chopra's key (1967) to genera, and it agrees it all respects with the description of *Xenogenus* in Göllner-Scheiding's revision of the genus (1980) and with the characters I listed in restoring the genus from Harmostini (see Brailovsky and Soria 1980) to Chorosomatini (Schaefer 1994). There can be no doubt that Barber (1926) and Göllner-Scheiding (1980) correctly removed *Darmistidus* from Alydidae, and correctly placed it in the rhopalid genus *Xenogenus*.

Acknowledgments.—I am grateful to M. Webb (The Natural History Museum, London) for the loan of the syntype of *Darmistidus maculatus* Uhler. I also thank T.J. Henry (Systematic Entomology Laboratory, USDA, National Museum of Natural History, Washington, D.C.) for information about that Museum's holdings, and for general discussion. Finally, I am deeply grateful to an anonymous reviewer, who improved this note markedly.

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NOTE

First Report of *Ochlerotatus condolescens* (Dyar and Knab) (Diptera: Culicidae) in the United States

A species of mosquito, *Ochlerotatus* (*Ochlerotatus*) *condolescens* (Dyar and Knab), new to the United States and to Florida has been found in Monroe County, Florida. It belongs to the Scapularis Group, Infirmatus Subgroup of the genus *Ochlerotatus* (Arnell 1976) and closely resembles *Oc. infirmatus* (Dyar and Knab) with which it has been confused. Hughes (1961) reported a single female intercepted on an airplane arriving in the United States. Whether it is a new introduction or an unrecognized indigenous species is unknown.

One first female of *Oc. condolescens* was collected on VI/19/00 in a dry ice-baited American Biophysics Company light trap on HOWE KEY (24°73′64″N, 81°40′33″W) (J. Vlach). In addition, I have seen a total of 12 ♀ and 1 ♂ as follows: ANNETTE KEY (24°74′57″N, 81°38′47″W), VII/11/00, 1 ♀ (J. Vlach), KEY LARGO (25°14′28″N, 80°W), Solid Waste Transfer Station, VIII/20/02, 1 ♂; Ocean Reef, IX/17/02, 2 ♀; Gun Club, IX/17/02, 2 ♀; Crocodile Lake, IX/12/02, 1 ♀ (D. DeMay); BIG PINE KEY (24°66′78″N, 81°35′63″W), X/26/02, 5 ♀, VACA KEY (24°72′17″N, 81°08′23″W), X/28/02, 1 ♀, (L. Hribar), all collected in light traps. There is evidence that it may be common. I have the records of 177 adult females from Big Pine Key, Sugarloaf Key, Boca Chica Key, and Key West City captured during 2002 for virus isolation and identified as *Ochlerotatus infirmatus* (Dyar and Knab) based on the presence of the large white scutal patch, a character shared with *Oc. condolescens*. Other species trapped with it were *Ochlerotatus tortilis* (Theobald), *Oc. taeniorhynchus* (Wiedemann), *Culex iolambdis* Dyar, *Cx. nigripalpus* Theobald, *Cx. peccator* Dyar and Knab and *Cx. atratus* Theobald.

The female of *Oc. condolescens* is recognized by the scutum with a broad anterior patch of white scales, no knee spots of white scales on the femora, broad, basal bands of white scales on abdominal terga II–VI (see Fig. 1) and claws of hindleg without a submedian tooth, whereas *Oc. infirmatus* also has the scutum with a broad patch of white scales and no femoral knee spots but the abdominal terga II–VI are entirely dark-scaled except for lateral triangular basal white patches and the claws on the hindlegs have a submedian tooth. Like *Oc. infirmatus, Oc. condolescens* has abdominal sterna I–VII entirely white-scaled. The male genitalia of *Oc. condolescens* has fewer than 60 setae on the sternomesal aspect of the gonocoxite between the basal dorsomesal lobe and the gonostylus while *Oc. infirmatus* has about 75 (Arnell 1976). Surprisingly, the immature stages of *Oc. condolescens* are unknown. However, Perez Vigueras (1956) described what he believed was the larva from French Guiana. Arnell (1976) maintained that the larva is unknown and that the species is not known outside the Greater Antilles.

Knight and Stone (1977) reported *Oc. condolescens* from the Caribbean Islands through Central and South America to Argentina; however, Arnell (1976) restricted it to the Bahama Islands, Cuba, and the Cayman Islands, claiming that records from the Neotropical countries were misidentifications.

Little is known about its bionomics and public health importance. Arnell (1976) did report that adults were taken biting man in deep to partial shade in late afternoon. It appears to be firmly established in Monroe County based on the number of adults which have been collected thus far

Fig. 1. *Ochlerotatus condolescens* adult female showing white scale patch on the scutum and the basal white bands on the abdominal terga.

I am indebted to the following: J. Vlach for first realizing that this mosquito was different and calling it to my attention, and L. Hribar and D. DeMay for collecting and sending specimens. Thanks goes to M. Cutwa for photographing the female and to Drs. G. F. O'Meara and J. F. Day for reviewing the manuscript. This is Florida Agricultural Exteriment Station Journal Series No.R-09380.

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NOTE

A New Specimen of Fossil Mutillidae (Hymenoptera) from Dominican Amber

Fossil velvet ants, or mutillids, are extremely rare and to date all except two have been limited to Palearctic forms. Menge (1856) found six specimens of this family in Baltic amber and Brischke (1886) cited another three from the same deposits. Larsson (1978) mentioned an additional three in the Copenhagen collection of Baltic amber insects. To our knowledge, none of the above were ever described. Scudder (1891) referred to an undescribed *Mutilla* from the mid-Oligocene beds (not amber) located in Brunstatt, Alsatia (now Alsace), in northeastern France.

Bischoff (1915) described seven species of fossil mutillids from Baltic amber, placing them in a new genus, *Protomutilla.* Krombein (1979) suggested that at least one of those species may not be correctly assigned to the family Mutillidae. However, Bischoff's paper still appears to have been the first descriptions of fossil mutillids.

Sharov (1957) described another new species of aculeate Hymenoptera from the Cretaceous deposits of Siberia, which was ultimately assigned to Mutillidae. That fossil specimen, estimated to be about 80 million years old, was called *Cretavus sibiricus* Sharov, for which the author created a new family, Cretavidae. Rasnitsyn (1975) later placed it in the family Mutillidae.

Manley and Poinar (1991) described *Dasymutilla dominica* from Dominican amber estimated to be from 25 to 40 million years old. That represented the first record and description of a fossil mutillid from the New World. *Dasymutilla albifasciatus* Manley and Poinar, another new species of fossil *Dasymutilla* from Dominican amber, was subsequently described (Manley and Poinar 1999).

We now have a third fossil specimen of Mutillidae. This specimen, too, was obtained from mines in the Cordillera Septentrional of the Dominican Republic. Dominican amber was produced by the leguminous tree, *Hymenaea protera* Poinar (1991). A reconstruction of the Dominican amber forest based on amber fossils indicated that the climate was similar to that of a tropical moist forest (Poinar and Poinar 1999).

Dating of Dominican amber is still controversial with the latest purposed age of 20 to 15 million years ago based on foraminifera (Iturralde-Vincent and MacPhee 1996), and the earliest of 45 to 30 million years ago based on coccoliths (Cêpek, in Schlee 1990). A range of ages for Dominican amber may be likely since the amber fossils are associated with turbiditic sandstones of the Upper Eocene to Lower Miocene Mamey Group (Draper et al. 1994). Dominican amber is secondarily deposited in sedimentary rocks, which makes a definite age determination difficult (Poinar and Mastalerz 2000).

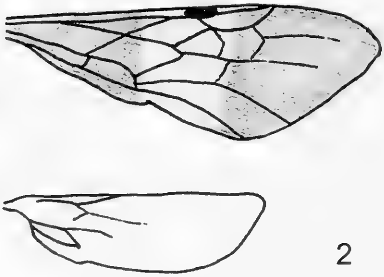
The present piece of amber containing the fossil mutillid is probably between 20 to 40 million years old. It is roughly triangular in shape, with the sides measuring 12 mm by 10 mm by 8 mm (Fig. 1). The thickness of the piece varies from 3–7 mm and the weight is 0.4 g. The amber was reshaped and repolished (GOP) to obtain the best viewing angle.

Many of the key characters cannot be seen in this specimen, thus making it impossible to determine its identity with certainty. However, it is a male, and by virtue of such characters as the shape of the head and eyes, the shape of the mesosoma, and the attachment of the first metasomal segment to the second, it can be placed in the genus *Dasymutilla* Ashmead. In general ap-

1

Fig. 1. Photograph of the piece of amber and the *Dasymutilla* inclusion.

pearance it resembles *D. dominica.* The specimen itself is about 5.5–6.0 mm in length, and the integument is entirely black. The holotype of *D. dominica* has the wings chopped off near the base, so little could be said about them (Manley and Poinar 1991). The wings of this specimen are clearly visible and are banded (Fig. 2). This character is one shared by only a few other species of Mutillidae. While not a lot can be said about this specimen, the mere fact that it represents only the third known specimen of fossil mutillid from the New World makes it noteworthy. The specimen is deposited in the Poinar amber collection, Department of Entomology, Oregon State University, Corvallis, Oregon.



2

Fig. 2. Sketch of the wings of the amber *Dasymutilla* specimen showing the banded pattern of the forewing

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OBITUARY

Jake Brodzinsky (1918–2003); Dominican Amber Dealer

Jake talking with some amber miners and a young girl in the Cordillera Septentrional of the Dominican Republic (photo taken in 1986 by G. Poinar).

Jake was born in Buffalo, New York, on January 17, 1918. After attending secondary school in upstate New York, he studied Forest Management at Syracuse University. He was drafted into the Corps of Army Engineers during World War II and sent to Europe in 1942. He served as an army intelligence officer for 20 years, then retired and worked as a civilian for the Foreign Science and Technology Center.

Jake's introduction to amber came late in life, only after he met and married Marianela Lopez-Penha in Washington, DC, in 1964. Being a native of the Dominican Republic, Marianela persuaded Jake to start an amber business that was originally housed in Charlottesville, Virginia. The pair concentrated on Dominican amber jewelry but in 1980 left that enterprise, moved to the Dominican Republic, and set up the corporation, Amberica, Inc. with an emphasis on amber fossils. Jake soon learned that entomologists wanted only specific fossils and in order for him to furnish these, he needed to know how to distinguish the different insect families. So he bought a microscope and a basic entomology text and with some professional help, soon learned how to identify insects in amber.

Jake became known around the world for securing and supplying a range of invertebrate and plant fossils to scientists. Many came to the Dominican Republic to examine his collection and personally select choice specimens. For a number of years, Jake would pack up a group of specimens and take them to the annual meetings of the Entomological Society of America, where he made personal contact with many entomologists.

When my wife and I organized an expedition to the Dominican Republic amber mines in 1986, Jake served as an indispensable guide during the entire trip, which included a "hole up" in a home during an anti-American demonstration that lasted several days. Our adventures on this trip are described elsewhere (Poinar and Poinar 1994). The miners, who knew him as "Jacobo," were always pleased when Jake brought people to their mines, especially those conducting scientific studies. Many of the amber pieces collected during this excursion were used to reconstruct the conditions that existed millions of years ago on Hispaniola (Poinar and Poinar, 1999).

One day in 1977, upon visiting the Smithsonian, Jake met Don Davis, who mentioned that the Smithsonian would be interested in having an opportunity to acquire a large collection of scientifically valuable amber specimens. Shortly after returning to the Dominican Republic, Jake started putting aside some of the more scientifically interesting fossils that passed through his hands. Soon he had collected several thousand pieces of considerable scientific value. His first collection, amounting to over 5,000 amber pieces, many with multiple insects, was sold to the Smithsonian Institution in 1985 and represents one of the most valuable collections of Dominican amber in the world today. Known as the Brodzinsky/Lopez-Penha collection, it has supplied many specialists with fascinating specimens for study. Several published accounts of this collection have appeared (Anonymous 1985, Harney 1985, Davis 1989).

After selling his first collection to the Smithsonian Institution, Jake built up additional collections, one of which was sold to the American Museum of Natural History in 1992. Jake continued collecting and distributing amber almost up to the time of his death.

The story of Jake's life shows how an amateur can teach himself a subject and make a contribution to a scientific discipline, in this case the field of insect paleontology, by furnishing research material to scientists around the world. In return for his assistance, many scientists named amber specimens after Jake. He and his wife are figured and portrayed as "people who have greatly aided scientists in the study of New World fossiliferous amber" (Poinar 1992).

Jake is survived by his wife, Marianela and two daughters, Raquel and Sibylla.

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OBITUARY

Richard C. Froeschner
(1916–2002):
Biographical Sketch, Described Taxa, and Publications

Richard C. Froeschner, circa 1985

Fig. 1. A round "tuit."

The passing of Dr. Richard C. Froeschner on May 2, 2002, brings to a close the long career of an eminent scientist devoted to entomology and helping others. Dick, as his friends called him, was a kind, gentle, shy man. Dick rarely gave advice, but he was a good listener who had an ability to let a person talk out loud and reach his own, but guided, conclusions. Those who knew Dick appreciated his friendship and subtle humor. One of his most famous lines was that he would finish a project when he got "*around to it*." Those closest to him knew that he would next pull from his desk drawer a "round tuit" (Fig. 1), which always received much-anticipated laughter. In keeping with his good cheer, he frequently complimented friends with a "Good job 99," a phrase borrowed from the old *Get Smart* television series.

Dick went out of his way to help others, particularly students and lay people, either by furnishing identifications or by explaining problems relating to household insects or to natural history in general. He was patient and kind to students, particularly when he saw exceptional potential. On occasion, Dick would include students as coauthors to stimulate and help teach them the details of publishing scientific papers. One recent visitor recalled with great admiration the gift of reprints and books Dick sent to him as a result of a much smaller request for a few key papers. This was typical of Dick when he saw a need.

During his many years at the Smithsonian, he was quoted regularly in newspapers and appeared on radio and television for the local as well as the foreign media. Although a heteropterist by profession, Dick was knowledgeable on a wide array of other insect groups. He was the resident cicada expert and regularly answered inquiries on the emergence of the various broods all over the country. He also published on other orders, including Coleoptera (Languriidae and Erotylidae), Neuroptera, and Orthoptera (his Master's thesis treated the Orthoptera of Iowa).

Dick was born in Chicago, Illinois, March 8, 1916, to immigrant German parents. At an early age the family moved to St. Louis, Missouri, where he attended elementary, junior high, and high school. During these formative years, he became intrigued with natural history. As a young boy, he enjoyed the powerful synergistic force of three, close, nature-loving brothers, who surely were a major stimulation in his development. From early collections of insects attracted to kerosene lamps, through the years of the "Froeschner Nature Club," and on to more sophisticated collecting techniques, Dick showed a strong interest in entomology. Several of his high school teachers, particularly Ms. Mary McCarty, saw his potential and provided assistance that allowed him to attend the University of Missouri in pursuit of his B.S., received in 1941. During these years, he worked at the Missouri Department of Agriculture on Japanese beetle surveys in the St. Louis area (1938–1940) and as a Taxonomic Entomologist at Jefferson City (1940–1941).

Early in his undergraduate days, he met University of Missouri Scientific Illustrator, Elsie M. L. Herbold, who soon became his companion and strongest supporter. On October 6, 1940, they were married and began a long and devoted relationship, combining Dick's scientific passion with Elsie's enviable artistic skills, that was to span more than 61 years.

From 1941 to 1945 he was variously employed as assistant state entomologist, nursery inspector, and state representative on the U.S. Department of Agriculture's *Parlatoria* Scale Insect Project. In 1945 he joined the Army, serving two years in various capacities from Entomology Technician working on mosquito and malaria control to Chief Ward Master at the MacDill Air Force Base Hospital, near Tampa, Florida. After the Service, from 1946 to1948, he served as Chief Curator and Acting Director of the Museum of Science and Technology at the St. Louis Academy of Sciences.

Dick received his M.S. from Iowa State College in 1951. During his Master's work on the "Orthoptera of Iowa," he was employed as an instructor from 1948 to 1949 and as an assistant professor during 1949–1954. He worked as a nursery inspector for the Iowa State Entomologist during the summers, gaining considerable practical experience.

Dick continued on to pursue his Ph.D. under Dr. Harry H. Knight, world renowned mirid specialist. It was during these years that he joined a group of graduate students who went on to become prominent heteropterists. He became life-long friends with well-known colleagues José C. M. Carvalho, Leonard A. Kelton, Joseph C. Schaffner, and James A. Slater. Not far behind the graduates students were the undergraduates John D. Lattin and John T. Polhemus. These must have been grand days at Iowa State College, which also boasted two other well-known hemipterists on the faculty, Drs. Carl J. Drake and Halbert M. Harris.

Upon completion of his doctorate, he joined the staff at Montana State College, Bozeman, as an assistant professor from 1954 to 1956 and associate professor from 1956 to 1960. In 1958, he received the school's Alumni and Student Council "Distinguished Teaching Award."

Despite his success and devotion to teaching, Dick's true love was research. In 1960, he accepted a research entomologist position with the United States Department of Agriculture in Washington, D.C. Disappointed with the heavy identification responsibilities that came with the position, he returned to Montana as an associate professor at the University of Montana, Missoula.

In 1963, Dr. J. F. Gates Clark, then chairman of the Department of Entomology at the United States National Museum (USNM), offered Dick a research entomologist position at the Smithsonian Institution, Washington, D.C. Without hesitation, Dick and family again pulled up roots and returned to the East. He devoted the remainder of his life researching Heteroptera at the USNM (now the National Museum of Natural History—NMNH), helping to build one of the world's largest and best-curated Heteroptera collections. Dick retired in 1995 at the age of 79. He continued driving into the museum from Falls Church, Virginia, on a regular basis until December 12, 2001, when poor health forced him to stay home. He passed away five months later.

Dick's contributions to entomology are numerous. His early teaching stimulated many students to go on to successful careers, but it is his research contributions that will have the longest influence. Dick's five-part series on the "Hemiptera of Missouri" is still remarkably useful after more than 40 years. The series contains identification keys and biological notes for all true bugs known from that state and is profusely illustrated by his talented wife, Elsie. It remains one of the most frequently cited treatises on North America Heteroptera. His 1960 monograph of the "Cydnidae of the Western Hemisphere" is perhaps his most outstanding, purely scientific, contribution. This masterful work puts the cydnids in phylogenetic context for the first time and provides revisions and keys to all known New World genera and species. Another major contribution is the 1988 *Catalog of the Heteroptera, or True Bugs, of Canada and the Continental United States.* As coeditor, Dick wrote large portions of the catalog introduction and authored 20 of the 45 family chapters, including the large families Coreidae, Pentatomidae, and Reduviidae. This major accomplishment was the first summation of the North America literature in more than 70 years. His "Heteroptera of Ecuador" (1981) and "Synopsis of the Heteroptera of the Galapagos Islands" (1985) have proved to be two of the most useful treatments of South American bugs ever published. The extensive literature reviews provided citations for original descriptions, revisions, and identification keys. He continued with this theme throughout his career, working on synopses and annotated lists for many Neotropical countries. Unfortunately, most remain incomplete. In 1999, however, he published an outstanding compilation of the amazingly rich fauna of Panama in his "True bugs of Panama" that included information on 51 families, 585 genera, and 1,330 species. Dick had nearly completed of the non-mirid Heteroptera for Chile, when declining health stopped progress on this monumental synopsis.

As Gary Hevel (2002. Ent News, Systematic Biology—Entomology Newsletter, Smithsonian Institution, National Museum of Natural History 16: 2–3) so nicely said, "Friends and colleagues will long remember this man of wisdom, humor, and devotion to his chosen field." During his career, Dick Froeschner published 131 entomological papers, mostly on Heteroptera, and treated taxa in 10 families and two suborders, describing new to science two subfamilies, eight genera, and 111 species.

Dick is survived by his wife Elsie; two daughters, Kay and Ellen; two grandchildren; and two great grandchildren. To learn more details about Dr. Richard C. Froeschner's life, I refer readers to the 1986 Festschrift [T. J. Henry and A. G. Wheeler, Jr. (eds.), Journal of the New York Entomological Society, 94(2)] published in his honor on the occasion of his 70th birthday. Articles by his wife Elsie; brothers Paul, the Reverend Robert, and the Reverend William Froeschner; former student Paul Eneboe, M.D.; and numerous colleagues reveal the high regard friends and colleagues held for Dick.

The Richard C. Froeschner Memorial Fund has been established to help purchase literature on Heteroptera at the Smithsonian Institution. Tax-deductible contributions may be sent to the Department of Systematic Biology, Division of Entomology, National Museum of Natural History, Smithsonian Institution, P.O. Box 37012, 10th Street & Constitution Avenue NW, Washington, D.C. 20013-7012.

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LIST OF DESCRIBED TAXA

AUCHENORRHYNCHA

MEMBRACIDAE

Telamona archboldi Froeschner, 1968

HETEROPTERA

ACANTHOSOMATIDAE

Hellica johni Froeschner, 2000
Hellica johnpolhemi Froeschner, 2000
Rolstonus Froeschner, 1997 (n. gen.)
Rolstonus rolstoni Froeschner, 1997

ARADIDAE

Brachyrhyncus pauper Kormilev & Froeschner, 1987
Calisiopsis brodzinskyorum Froeschner, 1992 (amber fossil)
Calisiopsis kormilevi Froeschner, 1992
Calisiopsis nigrotuberculata Froeschner, 1992
Calisiopsis tuberculata Froeschner, 1992
Mezira doesburgi Kormilev & Froeschner, 1987

Mezira vicina Kormilev & Froeschner, 1987

BLISSIDAE

Ischnodemus missouriensis Froeschner, 1944

COREIDAE

Ceraleptus denticulatus Froeschner, 1963
Ceraleptus probolus Froeschner, 1963

CYDNIDAE

Amnestus basidentatus Froeschner, 1960
Amnestus explanatus Froeschner, 1960
Amnestus foveatus Froeschner, 1960
Amnestus lenkoi Froeschner, 1975
Amnestus pequinus Froeschner, 1975
Amnestus radialis Froeschner, 1960
Amnestus sexdentatus Froeschner, 1960 (a jr. syn. of *A. radialis* Froeschner; syn. by Froeschner, 1981)
Amnestus trimaculatus Froeschner, 1960
Blaena blothroposa Froeschner, 1966
Blaena cirra Froeschner, 1966
Blaena coarctata Froeschner, 1960
Blaena mediocarinata Froeschner, 1960
Blaena multitrichia Froeschner, 1960
Blaena subsulcata Froeschner, 1960
Chilocoris incomptus Froeschner, 1967
Chilocoris neozealandicus Lariviere and Froeschner, 1994
Chilocoris peterseni Froeschner, 1967
Cyrtomenus bergi Froeschner, 1960 (n. n.)
Dallasiellus alutaceus Froeschner, 1960
Dallasiellus bacchinus Froeschner, 1960
Dallasiellus dilatipes Froeschner, 1960
Dallasiellus fusus Froeschner, 1960
Dallasiellus horvathi Froeschner, 1960
Dallasiellus interruptus Froeschner, 1960
Dallasiellus laevis Froeschner, 1960
Dallasiellus leurus Froeschner, 1975
Dallasiellus longirostris Froeschner, 1960
Dallasiellus megalocephalus Froeschner, 1960
Dallasiellus orchidiphilus Froeschner, 1960
Dallasiellus ovalis Froeschner, 1960
Dallasiellus puncticeps Froeschner, 1960
Dallasiellus puncticoria Froeschner, 1960
Dallasiellus reflexus Froeschner, 1960
Dallasiellus triangularis Froeschner, 1960
Dallasiellus vanduzeei Froeschner, 1960
Dearcla capensis Froeschner, 1961
Dearcla natalensis Froeschner, 1961
Dearcla paucivillosa Froeschner, 1961
Ecarinoceps Froeschner, 1960 (n. subg. of *Dallasiellus*)
Ectinopus muticus Froeschner, 1960
Garsauriinae Froeschner, 1960 (n. subfam.)
Macroscytus aquilus Froeschner, 1967
Macroscytus noonadanae Froeschner, 1967
Melanaethus aereus Froeschner, 1960
Melanaethus externus Froeschner, 1960
Melanaethus mixtus Froeschner, 1960
Melanaethus planifrons Froeschner, 1960
Melanaethus wolcotti Froeschner and Maldonado, 1993
Microporus shiromai Froeschner, 1977
Onalips bisinuatus Froeschner, 1960
Onalips completus Froeschner, 1960
Pangaeus bisetosus Froeschner, 1960
Pangaeus impressus Froeschner, 1960
Pangaeus neogeus Froeschner, 1960
Pangaeus pluripunctatus Froeschner, 1960
Pangaeus punctilinea Froeschner, 1960
Pangaeus punctinotum Froeschner, 1960
Pangaeus rugonotum Froeschner, 1960
Pangaeus quinquespinosus Froeschner, 1960
Pangaeus semibrunneus Froeschner, 1960
Pangaeus setosus Froeschner, 1960
Pangaeus tuberculipes Froeschner, 1960
Pseudopangaeus Froeschner, 1960 (n. subg. of *Dallasiellus*)
Rhytidoporus barberi Froeschner, 1960
Rhytidoporus obsoletus Froeschner, 1960
Scaptocorinae Froeschner, 1960 (n. subfam.)
Scaptocoris divergens Froeschner, 1960
Scaptocoris grossa Froeschner, 1960
Sehirus cinctus texensis Froeschner, 1960 (n. subsp.)
Tominotus albicostus Froeschner, 1960
Tominotus brevirostris Froeschner, 1960
Tominotus inconspicuus Froeschner, 1960
Tominotus unisetosus Froeschner, 1960

MIRIDAE

Atractotomus purshiae Froeschner, 1963
Hesperolabops mexica Froeschner, 1967
Larinocerus Froeschner, 1965 (n. gen.)
Larinocerus balius Froeschner, 1965

PENTATOMIDAE

Elsiella Froeschner, 1981 (n. gen.)

REDUVIIDAE

Phymata prolata Froeschner and Kormilev, 1990 (n. n.)

RHOPALIDAE

Jadera silbergliedi Froeschner, 1985
Niesthrea ashlocki Froeschner, 1989

TINIGIDAE

Acalypta emicata Froeschner, 1996
Acalypta laurae Froeschner, 1991
Acalypta ruhoffae Froeschner, 1976
Anommatocoris zeteki Drake & Froeschner, 1962
Carldrakeana Froeschner, 1968 (n. gen.)
Carvalhotingis Froeschner, 1996 (n. gen.)
Corythaica darwiniana Drake and Froeschner, 1967
Corythaica wolfiana Drake and Froeschner, 1967
Corythucha melissae Froeschner and Miller, 2002
Distocader Froeschner, 1968 (n. gen.)
Etesinalda Froeschner, 1996 (n. gen.)
Etesinalda laticosta Froeschner, 1996
Exulmus Froeschner, 1996 (n. gen.)
Gargaphia sanchezi Froeschner, 1972
Leptodictya archboldi Froeschner, 1968

Leptodictya fuscipes Froeschner, 1989
Leptopharsa bredini Froeschner, 1968
Leptopharsa gibbicarina Froeschner, 1976
Leptopharsa madrigali Froeschner, 1989
Leptopharsa reflexa Froeschner, 1989
Minitingis elsae Froeschner, 1968
Phatnoma biordinatum Froeschner, 1976
Phatnoma eremaea Drake and Froeschner, 1967
Pleseobyrsa nigribasis Froeschner, 1991
Sinalda haplotaxis Froeschner, 1969
Stragulotingis Froeschner, 1969 (n. gen.)
Stragulotingis englemani Froeschner, 1991
Teleonemia harleyi Froeschner, 1970

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dia Distant (Hemiptera: Cydnidae). Entomological News 71(10): 249–254.

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es southward into Maryland. Proceedings of the Entomological Society of Washington 73(3): 268.

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BOOK REVIEW

Fauna Iberica, Vol. 16: Hymenoptera, Cynipidae by José Luis Nieves-Aldrey, Museo Nacional de Ciencias Naturales Consejo Superior de Investigaciones Científicas, Madrid, 2001, 636 pp.; ISBN: 84-00-07810-1; about $40 + 4% IVA; see website: http://www.fauna-iberica.mncn.csic.es/faunai/homepage.html

This beautifully illustrated taxonomic treatise is 16th in a series of publications on selected (mostly invertebrate) taxa of the Iberian Peninsula. Although the text is in Spanish, its excellent illustrations, including scanning electron micrographs, black-and-white drawings and 106 color plates, make it a treat to open. Other than tables, keys and brief introductions, the text is organized by species and so well-illustrated that a Spanish-English dictionary is nearly unnecessary. Appendices include a 28 page Bibliography, Keys to Galls, Table of Host Plants, Table of Parasitoids and Inquilines, a Glossary.

The cynipid wasp fauna (gall-inducers and inquilines) of the 230,000 square miles of the Iberian Peninsula comprises 140 species in 26 genera. Each species is carefully described and well illustrated in this volume.

In the tribe Cynipini (oak gall-inducers) there are 58 species on 10 host oak species in the Iberian Peninsula. Most wasps in this tribe alternate generations, and both the unisexual and the bisexual generations are known for 39 of these species. Nieves-Aldrey indicates that he knows, but has not yet described, the alternate generations in an additional two species. Thus the biology is known in over 70% of the Cynipini here and the alternate generation is unknown for only 17 species. For some of these species one of the generations may have been lost during recent evolution.

As a contrast, in California, a land area of approximately 160,000 square miles or about 70% that of Iberia, there are 16 host oak species and about 122 described species in the Cynipini. However, our rich and diverse cynipid fauna is much less well-known than the Iberian relatives and we know the alternate generation for only about 24% of these species. Expanding to the entire United States, with an area of approximately 3,620,000 square miles, or nearly 16 times the area of Iberia, we find 573 Cynipini on 57 host oak species, and the alternate generation is known for only about 45 of these, less than 8%.

In addition to serving as a model to which we should aspire in studying Nearctic Cynipidae, this book also clarifies an enigma in the California cynipid fauna. *Plagiotrochus suberi* Weld forms galls on *Quercus suber* L., the imported cork oak. This is the only known species of *Plagiotrochus* in North America. Historical records show that this oak did not arrive in California prior to about 300 years ago, so the origin of this cynipid, whether by rapid evolution or alien introduction, has been questioned. Nieves-Aldrey synonymizes this species with the Palearctic *Plagiotrochus amenti* Kieffer 1901, showing that this cynipid crossed the ocean with its host plant.

This work embodies a goal for North American cynipid taxonomists. We must strive long and hard to characterize the Nearctic cynipid fauna, for which the most recent systematic treatments are nearly half a century out of date (see Weld 1956, 1959, 1960), as well as Nieves-Aldrey has accomplished for this portion of the Western Palearctic.

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BOOK REVIEW

Checklist of the Diptera of the Netherlands. By P. L. Th. Beuk, ed. KNNV Uitgerij, Utrecht <info@knnvuitgeverij.nl>. 2002. Includes CD/ROM. 448 pp. 11.35 Euros plus postage and handling.

This visually appealing volume, with CD version included, is the first complete checklist of Netherlands Diptera since that presented by De Meijere (1939). Listed here are nearly 5,000 species of flies known from the Netherlands, about a 50% increase since 1939. Stated purposes of the book include complementing the recent increase in knowledge of the European Diptera and supporting nature conservation and monitoring, in this case of the more minute and more precisely diagnostic faunal elements often overlooked in the emphasis on vertebrates and plants.

The introduction includes a history of lists of Netherlands Diptera, which means mostly those done by van der Wulp and de Meijere, with photos of both men, and an account of the life of this project, which began in 1991 but grew slowly until revived in 2000 by the late Volkert van der Goot, to whom the book is dedicated. A table lists the 105 Diptera families known from the Netherlands with the number of species in each. Chironomidae are much the most numerous family with 423 species represented, followed by Cecidomyiidae with 340, Syrphidae with 328, and Tachinidae with 315, the next largest families being several that hover around 250 species.

Beuk, editor of the volume, is also author or co-author of many family sections. Twenty-nine dipterists were involved in the project, 22 of them from the Netherlands, a remarkable number from a country roughly equivalent in size to Massachusetts and New Hampshire combined, even with about twice their population. The checklist is ordered by family, generally following the arrangement of the British Isles list (Chandler 1998). Within a family, subfamily to species levels are arranged in alphabetical order, with generic and specific names followed immediately by any synonyms used in the past for Netherlands species.

Each family begins on a fresh page, followed by the author name(s), a diagnosis, a description of the biology, annotated general references to publications on the family, references to publications that include Dutch records, and the list of species, with some explanatory notes. The diagnosis is often accompanied by an effective photograph or drawing of a representative adult. Any reader will wish all the families had an illustration and that some also showed a larval example. An excellent feature is a blue-highlighted line before each family list of species that gives comparative numbers of known species for each family in the Netherlands, Belgium, Germany, United Kingdom, and the world. This gives a good indication of the relative knowledge of the fauna in neighboring countries and among families.

A summary bibliography with unabbreviated journal names and an index of scientific names follow in small type. The CD-ROM, which fits into a jacket in the front cover of the book, is beautifully arranged, readily usable, completely searchable, and one can e-mail most of the chapter authors by just clicking the person's name.

Some quibbles: I noticed a few typographical errors or misspellings, including that of a fungus gnat named after me, an error in Table 2 gives 244 as the number of Syrphidae, but the chapter on that family gives the correct number of 328. Page numbers are unaccountably in tiny type. Otherwise, the book looks fine, is effective, folds flat on the table, and, yes, van der Goot would have been proud to see it.

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Book Review

The Ants of New Mexico (Hymenoptera: Formicidae). By William MacKay and Emma MacKay. The Edwin Mellen Press, Lewiston, New York. 2002. Hard bound. 5.7 × 9 in. ISBN 0-7734-6884-6. $129.00.

"Ants of New Mexico will set the standard for all future regional works on ants and other insects in both style and substance." So wrote Richard Fagerlund, B.C.E., in the brief forward to this book. He noted that it is student friendly but equally useful to professionals as well.

As the saying goes, you can't judge a book by its cover, but we all do; first impressions are important and *Ants of New Mexico* is not impressive. The cover is white with starkly contrasting black lettering. Throughout, text and keys are set up in dual columns, a format that does not permit easy scanning, particularly since the columns are routinely broken up by interspersed figures. Two plates of photographs at the end of the book are murky and a waste of time.

This book treats nearly 300 ant species, nearly one-quarter of which are species that the authors think might occur in New Mexico. According to the Abstract, 239 species are known to be present in New Mexico and 54 others (I counted 57) are included as possible members of that fauna. Some of the latter are unlikely candidates at best.

The ten page Introduction rambles, without being divided into discrete sections. The complex physiography and vegetation of New Mexico are each dismissed in a single paragraph, neither with reference to more comprehensive works. Two columns are devoted to general and more specific references on ants. The following five pages are spent on techniques for collecting, preserving and curating ants. It is chatty and verbose; the use of the second person ("you") I personally found a bit off-putting. The authors foster the impression that hand collecting is literally that: done with fingers or forceps; no mention at all is made of the use of an aspirator or, as some prefer, a small brush. The descriptions of various supplemental techniques (pitfalls, Berlese funnels, baiting, black lights) could have been more succinct; neither Malaise traps (for sexual forms) nor Winkler funnels (for litter inhabiting species) were mentioned.

Ants are routinely point-mounted, glued to the top of the point, with the apex between the meso- and metacoxae. This method of preparation is not mentioned. The authors recommend bending the tip of the point down and gluing the right side of the ant to the deflected point, a technique we are assured, that is ". . . most commonly used by other entomologists," a claim that is probably not true. They fail to point out that they are the only myrmecologists who advocate this lamentable method.

The remainder of the Introduction (2.5 pages) is devoted to ants as pets, the difficulties of identification, a bit about websites (but without mention of http://www.notesfromunderground.org) and a brief description of the "meat" of the book, systematic treatment (which the authors call a List) of the ants of New Mexico.

The next chapter, pp. 16–26, consists of an amply illustrated key to the genera of New Mexico ants. And, it is here that the dual column format becomes particularly aggravating. The figures are placed within the key, sometimes following a couplet, but more often between the two lugs, and always with an unnecessarily wordy caption to add to the confusion.

The "List of the ants of New Mexico" begins on p. 27, but it is not a list in the true sense. Rather, it is a systematic account of the ants, with keys, illustrations and maps. Each genus is briefly discussed and a key is given for the New Mexico species. Species accounts consist of a short Discussion of the salient features of each, including those that will distinguish it from similar taxa, followed by comments on Distribution, Habitat, and Biology.

The keys are generally reasonably straightforward, eschewing the brevity of telegraphic style (presumably thus more user-friendly). They are mostly original keys and work fairly well. Anyone using a couple of the keys is, however, going to receive a rude shock. The keys are for workers (queens and males generally receive short shrift, a common short-coming of most regional works). But, in the key to *Myrmica* three couplets utilize *male* characters only! Similarly, in the *Acanthomyops* key couplet 6 is for *queen* features only. The accompanying illustrations vary widely in quality, although most are adequate. In general, mesosomal shape is only approximate and the rendering of setae/hairs is sometimes horrendous. Especially awful are two figures in the *Solenopsis* key (figs. 274, 275), where the hairs are shown to be straight and stiff, rather than flexuous and tapering.

Some of the species included are those that the MacKays think might be found in New Mexico, but I find some choices a bit strange. For example, *Cephalotes rohweri* (Wheeler) should not be expected to occur in New Mexico. This species is found at mid-elevations in central Arizona, thence south into central Sonora, Mexico; it nests primarily in palo verde (*Cercidium* spp.) and not in "oak forests" as stated by the MacKays. Much the same would be true for *Leptothorax silvestrii* Santschi. Oddly, they include *Strumigenys louisianae* Roger as another "possible" (unlikely, in my view), but not *Pyramica,* a genus with better prospects. It is also unlikely that *Cyphomyrmex rimosus* (Spinola), a South American species, would be found in New Mexico; it is presently known in the U.S., only from a few southeastern states, in humid forest.

The Literature Cited is thorough and up-to-date.

This is followed by a Glossary. Most of the terminology is adequately described. But, there are a few oddities. Under Foramen there is a reference to "posterior lateral foramen" that has me puzzled. I find the definition for Lectotype confusing and the authors do not distinguish between Cotype and Paratype. One definition that is patently incorrect is that given for Metanotal suture—"suture separating the mesonotum from the propodeum." In fact, the metanotal suture lies between the metanotum and the propodeum or, as in most worker ants, between the mesonotum+metanotum and the propodeum. Other definitions are sometimes only partly correct, as is that for Scrobe, defined as a groove on the dorsum of the head for the reception of the antennal scape. Scrobes may alternatively be present on the side of the head or on the side of the mesosoma for the reception of a folded leg. The definition for Thorax is only more or less correct. The definition for Gena is incorrect.

Strangely absent from this book is a chapter devoted to what ants are and are not. There is no general account of ant biology and behavior. A chapter on ant morphology would have been very helpful to any student trying to identify ants. These omissions in a book supposedly directed more to the student/amateur rather than the professional myrmecologist are inexplicable.

This is a book that could have been much better. The writing style is verbose and unprofessional in most areas and sometimes downright opaque. There are occasional new words that pop up (e.g., "punctated" on p. 106), evidence of the limitations of the authors. The manuscript should have been subjected to wider peer review. The lack of a firm editorial hand and adequate proof-reading further detracted from this laudable, but flawed, effort.

As a book directed more to the student it is, in my opinion, less than it might have been and, at the same time, probably priced out of reach for most students and amateurs. It is certainly not a bargain. The intent is good and for that I would give the MacKays an "A", but for effort a "B−," and for overall product, a "C−". If this is to be the ". . . standard for all future regional works," it is a regrettably low one.

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SOCIETY MEETINGS

1,070th Regular Meeting—January 9, 2003

The 1,070th regular meeting of the Entomological Society of Washington (ESW) was called to order in the Cathy Kerby room of the National Museum of Natural History, Washington, D.C., by President Jon Mawdsley at 7:04 p.m. The meeting was attended by 16 members and 14 guests. The minutes of the 1,069th meeting were approved with modification.

There were no new applicants for membership. Six guests were introduced.

In miscellaneous business, President Mawdsley announced that the Executive Committee authorized $500 from ESW funds to support the 2003 Virginia Bioblitz. A vote was called on the proposal to combine the Corresponding Secretary and Membership Chair into a single position, Membership Secretary. It was passed unanimously.

For exhibits, Wayne Wehling and Walter Gould from APHIS brought to our attention the upcoming orchid and butterfly house in the Smithsonian Arts and Industries building. Art Evans announced that the 2003 Virginia Bioblitz will be held May 17–18 in Douthat State Park, Bath Co. Astrid Caldas mentioned that the popular University of Maryland Insect Summer Day Camp will continue this year. Dave Furth exhibited the richly illustrated "*Dragonflies and Damselflies of Northeastern Ohio*" field guide by L. Rosche, and "*Die Bombyces und Sphinges der Westpalaerktis*" Volumes 3 (Zygaenidae, by J. J. de Freina and T. J. Witt) and 4 (Sessiidae, by J. J. de Freina).

Dave Furth introduced the speaker, Dr. Gabriela Chavarria, last year's ESW President and Director of Conservation Policy, National Wildlife Federation. Her presentation, entitled "Capitol Hill-Topping in D.C. and Conservation Policy" was essentially a call for more biologists to join the ranks of policy-makers, against the backdrop of her personal journey along that track. Having started out in the academic world studying bumblebees, she envisioned having her own bumblebee hive full of active *Bombus* workers, that is, students. Instead, as she saw fellow Ph.D. students, jobless, give up biology and switch fields entirely, she entered the policy world. Now, six years later, she sees that she has done more for bumblebees as a policy maker than she would have had she set up her own lab. In conservation, in recent years there has been greater awareness of the need for trained biologists, and Dr. Chavarria has found that the research skills and informal academic network she developed in her doctoral work gave her the tools needed in the policy arena, in which science is just one aspect of decision-making.

The meeting was adjourned at 8:15 p.m. Refreshments were provided by the Society.

Respectfully submitted,
Stuart H. McKamey,
Recording Secretary

1,071st Regular Meeting—February 6, 2003

The 1,071st regular meeting of the Entomological Society of Washington (ESW) was called to order in the Cathy Kerby room of the National Museum of Natural History, Washington, D.C., by President Jon Mawdsley at 7:00 p.m. The meeting was attended by 16 members and 9 guests. The minutes of the 1,070th meeting were approved with modification.

There were no new applicants for membership or new members present. One guest was introduced.

For exhibits, Alma Solis passed around some color plates showing "fecal stalactites" in Pyralidae. Dave Furth had four new publications: "*Bees and Crop Pollination—Crisis, Crossroads, Conservation,*" edited by C. S. Stubbs and F. A. Drummond; "*A Guide to the Archives of the Royal Entomological Society,*" by B. Pedersen; "*Amphibiotic Insects of the Northeast of Asia,*" by A. Zasypkina and A. S. Ryabukhin; and a special bulletin of "*Nabesania,*" a journal of the Japanese Society of Coleopterology.

Dave Furth introduced the speaker, Dr. Robert A. Raguso, of the University of South Carolina. His talk was entitled "Moths as Pollinators: the Good, the Bad, and the Lazy." It consisted of an informal discussion of the different kinds of interactions between moths and flowers, the great majority of which rely on insect pollination to reproduce. Rewards include pollen, nectar, and oils, and these are advertised using a variety of visual, olfactory, and gustatory stimuli. Convergent evolution among moth-pollinated flowers is rampant, for example white flowers and deep nectaries, which force the moth to rub against the sexual parts of the flower. The nature of the moth-plant relationship varies from very loose (generalist flowers or generalist moths or both) to highly obligate. Dr. Raguso cited the famous example of the yucca moths, in which the reproduction of both species requires the other, but noted that there are cases of "cheaters" even in that system. Dr. Raguso lastly contrasted the pollination stimulus syndromes of hawk moth plants, which show little evidence of scent convergence, and noctuids, most of which will respond to a single, particular compound produced by many unrelated plants.

The meeting was adjourned at 8:30 p.m. Refreshments were provided by the Society.

Respectfully submitted,
Stuart H. McKamey,
Recording Secretary

1,072nd Regular Meeting—March 6, 2003

The 1,072nd regular meeting of the Entomological Society of Washington (ESW) was called to order in the Cathy Kerby room of the National Museum of Natural History, Washington, D.C., by President Jon Mawdsley, at 7:08 p.m. The meeting was attended by 17 members and 4 guests. The minutes of the 1,071st meeting were approved as read.

There were no new applicants for membership or new members present. Three guests were introduced.

For exhibits, Art Evans had "*Hofmann's Focus Guide to Butterflies of North America,*" by Hoffmann & Brock, which is filled with digitally enhanced photographs.

John Brown introduced the speaker, Dr. Stuart McKamey of the USDA Systematic Entomology Laboratory, who spoke about "Hopp(er)ing Through Mexico and Venezuela: Adventures in Leafhopper-hunting." This consisted of a travelogue of an October 2001 excursion with colleagues to arid and semideciduous habitats in the State of Jalisco, over the pine forests in Puebla, and through the wetter habitats along the Caribbean coast and inland mountains of Chiapas, and finally up through the arid region of Oaxaca. The field team collected by sweeping, visual search, UV-lights, and pyrethral canopy-fogging. The main hazards encountered included cow patties, flat tires, falling arboreal scorpions, killer bees, and corrupt Mexico City police. Dr. McKamey concluded the presentation with some recent video footage of violent riots in Caracas, which precluded a planned collecting trip to Venezuela.

The meeting was adjourned at 8:10 p.m. Refreshments were provided by the Society.

Respectfully submitted,
Stuart H. McKamey,
Recording Secretary

1,073rd Regular Meeting—April 3, 2003

The 1,073rd regular meeting of the Entomological Society of Washington (ESW) was called to order in the Cathy Kerby room of the National Museum of Natural History, Washington, D.C., by President Jon Mawdsley, at 7:05 p.m. The meeting was attended by 14 members and 8 guests.

The minutes of the 1,072nd meeting were approved as read.

There were no new applicants for membership or new members present. Three guests were introduced.

For exhibits, Dan Kyle had a collection of local marsh Orthoptera. Warren Steiner showed the book "*Review of Tenebrionidae of Benin*." Dave Furth showed some slides of the ALAS station, Costa Rica.

Dave Furth introduced the speaker, Dr. David Nickle of the USDA Systematic Entomology Laboratory, whose talk was entitled "Life in a Rainforest Canopy: an In-depth Study of Amazonian Grasshoppers, Katydids and Termites." The majority of the time focused on his findings about katydid ecology, biological traits, defensive strategies, and pairing behaviors, gathered over several years with a team of about 15 Earthwatch volunteers at Explorama Lodge, Peru. Collecting at mercury vapor lights, Malaise, night visual search, and canopy fogging, Dr. Nickle collected more species in an area the size of Washington, DC, than are found in all of the United States, among about 800 specimens per 2-week period. He discovered vertical preference among subfamilies. Dr. Nickle thinks of katydids as the "plankton of the forest" because they are an important source of food to many predators, especially bats, which hone in on their calls. In contrast, Dr. Nickle considers termites the "topsoil" of the rainforest because, in the almost complete absence of real topsoil, termites are the primary group breaking down leaves and wood, thereby releasing available nutrients.

The meeting was adjourned at 8:35 p.m. Refreshments were provided by the Society.

Respectfully submitted,
Stuart H. McKamey,
Recording Secretary

1,074th Regular Meeting—May 1, 2003

The 1,074th regular meeting of the Entomological Society of Washington (ESW) was called to order in the Cathy Kerby room of the National Museum of Natural History, Washington, D.C., by President Jon Mawdsley, at 7:09 p.m. The meeting was attended by 16 members and 9 guests. The minutes of the 1,073rd meeting were approved as read.

President-elect Eric Grissell announced the ESW annual banquet to be held June 4, 2003, and detailed the hightened security precautions.

There were no new applicants for membership or new members present. Five guests were introduced.

In miscellaneous business, a picture of meeting attendants was taken to show ESW Honorary President Don Anderson, who was unable to attend.

Dave Furth displayed the books "*Arthropods of Tropical Forests: Spatio-temporal Dynamics and Resource Use in the Canopy*" by Y. Basset, V. Novotny, S. E. Miller and R. L. Kitching (eds.), "*Special Topics in Leaf Beetle Biology*" by D. Furth (ed.), and "*Encyclopedia of Insects*" by V. H. Resh and R. T. Cardé (eds.). Warren Steiner displayed Volume 90 of the "*Faune de Madagascar*" series: "*Insecta Coleoptera Chironidae*."

Dave Furth introduced the speaker, Dr. Barry Knisely, of Randolf-Macon College, Virginia, who presented his research on "Tiger Beetle Conservation: Case Studies with Impacts, Management and Natural History." Dr. Knisely is using rare or endangered tiger beetles as flagship species to protect natural habitats. Tiger beetles as a group are, after butterflies, the most well studied regarding distribution, rarity, and biology in the United States, where 108 species and 211 subspecies occur. They also have a support group, which is a necessary ingredient to pursue listing by the Fish & Wildlife Service. Most tiger beetles are diurnal in open, barren habitats. Larvae are burrow-inhabiting, sit-and-wait predators in contrast to the adults who chase down their prey. The primary predators of larvae are tiphiid wasps, of adults, asilid flies, which catch them in flight. In terms of conservation needs, the official tally of listed species is one species endangered and two threatened, and three species are candidates for listing. The primary case study Dr. Knisely described was that of a subspecies endemic to the Coral Pink Sand Dunes in Utah, a state park popular with off-road vehicles that negatively impact the life cycle of the tiger beetles, which number about 2,000 individuals per year. After 8–10 years of study, Dr. Knisely's data has been pivotal in protecting, through a conservation agreement in lieu of federal listing, a critical area for the beetles, comprising about 80% of their population. Dr. Knisely also discussed two full species discovered in the 1980's that have restricted distributions. Both species are impacted by encroachment of vegetation that is closing up suitable breeding habitat. Dr. Knisely's work has been supported by the Bureau of Land Management and by the Fish and Wildlife Service. Those interested in further information are referred to the book "*The Biology of Tiger Beetles and a Guide to the Species of the South Atlantic States*" by C. B. Knisely and T. D. Schultz.

The meeting was adjourned at 8:30 p.m. Refreshments were provided by the Society.

Respectfully submitted,
Stuart H. McKamey,
Recording Secretary

1,075 Meeting—June 11, 2003

The 1075th meeting of the Entomological Society of Washington consisted of the Annual Banquet at the Uniformed Services University of Health Sciences in Bethesda, Maryland. A cash bar opened at 6:00 p.m. and the formal banquet followed at 7:00 p.m. Approximately 65 members and guests were in attendance. At 8:00 p.m. the speaker, Carll Goodpasture, an entomologist, geneticist and freelance photographer, was introduced by President-Elect Eric Grissell. The title of Carll's talk was "Entomological Crossingover: Where Art and Science Meet." The talk was illustrated with Carll's photographs and two DVD presentations. The meeting adjourned at about 9:30 p.m.

Submitted by
E. Eric Grissell,
President-Elect

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PROCEEDINGS
of the
ENTOMOLOGICAL SOCIETY
of
WASHINGTON

Volume 105

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President-Elect	E. E. Grissell
Recording Secretary	Stuart H. McKamey
Membership Secretary	Hollis B. Williams
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CANGES IN BYLAWS

The following bylaw changes were approved at the January 9,2003 regular meeting.

Article V. Section 5. The Membership Secretarty shall conduct all official correspondence of the Soceity except as otherwise provided, and shall keep a list of all members and their addresses. The Membership Secretary shall be responsible for processing application from prospective members and shall announce the names of the electee(s) at the regular meetings of the Society. The Membership Secretary shall cooperate with the Treasurer in maintaining an accurate membership list.

Remove Section 11 of Article V (Membership Chair).

Renumber Section 12 to Section 11 of Article V.

Renumber Section 13 to Section 12 of Article V.

Renumber Section 14 to Section 13 of Article V.

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
Revision of the Oriental Species of *Aphthona* Chevrolat (Coleoptera: Chrysomelidae), by Alexander S. Konstantinov and Steven W. Lingafelter. 349 pp. 2002	40.00
Revision of the Genus *Anoplophora* (Coleoptera: Cerambycidae), by Steven W. Lingafelter and E. Richard Hoebeke. 236 pp. 2002	30.00

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 *Blepharicera* Macquart (Diptera: Blephariceridae) of Eastern North America, by Gregory W. Courtney. 99 pp. 2000	14.00
No. 24	Holcocerini of Costa Rica (Lepidoptera: Gelechioidea: Coleophoridae: Blastobasinae), by David Adamski. 147 pp. 2002	18.00

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 on all 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, MRC 168, Smithsonian Institution, Washington, D.C. 20560-0168.

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