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The Nocturnal Bee Genus *Megaloptidia* (Hymenoptera: Halictidae)

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Abstract.—The nocturnal augochlorine bee genus *Megaloptidia* is revised and three species recognized; *Megaloptidia contradicta* (Cockerell), *M. nocturna* (Friese), and **M. saulensis Engel and Brooks** new species. The genus is newly diagnosed, distributional data given, and the male completely described for the first time. The first flower record for a species of this genus is given as *Dichorisandra ulei* (Commelinaceae). A lectotype and two paralectotypes are designated for *M. contradicta*. *Megalopta angusticeps* Friese is considered a junior synonym of *Megaloptidia nocturna* (new synonymy). *Megalopta pallitarsus* Friese, previously considered to be a species of *Megaloptidia*, is in fact a junior synonym of *Megommation insigne* (Smith) (new synonymy).

The neotropical halictine genus *Megaloptidia* Cockerell consists of three, rarely collected, nocturnal bees of the tribe Augochlorini. Individuals of *Megaloptidia* can be captured at lights during the night, however, aside from their nocturnal habit, the biology of *Megaloptidia* species remains unknown. One female of *Megaloptidia nocturna* (Friese 1926), however, has been collected at flowers of the monocotyledon *Dichorisandra ulei* (Commelinaceae). Members of *Dichorisandra* are nectarless and it is therefore believed that pollen is the only reward for floral visitors. *Dichorisandra* species possess poricidal anthers, suggesting "buzzing" as the means of freeing the pollen (i.e., the bee grasps the anther and buzzes its wings, thus translating the vibration to the anther and releasing the pollen through the apical pore). Most augochlorine species which have been studied are known to be buzz pollinators (e.g., Michener 1962, Rêgo and Albuquerque 1989, Renner 1989) and, in fact, the related *D. hexandra* is recorded to be buzz pollinated by the diurnal augochlorines *Augochloropsis* (*Paraugochloropsis*) *cupreola* (Cockerell 1900) and *Pseudaugochlora gra-*

minea (Fabricius 1804) (Sigrist and Sazima 1991). Within the Commelinaceae, *Dichorisandra* species are among the only ones to be open during the night (e.g., *D. hexandra* opens before dawn in southern Brazil) (Sigrist and Sazima 1991), making them suitable targets for nocturnal or crepuscular insects. Among related bee genera, floral associations are only known for *Megommation* (s. str.) (Moure 1943) which has been recorded at species of *Bauhinia* (Fabaceae) (Friese 1926) and *Ipomoeae* (Convolvulaceae) (Jörgensen 1912). There is nothing about the floral morphology of any of these plants which seems to readily explain the peculiarly modified mouthparts of these genera, which are extremely narrowed with a distinctly pointed galeal apex.

Megaloptidia was originally described by Cockerell (1900) as a subgenus of the common nocturnal augochlorine genus *Megalopta* Smith (1853) owing to its superficial similarity to this group. Cockerell distinguished his subgenus on the basis of wing venation. Moure (1958) redescribed the group, according it generic status for the first time, and recognized its affinity with

his genus *Megommation*. Eickwort (1969), in a revision of the genera and subgenera of Augochlorini, provided a more thorough description of the genus; however, he did not have the opportunity to examine the male terminalia thus the distal male sterna and genitalia remained undescribed. The genus is closely allied to the genera *Ariphanarthra* (Moure 1951), *Megommation* (s. lato), and *Micrommation* (Moure 1969). All of these genera share the distinctly narrowed labiomaxillary complex, pointed galeal apex, orthogonal epistomal sulcus, absence of the male labral distal process, narrow spiculum on the male eighth sternum, and the presence of a parapenial lobe in the male genitalia. The phylogenetic position of *Megaloptidia* will be further elaborated on in a forthcoming paper concerning the entire tribe (Engel in prep).

Herein we provide new descriptions for the genus and all included species. The male is thoroughly described for the first time and a key is presented for the identification of all three species.

MATERIAL AND METHODS

The following abbreviations are used for institutions where material used in this study is deposited: American Museum of Natural History, New York, New York, J.G. Rozen, Jr. (AMNH); Carnegie Museum of Natural History, Pittsburgh, Pennsylvania, R.L. Davidson (CMNH); Field Museum of Natural History, Chicago, Illinois, P.P. Parrillo (FMNH); Cornell University Insect Collection, Ithaca, New York, J.K. Liebherr and E.R. Hoebeke (CUIC); Natural History Museum of Los Angeles County, Los Angeles, California, R.R. Snelling (LACM); Instituto de Investigacíon de Recursos Biológicos, Alexander von Humboldt, Santa Fé de Bogotá, Colombia, F. Fernández (UNCB); Instituto Nacional de Pesquisas da Amazônia, Manaus, Amazonas, Brazil (INPA); Museo de Invertebrados 'G.B. Fairchild', Universidad de Panamá, Estafeta Universitaria,

Panamá City, Panamá, D. Quintero (MIUP); Museu Entomologico de Universidade Federal de Viçosa, Viçosa, Minas Gerais, Brazil (UFVB); Museum für Naturkunde, Humboldt-Universität, Berlin, Germany, F. Koch, A. Kleine-Möllhoff (ZMHB); United States National Museum, Smithsonian Institution, Department of Entomology, Washington, D.C., R.J. McGinley (USNM); Division of Entomology, Natural History Museum, University of Kansas, Lawrence, Kansas, R.W. Brooks (SEMC); G.A.R. Melo collection (GARM); Philadelphia Academy of Natural Sciences, Philadelphia, Pennsylvania, D. Azuma (ANSP).

A total of 67 specimens of *Megaloptidia* were located and examined in the course of this study. All measurements were made using an ocular micrometer on a WILD-M5a microscope. The abbreviation "o.d." in the descriptions refers to "ocellar diameter" and relates the approximate length of setae to the diameter of the median ocellus. S1, T1, and F1 are given as abbreviations for first metasomal sternum, first metasomal tergum, and first flagellomere respectively.

Genus *Megaloptidia* Cockerell

Megalopta (Megaloptidia) Cockerell 1900: 373. Type species: *Megalopta (Megaloptidia) contradicta* Cockerell 1900, by monotypy and original designation. Moure 1958: 180. Eickwort 1969: 442.

Diagnosis.—Individuals of *Megaloptidia* are robust bees which superficially resemble in general habitus species of the larger nocturnal genus *Megalopta* and the sole species of *Megommation* (s. str.). *Megaloptidia* differs from the former genus in the narrowed labiomaxillary complex, the serrate inner hind tibial spur, the irregular spacing of the distal hamuli, the narrow gena, the unmodified labral distal keel, the orthogonal epistomal sulcus, and the absence of lateral notches on the male S4. *Megommation* differs from *Megaloptidia* in the acute marginal cell apex, the deeply

concave clypeal apex, the extremely short and weakly border basitibial plate, and the medioapical processes on the male S3–4.

Description.—The following description is based on all three included species. FEMALE: Epistomal sulcus orthogonal. Clypeus and supraclypeal area strongly bowed, as in *Megommation* (Fig. 2). Malar space short. Mid-region of face gently sunken around antennal socket. Preoccipital ridge rounded. Inner orbit of compound eye strongly emarginate; eyes greatly enlarged, much broader than gena in profile (Figs. 2, 8, 14, 19); eye hairs short. Ocelli greatly enlarged (Figs. 1, 7, 13, 18), without impressed line running between lateral ocelli. Vertex extremely short, barely an ocellar diameter in length, usually less. Labral basal elevation orbicular, protuberant in profile, distal process narrowly triangular, labral teeth absent (Fig. 1). Mandible broad, subapical tooth well defined (Fig. 1). Hypostomal ridge carinate, not projecting beyond posterior margin of head, anterior angle rounded. Mouthparts greatly narrowed, approximately 10 times longer than wide (Fig. 4). Galeal base reaching to base of stipes, apex pointed, inner strip with setae; galeal comb absent; maxillary palp not greatly lengthened. V-shaped brace of salivary plate absent; combined length of labial palp segments 2 and 3 shorter than 1. Pronotal lateral angle obtuse, not produced; lateral and dorsal ridges rounded. Mesoscutum broadly rounded anteriorly; mesoscutal lip low and rounded. Tegula rounded. Propodeal dorsal ridge rounded; lateral ridge carinate, ridges slightly divergent; propodeum slightly narrowed posteriorly; pit of posterior face narrow. Wing hairs long; apex of marginal cell truncate (Fig. 3). Anterior basitarsal brush present. Inner hind tibial spur serrate, serrations sharp (Fig. 5). Basitibial plate narrowly rounded, all borders well defined. Division of T5 narrow. MALE: As for the female with the following modifications. Antenna of moderate length, reaching to posterior border of mesoscutum; scape long; F2 shorter than F1; sensory plate areas present. Labral basal elevation absent; distal process absent. Gradulus of T7 absent. S4 with depression along posterior margin. S8 with posterior margin produced into a short, blunt median projection; spiculum narrow. Gonobasal bridge narrow; dorsal lobes strong. Dorsal gonostylus a long thin process. Basal process of gonostylus absent. Parapenial lobe present. Ventral prong of penis valve present.

KEY TO SPECIES OF *MEGALOPTIDIA*

1. Propodeal lateral surface strongly punctured, punctures almost contiguous; length of propodeal triangle approximately equal to that of metanotum; mesepisternum strongly and closely punctured, punctures separated by less than a puncture width; integument between smooth (excluding hypoepimeron); mesoscutum punctured contiguously, integument between imbricate . . . . **M. contradicta** (Cockerell)
   – Propodeal lateral surface imbricate with punctures separated by 2–3 puncture widths; length of propodeal triangle little to much greater than that of metanotum; sculpturing of mesepisternum and mesoscutum variable, but mesoscutum never strongly punctured 2
2. Labrum and clypeus amber; mesepisternum minutely punctured, punctures separated by 3–4 times puncture width, at least on posterior half, integument between smooth or imbricate (excluding hypoepimeron); mesoscutum minutely punctured, punctures separated by 2–3 times puncture width; lateral ocellus almost touching compound eye, ocellocular distance 0.25 o.d. in female (Fig. 1), 0.33 o.d. in male (Fig. 7); frontal line very weakly produced in profile in female (Fig. 2); median ocellus wider than interantennal distance in female (Fig. 1); scopal hairs of hind femur and tibia amber . . . . **M. nocturna** (Friese)
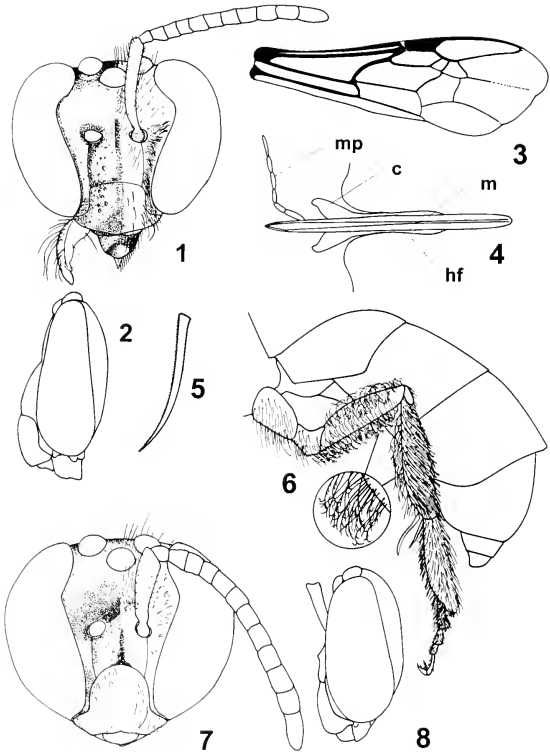
Figs. 1–8. *Megaloptidia nocturna* (Friese), 1–6 female, 7–8 male. 1, 2, head, front and side views respectively. 3, fore wing. 4, mouthparts excluding labium, ventral view, mp = maxillary palps, c = cardo, m = maxilla, hf = hypostomal fossa. 5, inner hind tibial spur. 6, hind leg and metasoma, side view, circle enlargement shows scopal hairs on S2 and S3. 7, 8, head, front and side views, respectively.

– Labrum and clypeus dark brown; mesepisternum closely and weakly punctured, punctures separated by less than a puncture width (excluding hypoepimeron); mesoscutum punctured, punctures weak and separated by 2–3 puncture widths centrally, laterally becoming separated by less than a puncture width; lateral ocellus removed from compound eye 0.5 o.d. (Fig. 18); frontal line protuberant in profile (Fig. 19); median ocellus narrower than interantennal distance (Fig. 18); scopal hairs of hind tibia black (those of femur amber) . .
.... *M. saulensis* n. sp.

Megaloptidia contradicta (Cockerell)
(Figs. 13–17, 20)

Megalopta (*Megaloptidia*) *contradicta* Cockerell 1900: 373. Schrottky 1902: 407. Friese 1926: 124.
Megaloptidia contradicta (Cockerell); Moure 1958: 180.

Diagnosis.—Labrum and apical ¾ of clypeus amber. Mesoscutum closely and coarsely punctured, punctures separated by less than a puncture width, except over central disc punctures becoming weaker and separated by 1–3 times a puncture width. Mesepisternum closely punctured, punctures separated by less than a puncture width, integument between punctures smooth; hypoepimeron smooth with a few widely spaced minute punctures. Scopal hairs of hind leg fuscous. Propodeal lateral surface strongly punctured, punctures nearly contiguous; length of propodeal triangle equal to that of metanotum. Only three specimens of this species were located, all from Cockerell's type series.

Description.—The following description is based on the lectotype. MALE: Total body length 11.3 mm; forewing length 8.6 mm. Head wider than long (Fig. 13). Distal margin of clypeus barely projecting below lower tangent of compound eye (Fig. 14); supraclypeal area wider than long, 0.59 times length of clypeus. Frontal line carinate from just below antennal sockets to just above sockets, ending at this point. Measurements of head of lectotype in mm: width 3.0; length (to apex of clypeus) 2.5; clypeal length 0.8; lower interorbital distance 0.9; upper interorbital distance 1.2;

interantennal distance 0.4; antennocellar distance (to median ocellus) 0.6; between lateral ocelli 0.4; median ocellus to lateral ocellus 0.1; lateral ocellus to compound eye 0.16; prementum length 1.9, width 0.18. Scape reaching past lateral ocellus, length 1.1; pedicel slightly longer than wide, length 0.2, width 0.18; F1 longer than wide and longer than F2, length 0.26, width 0.2; F2 as long as wide, length-width 0.22; F3–9 each longer than wide, individual lengths 0.24, widths 0.22; F10 longer than wide and longer than immediately preceding flagellomeres, length 0.26, width 0.22; F11 longer than wide and longer than all previous flagellomeres, length 0.42, width 0.22. Median line strongly impressed; parapsidal lines weak. Intertegular distance 2.2. Propodeal triangle about as long as metanotum, much shorter than scutellum. Basal vein distad cu-a by 2.5 times vein width; 1r-m basad 1m-cu by vein width; 2r-m distad 2m-cu by 4.5 times vein width, 2r-m weakly curved. First submarginal cell longer than second and third combined; second narrowed anteriorly; anterior border of third along Rs almost 2 times as long as anterior border of second, posterior border of third 2 times longer than anterior border; marginal cell length 1.2, width 0.3. Distal hamuli arranged 3-1-1-3. S5 apically emarginate and bent ventrally (Fig. 15). S6 apically emarginate and mediolongitudinally concave (Fig. 15). Male terminalia as in figures 16 and 17.

Clypeus and supraclypeal area finely imbricate, with a few weak punctures separated by 1–3 puncture widths on lateral borders. Face minutely and closely punc-
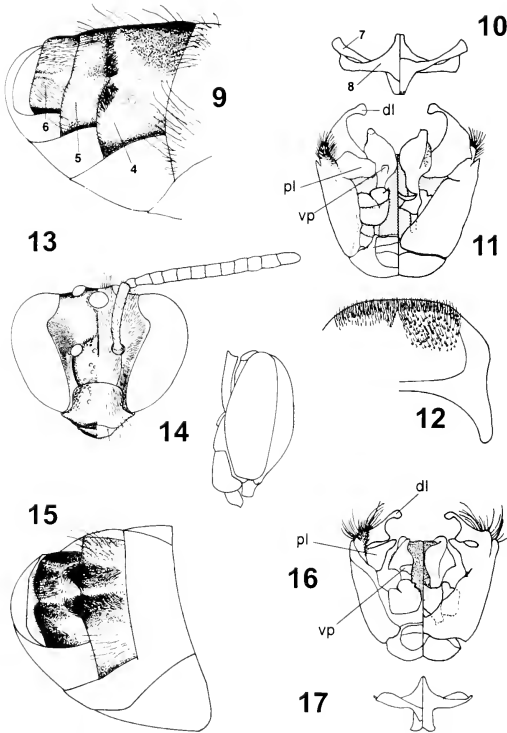
Figs. 9–17.   *Megaloptidia nocturna* (Friese), 9–12 male; *Megaloptidia contradicta* (Cockerell), 13–17 male. 9, metasoma, apical half, oblique view, numbers refer to sterna. 10, S7 and S8, dorsal view is right half and ventral view is left. 11, genital capsule, dorsal view is right half and ventral view is left, dl = dorsal gonostylar process, pl = parapenial lobe, vp = ventral prong of penis valve. 12, S6, ventral view. 13, 14, head, front and side views, respectively. 16, genital capsule, dorsal view is right half and ventral view is left. 17, S7 and S8, ventral view is right half and dorsal view is left.

tured, integument between imbricate. Vertex smooth and impunctate. Gena and postgena impunctate and finely imbricate. Pronotum finely imbricate. Mesoscutum closely and coarsely punctured, punctures separated by a puncture width or less, integument between punctures imbricate, medially punctures becoming weaker and more widely spaced, separated by 1–3 punctured widths. Scutellum with minute punctures separated by 1–2 puncture widths, integument between smooth. Metanotum sparsely and weakly nodulate, integument otherwise smooth. Preepisternum and mesepisternum closely punctured, punctures separated by a puncture width or less, integument between smooth. Hypoepimeron smooth, with a few minute punctures separated by 4–5 puncture widths. Metepisternum smooth. Propodeal triangle imbricate; lateral surface closely punctured, punctures separated by less than a puncture width; posterior surface smooth. Terga and sterna imbricate.

Head dark brown with a few weak blue-green highlights; labrum and apical three-quarters of clypeus amber; mandible dark brown; antennae brown. Mesosoma and metasoma dark brown; tegula amber and translucent along outer margins; legs dark brown, except amber on protarsus, apical four mesotarsomeres, and apical 2 metatarsomeres.

Pubescence generally pale or fuscous, fuscous hairs mostly on mesosoma and apical terga of metasoma. Scattered simple hairs (1 o.d.) on face, with suberect branched hairs (0.5 o.d.) along inner margins of compound eyes. Similar suberect and simple hairs on gena. Postgena with a few simple hairs (1.5–2 o.d.) on lateral and posterior borders. Hairs of face, gena, and postgena pale, those of vertex becoming fuscous. Pronotum with scattered simple hairs (1 o.d.) and laterally with extremely short, appressed branched hairs not obscuring the surface. Mesoscutum with scattered simple hairs (1 o.d.) and

shorter (less than 0.5 o.d.) branched hairs on lateral and posterior borders. Scutellum and metanotum with sparse simple hairs (1.5 o.d.). Pleura with scattered simple pale hairs (1–1.5 o.d.) and shorter (0.5 o.d. or less) suberect branched hairs. Hairs of forelegs pale or golden, outer margins with simple hairs (1–1.5 o.d.); mid legs with pale hairs except fuscous on basitarsus and outer margin of tibia, hairs simple, small tuft of closely packed hairs (1 o.d.) on inner basal margin of femur; hair of hind legs mostly fuscous, inner surface of basitarsus with stiff black hairs (1–1.5 o.d.). Terga with scattered simple hair (1–1.5 o.d.), becoming longer on lateral margins and more distal terga. Sterna with sparse simple hair (1–2.5 o.d.); hairs of S4 longest and concentrated on borders of apical depression and medially towards basal border; S5 with pair of apical submedian hair tufts (Fig. 15); hairs of S6 most numerous, more dense laterally (Fig. 15).

FEMALE: Unknown.

Type material.—BRAZIL: Pará: Lectotype #345, male, Benevides [1°22'S, 48°15'W], July (CMNH). Paralectotype, male, Santarem (CMNH). Paralectotype, male, Santarem, but lacking all metasomal segments except T1 and S1 and both antennae leaving only the scape, pedicel, F1 and F2 (ANSP).

Remarks.—In 1957 Padre Jesus S. Moure examined the material listed above and placed lectotype labels on the specimens, however, he failed to publish lectotype designations for this species. We now designate lectotype and paralectotypes for *Megaloptidia contradicta* using the same specimens. The lectotype specimen now bears a new label reading "LECTOTYPE: *Megalopta (Megaloptidia) contradicta* Cockerell, 1900; desig. M. Engel & R. Brooks", and the paralectotypes now have similar labels.

In Eickwort's (1969) study of the Augochlorini he referred to a male of *M. contradicta* (the paralectotype from ANSP des-

ignated above) along with a series of females he considered as possibly belonging to *M. contradicta*. This series of females from the AMNH are, in actuality, all of *M. nocturna*.

Megaloptidia nocturna (Friese)
(Figs. 1–12, 20)

Megalopta nocturna Friese 1926: 127.
Megalopta angusticeps Friese 1926: 127. **New synonymy.**
Megaloptidia nocturna (Friese); Moure and Hurd 1987: 242.
Megaloptidia angusticeps (Friese); Moure and Hurd 1987: 241.

Diagnosis.—Labrum and clypeus amber. Mesoscutum minutely punctured, punctures separated by 2–3 times a puncture width. Mesepisternum minutely punctured, otherwise integument smooth or imbricate; hypoepimeron as on mesepisternum although punctures more widely spaced. Scopal hairs of hind femur and tibia amber. Propodeal lateral surface imbricate with punctures separated by 2–3 times a puncture width; length of propodeal triangle little to much greater than that of metanotum. This is the most common of the three species with 62 specimens examined during the course of this study.

Description.—The following description is based on Friese's holotypes. MALE: Total body length 13.3 mm; forewing length 8.3 mm. Head wider than long (Fig. 7). Distal margin of clypeus barely projecting below lower tangent of compound eye (Fig. 8); supraclypeal area wider than long, 0.68 times length of clypeus. Frontal line carinate from just below antennal sockets to just above sockets, ending with acute projection (Fig. 8). Measurements of head of holotype in mm: width 2.8; length (to apex of clypeus) 2.5; clypeal length 0.8; lower interorbital distance 0.8; upper interorbital distance 1.1; interantennal distance 0.3; antennocellar distance (to median ocellus) 0.5; between lateral ocelli 0.3; median ocellus to lateral ocellus 0.04;

lateral ocellus to compound eye 0.08; prementum length 2.1, width 0.2. Scape reaching past lateral ocellus, length 1.0; pedicel slightly longer than wide, length 0.2, width 0.18; F1 longer than wide and longer than F2, length 0.24, width 0.18 (Fig. 7); F2 as long as wide, length–width 0.2; F3 and F4 each longer than wide, individual lengths 0.22, widths 0.2; F5 longer than wide, length 0.24, width 0.2; F6 longer than wide, length 0.26, width 0.2; F7 and F8 longer than wide, individual lengths 0.28, widths 0.2; F9 and F10 longer than wide, individual lengths 0.3, widths 0.2; F11 longer than wide and longer than preceding flagellomeres, length 0.44, width 0.2. Median line strongly impressed; parapsidal lines weak. Intertegular distance 1.8. Propodeal triangle longer than metanotum, slightly shorter than scutellum. Basal vein distad cu-a by vein width; 1r-m distad 1m-cu by 5 times vein width, intersecting second submarginal cell about half way through cell; 2r-m distad 2m-cu by 2 times vein width, 2r-m weakly curved. First submarginal cell longer than second and third combined; second narrowed anteriorly; anterior border of third along Rs about as long as anterior border of second, posterior border of third 2 times longer than anterior border; marginal cell length 2.5, width 0.5. Distal hamuli arranged 3-1-3. Male terminalia as in figures 10 and 11.

Clypeus and supraclypeal area finely imbricate, with a few weak punctures separated by 1–2 puncture widths on lateral borders. Face imbricate. Vertex smooth and impunctate. Gena sparsely and weakly nodulate, otherwise smooth. Postgena smooth. Pronotum smooth. Mesoscutum minutely punctured, punctures separated by 2–3 times puncture width, integument between punctures smooth and shining. Scutellum as on mesoscutum. Metanotum sparsely and weakly nodulate, integument otherwise smooth. Pre-episternum and mesepisternum minutely punctured, punctures separated by 3–4 times punc-

ture width, integument between smooth; hypoepimeron as on mesepisternum except minute punctures separated by 4 times puncture width. Metepisternum smooth. Propodeal triangle imbricate; lateral surface imbricate, with punctures separated by 2–3 puncture widths; posterior surface smooth. Terga and sterna imbricate, except T1 which is smooth.

Head dark brown with strong metallic green highlights; labrum and clypeus amber; mandible amber except red at apex; antennae brown. Mesosoma dark brown with strong metallic green highlights, except pronotum light brown and without such highlights. Legs pale brown. Metasoma dark brown.

Pubescence golden. Scattered simple hairs (1–1.5 o.d.) on face, with suberect branched hairs (0.5 o.d.) along inner margins of compound eyes. Similar suberect and simple hairs on gena, branched hairs becoming longer towards postgena. Postgena with scattered branched hairs (2 o.d.). Pronotum with scattered simple hairs (1 o.d.) and laterally with extremely short, appressed hairs. Mesoscutum with scattered simple hairs (1 o.d.) and shorter (less than 0.5 o.d.) branched hairs on lateral and posterior borders. Scutellum and metanotum with sparse simple hairs (1.5–2 o.d.) and more numerous shorter simple hairs (0.5 o.d.). Pleura with scattered simple pale hairs (1–1.5 o.d.) and shorter (0.5 o.d. or less) suberect branched hairs; metepisternum without longer simple hairs. Pubescence of legs simple (1–2 o.d.) Terga with scattered simple hair (1 o.d.), becoming longer on lateral margins and apical terga. Sterna with sparse simple hair (0.5–1.5 o.d.); S4 with a few simple hairs (0.5 o.d.) concentrated on borders of apical depression (Fig. 9); hairs of S6 most numerous, laterally more dense than median area.

FEMALE: As for the male with the modifications indicated below. Measurements from female type of M. angusticeps. Total body length 12.2 mm; forewing

length 8.7 mm. Head as in figures 1 and 2. Supraclypeal area 0.8 times length of clypeus. Head width 3.0; length (to apex of clypeus) 2.7; clypeal length 0.8; lower interorbital distance 0.9; upper interorbital distance 1.1; interantennal distance 0.3; antennocellar distance (to median ocellus) 0.6; between lateral ocelli 0.3; median ocellus to lateral ocellus 0.04; lateral ocellus to compound eye 0.08; prementum length 2.2, width 0.2. Scape reaching past lateral ocellus, length 1.4; pedicel slightly longer than wide, length 0.2, width 0.18; F1 longer than wide and longer than F2, length 0.24, width 0.22; F2 wider than long, length 0.2, width 0.22; F3 and F4 each as long as wide, individual lengths-widths 0.22; F5 and F6 longer than wide, lengths 0.24, widths 0.22; F7 and F8 longer than wide, lengths 0.26, widths 0.22; F9 longer than wide, length 0.3, width 0.22; F10 longer than wide and longer than previous flagellomeres, length 0.44, width 0.22. Intertegular distance 2.1. Wing as in figure 3; basal vein distad cu-a by vein width; 1r-m confluent with 1m-cu; 2r-m distad 2m-cu by 5 times vein width, 2r-m weakly curved. First submarginal cell longer than second and third combined; second narrowed anteriorly; anterior border of third along Rs slightly longer than anterior border of second, posterior border of third 2 times longer than anterior border; marginal cell length 2.6, width 0.6. Distal hamuli arranged 3-1-3.

Mesoscutum minutely punctured, punctures separated by 3–4 times puncture width, integument between punctures weakly imbricate and shining. Terga and sterna weakly imbricate, except T1 which is smooth.

Head dark brown with strong metallic green highlights; labrum and clypeus amber; supraclypeal area light brown medially; mandible amber except black at apex. Mesoscutum, scutellum, metanotum and propodeum brown with strong metallic green highlights; pronotum and pleura amber with metallic green highlights

fainter than those of mesoscutum. Legs amber. Terga amber, except apical margins brown; sterna amber.

Pubescence golden. Scattered simple hairs (1–1.5 o.d.) on face. Gena and postgena with branched hairs (1.5–2 o.d.). Pubescence of fore- and mid-legs as in male; hind legs with scopa formed of plumose hairs (2.5–3.5 o.d.) on trochanter, femur and inner margin of tibia. Terga with scattered simple hair (1–1.5 o.d.), becoming longer on lateral margins and apical terga. Sterna with sparse simple hair (1–1.5 o.d.).

Type material.—BRAZIL: Amazonas: Holotype, male, Faro, 23 January 1910, Ducke (ZMHB).

Additional material.—BRAZIL: Amazonas: 1 male, Parintins, 9 October 1919, Parish (FMNH). 1 male, Beruri, Rio Purus, 15 October 1991, G.A.R. Melo, sitting under leaf (GARM). 6 females, Hwy. BR 174, 86 km N Manaus, ZF6 km 9, 2°16'S, 59°56'W, 3 July 1986, M.V.B. Garcia, attracted to propane lantern at night (UFVB); 5 females, same except 4 July 1986 (UFVB); 2 females, same except (SEMC). 3 females, Reserva Ducke, 26 km NE Manaus, Itacoatiara Hwy., 12–23 May 1972, Munroe (SEMC). 2 males, Autaz-Mirim, Faz. São Lucas, 25 August 1994, João Vidal, malaise trap (INPA); 2 males, same except (SEMC); 1 male, same except 28 October 1994 (INPA). 1 female, Campus Universitario, Manaus, 7–24 September 1988, M. Castilho, J. Elias Bindo, Shannon trap, baited with feces (INPA). 2 females, Mun. Itacoatiara, Faz. Aruanã, AM010 km 215, 19–21 September 1990, C. Motta, R. Andreazze, R. Ferreira (INPA); 2 females, same except 18–19 September 1990, light trap (INPA). 1 female, Reserva Ducke, 9–22 September 1994, J. Rafael, J. Vidal, suspended malaise trap, 20 m (INPA). 1 female, Manaus, Campus Universitario, 21 June 1982, J. Rafael, malaise trap (INPA). 1 female, 26 km NE Manaus, Reserva Ducke, 6 October 1988, J. Raphael, suspended malaise trap, 10 m (INPA); 1 female, same except 9 May 1978, light trap,

J. Arias, N. Penny (INPA). 1 female, Rio Jau, Meriti, Mun. Novo Airão, 4–10 June 1994, J. Raphael (INPA). Pará: 4, females, Val de Cans. Belem., 20–21 November 1963, Oliveira, Wygodzinsky, at light (AMNH). 1 male, Baker (LACM). COLOMBIA: Dpto. Guaviare: 1 female, 1 male, Nukak Maku, Cerro Moyano, 200 m, 12 November 1995, malaise trap, F. Fernández (UNCB). ECUADOR: Sucumbios: 1 female, 0.5°S, 76.5°W, 290 m, Sacha Lodge, 13–23 June 1994, P. Hibbs, malaise trap (LACM). FRENCH GUIANA: 1 female (holotype of *Megaloptidia angusticeps*), Nouveau Chantier, Collection le Moult, June (ZMHB). 1 female, Saint-Laurent, du Maroni (AMNH). 1 female, Saül, 3°37'N, 53°12'W, 13–18 April 1983, S. Mori, ex: light trap (AMNH). 2 males, Roura, 18.4 km SSE, 240 m., 4°36'38"N, 52°13'25"W, 25–29 May 1997, J.S. Ashe and R.W. Brooks, FG1AB97-081, ex: flight intercept trap (SEMC). 1 male, Roura, 27.4 km SSE, 280 m., 4°44'20"N, 52°13'25"W, 23–24 May 1997, J.S. Ashe and R.W. Brooks, FG1AB97-022, ex: flight intercept trap (SEMC). 1 male, Roura, 27.4 km SSE, 280 m., 4°44'20"N, 52°13'25"W, 10 June 1997, J.S. Ashe and R.W. Brooks, FG1AB97-177, ex: flight intercept trap (SEMC). 1 male, Matoury, 41.5 km SSW on Hwy N2, 50 m., 4°37'22"N, 52°22'35"W, 29 May–9 June 1997, J.S. Ashe and R.W. Brooks, FG1AB97-170, ex: flight intercept trap (SEMC). GUYANA: Mazaruni-Potaro District: 1 female, Kartabo Point, 25–27 December 1983, W. Steiner, J. Byrd, J. Hill, F. Holtzclaw, malaise trap at edge of secondary forest and farmed field (USNM). PERU: Cuzco: 1 male, Quince Mil, 750 m, September 1962, L. Peña (CUIC). Huánuco: 1 female, Tingo Maria, 21 February 1972, J. Schuster, on flower of *Dichorisandra ulei*, 5:53am (CUIC). Madre de Diós: 1 male, Estacíon Pakítza, Reserva Manu, 18 June–4 July 1993, R. Cambra, T. Amorilla (MIUP). 1 female, Rio Tambopata Res., 30 air km SW Pto. Maldonaldo, 290 m, 16–20 November 1979, J. Heppner, subtropical
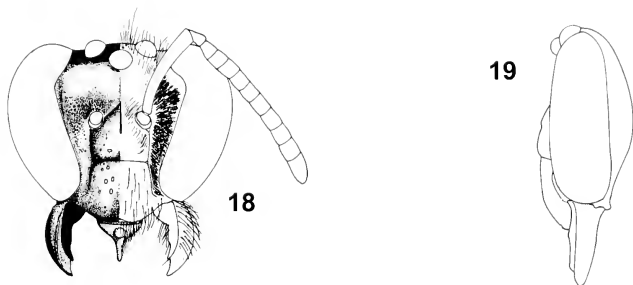
Figs. 18–19. *Megaloptidia saulensis* Engel & Brooks n. sp., 18, 19, female head, front and side views respectively.

moist forest (USNM). SURINAME: 3 females, Raleigh Vallen-Voltzberg Research Foengoe 4°43′N, 56°12′W, 26 January–15 February 1982, J. Carpenter, D. Trail (CUIC). VENEZUELA: Amazonas: 2 females, San Carlos de Río Negro, 1°56′N, 67°3′W, 6–12 December 1984, R. Brown (CUIC). 3 females, Camp IV, 0°58′N, 65°57′W, Cerro de la Neblina, 760 m, 15–18 March 1984, O.S. Flint, Jr., malaise trap over dry stream channel (USNM).

Flower records.—One female of *M. nocturna* has been collected on *Dichorisandra ulei* (Monocotyledonae: Commelinaceae), although there was no pollen in her scopa. This is the first floral association recorded for any species of *Megaloptidia*.

Variation.—As typical of nocturnal bees, *Megaloptidia nocturna* is lightly melanized throughout most of its Amazonian range. However, at the western edge of its distribution the male specimen from Colombia is light yellow brown and noticeably lighter than the brown Brazilian male specimens. This is odd since a female caught in the same trap on the same day is darker than the normal color of the Brazilian female specimens. The male specimen from Peru, Madre de Diós is almost black and much darker than the Brazilian material.

Megaloptidia saulensis Engel and Brooks, new species
(Figs. 18–20)

Diagnosis.—Labrum and clypeus dark brown. Mesoscutum weakly punctured, punctures separated by 2–3 times a puncture width over central disk, laterally punctures separated by less than a puncture width. Mesepisternum closely and weakly punctured, punctures separated by less than a puncture width; hypoepimeron with minute punctures separated by 2–3 times a puncture width. Scopal hairs of hind tibia black, those of femur amber. Propodeal lateral surface imbricate with punctures separated by 2–3 times a puncture width; length of propodeal triangle little to much greater than that of metanotum. This species is only known on the basis of two females.

Description.—The following description is based on the holotype. FEMALE: Total body length 12.4 mm; forewing length 8.8 mm. Head wider than long (Fig. 18). Distal third of clypeus projecting below lower tangent of compound eye (Figs. 18, 19);

supraclypeal area wider than long, 0.58 times length of clypeus. Frontal line carinate from below antennal sockets to just above sockets, ending with an acute projection and protuberant in profile (Fig. 19). Measurements of head of holotype in mm: width 3.4; length (to apex of clypeus) 2.8; clypeal length 1.0; lower interorbital distance 1.1; upper interorbital distance 1.4; interantennal distance 0.4; antennocellar distance (to median ocellus) 0.6; between lateral ocelli 0.4; median ocellus to lateral ocellus 0.08; lateral ocellus to compound eye 0.2 mm; prementum length 2.0, width 0.2. Scape reaching past lateral ocellus, length 1.5; pedicel slightly longer than wide, length 0.24, width 0.18; F1 longer than wide and longer than F2, length 0.26, width 0.22 (Fig. 18); F2 as long as wide, length-width 0.2; F3–6 each longer than wide, individual lengths 0.22, widths 0.2; F7 and F8 each longer than wide, individual lengths 0.24, widths 0.22; F9 longer than wide, individual lengths 0.26, widths 0.24; F10 longer than wide and longer than preceding flagellomeres, length 0.4, width 0.24. Median line strongly impressed; parapsidal lines weak. Intertegular distance 2.5. Propodeal triangle slightly longer than metanotum, about half length of scutellum. Basal vein distad of cu-a by vein width; 1r-m basad 1m-cu by vein width; 2r-m distad 2m-cu by 3 times vein width, 2r-m straight. First submarginal cell longer than second and third combined; second narrowed anteriorly; anterior border of third along Rs as long as anterior border of second, posterior border of third 2.5 times longer than anterior border; marginal cell length 2.4, width 0.6. Distal hamuli arranged 4-1-1-1-4.

Clypeus and supraclypeal area finely imbricate, with a few weak punctures separated by 1–2 puncture widths on lateral borders. Face imbricate with a few weak punctures along border with compound eye. Vertex, gena, and postgena smooth and impunctate. Pronotum weakly imbricate. Mesoscutum punctured, punctures separated by 2–3 times puncture width, integument between punctures imbricate and shining, except laterally punctures separated by less than a puncture width. Scutellum with sparse, minute punctures, integument smooth. Metanotum sparsely and weakly nodulate, integument otherwise weakly imbricate. Pre-episternum and mesepisternum punctured, punctures separated by less than a puncture width, integument between smooth; hypoepimeron as on mesepisternum except minute punctures separated by 2–3 times puncture width. Metepisternum smooth with a few minute punctures sparsely scattered. Propodeal triangle imbricate; lateral surface imbricate with punctures separated by 2–3 puncture widths; posterior surface smooth. Terga and sterna imbricate.

Head dark brown with metallic blue-green highlights, except labrum, mandible, clypeus, supraclypeal area without such highlights. Mesosoma dark brown without highlights, except scutellum, metanotum, and propodeal triangle amber. Legs brown. Metasoma dark brown.

Pubescence pale to golden. Scattered simple hairs (1–1.5 o.d.) on face, with suberect branched hairs (0.5 o.d.) along inner margins of compound eyes. Similar simple hairs on gena, hairs becoming longer towards postgena; postgena with scattered simple hairs (2 o.d.). Pronotum with scattered simple hairs (1 o.d.) and laterally with extremely short, appressed hairs. Mesoscutum with scattered simple hairs (1 o.d.) and shorter (less than 0.5 o.d.) branched hairs on lateral and posterior borders. Scutellum with sparse simple hairs (1.5–2 o.d.) and more numerous shorter simple hairs (0.5 o.d.). Longer hairs of mesoscutum and scutellum fuscous. Metanotum with sparse simple hairs (1.5–2 o.d.). Pleura with scattered simple hairs (1–1.5 o.d.) and shorter (0.5 o.d. or less) suberect branched hairs; metepisternum with longer simple hairs more dense on ventral half; pubescence of pre-episternum fuscous, remainder pale. Pubescence

Fig. 20. Distribution of *Megaloptidia* species. Circles represent locality records for *M. nocturna* (Friese), squares for *M. contradicta* (Cockerell), and the single triangle for *M. saulensis* Engel & Brooks.

of legs simple and amber (1–2 o.d.), except tarsomeres 1 and 2 (of all legs), apex of protibia, and entirety of mesotibia and metatibia, including tibial scopa. Terga with scattered simple hairs (1 o.d.), becoming progressively longer on lateral margins and more distal terga. Sterna with sparse simple hairs (1.5–2.5 o.d.), most with a few branches.

MALE: Unknown.

Type material.—FRENCH GUIANA: Holotype, female, Saül, 3°37′N, 53°12′W, 1983, S. Mori, #158 (AMNH). 1 paratype female, Saül, 3°37′N, 53°12′W, 1983, S. Mori, #157 (AMNH).

Etymology.—The specific epithet is derived from the type locality of the species.

SPECIES MISTAKENLY PLACED IN *MEGALOPTIDIA*

Moure and Hurd (1987), in a catalog of the Western Hemisphere halictid bee species, tentatively placed *Megaloptidia pallitarsus* Friese as a species of *Megaloptidia*. In actuality, examination of the holotype male for *M. pallitarsus* (ZMHB) reveals that this species is a junior synonym of *Megommation insigne* (Smith 1853). We therefore propose the following new synonymy:

Megommation insigne (Smith 1853)

Halictus insignis Smith 1853: 65.
Halictus cherazon Vachal 1904: 113.
Megalopta virgili Friese 1911: 454.
Megalopta (Megaloptella) ipomoeae Schrottky 1912: 271.
Megalopta pallitarsus Friese 1926: 125. **New synonymy.**
Megaloptidia pallitarsus (Friese); Moure and Hurd 1987: 242.

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Species Richness of Costa Rican Cenocoeliini (Hymenoptera: Braconidae): a Latitudinal and Altitudinal Search for Anomalous Diversity

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Abstract.—Latitudinal patterns of species diversity of New World Braconidae have been scarcely surveyed to date. Such patterns may be of biogeographical and ecological interest because some literature data suggest that some braconid subfamilies do not show an increase in species diversity towards the equator despite an increase of potential host species (i.e., "anomalous diversity"). In the present study, species diversity of a "presumptive" anomalous diverse braconid taxa, Cenocoeliini, was surveyed in Costa Rica. The results were compared with published distribution data of North American Cenocoeliini. Also, species richness and abundance of Cenocoeliini from sea-level to 3400 m altitude in Costa Rica were analyzed to compare latitudinal and altitudinal gradients in species diversity. Costa Rican Cenocoeliini were five times more speciose than those in Canada and USA combined. The increase in estimated species richness per unit area towards the equator of North American Cenocoeliini was similar to that of their most common hosts, Cerambycidae and Scolytidae, but exceeded that of the potential hosts in Costa Rica. Diversification in Costa Rican Cenocoeliini was partly influenced by adaptation to different host families and host substrates. Most species and individuals of Cenocoeliini were found at low altitudes (<500 m) in Costa Rica. Cenocoeliini were not encountered above 1600 m in Costa Rica, this being in contrast to their most likely hosts, Cerambycidae and Scolytidae, which also occurred at high altitudes. Larger-sized Costa Rican Cenocoeliini were often brightly colored suggesting an aposematic function towards visually-oriented predators. New World Cenocoeliini appeared to be tropical lowland-centered and this is expected to be rather an effect of temperature requirements than an effect of host-limitation.

Anomalous diversity is defined as a pattern in species richness "counter to the prevalent trend of increasing species number in a taxon with decreasing latitude" (Rathcke and Price 1976). Owen and Owen (1974) were the first investigators to show anomalous diversity for parasitic Hymenoptera of the family Ichneumonidae, despite an increase of numbers of potential host species towards the equator. Janzen and Pond (1975) found a similar pattern in species richness for parasitic Hymenoptera; they were less or equally speciose in Costa Rica compared to those occurring in a meadow in England. Several investigators noted that sweep-sample studies of parasitic Hymenoptera in

the tropics may provide biased results for large-sized parasitoids (>3 mm) in areas where small-sized parasitoids may be abundant (Hespenheide 1979; Morrisson *et al.* 1979). More recently, results of Malaise trap sampling revealed that some subfamilies of Ichneumonidae displayed anomalous diversity (Gauld 1986, 1987, 1995b). Several theories to explain latitudinal patterns in species diversity of parasitic Hymenoptera have been formulated: resource fragmentation (Janzen and Pond 1975; Janzen 1981), predation on hosts (Rathcke and Price 1976), predation on parasitoids (Gauld 1987), and the "nasty" host hypothesis (Gauld *et al.* 1992; Gauld and Gaston 1994). According to these the-

ories, different ecological groups of parasitic Hymenoptera are expected to show different patterns in latitudinal species diversity (Hawkins 1994).

To date, anomalous diversity has not been fully analyzed for New World Braconidae. Quicke and Kruft (1995) found some subfamilies of Braconidae (e.g., Alysiinae, Aphidiinae, Cheloninae) to be less speciose from northern (zone 3, 4) towards southern (zone 5) latitudes in the USA. This suggests anomalous diversity, however, these analyses did not include neotropical regions. Species richness of another group, Cenocoeliinae (i.e., Cenocoeliini), increased from northern to southern temperate regions, but did not increase from middle to lower latitudes in the USA (Quicke and Kruft 1995). Also, species richness of Cenocoeliini in southern temperate regions was equal to that of northern and central Mexico combined and to that of southern Mexico (data from Saffer 1982). To date, not more than two species of Cenocoeliini have been described from Costa Rica (Saffer 1977, 1982). Previous data, therefore, suggest a pattern of anomalous diversity in Cenocoeliini. The distribution of Central American Cenocoeliini, however, is less well documented than that of North America (Saffer 1982).

Cenocoeliini are diurnally active endoparasitic koinobionts of endophytic beetle larvae (van Achterberg 1994; Saffer 1982). In North America, Cenocoeliini were found to parasitize Cerambycidae (68% of recorded host species), Scolytidae (22%), and Buprestidae (Saffer 1982). Koinobionts are parasitoids which let their hosts continue to be mobile and defend themselves for a while after being parasitized. Koinobionts are expected to have more narrow host ranges than idiobionts (Askew and Shaw 1986; Gauld 1987; Hawkins 1994) and are often referred to as "specialist" parasitoids. Sheehan and Hawkins (1991), however, noted that comparisons of average host ranges between koinobionts and idiobionts have to be evaluated carefully. Specialist parasitoids (i.e., koinobionts) associated to endophytic hosts may show, as predicted by the theories of resource fragmentation and predation on parasitoids, a (very) strong decrease in species richness from the temperate to tropical zones (Table 4.2, Hawkins 1994). At the other hand, these parasitoids may also show, as predicted by the theory of predation on hosts and that of the "nasty" hosts, a weak decrease to increase in species richness towards the equator. Thus, based on parasitizing behavior, contrasting predictions could be made for species richness of Costa Rican Cenocoeliini.

Species richness along altitudinal gradients may demonstrate patterns similar to those of latitudinal gradients (Brown 1988; Stevens 1992). Noyes (1989) noted that in general species diversity of parasitic Hymenoptera in an Indonesian rain forest was the highest at low altitudes (< 1000 m). Also the highest diversity of their hosts, e.g. Lepidoptera, was found at low altitudes (Holloway 1986). This suggests that, if patterns in latitudinal and altitudinal species richness are similar, anomalous diversity should not occur among parasitic Hymenoptera. Results of an altitudinal transect study in the Venezuelan Andes by Janzen et al. (1976) showed that species richness of parasitic Hymenoptera was as high at 200 m as at 1600 m, but that it was lower at high altitudes (3550 and 3600 m). The decline of species richness of parasitic Hymenoptera between 1600 and 3550 m was smaller than the decline of species richness of most other groups of insects such as other Hymenoptera (ants, bees, aculeate wasps) and other insect orders (e.g., Coleoptera and Lepidoptera). This suggests that some groups of parasitic Hymenoptera show anomalous diversity along altitudinal gradients. At a lower taxonomic level, tropical altitudinal species diversity of Ichneumonoidea was found to differ among subfamilies (Gauld 1985; Gaston and Gauld 1993;

Gauld and Hanson, in press). Also, Ophioninae were found to have different patterns in altitudinal species diversities between tropical regions (Gauld and Hanson, in press).

As noted earlier, anomalous diversity has not been completely analyzed for New World Braconidae. Literature data suggest that the braconid tribe Cenocoeliini may show a decrease, or at least no increase, in species diversity towards the equator. Therefore, the aims of the present study were: 1) to determine whether species richness and α-index of diversity of the Cenocoeliini in temperate regions were higher than those in tropical regions, 2) to determine whether potential hosts of Cenocoeliini increased more in species richness towards the equator than their parasitoids, 3) to relate latitudinal species richness with altitudinal species richness, and 4) to determine whether abundance and species richness of Cenocoeliini were higher at intermediate and high than at low altitudes in Costa Rica. This research is the first in a series of analyses of different groups of Braconidae to be examined for species diversity in Costa Rica in relation to altitudes.

MATERIALS AND METHODS

The tribe Cenocoeliini is a monophyletic group in the Helconinae (Shaw 1995), although several authors placed the Cenocoeliini as the main tribe in a separate subfamily, Cenocoeliinae (van Achterberg 1984, 1993; Shaw and Huddleston 1991; Wharton 1993). Before the generic revision by van Achterberg (1994), most Cenocoeliini species were considered to be within the genus *Cenocoelius*.

Individuals of Cenocoeliini were collected with Malaise traps (85%) and the rest by hand netting in Costa Rica, mostly during the last 10 years. Hand collected specimens for this study were from H.A. Hespenheide (University of California, Los Angeles), F. Parker (University of Utah) and J.A. Ugalde (INBio, Instituto

Nacional de Biodiversidad, Costa Rica). Malaise traps were located in different habitat types and at different altitudes throughout Costa Rica as described by Gauld (1991, 1995a). Our analyses included ca 70 Malaise trap-years of samplings at ca 60 different sites. Therefore, sample coverage was expected to be reasonably representative for the Costa Rican fauna. From these samples, Braconidae were sorted and sent to the University of Wyoming for identification. Cenocoeliini were sorted and individuals were determined to morphospecies using the following set of characters: hindwing venation (relative length vein 1M+CU to 1M, and 1M to 1r-m); color patterns of head, mesosoma, metasoma, legs, ovipositor sheaths and antennae; body size; ovipositor length relative to forewing length; number of flagellomeres; and shape of apical flagellomeres. Additional characters, like sculpture patterns on the propisternum, apex of the propodeum, and vertex, were included to distinguish among presumptive sibling species complexes. Data by Saffer (1982) were used to compare species richness of Braconidae in North America with that in Costa Rica. Sample coverage and sample intensity for Mexico was relatively low and less representative for the area than those of Canada, USA and Costa Rica.

Two formulae were used to estimate expected species richness of the faunae (S^c) based on the numbers of individuals per species in a sample:

1. $S^{c1} = S^2/(S - S_1)$ (S_1 = total number of species with one individual)

2. $S^{c2} = S + ((S_1)^2/2S_2)$ (S_2 = total number of species with two individuals)

The first formula of expected species richness (S^{c1}) is derived from the formula of sample coverage $(1-(N_1/I))$: Fagen and Goldmann 1977). In this formula, I is the total number of behavior types observed and N_1 is the total behavior types ob-

served only once. I was substituted with S and N_1 with S_1. S^{c1} was calculated as the inverse of the sample coverage multiplied by the number of observed species (S). The second formula of expected species richness (S^{c2}), is that of Chao 1 as described in Colwell and Coddington (1994). In addition to species richness, α-index of diversity of the logarithmic series was calculated because of its good discriminant ability and its low sensitivity to sample size (Magurran 1988). To estimate species richness per unit area the formula $S_a = x/a^{0.25}$ was used (S_a = number of species per unit area, x = number of observed species in country or region, a = area of country or region (10^3 km²): MacArthur and Wilson 1967, Gaston et al. 1996). We also estimated species richness per unit area for the most important temperate hosts of Cenocoeliini, the Cerambycidae (data from Monne and Giesbert 1994) and the Scolytidae (data from Wood 1982; Wood et al. 1991).

To examine the effect of altitude on species richness of Cenocoeliini, we defined 4 altitude classes: low (0–500 m), low intermediate (500–1500 m), high intermediate (1500–2500 m) and high (>2500 m) altitudes. These altitude classes reflect the distribution of different habitat types as described by Gauld (1995a). We assumed that there was a linear relationship between sample effort (i.e., Malaise trap-months) and number of individuals caught in Malaise traps. Because seasonal variation in abundance of neotropical insects occurs (Owen and Chanter 1970; Wolda 1988, 1989; Wolda and Wong 1988), only Malaise traps which operated three or more consecutive months were included in the analysis, and abundances of Cenocoeliini were summed for several year-round Malaise trap samples. We estimated expected numbers of Cenocoeliini per altitude class by multiplying the total number of observed Cenocoeliini with the proportion of number of Malaise trap-months of a particular altitude class to the total

Table 1. Numbers of individuals (N), species richness (S), two estimates of expected species richness (S^{c1}, S^{c2}; see materials and methods), α-index of diversity, numbers of localities (loc) and averaged local species richness (S_{loc}) of Cenocoeliini from Canada and USA combined, Mexico and Costa Rica.

	Canada + USA	Mexico	Costa Rica
N	1108	51	301
S	11	13	57
S^{c1}	11	24	96
S^{c2}	11	22	123
α-index	1.665	5.291	20.822
loc	233	13	48
S_{loc}	1.1 ± 0.3	1.5 ± 1.0	2.8 ± 4.4
(range)	1–3	1–4	1–25

number of Malaise trap-months. We tested whether observed and expected numbers were equal between low (<500 m) and higher altitude classes combined using a chi-square test (Sokal and Rohlf 1981).

RESULTS

In total, 290 individuals of Cenocoeliini were found from 80,000 to 90,000 Braconidae sampled in Costa Rica. The individuals of Cenocoeliini were divided into 55 morphospecies. The two described Costa Rican Cenocoeliini species by Saffer (1977, 1982) did not match our individuals and were added to our morphospecies resulting in a total of 57 species and 301 individuals (Table 1). From this set of 57 species, 44 species belonged to Capitonius, and 7 species to Cenocoelius. Of the remaining species, 4 species may belong to Capitonius but are rather distinctive and 2 species belong to a new genus of Cenocoeliini. The species varied in size from 3 to 12 mm. The ovipositors were relatively long, 0.7 to 1.7 times the forewing length. About half of the individuals and species were relatively large, mostly >5 mm, and bright yellow-orange to red-orange and often partly black in color, with partly to completely darkened wings. Most other individuals were relatively small, <7 mm, and blackish, brownish or black and dull red

Table 2. Estimated species richness per unit area (S_a) of parasitoids (Cenocoeliini) and their most common temperate hosts (Cerambycidae and Scolytidae) for different geographical regions of North and Central America, using $S_a = x/a^{0.25}$ as a standard species–area relationship (see text). Between parentheses are the relative richnesses when the estimated species richness of Canada was set at 1.0.

Geographical region	Area (10^3 km^2)	Cenocoeliini S_a	Cerambycidae S_a	Scolytidae S_a
Canada (+Alaska)	11,496	0.39 (1.0)	29.4 (1.0)	17.3 (1.0)
USA (−Alaska)	7,828	1.17 (3.0)	85.8 (2.9)	50.3 (2.9)
Mexico	1,969	1.95 (5.0)	201.2 (6.8)	90.8 (5.2)
Costa Rica	51	21.36 (54.8)	260.1 (8.8)	155.3 (9.0)

to reddish brown in color with clear wings, sometimes with brownish spots on the forewings.

Highest species richness was found in Costa Rica and lowest species richness in Canada and USA combined (Table 1). Both estimators of expected species richness (S^{c1} and S^{c2}) predicted that in Mexico and Costa Rica about half of the total number of species have been caught to date. More species were found in 2 Costa Rican Malaise trap sites (Heredia Province, Biological Station of OTS La Selva, and Puntarenas Province, 24 km west of Piedras Blancas) than in all trap sites of Mexico or Canada and USA combined. The highest diversity (α-index) was found for Costa Rican Cenocoeliini, the lowest for those of Canada and USA combined.

The increase of estimated species richness per unit area for North American Cenocoeliini was similar to that of their most common hosts (Table 2). On average, 3 times more species per unit area occurred in the USA than in Canada and about twice as many species per unit area occurred in Mexico compared to the USA. In contrast, Costa Rican Cenocoeliini were 11 times more speciose per unit area than in Mexico, meanwhile the potential hosts increased only about 1.5 times in species richness per unit area for the same areas.

Cenocoeliini were most speciose at low altitudes in Costa Rica (Table 3). Specimens were not encountered above 1600 m and Cenocoeliini were, significantly, more

abundant at low (<500 m) than at higher (>500 m) altitudes.

DISCUSSION

The increase of species richness of Cenocoeliini from Canada to Mexico was equal to that of their common hosts and exceeded that of their potential hosts in Costa Rica. Hence, anomalous diversity could not be shown for New World Cenocoeliini. This is in contrast to the prediction by resource fragmentation (Janzen and Pond 1975; Janzen 1981) suggesting that tropical host trees and their associated host beetles are too widely distributed to be exploited by koinobiont parasitoids. To illustrate this fragmentation, one ha of tropical lowland rain forest in Costa Rica contained 3 to 4 times more tree species than one ha of the most diverse North American forests (Hartshorn 1983; Whittacker 1965). Also a 50 ha moderate diverse lowland rain forest in Panama contained an equal number of tree species as the whole of western North America, north of Mexico (Condit et al. 1996; Little 1980). Janzen's (1981) caveat to resource fragmentation was that tropical koinobiont parasitoids had developed a broader host range compared to temperate koinobionts, or that they had become very efficient in looking for sparcely distributed hosts. In the present study, this could not be analyzed for neotropical Cenocoeliini, partly due to the lack of host records. North American Cenocoeliini, on average,

Table 3. Total species richness (S), number of Malaise trap-months (# tm), observed (N_{obs}) and expected (N_{exp}) numbers of individuals of Cenocoeliini per altitude class in Costa Rica. Only Malaise traps which operated more than three consecutive months were included in the analysis. It was tested if the observed and expected numbers of Cenocoeliini were equal at low altitudes (<500 m) and at higher altitude classes combined using chi-square test.

Altitude class	S	# tm	N_{obs}		N_{exp}		χ^2 (df = 1)
≤500 m	48	546	219		155		78.27
500–1500 m	16	71	8		20		(P < 0.001)
1500–2500 m	5	138	7	15	39	79	
>2500 m	0	72	0		20		
Totals	57*	827	234		234		

* Twelve species occurred at the two lowest altitude classes; one species occurred from 0–1600 m. Individuals were not found above 1600 m altitude.

parasitize one to 4 different host species (Saffer 1982). This "narrow" host ranges would classify the North American Cenocoeliini as specialists, however, we have to be careful to generalize, because these host records were not complete (Shaw 1994).

Results of the present study showed that the increase in species richness per unit area of Cenocoeliini from Mexico to Costa Rica was 6 times larger than that of their potential hosts (Table 2). This suggests that Costa Rican Cenocoeliini parasitize a larger proportion of the Cerambycidae and Scolytidae, than those in North America. At the other hand, some Costa Rican Cenocoeliini may have adapted to other beetle families of beetles with a different biology. The only known host record from Cenocoeliini in Costa Rica was that of a species attacking seed-boring beetle larvae of the family Curculionidae (Saffer 1977). Long-term research on seed-boring beetles in Costa Rican dry forest (Janzen 1980), however, did not reveal additional observations of Cenocoeliini on seed-boring beetles (Janzen, pers. comm.). Five percent of our surveyed specimens of Cenocoeliini from Costa Rica were collected from treefalls by hand (Hespenheide, unpublished data) and other micro-habitats not were indicated on the collecting labels. We expect, therefore, that wood-

and bark-boring insects are the most likely host for Costa Rican Cenocoeliini.

In the present study, we found that fewer species of Cenocoeliini occur at intermediate than at low altitudes (Table 3). This is comparable to the reduction in species richness towards the equator (Table 1). But the decline in species richness of Cenocoeliini with altitude in Costa Rica was higher than expected. As shown in the present study, Cenocoeliini were not encountered at 2000 m in Costa Rica. At latitudes in temperate North America with a similar mean yearly temperature, however, 5 to 8 species of Cenocoeliini occurred (Quicke and Kruft 1995). In Costa Rica, seasonal changes in temperature are usually smaller than diurnally fluctuation in temperature (Gauld 1995a). In temperate regions this is often reversed. These differences in temperature regimes may affect species richness of New World Cenocoeliini.

Individuals of Cenocoeliini were not encountered at altitudes higher than 1600 m, even though a total of 150 Malaise trap-months located at 10 different sites were surveyed. This was an unexpected observation as potential hosts of Cenocoeliini have been observed at high altitudes. Cerambycidae are most abundant at low altitudes in Costa Rica but occur also at high altitudes up to timberline (3200–3400 m;

Lezama, pers. comm.). Scolytidae are known to be regularly encountered at high altitudes in Costa Rica (Wood *et al.* 1991). It is unlikely, however, that alternative hosts for Cenocoeliini, like larvae of seed-boring beetles do occur at high altitudes. Legume trees, of which the fruits are among the most frequently attacked by seed-boring beetles (Janzen 1980), are scarce at intermediate and absent at high altitudes (Holdridge *et al.* 1971). Also, Gaston and Gauld (1993) noted that Pimplinae (Icneumonidae) were more abundant at high altitudes than at low altitudes. In case species of Cenocoeliini would have been present at high altitudes in Costa Rica, they likely would have been collected in the Malaise traps. This suggests that host presence does not explain absence of Cenocoeliini at high altitudes in Costa Rica.

In the present study, it could not be determined if Cenocoeliini were scarce in Costa Rica or that it is difficult to sample them by using Malaise traps. On average, one individual of Cenocoeliini was caught per 3 to 4 Malaise trap-months. Trap efficiency for Cenocoeliini was twice as high at low altitude rain forests than at low middle altitude rain forest or low altitude dry forest. Also Cenocoeliini were most frequently caught during the dry season (Feb.–May; unpublished data). But even in the optimal habitat type and season, Cenocoeliini was never found to be abundant suggesting that they occur in low population densities.

Another remarkable result was that 77% of the Mexican and 60% of the Costa Rican species of Cenocoeliini were represented by one or 2 individuals. Estimated species richness of Mexican Cenocoeliini may have been underestimated as sample coverage by the Malaise traps in Mexico was low compared to those in Costa Rica and the USA and Canada combined.

Analyses of geographical distribution of Costa Rican Cenocoeliini could not be justified due to low numbers of individuals

in Malaise traps. The observed 24 Cenocoeliini species in the Pacific lowland rain forest around Golfo Dulce in Puntarenas Province shared 9 species with the 25 Cenocoeliini species in the Atlantic lowland rain forest of La Selva in Heredia Province. This species distribution of Cenocoeliini may suggest that many Costa Rican Cenocoeliini have a restricted geographical distribution according to Rapoport's Rule (Stevens 1989, 1992). It may also be a sample artifact due to the low number of individuals.

In the present study it was found that half of the Cenocoeliini and especially those larger than 5 mm were bright orange and black colored, often with partly or completely darkened wings. Saffer (1982) described 2 similar bright colored Cenocoeliini from southern tropical Mexico, but no such colored species from temperate North America. Bright colors are common in tropical parasitoids (Quicke 1986a; Shaw 1995). Bright colors occur in several other neotropical braconid subfamilies such as Agathidinae and Braconinae and they are characteristic for larger sized (>5 mm) diurnally active Braconidae with long ovipositors, which likely parasitize concealed hosts (Shaw 1995). In general, bright colors are characteristic for lowland insects where it occurs in up to 25% of insects and do not occur at high altitudes in Costa Rica (Janzen 1973). Quicke (1986b) noted that in general bright colors have a warning function towards visually-oriented predators (i.e., aposematic coloration). Bright colored tropical parasitic wasps may mimic stinging aculeates and some larger sized parasitoids are capable of stinging by themselves (Quicke 1986b). Other authors hypothesized that parasitoids may mimic unpalatable hosts such as Chrysomelidae (Gauld, pers. comm.) or Symphyta (anon. rev., pers. comm.). Gauld and Gaston (1994), suggested that parasitoids with bright colors may be unpalatable for predators after sequestering "nasty" tasting

secondary plant chemicals from their hosts. If the latter is true and the "nasty" host hypothesis has validity for Cenocoeliini, bright colored Cenocoeliini may attack seed-eating or phloephageous beetle larvae, rather than wood-living Scolytidae or Cerambycidae. Quicke (1986a) found homeochromatic assemblages for some large sized Braconidae and their potential hosts (i.e., Cerambycidae). Hespenheide (1996) showed that color patterns of Chrysomelidae may be substrate-related. More research is needed to elucidate the underlying defense mechanisms or other meaning of bright colors in large sized neotropical wood-boring braconid parasitoids.

The smaller sized Costa Rican Cenocoeliini from our survey were mostly less conspicuous colored than the larger sized ones. Many of these smaller sized Cenocoeliini may be ant-mimics, which is expected to occur frequently in neotropical Braconidae (Shaw 1995). This color pattern of presumably ant-mimics also occurred among North American Cenocoeliini (Saffer 1982). To date, possible behavioral and olfactorial cues involved in antmimicry of Braconidae have not been documented.

In conclusion, the results of the present study showed that the species diversity of the Cenocoeliini increases towards the equator. This is the normal pattern in latitudinal species richness (Fisher 1960; Pianka 1966; Stevens 1989; Wilson 1992). Thus, anomalous diversity was not observed for Cenocoeliini. The increase in species richness per unit area of Cenocoeliini from temperate North America to the Neotropics exceeded that of their potential hosts. In Costa Rica, species and individuals of Cenocoeliini were not found above 1600 m altitude, this is in contrast to their potential hosts which also occur at high altitudes. This suggests that species richness in Cenocoeliini is not host limited. The Cenocoeliini apparently is a tropical lowland-centered group of which a limit-

ed number of species have adapted to year-round cool conditions at lower montane rain forests and none to montane forests. Some other species have adapted to climatological conditions in temperate regions and evolved overwintering mechanisms (Saffer 1982).

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Sperm Development in the Imaginal Testes of *Aleiodes coxalis* (Hymenoptera: Braconidae: Rogadinae)

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Abstract—Spermatogenesis and spermiogenesis in the imaginal testes of the long-lived braconid wasp, *Aleiodes coxalis* (Spinola) has been investigated. The cyclostome group of braconid subfamilies, to which *Aleiodes* belongs, are considered to have unspecialised sperm, but in *Aleiodes* several aspects of spermatogenesis and morphology differ from that reported in other Hymenoptera, suggesting that reinterpretation of previously published studies may be necessary. In particular, the centriolar adjunct is found to lie between the nucleus and one of the pair of mitochondrial derivatives, resulting in the mitochondrial derivatives being offset longitudinally, giving the impression that the mitochondrial derivatives are of different lengths. A projection extends from the centriolar adjunct to the one mitochondrial derivative which abuts the nucleus. The shape change undergone by the nucleus during spermatogenesis is associated with an uneven distribution of peri-nuclear microtubules (microtubular manchette). These are not found over two extra-nuclear electron-dense regions, ('lateral plates') which appear to add increased rigidity to the nucleus at these points.

Very little is known about the sperm of Hymenoptera despite the fact that this is one of the largest and most diverse of insect orders (Jamieson 1987), and descriptions of spermatogenesis are limited to a handful of taxa, mostly bees and ants (Hoage & Kessel 1968, Hogge & King 1975, Cruz-Landim & Beig 1980). A recent survey of mature sperm morphology and ultrastructure across the order has revealed considerable variation between higher taxa that may be important for understanding phylogenetic relationships within the order (Quicke et al. 1992), some of the most extreme modifications occurring in the parasitic wasp family, Braconidae. In order to interpret the structures and modifications found in some braconid subfamilies it is first necessary to describe the 'normal' situation in that family.

The Braconidae is a large family of parasitic wasps comprising some 40 subfam-

ilies that can be broadly divided into two groups, the cyclostomes and the non-cyclostomes, which differ in morphology of the mouth and in their biology (Shaw & Huddleston 1991). In an initial survey (Quicke et al. 1992), it was found that in members of the cyclostome group of braconid subfamilies (e.g. Braconinae, Doryctinae and Rogadinae, the latter including *Aleiodes*) the sperm have a normal appearance, being between 80 and 170 μm long with the head (nucleus + acrosome) comprising 10 to 20% of the sperm's total length. However, nearly all non-cyclostomes have apomorphic sperm with total length between 10 and 20 μm, of which the head constitutes nearly 50%. Further, whilst the axonemes of the cyclostome braconid sperm have a normal 9+9+2 arrangement of microtubules, as found in most insects, those of the short apomorphic non-cyclostome sperm frequently have only one or no central microtubules. These features appear to be highly phy-

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logenetically informative and, in order better to understand their ontogenies, we have investigated spermatogenesis in a range of braconids. Here we report on that leading to the apparently unmodified sperm of the rogadine, *Aleiodes coxalis* (Spinola), which will form the basis for future comparisons. Despite the normal appearance and ultrastructure of the mature sperm in *Aleiodes*, spermatogenesis in this taxon exhibited several structures that do not appear to have been reported in other insects.

It has long been appreciated that the timing of spermiogenesis and spermatogenesis in insect testes is a reflection of the adult life span which may in turn be associated with the occurrence of sib-mating (Phillips 1970). Thus imaginal testes of species with short lived adults, such as mayflies (Needham et al. 1935) and caddis flies (Ross 1944), or those in which males almost invariably mate with their nearby sisters upon emergence such as many parasitic wasps, typically contain spermatids and spermatozoa, but no gonial and meiotic divisions, which would be completed in the pupal or nymphal stages. In contrast, meiotic and even gonial divisions often continue well into the imaginal stages in testes of long lived species (e.g. many beetles and dragonflies) which usually search for and mate with several unrelated females. Most rogadine braconid wasps, such as the *Aleiodes* species investigated here, are solitary parasitoids of Lepidoptera larvae and belong to the second category. Males fed on honey water will often live a month and sometimes considerably longer, and will mate readily throughout much of their adult life (M. R. Shaw pers. comm.). Indeed, some species are reluctant to mate immediately after eclosion and only start to mate once they have fed.

There are no papers on the ultrastructure of spermatogenesis in any member of the Ichneumonoidea, and the only parasitic Hymenopteran studied to date is the

pteromalid chalcidoid *Nasonia vitripennis* (Walker) (Hogge & King 1975).

MATERIALS AND METHODS

Adult *Aleiodes coxalis* (Spinola) were collected at Silwood Park (Imperial College) in 1995. Testes were dissected under 2% glutaraldehyde in phosphate buffered saline (pH 7.2), and fixed for two hours. Tissue was transferred to 2% osmium tetroxide in cacodylate buffer (pH 7.2) for 2 hr. After another buffer wash, tissue pieces were dehydrated to 50% ethanol and then further fixed with saturated uranyl acetate in 50% ethanol prior to complete dehydration, embedding in Epon resin and polymerisation overnight. Large silver sections were picked-up onto high resolution grids, stained with uranyl acetate and lead citrate and examined using a Phillips EM400 electron microscope.

RESULTS

Adult testes of *Aleiodes coxalis* contain follicles (seminal tubules) with multiple cysts present at various levels of maturity. Although neighbouring cysts can exhibit different stages of development, generally the more posterior the position along the testes the greater the proportion of later stages. Although most cysts contain spermatids, it is also possible to find in the adult indications of earlier stages of development. Primary spermatocytes still appear to be present some without any sign of a normal spindle and with a concentric arrangement of the endoplasmic reticulum around the chromosomes (Fig. 1 *long arrow*). Centriolar pairs are present in these cells (*arrowheads*), as are large numbers of small mitochondria. This appearance is considered indicative of an abortive first meiotic division; the result of incomplete centriolar polarisation. Centrioles are then extruded after meiotic multiplication by cytoplasmic blebbing (Fig. 2), where centrioles, attached to microtubules (Fig. 2a), are found incorporated into rounded portions of the plasma mem-

brane. This blebbing is also seen in secondary spermatocytes (which also exhibit loss of plasma membrane in larger whorls), although not all blebs exhibit centrioles (Fig. 2b *arrow*). Large numbers of polyribosomes are also present at this stage.

In the secondary spermatocytes it is difficult to find evidence of synaptonemal-like structures. At this stage the cells are considered to form a syncytium because of incomplete cytogenesis during the earlier mitotic division. The intercellular bridges (Fig. 3) linking the spermatocytes are difficult to identify as the cells can be very closely apposed. It is only during later spermiogenesis, with cell elongation, that the connections become apparent (Fig. 3a) with evidence of organelle continuity and possibly even intercellular movement of vesicles and granules (Fig. 3b). This has been suggested as being a method of transferring organelles from large to small spermatids where there is unequal division after the second meiotic division. No noticeable size difference was seen in *Aleiodes*.

Nebenkern formation occurs concomitantly with the above processes (Fig. 4). Mitochondria begin to accumulate in one area of the cell (Fig. 4a) where they fuse to form the beginnings of the nebenkern (Fig. 4b), a highly convoluted membranous organelle that is the precursor of the two mitochondrial derivatives. The development of the nebenkern into two labyrinthian networks has been linked with the appearance of microtubules in the cytoplasm. However, in *Aleiodes* microtubules appear to be a consistent component of the cytoplasm from earlier stages.

Flagellum growth (Fig. 5) is evident prior to nuclear condensation, commencing with the appearance of a basal body (Fig. 5a *arrowhead*) in a small depression of the nucleus (Fig. 5a *arrow*). The nuclear envelope thickens at this area (Fig 5b) and the doublet microtubules of the flagellum grow from the triplet microtubules of the

basal body (Fig 5b *arrow*). The flagella initially do not have accessory tubules (Fig. 5c). These appear to develop from sub-fibre b of each doublet as previously reported. The flagella/mitochondria axis is developed before this takes place (Fig. 5d *arrow*). Although spermiogenesis is advanced at this stage, separation following the last meiotic division in many cases is not complete and the nucleus still appears spherical. Nuclear condensation begins with the appearance of polarity in the nuclear membrane in the region closely apposed to the spermatid cell membrane (Figs 5d, 6 *arrowheads*) where the spermatid is attached to the wall of the cyst (a single epithelial layer with supportive and secretory functions). Microtubules appear around the nucleus but these are not evenly located; an arrangement which probably assists the complicated shape change that the nucleus undergoes.

The acrosome is detectable in early spermatid stages as an accumulation of a large number of small particles termed the proacrosomal granule (Fig. 7). During spermiogenesis the proacrosomal granule becomes located between the plasma membrane and the nucleus at the region of nuclear polarity (Fig. 8a). The acrosome is formed by a flattening of this structure and an indenting on the side apposed to the nucleus (Fig. 8b). A small protrusion is found anteriorly to the acrosome in the early spermatid (Fig. 8b *arrow*). This may represent an apical expansion of extra-acrosomal material, similar to that found in *Locusta migratoria* L. (Szöllösi 1974). However, the structure in *Aleiodes* appears to contain electron dense material. Whether this could be a separate structure, or represents a later stage of fusion of Golgi derived products, as found in the proacrosomal granule, is not clear. The situation is further complicated by the impression that the is distinct coated membrane which surrounds the acrosome and extends posteriorly over the anterior portion of the nucleus during development, at
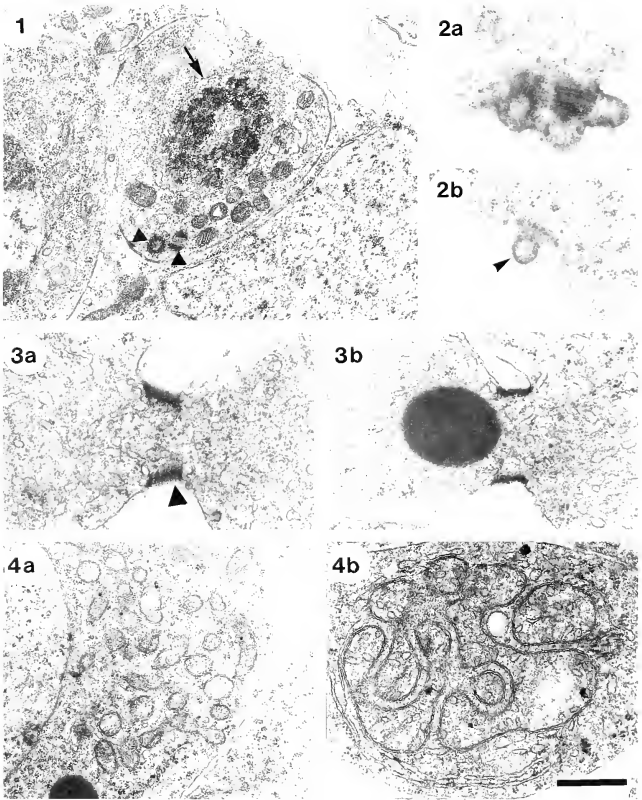
Figs. 1–4. 1, Primary spermatocyte from the testes of an adult male *Alenocles*, with anomalous metaphase plate formation, characterised by the absence of a normal spindle and a concentric arrangement of the endoplasmic reticulum around the chromosomes (*arrow*). Large numbers of small mitochondria and a centriolar pair (*arrowheads*), are also present. Scale bar = 0.5 μm. 2, Membrane blebbing during spermiogenesis: (a) loss of centrioles (attached to microtubules) through membrane blebbing; (b) membrane blebbing (*arrow*) without loss of centrioles. Scale bar a = 0.6 μm; b = 0.85 μm. 3, Syncytium formed by incomplete cytogenesis during mitotic division: (a) Intercellular bridges (*arrowhead*) link spermatocytes; (b) linkage provides a method for organelle movement between spermatocytes. Scale bar = 0.75 μm. 4, Nebenkern formation in the spermato-

least initially does not appear to be continuous with this granular tip. As the acrosome elongates an acrosomal rod (or perforatorium) develops, and extends from a depression in the nucleus and into the subacrosomal space formed during folding (Fig. 8c, *arrow*). The acrosomal rod becomes hollow as it develops (Fig. 8d), but does not occupy all of the large sub-acrosomal space (Fig. 8e). At this stage the complete structure is referred to as the acrosomal complex.

With the formation of the acrosomal complex and cell elongation, a distinct centriolar-adjunct appears in the spermatocyte (Fig. 9). It develops at the posterior nuclear pole adjacent to the forming basal body (Fig 9a). Unlike the situation in some other insect species (Gatenby & Tahmisian 1959, Breland et al. 1966) it does not appear to be forming around the centriole that is perpendicular to the axis of the flagellum. Instead, the basal body is located between the centriolar adjunct and the 'perpendicular' centriole; the ultimate fate of this second centriole is not clear. In transverse section, the axoneme is associated with one mitochondrial derivative and the sectioned centriolar adjunct (which in the past has been interpreted as a darkened mitochondrial derivative). In longitudinal section the centriolar adjunct can be seen to lie between the posterior pole of the nucleus and one of the mitochondrial derivatives (Fig. 9c), and is slightly more than 2μm long. The mitochondrial derivatives are thus offset longitudinally, with the other member of the pair abutting the nucleus. This may result in the appearance of the adult mitochondrial derivatives, where one member of the pair often seems to extend further posteriorly, possibly giving the erroneous impression that in fact the mitochondrial derivatives are of different lengths. This is a different arrangement from that previously reported for other related species. Furthermore, anteriorly, it can be seen that for part of the length of the centriolar adjunct, where the centriolar adjunct and one of mitochondrial derivatives lie side by side, there is an extension of the centriolar adjunct which surrounds the mitochondrial derivative on the side facing the centriolar adjunct (Fig. 9d). Interestingly in a rare teratological sperm-tail with two axonemes the centriolar adjunct was found to extend to enclose two mitochondrial derivatives. This contact is most evident in the region of the basal body and it is not clear if it actually extends into the flagellum proper as defined by the possession of both a ring of doublet microtubules and a central pair of microtubules.

The change in shape of the nucleus (Fig. 10) that occurs with the appearance of peri-nuclear microtubules is also marked by the formation of two extra-nuclear electron-dense regions (Fig. 10a, see also Fig. 6). Peri-nuclear microtubules are unevenly distributed and are not found over the extra-nuclear electron-dense regions, which we have called lateral plates, nor do they occur in the area of the nucleus that will be convex during the elongation process. The lateral plates appear to be the locus for shape changes that occur during the elongation of the nucleus. Condensation of the chromatin into coiled fibrillar threads then follows (Fig. 10b). In transverse section, as the nucleus elongates, the threads are found associated with that portion of the nuclear membrane that is adjacent to the region lacking microtubules (Fig. 10c). The side of the nuclear membrane surrounded by the full complement

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cyte: (a) Large numbers of small mitochondria accumulate in one area of the spermatocyte; (b) mitochondrial fusion occurs to form the labyrinthine network of the nebenkern, which will itself then give the two mitochondrial derivatives of the mature sperm. Scale bar a = 1.4 μm; b = 1.15 μm.
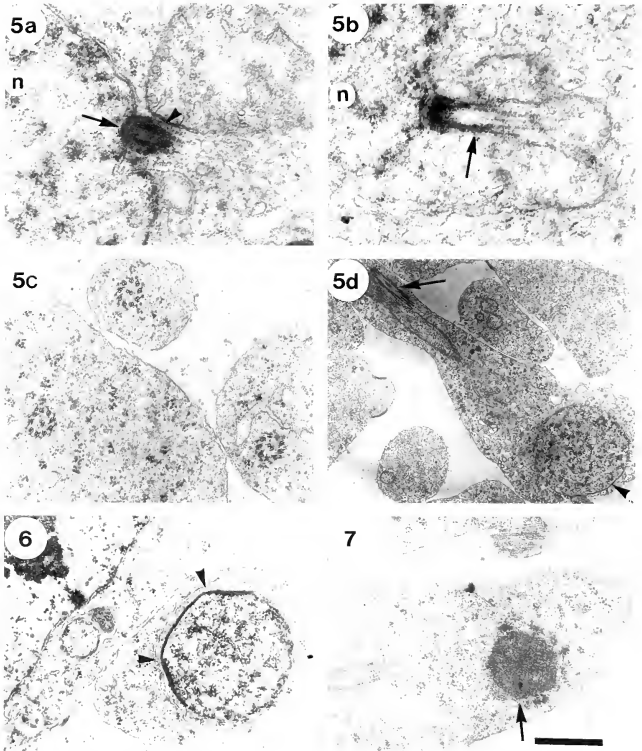
Figs. 5–7. 5, Flagellum formation during spermiogenesis: (a) the basal body (*arrowhead*) forms from the lateral centriole by insertion into a depression of the nucleus (*arrow*); (b) doublet microtubules (*arrow*) grow from the triplet microtubules of the basal body; (c) accessory tubules are absent at this stage, although a central pair of microtubules form in the developing axoneme post-basal body; (d) the flagella/mitochondria axis is developed (*arrow*) before the change in shape of the nucleus is found, although polarity in the nuclear membrane can be found. n = nucleus. Scale bar a, b = 0.7 μm; c = 0.8 μm; d = 3 μm. 6, Polarity of the nucleus develops prior to shape change with increased electron density of the nuclear membrane including the appearance of two extra-nuclear densities (lateral plates). Microtubules (*arrowheads*) appear around the nucleus. Scale bar = 1 μm. 7, Proacrosomal granule formed from small Golgi derived vesicles. Scale bar = 1 μm.
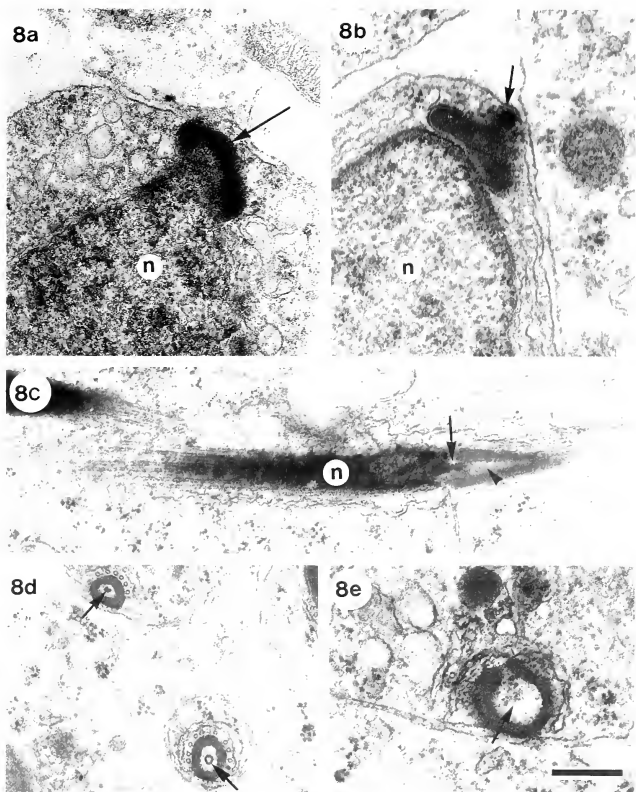
Fig. 8. Formation of the acrosomal complex during spermiogenesis. (a) the acrosome becomes located between the plasma membrane and the nucleus (*arrow*); (b) the acrosome indents to enfold the nucleus, and a small electron density is found anteriorly; (c) an acrosomal rod ('perforatorium' *arrow*) occupies the subacrosomal space formed during folding; (d) the perforatorium (*arrow*) is seen in transverse section to be hollow; (e) the subacrosomal space itself can be seen to be large and is not filled by the perforatorium for its entire length. n, nucleus. Scale bar a, c, d = 0.5 μm; b, e = 0.65 μm.
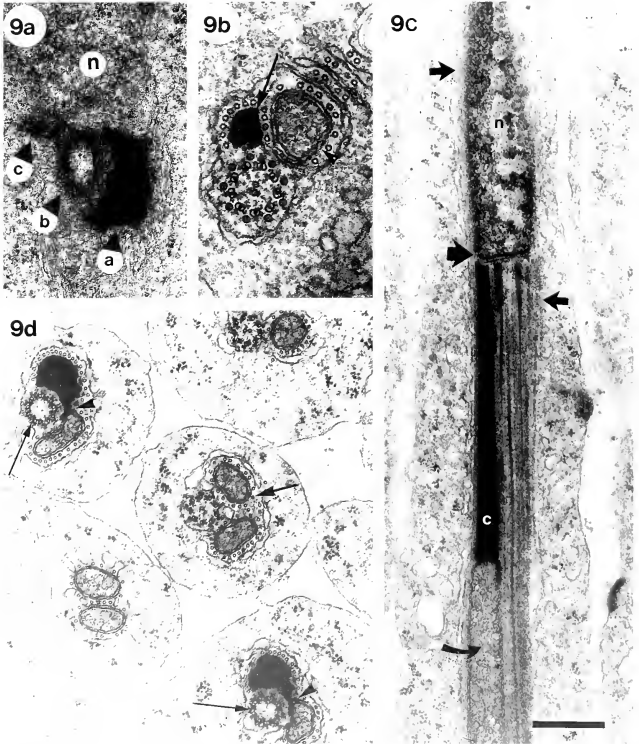
Fig. 9.   Centriolar adjunct formation during spermiogenesis: (a) arrangement of centriolar adjunct (*arrow*, 'a'), basal body (*arrow*, 'b') and perpendicular centriole (*arrow*, 'c'); (b) in transverse section the centriolar adjunct (*arrow*) and a single mitochondrial derivative (*arrowhead*) lie in parallel with the axoneme; (c) in longitudinal section the centriolar adjunct (c) abuts the nucleus anteriorly at the nuclear plate (large *arrow*) and a mitochondrial derivative (curved *arrow*) posteriorly. Microtubules (*arrows*) are evident lining the nucleus (n) and the developing axoneme; (d) at the level of the basal body (*arrows*) the centriolar adjunct (*arrowheads*) extends to contact and enclose the single mitochondrial derivative. Posteriorly to the centriolar adjunct two mitochondrial derivatives are found (*arrow*). Note also the absence of the central pair of microtubules in the basal bodies. n, nucleus. Scale bar a = 0.5 μm; b = 0.3 μm; c = 0.6 μm; d = 0.9 μm.
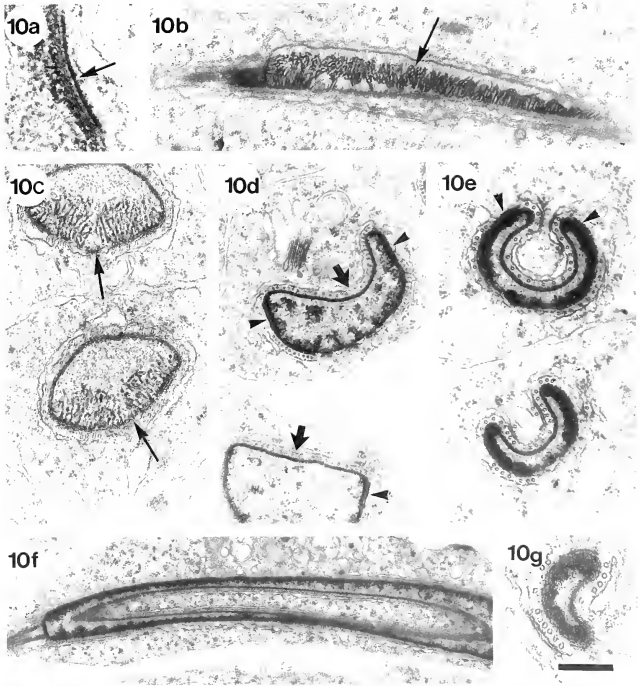
Fig. 10. Change in shape of nucleus during spermiogenesis: (a) extra-nuclear electron-dense region ('lateral plate', *arrow*) are produced upon nuclear shape-change; (b) condensation of the chromatin into coiled fibrillar threads (*arrow*); (c) the threads divide and become associated with that portion of the nuclear membrane on either side of the region lacking microtubules (*arrows*); (d) the side of the nucleus with the full complement of microtubules (*large arrows*) flattens, and then infolds with the lateral plates (*arrowheads*) providing a locus for shape change; (e) the chromatin becomes a layer on the outer surface of a horse shoe (*arrowheads*) that infolds to surround elements of the endoplasmic reticulum; (f) as the spermatocyte elongates the groove begins to disappear from the anterior and posterior ends; (g) the dense nuclear material then begins to redistribute more evenly around the nuclear membrane as the width decreases. Scale bar a = 40 μm, b = 1 μm, c, d, e = 0.6 μm; f = 1.2 μm; g = 1.7 μm.

of microtubules then flattens (Fig. 10d *arrow*), with the chromatin becoming a layer on the outer surface of the developing horse-shoe shape; as viewed in section (Fig. 10d *arrowhead*). The lateral plates become the linear portions of the outer surface of the arms of the 'horse-shoe' (Fig. 10e *arrowheads*); at the most extreme, the lateral arms (in transverse section) almost come into contact with one another. As the nucleus infolds, so elements of the endoplasmic reticulum, which surround the microtubules, become largely enclosed by the nucleus (Fig. 10e). It is not clear how this highly folded nucleus reaches the cylindrical shape of the adult sperm. As the sperm elongates it appears that the inverted side is flattened with the result that the grove begins to disappear from the anterior and posterior ends (Fig. 10f). The dense nuclear material then begins to redistribute more evenly around the nuclear membrane as the width decreases (Fig. 10g); however, intermediate stages are difficult to identify.

The axoneme itself develops into the 9+9+2 arrangement (Fig. 11a); 9 outer single accessory tubules, 9 doublets and 2 central single microtubules. Intratubular material is abundant (with radial spokes—Afzelius rays) and indications of the inner and outer dynein arms. Two deltoid bodies, (also referred to as triangular rods; Lensky et al. 1979) develop, but their exact derivation is not clear, although a membrane origin is apparent and a close association with the mitochondrial derivatives is probable. This is further supported by the observation that only one deltoid body is found at the level of the centriolar adjunct where there is only a single mitochondrial derivative. At the level of the two deltoid bodies is a single central rod, as previously reported in ant spermatozoa (Wheeler et al. 1990). This arrangement is maintained in mature sperm (Fig. 11b). By comparison with that of the spermatocyte, the nucleus of the mature sperm is homogeneous (Fig. 11c). The acrosome develops a

distinctive glycocalyx (Fig. 11c *arrowheads*) which extends over the anterior portion of the nucleus. The two mitochondrial derivatives show the offset arrangement that may be the result of the centriolar adjunct overlaying one of them anteriorly (Fig. 11c *arrows*). In addition an end piece with no mitochondrial derivatives is found (Fig. 11d *arrow*).

DISCUSSION

In the testes of imaginal male *Aleiodes* we have found structures indicative of early stages of sperm development. In particular, evidence for an abortive first meiotic division of the primary spermatocyte, a major feature of hymenopterous insects in which males are haploid, has been found. This appears to involve anomalous metaphase plate formation, probably caused by the absence of a normal spindle. This has been previously described in the drone of the bee *Scaptotrigona postica* by Cruz-Landim & Beig (1980), where it is characterised by the presence of a concentric arrangement of the endoplasmic reticulum around the chromosomes and the absence of a normal spindle. In *Aleiodes,* as in *S. postica,* this is connected to an anomalous movement of spermatocyte centrioles, which, instead of assuming polar locations, migrate to the cell surface and are lost by cytoplasmic blebbing (Hoage & Kessel 1968). The presence of such early stages of development in the adult supports our supposition that gonial development in this species could to be related to the life style of the adult. The relatively long adult life time of the male would seem to obviate the need for synchronous maturation of all the individual sperm cysts.

The manchette of microtubules that assembles around the developing spermatid nucleus appear to be important for nuclear compression and elongation (Baccetti 1972). The nuclear shape change found during development in *Aleiodes,* and the asymmetric distribution of microtubules,
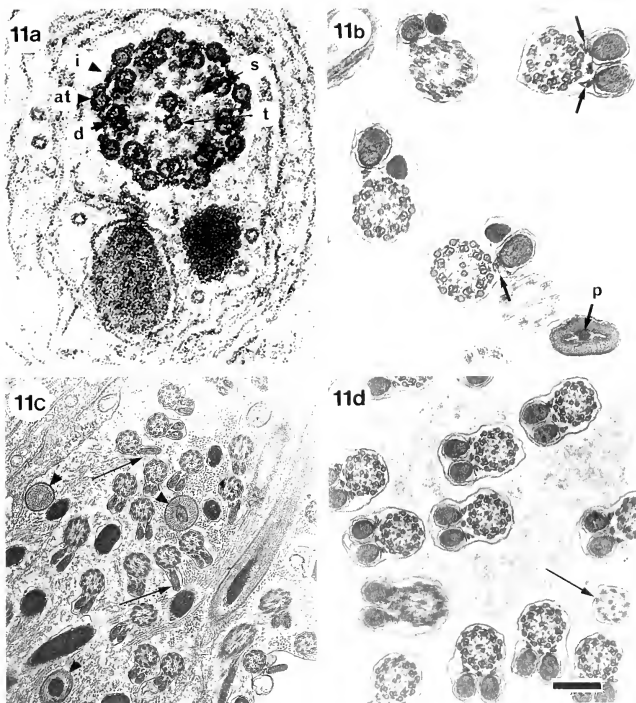
Fig. 11. Axoneme structure and the mature sperm:(a) The arrangement of 9 outer, singlet accessory microtubules (at), 9 doublet (d) and two single central microtubules (t) is evident in the later stages of spermiogenesis, with intratubular material (i) and prominent radial spikes (s); (b) two deltoid bodies (*arrows*) develop in association with the mitochondrial derivative except at the level of the centriolar adjunct where only one is found; (c) the mature sperm illustrates the uneven length of the mitochondrial derivatives (*arrow*) and the glycocalyx that develops around the mature acrosome (*arrowheads*); (d) the tail piece at the posterior of the sperm (*arrow*) contains only the 9+2 arrangement of doublet and single microtubules. Scale bar a = 100 μm; b = 0.25 μm; c = 0.75 μm; d = 0.4 μm; p = perforatorium.

have not previously been described for parasitic wasps. A gutter-shaped developmental stage of the nucleus occurs in some bugs (Lee & Lee 1992) but nuclear elongation is not accompanied by concavity in many other insects (e.g. Szöllösi 1975, Friedländer 1993, Wolf & Joshi 1995). In some caddis flies, in which the

spermatid nucleus transiently assumes a sickle shape, the microtubular manchette surrounding the nucleus is interrupted (Wolf & Klein 1995), as it is in the dragonfly, *Aeshna grandis* L., in which the elongating nucleus becomes locally compressed (Kessel 1966). The structures we have termed lateral plates, which occur between groups of microtubules of the microtubular manchette, do not appear to have been described previously in any insect.

The present study of spermiogenesis in *Aleiodes* has implications for published studies of the centriolar adjunct. The presence of a centriolar adjunct overlying only one of the mitochondrial derivatives has not to our knowledge previously been reported. In particular the connection from the centriolar adjunct to the mitochondrial derivative that abuts the nucleus is novel. This arrangement may be responsible for observations in related species suggesting that anteriorly there may be a particularly electron dense mitochondrial derivative (Quicke et al. 1992) or a region of overlap between the axoneme, nucleus and mitochondrial derivative (Chauvin et al. 1987)—i.e. some studies may have misinterpreted the centriolar adjunct as a particularly electron dense mitochondrial derivative. Further, the longitudinal offsetting of the mitochondrial derivatives caused by the interposition of the centriolar adjunct between one of them and the nucleus could be responsible for the appearance of some sections through the posterior region of the sperm, just before the tail piece, in which only one mitochondrial derivative is found. The presence of a single mitochondrial derivative in sections through this region prompted previous authors to conclude that mitochondrial derivatives are of different lengths, which has even been considered to be a characteristic, not just of the Hymenoptera, but of all holometabolous insect orders (Wheeler et al. 1990). However this result could be explained

simply by the arrangement of the centriolar adjunct. In the light of this finding in *Aleiodes*, it would be interesting to re-examine these previously reported groups for the presence of a similarly located centriolar adjunct. A large centriolar adjunct has been reported in ant spermatozoa (Wheeler et al. 1990), and was thought to distinguish this group from other Hymenoptera, such as bees, which appear to lack a homologous structure (Lensky et al. 1979, Cruz-Landim & Beig 1980). The arrangement of the centriolar adjunct in the ant spermatozoa, at least in longitudinal section, is similar to that of *Aleiodes*. However, in these the centriolar adjunct can be seen to overlie both mitochondrial derivatives.

The connection to the mitochondrial derivative is particularly interesting as it occurs at the level of the basal body where the two central microtubules are absent. The origin and exact function of the central pair is not known. A structural role for the central pair could imply a similar role for the centriolar adjunct and the latter could therefore be compensating for the absence of the central pair at the region of the basal body. However, some studies have provided evidence that the centriolar adjunct consists partly of RNA (Baccetti et al. 1969) and how this would be related to a structural role is uncertain.

The exact relationship between centrioles, the basal body, the centriolar adjunct and the developing axoneme in *Aleiodes* is not clear. In another parasitic wasp, the pteromalid *Nasonia vitripennis* (Walker), the distal centriole is reported to lengthen to form the basal body of the flagellum, and then, with the proximal centriole, form the ring centriole (Hogge & King 1975). This then associates with a spherical reticulate dense body, which forms adjacent to the nuclear membrane opposite a nuclear pore at the secondary spermatocyte stage. As maturation proceeds the proximal centriole is reported to become surrounded by granular material and

break down, with loss of material from the spherical, reticulate dense-body. The granular material, with presumably the remains of the proximal centriole is then thought to contribute to the centriolar adjunct. However, in *Aleiodes* such a straightforward relationship is not clear; in fact it appears as if the centriolar adjunct may develop prior to loss of the proximal centriole. Thus this may not contribute to the formation of the centriolar adjunct at all. In discussions of the centriolar adjunct in ant spermatozoa, Wheeler et al. (1990) suggest caution when applying this term, as the developmental homology to such structures in other species, such as mammals, has not been proven.

ACKNOWLEDGEMENTS

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Revision of the American Tiphiid Genus *Quemaya* Pate
(Hymenoptera: Tiphiidae: Brachycistidinae)

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Abstract.—The brachycistidine genus *Quemaya* is reviewed and six new species are described from southern California, Arizona, northern Mexico and Costa Rica, ***confusa, costaricensis, eurekaensis, megalops, mexicana,*** and ***sonorensis.***

The genus *Quemaya* Pate (1947) is an obscure group of nocturnal tiphiids originally known from five species described from the southwestern deserts of North America, as far south as Sonora, Mexico. In this paper we more than double the known species in this genus, and extend the known distribution hundreds of miles. Additionally, intensive collecting in Costa Rica by the Instituto Nacional de Biodiversidad and by Frank Parker has turned up a new species from the arid northwestern region of Costa Rica. This region appears to be the southernmost extension of this arid nearctic desert habitat.

These wasps are easily overlooked because of their small size, dark coloration and nocturnal habits. However, males are strongly attracted to ultraviolet light sources at night. Females are as yet unknown. The new Costa Rican species, *costaricensis,* has some characteristics unusual for *Quemaya,* including the tiny ocelli and sculptured propodeum, but still has the diagnostic features for the genus discussed below.

Quemaya is characterized by a combination of primitive and derived features. The wing venation is reduced (Figs. 10–17). The forewing has only one, or less commonly two, submarginal cells, one discoidal and one subdiscoidal cell, and the marginal cell is separated from the costal wing margin. In the hindwing the cubital vein is nearly straight meeting the transverse cubital vein at an angle much greater than 135°. *Quemaya* species lack the ventrally "tailed" antennal socket carina, forecoxal stridulatory structure, scrobal sulcus, mandibular carina, basal "ring" carina of the first gastral tergum, and carinate gastral sterna characteristic of other brachycistidine genera. Members of *Quemaya* all have a distinctly modified epipygium, that has sublateral carinae and an emarginate, truncate or convex apex (Figs. 18–21).

MATERIALS

Specimens in this study were obtained from: DAVIS—Bohart Museum of Entomology, University of California, Davis (S. L. Heydon); ITHACA—Department of Entomology, Cornell University, Ithaca, New York (J. Liebherr); LAWRENCE—Snow Entomological Museum, University of Kansas, Lawrence (R. Brooks); LOGAN—Department of Entomology, Utah State University, Logan (T. Griswold); OTTAWA—Canadian National Insect Collection, Agriculture Canada, Ottawa (L. Masner); RIVERSIDE—Department of Entomology, University of California, Riverside (S. Triapitsyn); SAN FRANCISCO—California Academy of Sciences, San Francisco (N. Penny); SANTO DOMINGO—Instituto Nacional de Biodiversidad, Santo Domingo de Heredia, Costa Rica (C. M. Rodríguez); TUCSON—University of Arizona, Tucson; WASHINGTON—U.S. Na-

tional Museum of Natural History, Smith-
sonian Institution, Washington, D. C. (A.
S. Menke, K. V. Krombein).

Two abbreviations are used below for
the sake of brevity; MOD = midocellus di-
ameter and F = flagellomere.

KEY TO SPECIES OF *QUEMAYA* (MALES)

1 Forewing with two submarginal cells (Figs. 10, 15, 16) 2
– Forewing with one submarginal cell (Figs. 11–14, 17) 5
2 Mandible with two apical teeth; distance between midocellus and closest eye margin less
   than 1.5 MOD (Fig. 1) . . . . *arenicola* Wasbauer
– Mandible with three apical teeth, one may be very small; distance between midocellus
   and closest eye margin more than 1.5 MOD 3
3 Mesopleuron densely punctate, with punctures evenly dispersed over entire surface and
   1–2 puncture diameters apart; propodeum coarsely sculptured with irregular demarcation
   between dorsal and posterior surfaces indicated by rugae . . . . *confusa*, new species
– Mesopleuron sparsely punctate, with punctures generally 4–6 puncture diameters apart,
   denser dorsally than posteroventrally, surface above midcoxa nearly impunctate; propo-
   deum smooth, without distinct punctation or rugosities, and no demarcation between
   dorsal and posterior surfaces 4
4 Midocellus separated from eye margin in frontal view by more than 2 MOD; epipygium
   apically bidentate . . . . *perpunctata* (Cockerell)
– Midocellus separated from eye margin in frontal view by more than 1 MOD but less than
   2 MOD (Fig. 6); epipygium apically flat and broadly triangular (Fig. 19) . . . *megalops*, new
                                                                                                          species
5 Gular carina with basal tooth-like projection near mandible (Fig. 25); clypeus transversely
   indented, without medial projection, arcuately raised apicomedially (Fig. 5); epipygium
   apex truncate (as in Fig. 21) . . . . *inermis* (Malloch)
– Gular carina simple; clypeus medially bulging or with medial tooth; epipygium various
   6
6 F-I and II subequal in length, about twice as long as broad or longer; epipygium apex
   strongly convex and lip-like (Fig. 20) . . . . *marcida* (Bradley)
– F-I shorter than II, and between I.2 and 1.8× as long as broad; epipygium apex medially
   emarginate or truncate 7
7 Midocellus larger, separated by 2 MOD or less from nearest eye margin; F-I 1.6× as long
   as broad or longer 8
– Midocellus small, separated by 3 or more MOD from nearest eye margin; F-I 1.5× as long
   as broad or shorter 9
8 Midocellus separated from nearest eye margin by 1.5 MOD or less; epipygial apex convex;
   clypeus with broad, blunt medial projection, bulging and strongly subtriangular in profile;
   forewing R1 vein strongly angulate near costal margin, marginal cell broadly parallel-
   sided (as in Fig. 15) . . . . *mexicana*, new species
– Midocellus separated from nearest eye margin by 1.8–2.0 MOD; epipygial apex bidentate;
   clypeus with narrow noselike or almost digitate medial projection; forewing R1 vein nar-
   rowly separated from stigma, curved or indistinguishable near costal margin . . . .
   . . . . *paupercula* (Bradley)
9 Midocellus five or more MOD from nearest eye margin (Fig. 3); F-I 1.2× as long as broad;
   F-II 1.4× as long as broad; epipygium apex truncate (as in Fig. 21); propodeum coarsely
   sculptured, with irregular, partial transverse carina (Fig. 24) . . . . *costaricensis*, new species
– Midocellus 3.0–3.5 MOD from nearest eye margin; F-I 1.5× as long as broad; F-II 1.7–
   1.9× as long as broad; epipygium apex truncate or emarginate; propodeum smooth with-
   out sculpturing or transverse carina 10
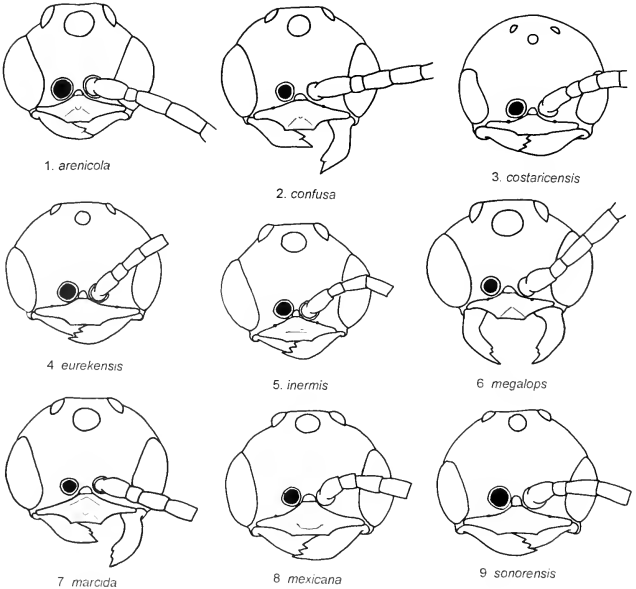
10 Clypeus with small, sharp medial projection, apical truncation 1.5 MOD wide (Fig. 4);
     epipygial apex medially emarginate, with sublateral carina . . . . . **eurekaensis**, new species
 –   Clypeus with broad, transverse medial projection subtended by discrete declivity, apical
     truncation 2 MOD wide (Fig. 9); epipygial apex truncate . . . . **sonorensis**, new species

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Quemaya arenicola Wasbauer
(Figs. 1, 10, 22)

Quemaya arenicola Wasbauer 1967:169. Holotype
male; California: Inyo Co., 6 mi w Glamis
(SAN FRANCISCO, type No. 9306).

Male.—Body length 4–6 mm; clypeus
with narrow apical truncation 0.6 MOD
wide (Fig. 1); mandible with two apical
teeth; gular carina simple; F-I and II length
twice breadth; interantennal distance 0.3
MOD wide; midocellus separated from
nearest eye margin by 1.1–1.2 MOD; fore-
wing with two submarginal cells, second
cell triangular or subquadrate, completely
underlying the first (Fig. 10); mesopleural
punctures 0.2–0.5 puncture diameter
apart; epipygium with sublateral carina

1. *arenicola*

2. *confusa*

3. *costaricensis*

4. *eurekensis*

5. *inermis*

6. *megalops*

7. *marcida*

8. *mexicana*

9. *sonorensis*

Figs. 1–9. Front view of male face, left antenna removed.
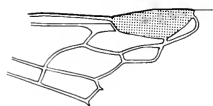
10. *arenicola*
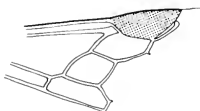
11. *costaricensis*

18. *confusa*
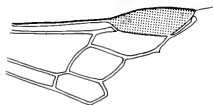
12. *eurekaensis*

13. *inermis*

19. *megalops*
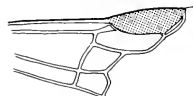
14. *marcida*
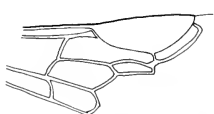
15. *megalops*

20. *marcida*
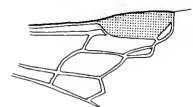
16. *perpunctata*
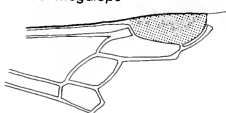
17. *sonorensis*

21. *eurekaensis*
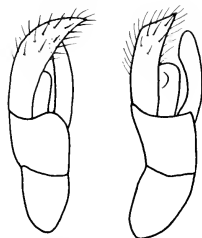
22. *arenicola*   23. *marcida*
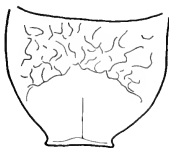
24. *costaricensis*
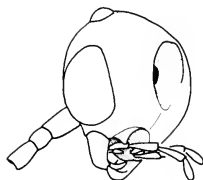
25. *inermis*

Figs. 10–25. Figs. 10–17. Forewing venation. Figs. 18–21. Apex of epipygum (last gastral tergum). Figs. 22–23. Lateral view of male genital capsule. Fig. 24. Posterior view of male propodeum. Fig. 25. Oblique posterior view of male head, showing genal tooth.

ending in an apical lobe, apical margin medially emarginate; paramere subapically expanded, apical margin linear terminating in acute ventral angle (Fig. 22). Body color reddish brown; antennae pale red; wing veins clear and at most faintly tinted with dark brown stigma.

Material examined.—84 specimens from California: Imperial, San Bernardino, Riverside and San Diego Co.; Arizona: Yuma Co.; Mexico: Baja California Norte and Sonora.

Discussion.—This is one of the few *Quemaya* species with two submarginal cells. It can be immediately distinguished from the others with similar venation by having only two mandibular teeth and large ocelli narrowly separated from the eye margin.

Quemaya confusa Kimsey and Wasbauer, new species
(Figs. 2, 18)

Male.—Body length 4–6 mm long; face (Fig. 2): clypeus medially projecting and nose-like in profile, apical truncation medially emarginate or slightly trilobate and 1.3 MOD wide; mandible with three apical teeth, two subsidiary teeth considerably smaller than apical one; gular carina simple; F-I and F-II 1.7× as long as wide; distance between midocellus and closest eye margin 2 MOD; interantennal space 0.5 MOD wide; mesopleural punctures 0.5–1.0 puncture diameter apart; forewing with one submarginal cell; marginal cell rhomboid, apically broad and R1 angulate; epipygium apicomedially emarginate, with two sublateral carinae forming an ovoid, slightly sunken, medial area and terminating in apical lobes (Fig. 18); paramere nearly parallel-sided, only slightly widened subapically before acute ventral angle. Body color black to dark brown; leg brown; antenna bicolored, paler ventrally than dorsally; wing veins pale brown-tinted, stigma dark brown; wing membrane untinted.

Etymology.—This species is named "confusa" because of the strong similarity

between it and other species of *Quemaya* found in the same localities.

Type material.—Holotype male: MEXICO: Sonora, 6 km nnw San Carlos, 11–15 July 1983, E. Fisher, malaise trap (DAVIS). Paratypes, 55 males (DAVIS, SAN FRANCISCO, RIVERSIDE, LAWRENCE, OTTAWA, WASHINGTON, TUCSON): two—USA: CALIFORNIA: Riverside Co., Blythe, 21 June 1963, F. D. Parker and L. A. Stange; one—Deep Canyon, 24 June 1964, E. I. Schlinger; one—Millard Cyn., 20 June 1963, E. I. Schlinger; two—Winchester, 10 July and 14 Aug. 1967, W. Icenogle; four—Imperial Co., 3 mi n Glamis, 15–16 Sept. 1977, M. Wasbauer & A. Hardy; one—Holtville, 8 July 1965, R. A. Flock; three—Chocolate Mts., Ogilby Rd., 3 mi s Jct. Hwy. 78, 16–21 Oct. 1977, M. Wasbauer; five—San Bernardino Co., 10 mi w 29 Palms, 27 May 1966, M. Wasbauer; two—NEW MEXICO: Dona Ana Co., Las Cruces, 2 June 1965, R. M. Bohart; one—2 mi. e Mesilla; ten—ARIZONA: Pinal Co., Marana, 6 July 1955, Butler & Werner; one—Maricopa Co., Gila Bend, Bohart & Butler, 12 Aug. 1954; one—Wickenburg, 10 Aug. 1950, H. K Lloyd; one—Pinal Co., 10 mi. s Toltec, 21 June 1953, T. R. Haig; nine—4 mi. se Casa Grande, 18 June 1964, Smith & Baker; one—Pima Co., Continental, 17 July 1966, H. K. Court; one—TEXAS: Brewster Co., Chisos Mts. 10–12 June 1908, Mitchell & Cushman; one—MEXICO: Sonora, Cocorit, 23 May 1968, Parker & Stange; one—11 June, F. D. Parker; two—18 mi. e El Puerto, 7 Aug. 1960, Arnaud, Ross & Rentz; four—40 mi. n Hermosillo, 8 Aug. 1960, Arnaud, Ross & Rentz; one—6 km nnw San Carlos, 11–15 July 1983; one—4.9 mi n Magdalena, Rt. 15, 25 Aug. 1964, M. E. Irwin.

Discussion.—*Quemaya confusa* is another species with two submarginal cells. It can be distinguished from other species with this kind of wing venation by the densely and evenly punctate mesopleuron, coarsely sculptured propodeum, and mandibles with the normal three apical teeth. This

species is probably most similar to *perpuncata* and *megalops*.

Quemaya costaricensis Kimsey and Wasbauer, new species
(Figs. 3, 11, 24)

Male.—Body length 4.0–5.5 mm; face (Fig. 3): clypeus flat in profile, with apical truncation 2.5 MOD wide; mandible with three apical teeth, preapical teeth subequal in length; gular carina simple; F-I length 1.2× breadth; F-II 1.4× as long as broad; interantennal distance 0.9 MOD wide; distance from midocellus to closest eye margin 5.7 MOD; mesopleuron with punctures 1–2 puncture diameters apart; forewing with one submarginal cell; marginal cell small, more than 3× as long as broad, widely separated from costal margin (Fig. 11); propodeum coarsely rugose dorsally, with broken irregular transverse ridge separating dorsal from posterior surfaces (Fig. 24) epipygium apicomedially truncate, with two sublateral carinae above apex forming an ovoid, slightly sunken medial area; paramere gently tapering, apicoventral angle narrowly rounded. Body color black; antenna bicolored, paler ventrally than dorsally; wing veins pale brown, stigma dark brown; wing membrane slightly brown tinted.

Etymology.—This species is named after the country of collection, which is the southernmost record for the tiphiid subfamily Brachycistidinae.

Type material.—Holotype male: Costa Rica: Guanacaste Prov., 14 km s Cañas, F. D Parker, 17 Feb. 1989 (LOGAN). Paratypes, 52 males (DAVIS, LOGAN, SANTO DOMINGO): eight—same data as holotype; one: 4–5 Mar. 1989; two—24 Feb. 1989; one—28–29 Jan. 1989; three—18 Feb. 1989; three—28 Feb. 1989; one—9 Mar. 1989; one—11–13 Jan. 1990; one—16 Feb. 1989; one—15–24 Feb. 1990; one—5 Mar. 1989; two—1–11 Feb. 1990; one—south of Cañas, 9–11 Feb. 1989, F. D. Parker; one—25–28 Feb. 1989; one—25 Feb.–8 Mar.

1989; twenty-one—Santa Rosa Natl. Pk., 21 Feb.–11–14 Mar. 1981.

Discussion.—There are many distinctive features of this species, which will immediately separate it from all other *Quemaya*, including: the tiny ocelli and small eyes, coarsely sculptured propodeum and short, broad flagellomeres. It is closest to *sonorensis* and *eurekaensis* based on the small ocelli, single submarginal cell and short broad flagellomeres.

Quemaya eurekaensis Kimsey and Wasbauer, new species
(Figs. 4, 12, 21)

Male.—Body length 3.5–4.0 mm; face (Fig. 4): clypeus with small, sharp medial projection, apical truncation 1.5 MOD wide; mandible with three apical teeth; gular carina simple, without tooth-like projection; F-I length 1.5× breadth; F-II length 1.9× breadth; interantennal distance 0.5 MOD wide; midocellus separated from nearest eye margin by 3.2 MOD; mesopleural punctures 3–6 puncture diameters apart; forewing with one submarginal cell (Fig. 12); epipygium with sublateral carinae each ending in an apical lobe, epipygial apex medially emarginate (Fig. 21); gonostylar shape apically narrowed into single acute apical angle. Body dark reddish brown, antennal and leg color pale reddish brown; wing veins untinted, except stigma dark reddish brown.

Etymology.—This species is known primarily from Eureka Valley, thus the name.

Type material.—Holotype male: California: Inyo Co., Eureka Valley, 13 July 1975, F. Andrews & A. Hardy (DAVIS). Paratypes, eight males (DAVIS, SAN FRANCISCO): six—same data as holotype; one—19 June 1972 Derham & Guiliani; one—Saline Valley dunes, 30 km e Independence, 26 May 1993, D. E. Russell, malaise trap.

Discussion.—The diagnostic features for *eurekaensis* are the small ocelli, separated from the eye margin by more than 3 MOD, medially emarginate epipygium

apex, and short F-I and II. This species is closest to *sonorensis* and less so *costaricensis*, but can be immediately distinguished from *sonorensis* by the sharp clypeal projection and emarginate epipygium. The larger ocelli and smooth propodeum will separate *eurekaensis* from *costaricensis*.

Quemaya inermis (Malloch)
(Figs. 5, 13, 25)

Brachycistis inermis Malloch 1924:23. Holotype male; Arizona: Higley (WASHINGTON).

Male.—Body length 3–4 mm; face (Fig. 5): clypeus transversely indented, without medial projection, apical truncation 0.9 MOD wide; mandible with three apical teeth, preapical teeth subequal; gular carina with tooth-like projection near base of mandible (Fig. 25); forewing with one submarginal cell (Fig. 13); F-I and II length 1.7× breadth; interantennal distance 0.8 MOD wide; midocellus separated from eye margin by 2 MOD; mesopleuron anterior part with punctures 1–3 puncture diameters apart, posteriorly nearly impunctate and polished; epipygium without sublateral carinae, only slightly indented apicomedially; paramere gently tapering, apicoventral angle narrowly rounded. Body color reddish brown; antenna paler than body; wing veins and stigma nearly colorless.

Material examined.—239 specimens from: California: Riverside, San Bernardino, and Imperial Cos.; Arizona: Yuma, Santa Cruz and Maricopa Cos. Nevada: Lincoln Co.; Mexico: Sonora and Baja California Norte.

Discussion.—This is the only *Quemaya* species with a tooth-like projection on the gular carina; a feature typically found in members of the genus *Brachycistis*. *Quemaya inermis* can be immediately recognized by the transversely medially indented clypeus, and the apically truncate epipygium.

Quemaya marcida (Bradley)
(Figs. 7, 14, 20, 23)

Brachycistis marcida (Bradley) 1917:283. Holotype male; USA: California, Imperial Co. (ITHACA).

Male.—Body length 3–5 mm; face (Fig. 7): clypeus with sharp medial projection, appearing nasiform in profile, apical truncation 1.7 MOD wide; mandible with three apical teeth; gular carina simple; F-I and F-II twice as long as broad; interantennal distance 0.6 MOD wide; midocellus separated from eye margin by 2.5 MOD; mesopleuron sparsely punctate, punctures 4–6 puncture diameters apart or more; forewing with one submarginal cell; marginal cell nearly parallel-sided, R1 vein strongly angulate and joining stigma at or below costal margin (Fig. 14); epipygium apicomedially rounded and lip-like, with sublateral carina beginning above lip (Fig. 20); paramere apically truncate with apical margin concave (Fig. 23). Body reddish brown to brown; antenna and legs paler reddish brown than body color, forewing veins pale brown tinted; stigma brown.

Material examined.—873 specimens from CALIFORNIA: San Bernardino, Riverside and Imperial Cos.; Arizona: Yuma and Cochise Cos.; Nevada: Nye; Mexico: Sonora.

Discussion.—As with the majority of *Quemaya* species, *marcida* has one submarginal cell in the forewing and a simple gular carina. However, of these species only *marcida*, *arenicola* and *perpuncata* have the first two flagellomeres twice as long as broad. *Quemaya marcida* is the only one that has the epipygial apex strongly convex and lip-like. Additionally, the ocelli are large and narrowly separated from the nearest eye margin.

Quemaya megalops Kimsey and Wasbauer, new species
(Figs. 6, 15, 19)

Male.—Body length 4–5 mm; face (Fig. 6): clypeus with large tuberculate medial projection, strongly nasiform in profile, apical truncation 0.9 MOD wide; mandible with three apical teeth, subsidiary ones considerably shorter than primary tooth; gular carina simple; F-I and II length 1.9–2.0× breadth; interantennal distance 0.5 MOD wide; midocellus separated from eye

margin by 1.6 MOD; mesopleuron nearly impunctate; forewing with two submarginal cells, the second large, nearly rectangular and Rs aligned with 2rs-m; marginal cell large and parallel-sided with R1 vein strongly angulate before joining stigma at costal margin (Fig. 15); epipygium apically truncate, with distinct sublateral carinae, flat medially (Fig. 19); paramere lanceolate, narrowly tapering apically. Body reddish brown to brown with yellow legs and antenna; wing veins and stigma transparent and lightly yellow tinted.

Etymology.—mega = large, *ops* = eyes; f. (Gr.). The name refers to the greatly enlarged eyes and ocelli.

Type material.—Holotype male: California: Riverside Co., 5 mi nw Desert Center, 22 Oct. 1955, M. Wasbauer (DAVIS). Paratypes: 7 males (DAVIS, RIVERSIDE, SAN FRANCISCO): one—same data as holotype; two: Indio, Aug. 1977, Allen and Duffy (DAVIS); one—Magnesia Cyn. 2 July 1952; one—Inyo Co., 7 mi nne Panamint Sprs., 15 May 1969, P.Rude; one—Arizona: Yuma Co., 4 mi w Salome, 8 June 1958, D & G. MacNeill; one—Mohawk, Apr. 1963, Timberlake.

Discussion.—This species most closely resembles *perpuncata* as both have two submarginal cells, a sparsely punctate mesopleuron and smooth propodeum. *Quemaya megalops* can be distinguished from *perpuncata* by the much larger ocelli, separated from the nearest eye margin by less than two midocellus diameters, pale stigma, and the very distinctive epipygium, which appears broadly triangular with the apex narrowly truncate. The wing venation is also diagnostic, with the second submarginal cell much larger than in other *Quemaya* species.

Quemaya mexicana Kimsey and Wasbauer, new species
(Fig. 8)

Male.—Body length 2.5–4.5 mm; face (Fig. 8): clypeus with broad, blunt medial projection, bulging and strongly subtriangular in profile, apical truncation 1 MOD wide; mandible with three apical teeth; gular carina simple; F-I–II 2.0–2.4× as long as broad; interantennal distance 0.4 MOD wide; midocellus separated from eye margin by 1.5–2.0 MOD; mesopleuron sparsely punctate, punctures 4–6 puncture diameters apart or more; forewing with one submarginal cell; marginal cell nearly parallel-sided, R1 vein strongly angulate and joining stigma at or below costal margin; epipygium apicomedially convex, otherwise similar to *sonorensis*; gonostylar apex truncate, with apical margin linear. Body brown to dark brown; antenna and legs paler reddish brown than body color, forewing veins pale brown tinted; stigma brown.

Etymology.—The name refers to the preponderance of specimens having been collected in northern Mexico.

Material examined.—Holotype male: MEXICO: Baja California Norte, 1 km s El Rosario, 24–25 July 1992, D. E. Russell, MT (DAVIS). Paratypes: 46 males (DAVIS): 37—Diablo Cyn, Dry Lake, 16 July 1979, D. Giuliani; four—same data as holotype; three—eastern base of Sierra de Juarez below Rumorosa, 11 Sept. 1961, I. L. Wiggins; one—USA: California, Andrade, 4 Aug. 1966, M. Wasbauer; one—Calexico, 19 June 1969.

Discussion.—This species closely resembles *marcida* as discussed under that species. However, *mexicana* can be readily distinguished from *marcida* by the shorter flagellomeres, broad blunt clypeal projection, and distinctively convex epipygial apex.

Quemaya paupercula (Bradley)

Brachycistis paupercula Bradley 1917:282. Holotype male; California: Calexico (ITHACA, type No. 129.1)

Male.—Body length 3–4.5 mm; clypeus with medial nose-like projection in profile, apical truncation 1.1 MOD wide; mandible with three apical teeth; gular carina sim-

ple; F-I and II length 1.6× breadth; inter-antennal distance 0.3 MOD wide; midocellus separated from eye margin by 1.9 MOD; mesopleural punctures almost absent; forewing with one submarginal cell; marginal cell narrow, closed on costal margin; epipygial apex truncate, subapically concave; paramere nearly parallel-sided, apex abruptly truncate, with acute ventral and dorsal angle and apical margin somewhat concave between. Body color dark brown; antenna paler than body; wing veins nearly colorless, except stigma dark brown.

Material examined.—109 specimens from California: Riverside, Imperial, Kern, San Bernardino and San Diego Co.; Arizona: Coconino, Yuma Co.; Nevada: Lincoln Co.; Texas: Brewster and and Presidio Co.; New Mexico: Dona Ana Co.; Mexico: Baja California Norte and Sonora.

Discussion.—*Quemaya paupercula* is one of the most commonly collected species of the genus. It is most readily confused with *eurekaensis*, which has a very restricted distribution. Both species have a medially emarginate epipygial apex, short flagellomeres, two submarginal cells and a simple gular carina. However, the larger size of the ocelli will readily separate *paupercula* from *eurekaensis*.

Quemaya perpunctata (Cockerell)
(Fig. 16)

Brachycistis perpunctata Cockerell 1896:291. Holotype male; New Mexico: Las Cruces (PHILADELPHIA).

Male.—Body length 4.0–5.5 mm; clypeus with low medial projection, apical margin 1 MOD wide; mandible with three apical teeth; gular carina simple; F-I length twice breadth; F-II 2.2× as long as broad; inter-antennal distance 0.5 MOD wide; midocellus separated from eye margin by 2.8 MOD; forewing with two submarginal cells, second cell triangular or subquadrate, completely underlying the first (Fig. 16); mesopleural punctures 1–2 puncture

diameters apart, nearly impunctate above midcoxa; epipygium with sublateral carinae each ending in an apical lobe, epipygial apex medially emarginate; paramere expanded subapically, apex truncate, apical margin linear, between two acute angles. Head and body dark brown to black, except antennae, clypeal apex, palpi and tegula reddish brown, mandibles and tarsi yellow, femora and tibiae brown; stigma dark brown, nearly black, veins brown.

Material examined.—249 specimens from California: San Bernardino, Riverside, Imperial and San Diego Cos.; Nevada: Lincoln Co.; Texas: Brewster Co.; Arizona: Yuma Co.; Mexico: Baja California Sur.

Discussion.—The most striking feature of this species is the wide range of variation in coloration. This variation appears to be geographically correlated. In California specimens some red is always present on at least the head. The prothorax and often the entire thorax may also be red, giving the specimen a strongly bicolored appearance. Otherwise, *perpunctata* can be recognized by having two submarginal cells, three mandibular teeth, propodeum without distinct sculpturing, and small ocelli.

Quemaya sonorensis Kimsey and Wasbauer, new species
(Figs. 9, 17)

Male.—Body length 3.5–4.0 mm; face (Fig. 9): clypeus with broad transverse medial projection subtended by discrete declivity, apical truncation 2 MOD wide; mandible with three apical teeth; gular carina simple; F-I length 1.5× breadth; F-II length 1.7× breadth; interantennal distance 0.7 MOD wide; midocellus separated from eye margin by 3 MOD; mesopleuron smooth, punctures 1–4 puncture diameters apart becoming sparser above midcoxa; forewing with one submarginal cell, venation as in *paupercula* (Fig. 17); epipygium apex truncate; paramere as in *costaricensis*. Body and antennal color pale

reddish brown; wing veins untinted, except stigma reddish brown.

Etymology.—The type series of this species is from Sonora, Mexico; thus the name.

Type material.—Holotype male: MEXICO: Sonora, 6 km nnw San Carlos, 11–15 July 1983, E. Fisher, MT (DAVIS). Paratypes: 11 males (DAVIS), same data as holotype.

Discussion.—The small ocelli, short flagellomeres, single submarginal cell, truncate epipygial apex and lack of a gular tooth distinguish *sonorensis* from most other *Quemaya* species, except *eurekaensis* and *costaricensis*. *Quemaya sonorensis* can be distinguished from these two species by the larger ocelli and flagellomeres I and II 1.5× as long as broad or longer, not shorter as in *costaricensis*, narrow clypeal truncation and broad transverse clypeal projection.

ACKNOWLEDGMENTS

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Geographic Variation of Sex Ratio in *Pelecinus polyturator* (Drury) (Hymenoptera: Pelecinidae)

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Abstract.—The relative abundance of males and females of *Pelecinus polyturator* (Drury) (Hymenoptera: Pelecinidae) was examined on the basis of specimens held in natural history collections. The species may be divided into two groups of populations. Those in the United States and Canada (between 28°N and 51°N) are primarily thelytokous: males form only 4% of the total number of individual specimens. Populations from localities 23°N and southward have a substantially higher frequency of males (36%). Within each group of populations, there is no demonstrable change in sex ratio with latitude. Male emergence dates generally precede those of females, but there seems to be no significant difference in the time period in which the two sexes are flying. Within the U.S. and Canada, the uncommon males are not randomly distributed.

The parasitoid wasp *Pelecinus polyturator* (Drury) (Hymenoptera: Pelecinidae) is a large and familiar inhabitant of moist deciduous forests in the Nearctic. Its range extends well beyond this, generally from southeastern Canada to central Argentina (Muesebeck 1979, Masner 1993). Surprisingly little is known of *Pelecinus* biology despite its relative abundance. The few published host records indicate that this wasp is an internal larval parasitoid of soil-dwelling Scarabaeidae (Coleoptera) (summarized in Lim *et al.*, 1980). One aspect of its biology that has received wide comment, however, is that males are extremely uncommon in the northern portion of the range.

Brues (1928) cited *Pelecinus polyturator* as an example of the phenomenon of geographic parthenogenesis. Arrhenotokous parthenogenesis is the most common mode of reproduction in the Hymenoptera, in which males are usually produced from unfertilized eggs. Thelytoky is not at all rare, being known from at least twenty families (Stouthamer *et al.* 1990). *Pelecinus* appears to demonstrate both modes: the-lytoky in the north temperate region and arrhenotoky elsewhere.

At the time that he wrote his paper Brues admitted that he had seen very few male specimens of *P. polyturator* from the United States or Canada. His analysis of the sex ratio of the species was anecdotal. His sampling of *Pelecinus* was never described and must have been quite limited (see below). Neither did he actually quantify observed sex ratios in tropical and temperate regions. Our purpose here is to quantify the issue of sex ratio variation in this wasp throughout its geographical range.

MATERIALS AND METHODS

Specimen data.—Our information on the distribution and relative abundance of males and females is based upon an extensive survey of the holdings of *Pelecinus* in natural history collections. Material for this study was borrowed or data acquired from 91 collections around the world (see Appendix). The information associated with specimens varies extensively in accuracy and completeness, especially given

the small size of the typical label attached to a specimen.

The data were transcribed and stored in a specimen-level relational database. The table structure is slightly modified from the information model developed by the Association of Systematics Collections (1993) and is implemented in the Oracle7® environment on a Silicon Graphics (UNIX) workstation. This combination of hardware and software was chosen to deal with the large numbers of specimens in insect collections and for its ability to interface with other software (geographic information systems, mapping software, and World Wide Web servers). The database stores all of the information on specimen labels (place, time, method of collection, etc.), characteristics of the specimens (e.g., sex, color pattern), source of material, and literature references. The relational structure allows the development of ad hoc queries unconstrained by the format of the original data. As such, the system is not only suited to the questions we ask here, but is also applicable to collection management, diversity assessments, taxonomic studies, host-parasitoid biology, etc. The database (Johnson & Musetti 1996), intended to represent the sum of documented geographic and temporal information available, contains data from 7,188 specimens of the genus *Pelecinus*.

Latitude and longitude of collecting localities were added where these could be determined with relative confidence. These are stored in two separate tables, for points and polygons, reflecting the level of accuracy of the cited collecting locality and our ability to locate the sites in atlases and gazeteers. Only those classed as "points" were used in the analyses below. In practice, this means that the collecting records for points consist of localities identified with specific populated places, recreational areas, manmade features (e.g., monuments), or geographic features such as mountains and lakes.

Brues (1928) pointed out that Neotrop-

Table 1. Numbers of specimens of males and females of *Pelecinus polyturator* used in analyses of sex ratio.

Latitude of localities	Number of ♂♂ [%]	Number of ♀♀ [%]	Total number
25°N–51°N	119 [4.2]	2723 [95.8]	2842
38°S–25°N	616 [38.4]	990 [61.6]	1606
Total	735 [16.5]	3713 [83.5]	4448

ical specimens of *Pelecinus* exhibit notable variation in color patterns. Many of these were described as distinct species in the early 19th Century, but the present taxonomic consensus (dating from Schletterer 1890) is that only a single species, *P. polyturator*, is recognized as valid. To avoid confounding data from possible distinct species, we chose to include in our analyses only those specimens conforming to the color pattern of specimens from the U.S. and Canada: the head, mesosoma, and metasoma are uniformly black or very dark brown, and the fore wings are clear or gradually infuscate toward the apex. A summary of the numbers of specimens used is presented in Table 1.

Analyses.—Coordinates of latitude and longitude of collecting localities were extracted from the database by sex. Brues (1928) asserted (as does conventional wisdom) that males and females are not identically distributed. This was tested by comparing the cumulative relative frequency distribution of specimens by 1° of latitude using the Kolmogorov-Smirnov test (Sokal & Rohlf 1995).

If there is variation in sex ratio among sites, especially over the vast area occupied by this species, one reason may be that northern females are substantially longer-lived as adults than males, thus leading to an overabundance of females in collection records. To examine this possibility, we sorted the collecting date records for specimens by sex and combined them into groups for each 10 degrees of latitude (from 50°N to 40°S). Collecting dates were expressed in terms of polar co-
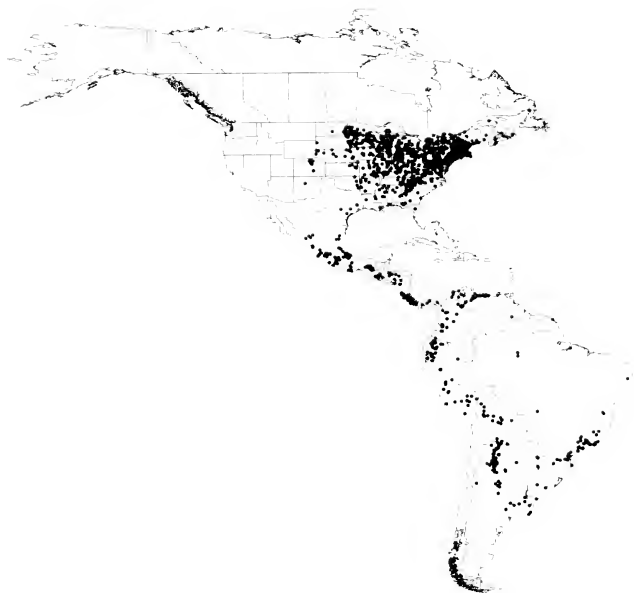
Fig. 1. World distribution of *Pelecinus polyturator*.

ordinates by Julian date (1–365) and mean and standard deviation of the dates were calculated for each sex in every 10° band.

Sex ratio data are expressed as the proportion of males in the total population of specimens. Specimens for every 5° band of latitude were pooled and the relationship between sex ratio and latitude of collection examined using regression. For reasons developed below, these data were partitioned into two groups north and south of 25°N. The two partitions then were separately analyzed for relationship between latitude and sex ratio. Finally, on the basis of this data partition, we exam-

ined the hypothesis that males in the U.S. and Canada are randomly distributed. Specimens were pooled from blocks of 5° of latitude and longitude and the observed number of specimens was compared using a χ^2 test with that expected using the observed sex ratio of all specimens north of Mexico.

RESULTS

The documented range of *Pelecinus polyturator* extends from a maximum of 51°N in Quebec and Ontario south to 38°S in Argentina (Fig. 1). The species does not occur in Chile or the West Indies (includ-

Fig. 2. Cumulative relative frequency distribution (%) of male and female specimens of *Pelecinus polyturator* by latitude. Localities grouped for every 1° of latitude. Maximum difference and probability of identity of distributions using Kolmogorov-Smirnov test.
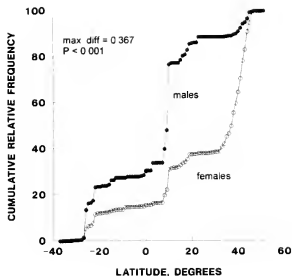

Fig. 3. Frequency distribution of collecting years of *Pelecinus polyturator*. Three specimens collected between 1804 and 1875 are not illustrated.

ing Trinidad). Specimens are otherwise found throughout South America, although material from the Amazon Basin is very scarce. In the United States, the range of the species extends west to 106° in Colorado and New Mexico. The species is apparently absent from peninsular Florida south of the Gainesville area.

The cumulative relative frequency distributions of the two sexes, pooled into 1° increments of latitude, is presented in Fig. 2. The comparison of these two distributions clearly leads to rejection of the null hypothesis that the two are identically distributed throughout America. Specimens of males are clearly more abundant outside of temperate North America.

Two possible sources of sampling error that could lead to the observation of highly skewed sex ratios are (1) the samples were taken in particular years in which one sex is either very rare or extraordinarily abundant, and (2) if populations are strongly protandrous or adult females survive much longer than males, then the apparent rarity of males in some areas may be a collecting artifact. The frequency dis-

tribution of collecting dates by year is illustrated in Fig. 3. The distribution of collecting dates for each sex were pooled into groups by 10° of latitude (Fig. 4); statistics for each sex in the latitudinal bands is presented in Table 2. The average collecting dates for males generally precedes those of females, but do not differ significantly. Further, it seems to be possible to find males through most of the flight time of females.

Figure 5 demonstrates a significant negative relationship between latitude and sex ratio (with southern latitude expressed as negative numbers). The observed sex ratio varies from 0.0–0.60, with an average of 0.19. Even cursory examination of the data reveals that this is not a continuous decrease in the frequency of males, but that the change to spanandrous populations (with <10% males) occurs rather abruptly. We have no knowledge of any specimens of *Pelecinus* collected between 23° and 28°N latitude, and the sex ratios on either side of this gap differ strongly. Therefore the data were partitioned into two components at 25°N (Fig. 6). Separate regression analyses result in a change in slope from negative to
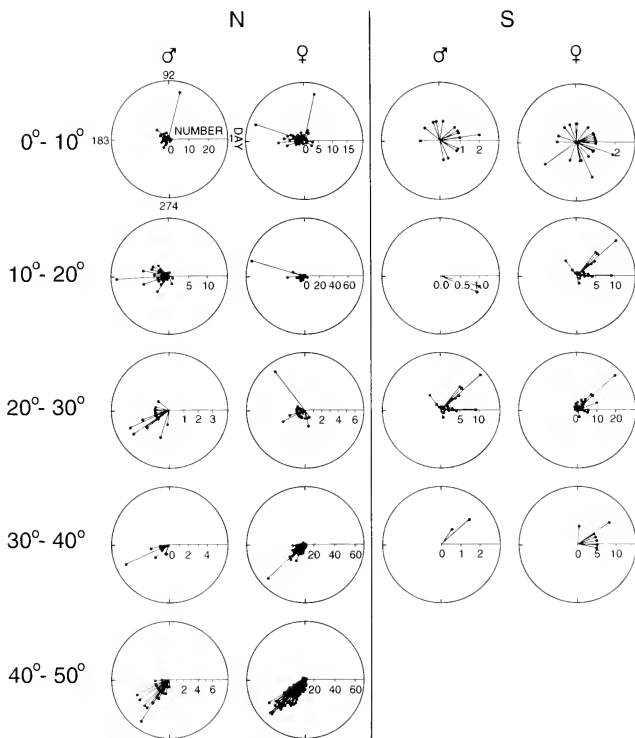
Fig. 4. Collecting dates for males and females of *Pelecinus polyturator*. Localities grouped for every 10° of latitude. Julian day 1 = 1 January; 92 = 2 April; 183 = 2 July; 274 = 1 October; N: north latitudes; S: south latitudes.

positive, but neither significantly differs from a slope of 0, i.e., there is no demonstrable relationship between latitude and sex ratio in the two groups. The average sex ratio for the southern populations is 0.36 (0.20–0.60), and that for the northern populations is 0.04 (0.00–0.06). Figure 7 maps the abundance of males and females in 5° blocks of latitude and longitude. Pooling specimens by latitude or

Table 2. Dates of collection of *Pelecinus polyturator* specimens, localities within 10° bands of latitude pooled together. $\bar{x}$: mean Julian date of collection (calendar date); sd: standard deviation; N: number of specimens.

Degrees latitude	North		South	
	♀♀	♂♂	♀♀	♂♂
0°–10°				
$\bar{x}$	144.7 (25 May)	153.4 (2 Jun)	22.7 (23 Jan)	344.8 (11 Dec)
sd	7.1	8.5	20.7	26.3
N	137	222	16	27
10°–20°				
$\bar{x}$	181.0 (30 Jun)	185.7 (5 Jul)	344.0 (10 Dec)	24.3 (24 Jan)
sd	4.8	5.4	0.5	17.9
N	133	390	2	11
20°–30°				
$\bar{x}$	209.3 (28 Jul)	195.5 (15 Jul)	39.0 (8 Feb)	37.5 (7 Feb)
sd	3.4	6.9	12.2	18.5
N	26	30	107	189
30°–40°				
$\bar{x}$	213.2 (1 Aug)	222.4 (10 Aug)	48.3 (17 Feb)	25.7 (26 Jan)
sd	2.3	3.4	0.8	22.0
N	18	897	3	8
40°–50°				
$\bar{x}$	228.1 (16 Aug)	230.7 (19 Aug)		
sd	2.4	2.8		
N	88	1277		

Fig. 5. Sex ratio for all specimens of *Pelecinus polyturator* (proportion of males in total) as a function of latitude, with regression and 95% confidence limits. Individual localities pooled for every 5° of latitude; south latitudes expressed as negative numbers.

longitude (Table 3) reveals that males do not appear to be randomly distributed through the U.S. and Canada.

DISCUSSION

Collecting records are not random samples and we recognize a number of possible biases in the data. Female *Pelecinus* are large and "unusual," easily identifiable, relatively slow fliers, and are often found resting on vegetation at heights accessible to collectors. Thus, females are commonly found in the holdings of even small collections and may be overrepresented. On the other hand, their numerical abundance and the fact that only a single species is recognized may cause experienced collectors to ignore them. Males may be relatively scarce in collections because their abundance in some areas may be truly low, or they may be overrepresented precisely because of their rarity, at least in the eyes of North American col-
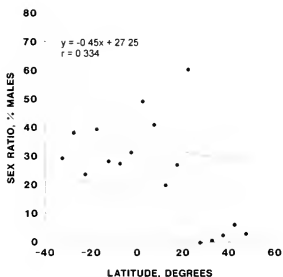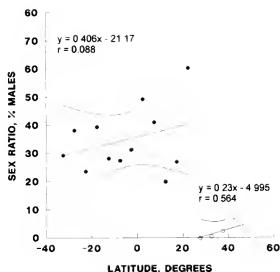
Fig. 6. Sex ratio for *Pelecinus polyturator* (proportion of males in total) as a function of latitude, with regression and 95% confidence limits. Data partitioned into two groups: localities north of 25°N, and localities south of 25°N. Individual localities pooled for every 5° of latitude; south latitudes expressed as negative numbers.

Table 3. Test of null hypothesis that male specimens in Fig. 7 are distributed randomly among blocks in the U.S. and Canada. When pooling by longitude, the specimens from the two westernmost columns of cells and the three easternmost columns of cells were summed to obtain expected numbers greater than five. Expected numbers of males based on overall sex ratio in America north of Mexico: 4.0% males. **: probability < 0.01; *: probability < 0.05.

	x^2	d.f
specimens in 5° blocks pooled by latitude	38.6**	2
specimens in 5° blocks pooled by longitude	10.2*	4

and is the only sample available from which to estimate the sex ratio. We believe that we can fairly judge the hypothesis presented by Brues with cautious use of the specimen data from collections.

Our survey of collections produced only 83 male specimens of *Pelecinus* that we are certain would have been available to Brues (i.e., collected in 1928 or earlier; a further 75 males have no year of collection on the label). Even on the basis of such limited data, it appears that Brues gener-

lectors. The magnitude and net effect of these biases are impossible to quantify. However these collections represent the material foundation upon which everything we know about this species is based

2 ♂ 94 ♀ 2.1%	8 ♂ 143 ♀ 5.3%	0 ♂ 26 ♀ 0.0%	0 ♂ 4 ♀ 0.0%	27 ♂ 89 ♀ 23.3%	0 ♂ 36 ♀ 0.0%	0 ♂ 4 ♀ 0.0%	0 ♂ 3 ♀ 0.0%	37 ♂ 399 ♀ 8.5%
1 ♂ 15 ♀ 8.3%	1 ♂ 55 ♀ 1.8%	2 ♂ 91 ♀ 2.2%	17 ♂ 292 ♀ 5.7%	9 ♂ 80 ♀ 10.1%	15 ♂ 343 ♀ 4.2%	10 ♂ 482 ♀ 2.0%	8 ♂ 19 ♀ 29.6%	0 ♂ 5 ♀ 0.0%	63 ♂ 1382 ♀ 4.4%
3 ♂ 30 ♀ 9.1%	0 ♂ 12 ♀ 0.0%	5 ♂ 70 ♀ 6.7%	0 ♂ 110 ♀ 0.0%	1 ♂ 203 ♀ 0.5%	5 ♂ 344 ♀ 1.4%	0 ♂ 7 ♀ 0.0%			14 ♂ 776 ♀ 1.8%
0 ♂ 2 ♀ 0.0%	0 ♂ 12 ♀ 0.0%	0 ♂ 39 ♀ 0.0%	0 ♂ 110 ♀ 0.0%	0 ♂ 3 ♀ 0.0%					0 ♂ 165 ♀ 0.0%
4 ♂ 45 ♀ 8.2%	3 ♂ 163 ♀ 1.8%	15 ♂ 316 ♀ 4.5%	17 ♂ 466 ♀ 3.5%	10 ♂ 397 ♀ 2.5%	47 ♂ 779 ♀ 5.7%	10 ♂ 525 ♀ 1.9%	8 ♂ 23 ♀ 25.8%	0 ♂ 8 ♀ 0.0%	114 ♂ 2722 ♀ 4.0%

Fig. 7. Numbers of males, females, and sex ratio (proportion of males in total) of thelytokous populations of *Pelecinus polyturator* in blocks of 5° latitude and longitude in the U.S. and Canada.

ally described the true situation: males are very scarce in temperate North America, and elsewhere they occur in numbers consistent with a 0.50 sex ratio. There is an abrupt transition between the two populations that corresponds with a geographical disjunction in southern Texas and northern Mexico. Further focussed collections are needed to determine whether this disjunction is real and, if not, what happens to the males in that area.

We cannot yet identify any diagnostic morphological differences between the northern thelytokous populations and the bisexual populations to the south. Specimens from southern Mexico (Chiapas) and Central America are often distinguishable, but typical black specimens are found from Mexico to Argentina. There is precious little information on the biology of *Pelecinus*, but Aguiar (1997) has recently described the copulatory behavior of individuals in Brazil, consistent with the idea that males in the tropics and south temperate regions are functional, i.e., that females do indeed mate.

Brues (1928) additionally speculated on the genetics of *Pelecinus*. He asserted that the largest specimens were found in the north and suggested that these may be tetraploid. The largest specimens we have seen, however, are from Argentina and a great range of sizes may be found even in single populations in the U.S. The size variation could be better explained by variation in host size than by invoking unexplored genetic mechanisms.

The discovery of the nonrandom distribution of males in the United States and Canada was particularly surprising. This could be the result of a statistical artifact or something unusual may be occurring in some populations. The most notable of these is a population near Ottawa, Ontario: male specimens have been consistently collected in this single site over a period of ten years. Young (1990) described a potentially similar situation in southern Wisconsin in which he suggested that a bisex-

ual population may have replaced the thelytokous strain. The Ottawa population could be a promising one upon which to focus in order to better understand the role of males in the northern temperate populations of *Pelecinus*.

ACKNOWLEDGMENTS

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APPENDIX

Sources of material. American Entomological Institute, Gainesville, FL; American Museum of Natural History, New York, NY; Academy of Natural Sciences, Philadelphia, PA; Buffalo Museum of Science, Buffalo, NY; California Academy of Sciences, San Francisco, CA; Albertson College of Idaho, Caldwell, ID; Carnegie Museum of Natural History, Pittsburgh, PA; Canadian National Collection of Insects, Ottawa, ON; Colorado State University, Fort Collins, CO; Cornell University, Ithaca, NY; Cambridge University Museum of Zoology, Cambridge, UK; Deutsches Entomologisches Institut, Eberswalde, Germany; University of New Hampshire, Durham, NH; College of Environmental Science & Forestry, Syracuse, NY; Denver Museum of Natural History, Denver, CO; Escuela Agrícola Panamericana, Zamorano, Honduras; Estación de Biología "Chamela", UNAM, San Patricio, Mexico; North Carolina Department of Agriculture; University of California, Berkeley, CA; Utah State University, Logan, UT; University of Wyoming, Laramie, WY; Fundação Instituto Oswaldo Cruz, Rio de Janeiro, RJ, Brazil; Field Museum of Natural History, Chicago, IL; Florida State Collection of Arthropods, Gainesville, FL; Instituto Miguel Lillo, San Miguel de Tucumán, Tucumán, Argentina; Instituto Nacional de Biodiversidad, Santo Domingo, Costa Rica; Illinois Natural History Survey, Urbana, IL; Instituto Nacional de Pesquisas da Amazonia, Manaus, AM, Brazil; University of Wisconsin, Madison, WI; Universidad Central de Venezuela, Maracay, Venezuela; Kansas State University, Manhattan, KS; Natural History Museum, Los Angeles, CA; Loyola University, Chicago, IL; M.A. Ivie private collection; Milwaukee Public Museum, Milwaukee, WI; Museum of Comparative Zoology, Cambridge, MA; Mississippi State University, Mississippi State, MS; Muséum d'Histoire Naturelle, Geneva, Switzerland; Universidad Nacional de La Plata, La Plata, Argentina; Muséum National d'Histoire Naturelle de Paris, France; Michigan State University, East Lansing, MI; Montana State University, Bozeman, MT; Museu de Zoologia da Universidade de São Paulo, São Paulo, SP, Brazil; North Carolina State University, Raleigh, NC; North Dakota State University, Fargo, ND; Naturhistorisches Museum, Vienna, Austria; Naturhistoriska Riksmuseet, Stockholm, Sweden; New York State Museum, Albany, NY; Oklahoma State University, Norman, OK; Ohio State University, Columbus, OH; P.K. Lago private collection; Peabody Museum of Natural History, Yale University, New Haven, CT; Pennsylvania State University, State College, PA; Purdue University, West Lafayette, IN; Museu Nacional, Rio de Janeiro, RJ, Brazil; Pontifícia Universidade Católica del Ecuador, Quito, Ecuador; Nationaal Naturhistorisch Museum, Leiden, The Netherlands; Royal Ontario Museum, Toronto, Ontario, Canada; R.S. Miller private collection; Rutgers State University, New Brunswick, NJ; R. Willis Flowers collection; South Dakota State University, Brookings, SD; Servicio Entomológico Autónomo, Nicaragua; University of Kansas, Lawrence, KS; Southern Illinois University, Carbondale, IL; Smithsonian Tropical Research Institute, Panama; Texas A&M University, College Station, TX; T.K. Philips private collection; University of Arkansas, Fayetteville, AK; University of Arizona, Tucson, AZ; Universidad de Concepción, Concepción, Chile; University of California, Davis, CA; University of Colorado, Boulder, CO; University of Connecticut, Storrs, CT; University of California, Riverside, CA; University of Delaware, Newark, DE; University of Georgia, Athens, GA; University of Louisville, Louisville, KY; University of Massachusetts, Amherst, MA; University of Mississippi, Oxford, MS; Museum of Zoology, University of Michigan, Ann Arbor, MI; University of Missouri, Columbia, MO; University of Minnesota, St. Paul, MN; Universidad Nacional Autónoma de México, Mexico City, Mexico; University of Nebraska State Museum, Lincoln, NE; National Museum of Natural History, Washington, DC; University of Vermont, Burlington, VT; Virginia Tech University, Blacksburg, VA; University of Idaho, Moscow, ID; James Entomological Collection, Washington State University, Pullman, WA; West Virginia University, Morgantown, WV; Humboldt Universität, Berlin, Germany; Zoologische Staatssammlung, Munich, Germany.

Parasitism of *Siphoninus phillyreae* (Homoptera: Aleyrodidae) by Aphelinid Parasitoids at Different Locations in Egypt

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Abstract.—Seven species of aphelinid parasitoids (Hymenoptera: Aphelinidae) were reared from second and third larval stages and pupae of pomegranate whiteflies, *Siphoninus phillyreae* (Haliday) (Homoptera: Aleyrodidae) from three locations in Egypt, during a one year survey (June 94–June 95). Three species, *Eretmocerus mundus* Mercet, *Encarsia davidi* Viggiani and Mazzone, and *E. galilea* Rivnay, were reported from Arish (Northeast Egypt). Parasitism was greatest (45.7%) in Arish during September 1994, of which 38% was caused by *E. mundus. Encarsia inaron* (Walker) was the dominant parasitoid of *S. phillyreae* in Giza (Central Egypt) and Assiut (Upper Egypt), with average parasitism rates of 38 and 46.5% over the year, respectively. In Giza, total parasitism reached a maximum of 80% during August 1994, with *Encarsia inaron* being responsible for 66.1%. In Assiut, parasitism peaked at 93.1% in August 1994 with *E. inaron* accounting for 78% of the total. *Eretmocerus diversiciliatus* Silvestri and *Encarsia lutea* (Masi) were reported only from Giza. *Eretmocerus corni* Haldeman was reported only from Assiut. These species had much less impact than *E. inaron* in both locations. The presence of different parasitoids at different locations was attributed to geographical factors as well as tolerance of the parasitoids to weather factors and probably availability of alternative hosts. A key for the reported parasitoids is presented.

The pomegranate whitefly, *Siphoninus phillyreae* (Haliday) (Homoptera: Aleyrodidae), is the most important pest of pomegranate in Egypt (Priesner and Hosny 1932). This insect's host range is restricted to deciduous fruit crops (Byrne et al. 1990). In Egypt, the host range of *S. phillyreae* includes apple, *Pyrus malus* L.; pear, *Pyrus communis* L.; quince, *Pyrus cydonia* L., and pomegranate, *Punica granatum* L. (Abd-Rabou 1990). Pomegranate orchards extend from the north coast to southern Egypt. Pomegranate leaves heavily infested with *S. phillyreae* have the demand for fluid transport substantially increased beyond the tree's normal capacity to respond. The loss of phloem fluids certainly represents a loss of potential productivity and probably contributes to the reported reduction in fruit size (Costacos 1963). Elwan (1982) studied the biology of *S. phillyreae* and showed that its developmental period varied according to temperature and relative humidity. Various aphelinid parasitoids (Hymenoptera: Aphelinidae) have been reported from *S. phillyreae*, including *Encarsia inaron* (Walker), *E. siphonini* Silvestri, *E. galilea* Rivnay, *E. hispida* De Santis, *E. pseudopartenopea* Viggiani and Mazzone and *Eretmocerus corni* Haldeman (Priesner and Hosny 1940; Mentzeloz 1967; Viggiani and Mazzone 1980a,b; Viggiani and Battaglia 1983; Rivnay and Gerling 1987; Polaszek et al. 1992). *Punica granatum* is a deciduous fruit crop which defoliates in winter.

The purpose of this study was to monitor the rate of aphelinid parasitism on *S. phillyreae* infested pomegranate leaves in three distinctive regions in Egypt, to assess the impact of biological control on the whitefly, and to determine in what ways it can be improved.

MATERIALS AND METHODS

Second and third larval stages and pupae of *Siphoninus phillyreae* were sampled
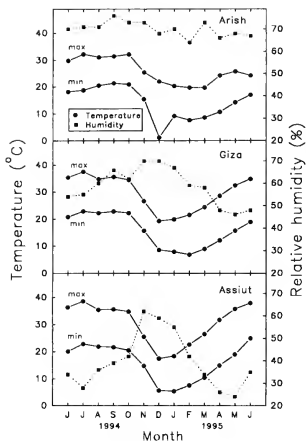
Fig. 1. Monthly mean maximum and minimum temperatures and percent relative humidity at the three locations over the survey period.

Table 1. Percent parasitism of *Siphoninus phillyreae* by different aphelinid parasitoids in Arish, Egypt.

Date	Whitefly individuals/ leaf	Percent parasitism		
		Er. mundus	En. davidi	En. galilea
June 1994	41.6	17.0	1.5	0
July	66.6	23.0	4.5	0.3
August	110.0	31	8	0.8
September	100.0	38	6.5	1.2
October	70.4	27	3	2.0
November	35.0	10	0.5	0.5
December	16.6	5	0	0
January 1995	—	—	—	—
February	—	—	—	—
March	—	—	—	—
April	—	—	—	—
May	—	—	—	—
June	32.6	13	1.1	0.8

— Data was not available because of defoliation.

on pomegranate leaves collected monthly (30 infested leaves per sample) from one site representing each of three distinctive regions in Egypt. The number of trees varied by location. Arish is located in Northeast Sinai (i.e., coastal area), Giza is located south of Nile Delta and Assiut in southern Egypt. Environmental data were obtained from local weather stations and mean monthly values were plotted in Fig. 1. Pomegranate trees in the three locations did not receive any chemical treatments except at the Assiut area, which was sprayed for stem borers during defoliation (i.e., January–February 1995). Defoliation time was longer in the Arish area than at Giza or Assiut. No data for the whitefly is presented during the defoliation periods. Pomegranate leaves were transferred to the laboratory in well-ventilated boxes. *S. phillyreae* eggs and first larval stages were

eliminated as well as other insects. Total number of *S. phillyreae* individuals in each stage were recorded per leaf. Each leaf was stored in well-ventilated glass emergence tube and monitored daily for parasitoid emergence. Parasitoid adults were slide mounted in Hoyer's medium and identified to species, and a diagnostic key was constructed for their identification.

RESULTS

Parasitoid species emerging from samples of *S. phillyreae* on pomegranate varied according to the area from which they were collected in Egypt. In the Northeastern Sinai, where Arish is located, *Eretmocerus mundus* Mercet, *Encarsia davidi* Viggiani, and *E. galilea* parasitized an average of 25% of the total *S. phillyreae* population. *Eretmocerus mundus* was responsible for 20.5% of the total parasitism and the other 4.4% by the other two parasitoids (Table 1). In the Arish area, parasitism peaked at 45.7% in September (Table 1). The parasitoid species reported from Arish area (i.e. *E. mundus, E. davidi* and *E. galilea*) were not recovered from samples in Giza or Assiut.

In Giza (Central Egypt), *S. phillyreae* was parasitized by *E. inaron, Eretmocerus diversicilatus* Silvestri, and *E. lutea* (Masi) at

Table 2. Percent parasitism of *Siphoninus phillyreae* by different aphelinid parasitoids in Giza, Egypt.

Date	Whitefly individuals/ leaf	Percent parasitism		
		En. inaron	*Er. diversiculatus*	*En. lutea*
June 1994	27.4	24.1	1.5	0.5
July	33.7	39.0	4.5	2.0
August	56.3	66.1	8.1	6.0
September	68.9	69.0	6.5	3.5
October	66.4	53.1	3.0	1.5
November	30.6	9.0	0.5	1.0
December	10.6	3.1	0.0	0.0
January 1995	—	—	—	—
February	—	—	—	—
March	—	—	—	—
April	—	—	—	—
May	17.3	0	0	0
June	22.1	25.0	1.1	1.0

— Data was not available because of defoliation.

Table 3. Percent parasitism of *Siphoninus phillyreae* by different aphelinid parasitoids in Assiut, Egypt.

Date	Whitefly individuals/ leaf	Percent parasitism	
		En. inaron	*Er. corni*
June 1994	70.1	50.0	9.0
July	113.8	73.0	12.1
August	189.0	78.0	15.1
September	177.8	66.0	17.1
October	140.4	45.1	19.1
November	100.0	20.0	14.0
December	20.7	18.0	10.0
January 1995	—	—	—
February	—	—	—
March	—	—	—
April	10.3	0.0	0.0
May	40.3	32.2	4.1
June	21	37.1	5.1

— Data was not available because of defoliation.

average rates of 38, 4.5, and 2.2%, respectively (Table 2). The maximum rate of parasitism reached 80% during August 1994, of which E. *inaron* was responsible for 66.1% of the total.

In Assiut, parasitism averaged 46.5% by E. *inaron* and 12% by *Eretmocerus corni* (Table 3). Parasitism peaked to 93.1% during August 1994, where E. *inaron* was responsible for 78% of the total.

All reported parasitoids were primary parasitoids except for *Encarsia* males that are known to be hyperparsites on females of their own species or other parasitoid species (Viggiani 1981). No hyperparasitism was observed.

DISCUSSION

The three areas of Egypt surveyed were distinctive in their locations as well as their weather (Fig. 1). The Arish area is located in Northeast Sinai and can be characterized by colder and longer winters, and higher relative humidity than in Giza or Assiut. Also, Arish is isolated from the other two locations by the vast desert area of the Sinai, which may account for difference in the S. *phillyreae* parasitoid complex. The parasitoid species

collected from Arish area were not reported in the other two locations. E. *inaron* was the dominant parasitoid of S. *phillyreae* in both Giza and Assiut. Both of these areas are in the Nile River Valley, south of Nile Delta with Assiut about 300 km south of Giza. *Encarsia lutea* and E. *diversicilatus* were obtained only in samples from Giza, while *E. corni* was recovered only from Assiut. Higher temperature in Assiut may correlate to both higher whitefly populations and higher rates of parasitism.

Encarsia davidi was recorded by Abd-Rabou (1994) as a parasitoid of *Aleurolobus niloticus* Priesner and Hosny on *Ziziphus spinachristi* in Egypt. *Encarsia galilea* was recorded by Abd-Rabou (1994) as a parasitoid of S. *phillyreae* on P. *granatum*. Priesner and Hosny (1932) recorded *Encarsia inaron* as a parasitoid of S. *phillyreae* on P. *granatum* and indicated a rate of parasitism as high as 80%. In our survey, the peak of parasitism by E. *inaron* occurred in September (69%) and in August (78%) in Giza and Assiut, respectively.

Encarsia lutea (Masi) was recorded by Abdel-Fattah et al. (1984) as a parasitoid of *Bemisia tabaci* (Genn.) on tomato plants, whereas *Eretmocerus corni* was recorded by Priesner and Hosny (1940) as a para-

sitoid of *B. tabaci* on *Lantana camara*. *Eretmocerus diversicilatus* was recorded for the first time from Egypt associated with *B. tabaci* by Khalifa and El-Khidir (1965), and *Eretmocerus mundus* has been recorded from Egypt on *B. tabaci* by El-Helay et al. (1971). In the present study, *E. mundus* was the dominant species in the Arish location, with the peak parasitism occurring in September (38%).

Parasitoid tolerance to different ranges

of temperature and relative humidity is not clearly known. The colder and longer winters of Arish, as well as lower humidity in Assiut, may be limiting factors controlling the presence and absence of each parasitoid species of *S. phillyreae*. In addition, the availability of alternate hosts for the parasitoids in the same area is probably another factor. Terminology used in the key follows that of Polaszek et al. (1992).

KEY TO APHELINID PARASITOIDS OF *SIPHONINUS PHILLYREAE* FROM EGYPT

1. Antennal flagellum 3-segmented in female, club one elongate segment, tarsi 4- segmented, male flagellum 1-segmented . . . . Genus *Eretmocerus* 2
 – Antennal flagellum 6-segmented in female, club 2–3 segments, tarsi 5-segmented, male flagellum 5 or 6-segmented . . . . Genus *Encarsia* 4
2. Mesoscutum with 2 pairs of setae, male pedicel dark brown 3
 – Mesoscutum with 3 pairs of setae, first funicle segment triangular, club 6–7 times as long as wide, male pedicel yellow . . . . *E. corni* Haldeman
3. First funicle segment quadrate, second funicle segment longer than wide, submarginal vein with 3 seta . . . . *E. mundus* Mercet
 – First funicle segment triangular, second funicle segment transverse, submarginal vein with 2 setae . . . . *E. diversicilatus* Silvestri
4. Head and mesosoma dark brown to black with 6–10 pairs of setae, metasoma yellow, antennal club 2-segmented . . . . *E. inaron* (Walker)
 – Entire body yellow or orange, or nearly so, metasoma tergite I often infuscate, antennal club 3 segmented 5
5. Valvular III dark brown, first funicle segment quadrate or wider than long, male funicle segments F1–F3 expanded 6
 – Valvular III yellow, first funicle cylindrical, 1.6–2.3 as long as wide, male unknown . . . . *E. galilea* Rivnay
6. Valvular III short, as long as width at base and 0.3 times as long as ovipositor, tibia II 1.0–1.1 times as long as ovipositor . . . . *E. lutea* (Masi)
 – Valvular III elongate, 2 times as long as width at base and 0.4 times as long as ovipositor, tibia II 0.8 times as long as ovipositor . . . . *E. davidi* Viggiani and Mazzone

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Revision of North American *Aleiodes* Wesmael (Part 2): the *apicalis* (Brullé) Species-group in the New World (Hymenoptera: Braconidae, Rogadinae)

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Abstract.—The *Aleiodes apicalis* (Brullé) species-group is defined to include the following previously described species: *apicalis* (Brullé, 1832), *grandis* Giraud, 1857 (=*Rhogas malaisei* Shestakov, 1940 NEW SYNONYMY), *parasiticus* Norton, 1869, *atriceps* Cresson, 1869, *abdominalis* Cresson, 1869, *rileyi* Cresson, 1869, *molestus* (Cresson, 1872) NEW COMBINATION, *schirjajewi* Kokujev, 1898, *convexus* van Achterberg, 1991 (=*Chelonorhogas rufithorax* Enderlein, 1912), and *brethesi* Shenefelt, 1975 NEW COMBINATION. One newly described species, *flavitarsus* Marsh and Shaw, is also included. The *apicalis* species-group is regarded as monophyletic based on the presence of dense setal mats on the apical metasomal terga of males. The genus *Dimorphomastax* Shenefelt, 1967 is synonymized under *Aleiodes*, and the species *Dimorphomastax peculiaris* Shenefelt, 1979 is regarded as a junior synonym of *Aleiodes atriceps* Cresson. *Rogas rufocoxalis* Gahan, 1917 is newly synonymized as a junior synonym of *Aleiodes molestus* (Cresson). A key to the New World species of the *apicalis* species-group is provided, and species treatments are given for Nearctic species, including diagnostic characters, distribution, and biological information.

The rogadine braconid genus *Aleiodes* Wesmael is worldwide in distribution, but is particularly species-rich in the Holarctic region. *Aleiodes* is diverse in North America, with at least 90 species in the United States and Canada (Shaw *et al.* 1997). This paper is the second contribution in a series of planned papers on *Aleiodes* species-groups, intended to provide a complete revision of the genus for North America. In this paper we treat a distinctive monophyletic assemblage, the species of the *Aleiodes apicalis* species-group, as it occurs in the New World region. All members of this group have dense setal mats on male terga 4–7 (Fig. 1). Our definition of the species-group includes all species known to us, worldwide. However, because our main intent is to provide a revision of North American species, species treatments are limited to the Nearctic fauna.

Since only one other New World species is known to us, this is included in the key for convenience. The European species are currently being revised by Kees van Achterberg and Mark Shaw.

Aleiodes species are koinobiont endoparasitoids of lepidopteran larvae, especially macrolepidoptera of the superfamilies Noctuoidea and Geometroidea, and to a lesser extent, Arctioidea, Sphingoidea, and Papilionoidea (Shaw *et al.* 1997). Members of the *apicalis* group, as far as known, are mostly parasitoids of Noctuidae. 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. The form of the mummy caused by a particular *Aleiodes* species is usually characteristic for that host and parasitoid, so the mummified remains are

of considerable diagnostic value and should be retained with the parasitoid, when reared. For more complete discussions of *Aleiodes* biology, readers may refer to Shaw (1983, 1994), Shaw and Huddleston (1991), Shaw (1995), and Shaw *et al.* (1997).

METHODS

Species covered in this paper can be identified as members of the subfamily Rogadinae using the keys of Shaw and Huddleston (1991), van Achterberg (1993), or Shaw (1995). Our definition of *Aleiodes* follows that of van Achterberg (1991), Shaw (1993), and Shaw *et al.* (1997). Specimens can be determined as *Aleiodes* using the keys of Marsh *et al.* (1987), van Achterberg (1991), or Shaw (1997). Specimens keyed through Marsh *et al.* (1987) will key to couplet 185, at which point they can be separated from *Rogas* by the presence of a discrete median carina on the propodeum, the lack of a foveate sternaulus on the mesopleuron, and the lack of a blunt basal tooth on the tarsal claw. In practice, more than 99% of U.S. and Canadian specimens encountered will be *Aleiodes*, as *Rogas s.s.* is only infrequently encountered north of Mexico (but increases in species richness in the neotropics). The species-groups of North American *Aleiodes* can be keyed using the key provided in Shaw *et al.* (1997). The species treated in this paper were formerly assigned to the *ductor* Thunberg species-group by Shaw *et al.* (1997) following a recent interpretation of that species by Papp (1985). However, Kees van Achterberg (pers. comm.) has indicated to us that previous interpretations of *ductor* are not correct, and that the species treated here are better called the *apicalis* species-group.

Terminology follows that used for *Aleiodes* by Shaw *et al.* (1997), Shaw (1993) and Marsh (1989). Microsculpture terminology follows that of Harris (1979). Wing venation terminology (see Fig. 16) follows that of Shaw (1997) and Shaw *et al.* (1997).

Abbreviations for museums are as follows: ANSP, Academy of Natural Sciences, Philadelphia; AEI, American Entomological Institute, Gainesville; AMNH, American Museum of Natural History, New York; CAS, California Academy of Sciences, San Francisco; CNC, Canadian National Collection, Ottawa; CUI, Cornell University, Ithaca; FSCA, Florida State Collection of Arthropods, Gainesville; HNHM, Hungarian Natural History Museum, Budapest; INHS, Illinois Natural History Survey, Urbana; MISU, Michigan State University, East Lansing; MSSU, Mississippi State University, Mississippi State; OKSU, Oklahoma State University; RMNH, Nationaal Natuurhistorisch Museum, Leiden; TAMU, Texas A. & M. University, College Station; UCD, University of California, Davis; UMSP, University of Minnesota, St. Paul; RMSEL, Rocky Mountain Systematic Entomology Laboratory, University of Wyoming, Laramie; USNM, U.S. National Museum of Natural History, Washington, D.C.

Authorship of species is attributed to the senior authors (PMM and SRS) in the order indicated.

ALEIODES APICALIS SPECIES-GROUP

Included species: apicalis (Brullé, 1832), *grandis* Giraud, 1857 (= *malaisei* Shestakov, 1940 new synonymy), *parasiticus* Norton, 1869, *atriceps* Cresson, 1869 revised combination (= *Dimorphomastax peculiaris* Shenefelt, 1979 new synonymy), *abdominalis* Cresson, 1869 (= *lectus* Cresson, 1869), *rileyi* Cresson, 1869 revised combination, *molestus* (Cresson, 1872) new combination (= *rufocoxalis* (Gahan, 1917) new synonymy), *schirjajewi* Kokujev, 1898, *convexus* van Achterberg, 1991 (= *Chelonorhogas rufithorax* Enderlein, 1912), *brethesi* Shenefelt, 1975 new combination (replacement name for *nigriceps* Brethes, 1909, preoccupied by *nigriceps* Wesmael, 1838), and *flavitarsus* Marsh and Shaw, new species.

Diagnostic characters.—Ocellar diameter small, ratio of ocellar diameter to distance
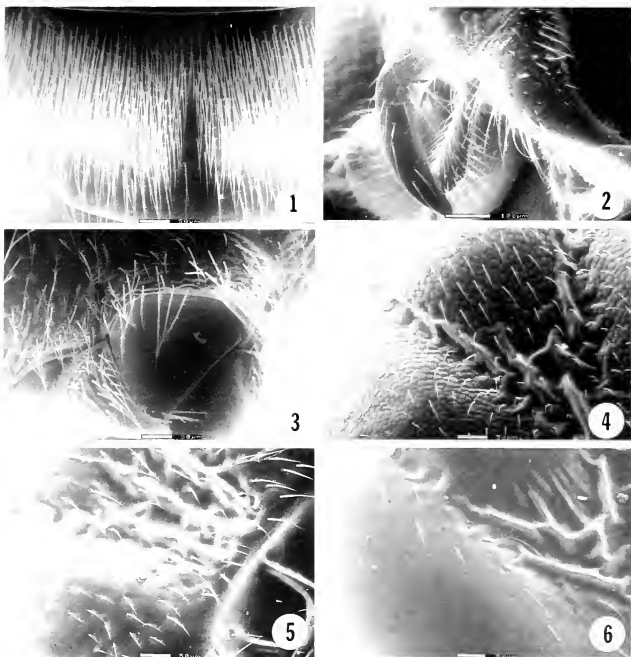
Figs. 1–6. Fig. 1. Densely setose metasomal tergum 4. *A. abdominalis*, male. Figs. 2–3. Mandible and oral space. 2. *A. atriceps*, male. 3. *A. abdominalis*, male. Figs. 4–6. Mesonotal sculpture. 4. *A. abdominalis*. 5. *A. parasiticus*. 6. *A. brethesi*.

between lateral ocellus and compound eye less than 1; occipital carina meeting hypostomal carina laterally; dense setal mat present on male terga 4–7 and subdivided medially (Fig. 1); medial ridge extending down frons 0.55 or more of distance from line between base of scape to clypeus; mesonotal disc sculpture finely granulate to smooth (Figs. 4–6), sparsely or not setose; tarsal claws strongly pectinate (Figs. 12–14).

Remarks.—A moderate-sized, circumpolar and neotropical monophyletic group, associated mostly with noctuids (see Fig. 15). There are some recorded associations with geometrids, lymantriids, pyralids, and even sawflies, but these need confirmation and the latter seems unlikely.

The dense setal mats on male terga 4–7 are undoubtedly synapomorphic. The function of the dense setal mats on male terga 4–7 is unknown, but perhaps they

may serve to disperse pheromones during courtship and mating.

Even fairly recently (Shenefelt, 1975; Marsh, 1979), species belonging in this group have been classified in several genera (*Aleiodes, Chelonorhogas, Dimorphomastax,* and *Rogas*). *Chelonorhogas* was synonymized with *Aleiodes* by van Achterberg (1991), but retained *Chelonorhogas* as a valid subgenus, to which the *apicalis*-group is assigned.

KEY TO NEW WORLD SPECIES OF THE *ALEIODES APICALIS* SPECIES-GROUP

1 Mandible of male with a large, curved, tusk-like accessory tooth situated near the posterior condyle (Fig. 2), or female with a small accessory tooth situated near the posterior condyle; oral space unusually large; southwestern U.S. and Mexico .. **A. atriceps** Cresson
 – Mandible normal and unmodified, lacking a large, tusk-like tooth (males) or small tooth (females) near the posterior condyle (Fig. 3); oral space smaller (Fig. 3) 2
2(1) Mesosoma (excluding legs) entirely black 3
 – Mesosoma color varying from entirely orange, to orange with extensive black markings posteriorly and laterally, but pronotum, mesonotum, and scutellar disc always colored bright orange 4
3(1) Hind tarsomeres orange to brown, similar to color of tibia; body length 6.0–8.0 mm; fore wing vein 1cu-a beyond vein 1M by less than 3 times its length; hindwing vein m-cu present (Fig. 16) .... **A. abdominalis** Cresson
 – Hind tarsomeres 1–4 yellow, much lighter than color of tibia; body length 4.5–5.5 mm; fore wing vein 1cu-a beyond vein 1M by 3 times its length; hindwing vein m-cu absent (Fig. 17) .... **A. flavitarsus** Marsh & Shaw, new species
4(3) Body entirely orange to orangish brown; mesonotum granulate and dull ....
 .... **A. rileyi** Cresson
 – Body only partly orange, head entirely black, legs, mesosoma, and apex of metasoma with variable black markings; mesosoma sculpture variable, but always somewhat shining and polished 5
5(4) Mesosoma entirely orange, legs entirely black; mesonotal disc entirely smooth and highly polished, virtually devoid of setae (Fig. 6); South American species ....
 .... **A. brethesi** (Shenefelt)
 – Mesosoma usually orange and black (rarely entirely orange), leg color orange and black, coxae at least always orange; mesonotal disc not so completely smooth, with numerous setal pits (Fig. 5); North American species 6
6(5) Hind femur and tibia banded, orange on basal half, black on apical half; northern species associated with boreal forests .... **A. parasiticus** Norton
 – Hind femur and tibia entirely black; southern species frequently associated with agroecosystems .... **A. molestus** (Cresson)

Aleiodes atriceps Cresson, revised combination
(Fig. 2)

Aleiodes atriceps Cresson, 1869, Amer. Ent. Soc. Trans. 2:380.
Dimorphomastax peculiaris Shenefelt, 1979, Proc. Ent. Soc. Wash. 81:133. New synonymy based on examination of holotype.

Diagnosis.—Body bicolored, head including antenna black, mandibles and palpi yellow, mesosoma varying from entirely black to entirely orange, tegula yellow, metasoma orange, legs orange, wings hyaline, veins brown except vein C+Sc+R and stigma yellow; body length, 6.0–7.0 mm; 46–53 antennomeres; malar space equal to basal width of mandible; oral opening circular, diameter equal to malar space in female and greater than malar space in male; ocelli small, ocellocular distance about twice diameter of lateral ocel-

lus; mandible in female with short triangular tooth at condyle, in male with large sickle-shaped tooth at condyle; occipital carina meeting hypostomal carina; head entirely coriaceous, sometimes smoother in male; pronotum rugose laterally; mesonotum and scutellum coriaceous, notauli weakly scrobiculate; mesopleuron smooth, subalar sulcus rugose, sternaulus absent; propodeum rugose, median carina complete; metasomal terga 1 and 2 costate-rugose, median carina complete; third metasomal tergum longitudinally costate over basal 0.25 to 0.5, smooth posteriorly; terga 4–7 in male with dense row of short yellow setae at base, and dense patches of yellow setae on each side of mid-line; fore wing with vein 1cu-a beyond vein 1M by distance nearly twice length of 1cu-a, hind wing with marginal cell gradually broadening to apex, vein RS straight on basal half and slightly bent downward on apical half, vein m-cu present; tarsal claws strongly pectinate with 6–7 stout teeth, apical 3 teeth of pectin about 0.75 as long as apical claw, remaining teeth gradually shorter towards base of claw; apical tibial spurs of male blunt.

Type material examined.—*Aleiodes atriceps* Cresson, holotype female, Mexico (ANSP). *Dimorphomastax peculiaris* Shenefelt, paratype female, Portal, Arizona (AEI).

Distribution.—Mexico, Arizona, and Texas.

Biology.—Unknown. Adults have been collected from July through December.

Comments.—Shenefelt (1975) classified *atriceps* under *Rogas*, but we are moving it here back to its original combination with *Aleiodes*. Although the unusual and distinctive shape of the mandible (Fig. 2) prompted Shenefelt (1979) to create a new genus for this species, we consider it to be only a specialized species of *Aleiodes* with peculiar mandibles. The species is, in most other characters, a typical *Aleiodes* and we consider the mandible shape, as well as the blunt tibial spurs of the male, to be autapomorphies. *Dimorphomastax* Shene-

felt, 1969 is therefore considered a junior synonym of *Aleiodes*, NEW SYNONYMY.

The unusual accessory mandibular tooth of this species is strongly sexually dimorphic (small triangular tooth in the female, large sickle-shaped projection in the male) suggesting a possible role in courtship and mating. The sexual dimorphism raises doubts about whether it may serve any primary cutting function, such as assisting in escape from the host mummy.

Aleiodes abdominalis Cresson
(Figs. 1, 3, 4, 7, 12, 16)

Aleiodes abdominalis Cresson, 1869, Amer. Ent. Soc. Trans. 2:379.

Aleiodes lectus Cresson, 1869, Amer. Ent. Soc. Trans. 2:379. Possible synonymy with *Aleiodes abdominalis* Cresson indicated by Cresson, 1869. Synonymized by Muesebeck & Walkley, 1951.

Diagnosis.—Body bicolored, head and mesosoma black, metasomal terga 1–3 orange, remainder of terga orange to black, antenna and legs orange, wings lightly dusky, veins brown, tegula yellow; body length, 6.0–8.0 mm; 54–63 antennomeres; malar space longer than basal width of mandible; face costate with distinct raised ridge between antennae, frons, vertex and temple coriaceous; oral opening circular, diameter about equal to basal width of mandible; propleuron rugose; mesonotum and scutellum finely coriaceous, notauli weakly scrobiculate and meeting in small rugose are before scutellum; mesopleuron smooth, subalar sulcus rugose, sternaulus absent; propodeum rugose-coriaceous, median carina on basal half only; first and second metasomal terga costate, median carina complete; third tergum costate at base, remainder smooth; apical terga of males, especially terga 4–7 densely covered with silvery setae, except along median line; fore wing with vein 1cu-a wing beyond vein 1M by distance greater than length of 1cu-a; hind wing with marginal cell gradually widening, vein RS slightly
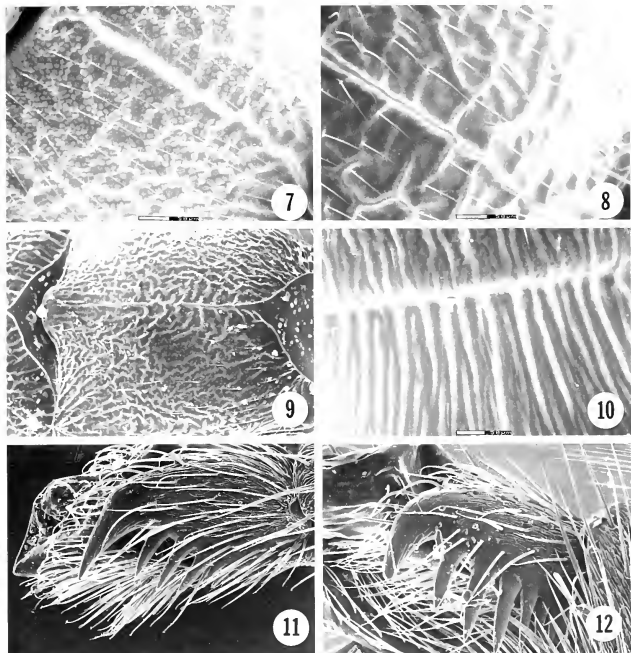
Figs. 7–12. Figs. 7–8: Propodeal sculpture. 7. *A. abdominalis*. 8. *A. parasiticus*. Figs. 9–10. Metasomal sculpture. 9. *A. brethesi*, first tergum. 10. *A. brethesi*, border of second and third metasomal terga. Figs. 11–12. Tarsal claws. 11. *A. parasiticus*. 12. *A. abdominalis*.

curved downward, vein m-cu present; tarsal claws strongly pectinate with 6–7 stout teeth, apical 3 teeth of pectin about 0.75 as long as apical claw, remaining teeth gradually shorter towards base of claw.

Type material examined.—*Aleiodes abdominalis* Cresson, holotype female, Pennsylvania (ANSP). *Aleiodes lectus* Cresson, holotype male, Illinois (ANSP).

Distribution.—Widely distributed in eastern North America from Quebec and Ontario south to North Carolina, west to South Dakota and Arizona; more commonly encountered in the eastern parts of its range.

Biology.—Unknown. One specimen from Maryland is associated with an undetermined noctuid. The mummy is dark brown, smooth, and about 1 cm long. Adults appear in early June in the north-
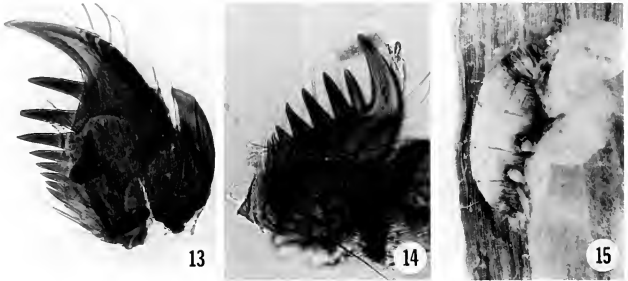
Figs. 13–15. Figs. 13–14. Compound microscope photographs of slide-mounted tarsal claws. 13. *A. rileyi*. 14. *A. molestus*. Fig. 15. Mummified plusiine noctuid host larva parasitized by *A. molestus*.

ern parts of its range; the specimens from Arizona were collected in late September.

Comments.—This is the most common member of the species-group with a mostly black body. The only other North American species in the group with an all-black mesosoma is *flavitarsus*, from which *abdominalis* can be distinguished by its larger body size (6.0–8.0 mm), fore wing vein 1cu-a beyond vein 1M by less than 3 times its length, and hindwing vein m-cu present (Fig. 16). The European species, *A. apicalis*, is also similar in body color and general appearance. However, *abdominalis* can be distinguished by its finely coriaceous to granulate mesonotum (Fig. 4), while the disc of the mesonotum is smooth-punctate in *apicalis*. Superficially, *abdominalis* is similar in color pattern (black and orange) to the very common species *A. terminalis* Cresson, but *terminalis* is a member of a different species-group, and can be easily separated by the species-group key provided in Shaw *et al.* (1997). Males of *terminalis* do not have densely setose metasomal terga 4–7.

Aleiodes flavitarsus Marsh and Shaw, new species
(Fig. 17)

Female.—Body color: head black, mandibles and mouthparts yellow, antenna light brown; mesosoma black, propleuron sometimes brown or orange; tegula yellow; legs yellow except apical tarsal segments, apical 0.25 of hind femur and apical 0.5 of hind tibia which are black; metasoma with segments 1–3 yellow-orange except tergum 1 black medially and tergum 3 black apically, segments 4–8 black; wings hyaline, veins light brown, tegula yellow. Body length, 4.5–5.5mm. Head: malar space short, equal to basal width of mandible and about eye height; temple narrow, about 0.5 eye width; occipital carina not quite meeting hypostomal carina; oral space small and oval, width equal to malar space and about 0.5 face height; 46–49 antennomeres, all flagellomeres slightly longer than wide, first slightly longer than second; ocelli small, ocellocular distance equal to or slightly greater than diameter of lateral ocellus; face rugulose-coriaceous with median carina between antennae; frons coriaceous; vertex and temples coriaceous; occiput smooth and shining; maxillary palpus not swollen; mandibles small, tips not overlapping when closed. Mesosoma: propleuron rugose, often smooth medially; mesonotum and scutellum coriaceous; notauli scrobiculate, meeting in small rugose area before scutellum; mesopleuron smooth and shining, rugose
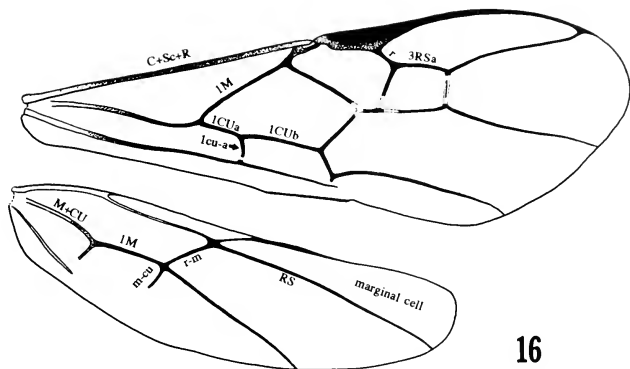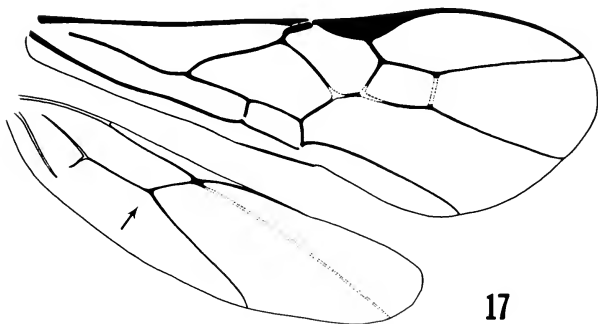
Figs. 16–17. Wings showing venation terminology. 16. *A. abdominalis*. 17. *A. flavitarsus*.

dorsally and in subalar sulcus; sternaulus absent; propodeum rugose-coriaceous dorsally, coriaceous laterally, median carina obscured apically. Legs: tarsal claws strongly pectinate with 4–5 stout teeth, apical 3 teeth of pectin about 0.75 as long as apical claw, remaining teeth gradually shorter towards base of claw; inner spur of hind tibia slightly less than 0.5 length of hind basitarsus; hind coxa smooth dor-

sally. Wings: hyaline; fore wing with vein r 0.5 length of 3RSa, vein 1cu-a beyond 1M by nearly 3 times length of 1 cu-a, vein 1CUa slightly longer than 1CUb; hind wing with vein RS straight, cell 1R1 gradually widening to wing apex, vein r-m slightly shorter than 1M, vein M+Cu slightly longer than 1M, vein m-cu absent. Metasoma: first tergum rugulostriate, median carina complete, length equal to apical width; second tergum rugulostriate, median carina complete; third tergum rugulostriate basally, smooth apically, median carina absent; fourth and following terga smooth; ovipositor short, about 0.5 length of hind basitarsus.

Male.—Essentially as in female.

Holotype.—Female: MICHIGAN: Marquette County, August 14, 1959, R. And K. Dreisbach. Deposited in USNM.

Paratypes.—CANADA, BRITISH COLUMBIA: 2 females, Gagnon Rd., 6 mi W Terrace, June 20, 1960, J. C. Chillcott, W. W. Moss; 4 females, Hixon, July 11, 1965–July 7, 1966, E. D. A. Dyer; 1 female, Terrace, July 9, 1960, W. R. Richards; 1 female, 10 km S Fernie, July 29, 1980, D. Williams. MANITOBA: 2 females, Big Eddy, em March 13, 1953, ex *Autographa* sp. NEW BRUNSWICK: 2 males, Kouchibougnac N.P., July 21, 1977, S. J. Miller. NEWFOUNDLAND: 1 male, Agr. Exp. Sta., St. John's, July 16, 1967, J. F. McAlpine. ONTARIO: 1 female, One Sided Lake, July 12, 1960, S. M. Clark; 1 male, North Branch, July 23, 1960, S. M. Clark; 1 male, Cumberland, June 13, 1975, L. Ling. QUEBEC: 1 female, 1 male, Parke Reserve, Kam. Co., July 5–12, 1957, G. E. Shewell. UNITED STATES, MAINE: 1 female, Oxford Co., Bryand Pond, July 23, 1976, leg. Heinrich. MICHIGAN: 1 female, Delta Co., August 6, 1959, R. & K. Dreisbach; 1 male, Houghton Co., August 20, 1959, R. & K. Dreisbach; 1 male, Schoolkraft Co., August 5, 1959, R. & K. Dreisbach. MINNESOTA: 1 female, Itasca St. Park, September 1927, S. Carthside. WASHINGTON: 1 female, Lake Cush-

man, July 22, 1917, A.L. Melander. Deposited in CNC, HNHM, MCZ, RMNH, RMSEL, USNM.

Distribution.—Widely distributed across Canada and the northern United States.

Biology.—Two specimens from Manitoba were reared from an unknown species of the genus *Autographa* (Noctuidae). Adults are active from late June through September. The specimens from Manitoba were labeled as emerging in March, but were probably collected during the previous summer and emergence may have been under laboratory conditions.

Comments.—This species is similar to *abdominalis*, but differs by its smaller body size (4.5–5.5 mm), vein 1cu-a of the fore wing being beyond vein 1M by three times its length (Fig. 17), by having hind tarsomeres 1–4 yellow, and by the absence of vein m-cu in the hind wing (Fig. 17).

Etymology.—The specific name is from the Latin *flavus* meaning yellow, in reference to the yellow hind tarsus.

Aleiodes molestus (Cresson), new combination
(Figs. 14, 15)

Rogas molestus Cresson, 1872, Trans. Amer. Ent. Soc. 4:188.
Rogas rufocoxalis Gahan, 1917, Proc. U.S. Natl. Mus. 53:207. New synonymy based on examination of holotype.

Diagnosis.—Body bicolored, mesonotum orange, mesopleuron and propodeum varying from entirely black to entirely orange, with various intermediate forms occurring, metasomal terga 1–3 always orange, rest of terga varying from orange to black, legs beyond coxae dark brown or black, wings slightly dusky, veins brown, tegula orange; body length, 5.0–7.0 mm; 45–47 antennomeres; malar space long, slightly greater than basal width of mandible; face, frons and vertex rugulose, temple smooth; mesonotum and mesopleuron smooth; propodeum rugose, median carina complete; first and second metasomal terga strigate-rugose to costate, median

carina complete; fore wing with vein 1cu-a beyond 1M by distance nearly twice length of 1cu-a; marginal cell of hind wing narrowest basally, gradually widening toward wing apex; tarsal claws strongly pectinate with 6–8 stout teeth, apical 3 teeth of pectin about 0.75 as long as apical claw, remaining teeth gradually shorter towards base of claw.

Type material examined.—*Rogas molestus* Cresson, holotype female, Texas, G.W. Belfrage collection, [USNM]. *Rogas rufocoxalis* Gahan, holotype female, Colorado, Rocky Ford [USNM].

Distribution.—South Dakota south to Arkansas, Louisiana, Texas, and Mexico, west to Wyoming, Utah, Arizona, and southern California.

Biology.—Although *A. molestus* is commonly collected by Malaise trap, sweep net, or at lights, verified rearing records are less common. In the USNM collection there are single specimens labelled as reared from several plusiine and noctuine species including *Autoplusia egena* (Gn.), the soybean looper, *Pseudoplusia includens* (Wlkr.), the cabbage looper, *Trichoplusia ni* (Hbn.), and the variegated cutworm, *Peridroma saucia* (Hbn.). The known hosts are all generalist feeders on a variety of low vegetation including numerous crop species. Adults have been collected from late April through mid-September in the southern parts of its range.

Comments.—*A. molestus* is a fairly common midwestern and southern species favoring open fields, low vegetation, and agroecosystems. It belongs to the *parasiticus* assemblage, comprising *parasiticus* Norton, *molestus* (Cresson) and *brethesi* (Shenefelt), all of which have an orange mesonotum that is smooth and shining (as in Figs. 5–6) and well-developed longitudinal sculpture on tergum 2+3 (as in Fig. 10). *A. molestus* differs from *parasiticus* by having the legs entirely dark brown or black beyond the coxae (the femorae and tibiae are banded in *parasiticus*). It differs from *brethesi* by having orange coxae,

while the legs are entirely black in that South American species.

There is considerable variation in the extent of dark coloration on the mesopleuron and propodeum in *molestus*, consequently *rufocoxalis*, which differs only by having an entirely orange mesosoma, cannot be held as a valid species. In his description of *rufocoxalis*, Gahan (1917) stated that "it would not be surprising if it (*rufocoxalis*) would ultimately turn out to be merely a color variety of Cresson's species (*molestus*)." Indeed, although sometimes the mesopleuron and propodeum are entirely black, intermediates with less dark color and orange patches showing through are fairly common, so it would appear that Gahan's prediction is correct.

Aleiodes parasiticus Norton
(Figs. 5, 8, 12)

Aleiodes parasiticus Norton, 1869, Trans. Amer. Ent. Soc. 2:327.

Diagnosis.—Body bicolored black and orange, head black, antenna orange basally to black apically, mesosoma orange except mesopleuron below subalar sulcus and propodeum black, first and second metasomal terga orange, third tergum orange on basal 0.5, black on apical 0.5, remainder of terga black, fore and middle legs orange except apical tarsomeres black, hind coxa and trochanters orange, hind femur orange on basal 0.66, black on apical 0.33, hind femur yellow on basal 0.5, black on apical 0.5, hind tarsus orange except apical tarsomere black, wings lightly dusky, veins brown, tegula yellow; body length, 5.0–7.0 mm; face costate, frons and vertex rugose, temple punctate, occipital carina scrobiculate; malar space longer than basal width of mandible and about 0.5 eye height; ocellocular distance longer than diameter of lateral ocellus; pronotum rugose; mesonotum smooth, mesopleuron smooth medially, subalar sulcus and sternaulus rugose; propodeum rugose dorsally, punc-

tate laterally, median carina complete; first and second metasomal terga costate-rugose, median carina complete, third tergum costate on basal 0.5, smooth on apical 0.5, median carina absent, remainder of terga smooth, fourth-seventh terga of male with dense patches of setae on apical 0.5 on each side of mid-line; fore wing with vein 1cu-a beyond 1M by distance twice length of 1cu-a, marginal cell of hind wing gradually widening, vein RS straight, vein m-cu absent; tarsal claws strongly pectinate with 5–6 stout teeth, apical 3 teeth of pectin about 0.75 as long as apical claw, remaining teeth gradually shorter towards base of claw.

Type material examined.—*Aleiodes parasiticus* Norton, holotype female, Connecticut (MCZ).

Distribution.—Eastern Canada and United States south to Maryland, west to North Dakota, Wyoming, and Colorado.

Biology.—We have examined specimens from the CNC and USNM collections labelled as reared from the plusiine noctuids *Anagrapha falcifera* (Kby.) and *Syngrapha epigaea* (Grt.). The former is a generalist on low plants including blueberries and clover, while the later is a generalist feeding on conifers including pines, spruces, and firs. The mummy formed is typically cream-colored and fairly smooth. Norton (1869) and Shenefelt (1975) listed this species as having been reared from the diprionid sawfly *Neodiprion abietis* (Harris) on *Abies,* but this seems very unlikely. Adults of *A. parasiticus* are active from late May to early September.

Comments.—*A. parasiticus* is similar to *molestus,* but *parasiticus* differs in having the posterior femur and tibia banded (orange on basal 0.5, black on apical 0.5). *A. parasiticus* is a distinctly northern species associated with boreal forests, while *molestus* is a midwestern and southern species favoring drier and more open habitats, including agroecosytems.

Aleiodes rileyi Cresson, revised combination
(Fig. 13)

Aleiodes rileyi Cresson, 1869, Trans. Amer. Ent. Soc. 2:382.

Diagnosis.—Body unicolored orange or honey yellow, flagellum black, wings hyaline, veins brown, stigma yellow to light brown; body length, 5.5–8.0 mm; 53–55 antennomeres; malar space short, about equal to basal width of mandible and 0.25 eye height; ocelli large, ocellocular distance equal to or slightly less (about 0.75) diameter of lateral ocellus; oral opening small and circular, diameter about equal to basal width of mandible; face rugose, frons smooth, vertex and temple coriaceous; occipital carina not meeting hypostomal carina; pronotum procate; mesonotum and scutellum coriaceous; mesopleuron smooth, subalar sulcus rugose, sternaulus absent; propodeum rugose dorsally, coriaceous laterally, median carina complete; first and second metasomal terga rugose costate, median carinae complete; third tergum costate on basal 0.33, smooth or weakly coriaceous on apical 0.66, sometimes entirely smooth or weakly coriaceous, median carina absent; remainder of terga weakly coriaceous; terga 4–6 in male with lateral patches of dense gold hair; fore wing with vein 1cu-a beyond 1M by distance slightly greater than length of 1cu-a; hind wing with vein RS arched in middle, marginal cell narrowest in middle; tarsal claws strongly pectinate with 7–8 stout teeth, apical 3–4 teeth of pectin about 0.75 as long as apical claw, remaining teeth gradually shorter towards base of claw.

Type material examined.—*Aleiodes rileyi* Cresson, holotype female, Missouri (ANSP).

Distribution.—Connecticut south to Florida, west to Michigan, Kansas, and Saskatchewan. It probably occurs throughout the eastern half of North America.

Biology.—We have examined specimens

from the CNC, INHS, and USNM collections labelled as reared from the noctuids *Acronycta oblinata* (J.E. Sm.), *Melanchra picta* (Harr.), and *Nephelodes minians* Gn., the lymantriid *Dasychira vagans* (B. & McD.), and possibly the pyralids *Ostrinia obumbratalis* (Led.), and *O. penitalis* (Grt.). The known hosts are all generalist feeders on a variety of low vegetation, shrubs, and low trees such as willows. Adults of *Aleiodes rileyi* are active in Florida as early as January, but in northern parts of its range (Illinois) adult activity is in late summer (August).

Comments.—Marsh (1979) classified *rileyi* under *Rogas*, but we are moving it here back to its original combination with *Aleiodes*. *A. rileyi* is quite distinctive by being the only member of the species-group that is entirely orange; all other North American species in the *apicalis*-group have at least some black coloration on the body.

ACKNOWLEDGMENTS

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Territoriality and Mating Behavior of *Sphex pensylvanicus* L. (Hymenoptera: Sphecidae)

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Abstract.—Daily observations were made on nine individually marked males of *Sphex pensylvanicus* in upstate New York during 25 July–8 August 1982. Males occupied territories on or near a grate atop a storm sewer drain in which 12 females nested. They obtained honeydew at a maple tree and slept and fed on white sweet clover growing on a nearby hillside. The following maintenance and reproductive activities of males were defined: (1) perching at stations, (2) swivelling, (3) cleaning, (4) wing raising, (5) defecating, (6) spontaneous flights, (7) feeding flights, (8) pouncing on conspecific males, (9) pursuit flights, (10) grappling, (11) trailing conspecific females, (12) clasping conspecific females, and (13) copulation. Aggressive interactions between territorial conspecific males occupied more time than all other maintenance and reproductive activities combined.

Almost nothing was known about the behavior of male solitary wasps until Lin's (1963) study of male territoriality in *Sphecius speciosus* (Drury), the cicada killer. Recent interest in male behavior surfaced following the revival of Darwin's (1859) sexual selection theory, especially as championed by Trivers (1972) and his contemporaries. The activities of male solitary wasps are primarily aimed at obtaining matings. Males feed on nectar, rest on plants or in burrows, or bask in the sun when not in pursuit of females (Evans and O'Neill 1988). Males of most species of Sphecidae are free from parental duties and their reproductive success is solely determined by the number of eggs they fertilize. In other words, males of most species contribute little more than genes to their offspring.

Male solitary wasps tend to emerge before the females, a phenomenon known as protandry (Evans 1966). Circumstantial evidence suggests that females of most digger wasps mate only once during their lifetime (Alcock et al. 1978). Although

nesting may extend for several weeks in certain species of Sphecidae (Hager and Kurczewski 1986, Kurczewski 1997), copulations in most species take place only during the first week or two. The majority of contacts between males and females do not end in successful copulation (O'Neill 1979). Once females are actively nesting, they rebuff all attempted matings by males (Evans and O'Neill 1988). The relative low fecundity of the females may mean that they actually gain little from additional matings (O'Neill 1985). Alcock et al. (1978) address the costs and benefits associated with multiple matings in species of aculeate Hymenoptera.

Territoriality, as defined by spacing, maintenance of stations, and aggressive encounters between conspecific males, does not occur in all sphecid wasps (Hager and Kurczewski 1985). But, it can be exaggerated in some species (Minkiewicz 1934, Lin 1963, Evans and O'Neill 1988). Males may establish stations or territories near prominent landmarks on the ground (*Astata*, Minkiewicz 1934; *Tachysphex*, Kur-

czewski 1966) or emergence holes (*Sphecius*, Lin 1963), or they may scent mark plants to attract females to a site (*Philanthus*, Evans and O'Neill 1988). The establishment and maintenance of stations or territories clearly facilitates mating between resident males and females in the vicinity (Alcock et al. 1978).

Studies on the behavior of male solitary wasps lag far behind those on female nesting behavior (Evans 1966, Alcock et al. 1978, Evans and O'Neill 1988). Male solitary wasps are often smaller, shorter lived, and do not maintain a nest making them more inconspicuous to the average observer (Kurczewski 1966, Hager and Kurczewski 1985). Among the species of Sphecinae (R. Bohart and Menke 1963, 1976), many of the studies on male behavior involve the genus *Ammophila* (Turner 1912, Baerends 1941, G. Bohart and Knowlton 1953, Olberg 1959, Powell 1964, Hager and Kurczewski 1985). Little is known about territoriality and male behavior in the genus *Sphex* including the nearctic *S. pensylvanicus* Linnaeus, the Great Black Wasp of John Bartram (Rau 1944). Rigley and Hays (1977) noted dominance, grappling, and attempted copulation in a few males of *S. pensylvanicus*. Gillaspy (1962) described mating behavior in the nearctic *S. tepanecus* Saussure. Janvier (1928) noted perching and grappling in the neotropical *S. latreillei* Lepeletier. Surprisingly, nothing is known of male behavior in a common nearctic species, *S. ichneumoneus* (Linnaeus)(Brockmann 1980).

My paper presents new and interesting information on the behavior of males of *S. pensylvanicus* and provides a verbal outline of the mating system employed by this species. The literature on reproductive behavior in sphecids is depauperate and observations such as those reported herein are needed to rectify this situation. Territoriality and mating behavior in this species were observed concurrent with an investigation on the sequential daily activities of the females (Kurczewski 1997). I

chronologically sequenced and described individual male behaviors, especially those connected with spacing, aggression, and copulation, and attributed possible significance to them, thereby adding to the overall knowledge of male behavior in the family Sphecidae.

METHODS

Males of *S. pensylvanicus* were observed on a daily basis, weather permitting, from 25 July to 8 August 1982 from 0730 to 2100 hrs (EDT). The study area was examined before and after these dates and there was no sign of male activity. One must assume, therefore, that the males had not emerged before 25 July and either had died or left the area after 8 August. Nine males each were color-coded by placing a drop of Testor's model paint on their mesoscutum with a tiny paint brush from which had been removed most of the hairs. The activities of these males were observed and recorded at or near a storm sewer grate for a total of 62.5 hrs during 10 of the 15 days that they were in evidence. The individual life spans of the nine males was only 10–14 days, with three males living an entire two-weeks-long period. I similarly marked all 12 females from this aggregation thus yielding a secondary sex ratio of 3:2 in favor of females. One male and one female each were collected before individually marking them and placed as voucher specimens in the insect museum of the State University of New York College of Environmental Science and Forestry, Syracuse, New York.

Territoriality in this species facilitated simultaneous observation of all nine males; however, some time was allocated to observe certain focal males more extensively during fixed observation periods. Individual male behaviors were described and chronologically sequenced. Particular emphasis was placed on reproductive behavior as it occurred near a storm sewer drain in which the females nested. Less

emphasis was placed on male maintenance behaviors such as feeding, sleeping, and basking in the sun that took place away from this site.

EMERGENCE AND LOCATION OF STUDY

Both males and females emerged from soil near a broken tile at the bottom of the sewer drain situated in an asphalt driveway beside the Marcellus Senior High School, Marcellus, Onondaga County, New York. Three males emerged on 25 July 1982, two days before the first female appeared. The emergences of the other six males shortly thereafter (27–31 July 1982) were interspersed among those of early emerging females. Behavior that represented aspects of territoriality such as spacing, maintaining stations, and aggression between conspecific males was focused on a 70 × 70 cm grate atop the 70 cm-deep drain in which the females nested (Fig. 1, Kurczewski 1997). Males also visited a maple tree 13 m south of the sewer drain in order to obtain honeydew, and slept and fed at a stand of *Melilotus alba* (white sweet clover) 55 m away (Fig. 2, Kurczewski 1997). Both males and females fed on the flowers of other plant species nearby but not as frequently as at the florets of white sweet clover, probably because this species was more abundant in the vicinity (Kurczewski 1997).

The nine males left their sleeping roosts on white sweet clover daily on warm sunny days, occasionally fed on nectar or basked in the sun, and then made low circling or figure-8 flights over the sewer grate as early as 0828–0837 hrs (EDT) at an air temperature as low as 16°C. They stationed themselves on and/or near the grate from 0845 to 1643 hrs, and once as late as 1818 hrs, at air temperatures of 16.5–26°C. Males interrupted this territorial activity to feed on the flowers of *Melilotus alba* from 1125 to 1800 hrs at air temperatures of 23–26°C. They circled the drain in flight between 1819 and 2019 hrs,

alit briefly on or entered through openings in the sewer grate, but then quickly exited and flew to sleeping roosts. Males did not maintain stations at or near the grate during this time. They did not make extensive and intricate flights for the purpose of orientation to the immediate environs as did the provisioning females (Kurczewski 1997).

MALE ACTIVITY

The following activities of male *S. pensylvanicus* were delineated: (1) perching at stations, (2) swivelling, (3) cleaning, (4) wing raising, (5) defecating, (6) spontaneous flights, (7) feeding flights, (8) pouncing on conspecific males, (9) pursuit flights, (10) grappling, (11) trailing conspecific females, (12) clasping conspecific females, and (13) copulation. Definition and significance of these activities are as follows:

(1) *Perching at stations.*—Males perched on or near the sewer grate with mid- and hindlegs outstretched yet raised and wings folded flat on the dorsum. They periodically moved their head or anterior body from side to side. While perching, males moved their antennae or held them still in an upward and outward attitude. The forelegs were either "fishhooked" medially or held backward beneath the body, raised above the substrate, and moved back and forth slowly or in short rapid bursts. Positioning by certain males close to the grate openings gave them a decided advantage over males stationed farther away with respect to access to entering or exiting females. These males subsequently obtained more claspings and copulations than males stationed farther from the sewer grate (see below).

Following emergence and through the first week of nesting, males maintained stations near the female nesting site. Males spent much time at a preferred site or station; however, most males maintained several stations in close proximity moving from one to another throughout the day.

On 27 July 1982, five males perched at stations on or near the sewer grate. Two of the males occupied opposite ends of the grate, being only 50–70 cm apart. The other three males were located near the grate at cardinal points of the compass, each less than 1 m from the two males. The males near the grate were not allowed to approach the males on the grate any closer than this without being chased away. On the following day, four additional, newly emerged males took up stations near the grate less than 1 m from the older males. Nine males now maintained one or more stations within a diameter of 2 m from the grate. The two males stationed on the grate and a third male nearest the grate perched at their stations for periods of 20–150 min ($\bar{x}$ = 37.9 min, n = 37 observations), except for chasing away conspecific males, females, and other insects, and making periodic flights with no discernible function. The six most peripherally situated males, on the other hand, perched for an average of only 3.8 (<1–7) min (n = 41) and then flew away for 1–71 ($\bar{x}$ = 32.4, n = 41) min before returning. In other words, the three males nearest the grate spent most of their time on or near it whereas the six males positioned peripheral to the grate occupied most of their time away from it.

The two males perching on the grate often approached to within 30 cm of one another without any apparent sign of interference between them. When one of the males flew away to feed, the other male encroached on his territory often temporarily appropriating some of the stations. Such replacement implies that males compete for stations, the defense of which clearly represents a form of territoriality. The spacing distance of about 1 m between most territorial conspecific males probably diminished the amount and intensity of aggressive interaction between them and thereby increased their chance for successful copulation but I have no concrete evidence to substantiate this.

(2) *Swivelling.*—Males often moved or turned their entire body to face in a slightly different direction. This movement was made so smoothly that the wasps appeared to be on a swivel. Swivelling was, therefore, a ramification of perching. Change in vantage ground by certain males may have ensured that they would not miss viewing females approaching or exiting the drain.

(3) *Cleaning.*—Males frequently cleaned their antennae, compound eyes, and mouthparts with the forelegs, and their wings and abdomen with the hindlegs. Wing and abdominal cleaning followed 63 flights during which a male pursued another male, female, or other insect. Only five times did a male land from such a flight without cleaning. Cleaning of the antennae, eyes, and mouthparts occurred seemingly spontaneously with or without the presence of another insect.

(4) *Wing raising.*—Males perching at stations often held the wings outward at an angle or raised and flicked the wings repeatedly. The former behavior was not observed to be associated with any specific incident. Sixty-one times wing flicking was associated with the appearance of a conspecific male, female, or other insect. After the intruder passed by, the perched male either lowered the wings onto the dorsum or cleaned the wings with the hindlegs and then lowered them. Raising and flicking the wings followed wing cleaning invariably followed the pursuit in flight of another male and landing (see above). The two males stationed only 50–70 cm apart on the grate often wing flicked upon visible movement of the other. Raising and flicking the wings may have represented an intention movement to fly as this behavior was performed usually at the appearance of another male, female, or other insect.

(5) *Defecating.*—The two males stationed on the sewer grate for long periods of time periodically discharged a viscous liquid from the anus to a distance of 10–20 cm.

Often, this fluid was squirted in two or three directions by the wasp moving his abdomen to a slightly different angle.

(6) *Spontaneous flights.*—Every 1–8 ($\bar{x}$ = 2.1, n = 78) min, a male made a short brief flight of no discernible function directly away from his station, turned 180°, and returned along the same route to resume perching. Such flights were often less than a meter in length and of only 1–2 sec duration, but occasionally they were as long as 3–6 m and several seconds in duration. They were usually made in different, sometimes opposite, directions from a station. Possible functions of these flights include moving into cooler strata of air to reduce body temperature or surveillance of the immediate area and its occupants.

Other flights made by males were slower, more deliberate, and longer in distance and duration. They were more or less straight in line, often repeatedly covered the same ground, were 1–2 m in length or longer, and invariably lasted for more than a second or two. Some flights took the form of repetitive short distance figure 8's. The longer flights possibly function in helping locate receptive females.

(7) *Feeding flights.*—Periodically, males temporarily left their perches and flew to a nearby maple tree where they obtained honeydew or to a stand of white sweet clover from which they gathered nectar. As many as six males were simultaneously seen in the maple tree or feeding on *Melilotus alba* from late morning to early evening. Flowers of other plant species nearby such as Queen Anne's lace or wild carrot, goldenrod, yarrow, and white clover were visited less frequently for nectar.

(8) *Pouncing on conspecific males.*—When males at adjacent stations moved closer than 30 cm apart, one of them often made a short pouncing flight at the other wasp. The latter frequently flew out of reach of the former and then sometimes was pursued in a low, sinuous flight for a short distance. Less commonly the two individuals, after making contact, grappled with

one another. This behavior may have reinforced the spacing of individual males.

(9) *Pursuit flights.*—Males maintaining stations near the female nesting site frequently flew at other males flying close to the sewer grate or at neighboring males if they approached too closely. Two wasps stationed on the grate periodically chased more peripherally located males in sinuous or figure-8 flights, 1–2 m above the ground, to distances of 3–5 m. Some of these flights transformed into ascending spiral flights, 3–4 m high. Continuous pursuit flights sometimes lasted for as long as 1.5 min. Regardless of the form of the flight, as many as four or five males participated in a single chase with distances of 20–30 cm separating individuals in tandem. After several seconds, such flights broke up into pairs of males or three individuals involved in chases. Flights terminated when the participants returned to their respective stations on or near the grate. Some chases involving two or three males continued into and out of the sewer drain. Physical contact occurred only rarely between males in pursuit of one another. In such cases one wasp grasped another, both fell to the ground, they grappled for several seconds, separated, and then flew to respective stations.

In addition to chasing conspecific males and females, territorial males also pursued dragonflies, moths, butterflies, horseflies, and other wasps and bees. The initiation of chasing depended entirely upon the visible presence of another insect, especially a conspecific. When other males were in the vicinity, males left their stations, took flight, and were air-borne continuously until the visitors(s) left the area. The sight of a non-provisioning female entering or exiting through the sewer grate often incited males stationed nearby to act aggressively toward one another and this frequently led to pursuit flights. By chasing other males out of the immediate area, males stationed on or near the grate would have more mating opportunities

available to them. Such males, in fact, did obtain more copulations with females than males situated on the periphery of the aggregation. Where all males were viewed simultaneously, the three males perching on or near the grate obtained eight (67%) of the 12 observed matings while the six males positioned farther away gained only four (33%). The three wasps stationed on or near the grate drove away all other males and permitted females to freely fly into the nesting area. However, copulations were successful only with females exiting through openings in the grate. Copulations with females entering the sewer drain were invariably unsuccessful.

(10) *Grappling.*—When two males approached to within 30 cm of one another they leapt at each other, held one another in a venter to venter position with the legs, and bit with the mandibles. Such grappling occurred in both anterior-anterior and anterior-posterior body positions. Grappling invariably ensued when a resident male pounced upon an intruding male flying low near the grate. Such wasps either separated in flight and returned to their respective stations or fell to the ground, making a buzzing noise, and continued grappling. Males stationed next to one another on or near the grate grappled for 2–20 ($\bar{x}$ = 11.8, n = 13) sec, separated, and flew to respective stations. One male stationed on the grate twice grappled with and drove away a larger intruder from a peripheral station. On three occasions two or three grappling males fell through openings in the sewer grate, disappeared from view, and resurfaced in tandem flight 3–5 sec later. After exiting, the three grappling males resumed grasping one another in flight above the grate with the legs and continued biting with the mandibles. Bouts of grappling even took place within ascending spiral flights up to 3–4 m in height. Much grappling occurred when non-provisioning females flew into the area by-passing the stations

of adjacent males. One to several males pursued such an incoming female, immediately bringing them into close contact with one another. They briefly grappled with each other, one chased another away, and the victor continued to pursue the female in flight. Spacing, an expression of territoriality in males maintaining stations near female nests, was clearly established through bouts of grappling. Such premier positions often facilitated successful copulation (see above).

(11) *Trailing conspecific females.*—During the height of male activity the trailing and/or pursuit of conspecific females was secondary to chasing other males. In fact, many females were allowed into the nesting area and permitted to land without being chased or contacted by males. Nonetheless, some non-provisioning females flying near but not entering the sewer grate were pursued by territorial males for distances of 1–4 m after which the male returned to his station. In addition, males stationed on the grate sometimes followed females in flight into and out of the sewer drain and often interfered with females making orientation flights. Orienting females were pounced upon, bumped, and jostled in mid-air before they flew away. However, males did not pursue females whose orientation flights took them away from the drain. Attempts by males to contact females in flight probably served as a prelude to mating, but other males in the vicinity constantly disrupted copulation efforts.

(12) *Clasping conspecific females.*—Males clasped females by flying onto their dorsum and holding them with the legs. Females so grasped were deprived of the use of their wings and either plummeted downward to the ground from heights of 30 cm to 2 m or glided onto a nearby lawn, 2–4 m from the grate. Such clasped wasps rolled over several times while making a buzzing sound as the female attempted to escape. Sometimes the male was dorsum down, still retaining his

grasp of the female which was also dorsum down with her legs dangling in the air. One pair remained clasped together for 3 min as they continually rolled over and twisted on the ground while making a constant buzzing sound. They eventually separated but the male clasped the female again and repeated his attempted copulation for an additional 1.5 min. Unsuccessful copulation in the form of clasping, however, usually lasted only 5–45 ($\bar{x}$ = 18.7, N = 14) sec. Following attempted copulation, males cleaned the sides of their abdomen alternately with the hindlegs and their eyes, antennae, and mouthparts alternately with the forelegs. Clasping of females by males preceded mating but most such engagements never went to completion.

(13) *Copulation.*—Twelve of 29 (41%) pairings that began as clasping culminated in several minutes-long matings. Genitalic union was not achieved in 17 pairings that dissolved after 5 sec-4 min ($\bar{x}$ = 47.8 sec) of clasping. The twelve apparently successful matings were observed between 1021 and 1231 hrs during 27–31 July 1982. This period, when males were 2–6 and females only 1–4 days old, represented the pinnacle of reproductive activity insofar as frequency of claspings and copulations. Attempted copulations were sparse before and after this time. Matings were not seen during the second week of a male's life.

Successful copulation proceeded through a sequence of behaviors. Males always mounted females dorsal side up in a head above head position. Usually, the male remained on top with the female on the bottom. However, sometimes the male was on his side or, rarely, on his back holding the female ventral side up with her legs dangling in the air. Regardless of orientation, the male retained his grasp of the female by using his legs to grip her wings, body, and legs.

In the beginning stages of copulation, a male stroked a female's antennae with his antennae. This behavior seemingly aided in keeping her acquiesced. When the female became restless, she sporadically produced a buzzing sound. In order to contact her genitalia, the male rubbed the sides of his abdomen against the underside of the female's abdomen. The male's abdomen had to be telescoped and the female's abdomen mildly contracted to execute coupling. The last half of his abdomen had to be twisted nearly 45° and the female's abdomen turned somewhat. Once coupling was achieved, periodic sound production ceased. There was some rhythmic abdominal movement from both participants during copulation.

Males and females remained coupled for an average of 5.1 (R = 2.5–14.0, N = 12) min. Following an apparently successful copulation, the female feebly attempted to release herself from the male by slowly moving her legs and antennae and twisting her head in an arc. In some cases, the female tried to break loose by walking on the substrate dragging the attached male behind. Coupling, separation, and recoupling of male and female occurred up to three times in certain pairs. The arrival of other males or, rarely, females often led to disruption of mating and, almost invariably, to dissolution of the pairing. Twice, intruding females entering the mix led to genitalic separation and cessation of mating. Seven times an intruding male mounted the first male while he was mating, dislodged him, and disjoined the coupling. Recoupling by the original pair was sometimes achieved after such a disruption.

Once, as many as three males attempted to copulate with a single female, the participants being stacked in a pile atop one another. The pile of bodies kept falling to one side, but the pedestal male retained his grasp of the female and the other males their grasp to one another. Whether the pile remained upright or fell onto its side made no difference in the respective positioning of the males, probably because

the pedestal male was holding the bases of the female's wings with his forelegs and ad infinitum. After 35 sec, the uppermost male flew away for a few seconds only to return and rejoin the pile. In his absence, the remaining two males each tried to make genitalic contact with the female by fencing for prime position with the ends of their abdomens. Sound production occurred on and off during the entire attempted copulation. After 4 min of remaining together, the participants separated and flew away without successfully mating.

Male activity summary.—The activities of four focal males stationed on or near the grate were observed and recorded for 30 min-long periods at air temperatures of 23–24°C between 1015 and 1553 hrs on 29–31 July 1982 for the purpose of summarizing and ranking them. Of the combined 120 min spent by these males, 67 (56%) min were utilized for flying, chasing, and grappling, 43 (36%) min for perching, swivelling, cleaning, wing raising, and defecating, 6 (5%) min for clasping and copulating, and 4 (3%) min for feeding on honeydew and the flowers of white sweet clover. The large proportion of time spent air-borne by these males coincided with the presence of conspecific males and females in the area. Ninety percent of the time (60/67 min) used for flying, chasing, and grappling by males stationed on or near the sewer grate included the intrusion of conspecific males stationed nearby.

DISCUSSION

Male solitary wasps often emerge one or a few days before the females (Evans 1966). This trend, known as protandry, and an overall shorter flight season synchronize male activity with female emergence (Evans and O'Neill 1988). Early emergence of males gives them an opportunity to mate with unmated, recently emerged females (Bulmer 1983). One-third of the males of *Sphex pensylvanicus* that I studied emerged two days before the remainder of the males and the first females. The early emerging males were more successful in establishing stations near the female nesting site than later emergents and this eventually resulted in a higher proportion of matings for these individuals.

Rigley and Hays (1977) noted a "dominance order" among males of *Sphex pensylvanicus* for about a week during the "latter part" of July before the females started provisioning. One male positioned himself nearer the female burrows than two other males, continually chased them from the area, occasionally caught and grappled with them, and temporarily drove them away. The "dominant" male "solicited" females at their burrow entrances by repeatedly flicking his wings, flew after females as they exited their entrances, clasped them in flight, disappeared from view, and then returned 2–5 min later to resume perching near the nests.

Behavior of male sphecid wasps is predominantly directed toward obtaining matings (Hager and Kurczewski 1985, Evans and O'Neill 1988). Males of many digger wasp species maintain territories or perches near female nests in order to gain a reproductive advantage (Lin 1963, O'Neill 1979, Evans and O'Neill 1988). Copulatory attempts near nesting sites underline the importance of territories or perches to facilitate mating (Alcock et al. 1978). In *Sphex pensylvanicus*, females often nest aggregatorily in one area (Reinhard 1929, Frisch 1938, Rigley and Hays 1977, pers. obs.). Males establish stations near the female nests, the two sexes are continually brought into contact with one another, and mating is expedited.

Male territoriality, as defined by spacing, maintenance of stations or perches, and aggression between conspecifics, has been demonstrated for a number of sphecids (Lin 1963, Evans 1966, Kurczewski 1966, Alcock et al. 1978, O'Neill 1979, Evans and O'Neill 1988, Hastings 1989). Applying this definition to *Sphex pensyl-*

vanicus, territoriality clearly is operational among the males (Rigley and Hays 1977, pers. obs.). In this species spacing and station maintenance and defense may function in reducing conflict between conspecific males and promoting successful copulation.

Although mating is the ultimate goal of male digger wasps, aggressive interactions between conspecifics are clearly the most conspicuous activities of territorial males (Evans and O'Neill 1988). More than 90% of the time spent by males of *Sphex pensylvanicus* during a three day-long observation period involved aggressive activities connected with territoriality. Males used most of this time in making flights, grappling with and pursuing other males, and vigorously defending stations against conspecifics. Males of *Sphex pensylvanicus* utilized only about 5% of their available time for clasping and mating. Some males, in fact, consistently ignored females flying into the area in order to pursue other males. However, if a male spends too much time on aggressive interactions with conspecific males, he wastes time and energy that could be used for locating and contacting females (O'Neill 1979).

Copulation in *Sphex pensylvanicus* is similar in configuration and relative positions of male and female to that of other sphecines, especially members of the genus *Ammophila* (Turner 1912, Baerends 1941, Olberg 1959, Powell 1964, Hager and Kurczewski 1985). In the former species, duration of coupling is apparently briefer than in species of *Ammophila* and the male and female abdomens are held outward rather than raised upward. Uncoupling and recoupling are characteristic features of copulation in both *Sphex* and *Ammophila* (Baerends 1941, Olberg 1959, Hager and Kurczewski 1985, pers. obs.). Coupling, separation, and recoupling in certain pairs of *Sphex pensylvanicus* occurred up to three times during one copulation event. Disruption of matings by conspecifics occurs frequently in *Ammophila* and *Sphex.* Two or more males attempting to mate with a single female and, in the process, disengaging the initial coupling appears to be a common strategy in both genera. In such a case an intruding male may benefit immediately or later via successful copulation with the disjoined female (Hager and Kurczewski 1985).

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The Effects of Cavity Diameter and Length on the Nesting Biology of *Osmia lignaria propinqua* Cresson (Hymenoptera: Megachilidae)

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Abstract.—When offered equally available trap-nests of 6, 7, or 8 mm diameter and 80, 140, or 230 mm length, *Osmia lignaria propinqua* Cresson females chose significantly more of the deepest cavities for nesting and produced 69% of their offspring in them. Proportionately more females were produced in both years in cavities of greater length and diameter. Male and female weight varied between years, cavity lengths, and cavity diameters. Mortality was not significantly related to either nest diameter or length. Nesting parameters of ten species of megachilid bees showed a positive significant relationship between both female body width and nest cavity diameter and female body length and cavity length. However, there was no relationship between female body width or length and number of cells per nest.

The cavity or wood-nesting wasps and bees (Malyshev 1935; Krombein 1967), with species found in several families (Krombein 1967; Evans and West-Eberhard 1970; Stephen et al. 1969; Gauld and Bolton 1988), represent one of the biological groupings within the Hymenoptera. These provisioning wasps and bees use natural cavities for the placement of food for rearing their offspring (Krombein 1967). Two quite different life histories exist in the group (Evans and West-Eberhard 1970). The primitive members never developed the ability to make a nest, whereas the advanced members typically make a series of cells, separated by partitions. The latter group has received much attention because of the development of the technique of "trap-nesting" (Krombein 1967) and their economic value as managed pollinators (Torchio, 1987, 1990; Bosch et al. 1992).

Evidence supporting Fisher's sex ratio theory (Fisher 1958) has come from both natural history observations on cavity nesting bees and wasps (Rau 1928, 1937; Malyshev 1935; Krombein 1967; Danks 1970, 1971; Maeta 1978) and experimental

studies (Stephen and Osgood 1965; Gerber and Klostermeyer 1972; Phillips and Klostermeyer 1978; Torchio and Tepedino 1980; Cowan 1981; Freeman 1980; Tepedino and Torchio 1982a, 1982b, 1989; Tepedino and Parker 1983, 1984; Frohlich and Tepedino 1986; Johnson 1988, 1990; Sugiura and Maeta 1989; Bosch 1994). The resource quality model of cavity size (Charnov 1982) appears to be the dominant factor in the facultative sex ratios observed. Female parents of these sexually dimorphic species produce a greater proportion of progeny of the larger sex (usually females) in wider diameter cavities, and/or additional progeny of the smaller sex (usually males) in narrowed cavities. Size distribution of nest cavities available to the parent generation will shift sex ratios; more males are produced in narrow cavities, and more females are produced in wide cavities (Charnov et al. 1981).

The genus *Osmia* contains several species that have been developed as commercial pollinators of fruit crops (Maeta 1978, Torchio 1987, 1989, 1990, Bosch 1994). Much of the biological information obtained concerns the procurement and uti-

lization of these species as pollinators. It has already been well established that both the sex ratio and the weight of individual bees of *Osmia lignaria propinqua* Cresson increased with cavity diameter (Torchio and Tepedino 1980; Tepedino and Torchio 1982a, 1982b, 1989). Bosch (1994) found that when *Osmia cornuta* Latr. was given a choice of cavity lengths for nesting they preferred the longest cavity. Maeta (1978) reported the use of an average cavity length and diameter for five Japanese *Osmia* species when given an assortment of diameter and length reeds for nesting.

Osmia l. propinqua has not been offered trap-nests of varying length (Torchio 1976, 1984a, 1984b, 1985). This paper examines the combined effects of cavity diameter and length on cavity acceptance, cavity use, offspring weight and sex, mud use for cell partitions and plugs, and mortality in *Osmia lignaria propinqua*. Also, the relationship of average female body size to average cavity selection in other cavity nesting megachilid bees is examined.

MATERIALS AND METHODS

Osmia l. propinqua individuals were obtained from trap-nests placed out during the spring and summer of 1991 and 1992 in Lake City, Modoc Co., California. Trapnest were pine blocks drilled with 6, 7, or 8 mm holes to a depth of 80, 140, or 230 mm. Trap-nests were bundled together in groups of nine, one each by diameter and length, and 30 bundles or 270 nesting cavities were placed in each of four wooden boxes (30 × 30 × 60 cm) supported by metal fence posts 1.5 m off the ground. Trap-nest openings faced southeast. Boxes were placed out in mid March near the edge of two mixed fruit (apricots, apples, pears, peaches and plums) orchards and were from 100 to 200 m apart. With the onset of apricot bloom, trap-nests were checked daily for nesting. Completed, plugged nests were marked and dated. Trap-nests were removed in September, x-

rayed, and held out-doors in Reno, Washoe Co., Nevada. In March, nests were opened and nesting information was recorded and adult bees were weighted. Temperature and precipitation were recorded daily from a station adjacent to one orchard. The duration of seasonal nesting activity was based on daylight temperatures above 15°C on precipitation free days (Torchio 1976).

Mean body lengths and widths for female *Osmia* were from Sandhouse (1939), Yasumatsu and Hirashima (1950), Rust (1974), and Peters (1977); for *Hoplitis* from Michener (1947); and for *Megachile* from Mitchell (1962).

Analysis of variance (GLM in SAS 1990) was used for all comparative analyses between years, cavity diameters, and cavity lengths and the cells per nest, mud per cell per nest, placement of first and last cell in a nest, and percentage (arcsine transformation) of mortality per nest using Type III sums of squares due to unequal observations (Cody and Smith 1991). Duncan's multiple-range test was used for multiple comparisons when analysis of variance indicated a significant difference. Female body part measurements were compared to nest dimensions using linear regression. Chi-square test and G-test (Sokal and Rohlf 1969) were used to compare trapnest usage patterns.

RESULTS

In 1991, nesting began on 4 May: on 22 May the first nest was completed. Forty-three days (4 May to 15 June) passed to accumulate 200 hours of 15°C or greater temperatures. During that period, rain or snow (57 mm precipitation) fell on 11 days and an additional three days were below 15°C. In 1992, nesting began on 14 April: on 29 April the first nest was completed. Thirty-four days (14 April to 17 May) passed to accumulate 200 hours of 15°C or greater temperatures. During that period, rain (20 mm) fell on two days and another six days were below 15°C.

Table 1. Nests and cells produced by *Osmia lignaria propinqua* in cavities with 6, 7, and 8 mm diameters and 80, 140 and 230 mm lengths in 1992 and 1993 at Lake City, California.

Diameter	Nests			Cells			Cell Mean ± SD
	1991	1992	Total	1991	1992	Total	
				80 mm length			2.8 ± 1.2
6.0	4	3	7	14	7	21	
7.0	0	2	2	—	6	6	
8.0	1	2	3	3	10	13	
				140 mm length			5.4 ± 2.2
6.0	7	9	16	43	38	81	
7.0	6	5	11	39	22	61	
8.0	7	3	10	47	13	60	
				230 mm length			8.1 ± 4.0
6.0	12	9	21	101	55	156	
7.0	7	10	17	70	62	132	
8.0	12	9	21	117	78	195	
				Totals			
	56	52	108	434	291	725	
	Total Nest Mean ± SD			Total Cell Mean ± SD			
	7.7 ± 3.4			5.4 ± 3.6			

A total of 108 nests containing 725 cells were produced (Table 1). Most nests (59) and cells (482) were approximately evenly divided among the 6 mm, 7 mm, and 8 mm diameter long cavities (230 mm) (Table 1). The least number (12) and cells (40) were in the 6 to 8 mm diameter by 80 mm short cavities. The distribution of nests was significantly different from the availability of cavities for nesting ($\chi^2 = 35.23$, df = 8, P < 0.001). Partitioning the nests by cavity length and cavity diameter showed no significant pattern (G = 2.66, df = 4, 0.75 > P > 0.50).

The mean number of cells per nest was significantly different between the years with more cells in 1991 than in 1992 (F = 4.51, P = 0.03). Cell distribution paralleled nest distribution with significantly more cells in longer cavities (F = 15.42, P < 0.001) but a similar number of cells in all cavity diameters (F = 0.4, P = 0.66). Nests in 230 mm length cavities contained significantly more cells than did nests in 140 mm and they contained more than did nests in 80 m cavities (Table 1).

The distribution of adults by cavity length was 69% in 230 mm cavities, 28% in 140 mm cavities, and 3% in 80 mm cavities and by cavity diameter was 32% in 6 mm cavities, 30% in 7 mm cavities, and 38% in 8 mm cavities. Five hundred and forty-nine adults (317 males and 232 females) were produced (Table 2). In 1991, 312 adults (166 males and 146 females) were produced, and in 1992, 248 adults (151 males and 86 females) were produced. The distribution of males or females by cavity length was similar to the distribution of all individuals. However, the distribution of males or females by cavity diameter showed different patterns with the number of males decreasing with increasing cavity diameter (6 mm—44%, 7 mm—30%, and 8 mm—26%) and the number of females increasing with increasing cavity diameter (6 mm—17%, 7 mm—30%, and 8 mm—53%).

Both male and female weights showed a significant year by cavity length by cavity diameter interaction (males F = 3.81, P = 0.02; and females F = 3.88, P = 0.02) and were thus separated by year to ex-

Table 2. Male and female production by *Osmia lignaria propinqua* in cavities with 6, 7, and 8 mm diameters and 80, 140, and 230 mm lengths in 1991 and 1992 at Lake City, California.

Diameter	Males			Females		
	1991	1992	Total	1991	1992	Total
	80 mm length					
6.0	0	5	5	0	1	1
7.0	0	1	1	0	0	0
8.0	1	2	3	2	5	7
Total			8			8
	140 mm length					
6.0	27	26	53	7	3	10
7.0	18	13	31	16	5	21
8.0	14	4	18	13	8	21
Total			102			52
	230 mm length					
6.0	46	35	81	20	8	28
7.0	34	28	62	24	24	48
8.0	26	37	63	64	32	96
Total			206			172
	Totals					
	166	151	317	146	86	232

amine the effects of cavity length and diameter on individual weights (Table 3).

In 1991, male weights differed significantly among cavity lengths (F = 23.5, P = 0.0001), cavity diameters (F = 7.79, P = 0.001), and the cavity length by diameter interaction (F = 130.5, P = 0.01) (Table 3).

Males in 80 mm length cavities were heavier than males in 140 mm or 230 mm cavities. Males in 8 mm diameter cavities were heavier than males in 7 mm or 6 mm cavities. However, in 1992 male weights were not significantly different in cavity lengths, cavity diameters, or cavity length by diameter interaction.

In 1991, female weights in were significantly different for cavity lengths (F = 6.75, P = 0.002), cavity diameters (F = 2.72, P = 0.07), and the cavity length by diameter interaction (F = 2.94, P = 0.06) (Table 3). Females in 80 mm cavities were significantly heavier than females in 140 mm or 230 mm. Females in 6 mm cavities were significantly lighter than females in 7 mm or 8 mm cavities. However, in 1992 female weights were not significantly different among cavity diameters or in cavity lengths and or their interaction.

The sex ratios based on mean weight of all males and females ranged from 1.2:1 to 1.9:1 (males: females) and were slightly different between years (Table 4). Sex ratios increased in both years with increasing cavity lengths (1.2:1 to 1.8:1) but not diameters (1992—1.6:1 to 1.9:1 and 1991—1.6:1 to 1.5:1).

The amount of mud used for each cell per nest was significantly different be-

Table 3. Mean weights and standard deviations (mg) of male and female *Osmia lignaria propinqua* produced in cavities with 6, 7, and 8 mm diameters and 80, 140, and 230 mm lengths in 1991 and 1992 at Lake City, California. * equals one individual.

Parameter	Males		Females	
	1991	1992	1991	1992
	Cavity diameter			
6.0	35.8 ± 5.7	34.2 ± 4.8	56.8 ± 11.2	54.8 ± 7.6
7.0	36.0 ± 7.3	35.1 ± 5.8	63.3 ± 9.1	59.7 ± 11.6
8.0	44.9 ± 9.5	32.6 ± 6.9	68.9 ± 12.7	61.7 ± 12.6
	Cavity length			
80	70.9*	32.6 ± 5.6	83.7 ± 5.5	53.2 ± 4.1
140	40.6 ± 6.5	35.3 ± 5.1	67.9 ± 10.2	62.2 ± 12.1
230	33.7 ± 5.2	33.4 ± 6.1	61.8 ± 11.7	60.6 ± 12.3
	Total			
Total	37.7 ± 5.1	33.9 ± 5.8	64.1 ± 10.1	60.3 ± 11.4

Table 4. Sex ratio of *Osmia lignaria propinqua* produced in cavities with 6, 7, and 8 mm diameters and 80, 140, and 230 mm lengths in 1991 and 1992 at Lake City, California.

Parameter	1991	1992
	Cavity diameter	
6.0	1.6:1	1.6:1
7.0	1.7:1	1.7:1
8.0	1.5:1	1.9:1
	Cavity length	
80	1.2:1	1.6:1
140	1.7:1	1.8:1
230	1.8:1	1.8:1
	Totals	
Total	1.7:1	1.8:1

Table 5. Percent mortality in *Osmia lignaria propinqua* cells produced in cavities with 6, 7, and 8 mm diameters and 80, 140, and 230 mm lengths in 1991 and 1992 at Lake City, California.

Diameter	1991	1992	Total
	80 mm length		
6.0	100.0	14.3	71.4
7.0	—	83.3	83.3
8.0	0.0	30.0	23.1
	140 mm length		
6.0	20.9	23.7	22.2
7.0	12.8	18.1	14.7
8.0	42.5	7.6	35.0
	230 mm length		
6.0	34.6	21.8	30.1
7.0	17.1	16.1	16.6
8.0	23.1	11.5	18.5
Total for:	80 mm 60.0,	140 mm 23.7,	230 mm 21.7
Total for:	6 mm 31.0,	7 mm 18.1,	8 mm 22.4
TOTAL	28.1	18.5	24.2

tween years (F = 7.32, P = 0.008) with less mud used in 1991 (mean 92.2 ± 33.2 mg versus 1992—mean 155.2 ± 95.3 mg). Mud investment per cell by cavity length and diameter was also significantly different (cavity length F = 6.46, P = 0.002, cavity diameter F = 16.4, P = 0.001). There was more mud per cell in the 80 mm cavities (163.3 ± 85.0 mg) when compared to the 140 mm (116.9 ± 77.8 mg) and 230 mm (117.7 ± 73/2 mg). The 6 mm diameter cavity nests contained less mud per cell (88.7 ± 36.9 mg) than either the 7 mm (146.0 ± 68.9 mg) or 8 mm (145.6 ± 102.9 mg).

Bees using 230 mm length cavities placed the first cell not at the bottom of the cavity but at an average of 21.4 ± 35.2 mm from the bottom of the cavity. Bees nesting in 80 or 140 mm length cavities place the first cell at the bottom of the cavity. The last cell in a nest was significantly closer to the entrance in 80 mm cavities (mean 33.7 ± 15.8 mm) than in either 140 mm (mean 50.7 ± 27.5 mm) or 230 mm (mean 75.1 ± 54.4 mm) cavities (F = 5.17, P = 0.007). For both the placement of the first and last cell in a nest, neither year, cavity diameter, or any of the interactions were significant.

The percent mortality averaged 24.2% for all cells produced and was not signif-

icantly different between years or among cavity lengths, cavity diameters, or any of the interactions (Table 5). Chalk brood (*Ascosphaera torchioi* Youssef and Mc-Manus) caused the greatest loss in 1991 (15.6%) whereas egg death or failure to hatch caused the greatest loss in 1992 (7.5%) (Table 6). Chalk brood was the overall highest mortality factor (10.9%).

Nesting parameters of ten species of megachilid bees have been reported on where they were provided with a choice of cavity lengths (Table 6). There was a positive relationship between female mean body width and mean preferred cavity diameter (Y (cavity diameter) = 1.10 + 1.50X (body width); F = 2.62, P = 0.144). The relationship became significant when *Osmia marginata* was removed from analysis (Y (cavity diameter) = −0.48 + 1.84X (body width); F = 16.6, P = 0.005). *Osmia marginata* does not place cells in a linear series in large diameter cavities, but fits cells to the cavity dimension that allows a maximum use of the space (Tepedino and Parker 1983). Female mean body length and mean cavity length also showed a significant positive relationship

Table 6. Female size and nest parameters of megachilid bees from studies where different length cavities were available for nesting.

Species	Female size		Nest characteristics			Reference
	Mean width (mm)	Mean length (mm)	Mean diameter (mm)	Mean length (mm)	Mean # of cells	
			Osmia			
imaii	3.2	8.7	5.3	9.9	8.9	Maeta 78
taurus	4.1	11.0	6.8	14.9	9.0	Maeta 78
cornifrons	3.5	9.7	5.8	14.8	8.0	Maeta 78
pedicornis	4.3	12.5	6.7	14.6	6.8	Maeta 78
excavata	3.8	10.7	6.5	15.0	7.2	Maeta 78
cornuta	4.0	12.0	8.0	17.1	4.0	Bosch 94
marginata	3.5	9.0	9.0	9.0	8.2	Tepedino & Parker 83
lignaria	3.8	11.5	6.9	18.2	6.6	present
			Hoplitis			
fulgida	3.5	9.7	6.0	8.5	4.9	Tepedino & Parker 84
			Megachile			
rotundata	3.0	8.5	4.9	7.8	6.3	Gerber & Klost. 72

(Y (cavity length) = −9.95 + 2.22X (body length); F = 17.18, P = 0.003). There was no relationship between female body width or length and the mean number of cells per nest.

DISCUSSION

Females of *Osmia l. propinqua* chose significantly deeper drilled holes in trap-nests when presented with an equal distribution of cavity lengths for nesting. These deeper holes were filled with more cells and offspring. However, females showed no preference for a particular diameter trap-nest from within the range available. This nest selection pattern was observed in both years. In similar studies, Bosch (1994) found a significant preference in *Osmia cornuta* for longer cavities for nesting (12, 15, or 21 cm, cavity diameter was 8 mm) and produced more cells in them. *Osmia marginata* Michener females preferred nest-traps in drilled elderberry (*Sambucus* spp.) stems with the longest (90 mm) and widest (9 mm) cavities (Tepedino and Parker 1983). They produce significantly more cells in them. Tepedino and Parker (1984) observed the same selection pattern in *Hoplitis fulgida*

(Cresson) nesting in drilled elderberry stems. The opposite cavity usage pattern was observed in the completed nests of *Megachile rotundata* (F.) which decreased from 100% in 1.25 and 2.5 cm length cavities to 16% in 15 cm cavities (Stephen and Osgood 1965). However, nest utilization increased as cavity diameter increased from 4.0 to 6.0 mm. Gerber and Klostermeyer (1972) also found *Megachile rotundata* to use more short (4 cm compared to 8, 12 or 16 cm length cavities) trap-nests for nesting in a three years study. However, unlike the Stephen and Osgood (1965) results, Gerber and Klostermeyer (1972) found more cells were produced in 8 to 16 cm length cavities.

Maeta (1978) provided *Osmia imaii* Hirashima, *O. taurus* Smith, *O. cornifrons* (Radoszkowski), *O. pedicornis* Cockerell, and *O. excavata* Alfken with a broad selection of reed cavities for nesting (4 to 11.9 mm in diameter and 3 to 33 cm in length). His presentation of nesting materials attempts to represent what is most likely available to the species in nature and consequently the usage preference observed best represents the species natural usage patterns (Table 6).

The general pattern of cavity choice suggests that female size dictates her choice in both the diameter and length of cavity. This assumes that within the natural habitat there exists a variety of cavities for nesting and that females visit several cavities before making a selection. Selection of a short cavity will require finding a second or even third cavity to continue the nesting process. Selection of a long cavity simply requires the female to initiate cell construction at the "average" depth to maximize the cells or offspring produced. The bee is leaving unused cavity behind the first cell. The presence of an empty space behind the last cell was evident in only in the 230 mm long cavities. Maeta (1978) found an increasing percentage of empty spaces with increasing cavity length in all five *Osmia* species studied.

Cavity selection for nesting affects the general population structure of the species. All studies show that selection of long wide cavities allows females to produce more cells with larger offspring, and more females (Stephen and Osgood 1965, Gerber and Klostermeyer 1972, Maeta 1978, Tepedino and Parker, 1983, 1984, Frohlich and Tepedino 1986, Tepedino and Torchio 1989, Sugiura and Maeta 1989, Bosch 1994). In bee species that excavate a tunnel in a twig or stem and then construct and provision linear series of cells there is no relationship between tunnel diameter or tunnel length and the sex ratio of the offspring (Garofalo et al. 1981 for *Lithurgus,* Johnson 1988 for *Ceratina,* and Watmough 1983 for *Xylocopa*).

Why should short narrow cavities be selected by any individual females? The answer is variation both in body size and cavity size. Females are selecting from an large assortment of potential nest cavities the cavity that best matches their body width configuration. Selection of short cavities is difficult to interpret. Why should a female invest more time in foraging for and constructing cell partitions

and nest plugs than in offspring production? Jayasingh and Taffe (1982) and Rust (1993) have reported on the greater cost to produce offspring in short cavities. Rust (1993) has also shown that nest plugs cost more to produce than cell partitions in *O. l. propinqua* and *Osmia ribifloris* Cresson. He suggested that a nest should contain four or more cells to equalize the extra cost of nest plug. Individuals nesting in the 80 mm length cavities were producing on average only 2.8 cells and used significantly more mud per cell than in the other cavity length nests.

The selection of a short cavity also implies that the female must spend additional time searching for a second and perhaps third cavity for nesting. Naturally occurring nest sites must be considered as clumped; beetle borings in dead trees and logs, shrubs with hollow stems, etc. This clumped distribution suggests that new site searching may be minimal. Tepedino and Torchio (1989) showed no pattern or preference for a given diameter nest when *O. l. propinqua* searched for and initiated a second or third nest.

Parasite or predator load may be a strong selective factor favoring females that select several different nest sites. Both parasite and predator build-up can become a serious problem with high mortality in commercial populations of cavity nesting bees (Torchio 1970, 1972; Stephen and Undurraga 1978; Eves et al. 1980). Females selecting one long cavity will be at a disadvantage in a high density parasite or predator site.

The overall immature mortality in *O. l. propinqua* was low, less than 30%, and is similar to other reports on cavity-nesting, non-social bees and wasps (Krombein 1967, Danks 1971, Raw 1972, Cross et al. 1975, Freeman 1977, Maeta 1978, Taffee 1979, Smith 1979, Jayasingh and Freeman 1980, Tepedino and Frohlich 1982, Tepedino and Parker 1983, 1984). The various mortality agents or factors were unrelated to either nest diameter of length in the

present study. Chalk brood was the only agent to showed a substantial yearly change. Rust and Torchio (1991) also reported extreme year to year variations in chalk brood mortality within populations of *O. l. propinqua*. Tepedino and Parker (1983) reported a significantly greater mortality due to developmental failure in large diameter, long nests of *O. marginata*. They suggest the reason to be a departure in cell construction from a linear array of cells to an array of cells perpendicular to the long axis of the cavity. There was no difference in parasite or predator attacks in the various nests. In *Hoplitis fulgida*, Tepedino and Parker (1984) found significantly less mortality in the short, least used nests.

Since several species of *Osmia* and *Megachile rotundata* have been developed for commercial pollination (Torchio 1987, 1990), the choice of the appropriate cavity size is paramount to maximize pollinator production in a management strategy. The economics of producing effective commercial nest cavities requires the availability of materials and tools to manufacture the "average" cavity for a commercial population. This cavity may not be the optimum for the species. The choice of the standard length (15 to 17 cm) drill bits and the difficulties of obtaining wood with grain pattern suitable for the manufacture of "bee boards" with many straight, close, deep holes (greater than 17 cm) resulted in the production the commercial nest cavity for *O. l. propinqua* of a 7 × 170 mm paper soda straw inserted into a 8 × 170 mm hole in redwood (see Torchio 1982a, 1982b for details). This nest cavity allows for the production of sustainable populations of *O. l. propinqua* for both apple and almond pollination. My study suggests that holes deeper than 170 mm should be provided for *O. l. propinqua* to maximize its offspring production even in a commercial situation.

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A New Species of the Baltic Amber Bee Genus *Electrapis* (Hymenoptera: Apidae)

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Abstract.—**Electrapis stilbonota**, a new species of fossil bee is described and figured from two female specimens preserved in a single piece of Eocene Baltic amber. The species is assigned to a new subgenus, **Melikertes** n. subg., characterized by the sparse hairs of the scutellum, outwardly curved scape, few distal hamuli, absence of hind tibial spurs, tear-drop shaped tegula, and absence of setal bands on the apices of the metasomal terga. The specimens of *E. stilbonota* are morphologically workers and were presumably from a highly eusocial colony. The classification of *Electrapis* among apines is briefly discussed, and the subtribe Electrapina proposed to accommodate the genus. The proposal that *Electrapis* and its presumed sister, *Apis*, coexisted in time is briefly examined and found to be unsupported.

The Eocene Baltic amber contains a fascinating, although uncommon, bee fauna. Those few specimens that are known present the picture of an assemblage of groups unlike anything seen today. Of the species represented in the Baltic amber only one is currently assigned to a modern genus, this being *Andrena wrisleyi* Salt (1931), although the generic assignment of this species is of considerable question and it is possibly a melittid (Michener and Poinar 1996). The remainder, however, are assigned to extinct genera whose affinities are difficult to ascertain and in some cases cannot confidently be placed to tribe. By comparison, bees of the Dominican amber, which is Oligo-Miocene in age (Grimaldi 1995), are referable to modern day genera or extinct groups closely allied to extant genera (Engel 1995, 1996, 1997, Michener and Poinar 1996, Rozen 1996).

In 1909 Prof. Theodore D.A. Cockerell described a number of Baltic amber Hymenoptera among which was the genus *Electrapis* (1909a). The genus is a member of the corbiculate apine tribe Apini which contains only one other genus, the familiar honey bees (*Apis* L.). *Electrapis* was erected to accommodate the type species *Apis meliponoides* Buttel-Reepen (1906) which, as the specific epithet suggests, possessed characters both Buttel-Reepen and Cockerell took to be intermediate between the Apini and their sister tribe, the Meliponini (the stingless bees). Since the time of its description, *Electrapis* has acquired a total of nine species segregated into three subgenera. Table 1 summarizes the current classification of the known species.

Herein I describe a tenth species of *Electrapis* and assign it to a new subgenus, *Melikertes*. In the descriptions the following abbreviations are used for morphological terms: F, flagellomere; S, sternum; T, tergum. All measurements were made using an ocular micrometer on a WILD-M5a microscope and are in millimeters. All measures are approximate since the best position for viewing a specific structure was not always achievable owing to the curvature of the amber surface. Measurements which were not possible to make for a given specimen are indicated by an asterisk (*). Values given in the specific description are for the holotype with the corresponding measure of the paratype indicated in brackets.

Table 1. Current classification of *Electrapis* species. *Electrapis proava* (Menge) is tentatively included in the subgenus *Melikertes*.

Subgenus	Species	Reference
Electrapis s.str.	*meliponoides*	Buttel-Reepen 1906
Electrapis s.str.	*tornquisti*	Cockerell 1909b
Electrapis s.str.	*apoides*	Manning 1960
Electrapis s.str.	*minuta*	Kelner-Pillault 1970
Electrapis s.str.	*bombusoides*	Kelner-Pillault 1974
Protobombus	*indecisus*	Cockerell 1909a
Protobombus	*tristellus*	Cockerell 1909a
Roussyana	*palmnickenensis*	Roussy 1937
Melikertes	*stilbonota*	present study
?	*proava*	Menge 1856

Genus *Electrapis* Cockerell
Melikertes Engel, new subgenus

Diagnosis.—*Roussyana*-like species without dense pubescence covering the scutellum; hairs generally sparse, never obscuring integument. Clypeus flat. Labrum U-shaped, broader than long, with apical fringe of simple hairs, hairs laterally short, becoming longer by middle. Labial palpus four segmented, basal segment longest, almost as long as following three segments combined. Minute flabellum at apex of glossa. Antennae set well below mid-line of face; scape slightly curved outwards at apex, inner concave surface without pubescence; pedicel longer than F1; F1 as long as F2 and F3 combined. Compound eyes bare. Face relatively flat. Vertex scarcely elevated above ocelli; preoccipital ridge with a weak carina behind vertex, becoming rounded by gena (Fig. 3). Mesoscutal anterior border weakly rounded, nearly straight; median line and notauli not apparent, parapsidal lines faintly evident. Tegula tear-drop shaped, with blunt apex pointing posteriorly. Scutellum not bulging, surface flat, not reaching back to obscure portions of the metanotum; anterior border nearly straight medially, posterior border broadly rounded. Strigular concavity set on a slightly protuberant shelf; velum and malus simple, velum not divided. Mesocoxae separated medially.

Hind tibia without inner apical spurs; corbicula comprising apical three-quarters of hind tibia, posterior apical border rounded; corbicular surface glabrous and not strongly depressed, with a few sparsely scattered long simple hairs, otherwise hairs restricted to tibial lateral borders, such hairs long and branched; inner surface of tibia with a dense medial field of extremely short, simple hairs; strong rastellum on inner apical surface of hind tibia, extending the full width of tibial apex; penicillum absent; hind basitarsus roughly quadrangular, about as broad at base as at apex; attachment to tarsomere 2 set forth on short distal process on anterior border; auricle present; inner surface of hind basitarsus with series of stiff setal rows (as in *Apis*); claw with minute tooth on lower third of inner margin. Pterostigma small; distal wing venation strong; posterior border of second submarginal cell extended posteriorly (Fig. 4), greatly narrowed anteriorly; basal vein basad cu-a, vein relatively straight; cu-a curved outwards, not orthogonal with Cu or A; less than 10 hamuli on anterior margin of hind wing; jugal lobe present, just over one half length of vannal lobe; jugal and vannal incisions shallow. Metasoma without distal rows of hair on terga (Fig. 3).

Type species.—*Electrapis* (*Melikertes*) *stilbonota* Engel, new species, present designation.

Etymology.—The subgeneric name is taken from the mythology of ancient Crete. Melikertes (meaning "honey-cutter") was associated with Corinth and Melissa, priestess to the mother-goddess Demeter.

Remarks.—*Electrapis proava* is possibly misplaced in *Roussyana* and should be included in *Melikertes*. Official transfer of this species will have to wait, however, until *E. proava* can be studied in more detail.

Electrapis (*Melikertes*) *stilbonota* Engel, new species
(Figs. 1–5)

Description.—FEMALE (male unknown): Body form *Trigona*-like. Total

Figs. 1–2. *Electrapis (Melikertes) stilbonota* new species. 1, holotype, dorsal view. 2, paratype, lateral view.

body length 3.76 [3.72]. Head wider than long (length 1.10 [1.12], width * [1.32]). Inner margins of compound eyes straight, nearly parallel; upper interorbital distance 0.84 [0.86]; lower interorbital distance * [0.82]; eye length 0.74 [0.76], width 0.32 [0.30]. Gena width 0.28 [0.24]. Mandible with two blunt denticles on upper half of apical margin, length 0.50 [0.44]; malar space length 0.04 [0.06]. Labrum length (median) 0.20 [0.24], width (basal) 0.44 [0.44]; clypeus length * [0.18], width * [0.64]; clypeoantennal distance 0.08 [0.08]. Scape length 0.36 [0.36]; pedicel length 0.10 [0.06]; flagellum length 0.88 [0.86]; F1 length 0.10 [0.10]; F2 length 0.04 [0.04]; F3 length 0.04 [0.04]; F10 length 0.18 [0.18]; F6–10 with dense sensillar plates on inner surfaces; interantennal distance * [0.20]; antennal-ocellar distance 0.58 [0.56]. Median ocellus diameter 0.12 [0.12]; distance between lateral ocelli 0.26 [0.26]; distance between median ocellus and lateral ocel-

lus 0.08 [0.08]; distance from lateral ocellus to eye 0.28 [0.28]; distance from lateral ocellus to occiput 0.16 [0.16]. Mesosoma length 1.34 [1.32]; intertegular distance 0.82 [0.80]; mesoscutum length 0.64 [0.60]; scutellum length 0.26 [0.28], width 0.48 [0.44]; metanotum length 0.04 [0.04]; propodeal triangle over four times longer than metanotum, length 0.18 [0.18]. Mesocoxae separated by more than mesocoxal width; hind tibia length (median) 1.02 [1.02], width (basal) 0.12 [0.12], width (apical) 0.28 [0.30]; hind basitarsus length 0.36 [0.32], width 0.28 [0.28]. Wings hyaline, all veins brown and strong; basal vein basad cu-a by 2 times vein width; pterostigma small; 1m-cu bisecting second submarginal cell; 2r-m distad 2m-cu by 1.5 times vein width; marginal cell length 0.84 [0.86], width 0.24 [0.22]; first submarginal cell shorter than second and third combined; length of anterior border of second submarginal cell one-tenth that of posterior

border; length of anterior border of third submarginal cell half of that of posterior border, just over 3 times length of anterior border of second submarginal cell; forewing length 3.00 [3.16]; venation of forewing depicted in figure 4; six distal hamuli on outer margin of hind wing; cu-a of hind wing orthogonal to M+Cu; hind wing length 2.08 [2.16]; venation of hind wing depicted in figure 5. Metasoma length 1.32 [1.28].

Integument over entire bee smooth and glabrous, except on metanotum where the integument is apparently rugulose. S3–6 apparently weakly nodulate, nodules scattered over the surface, integument between nodules smooth and shining as on previous sterna. Color not well preserved, apparently dark brown to black, metallic and shining, without any maculations.

Pubescence generally pale. Hairs of face widely scattered, simple, and short. Such hairs becoming longer by vertex. Gena with simple, short, suberect hairs. Postgena with long, simple hairs sparsely scattered over integument. Pronotal collar without pubescence; pronotal border with mesoscutum with short, simple hairs; lateral surface with similar minute hairs, such hairs appressed to surface, not obscuring integument. Mesoscutum with scattered simple hairs, more sparsely scattered and shorter over central disc, those hairs on anterolateral borders with a few short branches. Scutellum like that of mesoscutum except pubescence longer and restricted to posterior border. Metanotum with dense, minute, simple hairs, not obscuring the surface. Hypoepimeron without pubescence; mesepisternum with scattered simple hairs, becoming longer ventrally, central disc, however, without hairs. Propodeal triangle and posterior surface without pubescence; lateral surface with scattered long simple hairs and shorter, appressed hairs, partially obscuring the surface. Pubescence of fore- and midlegs generally simple and scattered, except inner surfaces of midtrochanter and femur without pubescence, and outer surface of mid-

tibia with dense, branched hairs. Inner surface of hind femur and trochanter without pubescence, except apical quarter of femur with dense field of minute hairs similar to those on inner surface of hind tibia (see generic diagnosis). Eight comb rows on inner surface of hind basitarsus; outer surface with scattered, long, simple hairs. T1 without hairs over median disc, a few simple hairs on lateral borders. T2 as on T1, except a few simple hairs on posterolateral borders. T3 with simple hairs, longer than those of T1–2, sparsely scattered over central disc, more concentrated on lateral margins. T4–6 similar to T3. Sterna with sparsely scattered simple hairs.

Material examined.—Holotype: female (Figs. 1 & 3), worker, Samland, Eocene Baltic amber, specimen In. 17778, Department of Palaeontology, the Natural History Museum (British Museum, London). Paratype: female (Figs. 2, 4–5), worker, same piece of amber, same accession information as holotype.

Preservation.—The bees presented herein are exceptionally well preserved. The only hindrance to their examination is the uneven surface of the amber and the small block of storage media they are preserved in. A few small fracture planes arising from the wings do not obscure any important structures, although one small fracture near the face of the holotype specimen obscures some features of the clypeus and lower face. A bit of mold on the legs along with the remains of what might have been collected pollen in the corbicula, while slightly demoting them from perfect specimens, does not detract in any significant way from examining their morphology. The inner teeth of the claws are minute and difficult to see. The best view of these structures can be achieved by back-lighting the specimens and examining the extended hind legs.

Etymology.—The specific epithet is derived from *stilbo* (Gr. shine) and *noton* (Gr. back), and is a reference to the glabrous
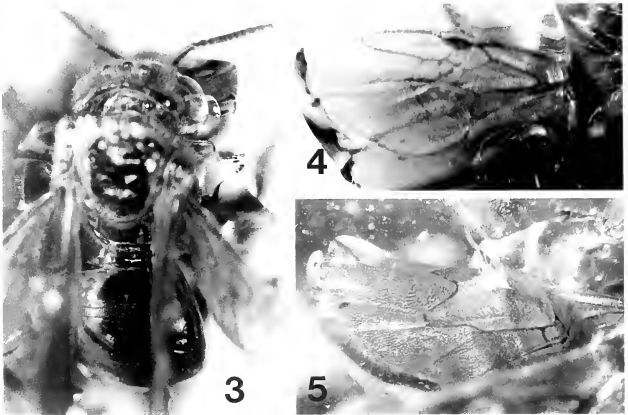
Figs. 3–5. *Electrapis* (*Melikertes*) *stilbonota* new species. 3, close-up of holotype, dorsal view, showing integument of metasoma and propodeal triangle as well as vertex and preoccipital ridge. 4, left forewing of paratype. 5, left hind wing of paratype.

integument of the dorsum, in particular that of the propodeal triangle.

DISCUSSION

Bees of the tribes Apini and Meliponini are all advanced eusocial, except for a few parasitic forms among the stingless bees (Michener 1974), and, based on their sister-group relationship (Chavarría and Carpenter 1994), presumably inherited this aspect of their biology from a common ancestor that was similarly eusocial. The phylogenetic position of the genus *Electrapis* within the tribe Apini suggests that species of *Electrapis* were also highly eusocial with a well developed caste system. Also suggestive of eusociality among *Electrapis* species is the fact that the specimens described herein are morphologically workers. In many eusocial species the loss of ovarian development in the worker caste results in a greatly reduced metasoma, a feature seen in both speci-

mens. Similar lines of evidence were used to make the inference that the oldest known fossil bee, *Trigona prisca*, was a worker of a similarly advanced eusocial society (Michener and Grimaldi 1988a, b).

While *Electrapis* runs to the tribe Apini in Michener's (1990) key to the corbiculate bee tribes (treated as subfamilies of Apidae in that work), there are significant enough differences between *Electrapis* and its sister *Apis* which would more than justify placing *Electrapis* in a tribe of its own. Recognition of a separate tribe for these bees, however, would obscure the relationship of *Electrapis* with members of the Apini as both possess a jugal lobe, bifid claws, complete distal wing venation, and a marginal cell apex gently pulled away from the anterior wing margin. A more practical approach to the problem is the recognition of subtribes, retaining a broadly defined Apini. The separation of

Table 2. Brief summary of the subtribal classification of Apini Latreille (based on worker caste). An elaboration of each character is given in the text.

	Apina	Electrapina
Eye hairs:	present	absent
Labral apex:	concave	convex
Mandible:	without dentition	with or without dentition
Vertex:	short	long
Scutellum:	bulging	weakly convex or flat
Propodeum:	short, declivious	long, not declivious
Mesocoxae:	nearly meeting	well separated
Marginal cell:	reaching wing apex	not reaching wing apex
Marginal cell:	not tapering	gently tapering
Basal vein:	distad cu-a	basad to just distad cu-a

these subgroups is as follows (a summary of the differences is given in Table 2):

Electrapina (new subtribe containing only the typical genus *Electrapis*): Compound eyes without hairs; labral apex convex; mandible with or without dentition; malar space extremely short, much less than basal width of mandible; vertex as long as ocellar diameter, or more; scutellum not bulging, surface weakly convex to flat; propodeal triangle with defined surface, not declivious; mesocoxae separated by at least their width; marginal cell not reaching wing apex, gently tapering over its length; basal vein basad to just distad cu-a, never strongly distad (7 times vein width or more).

Apina: Compound eyes covered with long hairs; labral apex gently concave; mandible lacking dentition; malar space as long as, or longer than basal width of mandible; vertex extremely short, much less than ocellar diameter; scutellum strongly convex and bulging, obscuring metanotum and propodeal triangle; propodeal triangle extremely short and declivious; mesocoxae nearly meeting medially; marginal cell long, nearly reaching wing apex, not gently tapering over its length; basal vein confluent (in some fossil *Apis*) to strongly distad cu-a (over 7 times vein width).

Arillo *et al.* (1996) have recently suggested that *Apis* and *Electrapis* overlapped in geologic time. Specimens of *Electrapis* are only known from the Baltic amber which is Eocene in age (Kosmowska-Ceranowicz 1987, Kosmowska-Ceranowicz and Müller 1985) while *Apis* species are unknown until the middle Oligocene (Culliney 1983, Engel in press, Michener 1990, Ruttner 1988, Zeuner and Manning 1976). Thus, the little available evidence in no way suggests that these taxa were coincident in time. Arillo *et al.* (1996) are correct, however, in their assertion that there is no reason to believe *Electrapis* is the direct ancestor of the true honey bees, *Apis*, as has been done by some earlier authors (e.g., Statz 1931, Zeuner and Manning 1976). Lastly, these authors have peculiarly used invalid family-group names for bees. For example, they refer to Michener (1986) for the recognition of Rophitidae in place of Halictidae. In fact, Michener (1986) clearly advises the use of Halictidae (even in his fairly short abstract), a proposal which was later supported by Michener (1991) and validated by the International Commission on Zoological Nomenclature (1993). Therefore, these authors should not be followed in their use of family-group names for bees.

ACKNOWLEDGMENTS

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NOTE ADDED IN PROOF

A paper has recently reached me concerning a Middle-Eocene bee from Germany which is attributable to *Electrapis* [H. Lutz. 1993. *Eckfeldapis electrapodes* nov. gen. n. sp., eine "Honigbiene" aus dem Mittle-Eozän des "Eckfelder Maares" bei Manderscheid/Eifel, Deutschland (Hymenoptera: Apidae, Apinae). *Mainzer naturwissenschaftliches Archiv* 31:177–199]. This bee is clearly a species of *Electrapis* s. str. and, based on the wing venation, appears most similar to *E. apoides*. I, therefore, here synonymize *Eckfeldapis* (**new synonymy**) with *Electrapis*, and place its only included species as a species of the latter: *Electrapis (Electrapis) electrapodes* (Lutz), **new combination**. It must also be noted that Lutz's figure 3h, labeled as the wing venation of *Apis mellifera*, should be disregarded as it resembles very little the venation of this species (particularly in the position of the basal vein and cu-a).

Neotropical Eucoilidae (Cynipoidea) Associated with Fruit-infesting Tephritidae, with New Records from Argentina, Bolivia and Costa Rica

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Abstract.—Host and distribution records are presented for five species of Neotropical Eucoilidae (Hymenoptera: Cynipoidea) reared in association with fruit-infesting Tephritidae. All previously recorded tephritid host associations for New World species are critically reviewed with the conclusion that several of these records are doubtful. Members of the genera *Aganaspis* and *Odontosema* are confirmed as parasitoids of *Anastrepha* and *Ceratitis*. Based on isolated puparia, *Dicerataspis* and *Lopheucoila* are recorded as parasitoids of Drosophilidae and Lonchaeidae, respectively. It is suggested that *Dicerataspis* is unlikely to attack Tephritidae, and records of *Lopheucoila* from Tephritidae require confirmation. One new species reared from Tephritidae, *Aganaspis nordlanderi* **Wharton**, is described.

The Eucoilidae are solitary endoparasitoids that oviposit in the larval stage of cyclorrhaphous Diptera and emerge as adults from the host puparium. Several eucoilid species have been implicated as important natural enemies of different phytophagous dipteran species (Wishart and Monteith 1954, Harding 1965, Valladares et al. 1982, Johnson 1987), and two species have been used for the biological control of fruit fly pests (Clausen 1978). The Asian species *Aganaspis daci* (Weld) has been introduced to the New World, and the Neotropical endemic *Aganaspis pelleranoi* (Brèthes) was reared and released from 1941 to 1945 in several areas of Tucumán, Argentina (Nasca 1973). At present, *A. pelleranoi* is being mass-produced in Metapa de Dominguez, Chiapas, Mexico (Ruiz et al. 1996).

Members of the genus *Aganaspis* are the only eucoilids thus far utilized in biological control efforts against Tephritidae. The two species involved, *A. daci* and *A. pelleranoi*, are also the only eucoilids attacking tephritids for which biological information other than host records has been published. Different aspects of the basic biology of *A. daci* were studied in the laboratory associated with programs directed against *Bactrocera dorsalis* (Hendel) in Hawaii (Clausen et al. 1965) and *Anastrepha suspensa* (Loew) in Florida (Nuñez-Bueno 1982). This species has also been introduced to Mexico (Jimenez-Jimenez 1956) and Costa Rica (Wharton et al. 1981, Jiron and Mexzon 1989). Establishment in Mexico and Costa Rica is doubtful, but in Florida it is established on *Anastrepha suspensa* (Loew), though in low numbers (Baranowski et al. 1993). A detailed biology of *A. pelleranoi* was given by Ovruski (1994a, 1994b).

The aim of this note is to provide preliminary information on the diversity of eucoilid species associated with tephritid fruit flies in the Neotropics, and clarify the status of species previously recorded as tephritid parasitoids. While several species have been associated with tephritids, few of these have been reared from puparia that were sufficiently isolated to enable

verification of the host. Data presented
here are based on surveys of tephritid par-
asitoids and on literature records.

MATERIALS AND METHODS

Fruits damaged by tephritid larvae
were collected from 1991 to 1994 in Tu-
cumán, Catamarca and La Rioja provinces
in northwestern Argentina, and from Au-
gust, 1979 through November, 1982 in the
provinces of Alajuela, Cartago, Guana-
caste, Heredia, Limón, Puntarenas, and
San José in Costa Rica. Additional eucoilid
specimens were also received from Boliv-
ia, and all reared material housed in the
U. S. National Museum of Natural Histo-
ry, Washington, D. C. (USNM) was ex-
amined. Samples collected in Argentina
and Costa Rica consisted of fallen fruit
and fruit still on the tree. In Argentina,
fruit samples were placed in styrofoam
boxes with damp sand in the bottom as a
pupation substrate. Fruit fly puparia were
recovered weekly and transferred to a
closed wooden box for holding until emer-
gence of flies or parasitoids. The proce-
dure differed slightly for the samples from
Costa Rica (Wharton et al. 1981), where
81,279 puparia were isolated (most of
them in individual vials) for verification of
host records. Tephritids of the genera
Anastrepha Schiner and *Ceratitis* MacLeay
(or their parasitoids) accounted for 69,012
of these puparia, with *C. capitata* repre-
senting 64.8% of the total tephritids. Lon-
chaeidae (also discussed below) were rep-
resented by 4583 puparia.

Specimens reported on here are housed
at Museo de La Plata, Argentina (MLP),
Museo de Ciencias Naturales Bernardino
Rivadavia, Buenos Aires, Argentina
(MBR), Instituto Fundación Miguel Lillo,
Tucumán, Argentina, Texas A&M Univer-
sity, College Station (TAMU), and USNM.
Measurements for the description of the
new species are as described by Nordlan-
der (1978, 1982).

RESULTS AND DISCUSSION

Several species of Eucoilidae, represent-
ing at least five genera, have been reared
in association with fruit-infesting tephri-
tids. Most of the species are almost cer-
tainly attacking other Diptera associated
with ripe and decomposing fruit (e.g. Dro-
sophilidae, Lonchaeidae, Phoridae, Neri-
idae). We have verifiable host records
from Tephritidae for *Aganaspis* and *Odon-
tosema*. The published records for *Dicera-
taspis*, *Lopheucoila*, *Rhoptomeris*, and *Try-
bliographa* attacking tephritids in the New
World need confirmation. Species of the
genus *Leptopilina*, well-known parasitoids
of Drosophilidae, may also be reared com-
monly from rotting fruit. Though Droso-
philidae tend to colonize fruit after te-
phritids, fallen, broken fruit may have
more rapidly decaying portions inhabited
by Drosophilidae at the same time as more
sound portions still inhabited by tephritid
larvae. Since fruit is often collected and
reared in bulk, it is easy to obtain parasit-
oids of both Drosophilidae and Tephriti-
dae, for example, from the same sample.
Unless puparia are isolated individually,
correct host associations cannot be made.

These seven genera may be separated
by the characters in Table 1. Additionally,
Lopheucoila is unique within this group of
genera in having a small spine on the dor-
sal plate of the scutellum and longitudinal
ridges on the mesoscutum. See also papers
by Weld (1952), the updated classification
by Nordlander (1978, 1980, 1981) and the
description of *Aganaspis* by Lin (1987).

Aganaspis Lin

The genus *Aganaspis* was relatively re-
cently described (Lin 1987) to accomodate
four species from southeast Asia (Taiwan
and Malaysia). One of these species, *A.
daci* (Weld), was originally described in
Trybliographa (Weld 1951b) but its generic
placement had always been problematic
(Kerrich and Quinlan 1960, Nordlander
1981). *Aganaspis daci* is the only one of the

Table 1. Genera of Eucoilidae reported from fruit-infesting Tephritidae in the Neotropics compared with *Leptopilina*, parasitoids of Drosophilidae commonly reared from the same fruits.

Genus	Scutellar disc posteriorly in dorsal view	Fore wing	Posterior-dorsal margin of pronotal plate	4th antennal segment (2nd flagellomere) of male	Anterior and posterior parts of pronotal plate fused or separate laterally
Aganaspis	rounded or truncate or weakly bi-lobed	distinctly setose	protruding above anterior margin of mesoscutum; deeply concave medially	$4 \leq 3$ not bent	widely to narrowly separated
Dicerataspis	bifurcate, with 2 tooth-like lobes directed posteriorly	distinctly setose	weakly protruding above anterior margin of mesoscutum; undulant, with 4 rounded lobes	$4 < 3$ not bent	contiguous or narrowly separated
Lopheucoila	weakly dentate, with 4 lobes; somewhat truncate	bare or nearly so	protruding above anterior margin of mesoscutum; deeply concave medially	$4 < 3$ not bent	fused or contiguous
Odontosema	bifurcate, with 2 tooth-like lobes directed posteriorly	bare or nearly so	protruding above anterior margin of mesoscutum; deeply concave medially	$4 < 3$ not bent	fused or contiguous
Rhoptromeris	rounded or truncate	distinctly setose	not protruding above anterior margin of mesoscutum; evenly rounded or very weakly concave medially	$4 > 3$ bent outwardly	fused
Trybliographa	rounded or truncate	distinctly setose	not protruding above anterior margin of mesoscutum; evenly rounded or very weakly concave medially	$4 \leq 3$ not bent	fused
Leptopilina	rounded or truncate	distinctly setose	not protruding above anterior margin of mesoscutum; evenly rounded or very weakly concave medially	$4 > 3$ usually bent	widely separated

four originally included species for which hosts have been recorded. Nordlander (in litt.) suggested that the New World species *pelleranoi* should also be placed in *Aganaspis*. This transfer was made by Ovruski (1994a), bringing the total number of species in *Aganaspis* to five. All four of the Old World species have distinctly setose eyes (more noticeable in the female), while those from the Neotropics do not. This is one of the easiest ways to recognize *A. daci* in those areas of the New World where it has been introduced.

The placement of *pelleranoi* and *nordlanderi*, n. sp. (described below) in *Aganaspis* broadens the limits of this genus, and opens up the possibility that several of the Neotropical species formerly placed in either *Trybliographa* or *Pseudeucoila* may actually belong here. As indicated by Nordlander (1981, Table 2), several generic names are available for these species, and placement of most of the previously described species will not be possible without a revision of the entire group. Collection records (e.g., Weld 1932) and label data on specimens in the USNM suggest that several of these species have been reared from tephritids, but most records are not sufficiently precise to preclude the possibility that the actual hosts may be other fruit-inhabiting flies. See further discussion below under *Trybliographa*.

Aganaspis pelleranoi (Brèthes)

De Santis (1965) placed *Ganaspis carvalhoi* Dettmer, 1929 as a junior subjective synonym of *Eucoila pelleranoi* Brèthes, 1924. The senior author has confirmed this synonymy through comparison of one of Dettmer's syntypes in USNM with one of the syntypes of *pelleranoi* from the Brèthes collection (MBR). Both types match the specimens we reared from Argentina and Costa Rica, confirming their identity as *pelleranoi*.

Known hosts and distribution records of *A. pelleranoi* are as follows:

Hosts.—*A. ludens* (Loew), *A. obliqua* (Macquart) (Aluja et al. 1990), *A. serpentina*

(Wiedemann) (Costa Lima 1940), *A. striata* Schiner (Clausen 1978), *A. distincta* Greene (Katiyar et al. 1995), *A. fraterculus* (Wiedemann) (Brèthes 1924), *Ceratitis capitata* (Wiedemann) (De Santis 1965), and *Rhagoletis turpiniae* Hernández-Ortiz (Hernández-Ortiz 1993). The records from "*Lonchaea sp.*" and "*L. pendula* Bezzi" (Borgmeier 1935 and Costa Lima 1948, respectively) are suspect, and require verification. As noted by McAlpine and Steyskal (1982), the name *pendula* has been misapplied on numerous occasions to Neotropical lonchaeids of the genus *Neosilba* McAlpine that have been reared from fruit. Our own records suggest that *A. pelleranoi* may only rarely attack lonchaeids. Of 295 specimens of *A. pelleranoi* that we reared from isolated puparia in Costa Rica, 191 (64.7%) were from *C. capitata* (mostly in coffee), 81 from *Anastrepha* (nearly all *A. striata*), and only two were from a lonchaeid (*Neosilba batesi* (Curran), **new record**). Twenty-one other specimens of *Aganaspis* were also reared from *Neosilba* in Costa Rica, but these are only tentatively assigned to *pelleranoi* because of slight but consistent color differences relative to the other specimens of *A. pelleranoi* reared during these studies.

We reared *A. pelleranoi* from infested fruits of the following species: *Casimiroa edulis* Llave and Lex., *Citrus aurantiifolia* (Christm.) Swingle, *Coffea arabica* L., *Ficus carica* L., *Juglans australis* Grisebach, *Prunus domestica* L., *Prunus persica* (L.) Batsch, *Psidium guajava* L., *P. friedrichsthaliamum* (O. Berg) Niedenzu, *P. littorale* Raddi (=*cattleianum*), *Syzygium jambos* (L.) Alston, and *Terminalia catappa* L. These data, together with previously published records, suggest that *A. pelleranoi*, like several of the other commonly encountered tephritid parasitoids, has little or no host plant preferences. See additional comments below under discussion of *Odontosema*.

Distribution.—Argentina: Buenos Aires, Misiones, Salta, Tucumán, Jujuy, Corrien-

tes (De Santis 1967, Diaz 1986), La Rioja and Catamarca (**new records**); Bolivia: Santa Cruz de La Sierra (**new record**); Perú (Clausen 1978); Brazil (Dettmer 1929); Venezuela (Katiyar et al. 1995); Colombia (Yepes and Velez 1989); Costa Rica (Wharton et al. 1981); El Salvador (Ovruski et al. 1996); and Mexico (Aluja et al. 1990). There are also specimens in the USNM from Panama, Guatemala, and Belize (all **new records**).

During the survey for tephritid parasitoids in Costa Rica (Wharton et al. 1981), several species resembling *A. pelleranoi* were reared. Only one of these was repeatedly reared from tephritids, and it is described next.

Aganaspis nordlanderi Wharton, new species
(Figs. 1, 3, 4, 6–8, 10, 12)

Quantitative measurements, based on 5 females and 2 males, are presented either as ranges or means to the nearest 0.05.

Female (Fig. 1).—Body length 2.3–3.5 mm; fore wing length 2.3–3.1 mm.

Head in dorsal view 1.05–1.15 times wider than mesoscutum; 1.75–1.90 times wider than long, when length measured in profile; temples strongly receding in dorsal view. Frons, vertex, and occiput bare; eyes without visible setae at 50×. Face shining, unsculptured; malar sulcus a weak, narrow groove, without additional striae; antennal base elevated, especially laterally, forming shallow depression between antenna and eye. Posterior ocelli widely separated: distance between them 1.2–1.3 times distance between posterior ocellus and eye. Antenna (Fig. 4) short, about 2.5 times height of head; without distinct club, the segments gradually broadening distally, first 4–5 flagellomeres weakly clavate: each slightly broader subapically than medially; first flagellomere slightly shorter than second, relative lengths, first 8 flagellomeres: 1.0:1.1:1.1: 1.05:1.0:1.0:0.95:0.95; ratio of length to maximum width, first 8 flagellomeres: 2.4:

2.3:2.2:2.0:1.9:1.8:1.65:1.55; flagellomeres each with 3–5 whorls of setae.

Mesosoma 1.25 times longer than high; 1.6 times longer than wide; 1.3 times higher than wide. Pronotal collar (Figs. 1, 6) distinctly protruding above anterior margin of mesoscutum in lateral view, deeply bilobed; median bridge wider than anterior ocellus; lateral arms of anterior and posterior parts narrowly but distinctly separated; posterior part of pronotal plate with a few, completely decumbent setae, otherwise bare and polished, 2.3–2.8 times wider than median bridge. Mesoscutum divided into three parts of approximately equal width by two longitudinal rows of 5–6 decumbent setae per row; margin with scattered setae separated from each other by their own length; short, shallow, crescentic grooves present on posterior half directly anteriad lateral bars of scutellum. Scutellar disc (Figs. 7, 8, 10) distinctly reticulate, with dorsoposteriorly-directed setae somewhat longer than in *pelleranoi*; in dorsal view (Fig. 8) disc slightly excavated medially, and thus weakly bilobed, the lobes protruding slightly beyond cup; posterior margin of disc sinuate in profile; height of posterior margin of scutellum about 1.5 times length (in lateral view) of flat portion of cup; scutellar cup (Fig. 8) large, broadly tear-drop shaped, with posterior margin weakly rounded, nearly truncate, anterior margin short, not extending through scutellar fovea, surface nearly flat, not drooping posteriorly, shallowly excavated medially, with only one or two punctures and 2–4 short, erect setae laterally; width of cup 0.5–0.6 times width of disc. Fore wing (Fig. 12) 2.6–2.9 times longer than wide; marginal setae short, longest subapical seta 0.08–0.1 times maximum width of wing; radial cell deep, completely open along wing margin, second radial abscissa 2.7–3.1 times longer than first; costal cell densely setose, ventral surface with 3–4 longitudinal rows of setae. Mid and hind coxae (Fig. 1) with extensive patches of
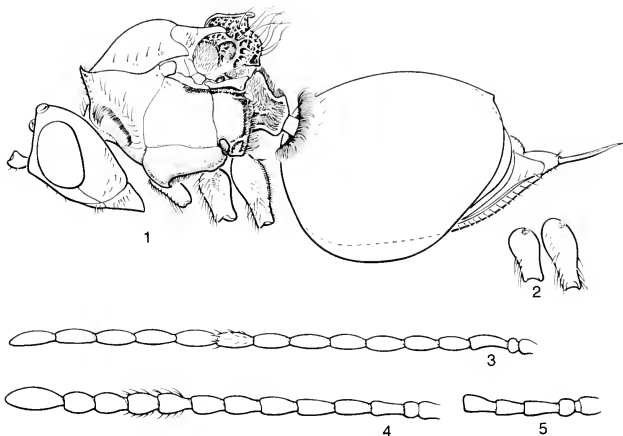
Figs. 1–5. *Aganaspis* spp. 1, *A. nordlanderi*, habitus. 2, *A. pelleranoi*, mid and hind coxae, lateral view, showing small patches of dense setae dorsoposteriorly. 3, *A. nordlanderi*, male antenna, setae not shown except for 8th flagellomere. 4, *A. nordlanderi*, female antenna, setae not shown except along margins of 7th and 8th flagellomeres. 5, *A. pelleranoi*, basal 5 antennal segments of female.

dense setae, patch on mid coxa extending about half length of coxa from base, patch on hind coxa extending more than half length of coxa.

Second metasomal tergum 1.0–1.1 times length of mesosoma.

Male.—As in female except as follows: head in dorsal view 1.15–1.2 times wider than mesosoma; antenna (Fig. 3) long, 3.2–3.3 times height of head; relative lengths, first 5 flagellomeres: 1.0:0.8:0.9:0.95:0.95, ratio of length to maximum width, flagellomeres 1–5 and 10: 2.85:2.05:2.25:2.25:2.3: 2.6; mesosoma 1.2 times longer than high;

fore wing 3.6–3.75 times longer than wide; second tergum 0.85–0.9 times length of mesosoma. Color. Head and mesosoma black except pedicel and basal flagellomeres usually dark reddish brown, flagellomeres gradually darkening apically, more rarely with antenna entirely dark brown to black; gaster reddish-orange, except apical terga black posteriorly; legs red-brown (slightly browner than gaster).

Hosts.—The specimens forming the type series were reared from individually isolated puparia of *Ceratitis capitata* and *Anastrepha striata*, and the puparia from which

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Figs. 6–11. *Aganaspis* spp, mesosoma. 6, *A. nordlanderi*, pronotum in dorsal view. 7, *A. nordlanderi*, propodeum in posterior view, showing posterior portion of scutellum, setae not shown except portion of basal ring on metasoma. 8, *A. nordlanderi*, scutellum in dorsal view. 9, *A. pelleranoi*, scutellum in dorsal view. 10, *A. nordlanderi*, scutellum in lateral view. 11, *A. pelleranoi*, scutellum in lateral view.
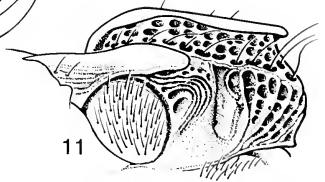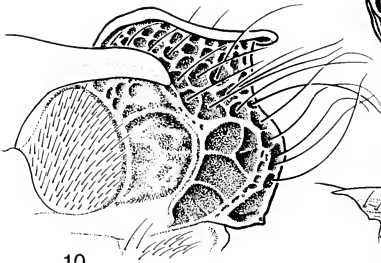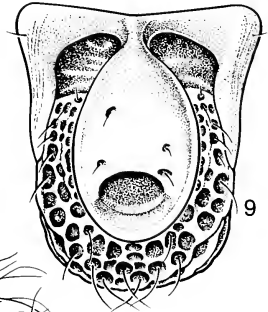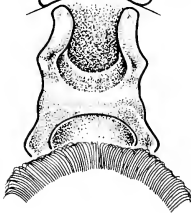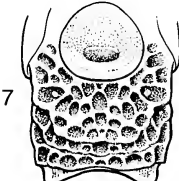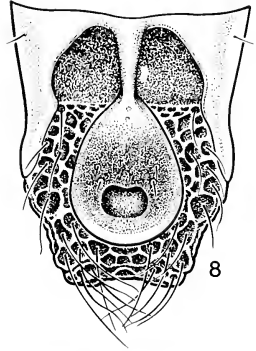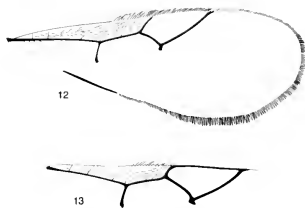
Figs. 12, 13. *Aganaspis*, fore wings. 12, *A. nordlanderi*, showing setal pattern in costal cell, marginal setae, and shape of radial cell, other setae not shown. 13, *A. pelleranoi*, showing relatively reduced pattern of setae in costal cell and closed radial cell.

they emerged are pinned with the parasitoids.

Holotype female.—"Costa Rica: Cartago Turrialba, Catie 10.vii.1980 ex: guava R. Chavez." Reared from *Anastrepha striata* in guava. Deposited in USNM. Paratypes (TAMU), all reared from *Ceratitis capitata* in Costa Rica: 3 females, 2 males, same locality, 8-vi-1980, 26-vi-1980, 30-ix-1981, and 8-vi-1982, J. Duran and R. Chavez, collectors, from coffee and naranja agria; 1 female, Puntarenas, San Vito, 23-ix-1980, R. Chavez, from guava.

Diagnosis.—This species differs from *pelleranoi* in the more densely setose costal cell of the fore wing (with only a single longitudinal row of setae on ventral surface in *pelleranoi*: compare Figs. 12 and 13), the completely open radial cell, the more extensively furry hind coxa (Fig. 1 vs. Fig. 2), the smaller scutellar cup (width of cup/width of disc = 0.55 in *nordlanderi* vs. 0.75 in *pelleranoi*; scutellar cup extending nearly to anterior margin of scutellar fovea in *pelleranoi*: compare Figs. 8 and 10 with Figs. 9 and 11), and the relative proportions of the flagellomeres (Fig. 4 vs. Fig. 5) and first and second radial abscissae.

Discussion.—*Aganaspis nordlanderi* has a distinctly smaller scutellar cup than either *pelleranoi* or *daci*, and the surface is not

quite as flat as in these two other species. The first flagellomere of the female is also slightly shorter than the second in *nordlanderi* but slightly longer than the second in *pelleranoi* and *daci*. Otherwise, *nordlanderi* and *pelleranoi* share several features which suggest that they are more closely related to each other than either is to *daci* and the other Old World species of *Aganaspis* described by Lin (1987). This relationship between the New World species is based on the absence of distinct setae on the eyes, the shape of the scutellar disc which protrudes posteriorly beyond the cup, the lack of a deep, median depression in the posterior margin of the metapleuron, and the more elongate basal flagellomeres and less distinctive club of the female antenna. Until the genera occurring in the Neotropical Region become better known, we prefer to retain *pelleranoi* and *nordlanderi* in *Aganaspis*, with the full realization that this placement may need to be reconsidered at some later date.

Dicerataspis Ashmead

There are two described species, and Weld (1952) recorded an additional, apparently undescribed species from Florida. The genus is known from Mexico and Florida south through the Caribbean to Brazil and Argentina (Weld 1921, 1952, Diaz 1974). The species have not been revised, and most of the reared material in the USNM has been tentatively associated with the name *D. grenadensis* Ashmead, 1896. At least two species are represented in our material from Costa Rica. The species differ in the sculpture of the scutellum, infumation of the wing, and shape of the radial cell. A revision of the genus is needed before species names can be assigned with any degree of confidence.

Based on records in the USNM, largely from the rearings by Zetek in the Panama Canal Zone, members of this genus have been reared from a variety of fruits (*Ficus, Labatia, Psidium, Carica,* and *Anacardium*) in association with several different spe-

cies of the tephritid genus *Anastrepha*. *Dicerataspis* has also been associated with one species of *Rhagoletis* from Mexico (Hernández-Ortiz 1993). However, precise associations have rarely if ever been made. Our own material was reared in association with *Anastrepha fraterculus* and *Anastrepha* sp. from *Psidium guajava* (guava) in Tucumán, Argentina, and from Drosophilidae in peaches and guava in Costa Rica. The single specimen from guava in Costa Rica was reared from a carefully isolated drosophilid puparium and represents the first specific, verified host association to our knowledge. All of our other material was batch-reared, and could not be directly associated with the individual puparia from which they emerged. The specimens from guava in both Costa Rica and Argentina agree most closely with the description of *D. grenadensis*.

Given the small size of the species of *Dicerataspis* and their development as solitary parasitoids, normal hosts are likely to be drosophilids or other small Diptera in fruit, rather than tephritids. Parasitism of *Anastrepha* or other tephritids needs verification.

Lopheucoila Weld

Weld (1951a) described the genus *Lopheucoila* for three New World species, only one of which, *L. anastrephae* (Rohwer), has ever been associated with specific hosts. *Lopheucoila anastrephae* was originally described from specimens supposedly reared from *Anastrepha* sp. in Trinidad (Rohwer 1919). Weld (1951a) subsequently reported this species from *A. fraterculus* in Panama and *Lonchaea* sp. in Brazil, as well as from Mexico and Peru (unassociated with hosts). As noted above under the discussion of hosts of *A. pelleranoi*, the Brazilian record from *Lonchaea* undoubtedly refers to a species of *Neosilba*. All of the specimens of *Lopheucoila* reared from Argentina and Costa Rica during the present study were *L. anastrephae*, based on comparison with type material of the three described species housed in the USNM.

In Argentina, *L. anastrephae* was obtained from guava fruits in association with *A. fraterculus* and *Anastrepha* spp. In Costa Rica, it was reared from coffee, guava, papaya, sour orange (*Citrus aurantium* L.), and tangerine (*Citrus reticulata* Blanco), and only from Lonchaeidae. All 74 specimens collected in Costa Rica were reared from isolated puparia of *Neosilba batesi* (Curran), the most abundant of the two species of Lonchaeidae in the Costa Rican samples. Although 69,000 puparia of *Anastrepha* and *Ceratitis* were collected from 1979–1982 in Costa Rica, *L. anastrephae* was never reared from a tephritid during this period.

Odontosema Kieffer

Kieffer (1909) based the genus *Odontosema* on a single species from Brazil. Borgmeier (1935) later described a second brazilian species, *O. anastrephae* Borgmeier, collected in association with *A. fraterculus* from guava. One undescribed species has been recorded from *A. striata* and *A. fraterculus* in guava in Veracruz, Mexico (Hernández-Ortiz et al. 1994), and an unidentified *Odontosema* species was reared from *A. fraterculus* in fruit of four species of Myrtaceae in southern Brazil (Salles 1996). In Costa Rica, *O. anastrephae* has been reported from *C. capitata* and *Anastrepha* spp. inhabiting several different fruits (coffee, orange and guava) (Wharton et al. 1981). *Odontosema* is probably widely distributed throughout the Neotropical Region, but at present it has only been recorded from Brazil (Borgmeier 1935, Costa Lima 1948, Salles 1996), Costa Rica (Wharton et al. 1981) and Mexico (Hernández-Ortiz et al. 1994, Lopez et al. 1996).

Odontosema anastrephae was collected only in Costa Rica, and was not found in Argentina during the present study. This species showed distinct host preferences, with 74% of the 193 reared individuals coming from *Anastrepha* in guavas. An ad-

ditional 15.5% of the reared individuals were from *C. capitata* in citrus. Coffee, the most heavily sampled fruit in Costa Rica, yielded only four individuals. Only 2% of the individuals were reared from Lonchaeidae (all on citrus), with the remaining 98% on either *Anastrepha* or *Ceratitis*. These results are in direct contrast with those for *A. pelleranoi*, which was collected predominantly from *C. capitata* in coffee in Costa Rica. Slightly less than half as many *A. pelleranoi* were reared from *Anastrepha* in guava as from *Ceratitis* in coffee. The pattern of host utilization by *A. pelleranoi* can thus be directly correlated with sampling frequency, with the mostly commonly sampled fruits and tephritids yielding the greatest numbers of *pelleranoi*.

Rhoptromeris Förster

Only one species of this genus has been associated with tephritid fruit flies. This species, *R. haywardi* (Blanchard 1947), was originally included in *Eucoila* and later transferred to *Rhoptromeris* (De Santis 1967). *R. haywardi* was described from Argentina and Uruguay (Blanchard 1947) and has been reared in association with *A. fraterculus* and *C. capitata* (De Santis 1967), as well as *Anastrepha* spp., from *Carica quercifolia* Hill, *Ficus carica*, *Phoebe porphyria* Gris, *Psidium guajava*, and *Prunus persica* in Tucumán (Turica and Mallo 1961). Despite intensive surveys of fruit fly parasitoids that were conducted in several areas of the province of Tucumán for this and related studies (Ovruski 1995) the host fly and host plant associations recorded by Turica and Mallo have not been verified.

Nasca et al. (1980) obtained exceptionally large numbers of *R. haywardi* and the diapriid *Trichopria anastrephae* Costa Lima (nearly 3,500 and 1,000 individuals respectively) by using a modified model of Hayward's (1940) parasitoid fly-trap. This collecting method consisted of a pit in the soil beneath the host plant into which fallen host-fruit were placed, the pit was then covered with a thin sieve permitting only

the capture of parasitoids. It is very likely this method facilitated the production of drosophilids and their parasitoids. For example *T. anastrephae* is also known to attack drosophilids (Turica and Mallo 1961). This, together with our failure to rear *haywardi* from tephritid puparia in the province of Tucumán, lead us to question the recorded host associations of this species. Parasitism of Tephritidae needs to be verified.

The generic placement of this species also needs verification following Nordlander's (1978) revision of *Rhoptromeris*. As restricted by Nordlander (1978), *Rhoptromeris* consists of parasitoids of Chloropidae and other small dipterous larvae such as those that commonly breed in the base of grass stems (Poaceae), and it is unlikely that *haywardi* belongs to this largely Holarctic genus.

Trybliographa Förster

Several eucoilids associated with fruit-infesting Diptera in the Neotropical Region have been placed in the genus *Trybliographa* at one time or another. These include species placed in *Pseudeucoila*, a junior synonym of *Trybliographa* (Hellén 1960, Nordlander 1980), as well as various subgenera of either *Trybliographa* or *Pseudeucoila* (Weld 1952). Three of these, including the species originally described as *Trybliographa daci* by Weld (1951b), are treated above under the genus *Aganaspis*. Most of the others, however, cannot be readily assigned to genus at the present time because the Neotropical genera are badly in need of revision. These species appear to belong to what Nordlander (1982) referred to as the *Ganaspis* group of genera. Nordlander (1981, 1982) discussed some of the problems associated with the *Trybliographa* and *Ganaspis* groups of genera, presented a list of generic names that he considered valid, and provided useful information on the location and status of the type material. According to Nordlander (1981), *Trybliographa* is predominantly

Holarctic. It is therefore unlikely that any of the species previously associated with fruit-infesting Diptera in the neotropics belong to this genus. We have examined several such specimens in the USNM collection of *Trybliographa* and *Pseudeucoila* labelled as reared from tephritids or other fruit-infesting flies, and were unable to discover any that belong to *Trybliographa* s. s. as defined by Nordlander (1981). Aside from the species now transferred to *Aganaspis*, we are aware of only two other species that have been described, and for which tephritid hosts have been reported (additional records available to us are largely in the form of unpublished label data). These are *brasiliensis* von Ihering, 1905 and *hookeri* Crawford, 1913.

Von Ihering's species was first described as *Hexamerocera brasiliensis* and later as *Eucoela (Hexamerocera) eobrasiliensis* (von Ihering 1914). It was transferred, along with the subgenus *Hexamerocera*, to *Pseudeucoila* by Weld (1932). Nordlander (1978), however, treated *Hexamerocera* as a synonym of *Rhoptromeris*. *Pseudeucoila*, as noted above, is now a synonym of *Trybliographa*. Von Ihering's *brasiliensis* does not fit the current definition of either *Rhoptromeris* or *Trybliographa*, and thus, like *haywardi*, remains unplaced in the Eucoilidae.

Von Ihering's *brasiliensis* is known from Brazil and Panama (Borgmeier 1935) and it was introduced into Puerto Rico during 1935–37 along with other unidentified eucoilid species to aid in the control of *A. obliqua* and *A. suspensa* (Bartlett 1941). The recorded hosts were *A. fraterculus*, *Anastrepha* sp., *C. capitata* and Drosophilidae (Borgmeier 1935, Costa Lima 1948). The type material was collected from peaches, where it was thought to be a parasitoid of *A. fraterculus* (von Ihering 1905). Though von Ihering (1912) provides evidence to support his view of *brasiliensis* as a parasitoid of *Anastrepha*, the actual host was not identified and the possibility that this is a drosophilid parasitoid (because of its small size) cannot be discounted. Hosts for this species thus need verification.

Crawford's *hookeri* was originally described in *Ganaspis*, but was placed under *Hexamerocera* by Weld in his arrangement of the USNM collection (though formal transfer to *Pseudeucoila (Hexamerocera)* was apparently never published). This is a similarly diminutive species, and therefore unlikely to be a parasitoid of *Anastrepha*, as originally recorded. Both *hookeri* (from Puerto Rico) and *brasiliensis* have a complete hairy ring at the base of the second tergum, unlike similarly-sized species of *Leptopilina*, in which the second tergum is bare dorso-medially. The scutellar cup is much larger in *brasiliensis* than it is in *hookeri*.

CONCLUSIONS

Information on host specificity in eucoilids is largely lacking other than for the work by van Alphen, Vet and colleagues on species of *Leptopilina* attacking Drosophilidae (e.g. van Alphen et al. 1991, Poolman Simons et al. 1992). There are often many species of Diptera, representing several families, present in fruit attractive to eucoilids. Thus, in order to assess host specificity accurately, it is essential to verify all records by isolating individual puparia or exposing known hosts to ovipositing females. For many of the older records (including label data from unpublished studies), host associations were based on eucoilids reared from bulk samples of fruits containing pest tephritids. These must be viewed with caution because of the inevitable inclusion of other flies, such as drosophilids and lonchaeids, in these samples.

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NOTE

First Chromosome Record for the Family Dryinidae: The Karyotype of *Anteon brevicorne* Dalman (Hymenoptera: Chrysidoidea)

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Though karyotypes of some members of the superfamily Chrysidoidea have been examined during the last few years (Hoshiba and Imai 1993, Gokhman and Quicke 1995, Quicke and Gokhman 1996), the family Dryinidae remains totally untouched by chromosomal investigation. We have studied for the first time chromosome number and karyotype of the dryinid, *Anteon brevicorne* Dalman. Chromosome preparation was obtained from an adult wasp collected from the wild at the Botanical Garden, Moscow State University, Moscow, Russia, in May 1997. Preparation was made according to the previously described protocol (Gokhman and Quicke 1995). Chromosomes were subdivided into four groups—metacentrics, submetacentrics, subtelocentrics and acrocentrics following Levan *et al.* (1964) and Imai *et al.* (1977). The voucher specimen is deposited in the Zoological Museum, Moscow State University, Moscow, Russia.

RESULTS

Eleven well-spread metaphase plates were obtained from the individual studied, all of them having the same diploid chromosome number, $2n = 10$ (Fig. 1). All chromosomes are obviously two-armed and thus arm number (NF) in this species is 20. The karyotype comprises three pairs of submetacentric chromosomes and two pairs of subtelocentric ones. However, all chromosomes differ notably in size, each chromosome pair being at least about 1.5

times longer or shorter than the others. Submetacentrics of the first two pairs are the longest in the set (3–4 μm), those of the third pair are the shortest (0.5 μm), and subtelocentrics are of intermediate length (1–2 μm).

DISCUSSION

The above results, together with accumulated data on chromosomes of the other Chrysidoidea, provide qualitatively new karyotypic information for the superfamily. First, chromosome number of *A. brevicorne* is the lowest in the Chrysidoidea and one of the lowest in all aculeate Hymenoptera. Except for a few ant species, only four predominantly unrelated members of the Aculeata (although two of them belong to the bee genus, *Andrena*) were reported to have *n* values of 5 or fewer (Goodpasture 1974, Hoshiba and Imai 1993). Second, the chromosome set of *A. brevicorne* is highly asymmetric (White 1973), apart from karyotypes of the other Chrysidoidea, where chromosomes show a continuous gradation in length (see for example Hoshiba and Imai 1993, Fig. 2c and 8c, and Quicke and Gokhman 1996, Fig. 1c). Finally, ranges of variation in chromosome number in all studied families of the Chrysidoidea do not overlap. Specifically, *n* values of 10–14, 19–21 and 5 were found in the Bethylidae, Chrysididae and Dryinidae respectively. Though it is difficult at present to determine pathways of karyotype evolution in the Chrysidoidea, low chromosome number and

Fig. 1.   Karyotype of *Anteon brevicorne*. Scale bar indicates 1 μm.

karyotype structure found in the Dryinidae and perhaps resulted from multiple chromosome fusions suggest that those features may be apomorphic together with the other apomorphies of this specialized group (Brothers and Carpenter 1993). However, further chromosomal investigation of the Dryinidae and other Chrysidoidea will be necessary to confirm this assumption.

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NOTE

A Putative Pheromone-gland Associated Modification of the Hind Tibia in *Vipio moneilemae* (Hymenoptera: Braconidae: Braconinae)

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More is known about the pheromone and other exocrine glands of braconid wasps than any other group of parasitic Hymenoptera, although behavioural evidence suggests that they are present in many if not all groups and that their products collectively have a variety of roles including mate location, host marking, defence and spacing (Quicke, 1997). The majority of pheromone glands identified to date are located in the metasoma (Weseloh 1980; Tagawa 1983; Buckingham and Sharkey 1988; Quicke 1991; Field and Keller 1994; Quicke *et al.* 1996, 1997) although recent studies have indicated that the antennae also have a wide range of intrinsic glands that are involved in courtship as well as host assessment (Bin *et al.* 1986, 1989; Isidoro and Bin 1995; Isidoro *et al.* 1996). Here we describe and illustrate a modification of the hind tibia of a braconine wasp, *Vipio moneilemae* Gahan, that was noticed during revision of the North American species of *Vipio* (Inayatullah *et al.* 1998). The morphology of the structure suggests that it is yet another exocrine gland, and its presence only in males further suggests that, if the newly described structure is associated with a gland, then this may be a release site for sex pheromones. It is worth noting that the hind tibia of an unrelated braconid, the chelonine *Ascogaster reticulatus* Watanabe, has been

identified as the source of a sex pheromone, but in this case the glands are present only in females (Kainoh and Oishi 1993). Males of this species apparently follow female pheromone trails as do the males of the aphelinid *Aphelinus asychis* Walker (Fauvergue *et al.* 1995).

The male hind tibia of *V. moneilemae* is especially thickened for most of its length (Figs. 1, 3) whereas that of the female (Fig. 2, 4) is essentially unmodified. Along almost the whole of the dorsal surface of the male hind tibia, there is a deep groove bordered laterally by a distinct ridge on both the inner and outer sides. Within this groove, there is a dense arrangement of setae that point somewhat posteriorly and whose tips converge towards the mid-line of the groove (Figs. 5, 6). In some uncleaned specimens, the setae are covered by a deposit, perhaps the dried secretion of an associated gland, though this has not been confirmed. We were not able to see any cuticular pores but these may be small and the setae obscured the view of most of the floor of the groove. The arrangement and close-spacing of the setae in the tibial groove suggest that they could act as a wick and provide an increased evaporative area for the release of pheromones; similar evaporative setal structures have been found associated with the metasomal glands of agathidine braconids (Bucking-
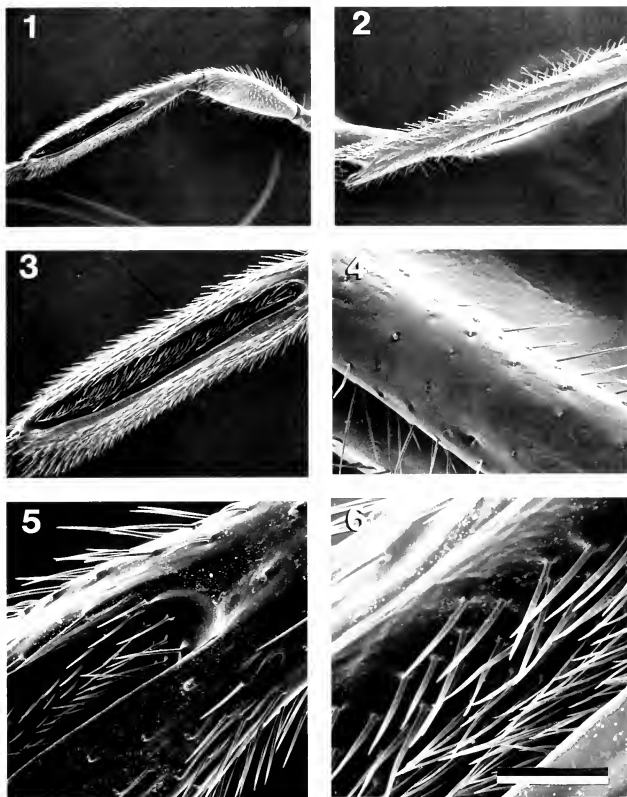
Figs. 1–6. Features of the hind leg of *Vipio monetlemae*: 1, 3, 5, 6, male leg showing swollen tibia with dorsal groove and associated setal arrangement; 2, 4, female showing unmodified tibia. Scale bar: 1 = 860 μm; 2, 3 = 380 μm; 4 = 136 μm; 5 = 100 μm; 6 = 50 μm.

ham and Sharkey 1988). No similar structures have been found on the legs of any other species of *Vipio*, nor on those of other braconines.

Vipio species are idiobiont larval ectoparasitoids of concealed hosts living in wood. Unfortunately, very little is known about *V. moneilemae* apart from the fact that it has been reared from a species of *Moneilema* (Cerambycidae) in Mexico (Gahan 1930), and it is known from only a handful of specimens from Mexico and the southern USA (California, Texas, Utah: most of the known specimens are in the United States National Museum of Natural History). The majority of parasitic wasps are protandrous, and the males of many that attack wood-boring hosts congregate at sites from which females are about to emerge, and where a variety of competitive tactics may ensue. If the structure seen on the hind tibia of male *V. moneilemae* is indeed associated with a sex pheromone gland, it may suggest a radically different mating strategy.

Large putative sex pheromone glands are found in the metasomata of males of many genera of braconines (Quicke 1991) as well as in a range of other braconids such as many opiines, alysiines and agathidines (Buckingham and Sharkey 1988). Most work, including the chemical analysis of glandular products, has been carried out on those of some Opiinae (Williams *et al.* 1988) and it has been proposed that these have a role in courtship although a defensive role cannot be excluded. Without doubt, more work needs to be done on the roles of male exocrine glands in the Braconidae and other parasitic wasps.

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NOTE

A Note on the Mating Behavior of *Anoplius amethystinus* Fabricius (Hymenoptera: Pompilidae)

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To date, nothing has been reported on the biology of *Anoplius* (*Notiochares*) *amethystinus* Fabricius, a widespread New World pompilid ranging from Argentina to parts of the southern United States (California, Arizona, New Mexico, Texas, Georgia, Florida) (Wasbauer & Kimsey 1985). A handful of remarks may be found on the biology of related species; to this growing knowledge we add the following observations on *A. amethystinus*.

The encounter occurred in the Riverside Pine Island (longleaf pine (*Pinus palustris* Miller) woods) of the Ocala National Forest, Florida (29°25'N, 81°47'W). On 11 April 1997, around noon on a lightly overcast day, we noticed a group of male pompilids in the tire rut of a seldom-used, sandy dirt road. Our presence scattered them, but as soon as we stepped back 1–2 meters, they returned to an oblong area of sand (about 10 by 30 cm) in which it appeared that the surface debris of pine needles, dead leaves, and small twigs had been displaced to the periphery by the activities of the male wasps. We counted 12–15 males in this space at any one time, some flying off occasionally to circle the area or to visit nearby shrubs. They walked around in small circles, flicking their wings and drumming their antennae on the ground. They did not fight or otherwise respond to each others' presence, although in their tight quarters they often touched each other.

After watching for a few minutes and capturing some of the males that flew out from the group, we swept aside the loose sand (about 5 mm deep) in the clear area, and then started excavating the compacted, cement-like sandy substrate. A few millimeters down we found the opening of a burrow (6 mm diameter) with a pompilid female near the top, scraping at the sand in an apparent effort to dig herself out: her wings were open and dry, and she flew directly into the waiting net. When we stepped aside, 4 or 5 males returned; several popped headfirst into the burrow, then backed out after a few seconds. Further excavation revealed an empty nest similar to those reported for *Anoplius* (*Pompilinus*) *tenebrosus* Cresson, *A.* (*P.*) *viaticus* L. (Alm & Kurczewski 1984), and *A.* (*Arachnophroctonus*) *apiculatus pretiosis* Banks (Kurczewski & Spofford 1986): exit tunnel straight, ca. 5 cm long, angled 50–60° from surface, with terminus unicellular and widened only very slightly.

Similar behavior in male *Anoplius* has been reported in a few other species. Rau (1922) found four males of *A.* (*Notiochares*) *atramentarius* Dahlbom gathered around a

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newly emerged female, and males of *A. tenebrosus* (Alm & Kurczewski 1984) and *A. apiculatus autumnalis* Banks (Evans et al. 1953) have been observed to fly low over sandy areas and occasionally alight. These observations and ours are consistent with the suggestion of Evans et al. (1953) that mating may only be successful with virgins in some species (but do not rule out other strategies). Such behaviors also imply the use of pheromones in combination with habitat cues in locating female emergence areas, and our observations in particular suggest that antennation of the ground may be involved in location of females at short range.

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BOOK REVIEW

Annotated Keys to the Genera of Nearctic Chalcidoidea (Hymenoptera). Gary A. P. Gibson, John T. Huber and James B. Woolley (Editors.). NRC Research Press, Ottawa, 1997. xi+794 pp. Price: Canada CAN$64.95, other countries the equivalent of US$64.95 (hardcover). ISBN 066016669-0.

It has been said that it is dangerous to study the Parasitic Hymenoptera, for those who do are inclined to become alcoholics or end up in mental institutions. Notions of such despair undoubtedly stem from the daunting task that confronts those who venture to unravel the identity of this vast and taxonomically complex assemblage of enigmatic wasps.

The superfamily Chalcidoidea alone comprises close to 19,000 valid species in 2,000 genera, with estimates of the actual number of species ranging from between 60,000 to 100,000 world wide. Compounding the difficulties in coming to grips with the identity of this bewildering array of mostly poorly known taxa is the plethora of scattered and often inaccessible descriptive literature spanning some 200 years of taxonomic endeavour on the group. The task is made even more arduous by a shortage of essential identification tools such as modern catalogues, revisions, keys and adequately documented reference collections. In Britain, arguably the cradle of Chalcidology, there are for instance no modern identification keys for more than half of the 5,000 or so species of Hymenoptera (Weeks et al. 1997, Bull. Ent. Res. 87: 203), many of which belong to chalcidoid groups.

What is clearly needed, is to take stock of what is known, collate and synthesize the vast pool of scattered knowledge, much of which is buried in a few inquiring minds, and make it readily accessible in such a way that it is both palatable and of practical value to all. Indeed, this is not only imperative in giving credence to the ideals of the Convention on Biological Diversity, but also in proving the worth of insect systematists in a world of changing attitudes to science.

The 17 authors of Annotated Keys to the Genera of Nearctic Chalcidoidea receive full credit for having done exactly that. In harnessing their collective skills to the full they have produced an outstanding synopsis of the 19 families and 706 chalcidoid genera known to occur in the region. But the true value of this book lies far beyond that of a manual merely for identifying specimens. It is also an impressive reference work, crammed with invaluable nomenclatural, bibliographical and host information on the Nearctic chalcidoid fauna.

The book comprises 22 chapters. The introduction, which contains interesting background information on the history of Chalcidology in North America, numbers of taxa and the rate at which genera have been described from the region through the years, is followed by a chapter on morphology. Morphological terms pertaining to the keys and various family diagnoses are conveniently highlighted in bold, clearly explained and depicted in a series of uncluttered line drawings and good quality scanning electron micrographs. For quick reference, terms are listed alphabetically in a separate appendix with their abbreviations and reference to figures. A second appendix cross-references the abbreviations with terms. The disadvantage of having this information separate, and not in figure legends below the plates, is that some paging is required to determine the meanings of the abbreviations depicted in the illustrations.

Chapter three provides, besides a key to

families, an overview of the Chalcidoidea and covers topics such as recognition of the group, mode of parasitism (feeding types), host ranges and relationships, behaviour, collecting methods and voucher specimens. Written in clear language, this is essential reading matter which should appeal in particular to the non-specialist seeking general background information on the superfamily at a glance.

The family key is primarily a derived combination of those found in A Handbook of the families of Nearctic Chalcidoidea and Hymenoptera of the World. In recognizing 19 families, the authors have opted for the traditional system of classifying chalcidoids at this level. Considering the intended purpose of the book and the instability of the higher classification of these wasps, in which anything from nine to 24 families have been recognized, this is a sensible choice.

Preceding the key is a flow chart which gives a pleasing visual impression of how the 19 families are keyed out in the 40 couplets. The key itself is visually less pleasing. Placing the figures associated with each alternate of a couplet directly above it allows for easy comparison between figures and text, but often results in insufficient space for both alternates on the same page. Consequently, many pages are left with unsightly blank spaces, while the alternates of some couplets appear on different pages, making comparisons somewhat cumbersome. More important though, is the fact that the key works well. Evidently, much careful thought has gone into making it both accurate and workable for the novice and specialist alike. Chosen for diagnostic reliability rather than convenience, the characters are not necessarily "easy" to use, but being appropriately and clearly illustrated there should be no problem in keying specimens out.

The bulk of the remaining text is devoted to the family treatments. Each of the 19 chapters reviews one family and includes, apart from a generic key, sections on its

recognition, systematics, biology, fauna and literature. For larger families a useful index to genera based on couplet numbers is also included. These topics are all well covered, serving as a concise and informative introduction to the 19 families as represented in the Nearctic region.

In essence, this book is all about generic keys to Nearctic chalcidoids, and its real value will ultimately be judged by how well these keys perform. So I decided to put some of them to the test, selecting specimens not only from the Nearctic region, but also from further afield. The results were excellent, bearing testimony to the skilful and competent way in which these keys have been constructed. The contents of the couplets are unambiguous and the taxonomic language easy to comprehend. I was pleased to see that the authors have, in all but one of the tested keys, managed to avoid using the handy but dreadful "either/or" method of separating taxa. All of this adds much to the relative ease with which the user is guided through the keys, even in the case of genera which are difficult to define. Although these keys have been designed specifically for the Nearctic region, they will, if used with the necessary insight and care, also serve as a very useful tool in the study of extra-limital forms, as was evident from the large selection of Afrotropical specimens which keyed out perfectly well. Greatly enhancing the value of these keys are brief annotations to each genus comprising references to existing species keys, estimated number of species, known distribution and host range in the region.

The use of the keys is facilitated by 1,880 line drawings and scanning electron micrographs which, despite the inputs from a variety of illustrators, are of a consistently high aesthetic and technical standard. With the intended readership of the book in mind, a few more eye-catching habitus drawings, which are completely lacking for some families, would have added a special touch.

The book concludes with four very useful indices. The first one comprises about 130 generic and subgeneric chalcidoid names (with their nomenclatural fate) which have become invalid since publication of the most recent (1979) edition of Catalog of Hymenoptera in America North of Mexico. Following this index are separate lists of plant and animal hosts, and supraspecific chalcidoid names.

In summary, I applaud the contents of this book, hence the lack of any serious criticism. Naturally, this is not the last word on the supraspecific identity of Ne-arctic chalcidoids, for our knowledge and understanding of the fauna is far from complete. But the authors have succeeded admirably in synthesizing what is presently known while providing an excellent framework for further revisionary work on the group. I recommend this book as an indispensable reference and identification tool for anyone, specialists and generalists alike, involved in the study of parasitic wasps.

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MANUAL OF THE NEW WORLD GENERA OF THE FAMILY BRACONIDAE

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This 439 page, multiauthored identification manual presents illustrated keys to the 34 subfamilies and 404 genera of the family Braconidae from the New World. Information about all New World genera described up to 1994 is included. The manual consists of 37 chapters by world authorities plus an index to generic names including subgenera and synonyms, and an appendix listing all the New World genera alphabetically by subfamily. The first chapter provides an introduction including a review of braconid biology, literature, classification, biogeography, collection and curation, and a discussion of the manual format. The second chapter is an extensive illustrated discussion of braconid morphology and terminology used in the keys. The third chapter is a fully illustrated key to the New World subfamilies of the Braconidae. The New World subfamilies are then presented separately in the remaining 34 chapters. For each, a key to the New World genera is included. Each of these keys is annotated to include estimated number of species, distribution, hosts, and critical references for each genus. Each subfamily chapter is extensively illustrated and the entire manual contains over 750 line drawings and scanning electron micrographs.

A valuable identification tool for biological control workers and museum curators

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All papers will be reviewed by at least two referees. The referees will be chosen by the appropriate subject editor. However, it would be helpful if authors would submit the names of two persons who are competent to review the manuscript.

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A Revision of the Philomastigine Sawflies of the World (Hymenoptera: Pergidae)

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Abstract.—The world genera and species of Philomastiginae (*Cerospastus* Konow, *Ecopatus* Smith and *Philomastix* Froggatt) are revised and an illustrated, identification key is provided. *Cerospastus volupis* Konow and *Ecopatus penai* Smith from South America and *Philomastix nancarrowi* Froggatt, *P. macleaii* (Westwood) and *P. xanthophylax* sp. n. from eastern Australia are described or redescribed. Larvae of *C. volupis* feed on foliage of species of *Nothofagus* (Fagaceae); those of *Philomastix* on foliage of *Rubus* (Rosaceae) or *Alphitonia* (Rhamnaceae). All species of *Philomastix* exhibit maternal guarding of eggs and larvae. The trans-Antarctic distribution of the Philomastiginae suggests a Gondwanan origin for the subfamily.

Distinctive Gondwanan elements are now known within numerous Australian families of Hymenoptera (Naumann 1991). Over a dozen families or subfamilies and even a few genera are shared by Australia and South America or by Australia, South America, New Zealand and southern Africa. Examples of such trans-Antarctic distribution patterns can be found among the Symphyta, Megalyroidea, Evanioidea, Ichneumonoidea, Proctotrupoidea, Platygasteroidea, Chalcidoidea, Vespoidea and Apoidea and include phytophages, parasitoids and predators. Generally these Gondwanan elements are readily recognisable as archaic clades within their respective superfamilies or families. Some, such as the parasitoid genus *Monomachus* Klug (family Monomachidae) are morphologically conservative and comprise in total only a few dozen species (Johnson 1992). Some, such as *Monomachus*, are very rarely collected or are restricted to temperate, forest habitats. In contrast such Gondwanan groups as the thynnine Tiphiidae are spectacularly varied and speciose; the many hundreds of species (Naumann 1991) occur over a wide range of habitats and some of these species are extremely common.

Seven subfamilies or tribes of Symphyta, the Dereycyrtinae (Xiphydriidae), the Guiglini and Leptorussini (Orussidae), the Scobini (Argidae), and the Pergulinae, Perreyinae and Philomastiginae (Pergidae) all exhibit trans-Antarctic distribution patterns. The Dereycyrtinae comprises the monotypic *Austrocyrta* Riek in Australia and three genera totalling sixteen species in South America (Smith 1988; Smith 1995). Larvae of this subfamily are unknown but probably develop within wood. The Guiglini comprise six Australian and two New World species, and the Leptorussini consist just a South American species, five Australian species and a species in South Africa (Smith 1988). All orussid larvae are believed to be ectoparasitic on the larvae of wood-boring beetles and siricid wood wasps. The orussid tribe Ophrynopini, with representatives in south-east Asia and South America might also be considered to be a "trans-Antarctic" taxon (N. Springate, pers.comm.). The Scobini comprise *Scobina* Lepeletier and Serville, a common New World genus of

about 50 species, and *Antargidium* Morice, an Australian genus of six species (Naumann 1991). Larvae of two species of *Scobina* feed on *Sida* Linnaeus (Malvaceae) but nothing is known of the biology of *Antargidium*. The subfamily Pergulinae (Pergidae) comprises the genus *Haplostegus* Konow with fifteen species in South America and the monotypic *Pergula* Morice in south-western, mainland Australia (Smith 1990). The biology of the single, rare species of *Pergula* is unknown but larvae of the South American pergulines have been recorded feeding on Myrtaceae, especially *Psidium guajava* L. (guava). Perreyinae are represented on the western side of the Pacific ocean by two species with flightless females (described respectively from Sulawesi and New Guinea) and east of the Pacific by about 80 species in South America (Smith 1990). Larvae of South American species feed variously on Asteraceae and Malvaceae. The Philomastiginae consists of two monotypic South American genera, *Cerospastus* Konow and *Ecopatus* Smith, and three eastern Australian species of *Philomastix* Froggatt (Fig. 75). The two previously described species of *Philomastix* are well known species of tropical and subtropical rainforests. Their larvae feed on the foliage of species of *Rubus* L. (Rosaceae) (Leask 1944) or *Alphitonia* Reissek ex Endl. (Rhamnaceae) (Jackson 1993) and females are commonly encountered standing guard over egg batches and young larvae (Fig. 72). Members of the subfamily can be recognised using the keys of Smith (1990) and Naumann (1991).

The present paper revises the generic diagnoses and key of Smith's (1990) treatment of the South American Philomastiginae, redescribes all previously named species, describes a new species of *Philomastix* from south-eastern Queensland (Fig. 1), and collates all known biological and distributional data on the subfamily. Morphological and biological studies of the larvae of *Philomastix* are continuing (Groth and Naumann unpublished).

Fig. 1. *Philomastix xanthophylax*. Scale line = 2mm.

TERMINOLOGY

The morphological terminology used here follows Goulet and Huber (1993).

DEPOSITORIES

AMSA	Australian Museum, Sydney, Australia
ANIC	Australian National Insect Collection, CSIRO Division of Entomology, Canberra, Australia
BPBM	Bernice P. Bishop Museum, Honolulu, Hawaii, U.S.A.
CNC	Canadian National Collections of Insects, Arachnids and Nematodes, Ottawa, Canada
BCRI	Biological and Chemical Research Institute, N. S. W. Department of Agriculture, Rydalmere, Australia
BMNH	The Natural History Museum, London, U. K.
DEIC	Institut für Pflanzenschutzforschung der Akademie der Landwirtschaftswissenschaften (formerly:Deutsches Entomologisches Institut, Eberswalde, Germany)
FCNI	State Forests Research Institute, Beecroft, Australia

HGCN   H. Groth Collection, "Timbar-
        rah," via, Crows Nest, Australia
MVMA   Museum of Victoria, Mel-
        bourne, Australia
UMO   Hope Department of Entomol-
        ogy, University Museum, Ox-
        ford, U. K.
QMBA   Queensland Museum, Brisbane,
        Australia
QDPI   Entomology Collection, Queens-
        land Department of Primary In-
        dustries, Brisbane, Australia
SAMA   South Australian Museum,
        Adelaide, Australia
UQIC   Department of Entomology,
        University of Queensland, Bris-
        bane, Australia
USNM   National Museum of Natural
        History, Smithsonian Institu-
        tion, Washington, D. C., U. S. A.

PHILOMASTIGINAE Rohwer

Pterygophorinae (part): Froggatt 1890b: 696;
    Ashmead 1898: 231.
Ptergophorides (part): Konow 1898: 248; Ko-
    now 1905b: 37.

Philomastiginae Rohwer 1911a: 220; Benson
1935: 224; Benson 1938: 379; Riek 1970a: 891;
Riek 1970b: 218; Smith 1978: 159; Naumann
1984: 345, 347; Smith 1990: 13, 21–23; Nau-
mann 1991: 934–935; Macdonald and Ohmart
1993:493–495.

Diagnosis.—Antenna 14–21-segmented,
filiform in female, serrate in male. Head
capsule open (neither postgenae nor hy-
postomae forming continuous bridge be-
tween occipital and foramen and oral fos-
sa). Maxillary palp 4- or 6-segmented; la-
bial palp 3- or 4-segmented. Labium api-
cally single or tri-lobed. Ventral arms of
cervical sclerites pointed, neither meeting
nor forming precoxal bridge with proster-
num; notauli complete; mesothoracic ster-
nopleural suture present; distance be-
tween cenchri less than half width of cen-
chrus. Mid- and hind tibia each with pre-
apical spine; foretibia with 2 apical spines.
Costa of forewing narrower than intercos-
tal area; forewing without anal cell. Ab-
dominal tergum 1 sclerotised.

KEY TO GENERA OF PHILOMASTIGINAE

1. Maxillary palp 4-segmented; labial palp 3-segmented, apical segment with large sensory
   cup occupying more than half length of segment (Fig. 70), maxillary palp with smaller
   sensory cup; labium single lobed; female without cercus . . . . *Philomastix* Froggatt
 – Maxillary palp 6-segmented; labial palp 4-segmented, apical segments without sensory
   cup; labium tri-lobed; female with cercus 2
2. Forewing with 4 cubital cells (1R1, 1Rs, 2Rs, 3Rs) (Fig. 4); forewing radial cell closed; fourth
   maxillary palp segment slender (Fig. 9); antenna of female weakly clavate (Fig. 3); meso-
   scutum conspicuously setose . . . . *Cerospastus* Konow
 – Forewing with 2 or 3 cubital cells; fore-wing radial cell open (Fig. 5); fourth maxillary palp
   segment apically distinctly wider than other segments (Fig. 8); antenna of female not cla-
   vate (Fig. 2); mesoscutum almost devoid of setae . . . . *Ecopatus* Smith

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PHILOMASTIX Froggatt

Philomastix Froggatt 1890a: 487–488; Froggatt
1890b:696; Froggatt 1901: 1070; Dalla Torre
1894: 308; Ashmead 1898: 231; Konow 1898:
248, 249; Konow 1905: 36–37; Schulz 1906:
81–82; Rohwer 1911: 87; Morice 1919: 248,

255, 287; Tillyard 1926: 265; Benson 1935: 224;
Benson 1938: 379–380; Riek 1970a: 880, 889,
891; Smith 1978: 159; Smith 1990: 21–23; Pag-
liano and Scaramozzino 1990: 157; Abe and
Smith 1991: 65; Naumann 1991: 926, 933, 935;
Macdonald and Ohmart 1993: 493–496; Nau-
mann 1994: 414–415. Type species: *Perga nan-*
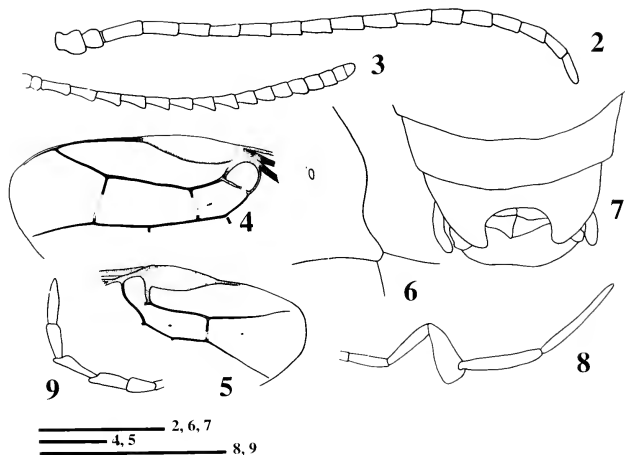
Figs. 2–9. *Ecopatus penae, Cerospastus volupis*: 2, *E. penae*, female antenna; 3, *C.volupis*, female antenna; 4, *C. volupis*, forewing (part); 5, *E. penae*, forewing (part); 6, *E. penae*, lateral panel of first abdominal tergum; 7, *C. volupis*, apex of male abdomen, dorsal view; 8, *E. penae*, maxillary palp palp; 9, *C. volupis*, maxillary palp. Scale lines = 1.0 mm.

carrowi Froggatt (designated by Rohwer 1911).

Perga Leach: Westwood 1880: 372; Kirby 1882: 26. Dalla Torre 1894: 351. (part)

Heptacola Konow: Konow 1905a: 167 (part)

Female.—Vertex conspicuously setose. Face with some fine microsculpture. Malar space narrower than diameter of anterior ocellus. Antenna 14–19-segmented, weakly serrate, not clavate. Right mandible simple (Fig. 69). Maxillary palp 4-segmented, filiform (Fig. 70); apical segment with conspicuous sensory cup, this less than half as long as segment. Labial palp 3-segmented, apical segment with conspicuous sensory cup, this more than half as long as segment. Labium single lobed. Thorax dorsally conspicuously setose. Notauli, median mesoscutal line deeply impressed. Mesoscutellum swollen so that posterior margin concealed from above. Mesepisternum with tubercle. Metascutellum in form of transverse band. Forewing with closed radial cell and 4 cubital cells (e.g. Fig. 1). Median, second cubital and third cubital cells each with nygma (small, corneous spot). Abdominal terga dorsally densely setose. Second tergum predominantly smooth. Cercus absent. Ovipositor sheath posteriorly strongly expanded, in posteroventral view with prominent, flattened, semicircular surface (e.g. Fig. 21).

Head, mesoscutellum, metascutellum orange-yellow. Legs brown to dark brown. Wings with background smokey brown appearance, especially in female. Costal cell of fore wing distinctly more darkened than remainder of wing.

Male.—Antenna 15–21-segmented, stronglyserrate (e.g. Fig. 11). Eighth tergum pos-

teriorly with moderate or very weak emargination (e.g. Fig. 20).

Discussion.—Larvae of *Philomastix* have long been known to feed externally on leaves of various shrubby and scandent species of *Rubus* (known as blackberries or native raspberries) (Leask 1944). More recently (present paper and Jackson 1993) *Philomastix* larvae have been discovered defoliating trees of the genus *Alphitonia* (Figs. 72–74). Two species of *Alphitonia* are attacked: *Alphitonia petriei* Braid & C. T. White, the pink ash, which is widespread in Queensland and the northern part of the Northern Territory, and *Alphitonia excelsa* (Fenzl) Benth., the red ash, which occurs in rainforests and eucalypt woodlands of Queensland, New South Wales, and the northern parts of the Northern Territory and Western Australia (Francis and Chippendale 1970; Lazarides and Hince 1993). The hosts of *Philomastix* are thus a shrub and a tree from different plant families. *Rubus* and *Alphitonia* do have at least one, ecological characteristic in common—both are pioneer species. Various *Rubus* are well known species of paths, clearings and margins of closed forests and *A. petriei* is the most prominent recolonising tree species in upland rainforest clearings in north Queensland (Jackson 1993).

A species of "*Philomastix*" has been recorded feeding on *Eucalyptus* sp. at Launceston, Tasmania (Anonymous 1980). This is almost certainly a misidentification: it is the only record of a eucalypt as host and we have seen no authentic specimens of *Philomastix* from Tasmania in the course of this revision.

Philomastix does not occur over the entire range of its host plants. The sawfly genus is restricted to the eastern Australian states of Queensland and New South Wales between the latitudes 16°S and 35°S. However *Alphitonia* occurs beyond this range in the Northern Territory and Western Australia and suitable species of *Rubus* are common in Victoria (Bruzzese 1980).

P. nancarrowi and *P. macleaii* are strictly allopatric (Fig. 76). *P. nancarrowi* is confined to the rainforests and closely adjacent eucalypt woodlands of the Queensland Wet Tropics between the northern end of the Atherton Tableland and the Mount Spec-Paluma area. Almost all specimens have been collected at altitudes above 500m. *P. macleaii* is very widely distributed from Eungella in central Queensland to the Illawarra district in south-eastern New South Wales. It occurs in tropical, subtropical and temperate rainforest and nearby moist woodlands. In the northern parts of its range (Eungella, Kroombit tops, Bunya Mountains) *P. macleaii* is not known below 1000m but south of about Brisbane it occurs near sea level. The region of eastern Queensland between Paluma and Eungella which separates *P. nancarrowi* and *P. macleaii* is relatively dry; the vegetation is dominated by eucalypt woodland and there are no significant patches of rainforest. North from Paluma the so-called "base-of-peninsula" rainforest system stretches with some interruptions to Cooktown. On the other hand Eungella stands as the northern extremity of a rainforest system that extends, also with interruptions, all the way to southern New South Wales. There are taxonomic discontinuities in several orders of insects (especially mesothermic Odonata, Plecoptera and Megaloptera) at the gap between Paluma and Eungella (Kikkawa et al. 1981; Watson and Theischinger 1984) and these are thought to reflect Pleistocene fluctuations in climate. During Pleistocene glacial periods, increased aridity resulted in a contraction of the rainforests and a pronounced inhospitable gap between moist refugia north of Paluma and south of Eungella. Presumably vicariance speciation occured on either side of this barrier within *Philomastix* and various odonate, stonefly and alderfly genera.

P. xanthophylax has a much more circumscribed distribution pattern (Fig. 76). It has been collected in moist woodlands

rather than rainforest but in the Brisbane area it is sympatric with *P. macleaii*. There is at present no model to explain the origin of this species.

The oviposition behaviour of *Philomastix* is unusual for a pergid sawfly. The adult female pierces the leaf of the host plant, pushes each elongate egg through the perforation, and attaches one end of the egg to the underside of the leaf (Macdonald and Ohmart 1993). The other end of the egg is pushed free of the lower surface of the leaf. The more typical behaviour for pergids is to cut a shallow slit in the host plant and insert the egg into this slit. The lancet of most pergids is saw-like in appearance but the lancet of *Philomastix* (Figs. 22, 39, 58, 71) is auger-shaped, presumably to facilitate the "pierce-and-push" oviposition habit.

All species of *Philomastix* exhibit mater-

nal care. Females stand over or near their egg masses and young larvae (Fig. 72). When disturbed they shake from side to side and rapidly vibrate their wings to produce a loud buzzing sound. Females will guard their offspring, usually from a position on a petiole or stem, and have been observed to guide larvae to new leaves (Leask 1944). Females eventually die at their post, and sometimes dozens of dried bodies remain hanging on defoliated host plants. Parental defence of offspring is widespread within the Symphyta. It has been recorded in three other subfamilies of Pergidae (Naumann 1984; Macdonald and Ohmart 1993) and in the Pamphiliidae (Kudô et al. 1992). In those species which have been studied quantitatively it has been shown that female guarding reduces predation on eggs by other arthropods.

KEY TO SPECIES OF *PHILOMASTIX*

1 Female; abdomen with saw-like ovipositor often concealed within sheath (Figs. 1, 21, 46, 55) 2
– Male; ovipositor and sheath absent 4
2 Abdomen orange-yellow (Fig. 1); antennal flagellum black; ovipositor sheath posteromedially dentate (Figs. 54, 55) .... ***xanthophylax*** sp.n.
– Abdomen with extensive dark brown, black and cream markings (Figs. 21, 46); antennal flagellum orange-yellow; ovipositor sheath not posteromedially dentate (Figs. 21, 46) 3
3 Mesoscutellum usually with posterolateral tubercles (Figs. 30–34); mesepisternal tubercle strong (Fig. 38); abdominal terga 3–5 usually with cream, lateral maculae visible from above (Fig. 62); posterolateral margin of first abdominal tergum weakly curved or straight (Fig. 37), spiracle separated from margin of tergum by a distance 0.9–1.1 times maximum diameter of spiracle .... ***macleaii*** (Westwood)
– Mesoscutellum without posterolateral tubercles (Fig. 16) although sometimes posteriorly emarginate; mesepisternal tubercle usually weak (Fig. 26); abdominal terga 3–5 without lateral, cream maculae visible from above (Fig. 64); posterolateral margin of first abdominal tergum strongly curved almost angulate (Fig. 19), spiracle separated from margin of tergum by a distance 1.6–1.7 times maximum diameter of spiracle .... ***nancarrowi*** Froggatt
4 Mid lobe of mesoscutum with brown to black coloration reaching anterior margin (Fig.63); diameter of anterior ocellus 0.9–1.0 times minimum distance between antennal sockets; sixth abdominal tergum with lateral, cream or orange-yellow macula visible from above (Fig. 63); mesoscutellum usually with posterolateral tubercles .... ***macleaii*** (Westwood*)*
– Mid lobe of mesoscutum reddish orange anteriorly and brown to black posteriorly or lobe entirely reddish orange; diameter of anterior ocellus approximately 0.7 times minimum distance between antennal sockets; sixth abdominal tergum usually without orange or yellow maculae visible from above; mesoscutellum without tubercles, although posterior margin sometimes distinctly concave 5
5 Seventh abdominal tergum with widely separated, yellow or orange maculae; posterolat-

eral margin of first abdominal tergum strongly curved, almost angulate (as in Fig. 19); mesoscutellum posteriorly weakly emarginate (Fig. 17) or straight . . . . . *nancarrowi* Froggatt
– Seventh abdominal tergum with yellow or orange band across posterior margin, band sometimes narrowly interrupted medially; posterolateral margin of first abdominal tergum weakly curved (as in Fig. 53) or straight; mesoscutellum posteriorly straight or weakly convex . . . . *xanthophylax* sp.n.

Philomastix nancarrowi Froggatt
(Figs. 10–26, 64–66, 76)

Philomastix nancarrowi Froggatt 1890a: 488–489; Froggatt 1890b: 696; Konow 1898: 250; Schulz 1906: 82–83; Rohwer 1911B: 87; Morice 1919: 287–288, Plate XI, fig. 13, Plate XII, figs 5,6, Plate XIII, fig. 15; Leask 1943: 2; Leask 1944: 1–3; Smith 1978: 159; Bruzzese 1980: 4; Abe and Smith 1991: 65; Macdonald and Ohmart 1993: 493–494; Naumann et al. 1994: 71.
*Philomastix naucarrowi*: Dalla Torre 1894: 308; Konow 1905: 37; Rohwer 1911: 87. (Misspelling)
nec Philomastix nancarrowi : Forsius 1927: 283. (Misidentification)

Female.—Body length 9.5–11.0 mm. Forewing length 10.6–12.3 mm. Distance between antennal sockets 2.8–3.9 times diameter of anterior ocellus. Antenna (Fig. 10) 15–18-segmented; apical 2–4 segments sometimes fused so that antenna apparently 13–16-segmented (traces of intersegmental sutures sometimes present). First flagellar segment 2.8–3.8 times longer than wide. Second flagellar segment 1.7–1.9 times wider apically than basally. Mesoscutellum without posterolateral tubercles, posteriorly rounded or weakly emarginate (Fig. 16); anterodorsal surface flat (Fig. 15) to weakly concave. Mesepisternal tubercle weak (Fig. 26). Ovipositor sheath not posteromedially dentate (Fig. 21). Posterolateral margin of first abdominal tergum strongly curved (Fig. 19), almost angulate, spiracle separated from margin by a distance 1.6–1.7 times maximum diameter of spiracle. Lancet as in Figs. 22–25, about 8 ctenidia terminating in dorsal tooth, anterior teeth weak

Flagellum orange-yellow. Mid lobe of mesoscutum orange-yellow (Fig. 64). Each lateral lobe of mesoscutum with large, dark brown to black macula occupying most of length of lobe. Mesepisternum with broad, brown band adjacent to sternopleural suture (Fig. 66). Mesosternum brown with narrow, orange-yellow band along anterior and lateral margins. Metascutum orange-yellow to pale brown, usually not much darker than cenchri. Forewing with broad, transverse, brown band; cell 1M usually completely brown (Fig. 12) or forewing entirely brown (Fig. 13). Abdomen predominantly dark coloured with some metallic reflections. Abdominal tergum 1 orange-yellow to pale brown. Terga 3–5 dark brown, black or metallic blue. Terga 6 and 7 each with cream, lateral macula; maculae narrowly separated middorsally by dark brown or black, or maculae contiguous. Tergum 8 cream. Tergum 9 orange-yellow. Abdominal sterna 2 and 3 at least in part orange-yellow or cream. Sterna 4–7 dark brown to black. Ovipositor sheath orange-yellow.

Male.—Body length 7.1–9.4 mm. Forewing length 7.1–8.1 mm. Distance between antennal sockets 1.7–2.0 times diameter of anterior ocellus. Antenna (Fig. 11) 15–17-segmented, apical 2 segments sometimes fused. First flagellar segment 1.6–2.0 times wider than long. Second flagellar segment 1.8–2.2 times wider apically than basally. Mesoscutellum sometimes distinctly emarginate posteriorly (Fig. 17); anterodorsal surface usually more concave (Fig. 14). Mesepisternal tubercle as in female. Tergum 8 posteriorly with deep emargination (Fig. 20). Genitalia as in Fig. 18, paramere moderately broad, gonolacinia not strongly hooked, penis valve truncate.
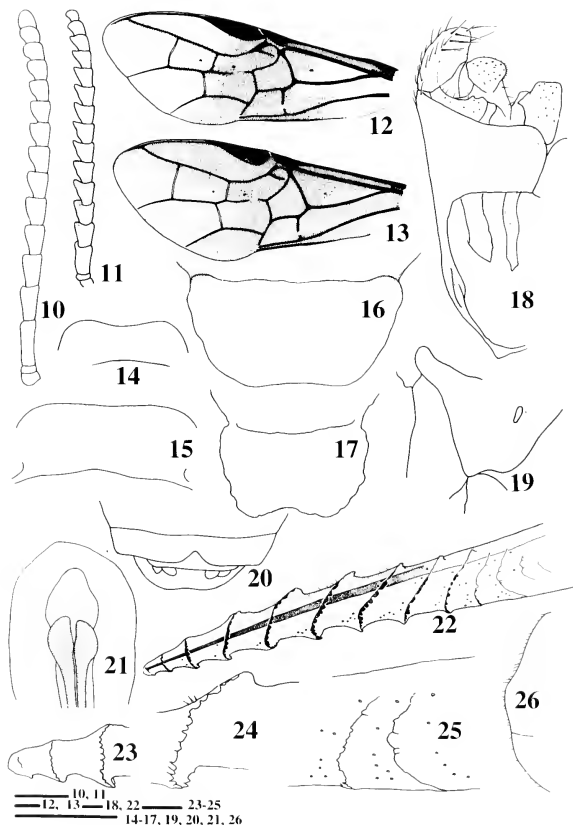
Figs. 10–26. *Philomastix nancarrowi*: 10, female antenna; 11, male antenna; 12, 13, forewings; 14, male meso-scutellum, surface contour as seen from rear of insect; 15, female mesoscutellum, surface contour as seen from rear of insect; 16, female mesoscutellum, dorsal view; 17, male mesoscutellum, dorsal view; 18, male genitalia, dorsal view; 19, lateral panel of first abdominal tergum; 20, apex of male abdomen, dorsal view; 21, apex of ovipositor sheath, posteroventral view; 22–25, lancet; 26, mesepisternum, profile. Scale lines = 1.0 mm for 10–17, 19–21, 26; = 0.1 mm for 18, 22–25.

Clypeus and labrum creamy white. Mid lobe of mesoscutum anteriorly orange-yellow, posteriorly brown (Fig. 65). Lateral lobe of mesoscutum entirely brown to dark brown. Abdominal terga 5 and 6 without orange-yellow, lateral maculae. Tergum 7 with lemon-yellow, lateral macula.

Type.—Holotype female, Cairns (ANIC, on permanent loan from Macleay Museum, University of Sydney, examined).

Material examined.—Queensland: 1 female, Myola, 1909 (ANIC); 10 females, 22 males, Kuranda, IV. 1902, R. E. Turner (BMNH, USNM, QMBA); 1 female, same locality, 3. V.-20. VI. 1913, R. E. Turner (BMNH);1 male, same locality, 15. IV. 1931, A. N. Burns (MVMA); 1 female, same locality, H. J. Carter (AMSA); 1 female, 2 males, 1.5 km SE Kuranda, 16–17. V. 1980, I. D. Naumann, J. C. Cardale (ANIC); 2 females, Barron Falls, via Kuranda, 16. VI. 1971, E. F. Riek (ANIC); 1 female, Cairns, 1905, H. Elgner (ANIC); 1 male, Cairns district, F. P. Dodd (SAMA); 1 female, Danbulla (forestry Reserve), 14. V. 1959, G. W. S. (BMNH);1 female, Mt Baldy,approximately 8 km W of Atherton, 13. I. 1977, M. S. and B. J. Moulds (AMSA); 1 male, 12 miles (19.3 km) from Ivanhoe (?Mine), 5. III. 1961, R. Straatman (ANIC); 1 female, Herberton, 17. III. 1922 (QMBA); 1 female, same locality, 30. V. 1943, M. F. Leask (QMBA); 4 females, same locality, 4. VI. 1944, M. F. Leask (AMSA); 3 females, Eubenangee, 14. V. 1950, G. Brooks (MVMA); 1 female, Bartle Frere, 5. V. 1928 (QDPI); 1 female, Laceys Creek, Mission Beach, 22. IV. 1970, S. R. Curtis (ANIC); 1 female, Tully, 24. IV. 1931, A. N. Burns (MVMA); 1 female, 4 miles (6.4 km) W Paluma, 13. IV. 1969, I. F. B. Common, M. S. Upton (ANIC); 2 females, Paluma, II.-IV. 1992, R. Jackson (ANIC);18 females, Little Crystal Creek, Mt Spec, 16. V. 1971, E. F. Riek (ANIC). Unlocalised: 2 females, "North Queensland," V. 1944, M. F. Leask (QMBA); 1 female, "Atherton Tableland," 14. III. 1934 (QDPI); 1 female, "Atherton Tableland," 19. III. 1958, N. H. L. Krauss (USNM); 1 female (QMBA).

Distribution.—See Fig. 76. The series split between the BMNH, USNM and QMBA is labelled "Cairns Kur 4. 02." I have interpreted this as meaning that the specimens were collected at Kuranda, a well known entomological collecting locality approximately 15 km north west of Cairns. Locality labels for specimens collected at Kuranda during the early 1900s commonly bear the additional information "Cairns" or "Cairns district." The collector's name is omitted from the USNM and QMBA specimens. Forsius (1927) recorded *P. nancarrowi* (and *P. macleaii*) from specimens collected at Dorrigo, in north eastern New South Wales by W. Heron and deposited in the SAMA. I have re-examined these specimens and all are clearly identifiable as *macleaii*.

Discussion.—One male from Mt Lewis, north Queensland listed below under "Other material examined", differs significantly from the description of *P. nancarrowi* males given above. In the Mt Lewis male the mesoscutellum is rather truncate posteriorly and thus approaches the tuberculate condition of *P. macleaii*; tergum 8 is only weakly emarginate; the dark brown coloration of the vertex does not extend to the posterior surface of the head; and the the clypeus, labrum and mesoscutum are all orange-yellow. The specimen may represent an extreme of variation in *P. nancarrowi* or an additional, undescribed species. It is perhaps not surprising that an anomalous *Philomastix* occurs on Mt Lewis. The mountain is the most northerly, known locality for the genus. It is part of the Carbine Tableland, a discrete, rainforest-covered upland remarkable for the uniqueness of its fauna. The Carbine Tableland supports the highest number of endemic vertebrate species in the Queensland Wet Tropics (Nix 1991) and Mt Lewis itself harbours several endemic species of insects: a stag beetle of the genus *Sphaenognathus* Buquet which is

known elsewhere only from the Black-down Tableland in central Queensland and Andean South America (Moore 1978; Monteith 1996), a primitive leafhopper representing a tribe otherwise unknown from Australia but recorded from Madagascar, New Zealand, Chile and Juan Fernandez and a species of flightless dung beetle (Kikkawa et al. 1981).

Larval host plants.—Rosaceae: *Rubus rosifolius* Sm. (Leask 1943, 1944); *Rubus hillii* F. Muell.(Leask 1944; Bruzzese 1980); *Rubus moluccanus* L. (Bruzzese 1980). Rhamnaceae: *Alphitonia petriei* (Jackson 1993).

Other material examined.—QUEENSLAND: 1 male, Mt Lewis, via Julatten, 4. V. 1970, S. R. Curtis (ANIC).

Philomastix macleaii (Westwood)
(Figs. 27–47, 62, 63 76)

Perga macleaii Westwood 1880: 372–373, Plate XXXV, fig. 2.; Kirby 1882: 26.

Perga macleayi : Dalla Torre 1894: 351 (unjustified emendation).

Heptacola macleayi : Konow 1905a: 167.

Philomastix macleaii : Froggatt 1918: 671; Smith 1978: 159; Bruzzese 1980: 4; Smith 1980: 342; Macdonald and Ohmart 1993: 493–494; Naumann 1993: 8, 115, 183.

Philomastix macleayi : Morice 1919: 248, 265, 287–288; Tillyard 1926: 265, Plate 21, fig. 2; Forsius 1927:283 (part).

*Philomastix nancarrowi* : Forsius 1927: 283 (misidentification).

Philomastix glabra Froggatt 1890a: 489–490; Froggatt 1892: 201; Konow 1898: 248; Froggatt 1901; 1070; Schulz 1906: 83–84. (Synonymised, with *macleaii* by Froggatt 1918: 671.)

Philomastix glaber : Froggatt 1890b: 696; Froggatt 1893: 201; Froggatt 1901: 1070, Plate; Froggatt 1907: 73, Plate XI; Froggatt 1918: 671.(Misspelling of *glabra*).

Female.—Body length 12.0–14.3 mm. Forewing length 12.2–13.7 mm. Distance between antennal sockets 2.2–2.6 times diameter of anterior. Antenna (Fig. 27) 17–19-segmented; apical 2–3 segments sometimes fused so that antenna apparently 15–18-segmented. First flagellar segment

2.5–2.9 times longer than wide. Second flagellar segment 1.6–1.9 times wider apically than basally. Mesoscutellum usually with posterolateral tubercles (Figs. 30–34); anterodorsal surface distinctly (Fig. 36) or weakly (Fig. 35) concave. Mesepisternal tubercle strong (Fig. 38). Posterolateral margin of first abdominal tergum weakly curved (Fig. 37) or straight, spiracle separated from margin by a distance 0.9–1.1 times maximum diameter of spiracle. Ovipositor sheath not posteromedially dentate (Fig. 46). Lancet as in Figs. 39–42, about 5 ctenidia terminating in dorsal tooth.

Flagellum orange-yellow. Mid lobe of mesoscutum usually with large, brown macula occupying more than half of length of lobe (Fig. 62); mid-lobe sometimes uniformly orange-yellow. Lateral lobe of mesoscutum with large, dark brown to black macula occupying most of length of lobe. Mesepisternum usually with broad, brown band adjacent to sternopleural suture. Mesosternum usually brown to anterior margin and sternopleural sulcus, sometimes entirely orange-yellow. Metascutum brown to dark brown, usually distinctly darker than cenchri. Forewing (Fig. 47) with narrow, transverse, brown band; cell 1M rarely completely brown. Abdomen predominantly dark coloured with some metallic reflections. Abdominal tergum 1 dark brown to black. Tergum 2 brown to black or metallic blue, on each side with large, cream, macula. Terga 3 and 4 dark brown, black or metallic blue, with smaller, cream lateral maculae. Terga 5, 6 and 7 each with large, cream, lateral macula; maculae narrowly separated by dark brown or black, or contiguous. Tergum 8 anteriorly dark brown to metallic blue (usually concealed by preceding tergum), posteriorly cream. Tergum 9 dark brown to black. Abdominal sterna 1 and 2 at least in part yellow or cream. Sterna 3–6 dark brown to black. Ovipositor sheath orange-yellow, with or without dark brown markings.
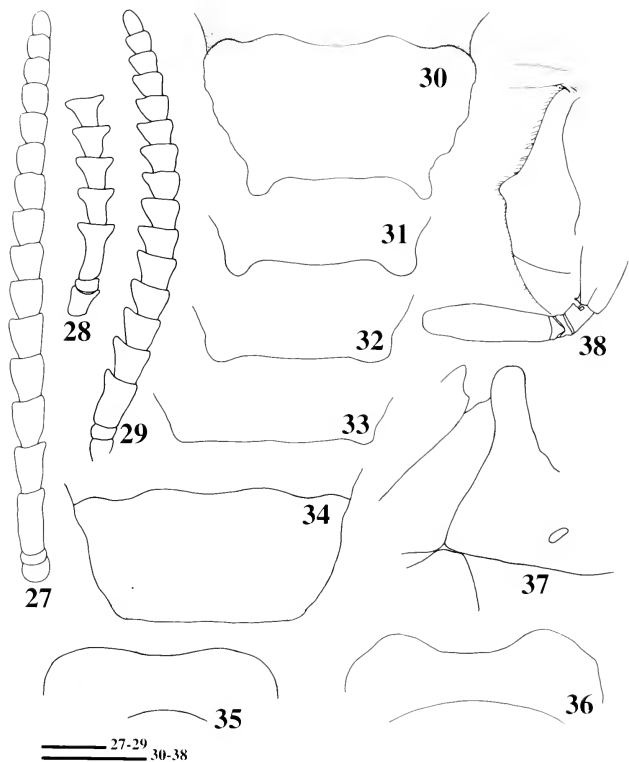
Figs. 27–38. *Philomastix macleaii*: 27, female antenna; 28, male antenna, basal antennomeres, frontal view; 29, male antenna, lateral view; 30–34, mesoscutellum, dorsal view, variation in shape; 35, 36, mesoscutellum, variation in surface contour as seen from rear of insect; 37, lateral panel of first abdominal tergum; 38, mesepisternum, profile. Scale lines = 1.0 mm.

Male.—Body length 11.0–12.8 mm. Forewing length 7.4–11.4 mm. Distance between antennal sockets 1.0–1.3 times diameter of anterior ocellus. Antenna (Figs. 28, 29) 18–21-segmented; apical 2 segments sometimes fused (occasionally without trace of sutures) so that antenna apparently 17–21-segmented. First flagel-
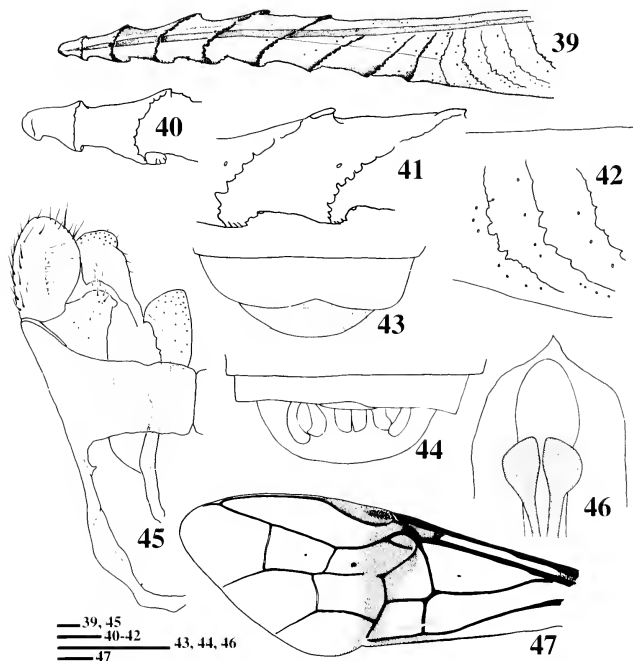
Figs. 39–47. *Philomastix macleaii*: 39–42, lancet; 43, 44, apex of male abdomen, dorsal view; 45, male genitalia, dorsal view; 46, apex of ovipositor sheath, posteroventral view; 47, forewing. Scale lines = 0.1 mm for 39–42, 45; = 1.0 mm for 43, 44, 46, 47.

lar segment 1.2–1.6 times longer than wide. Second flagellar segment 1.9–2.4 times wider apically than basally. Mesoscutum and mesepisternal tubercle as in female. Tergum 8 posteriorly with shallow emargination (Fig. 43, 44). Genitalia as in Fig. 45, paramere broad, gonolacinia not strongly hooked, penis valve apically rounded.

Clypeus and labrum orange-yellow.

Mesoscutum entirely brown to dark brown (Fig. 63). Abdominal terga 5 and 6 with orange-yellow, lateral macula. Tergum 7 with lemon yellow, lateral macula.

Types.—*P. macleaii*: holotype female, "Australia" (UMO; examined). *P. glabra*: 4 syntypes, "Australasia," Dunoon, Richmond River (ANIC, on permanent loan from Macleay Museum, University of Sydney, examined).

Other material examined.—Queensland: 1 male, Mt William, Eungella National Park, 1100–1200 m,19. IV. 1979, G. B. Monteith (QMBA); 1 male, Olmara Hills, via Dalrymple Heights, 1000m, 5. IV. 1975, D. K. McAlpine (AMSA); 1 female, Eungella, 25. IV. 1931, W. A. McDougall (QDPI); 1 female, Three Moon Creek, Kroombit Tops, 3–4 II. 1984, G. B. Monteith, C. Hagen, D. Yeates (QMBA); 1 female, Kroombit Tops, 1000–1100 m, 22–26. II. 1982, G. B. Monteith, G. Thompson, D. Yeates (QMBA); 1 female, Forest Station, Bulburin State Forest, 600 m, 12–13. IV. 1974, I. D. Naumann (UQIC); 2 females, Imbil, 13. V. 1937, 30. III. 1938, A. R. Brimblecombe (QDPI); 1 female, Palmwoods, 15. IV. 1911, Miss Ede (QMBA); 1 female, Montville, C. Deane (UQIC); 1 female, 6 males, Mt Kiangarow, Bunya Mountains, 27. I.1993, K. J. and C. L. Lambkin (QMBA, ANIC); 1 female, Bunya Mountains National Park, 11–13. XII. 1979, M. Schneider (UQIC); 1 female, Mt Glorious, 4. IV. 1959, K. H. L. Key (ANIC); 1 female, same locality, II. 1960, J. Bryan (UQIC); 2 females, same locality, 853 m, 13. III. 1960, R. Straatman (ANIC); 1 female, 1 male, same locality, 5–8. II. 1961, 10. IV. 1962, J. L. and M. Gressitt, Malaise trap (BPBM, USNM); 2 females, same locality, 17. I. 1963, T. Brooks (BPBM, USNM); 1 female, same locality, 1. II. 1968, H. McDougall (UQIC); 1 male, Mt Tenison-Woods, 4. II. 1983, G. Daniels (UQIC); 1 female, Highvale, 12. III. 1960, A. Cameron (UQIC); 1 female, Brisbane, 24. III. 1929, L. F. (MVMA); 1 male, same locality, III. 1953, L. W. Rule (UQIC); 5 females, Brookfield, 30. III. 1990, 2. IV. 1990, 10. IV. 1993, 20. IV. 1994, J. Grigg (UQIC, ANIC); 1 male, Toowoomba, 30. XII. 1917, J. A. Bock (UQIC); 1 female, Mt Tamborine, 1893, C. Wild (QMBA); 1 female, same locality, 20. II. 1911, W. W. Froggatt (ANIC); 1 female, same locality, 1923, W. H. Davidson (QMBA); 1 female, same locality, 21. II. 1927, H. Hacker (QMBA); 1 female, same locality, C. Deane (UQIC); 1 female, same locality (QDPI); 1 female,

Boonah, 5. IV. 1948 (QDPI); 1 female, Canungra, 7. IV. 1928 (QDPI); 1 female, Cunningham's Gap, 800m, R. Eastwood (UQIC); 1 female, same locality, III. 1972, R. Baldwin (QMBA); 1 female, 1 male, Beechmont, 1. II. 1972, A. and G. Daniels (AMSA); 1 male, Mt Huntley, 1250 m, 29–30 I. 1993, G. B. Monteith (QMBA); 1 male, Bald Mountain, 1219 m, 28–31 I. 1972, 1. D. Naumann (UQIC); 3 females, Upper Nerang, III. 1891, H. Tryon (QMBA, QMBA); 1 female, Upper Currumbin, 27. IV. 1932, L. Franzen (MVMA); 3 females, 1 male, McPherson Range, XI. 1928, A. J. Turner (MVMA); 1 male, same locality, H. Tryon (QDPI); 6 females, Lamington National Park, (some labelled 300 feet = 914 m), 2–3. I. 1921, 26–27. II. 1921, 1–11. III. 1921 (QMBA); 7 females, same locality, XII. 1921, H. Hacker (QMBA, ANIC); 2 males, same locality, 900–1000m, 16–18. II. 1964, J. Sedlacek (BPBM); 1 female, same locality, 930 m, 3 II. 1983, W. C. Paine (ANIC); 2 females, same locality, 914 m, 6–7. III. 1980. H. E. Evans, A. Hook (UQIC); 1 female, Binna Burra, I. 1943 (QDPI); 3 females, 2 males, Springbrook, 1930, R. Blackwood (MVMA, ANIC); 1 female, same locality, 2. XI. 1961, I. C. Cunningham (UQIC).New South Wales: 1 female, 2 males, Mt Clunie, 16. XII. 1972, I. D. Naumann (UQIC); 4 females, Tweed River, 1897 and no date (BRI, USNM, BMNH); 1 female, same locality, 1920, W. W. Froggatt (BMNH); 1 female, Wiangaree State Forest, 12. II. 1978, K. Walker (UQIC); 2 males, Richmond River (BRI); 1 male, Huonbrook, 2. III. 1964, D. K. McAlpine (AMSA); 6 females, 1 male, Glen Innes, 17 II. 1974, M. S. Moulds (AMSA, ANIC); 1 female, same locality, 19. I. 1975, R. Gallagher (BRI); 2 females, Platypus Flat camp, Wild Cattle Creek State Forest, 7 IV. 1993, C. Reid (ANIC); 1 female, 1 male, Guyra, II. 1949, A. Dyce (ANIC); 2 females, Ulong, III. 1920, W. Heron (AMSA); 11 females, Brooklana, 1929, W. Heron (BMNH, AMSA, ANIC); 1 female, Coffs Harbour, 11. I. 1950, F. D.

(MVMA); 11 females, Dorrigo, W. Heron (BMNH, MVMA, SAMAA, AMSA); 1 female, same locality, 914 m, G. Heron (USNM); 2 females, same locality (QMBA, BMNH); 1 male, same locality, 914 m, 17. II. 1932, P. J. Darlington (USNM); 1 male, same locality, 12 II. 1968, D. H. Colless (ANIC); 1 female, same locality, 14. II. 1981, D. A. Doolan (AMSA); 1 female, same locality, 13. II. 1984, L. Masner (CNC); 4 females, 1 male, Deer Vale, 12–13. I. 1931, 13. I. 1933, A. N. Burns (MVMA); 2 females, same locality, 30. I. 1972, G. Daniels (AMSA); 1 female, 4 males, Ebor, I. 1934, F. E. Wilson (MVMA, ANIC); 3 females, same locality, 12. XII. 1962, T. V. Bourke (BRI); 2 females, 3 males, Armidale, 5. II. 1915 (QMBA); 3 females, Bellangry, 2. V. 1894, W. W. Froggatt (ANIC, BRI, MVMA, CNC); 4 females, Hanging Rock, 7. I. 1955, K. M. Moore (FCNI); 1 female, Elands, 30. I. 1928 (BRI); 1 female, Comboyne Scarp, near Upper Lansdowne, 6. IV. 1987, D. K. McAlpine, S. Day, R. de Keyzer (AMSA); 1 female, Dingo State Forest, 26–27. II. 1981, G. and T. Williams (AMSA); 1 female, Bay's Hill, Taree, 28. III. 1992, G. Williams (AMSA); 9 females, 2 males, Tuncurry, 21 III. 1931, 15–25. III. 1932, no date, J. Parkes (AMSA, ANIC); 1 female, Upper Allyn River, 6. IV. 1958, R. Mackay (AMSA); 1 female, Upper Allyn, near Eccleston, 10 III. 1970, D. K. McAlpine, G. Holloway (AMSA); 1 female, 1 male, same locality, 26. II. 1970, D. K. McAlpine (AMSA); 1 female, same locality, 16. II. 1967, D. K. McAlpine (AMSA); 6 females, Maitland, 1892, W. W. Froggatt (ANIC, MVMA, USNM, BMNH); 1 female, Olney State Forest, 15. III. 1986, J. Grigg (UQIC); 5 females, Ourimbah, IV. 1904, S. W. Jackson (AMSA); 1 female, Narara, 23 I. 1911 (AMSA); 1 female, same locality, 2. III. 1950, P. C. Hely (BRI); 2 males, Upper Colo, 10. III. 1990, G. R. Brown, M. A. Terras (BRI); 4 females, 8 males, Mt Wilson, 4. I. 1931, A. N. Burns (MVMA); 1 female, same locality, 7 II. 1959, D. K. McAlpine (AMSA); 1 female, same locality, II. 1921 (AMSA); 1 male, same locality, 1067 m, I. 1932, P. J. Darlington (USNM); 1 female, Hartley Vale, 29. III. 1975, G. Daniels (AMSA); 3 females, Mt York, 21. III. 1964, D. K. McAlpine (AMSA, ANIC); 2 males, Katoomba, 26. I. 1955, K. M. Moore (FCNI); 2 females, 1 male, same locality, 21. II. 1969, G. Hardy (AMSA); 2 females (with eggs), Woodford, 28. II. 1984, M. Hill (BRI); 1 female, 2 males, Beecroft, 18. II. 1968, O. M. Williams (BRI, ANIC); 2 females, same locality, 18. III. 1967, C. E. Chadwick (BRI, ANIC); 5, females, Glenbrook, III. 1994, L. Turton (BRI, ANIC); 1 female, 2 males, Lane Cove, 27. IV. 1946, 30. III. 1947, 3. IV. 1948 (AMSA); 1 male, Sydney, 13. III. 1932, G. A. Waterhouse (MVMA); 1 female, same locality, III. 1949, A. Dyce (ANIC); 1 female, same locality, III. 1977, D. Clyne (ANIC). 1 male, Heathcote, 20. III. 1952, L. Cascysand (BRI); 1 female, Heathcote National Park, 24. IV. 1994, Cowdrey (AMSA); 2 males, Mt Keira, 23. II. 1983, G. A. Holloway (AMSA); 1 male, Jamberoo Mtn, 16. II. 1963, C. E. Chadwick (BRI); 1 male, Jamberoo, 11. I. 1950 (AMSA). Unlocalised: 1 female, 1 male, W. Heron (BMNH); 2 females, 1 male (QDPI); 1 female (MVMA); 3 females, 1 male (UQIC); 1 female (QMBA); 1 female (ANIC).

Distribution.—See Fig. 76. Several females in the ANIC and the BMNH are labelled "Brooklana Sydney." Since Brooklana and Sydney are approximately 400 km apart, clearly mislabelling has occurred. Reliably labelled specimens indicate that *P. macleaii* occurs at both Brooklana and Sydney. *P. macleaii* was not recorded from Victoria by Bruzzese (1980) in a survey of insects on *Rubus*.

Larval host plants.—Rosaceae: *Rubus moluccanus* L. (Froggatt 1893); *Rubus rosifolius* Smith.

Discussion.—There is some variation in wing venation. In the forewing, R1 may continue beyond the junction with Rs. In the hindwing cross-vein m-cu may be
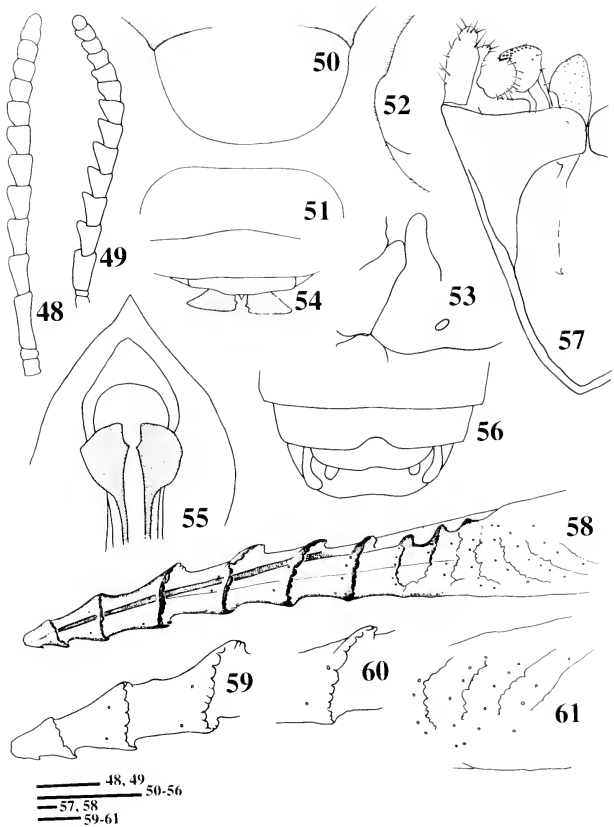
Figs. 48–61. *Philomastix xanthophylax*: 48, female antenna; 49, male antenna; 50, mesoscutellum, dorsal view; 51, mesoscutellum, surface contour as seen from rear of insect; 52, mesepisternum, profile; 53, lateral panel of first abdominal tergum; 54, apex of ovipositor sheath, dorsal view; 55, same, posteroventral view; 56, apex of male abdomen, dorsal view; 57, male genitalia, dorsal view; 58–61, lancet. Scale lines = 1.0 mm for 48–56; = 0.1 mm for 57–61.
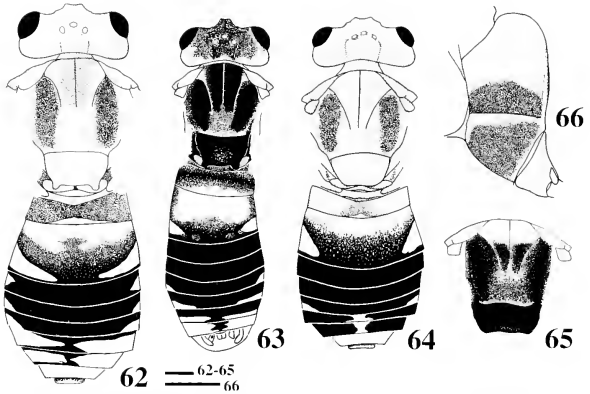
Figs. 62–66. *Philomastix* spp.: 62, *P. macleaii*, female, dorsal view; 63, *P. macleaii*, male, dorsal view; 64, *P. nancarrowi*, female, dorsal view; 65, *P. nancarrowi*, male thorax (part), dorsal view; 66, *P. nancarrowi*, female mesepisternum, lateral view. Scale lines = 1.0 mm.

present or absent. The mesoscutellar tubercles are usually strong (Figs. 30, 31) but may be weak (Fig. 32), absent on one side (Fig. 33) or absent altogether (Fig. 34). Cell 1M is usually at least in part hyaline proximally, but in the female from Eungella cell 1M is entirely dark and the infuscation extends to cell R.

Philomastix xanthophylax Naumann and Groth, sp. n.
(Figs. 1, 48–61, 67–74, 76)

Female.—Body length 9.0–12.0 mm. Forewing length 9.4–11.5 mm. Distance between antennal sockets 2.2–2.6 times greater than diameter of anterior ocellus. Antenna (Figs. 48, 67) 14–16 segmented;
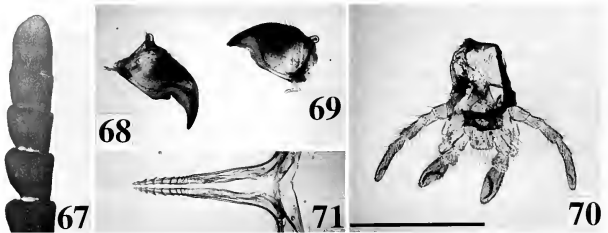
Figs. 67–71. *Philomastix xanthophylax*: 67, female, apical antennomeres; 68, left mandible; 69, right mandible; 70, labium, maxilla; 71, lancets, ventral view. Scale line = 1.0 mm, for 68–70; see 48, 58 for scale to 67, 71.
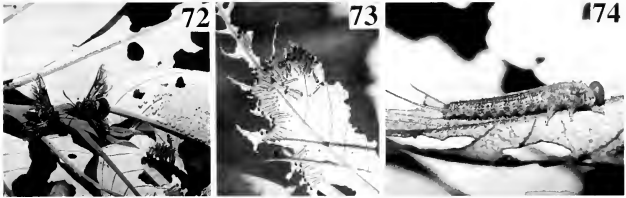
Figs. 72–74. *Philomastix xanthophylax* on *Alphitonia excelsa*; 72, two adult females, one guarding egg mass, other guarding batch of first instar larvae; 73, batch of first instar larvae; 74, third instar larva. Adult sawflies in 72 each approximately 9.5 mm long; larvae in 73, 74 approximately 5 and 17 mm long respectively.

apical 2–5 segments sometimes fused so that antenna apparently 12–13-segmented. First flagellar segment 2.9–3.0 times longer than wide. Second flagellar segment 1.8–1.9 times wider apically than basally. Mesoscutellum without posterolateral tubercles (Fig. 50); anterodorsal surface more or less flat (Fig. 51). Mesepisternal tubercle weak (Fig. 52). Posterolateral margin of first abdominal tergum weakly curved (Fig. 53) or straight, spiracle separated from margin by a distance 1.2–1.3 times maximum diameter of spiracle. Ovipositor sheath posteromedially dentate (Figs. 54, 55). Lancet as in Figs. 58–61, 71, about 8

ctenidia terminating in dorsal tooth, antior teeth strong.

Flagellum black (Fig. 1). Mid lobe of mesoscutum orange-yellow. Lateral lobe of mesoscutum orange-yellow, sometimes with small, brown macula less than half as long as lobe. Mesepisternum without brown band adjacent to sternopleural suture. Mesosternum brown, with orange-yellow band along anterior and lateral margins. Metascutum and cenchri orange-yellow. Forewing with narrow, transverse, brown band; cell 1M not completely brown. Abdomen entirely orange-yellow.
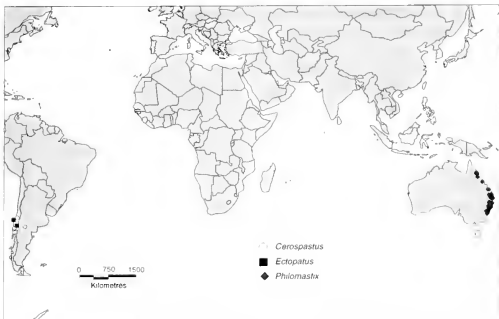
Male.—Body length 7.3–8.9 mm. Fore-

Fig. 75. Distribution of Philomastiginae: world distribution of *Philomastix*, *Cerospastus* and *Ecopatus*.
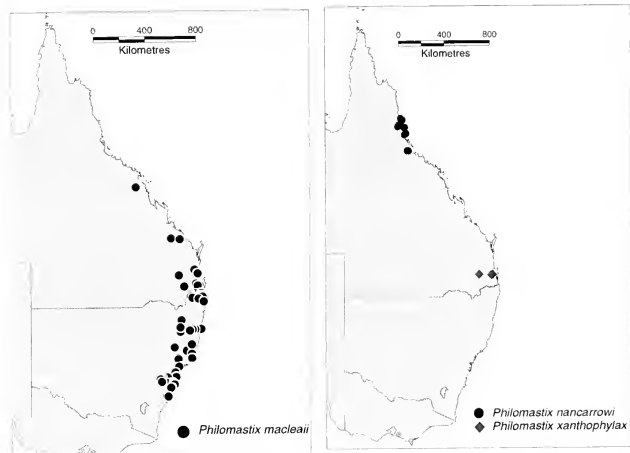
Fig. 76.   Australian distribution of *Philomastix nancarrowi*, *P. macleaii* and *P. xanthophylax*.

wing length 6.5–8.8 mm. Distance between antennal sockets 1.3–1.7 times greater than diameter of anterior ocellus. Antenna (Fig. 49) 15-segmented. First flagellar segment 1.7–1.8 times longer than wide. Second flagellar segment 2.0–2.1 times wider apically than basally. Mesoscutellum without posterolateral tubercles; dorsally slightly concave. Mesepisternal tubercle weak. Abdominal tergum 8 posteriorly with deep emargination (Fig. 56). Genitalia as in Fig. 57, paramere slender, gonolacinia strongly hooked, penis valve apically rounded.

Clypeus and labrum lemon-yellow. Mid-lobe of mesoscutum orange-yellow. Lateral lobe of mesoscutum entirely brown to dark brown. Abdominal terga 5 and 6 without orange-yellow, lateral maculae. Tergum 7 with lemon-yellow, lateral macula.

Material examined.—Holotype female,

27.28S 151.56E, 10 km N Toowoomba, Queensland, 12. IV. 1992, H. Groth (ANIC). Paratypes: Queensland: 2 females, same data as holotype (ANIC, HGCN); 8 females, same locality and collector as holotype, 3. IV. 1991, 1. III. 1992, 29. III. 1992, 16. III. 1992 (ANIC, BMNH, USNM, HGCN); 4 males, same locality and collector as holotype, but labelled "Highfields," reared from eggs collected V. 1992, emerged as adults 30. III. 1993, 22. IV. 1993, 24. IV. 1993, 26. IV. 1993 (ANIC, HGCN); 3 females, 4 males, Brookfield, 22. III. 1994, 29. III. 1994, 3. IV. 1994, J. Grigg (UQIC, ANIC); 2 females, Bellbird Park, Brisbane, IV. 1994, R. Nattrass (QMBA).

Etymology.—The species name is derived from the Greek words *xanthos*, yellow or golden, and *phylax*, a guard, with reference to the maternal guarding behaviour common to all species of *Philomastix*.

Distribution.—See Fig. 76.

Larval food plants.—*Alphitonia excelsa* (Fenzl) Benth. (Rhamnaceae).

Discussion.—There is conspicuous variation in wing venation within the type series. In the forewing: (1) R1 sometimes continues as a short spur beyond the junction of R1 and Rs; (2) there may be one, two or no cross-veins between C and R; (3) there may be an incomplete cross-vein distal to 3r-m; and (4) a diagonal vein sometimes defines a small, triangular cell in the anterobasal corner of cell 3M. In the hindwing cross-vein m-cu is rather variable: (1) it may be present or absent; (2) it may curve smoothly into CuA, in which case there is no distal abscissa of CuA; (3) it may join M before or after the junction of cross-vein 2r-m and M.

CEROSPASTUS Konow

Cerospastus Konow 1899: 404–405; Konow 1905: 36–37; Rohwer 1911: 76. Benson 1935: 224. Benson 1938: 379; Pagliano and Scaramozzino 1990: 58; Smith 1990: 21–23; Abe and Smith 1991: 18. Type species: *Cerospastus volupis* Konow (by monotypy).

Ceratospastus: Schulz 1906: 84 (unjustified emendation).

Female.—Vertex conspicuously setose. Face with some fine microsculpture. Malar space narrower than diameter of anterior ocellus. Antenna (Fig. 3) 14-(-20, Smith 1990) segmented, weakly serrate, weakly clavate. Right mandible simple (Smith 1990). Maxillary palp (Fig. 9) 6-segmented, filiform, without sensory cup. Labial palp 4-segmented, without sensory cup. Labium tri-lobed. Thorax dorsally conspicuously setose. Notauli, median mesoscutal line deeply impressed. Mesoscutellum not swollen, posterior margin visible from above. Mesepisternum without tubercle. Metascutellum not band like. Forewing (Fig. 4) with closed radial cell and 4 cubital cells; median and second cubital cells each with nygma. Abdominal terga not conspicuously setose. Second tergum predominantly fine transversely striate. Cer-

cus present. Ovipositor sheath not strongly expanded posteriorly.

Male.—Antenna 20-segmented (19–21 according to Smith 1990), strongly serrate. Median cell of forewing without nygma. Eighth tergum posteriorly with very deep, broad emargination (Fig.7).

Cerospastus volupis Konow
(Figs. 3, 4, 7, 9, 76)

Cerospastus volupis Konow 1899: 404; Konow 1905: 37; Rohwer 1911: 76; Smith 1978: 160; Oehlke and Wudowenz 1984: 419; Pagliano and Scaramozzino 1990: 58; Smith 1990: 22–23; Smith 1993: 11.

Female.—Body length 10.0–11.5 mm. Forewing length 11.0–12.0 mm. Distance between antennal sockets 1.2–1.7 times greater than diameter of anterior ocellus. First flagellar segment 2.5 times longer than wide. Second flagellar segment 1.7–2.0 times wider apically than basally. Mesoscutellum without posterolateral tubercles, posterior margin convex; dorsal surface weakly convex. Mesepisternum without tubercles. Posterolateral margin of first abdominal tergum smoothly curved or slightly angulate, spiracle separated from margin by a distance 0.5–1.3 times maximum diameter of spiracle. Ovipositor sheath not posteromedially dentate. Lancet as in Smith (1990: Fig. 34).

Flagellum very pale brown, scape and pedicel orange-yellow. *Either:* head predominantly orange-yellow; upper frons with transverse brown joining upper extremities of compound eyes and encompassing ocellar triangle; *or* most of frons, lowermost gena, vertex medially brown. Mandibles brown, remaining mouthparts orange-yellow. Thorax and legs predominantly orange-yellow to cream. Mesonotum orange-yellow, with brown maculae occupying either most of length of mid and lateral lobes or only anterior half of lateral lobe. Cenchri, metascutum, most of mid and hind tarsi, first abdominal tergum and sometimes also ventral surfaces of thorax brown to pale brown. Remain-

der of abdomen orange to yellow. Wings hyaline with faint yellow tinge.

Male.—Body length 7.5 mm. Forewing length 7.3 mm. distance between antennal sockets 0.7–0.8 times greater than diameter of anterior ocellus. First flagellar segment 1.3 times longer than wide. Second flagellar segment 2.4 times wider apically than basally. Mesoscutellum, mesepisternum as in female. Genitalia as in Smith (1990: Fig. 31).

Head, thorax predominantly black to dark brown. Antenna pale brown. Clypeus orange-brown. Mandibles red-brown. Maxilla, labium orange-yellow. Spiracular lobe of pronotum orange-yellow. Legs orange to yellow. Abdomen dorsally dark brown to brown, ventrally orange to yellow. Wings hyaline with faint brown tinge.

Type.—Lectotype female (designated by Smith 1990), Valdivia, Chile, 1897, Lossberg (DEIC; examined).

Other material examined.—1 female, 1 male, Parque Nac. Conguillio. Province Temuco, Chile, 31. XII. 1976, O. Puentes (USNM).

Distribution.—Known only from a few specimens from central western Argentina (Neuquén Province) and central Chile (Cautin, Malleco, Maule and Valdivia).

Larval host plant.—*Nothofagus* sp. (Fagaceae) (Smith 1990).

ECOPATUS Smith

Ecopatus Smith 1990: 23–24. Type species: *Ecopatus penai* Smith (by original designation and monotypy).

Female.—Vertex almost bare. Face almost completely smooth. Malar space very slightly wider than diameter of anterior ocellus. Antenna (Fig. 2) 18-segmented (20–21 according to Smith 1990), filiform, not clavate. Right mandible with 2 inner teeth. Maxillary palp (Fig. 8) 6-segmented, 4th segment apically distinctly wider than other segments; apical seg-

ment without sensory cup. Labial palp 4-segmented, apical segment without sensory cup. Labium tri-lobed. Thorax dorsally almost bare of setae. Notauli, median mesoscutal line shallow. Mesoscutellum not swollen, posterior margin visible from above. Mesopleuron without tubercle. Metascutellum not band like. Forewing (Fig. 5) with open radial cell and 2–3 cubital cells; median and second cubital cells each with nygma. Abdominal terga dorsally not conspicuously setose. Second tergum with faint, reticulate microsculpture. Cercus present. Ovipositor sheath not strongly expanded posteriorly.

Male.—Unknown.

Ecopatus penai Smith
(Figs. 2, 5, 6, 8)

Ecopatus penai Smith 1990: 24–25.

Female.—Body length 6.0–7.0 mm. forewing length 7.7 mm. distance between antennal sockets 2.3–2.4 times greater than diameter of anterior ocellus. first flagellar segment 3.6–3.7 times longer than wide. Second flagellar segment 1.1–1.2 times wider apically than basally. Mesoscutellum without tubercles; anterodorrsal surface convex. Mesepisternum without tubercle. Posterolateral margin of first abdominal tergum sinuate (Fig. 6), spiracle separated from margin by distance 4.6 times maximum diameter of spiracle. Ovipositor sheath not medially dentate. Lancet as in Smith (1990: Fig. 39).

Head, thorax, abdomen predominantly dark brown to black. Following orange, orange-yellow to cream: scape or scape and pedicel, frons just above and below antennal sockets, clypeus, mandible (excluding red-brown teeth), maxilla, labium, posterior margin of pronotum, tegula, axillar sclerites, large macula anterodorsal to extremity of mesepisternum, legs (except pale brown extremities of tarsi), abdomen ventrally. Wings uniformly strongly brown tinged.

Types.—Holotype female, Caramavida,

Province Arauco, 5–10. II. 1953, L. Peña (USNM; not seen). Paratypes: 2 females, same data as holotype (not seen); 1 female, Curacautin, Rio Blanco, 27–31. I. 1950, L. Peña (USNM) (examined).

Distribution.—Known only from a few specimens from central Chile (Araucan and Curacautin Provinces).

Larval host plants.—Unknown.

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A New Species of *Ibalia* from Borneo, with a Revised Phylogeny and Historical Biogeography of Ibaliidae (Hymenoptera: Cynipoidea)[1]

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Abstract.—*Ibalia kalimantanica* Liu from eastern Kalimantan, Borneo, is described here as a new species. Reanalysis of a previously published character matrix of the family Ibaliidae with the new species included shows that *I. kalimantanica* belongs to the subgenus *Tremibalia* and is the sister species to the clade of ((*I.mirabilis*, *I. japonica*), *I. hunanica*). Biogeographical analysis of the expanded data set strengthened support for an earlier hypothesis concerning the historical biogeography of the Ibaliidae postulating early radiation of the family in the eastern Palaearctic—Oriental region. The separation of the *I. kalimantanica* clade is suggested to have been caused by changes of land area configuration in Southeast Asia as a result of global sea level changes during late Oligocene to early Miocene.

The Ibaliidae constitute a small family of parasitic cynipoids comprising nineteen known species, of which all but one are restricted in the Northern Hemisphere. The species belong to the three genera *Eileenella* Fergusson, *Heteribalia* Sakagami and *Ibalia* Latreille. They parasitize siricid woodwasps, both in conifers and hardwoods, and some species of *Ibalia* have been used in the biological control of siricid pests in conifer plantations. Ibaliidae is of interest owing to its near-basal phylogenetic position within the superfamily Cynipoidea (Ronquist 1995). Recently, Liu & Nordlander (1992, 1994) studied the North-American species of the Ibaliidae and presented a review of the world species of the family, and Nordlander et al. (1996) studied their phylogeny and historical biogeography. In this study, a new species of *Ibalia* Latreille is described from

the tropical rain forests of eastern Kalimantan, Borneo, Indonesia. The character matrix of Nordlander et al. (1996) has been reanalyzed in order to determine the phylogenetic position of the new species in relation to other *Ibalia* species, and to investigate whether the topology of the phylogenetic tree of the genus would be thus affected.

Species of *Ibalia* have previously been described only from the Northern Hemisphere; the new species represents the first tropical species of the genus. The only other tropical ibaliid species, *Eileenella catherinae*, is from New Guinea, and is the sister species to all other ibaliids (Fig. 2). Therefore, the phylogenetic position of the new *Ibalia* species will provide new evidence for testing the previous biogeographical scenario of Nordlander et al. (1996).

MATERIALS AND METHODS

Terminology used in this article follows that of Ronquist and Nordlander (1989) and Liu and Nordlander (1994).

Only a single female of the new species was available. The character-state coding of the new species was made in compari-

Table 1. Character states for *Ibalia kalimantanica*. Characters and character states are coded as in Nordlander et al. (1996), with the following addition of character state: Character 55. Sculpture of mesopleural speculum: (2) distinctly vertically costate with secondary irregular foveolate sculpture. The table is supplementary to the previously published matrix including all the other species.

Taxon	Character							
	1	6	11	16	21	26	31	36
I. kalimantanica	11???	11100	10100	01–00	0–011	00–10	00120	010–1

son with representatives of the genus *Heteribalia* Sakagami and each of the two subgenera of *Ibalia*, as well as of the outgroups Liopteridae and *Eileenella* Fergusson.

The characters and character coding were the same as in the previous cladistic analysis of the Ibaliidae (Nordlander et al. 1996). For characters 31, 34, 35, and 69, a polymorphic condition was coded as a separate, intermediate state and each step was given the weight 0.5, so that a change between non-polymorphic states would count as one step instead of two. Of the multi-state characters, characters 6, 45, 52, 63, 66, 67, and 80 were unordered; the others were ordered in the sequence 012. The only change in relation to the previous study was that an autapomorphy for *I. kalimantanica* required additional state for character 55 (see Table 1).

Methods used for phylogenetic and biogeographical analyses were in general as described in Nordlander et al. (1996), with some minor modifications. As in Nordlander et al. (1996), PAUP 3.1 were used for

Fig. 1. *Ibalia kalimantanica*, new species.

phylogenetic analysis, but less extensive options were adopted when calculating support indexes for the branches. Options for bootstrapping included heuristic search, random addition sequence, 1000 replications, and for each replication tree search options are simple addition sequence and tree bisection reconnection (TBR) swapping. The decay index (or Bremer support), the number of extra steps needed to break up the group, were obtained using branch and bound search and simple addition sequence. For biogeographical analysis, the previously defined distribution area Eastern Palaearctic + North-east Oriental was extended to include oceanic Southeast Asia, and defined as Eastern Palaearctic + Eastern Oriental. DIVA1.1 was used in the present study for historical reconstruction (Ronquist 1996, 1997). It is basically the same version (DIVA 1.0) used by Nordlander et al. (1996), but with some performance improvements (Ronquist 1996) that should not affect comparison of the results.

Ibalia (Tremibalia) kalimantanica Liu, new species
(Fig. 1)

Female.—Body length 10.0 mm. *Coloration:* Head yellow except eyes, upper face, and a narrow longitudinal median strip through lower face, which are black. Flagellomeres 4–10 of female antenna white to pale, contrasting with the remaining darker antennal segments. Pronotum pale yellow with anterior plate of pronotum medially, dorsal pronotal area entirely, and lateral pronotal area posteriorly black.

Table 1. Extended.

41	46	51	56	61	66	71	76	81
0–012	01111	00102	10100	0–011	11001	?100?	– – – –	– –

Mesothorax mainly black, a small area posteriorly on mesoscutum, mesopleural triangle entirely, and a broad transverse band across middle of scutellum yellow. Metathorax and propodeum black. Legs yellow with dorsal parts of coxa, trochanter, and femur yellow to brown. Metasoma pale yellow with three narrow, transverse to oblique, dark brown strips (Fig 1).

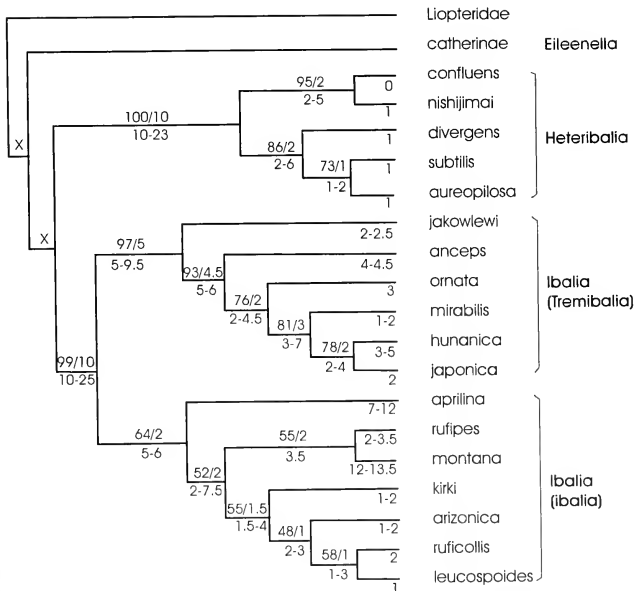*Head.*—Vertex rather weakly longitudi-

Fig. 2. Shortest tree of interspecific relationships in the Ibaliidae according to the previous analysis by Nordlander et al. (1996). Figures above and below branches as in Fig. 3.

nally carinate and with rather dense, appressed pubescence. Upper face completely rugose; antennal scrobes indistinctly delimited by a lateral carina and not distinctly depressed. Gena largely glabrate with shallow foveae, postero-ventrally distinctly costate. Eye length about 3.1 times length of malar space.

Antenna.—Female with 11 flagellomeres; 2nd flagellomere distinctly longer than 1st (F2/F1 = 4/3).

Mesosoma.—Pronotal crest without medial incision. Pronotum costate almost entirely, covered with dense, adpressed pubescence. Propleuron protruding strongly ventrally. Scutellar foveae rugose, separated by median carina. Posterior processes of scutellum raised weakly posteriorly. Distance between outer sides of posterior scutellar processes about 0.7 times maximum width of scutellum. Femoral groove of mesopleuron almost smooth with faint longitudinal carination ventrally; speculum vertically striate with secondary irregular foveolate sculpture. Metepisternum with vertical costulae. Anterolateral propodeal process distinct; posterior propodeal process low; lateral propodeal carina not elevated medially.

Wings.—Forewing subhyaline with wide dark strip along outer margin and distinct, narrow, dark band between

Rs+M and Cu1 (behind submarginal cell) along outer side of M. Areolet present and very small. Hindwing faintly fuscous along outer margin; with three hamuli.

Legs.—Anterior lateral crest of metacoxa rounded and low. Anterior mesotibial spur present. Anterior apical process of 2nd metatarsomere reaching to middle of 4th tarsomere.

Metasoma.—Metasoma as long as head and mesosoma combined. Tergum 8 with sparse hairs.

Male.—Unknown.

Biology.—Unknown.

Distribution.—Indonesia: E. Kalimantan, Borneo.

Type material.—Holotype, ♀, INDONESIA: Eastern Kalimantan, Kayan-Mentarang Natural Reserve, WWF Station, Lowland Dipterocarpus Forest (2°52'N, 115°49'E), Malaise Trap head, iii.1993 (D.C. Darling and U. Rosichon) (Museum Zoologi Bogor, Indonesia).

For a comprehensive comparison with other species of the family Ibaliidae, the character matrix of Nordlander et al. (1996) should be consulted. For identification, *I. kalimantanica* may be keyed out by introducing an additional couplet 3a following the second item of couplet 2 in Liu & Nordlander's (1994) key to the world species of *Ibalia*:

3a. Female antenna contrastingly colored with flagellomeres 4–10 white and the remaining segments dark. Upper face lacks regular sculpture. Speculum vertically striate. Posterior processes of scutellum posteriorly only weakly raised ... *I. kalimantanica* Liu, new species
–　　Female antenna evenly light yellow to dark brown throughout or becoming darker toward apex, but never with contrasting colors. Upper face longitudinally or transversely carinate at least in antennal scrobes. Speculum finely striolate longitudinally. Posterior processes of scutellum raised distinctly posteriorly 3

REVISED PHYLOGENY AND HISTORICAL BIOGEOGRAPHY OF IBALIIDAE

The sum of minimum and maximum possible lengths over all characters in the data matrix of Nordlander et al. (1996, Table 1) was 99 and 414 respectively. Parsimony analysis using the branch-and-bound algorithm of PAUP resulted in one optimal tree of length 149 (CI = 0.67, RI = 0.84). Compared with Nordlander et
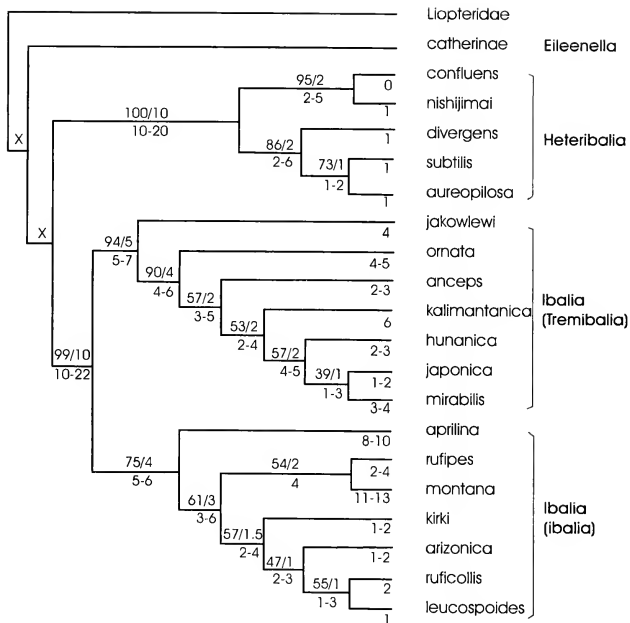
Liopteridae

catherinae — Eileenella

confluens ⎫
nishijimai ⎪
divergens ⎬ Heteribalia
subtilis ⎪
aureopilosa ⎭

95/2 2-5 | 0, 1

100/10 10-20

86/2 2-6

73/1 1-2 | 1, 1

X

jakowlewi ⎫
ornata ⎪
anceps ⎪
kalimantanica ⎬ Ibalia (Tremibalia)
hunanica ⎪
japonica ⎪
mirabilis ⎭

94/5 5-7 | 4

90/4 4-6 | 4-5

57/2 3-5 | 2-3

53/2 2-4 | 6

57/2 4-5 | 2-3

39/1 1-3 | 1-2

3-4

X

99/10 10-22

aprilina ⎫
rufipes ⎪
montana ⎪
kirki ⎬ Ibalia (Ibalia)
arizonica ⎪
ruficollis ⎪
leucospoides ⎭

75/4 5-6 | 8-10

54/2 4 | 2-4

61/3 3-6 | 11-13

57/1.5 2-4 | 1-2

47/1 2-3 | 1-2

55/1 1-3 | 2, 1

Fig. 3. Shortest tree of interspecific relationships in the Ibaliidae, obtained with the branch-and-bound algorithm of PAUP (length = 149, CI = 0.67, RI = 0.84). Shown above each branch in the tree is the support for the corresponding clade, measured as the percentage with which the clade appeared among the shortest trees in 1000 bootstrap replications of the analysis, followed by the decay index (or Bremer support). Below each branch are the minimum and maximum number of character changes along that branch. Clades marked 'x' were constrained to be monophyletic according to results of Ronquist (1995).

al.'s previous optimal tree (length = 141, CI = 0.67, RI = 0.85), the new tree is almost identical in terms of fitness. Compared with the earlier phylogeny of Ibaliidae (Fig. 2) as presented by Nordlander et al. (1996), the topology of the phylogenetic tree remained unchanged with the addition of *I. kalimantanica*, except for two local changes within the *Tremibalia* clade.

The first change concerns the relative relationship within the clade (*I. mirabilis* Yasumatsu, *I. japonica* Matsumura, *I. hunanica* Liu & Nordlander), and the other concerns the relative positions of *I. anceps* Say and *I. ornata* Belizin (Figs. 3, 4). The monophyly of *Ibalia* (*Ibalia*) became better supported after the inclusion of *I. kalimantanica* in the analysis, the bootstrap value
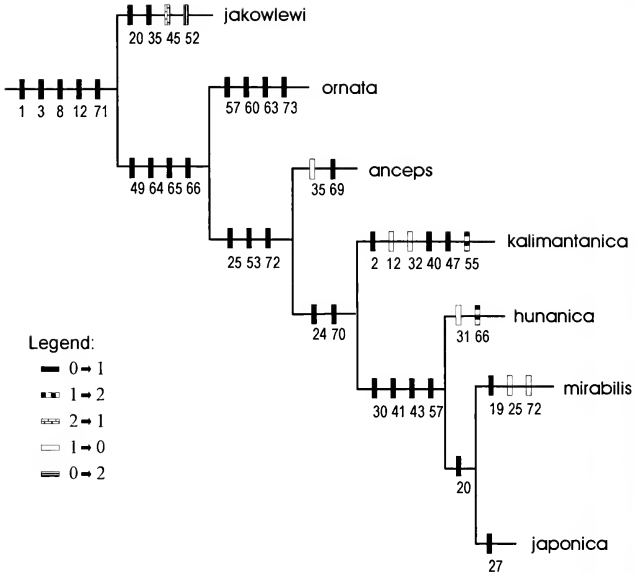
Fig. 4. The clade of *Ibalia* (*Tremibalia*) of the shortest tree with all character changes that could be mapped unambiguously.

increased from 64% to 72% and Bremer support from 2 to 4.

As a result of the changes in tree topology, the previously suggested Eocene-Oligocene separation of *I. anceps* (ca 33–34 MYA) in the subgenus *Tremibalia* is now one node further from the base of the tree (Nordlander et al. 1996). The origin of the Ibaliidae, based on node/branch distance calculation, is now estimated to be about 160 MYA, a negligible difference from the previous estimate of 150 MYA with regard to potential calculation errors. The estimated time for the origin of the Ibaliidae is still the Late Jurassic.

An exact search of the updated distribution matrix using DIVA 1.1 resulted in one single reconstruction of the distribution history requiring nine dispersals (Fig. 5). The present reconstruction postulates a center of origin for *Heteribalia* and *Ibalia* in the Eastern Palaearctic—North Oriental region, and is in complete accordance with that preferred by Nordlander et al. (1996, Fig. 7).

The separation of the *I. kalimantanica* clade probably resulted from a dispersal within the Oriental as early as in the end of Oligocene (29–24 MYA) and its subsequent isolation from its sister clade. The

E. catherinae

H. subtilis

H. aureopilosa

H. divergens

H. nishijimai

H. confluens

I. (T.) mirabilis

I. (T.) japonica

I. (T.) hunanica

I. (T.) kalimantanica

I. (T.) anceps

I. (T.) ornata

I. (T.) jakowlewi

I. (I.) aprilina

I. (I.) rufipes

I. (I.) montana

I. (I.) kirki

I. (I.) arizonica

I. (I.) ruficollis

I. (I.) leucospoides

Legend:
A = West Nearctic
B = East Nearctic
C = West Palaearctic
D = East Palaearctic
    and East Oriental
E = New Guinea
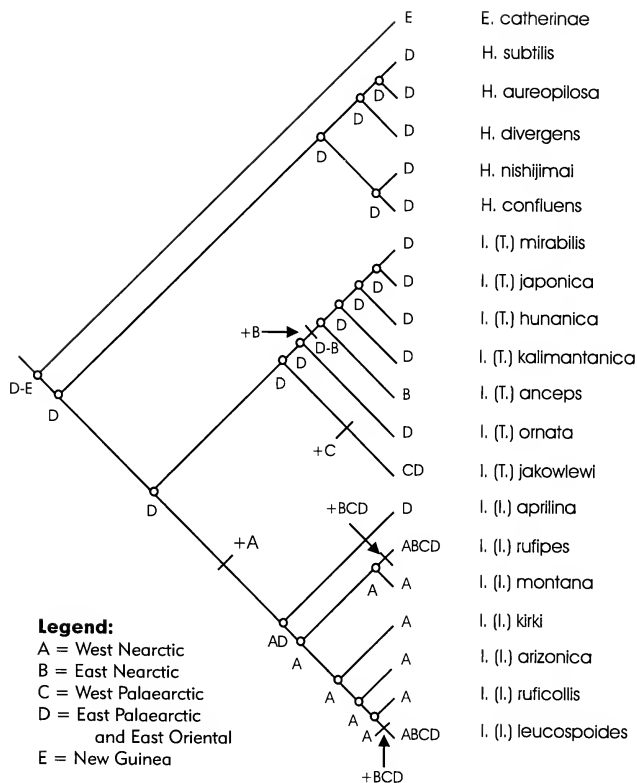
Fig. 5. Reconstruction of ancestral distribution of Ibaliidae using DIVA 1.1 resulted in one exact solution that requires nine dispersals. Dispersal events are indicated on the branches, and implied between-area vicariance events are indicated by hyphens in the ancestral distributions.

land area configuration of the Southeast Asia has varied greatly since late Oligocene as a result of global sea level changes (Heaney 1991). The global sea levels remained high from Palaeocene through Oligocene (65–30 MYA). By late Oligocene (29 MYA) there occurred a spectacular fall in sea level to about 250 m below the pres-

ent level, and it then recovered to present level by end of Oligocene (24 MYA). From then onwards the sea levels progressively rose, with minor drops, to about 220 m above the present level in the middle Miocene (13 MYA). This was followed by several cycles of fluctuating sea levels (Hutchison 1989). During times of low sea levels, Sumatra, Java and Borneo were part of a peninsula projecting south from continental Asia (often referred to as Sundaland) (Morley & Flenley 1987, Heaney 1991), facilitating the dispersal of the stem species of *I. kalimatanica* and its sister species from the continental Asia to Borneo, and the continuous ancestral distribution was subsequently split when sea level rose again. Although, any of these sea level cycles could have been responsible for the speciation of *I. kalimantanica*, the many autapomorphies of *I. kalimantanica* and the rather many synapomorphies for its sister group indicates that the event probably occurred rather early. Using the same dating method as in Nordlander et al. (1996), the vicariant event separating *I. kalimantanica* from its sister species was estimated as having occurred at about 21 MYA. This is in general accordance with the sea level recovery since late Oligocene from the late Oligocene dramatic drop, which could have facilitated the dispersal of the ancestral species.

ACKNOWLEDGMENTS

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Taxonomy, Mature Larva, and Observations on the Biology of *Gnamptopelta obsidianator* (Brullé) (Hymenoptera: Ichneumonidae, Ichneumoninae)

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Abstract.—The two nominal species in *Gnamptopelta*, *G. obsidianator* (Brullé) and **G. austrina (Cresson)**, do not merit separate species or subspecies status, and the latter is synonymized under the former; the genus is hence monotypic. Specimens reared from *Amphion floridensis* (B.P. Clark) (Lepidoptera: Sphingidae), probably attacked in captivity, represent the first verified host record for *Gnamptopelta*. A description of the mature larval exuviae is provided. Observations of the wasps in the field and in captivity suggest that *G. obsidianator* directs its host-searching to grapevines (*Vitis* spp.), and that its host range may not include all grapeleaf-feeding sphingids.

Gnamptopelta obsidianator (Brullé) is one of the largest ichneumonids in eastern North America and one of the most striking, with its black body, yellow antennae, and, in some southern populations, extensive reddish coloring of the head and anterior mesosoma. While it is commonly collected on the wing and is well represented in collections, no credible hosts have previously been reported. The genus is currently placed in the Trogini, subtribe Callajoppina; nearly all recorded callajoppine hosts are Sphingidae (Heinrich 1962). Heinrich (1977) noted that *G. obsidianator* frequents grapevines, which are the food plants for at least 10 sphingids in North America (Forbes 1948; Hodges 1971). Thus, guided by taxonomic inference and a few incidental observations, we set out to identify the hosts of *G. obsidianator* by rearing *Vitis*-feeding sphingids.

We also decided to use this opportunity to clarify the status of species within *Gnamptopelta* Hopper, in which two species, *obsidianator* (Brullé) and *austrina* (Cresson) were originally included. Sub-

sequent authors (Townes and Townes 1951; Heinrich 1962, 1977; Carlson 1979) have considered *austrina* to be a subspecies of *obsidianator*, although Heinrich (1977) hedged that the subspecies could be "ecologically differentiated species parasitizing 2 different hosts living on the same plant."

The *Gnamptopelta* specimens examined in this study are in the American Entomological Institute (Gainesville, Florida: AEIC) and the Florida State Collection of Arthropods (Gainesville, FL: FSCA).

TAXONOMY

Heinrich (1962) placed *Gnamptopelta* in the tribe Trogini, subtribe Callajoppina, which also contains the genera *Afrotrogus*, *Callajoppa*, *Catadelphus*, *Conocalama*, *Dinaetha*, *Holojoppa*, *Pepsijoppa*, *Stirojoppa*, *Tmetogaster*, *Tricyphus*, and *Yeppoona* (Ward and Gauld 1987; Yu and Horstman 1997). All reliable host records indicate that these genera parasitize only Sphingidae.

Hopper (1939) erected *Gnamptopelta* for two North American species, *Trogus obsidianator* Brullé and *Trogus austrinus* Cres-

son. These were distinguished on the basis of color: *G. austrina*, found in South Carolina, Georgia, and Florida, had the head and anterior mesosoma reddish while *G. obsidianator*, found in the remaining part of eastern North America west to the Rocky Mountains, had the entire body black except for the yellowish-white paraocular area. With the exception of Townes (1944), later authors (Townes and Townes 1951; Heinrich 1962, 1977; Carlson 1979) have treated *austrina* as a subspecies of *obsidianator*. Heinrich (1962) could not decide whether the taxa represented two species or a single species with two color forms. After studying the Florida ichneumonine fauna (Heinrich 1977), he concluded that for *Gnamptopelta*: 1) "*austrina* . . . occupies the peninsula of Florida except its most northern part, and that the uniformly black *obsidianator* occupies the entire eastern territory of continental North America, including the base of Florida"; 2) "Very sporadically, however, *obsidianator* also occurs in the territory of *austrina*, and likewise, sporadically, *austrina* is found in the southern parts of the territory of *obsidianator*"; 3) ". . .it also must be mentioned that "intergrades" between the 2 forms have never been found" (*op. cit.*, p. 285).

Our examination of over 550 *Gnamptopelta* specimens reveals that, contrary to Heinrich's assertions, intermediates do occur and all are found in Florida. Most of these individuals are found north of Ocala, in the northern third of the state (above 29°N). Black and intermediate specimens are found throughout the flight period (mid-February through mid-November); there is no sex bias in the color forms. An interesting series of eight males was collected at the American Entomological Institute in March and April of 1986 [AEIC]. Every variation is present, from uniformly black with no reddish markings to the extreme of an entirely reddish head, reddish anterior mesosoma, and reddish postpetiole. This series alone refutes the notion of two separate entities. We there-

fore place *austrina* as a junior synonym of *obsidianator* (**NEW SYNONYM**), noting a particularly apt remark that summarizes the past *Gnamptopelta* literature: ". . .too much time has been wasted on trying to assemble data, much of it illusory, to maintain already proposed names for subspecies" (Franclemont 1973).

All records to date indicate that *G. obsidianator* does not occur west of the front range of the Rocky Mountains. We have, however, seen one specimen from California ("Merced Co.; Los Banos National Wildlife Refuge, 4 mi. N. Los Banos; 12-vi-1981; D. Jamieson"; FSCA). It is uniformly black and identical to specimens from the northeastern part of the range. Queries of the major California collections have not revealed any more specimens from the West Coast. At this time, we consider the specimen to be mislabeled or perhaps the result of an import to the area.

MATURE LARVA OF *GNAMPTOPELTA OBSIDIANATOR*

Materials and Terminology.—The terminology of the cephalic sclerites of the mature larva is that of Gillespie and Finlayson (1983) and Short (1978), with modifications by Wahl (1990). The epistomal suture is the lateral groove between the anterior tentorial pits (Matsuda 1965). It is present as a distinct depression in mature ichneumonid larvae. Although the area is usually unsclerotized, a continuous sclerotized band extends across it in the Anomaloninae, Ichneumoninae, Metopiinae, and Pimplini (and isolated taxa in other subfamilies). Previous ichneumonid workers have referred to this area as the "epistoma," including in it the portion of the pleurostoma above the superior pleurostomal process. This use of "epistoma" should be eschewed. We suggest the following descriptive terms: a) epistomal suture unsclerotized; b) epistomal suture partially unsclerotized, medially incomplete (as in *Cryptus albitarsis* (Cresson); Short 1978: fig. 238); c) epistomal suture
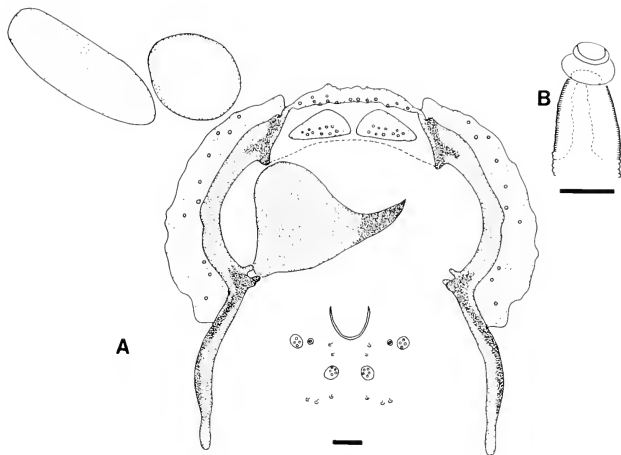
Fig. 1. Mature larva of *Gnamptopelta obsidianator*: (a) cephalic sclerites, (b) prothoracic spiracle. The scale lines represent 0.1 mm.

completely sclerotized forming an *epistomal band*.

Methods of larval preparation are those of Wahl (1989). Wahl's notation for larval preparations follows the museum acronym. It consists of his initials, the day, month, year, and a letter designating the individual preparation.

Description.—Epistomal band present, with 14 pores. Labral sclerite, hypostomal spur, stipital sclerite, labial sclerite, and prelabial sclerite, absent. Clypeolabral plates present and triangular in outline, not connected to epistomal band, and not joined or touching medially. Pleurostoma and hypostoma strongly sclerotized. Accessory pleurostomal area moderately sclerotized. Hypostoma straight, posterior end not elongate or upcurved. Accessory reticulate sclerotization prominent. Maxillary palpus with four sensilla and an adjacent sclerotized seta; labial palpus with five sensilla and four adjacent setae. Mandible strongly and uniformly sclerotized; blade about 0.4× as long as mandible, without denticles. Antenna disc-like, rim moderately sclerotized; central papillus absent. Parietal band present and weakly sclerotized. Prothoracic spiracle as in fig. 1b: atrium with width about 0.7× as long as closing apparatus and interior with numerous long heavy spines; atrial opening with conspicuous rim; closing apparatus adjacent to atrium. Skin smooth, with widely scattered setae and without spines.

Fig. 1 illustrates the cephalic sclerites and prothoracic spiracles of the mature larva; it is a composite of two individuals collected in the Ocala National Forest (USA: Florida; Marion Co.; Lake Delancy campground area, 5.5 miles N-NW Salt Springs, 29° 25'N, 81° 47' W; K.R. Sime & D.B. Wahl; emerged 31 May 1997 [AEIC: DBW 1.vi.1997a] and emerged 19 June

1997 [AEIC: DBW 20.vi.1997a], both from *Amphion floridensis*). The characteristic absence of the labial sclerite in ichneumonines resulted in distortion of the labial region in both preparations. Consequently, placement of the salivary orifice, palpi, and associated setae is only approximate.

Discussion.—Short (1978) and Gillespie and Finlayson (1983) provide keys to final-instar larvae of ichneumonine tribes and genera. Townes and Heinrich differed regarding placement of the Callajoppina. Short follows Townes (Townes et al. 1961) in placing them in the Heresiarchini ("Ichneumonini" of Short); Finlayson accepts Heinrich's placement of these genera as the subtribe Callajoppina in the Trogini (her "Trogusini"). Both sets of keys will take *Gnamptopelta* to the correct group of genera. Further use of Short will run *Gnamptopelta* to *Callajoppa*; Gillespie and Finlayson will key it to *Conocalama*. Modification of these keys will not, in our opinion, be useful. Both are inadequate samples of the world ichneumonine fauna: of approximately 370 genera worldwide (Wahl 1993), Gillespie and Finlayson treat 25 and Short 53. Any attempted corrections of the generic keys will risk defeat when the next previously undescribed larva is found.

BIOLOGY OF *GNAMPTOPELTA OBSIDIANATOR*

Observations.—Field work was conducted in the Ocala National Forest, in north-central Florida (29° 25'N, 81° 47' W), where both grape and *G. obsidianator* are abundant in the spring (March to May). The study site is part of an extensive stand of longleaf pine (Pinaceae: *Pinus palustris* Miller), with an open understory dominated by wiregrass (Gramineae: *Aristida stricta* Micheaux) and scattered low shrubs, chiefly scrubby oaks (Fagaceae: *Quercus marilandica* Muenchhausen and *Q. laevis* Walter), and pawpaw (Annonaceae: *Asimina speciosa* Nash and *A. obovata* Willdenow). Two species of grape are

Table 1. Summary of field observations of female *obsidianator*. Identification of plants landed upon with searching times, recorded when possible, in parentheses (seconds) of *Vitis* species. Before 8 April we had not confirmed the identities of *Vitis* species.

Wasp No.	Searching Sequence
1 (23 March)	*Vitis* (2-3s); *Vitis* (2-3s); *Vitis* (2-3s)
2 (23 March)	*Quercus* (<1s); *Quercus* (<1s); *Vitis* (25s); *Vitis* (lost)
3 (23 March)	*Vitis* (2-3s); *Vitis* (2-3s); *Vitis* (2-3s)
4 (23 March)	*Vitis* (2-3s); *Vitis* (2-3s); *Quercus* (2-3s)
5 (23 March)	*Vitis* (2-3); *Vitis* (2-3s); *Quercus* (2-3s)
6 (8 April)	*V. rotundifolia* (>20s); *V. aestivalis* (10s)
7 (8 April)	*V. aestivalis* (captured after 2-3s)
8 (17 April)	*V. rotundifolia* (>60s)
9 (24 April)	*V. aestivalis* (captured after 2-3s)

found here, both extremely common and often covering large expanses: *Vitis aestivalis* Micheaux and *V. rotundifolia* Micheaux. In 1997, most grape plants of both species were fully leafed out by the middle of March, and both continued to put out new leaves throughout the spring. A few *G. obsidianator* were seen as early as 10 March; the peak of abundance appeared to be during the last week of the month, when for a few days 12–15 wasps were seen each day. From then until the middle of May, when observations ceased, we usually saw 1–3 individuals in the course of 4–5 hours spent almost every day in the field.

Males fly rapidly, 2–3 meters above the ground, land rarely, and follow wide circuits in patches of forest abounding in grapevines. They were perhaps patrolling areas in which females were likely to eclose or to enter in the course of searching for hosts, although we witnessed no encounters between the sexes.

The females as well as the males are associated with grape at this field site. The females also fly quite fast, but land often. Table 1 summarizes our observations of searching behavior. Females appear to fly deliberately from one grape patch to the next, less often landing on other common low shrubs, which were usually surround-

ed by if not overlaid with grapevines. The wasps land on the upper surface of the leaf and tap it several times with the ventral surfaces of the antennae; usually, the inspection lasted just a few seconds, and the wasp then proceeded to the next plant, but in some cases the wasps stayed longer and conducted a thorough search of nearby leaves and stems. We suspect that the length of the search might be related to the presence of feeding damage or other traces left by host larvae (Vinson 1984). However, we observed no encounters with hosts in the field: the leaves searched, including those examined for just a few seconds, often bore herbivore damage, but we never found larvae in their vicinity.

Between 31 March and 2 May 1997 we collected 66 sphingid larvae on *Vitis*. We reared them in small groups (3–10 larvae) in plastic boxes which we supplied with fresh grape leaves every 1–2 days. Using Forbes's (1948) key, we were able to identify the caterpillars to species when they reached the 4th instar (and confirmed the identifications when adults emerged). All were macroglossine sphingids: *Darapsa myron* Cramer (33 reared to pupation), *Amphion floridensis* B.P. Clark (= *nessus* Cramer) (5 reared), and *Eumorpha achemon* Drury (2 reared). Larval mortality was due to braconid parasitism (*Aleiodes texensis*) killing 4th instars (10 victims, all *D. myron*) and unknown causes among 2nd-instar larvae (too small to identify). Of the *D. myron* and *A. floridensis* found during the first two weeks (about 45 larvae), all but one were small second and third instars; later collections included a few 4th and 5th instars. The two *E. achemon* larvae were found side-by-side on April 26 as very nearly mature 5th instars.

All larvae were found on *V. aestivalis*. Although we often found compelling feeding damage on *V. rotundifolia*, and this plant was inspected both by us and by *Gnamptopelta* females, we found no sphingid larvae on it: if not coincidence, this could be evidence for an oviposition pref-

erence in the adult sphingids, or for higher larval survivorship on *V. aestivalis*. Furthermore, in rearing the larvae, we found that they preferred to feed on *V. aestivalis* when both species of grape were in their boxes. This could reflect the habituation of the larvae to the plant on which they initially fed (Jermy 1987), or it could represent an inherently greater palatability of *V. aestivalis* to the larvae. As most of the larvae were *D. myron*, these observations may apply only to that species; the numbers of the other two species collected were too small for useful speculation. In addition, we noted that all larvae fed on full-sized leaves, never on the youngest leaves, which might represent an aversion to the denser pubescence of the youngest leaves (Southwood 1986) or perhaps to higher levels of allelochemicals (Feeny 1976).

The larvae of *D. myron* and *A. floridensis* have many habits that make them inconspicuous in the field. Whether feeding or resting, all instars are invariably on the undersides of the leaves, and they usually rest along the leaf veins, which the light-green young instars match particularly well in color and shape. Often the larvae rest on undamaged foliage one, two, or three leaves removed from the feeding site. The younger larvae feed in a distinctive fashion, by eating symmetrical holes on either side of the leaf, near the base, a pattern that blends extremely well with the deep rounded lobes and hollows of the leaves of *V. aestivalis*. Older larvae tend to feed along the edges of the leaf, eating off large pieces. Heinrich (1979) noted similar behaviors in the sphingid *Sphecodina abbotti* Swainson feeding on *V. vulpina* L. (in Minnesota) and suggested that this, along with the habit of staying under the leaves, conceals the caterpillars from predators that hunt by eye, particularly birds. We did not happen to observe any birds inspecting grapevines, but speculate that these behaviors may be somewhat effective against *G. obsidianator*. As the wasps

land initially on the top surface of the leaf, a caterpillar resting underneath may gain some extra time to fall off without being noticed, and its removal from the feeding site while resting might help frustrate a wasp that was initially attracted (by sight or by odor) to feeding damage (Vet and Dicke 1992).

Our observations of *G. obsidianator* and sphingid larvae in captivity suggest that letting go from the leaves is an effective means by which caterpillars elude wasps. We placed three field-caught females in a small glass aquarium (23-cm cube) with 4 larvae (at a time) feeding on grape sprigs. Some larvae (both *D. myron* and *A. floridensis*) dropped off their leaves as soon as wasps set foot on the leaves; others dropped only after the wasps' antennae or tarsi touched them. If the wasps tried to oviposit, the time it took them to bring their ovipositors into position, after making antennal contact, was long enough for the larvae to drop down and thus confound the oviposition attempt. Dropping appeared to be the main defense of smaller larvae; fourth- and fifth-instar larvae, when touched by a wasp, stayed put and swung their heads about with such violence as to parry any attempt at oviposition quite effectively, sometimes hurling the wasp against the side of the cage. The wasps, if not thrown, in many instances had so much difficulty inserting their ovipositors into the writhing caterpillars that they simply gave up.

When exploring the aquarium, the wasps tapped steadily with the extended antennae, lightly touching the apical quarter (flattened ventral surface) to the substrate. The wasps showed little interest in *D. myron* larvae, never attempting to sting them even after finding and examining them. In contrast, *A. floridensis* elicited great excitement: upon encountering a chewed leaf margin or a particle of frass, the wasps slowed their walking pace, vibrating the antennae much more rapidly and pressing them more firmly against the surface, with more of the antennal area, approximately the apical third, making contact. Upon finding *A. floridensis* larvae, the wasps tapped them for 1–2 seconds with the antennae and then turned around to sting. We witnessed six apparent ovipositions, by two females; it appears that the eggs may be inserted anywhere into the host's body apart perhaps from the head capsule. Attempts at oviposition occurred with third-, fourth-, and fifth-instar larvae (we did not expose younger larvae).

The *G. obsidianator* that we reared came from *A. floridensis* and resulted from those larvae exposed as 3rd and 5th instars. In total, we had six *A. floridensis* larvae that grew large enough to be identified: two went to term and emerged as moths, and four others were exposed, of which one died just before and one some time after pupation and two produced the wasps. Six of the *D. myron* larvae (also 3rd, 4th, and 5th instars) were exposed to the wasps and continuously observed, but no ovipositions were attempted with these larvae and all developed into adult moths.

The sphingids, parasitized and not, pupated by forming loose cocoons amid leaves and paper towels. The adult wasps emerged by cutting off the anterior 0.1 of the host pupa. Such an emergence hole is apparently characteristic of the Callajoppina (Mell and Heinrich 1931), and appears to be the primitive condition for the Ichneumoninae (Gillespie and Finlayson 1983). The ichneumonid's rudimentary cocoon, located in the detached anterior section, consists of a cap of dark brown silk just inside the cut margin.

Conclusions.—Although it was the most common grape-feeding sphingid at our field site in spring 1997, our observations suggest that *D. myron* is not a host of *G. obsidianator*. Of 33 larvae collected on plants exposed to a considerable population of *G. obsidianator*, no wasps emerged; the wasps showed no interest in this species in captivity (and much interest in *A.*

floridensis under the same conditions). It is possible that the larvae we collected were too small for successful oviposition or were not old enough to have spent much time exposed to wasps, thus lowering the probability of parasitism, or that parasitism rates are generally very low; however, the combined field and captivity observations argue that *D. myron* is at least not a preferred host.

That *A. floridensis* is a natural host is strongly supported by our successful rearing in captivity: a koinobiont larva-pupal endoparasitoid, *G. obsidianator* is not likely to develop successfully in randomly encountered moth larvae because it must survive the immunological defenses of the host and also coordinate its development with the onset of pupation in the host (Askew and Shaw 1986; Omata 1984). *Amphion floridensis* occurs throughout the geographical range of *G. obsidianator* and is thus potentially the sole host: its range is described as extending "from Florida, north to Nova Scotia, west to Calgary, Alberta, and south to Kansas" (Hodges 1971), and our queries of various collections expand this to central Colorado and southern Texas as well. In Florida, at least, the flight period of *G. obsidianator* coincides with the larval stage of *A. floridensis* (Kimball 1965). However, we can say nothing about *E. achemon*, because we found only two specimens and did not expose them to wasps; some 10 other sphingids feeding on grape in eastern North America (Hodges 1971) also demand investigation.

Hopper (1939) lists as a host *Papilio polyxenes* Fabricius (Lepidoptera: Papilionidae), referring to a New York list for which voucher specimens are unobtainable. As may be the case for many such isolated records (Shaw 1994), this one is almost certainly specious. This swallowtail is often reared by amateurs and professionals alike, as the caterpillar is quite striking and very often found on garden herbs and common roadside weeds (Um-belliferae). We have seen scores of specimens of *Trogus pennator* Fabricius (Ichneumoninae) reared from *P. polyxenes* in collections, but no reared *G. obsidianator*; a life-history study of *P. polyxenes* in central New York State, where *G. obsidianator* is common, found that about 10% of 128 pupae were parasitized by *T. pennator*, with a few other parasitoids occurring infrequently, but no *G. obsidianator* (Feeny et al. 1985).

We conclude that *G. obsidianator* parasitizes at least one species of *Vitis*-feeding sphingid. The degree of specialization within this group is unknown, but our observations of captive wasps suggest that *G. obsidianator* does not uniformly attack available sphingid species and that it could be restricted, at least locally in Florida, to *A. floridensis*. Our results support Heinrich's (1962) contention that the genera of the *Callajoppa* group are strictly parasitoids of Sphingidae.

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The Nesting Behavior and Dynamics of *Bicyrtes angulata* (F. Smith) with a Comparison to other Species in the Genus (Hymenoptera: Sphecidae)

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Abstract.—Data are presented on the nesting behavior and dynamics of a population of *Bicyrtes angulata* (F. Smith) found on the campus of the Universidade Federal de Minas Gerais, Belo Horizonte, Minas Gerais, Brazil. Many aspects of the biology of this population of *B. angulata* are similar to all (or the majority) of the 8 other species in the genus that have been studied in some detail. Other features were atypical in comparison, such as: (1) nesting in sandy soil far from water (2) constructing relatively short burrows (less than 10 cm on average) (3) taking more than two hours to dig a nest. New information is presented on the level of nest failure (roughly a third of all nests initiated are not completed), mortality (roughly 90% of all completed nests fail to produce adult wasps), and variability in egg to adult developmental time (44 to 375 days) due to bimodal prepupal dormancy. Factors affecting mortality are discussed, the most important being termites and ants. The number of nests made per female varied slightly over the year, this ratio being lowest in the dry season (winter and spring), and was not correlated with the total number of nesting females, thus suggesting that there is little or no competition for nesting space in the area. Possible alternative explanations for these patterns are offered, in relation to prey abundance and female mobility and longevity, and we suggest that the availability of suitable patches for nesting may potentially be of importance in the nesting dynamics of this species.

Of the 23 described species of *Bicyrtes*, 12 are found exclusively in South America, 8 in North America and 3 occur in both continents (see Bohart and Menke 1976 for distributions; Willink, 1947, revised the South American species). Their biology is largely either unknown or poorly known, with the exception of the North American *B. quadrifasciata* (Say) (see Evans 1966 for a review). Some additional information is available for *B. discisa* (Taschenberg), *B. simillima* (Smith) and *B. variegata* (Olivier) (Genise 1979, 1982), *B. cingulata* Burmeister (Evans and Matthews 1974), and also for the Cuban *B. spinosa* (Fabricius) (Sánchez and Genaro 1992). Few of the details of nesting and provisioning behavior have proven to be uniform across all species (see Discussion). Information on addition-al species should help address questions related to patterns of behavioral evolution within the genus.

Bicyrtes angulata (F. Smith) occurs in French Guiana, Paraguay, Argentina, and Brazil (Bohart and Menke 1976). Records for *B. angulata* in Brazil include some states in the North and Northeast (Nascimento and Overall 1980) and São Paulo (Martins 1991), but its biology was unknown until the present, and is compared here to what has been recorded for other species in the genus. This includes novel information on prepupal dormancy, and rates and causes of nest failure and mortality.

STUDY SITE AND METHODS

We observed an aggregation of *B. angulata* (147 marked nests in 1993 and 80 in
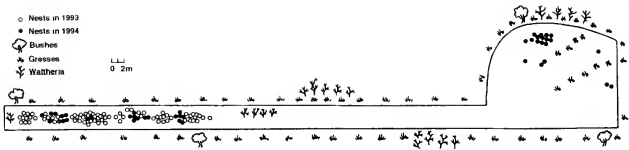
Fig. 1. Diagram of the nesting site of *Bicyrtes angulata* showing nest distributions in 1993 and 1994.

1994) on the Campus of the Federal University of Minas Gerais (UFMG), Belo Horizonte, Minas Gerais, Brazil, from January 1993 to June 1994. We spent a total of 556 hours making ad libitum and focal individual observations (*sensu* Martin and Bateson 1986), mostly between 0900 and 1200 h when the majority of nesting activity occurred, and opportunistically at the beginning and end of some days. The study site, Prefeitura, is a secondary growth, relatively undisturbed area, mostly covered with grasses, scattered bushes, and trees (including a few exotic and or-

chard species; see photo in Gaimari and Martins 1996). Nearby fields of corn, bean and manihot support a substantial population of *Waltheria americana* (Sterculiaceae), a weed whose flowers are commonly visited by *B. angulata* (Macedo and Martins 1998).

Most nests of *B. angulata* were concentrated in a 35 m long and 0.65 m wide strip of a dirt road (approx. 700 m² total) on a superficially compacted well-drained sandy soil. Nesting soil was completely free of vegetation and exposed directly to the sun (Figs. 1 and 2). We built a tem-

Fig. 2. Nesting site of *Bicyrtes angulata* showing the plastic-cup emergence traps.

porary fence around the nesting area to prevent vehicular and pedestrian traffic. In 1993 the area also contained numerous nests of other sphecid wasps: 193 of *Rubrica nasuta* (Christ) (Pimenta and Martins unpublished data), 54 of *Ammophila gracilis* Lepeletier (Gaimari and Martins 1996), 4 of *Bicyrtes discisa*, 4 of *Trachypus* sp., and 1 of *Prionyx fervens* (Linnaeus). There were also a few bee nests at the same time: 7 of *Centris aenea* Lepeletier, and 1 of *Megachile neoxanthoptera* Cockerell.

We marked and released 180 females (127 in 1993 and 53 in 1994) and 31 males (19 in 1993 and 12 in 1994) that were captured in or near the nesting site while either searching for a place to begin excavation, in the process of excavating a nest, flying in search of prey or in transit to the nest, or visiting the flowers of *Waltheria americana* (see Macedo and Martins 1998, for annual records of *B. angulata* visits to this plant). Numerous additional wasps were marked in areas outside the nesting area, but none of these wasps were subsequently encountered there. Wasps were restrained and marked individually with fast-drying non-toxic acrylic paint using combinations of 4 colored dots on the corners of the scutum, making it possible to observe individual variation in daily phenology, nesting (note that many marked females made no nests in the study site), provisioning, male behavior, longevity, interactions with other insects and plants, and movements in the aggregation and its surroundings. Adult longevity was calculated as the length of time between when a wasp was marked and the last time it was seen, and is thus likely to be a very conservative estimate, though many wasps were never seen again after marking (64 females and 21 males), and we did not include these individuals in the average. Differences between male and female longevity were tested using Student's t-test.

Nests were marked during interruptions in the nest excavation process, using 4 cm-long and 5 mm-wide aluminum arrows fixed to the ground with nails. Arrows were distinguished by colors corresponding to those of the resident female and/or by numbers. After observing a definitive nest closure, we nailed an emergence trap (a marked plastic cup) to the ground at the nest entrance (Fig. 2), to record egg-adult development time and the emergence of nest parasites. This also helped us to estimate the number of annual generations. Wasps from the first generation that emerged in the field or in the laboratory were marked and released in the study site, so as not to extirpate the population.

We excavated all 227 marked nests to determine their architecture and contents, assessing whether they were deserted, parasitized, destroyed by ants or termites, or completed. The status of the nests during the study was categorized as follows: (1) Deserted nests were those in which we observed a female working but which proved to be empty upon excavation (this class of nests thus includes both abandonment and female mortality events) (2) Parasitized nests were those in which parasites appeared in the emergence traps (3) Nests destroyed by ants or termites were those in which we found pieces of destroyed cocoons and prey remains (4) Completed nests were those that we observed being provisioned and in which we found all remains of cocoons and/or prey. Only nests which were not deserted were included in the analysis of nesting phenology and counts of nests per females.

We counted 307 prey that were consumed by larvae in 26 of the nests; it was possible to count the exact number of consumed prey because their heads and scuta remained intact in the cell. Eight days after provisioning ceased, seven nests were excavated to measure the time of development from egg to prepupae. The number of pores of 14 cocoons were counted and the larger and smaller diameter measured for 8 of them. We made casts of 2

Fig. 3. Architecture of the nest of *Bicyrtes angulata*.

completed nests with plaster of Paris to record their shape (Fig. 3), and casts of two incomplete nests. Nesting activity was measured as the number of nests initiated per month. We plotted the number of nesting females per month versus the average number of nests made per female to assess evidence for density-dependent effects. For quantitative measurements we calculated averages with standard deviations.

Voucher specimens of wasp and prey were deposited at the Laboratório de Ecologia e Comportamento de Insetos of the Departamento de Biologia Geral, ICB-UFMG, Belo Horizonte, MG, Brazil.

RESULTS

Nest excavation.—Over the entire study, a total of 180 females excavated 227 nests, and 80 of these females excavated at least one nest within a week of being marked. In 1993, the final nest density was approximately 16.5 nests/m². We also observed the origin of a new nest site in 1994, when 29 out of the 80 nests of *B. angulata* found were in an area close to, but separate from, the original site (Fig. 1).

Females walk in a slow and meandering path over the nesting site, occasionally antennating the ground, until they find a suitable spot (the selection criteria are unknown, but are likely to be tactile) and begin to dig. Females dig primarily with their mandibles, using the forelegs to scoop loosened soil backwards, throwing the soil out from under the body. This movement is accompanied by a rapid rocking motion of the body, lifting the abdomen each time the soil is thrown, and simultaneously tilting the head down over the soil. The excavated soil accumulates, forming a mound (tumulus) close to the nest entrance. Over the entire period of excavating a single nest, females spend an average of 2.26 ± 0.13 h (n = 4) actually digging the nest, but also 2.39 ± 0.24 h (n = 4) flying to and from the nests, or simply resting in the tunnel. Completed nests (n = 5 with all measurements taken) have a straight tunnel, 9.6 ± 1.1 cm long and 0.8 ± 0.1 cm in diameter, angled from 20° to 35° relative to the soil surface (Fig. 3), and ending in a single ellipsoid cell (only two nests had two cells) measuring 2.6 cm long by 1.2 cm in diameter (all 5 measured cells identical), at 5.6 ± 0.54 cm depth. Females typically complete nest excavation in the afternoon. Afterwards, they close the nest entrance and fly away to feed on nectar, and from March 16 to April 20, to sleep in mixed male/female aggregations on inflorescences of *Panicum maximum* (Poaceae), in proximity to adults of *Rubrica nasuta* (described below) (Fig. 4). No form of orientation flight was ever observed, either after nest construction, afternoon closure, or in between provisioning trips.

Nest provisioning.—Out of 227 nests, 147 were succesfully provisioned by 103 different females. Provisioning can occasionally start the same afternoon that nest excavation is finished (n = 2) but is generally begun the following day. In the latter case, by 0830 to 0900, the females return and open the nest entrances with their forelegs, using motions as described above. Hunting trips occur between 0845 and 1545 h. As they leave the nest for the first and all subsequent hunting trips, they emerge headfirst, and temporarily close the entrance by scooping the tumulus backwards into the entrance. However, sometimes nest entrances stay partially open due to careless and hasty closure. If heavy rains level off the mound, females still have little or no difficulty finding

Fig. 4. Mixed male-female sleeping site of *Bicyrtes angulata*.

their nest. Sometimes they seem confused initially, but soon find the nest entrance and reopen it.

Prey are immatures (sometimes adults) of *Megalotomus* sp. and *Apidaurus* sp. (Hemiptera: Coreidae: Alydini [=Alydidae]), accounting for 302 prey items; only one anomalous cell was found, containing 5 pentatomid nymphs. Each prey is stung and partially paralyzed, then the wasp flies back to the nest holding it venter up with her middle legs. She then removes the nest closure with her front legs, keeping the prey in the same position, and in this way she enters the nest headfirst. Once, after removing the nest closure, a female dropped the prey at the nest entrance, entered, came back out headfirst, grabbed the prey in her mandibles, and dragged it down to the cell by moving backwards. Hunting trip lengths are quite variable (45.6 ± 35.9 min., n = 13; range 1–95). After capturing the first prey and placing it in the nest, one egg is attached

erect on the metasternum between the middle or hind coxae, exactly as shown by Evans (1966:158). Since the time between the first and second provisioning trips can vary considerably, it appears that the egg may hatch either before or after the second prey is supplied, but in most cases it is probably after two or three prey are already in the nest.

Provisioning is progressive and somewhat lengthy, lasting approximately 6 consecutive days per nest (6.5 ± 0.53, n = 7), with roughly 12 prey per completely stocked cell (11.88 ± 4.46, n = 26; range 7–24). The final closure of completed nests begins with females scraping the tumulus into the nest entrance, as when making a temporary closure, but is somewhat more thorough, and this is followed by a bout of "hammering," during which a female delivers vigorous blows with the tip of the abdomen until the nest entrance is compacted and levelled. The egg-prepupa developmental period is rapid, as we found
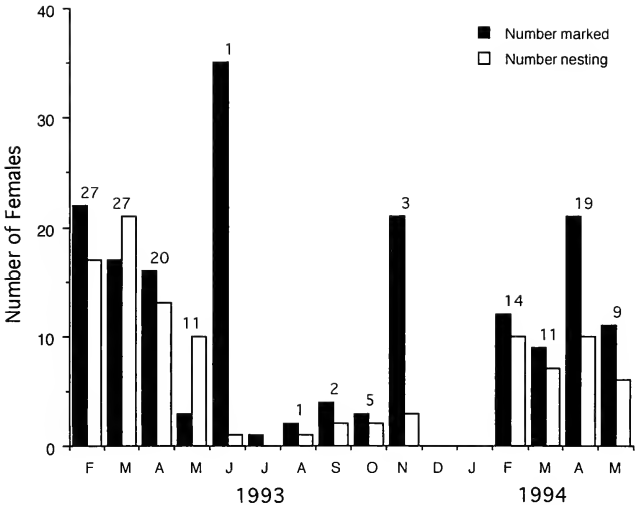
Fig. 5. Number of marked and nesting females of *Bicyrtes angulata* in 1993 and 1994. Numbers above the bars indicate the total number of nests constructed in that time interval.

prepupae already inside their cocoons (n = 7) when excavated 8 or 9 days after provisioning had ceased. Cocoons had 4 to 6 pores (5.5 ± 1.95, n = 14) and averaged 17 ± 0.9 mm long by 5.3 ± 0.06 mm (n = 8) in diameter. The entire cycle for a single nest, from first excavation to final closure, typically takes 8 days (8.5 ± 0.5, n = 6).

Seasonal phenology and demographic patterns.—Adults are found during the whole year, mainly visiting flowers, but nests are built mainly from February to May (midsummer and autumn; 85 of 97 provisioned nests in 1993, and all 50 in 1994; Fig. 5). The ratio of nests provisioned per nesting female was generally higher than one except in the winter and spring (June through November, Fig. 6; in October the ratio was higher because two females provisioned five nests in total). Overall, there is no relationship between the number of nesting females per month and the average number of nests per female per month. If we consider the number of nests relative to the total number of marked females, it is obvious that many females were present in the area that never made nests (in 7 of 14 months in which nesting was observed, there were more marked females alive than nests provisioned). Despite the fact that the range of number of nests per nesting female was one to seven, the average number of nests per marked female only varied from 1.0 to 1.5 in different months.

Females seem to feed on flowers in areas other than those in proximity to their nests; only three out of 77 females marked
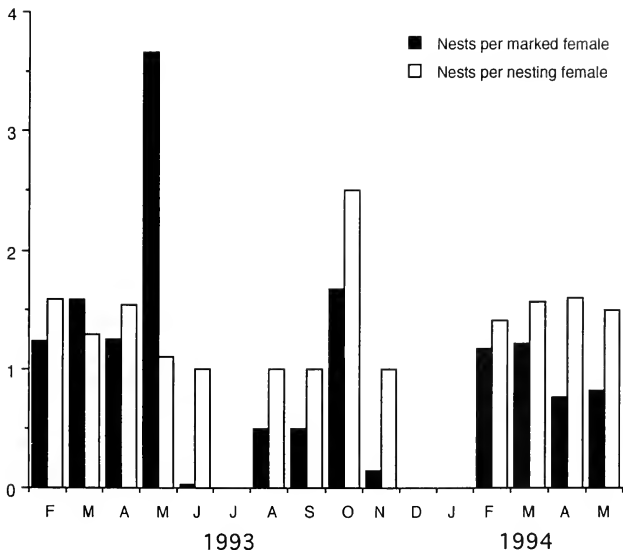
Fig. 6. Monthly ratio of number of nests to females of *Bicyrtes angulata* in 1993 and 1994.

on *W. americana,* close to the study site, were seen nesting in the aggregation. However, 77 out of 103 females that were marked while visibly searching for a place to begin excavation were later seen nesting there. Females stayed in the aggregation from 1 to 84 days (24.1 ± 17.5, n = 116). One female was observed nesting until the age of 65 days, with no apparent mandibular or wing wear over this time. The estimate of male longevity (31.4 ± 20.4 days, n = 10; range 3–56) was not significantly different from that of females (Student's t = −1.25, p > 0.2).

There are at least 2 annual generations, though these are staggered and overlap-

ping rather than synchronized and discrete (see Table 1). The range of time from oviposition to adult emergence was 44 to 375 days (200.1 ± 137.1, n = 13; Table 1). The origin of such variability is in the prepupal stage, which may remain dormant for widely varying intervals of time. This variability in dormancy can occur not only among but within the broods of individual females; two eggs from one female produced adult males after 55 and 375 days of development. The operational sex ratio at this site was apparently female biased; 15 wasps from the first generation emerged (in the field or from cocoons brought into the laboratory), of which 9

Table 1. Developmental intervals of *Bicyrtes angulata* (arranged by starting date).

Nest	Nest starting date	Nest closing date	Adult emergence date	# days egg-adult	Sex
1	12 Feb 1993	18 Feb 1993	16 Apr 1993	57	F
3	13 Feb 1993	19 Feb 1993	9 Mar 1994	375	M
2	16 Feb 1993	3 Mar 1993	27 Apr 1993	55	M
12	19 Feb 1993	26 Feb 1993	3 Feb 1994*	342	F
4	3 Mar 1993	9 Mar 1993	19 Aug 1993	163	M
10	8 Mar 1993	?	7 Feb 1994	ca. 310	F
13	17 Mar 1993	1 Apr 1993	30 Jan 1994	335	F
11	30 Mar 1993	13 Apr 1993	3 Feb 1994*	296	M
15	1 Apr 1993	13 Apr 1993	11 Apr 1994*	356	F
5	24 Apr 1993	6 May 1993	29 Jan 1994	328	F
7	1 May 1993	6 May 1993	4 Sep 1993	88	M
6	6 May 1993	?	31 Jan 1994	ca. 310	F
9	13 Oct 1993	28 Oct 1993	24 Jan 1994	88	F
8	28 Oct 1993	5 Nov 1993	24 Jan 1994	80	F
14	11 Feb 1994	22 Feb 1994	8 Apr 1994	44	M

* These individuals emerged in the laboratory.

were females (60%). We found 5.7 females per male (85% females) over the period of the study, though males were rarely seen on the aggregation and thus their abundance was likely underestimated.

Movement patterns and diel phenology.—Adults of *B. angulata* spend nights on plants. From March 16 to April 20, marked *B. angulata* and *R. nasuta* were seen sleeping on inflorescences of *Panicum maximum* (Fig. 4). The highest number of wasps seen in a single group was 17 *B. angulata* and 9 *R. nasuta* (J. F. Macedo, pers. comm.). Females leave the sleeping site between 0800 and 0830 h to take nectar prior to the start of nesting activities (other phenological data above). Usually after 1600 h, or when it is very cloudy, they return to the sleeping site. One day they left the sleeping site early, returned around 0900, but then resumed nesting activities between 0900 to 1000 h, when the sun began shining again. *B. angulata* comprised 34% of the individuals of the 29 bee and 51 wasp species visiting *Waltheria americana* between 1000 and 1200 h in April 1993 and April 1994 (Macedo 1995). The highest number of *B. angulata* seen on *W. americana* during one month was 35 females and 7 males in June 1993 at a site some distance from the nest-

ing site (despite the availability of flowers, no visits were observed on the same plants in June 1994, reflecting the large variation in the abundance of wasps between years).

Only 8 males were captured and marked (of 31 total) while they were patrolling the aggregation by flying close to the soil, continuously going back and forth. Occasionally they clashed briefly in mid-air with other males, females, or other insects flying in the patrolling area. The highest levels of patrolling activity were observed in April between 0845 to 1145 h, and 1300 to 1600 h. Despite the patrolling activity, copulation was never seen in the aggregation, nor on flowers of *W. americana* or in the sleeping site.

Four new adults were observed emerging from their cells between 1045 and 1145 h, and new adults were generally found in the emergence traps in the mornings, suggesting that there is a preferred daily emergence time.

Interactions with natural enemies and other insects.—The female actively defends the nest entrance against insects. Once, when an army ant trail crossed the entrance of one nest, the female tried to drive them out by touching them with its abdomen or

Table 2. Survivorship and success of *Bicyrtes angulata* nests.

Nest status			Number of nests per year		
			1993	1994	Total
Marked			147	80	227
Marked	Abandoned		46	30	76
Marked	Cast in plaster		4	0	4
Marked	Completed		97	50	147
Marked	Completed	Failed	83	49	132
Marked	Completed	Survived	14	1	15

hovering above them. However, we never observed females carrying ants into the air and dropping them a few cm away, as *Ammophila gracilis* did in our study site (Gaimari and Martins 1996). A butterfly that was flying repeatedly over a nest was also driven away by the resident female; in this case the wasp hovered above the butterfly, approaching and touching it several times until it was driven off. Aerial clashes were common between males and females of *B. angulata* and *R. nasuta*. Once, a female of *B. angulata* entered a nest of *R. nasuta* while the latter was discarding a prey item not consumed by her larva, and when the *Rubrica* returned, she found the *Bicyrtes* and drove her away. A few minutes afterwards, this female started to excavate her own nest close to that of the *Rubrica*.

Table 2 summarizes the fate of the nests initiated in 1993 and 1994. Out of 227 nests, 147 were completed; 76 were abandoned and four were cast in plaster; excluding the latter, then, some 34% of nests were abandoned. Apparent causes of nest abandonment were: excavation in hard soil (n = 8); proximity to ant nests (2); heavy rains (2); female disturbed by a female of *R. nasuta* (1); and the remainder (63) were due to unknown causes.

Of 147 provisioned nests, only 15 produced adult wasps; 100 were destroyed by ants (principally *Solenopsis* sp.) and termites; 16 experienced immature mortality of unknown nature; 7 pupae died due to flooding of the nesting site; 6 nests were

parasitized by *Ligyra morio* (Diptera: Bombyliidae; 5 adults emerged in 5 traps); one nest was apparently parasitized by *Metopia* n. sp. nr. *sinipalpis* (Diptera: Sarcophagidae: Miltogramminae; emerged in one trap), a major parasite of *Ammophila gracilis* in the study site (Gaimari and Martins 1996); and two nests were excavated prematurely to document egg placement on prey. Excluding the latter two nests, mortality of completed nests was approximately 90%. One entire aggregation of 25 marked nests was extirpated in 1991 by ants and termites at the Ecological Station of the UFMG.

DISCUSSION AND CONCLUSIONS

The data from this study are only exceeded by those available for *B. quadrifasciata*, obtained by several workers in numerous localities in the United States (see Evans 1966 for a review). As Evans (1966) has claimed, a detailed comparison of the behavior of the species of *Bicyrtes* requires that other species like *B. angulata* are studied in detail. Following Evans' (1966) summary of features of the ethology of the species of *Bicyrtes*, we have thus confirmed some general patterns within the few members of the genus that have been studied, as well as added new information (Tables 2, 3 and 4), though, as mentioned, only a few of the details of nesting and provisioning behavior are uniform across all species.

Adults of *B. angulata* are like all the other studied species in the genus in some

Table 3. Comparison of qualitative features of *Bicyrtes* nesting biology.

	angulata	discisa	variegata	smillima	quadrifasciata
Provisioning	progressive	mass	mass	mass	delayed
Prey paralyzation (partial)	yes	yes	yes	yes	?
Prey types*	N ≥ 4 (+A)	N ≥ 4	N5	N5	N
Prey families**	C	P	P	P	CPRLSCy
Foraging during morning-afternoon	yes	?	?	yes	yes
Mound (tumulus) near nest entrance	yes	yes	no	yes	no
Nests aggregated***	yes	no	yes	no	no
Accessory burrow	no	no	yes	yes	?
Sleep in accessory burrow	no	no	?	yes	?
Sleep in mixed association	yes	?	?	no	?
Citation****	present work	G1982	G1982	G1982	E1966

* N = nymphs (followed by instar numbers if specified), A = adults, (+A) indicates adults rarely taken.
** C = Coreidae (s.l.), P = Pentatomidae, R = Reduviidae, L = Lygaeidae, S = Scutelleridae, Cy = Cydnidae, Rh = Rhopalidae, Py = Pyrrhocoridae.
*** Statistics not available; category represents subjective evaluation of authors as to dispersion of nests relative to apparent available space.
**** G1982 = Genise 1982, E1966 = Evans 1966, E&M1974 = Evans & Matthews 1974, S&G1992 = Sánchez & Genaro 1992.

respects: (1) they are frequent visitors at flowers for nectar (they do not feed upon the prey they capture for their larvae) (2) they are solitary ground-nesting predators (3) prey are immature and/or adult heteropterans (4) nest closure is maintained while outside the nest (5) foraging is primarily in the morning and afternoon. Other features which appear similar to the majority of species studied include: (1) nesting in multispecies aggregations (2) sleeping on vegetation (3) partial paralysis of prey (4) nests with one or two cells (5) low nest angles (generally less than 45°).

Other features were atypical, such as: (1) nesting in sandy soil far from water (other species except for *B. spinosa* nest along water courses) (2) relatively short burrows (less than 10 cm on average) (3) more than two hours to dig a nest. The presence of a tumulus can neither be considered exceptional nor general, and for other features comparative information is lacking.

A few of these points merit further discussion. Despite the general tendency of *B. angulata*, like other species, to intersperse its nests with those of other digger wasp and bees, it tends to aggregate intraspecif-

Table 4. Comparison of quantitative features of *Bicyrtes* nesting biology.

	angulata	discisa	variegata	smillima	quadrifasciata
Number of cells per burrow	1–2	3	2–5	1	2–3
Number of prey per cell	7–24	16	3–6	11	8–11
Time to dig cell/nest (min)	146 ± 14	30	60	>60	60–120
Angle of entrance burrow	20°–35°	30°–35°	30°–35°	30°	30°–60°
Nest depth (cm)	5.6 ± 0.54	5	8–10	20	?
Nest length, burrow plus cell (cm)	9.6 ± 1.1	12	12	24	8–43
Lengt of cell (mm)	25–26	18–20	25–30	17	20–35
Width of cell (mm)	12–13	10–12	12–15	12	5–27.5
Number of pores in cocoon	5.5 ± 1.95	?	5	?	?
Egg-adult developmental time (days)	44–375	?	?	?	49
Number of generations per year	2	?	?	?	?

Citations as for Table 3.

Table 3. Extended.

ventralis	hadiens	cingulata	spinosa
delayed	?	progressive	progressive
?	?	?	no
N	N+A	N+A	N(+A)
CPRLSCy	PS	Rh	CPLSPy
?	?	yes	yes
no	no	no	yes
variable	?	?	variable
?	?	?	no
?	?	?	no
?	?	?	no
E1966	E1966	E&M1974	S&G1992

ic nests within these areas. As in its congeners, *B. angulata* maintains an outer closure at all times when the female is not in the nest, but no inner closure is ever made. Prey are Coreidae (sensu lato), indicating in our case a possibly high level of local specialization, compared for example with the Cuban generalist *B. spinosa* that preys upon several species of five heteropteran families (Sánchez and Genaro 1992). Additionally, the prey is partially paralyzed and carried in flight with the middle legs, clasped tightly beneath the base of the wasp's abdomen, and is not usually deposited on the ground at any time. The egg is laid in a semierect position on the mid-ventral line of the first prey item. Our observations established that *B. angulata* is a progressive provision-

Table 4. Extended.

ventralis	hadiens	cingulata	spinosa
1–2	2–5	1	1
3–11	10–23	?	?
60–120	?	?	?
45°	45°–60°	20°–45°	45°
4–8	8–13.5	8.5–10.5	4.5–8.5
20–30	12.5–18.5	12–14	9.9 ± 2.6
20–30	?	?	?
8–12	?	10–12	?
?	?	?	7.6 ± 1.54
?	40–42	?	?
?	2	?	?

er like *B. spinosa* and *B. cingulata*, though mass provisioning and delayed provisioning are found in other species.

Among the novel data for *B. angulata* is the huge variability in the time of prepupal dormancy within the same brood. This variability (sometimes called "parsivoltinism"; Torchio and Tepedino 1982) is scarcely documented for Nearctic and Neotropical species of solitary wasps and bees (see Evans 1966; Stephen et al. 1969; Evans and West-Eberhard 1970; Torchio and Tepedino 1982; Roubik 1989; Wcislo and Cane 1996). A comparable variability was also found for other species of solitary wasps and bees in the same study site and other sites in the Ecological Station of the UFMG (Martins et al. 1996; Almeida et al. 1997; Pimenta and Martins unpublished data). One of the possible interpretations for such a pattern is given by theories of risk spreading of reproductive effort (or "bet-hedging") in unpredictable environments (Danks 1987; Tauber et al. 1986). The possibility that parsivoltinism may help avoid predation or parasitism in some way seems reasonable, but we cannot confidently identify the precise mechanism of selection for such an adaptation in the present case. We do believe, however, that we can exclude variability in the occurrence of rains (as in deserts where similar insect life cycles occur, e.g. Hanski 1988), because our study site is strikingly seasonal and predictable in the occurrence of rains (see Martins and Antonini 1994) and dormancy seems to not correlate with rains (R. P. Martins unpublished data).

There is an apparent paradox in the data on number of marked females versus number of nests made (see Fig. 5). Many marked females visiting flowers at the study site did not nest there, so the total number of females exceeded the number of nests in 7 of the 14 months when females were present. Why are there so many active females that apparently not nesting? This same phenomenon occurs in *R. nasuta* (Pimenta and Martins un-

published data), and for that species, prey are seasonally distributed within the year, and the hypothesis is that females should wait for a burst of prey availability to make nests. It is likely that prey abundance for *B. angulata* also exhibits seasonal variation, because many plant-feeding insects in this environment have strongly seasonal life cycles, and a similar explanation may apply here. It is alternatively possible, though questionable, that these excess females were nesting elsewhere but all foraging in a limited area together; i.e., the females sampled at the flowers represented the combined population of several nesting areas. However, this was not the only patch of suitable flowers in the area, and there is no obvious reason why the wasps would be concentrated in this particular patch.

Because we found no relationship between the number of nesting females and the average number of nests per female, we suggest that crowding has no effect on the number of nests made in the aggregation, despite the preference to nest in a somewhat limited area. It is also possible that females made only one or two nests in the aggregation and then dispersed to other areas, given that a female can live for up to 84 days, yet few were in residence this long. That is, rather than interpreting the small number of nests per female as a result of high mortality, there may be some undetected nesting activity outside of the known aggregation area; further work with marked females might help resolve this. In either case, the availability of adequate patches (whether aggregations form in them or not) may be of primary importance in the nesting dynamics of this species. In addition to other forces that could potentially influence nesting dynamics is the frequent extirpation of nests or entire aggregations by termites and ants, and the high frequency of nest desertion, due to several causes. Therefore, the patchiness of the environment and the dynamics within the aggregations are likely to be crucial in the population dynamics of this species.

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Sexual Dimorphism Of Wasp Antennal Structure in Relation to Parasitic and Non-parasitic Behavior (Hymenoptera: Sphecidae)

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Abstract.—To assess the relationship between sensory ecology and behavior of non-parasitic and parasitic spheciforme wasps (Sphecidae), I measured the lengths of scapes, flagella, and body size (intertegular distance) of males and females of 29 species, representing 7 subfamilies and 26 tribes. Unlike a previous study with bees (Wcislo, 1995), spheciforme wasps show no consistent sexual dimorphism in relative antennal size for free-living versus parasitic species.

Brood parasitism (cuckoo behavior) and social parasitism have evolved repeatedly among bees, aculeate wasps and ants (e.g., Wcislo 1987; Wcislo and Cane 1996; Hölldobler and Wilson 1990; Cervo and Dani 1996). Parasites utilize host-derived resources (a nest, stored food, or worker labor) to rear their own offspring. Maternal behavior of parasitic and non-parasitic species differs (Wcislo 1987), while respective males do not differ essentially in mating behavior, although data are scant (e.g., compare Cederberg et al. 1984 with Alcock and Alcock 1983). Few studies have investigated the sensory ecology (*sensu* Dusenbury 1992) of parasitic and non-parasitic Aculeata to ascertain if differences in sensory structures co-occur with behavioral differences. Non-parasitic bees (Apoidea) usually are strongly sexually dimorphic for antennal structures; at a given body size, males tend to have shorter scapes and longer flagella (Wcislo 1995; Müller 1872). Parasitic bees, in contrast, usually are not sexually dimorphic for relative size of antennal structures. Among ants, a fusion of antennal flagellomeres is part of a syndrome of structural characters associated with parasitic behavior (Hölldobler and Wilson 1990).

Some clades of spheciforme wasps (= "Sphecidae" of Bohart and Menke 1976) together with the bees form a monophyletic group, Apoidea (e.g., Alexander 1992; Brothers and Carpenter 1993). Parasitism has evolved repeatedly in bees (e.g., Wcislo and Cane 1996), and has probably evolved twice among spheciforme wasps, once in the common ancestor of the genus *Stizoides* and once in the common ancestor of Nyssonini (see Bohart and Menke 1976). Thus, the evolution of parasitism among sphecid wasps provides additional examples to assess whether female parasites are similar to males in their sensory ecology and relevant structures. This note presents information on antennal size for parasitic and non-parasitic wasps (Sphecidae), as part of an on-going comparative study of the relationship between morphological and behavioral evolution within aculeate Hymenoptera (cf. Wcislo 1989).

MATERIALS AND METHODS

In an effort to minimize phylogenetic bias I used 29 species, representing 7 subfamilies and 26 tribes of the 10 subfamilies and 30 tribes that Menke (1997) lists for Sphecidae (see Appendix). Intertegular distances, scape length, pedicel length,

and total flagellar length was measured on 5 individuals of each sex using methods in Wcislo (1995). Values are reported as means with standard errors. Data were analyzed using SYSTAT (Wilkinson 1988) on a personal computer, unless otherwise indicated. Phylogenetic bias probably exists within these data due to nonindependence of the taxa (e.g., Harvey and Pagel 1991). There is, however, no widely-accepted phylogenetic hypothesis available for the taxa included here, and taxonomy may be a poor indicator of phylogeny (see discussion in Alexander 1992).

RESULTS

Parasitism is relatively rare among spheciforme wasps. Among non-parasitic species males and females, on average, were not significantly different in body size (mean intertegular distance in mm: females, 1.95 ± 0.17; males, 1.66 ± 0.15; Mann-Whitney U = 402.5, P > 0.2). The sexes did not differ in mean length of the flagella (in mm, females: 3.44 ± 0.46; males: 3.28 ± 0.39; Mann-Whitney U = 348, P > 0.8) (Figure 1, bottom). Males had significantly smaller mean scape length than females (in mm, females: 0.55 ± 0.053; males: 0.43 ± 0.04; Mann-Whitney U = 461, P = 0.02; Figure 1, top). Within species, non-parasitic females more frequently had a larger body size than males (two-tailed sign test, P < 0.05, T = 22, N = 26), and had longer scapes (two-tailed sign test, P < 0.05, T = 23, N = 23), but females did not have longer flagella (two-tailed sign test, 0.1 > P > 0.05, T = 17, N = 25) (sample sizes differ because ties were eliminated; Conover 1971). Regression equations for non-parasitic males versus females were not significantly different for scape or flagellum length as a function of body size (P > 0.05, comparing y-intercepts or slopes). Male and female parasites did not differ in body size, nor in lengths of scapes and flagella.
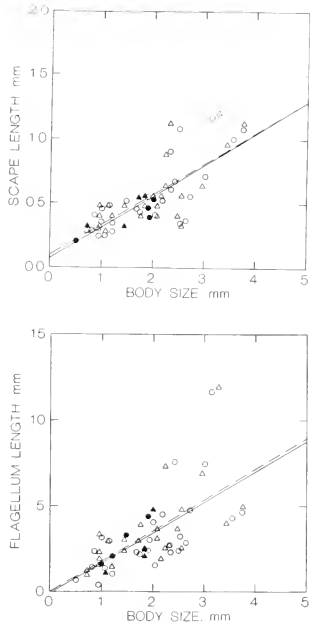
Fig. 1. Scape (top) and flagellum (bottom) length of spheciforme wasps as a function of body size (intertegular distance). Open circle = non-parasitic female; open triangle = non-parasitic male; closed circle = parasitic female; closed triangle = parasitic male.

DISCUSSION

Among non-parasitic spheciforme wasps females often are larger than males, and have longer scapes. Small samples preclude statistical analyses, but parasitic females are not conspicuously larger than conspecific males, and have similarly sized scapes and flagella. In contrast, a study of 114 bee species showed that 1) female non-parasitic bees of a given body size have

longer scapes but shorter flagella than con-specific males, and 2) for parasitic bees, scapes and flagella are similar in size, on average, between males and females of a species (Wcislo 1995; also Müller 1872). Since bees are closely related to, and probably arose from within spheciforme wasps (e.g., Alexander 1992), the sexual differences are probably derived among bees. Relative to non-parasitic females, female parasites may be more "male-like" in their search behavior, but pertinent data are scarce (refs. in Wcislo 1995). If substantiated, these behavioral differences can help explain similarities in sensory structures among males of parasitic and non-parasitic species and females of parasitic species, which differ from non-parasitic females.

Antennae have olfactory, gustatory, and tactile sensory receptors; they are used like calipers during nest construction; and they can be used to drum, tap, or stroke parts of the female's body (refs. in Wcislo 1995). The scape of some male spheciforme wasps is broadly expanded (e.g., *Dinetus*), like males of a parasitic bee, *Doeringiella* (Roig-Alsina 1989); these expansions may house glands for use during courtship and mating, as known for other Hymenoptera (Isidoro et al. 1996). The functional morphology of antennae has been studied for relatively few species, and typically only for one or two sensory modalities. Antennae have multiple functions, highlighting the need for more detailed studies relating behavior to an animal's sensory world ("umwelt"), as pointed out long ago by von Uexküll (1934).

ACKNOWLEDGMENTS

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APPENDIX

List of spheciforme wasp species from which antennal measurements were taken. * = parasitic taxon; ? = taxon is probably parasitic, but behavioral data are unavailable. Nomenclature follows Bohart and Menke (1976), as modified by Menke (1997).

AMPULICINAE

  AMPULICINI

  Ampulex compressa (Fabricius)

  DOLICHURINI

  Dolichurus corniculus (Spinola)

ASTATINAE

  DINETINI

  Dinetus pictus (Fabricius)

  ASTATINI

  Astata mexicana Cresson

PHILANTHINAE

  EREMIASPHECIINI

  Eremiasphecium schmiedeknechtii Kohl

  APHILANTHOPSINI

  Aphilanthops frigidus (Smith)

  PHILANTHINI

  Philanthus solivagus Say

  CERCERINI

  Cerceris frontata Say

PEMPHREDONINAE

  PSENINI

  Psenulus pallipes (Panzer)

  PEMPHREDONINI

  Stigmus americanus Packard

SPHECINAE

  AMMOPHILINI

  Ammophila polita Cresson

  SCELIPHRONINI

  Podium rufipes Fabricius

  SPHECINI

  Sphex dorsalis (=*singularis*) Smith

BEMBICINAE

  HELIOCAUSINI

  Heliocausus larroides (Spinola)

  MELLININI

  Mellinus arvensis (Linnaeus)

  STIZINI

  Bembicinus wheeleri Krombein & Willink
  Stizoides unicinctus (=*renicinctus*) (Say)

  GORYTINI

  Gorytes simillimus Smith

  *NYSSONINI

  Nysson (Epinysson) mellipes (Cresson)
  ?Synnevrus aequalis (Patton)
  Nysson simplicicornis Fox

  BEMBICINI

  Bembix texana Cresson

CRABRONINAE

  LARRINI

  Larra bicolor Fabricius

  MISCOPHINI

  Solierella plenoculoides (Fox)

  PALARINI

  Palarus latifrons Kohl

  TRYPOXYLONINI

  Trypoxylon lactitarse Saussure

  SCAPHEUTINI

  Scapheutes brasilianus Handlirsch

  CRABRONINI

  Crabro cribrellifer (Packard)

  OXYBELINI

  Oxybelus emarginatus Say

Systematics of Costa Rican *Meteorus* (Hymenoptera: Braconidae: Meteorinae) Species Lacking a Dorsope

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Abstract.—This study of the genus *Meteorus* (Hymenoptera: Braconidae: Meteorinae) treats the 19 known Costa Rican species that lack a dorsope (a pit on the dorsal surface of the first metasomal tergite). Fourteen new species all attributed to Zitani are described and illustrated: **M. alejandromasisi, M. camilocamargoi, M. coffeatus, M. corniculatus, M. desmiae, M. dos, M. mariamartae, M. megalops, M. micrommatus, M. pseudodimidiatus, M. rogerblancoi, M. sterictae, M. uno,** and **M. yamijuanum.** An identification key to 19 species is provided, including the previously described species: *M. congregatus* Muesebeck, *M. dimidiatus* (Cresson), *M. laphygmae* Viereck, *M. papiliovorus* Zitani, and *M. rubens* (Nees). Biological information, host associations, and cocoonforming behavior are included for *M. congregatus, M. rubens* and the new species *M. alejandromasisi, M. camilocamargoi, M. desmiae* and *M. sterictae.* This work provides the first record of *Meteorus* attacking Megalopygidae and Hesperiidae including *Chiomara asychis* (Stoll), *Pyrgus* sp., *Staphylus azteca* (Scudder), and *Staphylus* sp. Other new host records include the pyralids *Desmia tages* (Cram.), *Omiodes stigmosalis* (Warr.), and *Stericta albifasciata* (Druce), and the sphingids *Manduca sexta* (L.), and *Unzela japix* (Cram.). *Meteorus congregatus, M. dimidiatus,* and *M. rubens* are recorded for the first time in Costa Rica.

The Meteorinae is a moderately large, cosmopolitan subfamily with at least 183 described species worldwide. The subfamily consists of solitary or gregarious koinobiont endoparasitoids of larval Coleoptera and Lepidoptera (Muesebeck 1923; van Achterberg 1979; Huddleston 1980). The genus *Meteorus* Haliday is the most diverse and frequently encountered genus of the Meteorinae (*sensu* Shaw 1985, 1995; Maetô 1990b; Shaw and Huddleston 1991), and is the sister-group of the subfamily Euphorinae Foerster *s.s.* (Shaw 1985, 1988). For a detailed review of the biology of the Meteorinae see Shaw (1997), Zitani et al. (1997), Shaw (1995), and Shaw and Huddleston (1991).

There has been some revisionary work on the *Meteorus* species that occur in North America (Muesebeck 1923), Africa (Nixon 1943), the western Palearctic region (Huddleston 1980), and Australia and New Guinea (Huddleston 1983), but none for the Neotropical region. Although six species of *Meteorus* have been described from various localities in the neotropics (Shenefelt 1969), and the North American species *M. laphygmae* Viereck has been recorded from Costa Rica (Shenefelt 1969), the first new species from Costa Rica was described only recently (Zitani et al. 1997).

In order to keep the present work at a reasonable length only those species lacking a dorsope are treated here. A dorsope is a pit lying anterior to the spiracles on the dorsal surface of the first metasomal tergite; these pits occur in a pair (Fig. 1). Species lacking a dorsope (Figs. 3, 5) represent the majority of the material from the examined Costa Rican collections. This character has been used to separate spe-

cies of *Meteorus* by several previous authors (Muesebeck 1923; Huddleston 1980; Maetô 1989, 1990a). This group of species was also chosen because considerable biological information was available for 6 included species.

METHODS

Species treated in this work can be identified as members of the subfamily Meteorinae using the keys of Shaw (1995) or Shaw and Huddleston (1991). Specimens can be determined as *Meteorus* using the key of Shaw (1997) or Marsh *et al.* (1987).

Approximately 1,200 specimens of *Meteorus* were examined. The following institutions provided specimens for this study:

ANS: The Academy of Natural Sciences, Philadelphia, PA, USA.

INBio: Instituto Nacional de Biodiversidad, Santo Domingo de Heredia, Costa Rica.

PAS: The Polish Academy of Sciences, Warszawa, Poland.

RMSEL: Rocky Mountain Systematic Laboratory, University of Wyoming, Laramie, WY, USA.

USNM: United States National Museum, Smithsonian Institution, Washington, DC.

UCR: Museo de Insectos, Universidad de Costa Rica, San Pedro, San Jose, Costa Rica.

Specimens reared by D.H. Janzen and W. Hallwachs at the Area de Conservacion Guanacaste (ACG), Guanacaste Province, Costa Rica, are identified by a voucher number with "SRNP" in the middle. Each Janzen and Hallwachs rearing voucher number is for a single host larva. Information about the rearings can also be found at http://janzen.sas.upenn.edu/index.html.

The majority of the specimens were prepared and mounted at RMSEL using the technique of Sharkey (1988). Specimen label data were recorded exactly as they ap-

pear on the collection label to avoid misinterpreting data. However, when available, collection site information is added in brackets []. Authorship of all new species is attributed to the senior author (NMZ).

TAXONOMIC CHARACTERS AND TERMINOLOGY

The taxonomic characters used here follow the work of Huddleston (1980, 1983), Maetô (1989, 1990a), Shaw (1985), and Zitani *et al.* (1997). Microsculpture terminology follows that of Harris (1979). Morphological terminology follows Wharton *et al.* (1997).

As noted by Huddleston (1980), many characters of the head are important for distinguishing one species from another, especially the following: the size and degree of convergence of the eyes, width of the face in relation to the height, and the amount of twist of the mandibles. In this study, eye size was determined by the length of the eye, in anterior view, relative to the length of the head in anterior view. Eyes were designated as 'small' if the head height was equal to or greater than 1.6× the eye height in anterior view, and 'large' if the head height was less than 1.6× the eye height in anterior view. Eye convergence was designated as 'strongly convergent', 'convergent', or 'nearly parallel'. Eyes were called 'strongly convergent' if the maximum/minimum face width ratio was 1.7 or greater, 'convergent' if the maximum/minimum face width ratio was 1.4–1.7, and 'nearly parallel' if the maximum/minimum face width ratio was less than 1.4.

The amount of twist of the mandibles can sometimes be difficult to determine. An untwisted mandible, in anterior view, is flat and has two visible teeth. In a strongly twisted mandible it appears as though the ventral tooth has rotated to a position posterior to the dorsal tooth. Thus the mandible, in anterior view, has only one apparent tooth, and the apical

portion appears twisted (Fig. 9). Also, mandibles that are untwisted are usually larger (longer and broader in anterior view) than strongly twisted mandibles. Moderately twisted mandibles, where the ventral tooth has only partially rotated, are the most difficult to determine but are present in only two species, *Meteorus coffeatus* and *Meteorus micrommatus* (Fig. 10). Moderately twisted mandibles are also longer, and broader at the base, compared to strongly twisted mandibles.

The number of flagellomeres and size of the ocelli usually vary only slightly within a species, and these characters, therefore, are also useful (Huddleston 1980). In this text, the diameter of a lateral ocellus is expressed relative to the length of the ocellocular distance (distance from edge of lateral ocellus to border of compound eye). The acronym OCD is used for ocellar diameter, and OCOD for ocell-ocular distance. The term 'small ocelli' is used when the OCOD is greater than or equal to 1.5× OCD, and the term 'large ocelli' when the OCOD is less than 1.5× OCD. The width of the apical flagellomere was measured as the width of the base of the flagellomere.

Wing venation characters generally are not stable within species and therefore should not be used as diagnostic characters (Huddleston 1980). For example, the position of the forewing vein m-cu (whether it is antefurcal, interstitial, or postfurcal) often exists in two of these states within a species. One exception may be the shape of the forewing second submarginal cell, which appears to be stable in some species (e.g., *M. congregatus, M. papiliovorus*).

Muesebeck (1923) and Huddleston (1980) have pointed out the importance of: 1) the presence or absence of a dorsope

and 2) whether or not the ventral borders of the tergite are joined. Huddleston (1980) noted that when a dorsope is present it is distinct (Fig. 1), even if it is small, and that the ventral borders of the first tergite are never joined beneath, and usually widely separated (Fig. 2). In specimens where the dorsope is absent (Figs. 3, 5), the ventral borders are always touching or nearly touching (Figs. 4, 6), partially fused (Fig. 7) or completely fused (Fig. 8).

The length of the ovipositor was measured from the base of the hypopygium to the tip of the ovipositor and was expressed as relative to the length of the first tergite. The term 'long ovipositor' was used when the length of the ovipositor was equal to or greater than 2.0 × the length of the first tergite, and the term 'short ovipositor' was used when the length of the ovipositor was less than 2.0 × the length of the first tergite.

As noted by Huddleston (1980), color and body size are among the least stable characters and often vary within a species. The color of a specimen can vary depending on how it was preserved, how long it remained in alcohol before it was prepared, and exposure to light. Although the colors 'white' and 'yellow' are used in this text, often the specimens described as having these colors actually have a clear integument, and it is the internal tissues that provide the color. Overall, color is somewhat generalized in the species descriptions and should not be used without other diagnostic characters.

Specimens can have a variety of metasomal positions, therefore the body length is a combined measurement of the length from the head to the end of propodeum, added to the length from the base of the first tergite to the end of the metasoma (not including the ovipositor).


KEY TO COSTA RICAN *METEORUS* FEMALES WITHOUT A DORSOPE

1.   Mandible strongly twisted (Fig. 9); propodeum rugose (Figs. 15–16) or areolate-rugose (Fig. 17), but never carinate, with a distinct median and transverse carina creating very large, defined areolae (Fig. 18) 2
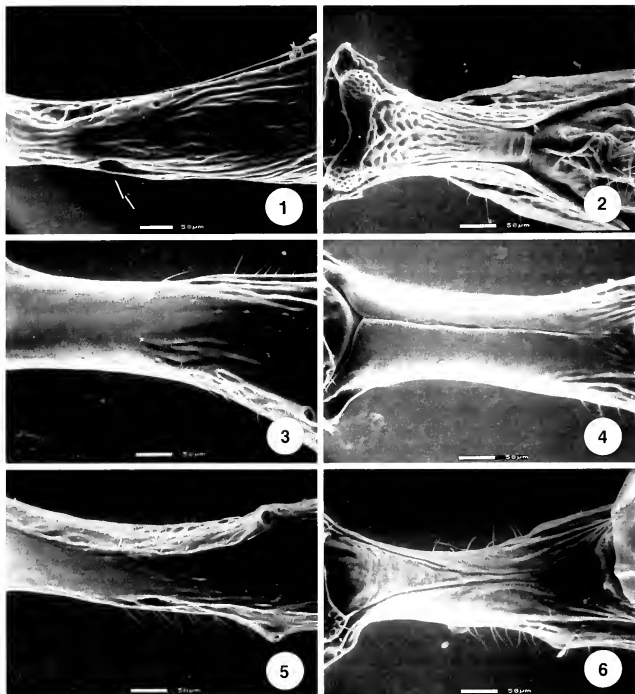
Figs. 1–6. 1, 3, 5. First metasomal tergite, dorsal view. 1, *Meteorus sp.*, dorsope present; 3, *Meteorus rogerblancoi*, dorsope absent, surface smooth and rounded; 5, *Meteorus pseudodimidiatus*, dorsope absent, surface not completely smooth and tergite flattened laterally. 2, 4, 6. First metasomal tergite, ventral view. 2, *Meteorus sp.*, (dorsope present) ventral borders widely separated; 4, *Meteorus rogerblancoi*, (dorsope absent) ventral borders of first tergite joined completely along basal ½ of segment and suture apparent; 6, *Meteorus dimidiatus*, (dorsope absent) ventral borders touching for only short distance apically.

–   Mandible moderately twisted (Fig. 10) or not twisted, broad and flat at base; propodeum carinate, with a distinct median and transverse carina creating very large, defined areolae (Fig. 18), or rugose (Figs. 15–16) 15

2(1).   Wings very dark, infused with blackish pigment, and second submarginal cell of forewing strongly narrowed anteriorly; forewing vein 3RSa usually much shorter than r, or some-
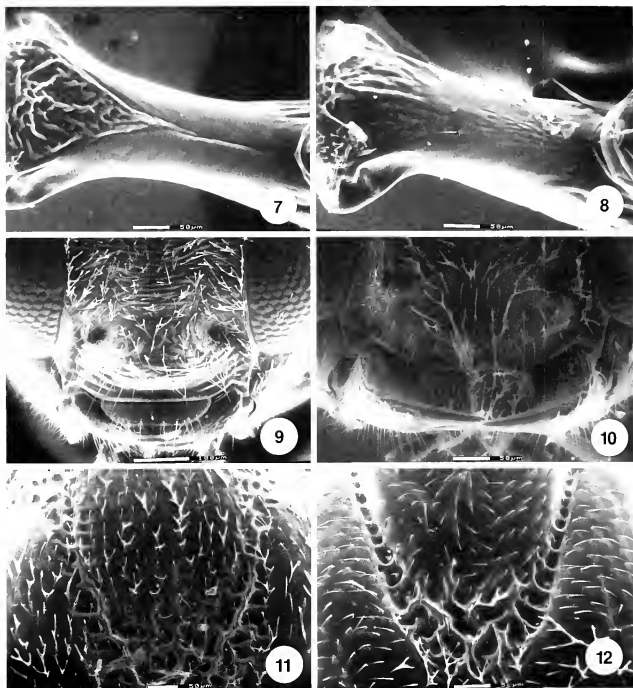
Figs. 7–12. 7–8. *Meteorus congregatus*, first metasomal tergite, ventral view (dorsope absent). 7, ventral borders partially fused (separated basally, fused apically); 8, ventral borders fused, no indication of suture. 9–10. Anterior view of head, 9, *Meteorus rogerblancoi*, mandibles strongly twisted, with one visible tooth; 10, *Meteorus coffeatus*, mandibles moderately twisted, with ventral tooth partially visible. 11–12. Mesoscutum, dorsal view, showing notauli. 11, *Meteorus rogerblancoi*, notauli not distinct, broad, rugose, and converge posteriorly in a rugose area; mesonotal lobes not well-defined; 12, *Meteorus megalops*, notauli distinct, linear, foveolate anteriorly, and converge posteriorly in a rugose area, mesonotal lobes well-defined.

times nearly equal; eyes small and nearly parallel; notauli distinct and linear, mesonotal lobes well-defined (Fig. 12) 3

–   Wings not dark, at most with brownish pigment; second submarginal cell of forewing not strongly narrowed anteriorly; forewing vein r usually much shorter than, or sometimes equal to, 3RSa; eyes small or large, convergent or nearly parallel; notauli distinct, linear and mesonotal lobes well-defined (Fig. 12), or not (Fig. 11) 4

3(2). Head height 2.0× eye height; occipital carina incomplete, widely separated medially (Fig. 23); first tergite with costae parallel, usually yellowish in color and only slightly darker apically, ventral borders fused (Figs. 7–8); highly gregarious (about 25–250 wasps per larva), attacking Sphingidae (Figs. 25–27) ...... *M. congregatus* **Muesebeck**

– Eyes somewhat larger, head height 1.7× eye height; occipital carina not complete but with only a small separation medially (Fig. 21); first tergite with costae convergent posteriorly, usually yellow basally, nearly black apically, ventral borders joined completely but not fused (Fig. 4); metasoma nearly black dorsally; solitary or gregarious, attacking Papilionidae (1–5 wasps per larva) (Fig. 28) .... *M. papiliovorus* **Zitani**

4(2). Ventral borders of first tergite not joined completely along basal ½ of segment (Fig. 6); notauli distinct, linear, and mesonotal lobes well-defined (Fig. 12), or not (Fig. 11) 5

– Ventral borders of first tergite joined completely along basal ½ of segment (Fig. 4) and notauli not distinct, broad, mesonotal lobes not well-defined (Fig. 11) 7

5(4). Notauli not distinct, broad, and mesonotal lobes not well-defined (Fig. 11) .... *M. rubens* **(Nees)**

– Notauli distinct, linear, and mesonotal lobes well-defined (Fig. 12) 6

6(5). Ovipositor long, equal to, or greater than 2.0× length of first tergite; malar space about equal to basal width of mandible .... *M. dimidiatus* **(Cresson)**

– Ovipositor short, less than 2.0× length of first tergite; malar space longer than basal width of mandible .... *M. pseudodimidiatus* **Zitani, new species**

7(4). Ocelli small (OCOD equal to, or greater than 1.5× OCD) 8

– Ocelli large (OCOD less than 1.5× OCD) 9

8(7). Occipital carina complete (Fig. 19), hind coxa rugolose ... *M. rogerblancoi* **Zitani, new species**

– Occipital carina not complete, poorly defined medially (Fig. 21), hind coxa polished, punctate .... *M. uno* **Zitani, new species**

9(7). Ovipositor short, less than 2.0× length of first tergite; tarsal claws with a well-defined lobe (Fig. 22) or without (Figs. 20, 24) 10

– Ovipositor long, equal to, or greater than 2.0× length of first tergite, and tarsal claws with a well-defined lobe (Fig. 22) 12

10(9). Occipital carina not complete, poorly defined medially (Fig. 21); longitudinal costae of first tergite parallel .... *M. alejandromasisi* **Zitani, new species**

– Occipital carina complete (Fig. 19); longitudinal costae of first tergite convergent posteriorly 11

11(10). Malar space length 0.5× length of mandible basally; frons with a median tubercle anterior to median ocellus; sternaulus foveolate, not broad (Fig. 14); hind coxa rugolose, with distinct but very fine carinae .... *M. dos* **Zitani, new species**

– Malar space greater than 0.5× mandible width basally; sternaulus rugose, broad, and long (Fig. 13); hind coxa rugolose-punctate .... *M. laphygmae* **Viereck**

12(9). First tergite laterally flattened (Fig. 5), and dorsal surface rugolose medially (costae not distinctly linear); eyes not so large and protuberant laterally ... *M. strictae* **Zitani, new species**

– First tergite not laterally flattened (Fig. 3), with longitudinal costae distinct, parallel, but sometimes convergent posteriorly and, eyes very large, strongly protuberant ... 13

13(12). Eyes convergent; clypeus somewhat flattened; occipital carina complete (Fig. 19); first tergite with costae somewhat convergent posteriorly; vertex not concave behind eyes .... *M. desmiae* **Zitani, new species**

– Eyes nearly parallel; clypeus not flattened; occipital carina not complete, poorly defined medially (Fig. 21); first tergite with costae parallel; vertex strongly concave behind eyes .... *M. camilocamargoi* **Zitani, new species**

14(1). Mandibles moderately twisted (Fig. 10) 15

– Mandibles not twisted 16

15(14). Malar space very short, 0.3× mandible width basally, eyes nearly touching base of
         mandible; eyes strongly convergent . . . . *M. coffeatus* Zitani, new species
  –   Malar space very long, 1.1× mandible width basally; eyes parallel . . . *M. micrommatus*
                                                                          Zitani, new species
16(14). Propodeum rugose, scutellar disc coarsely rugose and raised into a sharp point; eyes
         protuberant . . . . *M. corniculatus* Zitani, new species
  –   Propodeum carinate, with a distinct median and transverse carina creating very large,
         defined areolae (Fig. 18); scutellar disc rounded and smooth; eyes protuberant or not
         17
17(16). Eyes huge, bulging, and strongly convergent; antennae with 25 flagellomeres; large
         species, body length greater than 5.0 mm . . . . *M. megalops* Zitani, new species
  –   Eyes large but not huge and bulging; 19–20 flagellomeres, very small species, body
         length less than 4.0 mm 18
18(17). Notauli linear and converging posteriorly in a distinct V-shape; antennae with two
         white bands on F1–F3, and F9–F16; first tergite with very faint costae or none at all
         . . . . *M. mariamartae* Zitani, new species
  –   Notauli distinctly linear anteriorly but converging posteriorly in a rugose area (Fig.
         12); antennae without white bands; first tergite with distinct lateral costae . . . .
         . . . . *M. yamijuanum* Zitani, new species

Genus *Meteorus* Haliday

Meteorus Haliday 1835: 24.

Diagnosis for species lacking a dorsope:
Body color: variations of white, yellow,
orange, reddish-brown, brown, dark
brown, or nearly black. **Body length:** 2.5–
6.0mm. **Head:** maxillary palpi 6-segment-
ed; labial palpi 3-segmented; antenna with
19–34 flagellomeres, antennae filiform,
apical flagellomere pointed; head 1.1–1.4×
wider than high, head height 1.3–2.0× eye
height; eyes nearly parallel, convergent, or
strongly convergent in anterior view;
mandible strongly twisted, moderately
twisted, or not twisted; occipital carina
complete or incomplete. **Mesosoma:** no-
tauli and sternaulus present; epicnemial
carina present. **Legs:** tarsal claw lobed or
simple. **Wings:** vein m-cu antefurcal, in-
terstitial, or postfurcal. **Metasoma:** ventral
borders of first tergite fused completely or
partially, joined completely, but not fused,
along basal ½ of segment, or, meeting for
only a short distance; dorsal surface of
first tergite usually with costae posterior-
ly; metasoma polished dorsally, smooth
and shining; ovipositor 1.3–3.6× longer
than first tergite, usually straight but
sometimes curved.

### *Meteorus alejandromasisi* Zitani, new species
(Fig. 21)

Holotype female.—**Body color:** Yellow ex-
cept antennae light brown; metanotum
brown; propodeum brown dorsally and
posteriorly; hind leg with coxa and femur
brown apically, tibia and tarsus brown;
first tergite brown apically; T 2+3 brown
laterally, T 4 brown. **Body length:** 3.2 mm.
Head: antenna with 28 flagellomeres; fla-
gellar length/width ratios as follows: F1
= 2.5, F2 = 2.5, F3 = 2.5, F24 = 3.0, F25
= 3.0, F26 = 2.0, F27 = 2.0, F28 = 3.0;
head 1.2× wider than high, head height
1.6× eye height, eyes small but protuber-
ant, slightly convergent in anterior view;
maximum face width 1.3× minimum face
width; minimum face width 1.4× clypeus
width; malar space length 1.3× mandible
width basally; ocelli large, OCOD 0.9×
OCD; mandible strongly twisted; occipital
carina not complete, poorly defined me-
dially (Fig. 21). **Mesosoma:** notauli not
distinct, broad, rugulose, and mesonotal
lobes not well-defined (as in Fig. 11); scu-
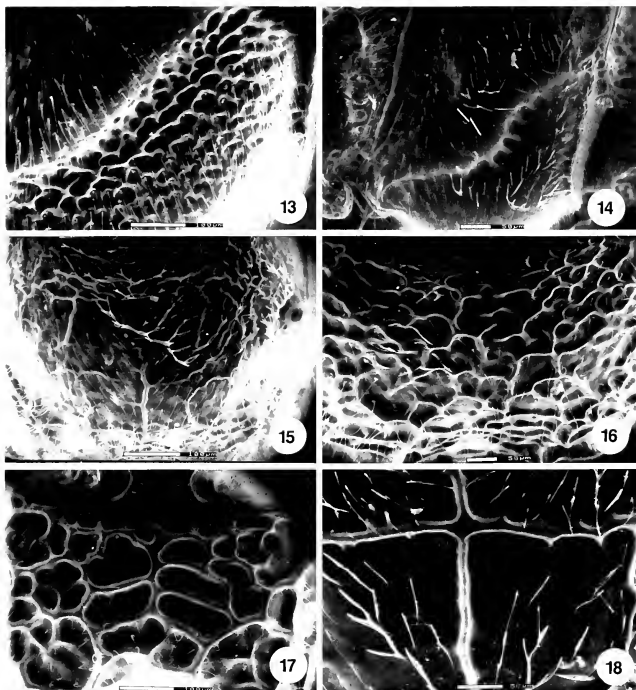
Figs. 13–18. 13–14. Mesopleuron, showing sternaulus. 13, *Meteorus laphygmae*, sternaulus broad and rugose; 14, *Meteorus yamjuanum*, sternaulus foveolate but not broad. 15–18. Propodeum, dorso-posterior view. 15, *Meteorus pseudodimidiatus*, showing finely rugose sculpturing; 16, *Meteorus rogerblancoi*, showing rugose sculpturing; 17, *Meteorus congregatus*, showing areolate-rugose sculpturing; 18, *Meteorus megalops*, showing carinate sculpturing. Notice a distinct median and transverse carina creating very large defined areolae.

tellar furrow with 3 carinae; sternaulus rugose, long but not broad; mesopleuron polished, shining around sternaulus; propodeum areolate-rugose, median depression weakly present. **Legs:** hind coxa rugulose; tarsal claw with a small lobe, strongly curved. **Wings:** forewing length 3.0 mm; vein m-cu interstitial; vein 3RSa 1.8× length of r. **Metasoma:** (as in Fig. 3); ventral borders of first tergite joined completely along basal ½ of segment (as in Fig. 4); first tergite dorsally longitudinally costate with costae parallel; ovipositor short, 1.8× longer than first tergite.
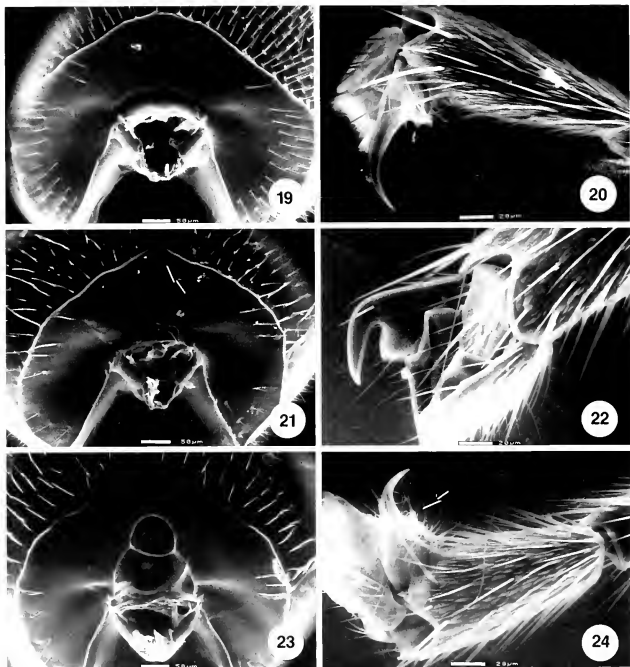
Figs. 19–24. 19, 21, 23. Posterior view of head showing occipital carina. 19, *Meteorus rogerblancoi*, occipital carina complete; 21, *Meteorus alejandromasisi*, occipital carina not complete, poorly defined medially; 23, *Meteorus congregatus*, occipital carina widely separated medially. 20, 22, 24. Tarsal claw. 20, *Meteorus megalops*, simple tarsal claw; 22, *Meteorus camilocamargoi*, tarsal claw with well-defined lobe and strongly curved; 24, *Meteorus pseudodimidiatus*, tarsal claw with small lobe or basal tooth

Variation of paratype females.—Brown areas vary from nearly black to nearly yellow; 26 flagellomeres; OCOD 1–1.3× OCD; forewing vein 3RSa 0.8× length of r, second submarginal cell slighty narrowed anteriorly; median depression of propodeum strongly present; dorsal costae of first tergite somewhat convergent posteriorly.

Variation of paratype males.—Brown areas vary from nearly black to nearly yellow; head height 1.8× eye height.

Cocoon.—Pale brown to brown, somewhat wooly, ovoid; length 3.9–4.1 mm,

1.6–1.8 mm wide medially; usually terminating anteriorly with a rounded nipple-like projection; not stuck together but often in a cluster and pointing outward from interior of caterpillar leaf shelter and next to dead or nearly-dead host; usually with anterior end attached to leaf substrate by a thread 0.7–2.0 mm in length which originates just posterior to adult emergence hole (note that thread originates from anterior end of cocoon and not the posterior end as is usual for *Meteorus*).

Material examined.—**Holotype female: COSTA RICA: Guanacaste Province:** ACG, Sector Horizontes, Vado La Esperanza, reared from last instar larva of *Staphylus* prob. *vulgata* (Moschler), 1993, Janzen & Hallwachs voucher 93-SRNP-5688. Deposited in RMSEL. **Paratypes: Guanacaste Province:** 8 females, 1 male, same data as holotype; 4 females, ACG, Sector Santa Rosa, Area Administrativa, reared fr. *Chiomara asychis* (Stoll), larva coll. 27 July 1993, wasps pupated 31 July, wasps eclosed 9 Aug., Janzen & Hallwachs voucher 93-SRNP-4212; 5 females, 1 male, ACG, Sector Santa Rosa, Cerco de Piedra, reared fr. *Pyrgus sp.*, larva coll. 25 Sept. 1993, wasps pupated 28 Sept., wasps eclosed 5 Oct., Janzen & Hallwachs voucher 93-SRNP-6387; 11 females, 1 male, ACG, Sector Cacao, Gongora, reared fr. *Staphylus sp.*, larva coll. 21 Aug. 1994, wasps pupated 4 Sept., Janzen & Hallwachs voucher 94-SRNP-6574; 4 females, ACG, Sector Cacao, Gongora, reared fr. *Staphylus sp.*, larva coll. 21 Aug. 1994, wasps pupated 9 Sept., Janzen & Hallwachs voucher 94-SRNP-6577. Deposited in INBio, UCR, RMSEL.

Distribution.—Known only from the holotype and paratype localities in the ACG (Sector Santa Rosa, dry forest, and Gongora, intergrade between wet and dry forest), Guanacaste Province.

Biology.—The rearing of this gregarious species (4–13 wasps per larva) constitutes the first record of *Meteorus* attacking Hesperiidae. All of the parasitized larvae were feeding on low plants in isolated dry forest old field succession. The type specimens were all reared from last instar larvae of Hesperiidae as follows: *Staphylus* prob. *vulgata* and *Staphylus sp.* feeding on Amaranthaceae, *Pyrgus sp.* feeding on *Sida rhombifolia* L. (Malvaceae), and *Chiomara asychis*, feeding on *Banisteriopsis muricata* (Cav.) Cuatr. (Malpighiaceae). Wasps pupated 3–4 days after collection of hosts and eclosed 7–9 days later.

Comments.—*Meteorus alejandromasisi* shares with *M. dos* and *M. laphygmae* the following combination of characters: strongly twisted mandibles, completely joined ventral borders of the first tergite, large ocelli, and a short ovipositor. *Meteorus alejandromasisi* can be distinguished from these species by an incomplete occipital carina. Intraspecific variation is high in this species.

Etymology.—This species is named in honor of Sr. Alejandro Masis in recognition of his outstanding interest in facilitating the parataxonomists in the Research Program of the ACG, and for being a major supporter of the Research Program activities and a Hesperiidae fanatic.

Meteorus camilocamargoi Zitani, new species
(Fig. 22)

Holotype female.—**Body color:** orange. **Body length:** 6.1 mm. **Head:** antenna with 35 flagellomeres; flagellar length/width ratios as follows: F1 = 2.6, F2 = 2.6, F3 = 2.0, F31 = 1.5, F32 = 1.5, F33 = 1.5, F34 = 1.5, F35 = 2.0; head 1.3× wider than high, head height 1.5× eye height, eyes large, nearly parallel in anterior view; maximum face width 1.3× minimum face width; minimum face width = clypeus width; malar space length = mandible width basally; ocelli large, OCOD 0.6× OCD; mandible strongly twisted (as in Fig. 9); occipital carina not complete, poorly defined medially (as in Fig. 21); vertex concave behind eyes. **Mesosoma:** notauli uncertain (see comments section); scutellar furrow

with 3 carinae; sternaulus rugose, not deep or broad but long; propodeum areolate-rugose (as in Fig. 17), median depression present. **Legs:** hind coxa punctate; tarsal claws lobed, strongly curved (Fig. 22). **Wings:** forewing length 4.6 mm; vein m-cu antefurcal; vein 3RSa 1.3× length of r. **Metasoma:** (as in Fig. 3); ventral borders of first tergite joined completely along basal ½ of segment (as in Fig. 4); first tergite with longitudinal costae parallel; ovipositor long, 3.5× longer than first tergite.

Variation of paratype female.—Body length 5.5 mm.

Variation of paratype male.—Unknown.

Cocoon.—Pale brown, ovoid; length 7.9 mm, 2.6 mm medially; does not terminate in a nipple-like projection; formed within the host cocoon; attached to the inside of the host cocoon by a thread, 0.7 mm in length, which originates from the wasp cocoon just posterior to the adult emergence hole (not from the posterior apex of the cocoon as is usual for *Meteorus*).

Material examined.—**Holotype female: COSTA RICA: Guanacaste Province:** ACG, Sector Santa Rosa, Casona, reared from *Omiodes stigmosalis* (Warr.) prepupa, 1978, Janzen & Hallwachs voucher 78-SRNP-143. Deposited in RMSEL. **Paratype: Guanacaste Province:** 1 female, same data as holotype except Janzen & Hallwachs voucher 78-SRNP-143.1. Deposited in RMSEL. It is not known to which specimen the cocoon belongs, deposited in RMSEL.

Distribution.—Known only from the type-locality, the dry forest of the ACG, Guanacaste Province.

Biology.—All type specimens were reared from larvae of the pyralid, *Omiodes stigmosalis,* feeding on *Ficus ovalis* Miq. (Moraceae). The host larva webs and mines through nearly ripe to fully ripe figs and turns them brown. The host larvae were collected 25 December 1978 and became prepupae 3 days later. The wasp lar-

vae emerged from the prepupae and formed cocoons within the host cocoon. The wasps eclosed 18 January 1979.

Comments.—*Meteorus camilocamargoi, M. desmiae,* and *M. sterictae* can be recognized by the following combination of characters: strongly twisted mandibles, first tergite with completely joined ventral borders, large ocelli, long ovipositor, and lobed tarsal claws. *Meteorus camilocamargoi* can be separated from these species by the following characters: first tergite not laterally flattened, parallel eyes, and a concave vertex. The type specimens were pinned through the mesonotum, therefore most of the notauli are destroyed.

Etymology.—This species is named in honor of Sr. Camilo Camargo in recognition of his extreme enthusiasm for facilitating the full computerization of the Research Program and other programs of the ACG, and being a major supporter of the Research Program activities.

Meteorus coffeatus Zitani, new species
(Fig. 10)

Holotype female.—**Body color:** brown except face light brown; mesosoma dark brown except fore and mid coxae yellow; legs brown; metasoma brown except first tergite dark brown; basal ⅔ of T 2+3 yellow. **Body length:** 4.0 mm. **Head:** antenna with 29 flagellomeres; flagellar length/width ratios as follows: F1 = 3.5, F2 = 3.5, F3 = 3.0, F25 = 1.5, F26 = 1.5, F27 = 1.5, F28 = 1.0, F29 = 2.0; head 1.2× wider than high, head height 1.6× eye height; eye small, strongly convergent in anterior view; maximum face width 1.7× minimum face width; minimum face width = clypeus width; malar space length 0.3× mandible width basally; ocelli small, OCOD 2.5× OCD; face polished, punctate; clypeus somewhat more convex than usual; antennal bases low on face; occipital carina complete; mandibles moderately twisted, broad and flat at base (Fig. 10). **Mesosoma:** notauli distinct, linear, and mesonotal lobes well-defined (as in Fig.

12); scutellar furrow with one median carina; sternaulus not broad or long, foveolate (as in Fig. 14); propodeum rugose, median depression absent. **Legs:** hind coxa polished, punctate; tarsal claws simple, swollen at base. **Wings:** fore wing length 3.8 mm; vein m-cu interstitial; vein 3RSa 1.7× length of r. **Metasoma:** ventral borders of first tergite separated basally, joined apically; first tergite dorsally longitudinally costate; ovipositor long, 2.6× longer than first tergite.

Variation of paratype female.—Forewing vein m-cu postfurcal.

Variation of paratype males.—T 2+3 almost completely yellow; eyes smaller, head height 1.8× eye height.

Cocoon.—Unknown.

Material examined.—**Holotype female: COSTA RICA: San Jose Province:** Zurqui de Moravia, 1600 m, vii. 1990, Paul Hanson. Deposited in RMSEL. **Paratypes: San Jose Province:** 1 female, Zurqui de Moravia, 1600 m, vii 1992, P. Hanson; 3 males, Zurqui de Moravia, 1600 m, iii 1991, P. Hanson. Deposited in INBio, UCR, RMSEL.

Distribution.—Known only from the holotype and paratype localities in San Jose Province.

Biology.—Unknown.

Comments.—*Meteorus coffeatus* and *M. micrommatus* both have moderately twisted mandibles but they can easily be separated by the size and degree of convergence of the eyes: *Meteorus coffeatus* has large convergent eyes whereas *M. micrommatus* has small parallel eyes. *Meteorus coffeatus* can easily be distinguished from the species with untwisted mandibles by the sculpturing on the propodeum.

Etymology.—From Latin meaning "the color of roasted coffee beans," for the brown body color of this species.

Meteorus congregatus Muesebeck
(Figs. 7–8, 17, 23, 25–27)

*Meteorus congregatus* Muesebeck 1939: 86.

Diagnosis of females.—**Body color:** yellowish-white except antennae black; head orange dorsally; pronotum orange dorsally; mesonotum orange; fore and mid legs darker with tarsi brown apically; hind leg with tibia dark brown apically, tarsus dark brown; first tergite light brown dorsally; metasoma light brown dorso-medially; wings very dark, infused with blackish pigment. **Body length:** 3.8–4.1 mm. **Head:** antenna with 27 flagellomeres; flagellar length/width ratios as follows: F1 = 2.5, F2 = 2.5, F3 = 3.0, F23 = 3.0, F24 = 3.0, F25 = 3.0, F26 = 2.0, F27 3.0×; head 1.1× wider than high, head height 2.0× eye height; antenna, nearly parallel in anterior view; maximum face width 1.1× minimum face width; minimum face width 1.3× clypeus width; malar space length 2.0× mandible width basally; face, clypeus polished, minutely punctate; ocelli small, OCOD 1.8–2.0× OCD; mandible strongly twisted; occipital carina incomplete, usually, but not always widely separated medially (Fig. 23). **Mesosoma:** notauli distinct, deep, foveolate, and mesonotal lobes well-defined; mesonotum polished, punctate, with short carina dorso-medially; scutellar furrow with one median carina; mesopleuron polished, punctate; sternaulus rugose; propodeum areolate-rugose, somewhat coarse (Fig. 17); median depression present. **Legs:** hind coxa smooth; tarsal claws simple, swollen basally. **Wings:** forewing length 3.3 mm; vein m-cu interstitial, antefurcal; vein 3RSa 0.6× length of r; second submarginal cell strongly narrowed anteriorly. **Metasoma:** (as in Fig. 3); ventral borders of first tergite partially fused (Fig. 7) or completely fused (Fig. 8); first tergite dorsally longitudinally costate, costae parallel; ovipositor short, thick at base, sometimes curved, 1.1–1.5× longer than first tergite.

Variation of males.—32 flagellomeres; head height 1.8× eye height.

Cocoon.—(Figs. 25, 27) A cluster of 25–250 pinkish-beige, wooly cocoons, all massed together next to host caterpillar
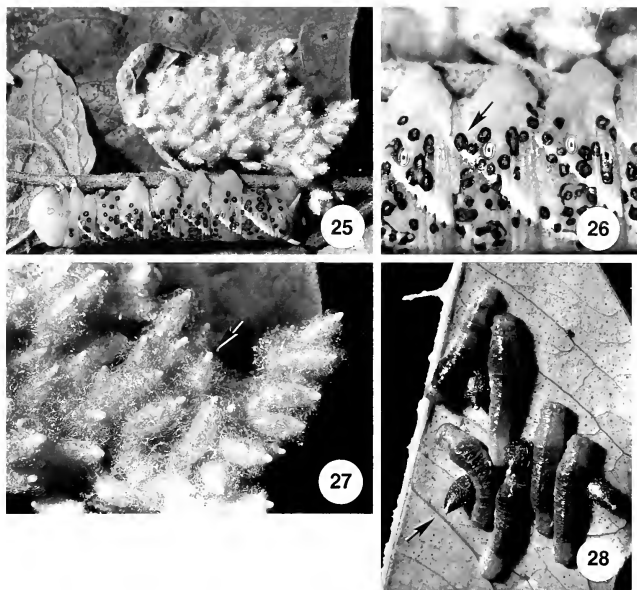
Figs. 25–28.   25–27. *Meteorus congregatus* and last instar host, *Manduca sexta*, at the ACG. Janzen & Hallwachs voucher 95-SRNP-7538. 25, Large cocoon cluster next to host cadaver; 26, Close-up ot host cadaver showing exit holes of *M. congregatus* larvae; 27, Close-up of cocoons. Notice cocoons terminate with a distinct nipple-like projection. 28. *Meteorus papiliovorus* cocoons next to host caterpillars, *Papilio anchisades*, at Santa Rosa dry forest, ACG. Notice cocoons terminate with a distinct nipple-like projection. Janzen & Hallwachs voucher 90-SRNP-2177.

and stuck to leaf substrate; each terminating with a distinct nipple-like projection.

Material examined.—**COSTA RICA: Guanacaste Province:** 51 females, 34 males, ACG, Sector Puente, Est. San Cristobal, 2 km W. of Dos Rios, reared from *Manduca sexta* (L.) larva on *Solanum torvum* Sw., larva collected 4 Aug. 1995, wasps eclosed 11–12 Aug. 1995, Janzen & Hallwachs voucher 95–7538; 92 females, 162 males, ACG, Sector Puente, Est. San

Cristobal, 2 km W. of Dos Rios, reared from *Manduca sexta* larva on *Solanum torvum*, larva collected 4 Aug. 1995, wasps eclosed 11–12 Aug. 1995, Janzen & Hallwachs voucher 95-SRNP-7539; 19 females, 7 males, ACG, [Sector El Hacha] Los Almendros, reared from *Unzela japix* (Cram.) larva, Janzen & Hallwachs voucher 96-SRNP-11208, 1996. Deposited in INBio, UCR, RMSEL.

Distribution.—Recorded only from local-

ities in wet forest of the eastern end of the ACG, Guanacaste Province, and in Panama (Canal Zone).

Biology.—*M. congregatus* is a gregarious species attacking sphingid larvae. A large number of wasp larvae (about 25–250) emerge from a single host larva. In Costa Rica *M. congregatus* was reared from *Manduca sexta* feeding on *Solanum torvum* (Solanaceae), and *Unzela japix* feeding on *Tetracera volubilis* L. (Dilleniaceae). Wasp larvae emerged from the last instar larva of the host (Figs. 25–27).

Comments.—*Meteorus congregatus* was described by Muesebeck (1939) from specimens reared from the larva of a sphingid, *Erinnyis ello* (L.), feeding on papaya, from Panama (Canal Zone). The Costa Rican specimens of *M. congregatus* show some morphological variation not discussed by Muesebeck in the original description: occipital carina with a wide separation medially (Fig. 23); ventral borders of first tergite partially or completely fused (Figs. 7–8); and ovipositor sometimes curved.

Meteorus congregatus is very similar morphologically to *M. papiliovorus*, and shares with *M. papiliovorus* and one other Neotropical species, *M. townsendi* Muesebeck, a Brazilian species, which has not been found to occur in Costa Rica, a narrowed second submarginal cell of the forewing. *M. congregatus* can be separated from these species by its widely separated occipital carina, fused ventral borders, and parallel costae of the first tergite. *M. congregatus* also has a cocoon that is very different from that of *M. papiliovorus* (Figs. 25, 28), and feeds on another family of Lepidoptera.

Meteorus corniculatus Zitani, new species

Holotype female.—**Body color:** body reddish-orange except antenna yellow basally, brown apically; legs yellow except mesothoracic leg with femur brown apically; metathoracic leg with femur, tibia, and tarsus brown apically; metasoma dark brown except first tergite orange. **Body length:** 4.5 mm. **Head:** antenna with 26 flagellomeres; flagellar length/width ratios as follows: F1 = 5.0, F2 = 5.0, F3 = 4.0, F22 = 2.3, F23 = 2.3, F24 = 2.0, F25 = 1.5, F26 = 2.7; head 1.3× wider than high, head height 1.5× eye height; eye large and protuberant, convergent in anterior view; maximum face width 1.4× minimum face width; minimum face width equal to clypeus width; malar space short, malar space length 0.5× mandible width basally; ocelli small, OCOD 2.3× OCD; face, clypeus polished; mandible not twisted. **Mesosoma:** notauli distinct, linear, foveolate, and mesonotal lobes well-defined; mesonotum polished except scutellar disc coarsely rugose and raised in a sharp point; scutellar furrow with a distinct median carina, two lateral carinae weakly present; mesopleuron rugose; sternaulus rugose, long and broad; propodeum coarsely areolate-rugose, median depression absent. **Legs:** hind coxa polished, punctate; tarsal claws simple (as in Fig.20). **Wings:** forewing length 3.6 mm; vein m-cu antefurcal; r 0.6× length of 3RSa; second submarginal cell quadrate. **Metasoma:** (as in Fig. 3); ventral borders of first tergite joined completely along basal ½ of segment; first tergite polished with faint costae posteriorly; ovipositor long, 2.2× longer than first tergite.

Variation of paratype females.—Body (except legs) almost entirely dark reddish-brown.

Variation of paratype male.—Antennae broken; head 1.2× wider than high; head height 1.8× eye height.

Cocoon.—Unknown.

Material examined.—**Holotype female: COSTA RICA: Puntarenas Province:** San Vito, Las Cruces, 1200 msnm, VIII–IX 1988, Coll. P. Hanson. Deposited in RMSEL. **Paratypes: Guanacaste Province:** 2 females, ACG, [Sector] Santa Rosa, Bosque Humedo-12-C, Malaise, Janzen & Gauld, 3.viii-24.viii.1985; 1 female, ACG, [Sector El Hacha] Los Almendros, E. Lo-

pez, 1 a 22 July 1992, L-N 334800, 369800, INBIO CR1000 735444; **Puntarenas Province:** 1 male, Rancho Quemado, 200 m, Peninsula de Osa, Oct 1992, M. Segura, L-S 292500, 511000 INBIO CR1000 969047; 2 females, San Vito, Estac. Biol. Las Alturas, 1500 m, vi. 1992, traps #1 & #2, Malaise, Paul Hanson; 1 female, R.F. Golfo Dulce, 3 km SW Rincon, 10 m, vii. 1991, Paul Hanson. **San Jose Province:** Zurqui de Moravia, 1600 m, viii. 1995, Malaise, Paul Hanson. Deposited in INBio, UCR, RMSEL.

Distribution.—Known only from the holotype and paratype localities in Guanacaste, Puntarenas, and San Jose Provinces.

Biology.—Unknown.

Comments.—This species has an unusual character found in no other *Meteorus* species: the scutellar disc is coarsely rugose and raised into a sharp point. In all other species the scutellar disc is rounded and smooth. The combination of the form of the scutellar disc, untwisted mandibles, and a coarsely rugose propodeum makes this species very easy to recognize.

Etymology.—Named for the form of the scutellar disc, from Latin meaning "having a horn-shaped appendage."

Meteorus desmiae Zitani, new species

Holotype female.—**Body color:** yellow-orange except head with temples and vertex black, antennae brown; pronotum black dorsally; propleura mostly black; mesonotum black; mesopleuron black anteriorly; propodeum dark brown dorsally; first tergite with lateral brown spots. **Body length:** 6.0 mm. **Head:** antenna with 31 flagellomeres; flagellar length/width ratios as follows: F1 = 3.5, F2 = 3.5, F3 = 3.0, F27 = 3.0, F28 = 2.0, F29 = 2.0, F30 = 2.0, F31 = 3.0; head 1.2× wider than high, head height 1.4× eye height; eye large and protuberant, ventral margin of eye nearly touching base of mandible; eyes slightly convergent in anterior view; maximum face width 1.6× minimum face width; minimum face width 0.8× clypeus width; malar space length 0.5× mandible width

basally; ocelli large, OCOD 0.5× OCD; face, clypeus punctate; clypeus somewhat flattened; mandible strongly twisted (as in Fig. 9); occipital carina complete (as in Fig. 19). **Mesosoma:** notauli not distinct, rugulose, and mesonotal lobes not well-defined (as in Fig. 11); mesoscutum polished, punctate, with median carina anteriorly; scutellar furrow with 3 distinct carinae; mesopleuron polished, punctate; sternaulus rugose, very long and extending dorsally; propodeum rugose, with two distinct carinae posterio-ventrad, median depression weakly present. **Legs:** hind coxa polished, punctate; tarsal claws lobed, strongly curved (as in Fig. 22). **Wings:** forewing length 4.6 mm; vein m-cu antefurcal; vein 3RSa 1.8× length of r. **Metasoma:** ventral borders of first tergite joined completely along basal ½ of segment (as in Fig. 4); first tergite dorsally longitudinally costate, costae parallel; ovipositor long, 2.5× longer than first tergite.

Variation of females.—Unknown.

Variation of paratype male.—Body length 5.0 mm; eyes nearly parallel, maximum face width 1.3× minimum face width; minimum face width equal to clypeus width; fore wing length 3.6 mm; vein 3RSa 1.3× length of r; hind coxa rugulose.

Cocoon.—Ovoid, brown; length 5.9 mm, 2.4 mm wide medially; formed within the remains of the larval leaf roll.

Material examined.—**Holotype female: COSTA RICA: Guanacaste Province:** [ACG, Sector Pitilla] Est. Pitilla, 700 m, 9 km S Sta Cecilia, P. Rios & C. Moraga, Oct 1990, L-N-330200, 380200, INBIO CR1000 398209. Deposited in RMSEL. **Paratype: COSTA RICA: Guanacaste Province:** 1 male with cocoon, ACG, [Sector] Santa Rosa, Casetilla Entrada, reared from *Desmia tages* (Cram.), 1983, Janzen & Hallwachs voucher 83-SRNP-574A. Deposited in RMSEL.

Distribution.—Known only from the holotype and paratype localities in the ACG, Guanacaste Province.

Biology.—The male paratype was reared

from a pyralid, *Desmia tages*, feeding on *Hamelia patens* Jacq. (Rubiaceae). This pyralid is a leaf roller/webber. The parasitoid emerged from the last instar larva.

Comments.—*Meteorus desmiae* shares with *M. camilocamargoi* and *M. sterictae* the following characters: strongly twisted mandibles, completely joined ventral borders of the first tergite, large ocelli, long ovipositor, and lobed tarsal claws. *Meteorus desmiae* can be separated from these species by its first tergite being not laterally flattened, convergent eyes, and complete occipital carina.

Etymology.—This species is named for the genus of the pyralid caterpillar it attacks, *Desmia*.

Meteorus dimidiatus (Cresson) (Fig. 6)

Perilitus dimidiatus Cresson 1872:83.

Diagnosis of females.—**Body color:** dark brown except antennae brown, orange around eyes, face yellow, pronotum yellow ventrally, legs yellow except hind leg with tibia and tarsus light brown, metasoma brown. **Body length:** 3.6 mm. **Head:** antenna with 27 flagellomeres; flagellar length/width ratios as follows: F1 = 4.0, F2 = 3.5, F3 = 3.0, F23 = 1.5, F24 = 1.5, F25 = 1.5, F26 = 2.0, F27 = 3.0; head 1.1× wider than high, head height 1.7× eye height, eye small, convergent in anterior view; maximum face width 1.4× minimum face width; minimum face width 1.1× clypeus width; malar space short, malar space length = mandible width basally; ocelli small, OCOD 2.0× OCD; mandible strongly twisted (as in Fig. 9); occipital carina not complete. **Mesosoma:** notauli distinct, finely areolate, and mesonotal lobes well-defined; scutellar furrow with one distinct median carina, 4 carinae weakly present; mesopleuron polished, punctate; sternaulus not deep or broad but long; propodeum finely areolate-rugose, with a weak carina medially (as in Fig. 15); median depression weakly present. **Legs:**

hind coxa polished, punctate; tarsal claws simple but swollen at base. **Wings:** forewing length 3.3 mm; vein m-cu post furcal; vein 3RSa 1.3× length of r. **Metasoma:** (as in Fig. 5); ventral borders of first tergite joined for only a short distance apically (Fig. 6); first tergite with lateral longitudinal carinae, rugulose medially; ovipositor long, 2.6× longer than first tergite.

Variation of males.—Unknown.

Cocoon.—Unknown.

Material examined.—**COSTA RICA: Guanacaste Province:** 1 female, [ACG, Sector Cacao, Estacion Cacao =] Estac. Mengo, S.W. Volcan Cacao, 1100 m IX–X 1989; 1 female, [ACG, Sector Cacao, Estacion Cacao =] Estac. Mengo, S.W. Volcan Cacao, 1100 m, 1988–1989] **Puntarenas Province:** 5 females, San Vito, Estac. Biol. Las Alturas, 1500 m, xii, 1991, Paul Hanson; 1 female, Estac. Biol. Las Alturas, xi 1991; 1 female, Estac. Biol. Las Alturas, i, 1992; 1 female Estac. Biol. Las Alturas, ii, 1992; **San Jose Province:** 1 male, Zurqui de Moravia, vi. 1990, 1600 m, P. Hanson; 1 female, Zurqui de Moravia, 1600 m, x–xii, 1990; 1 female, Zurqui de Moravia, iii, 1991; 2 females, Zurqui de Moravia, iii, 1992, P. Hanson. Deposited in INBio, UCR, RMSEL.

Distribution.—In Costa Rica Known from Guanacaste, Puntarenas, and San Jose Provinces. It is also widely distributed in North America and recorded from Patagonia (Shenefelt 1969).

Biology.—Unknown.

Comments.—*M. dimidiatus* and *M. pseudodimidiatus* are very similar morphologically, but can be separated by the length of the ovipositor and size of the eyes. These are the first records of *M. dimidiatus* in Costa Rica.

Meteorus dos Zitani, new species

Holotype female.—**Body color:** Head yellow, antenna black; mesosoma white except pronotum dark brown dorsally, mesonotum dark brown anteriorly and laterally, mesopleuron dark brown ven-

trally, propodeum dark brown dorsally and posteriorly, legs brown apically, hind coxa with dark brown patches laterally; metasoma white except first tergite dark brown apical ¾, T 2+3 dark brown laterally. **Body length:** 4.6 mm. **Head:** antenna with 28 flagellomeres; flagellar length/ width ratios as follows: F1 = 3.5, F2 = 3.0, F3 = 2.5, F24 = 2.5, F25 = 2.0, F26 = 2.0, F27 = 2.0, F28 = 2.5; head 1.2× wider than high, head height 1.3× eye height, eyes large and protuberant, ventral margins nearly touching base of mandible; slightly convergent in anterior view; maximum face width 1.3× minimum face width; minimum face width = clypeus width; malar space length 0.5× mandible width basally; ocelli large, ocell-ocular distance 0.8× greatest diameter of a lateral ocellus; mandible strongly twisted (as in Fig. 9); occipital carina complete (as in Fig. 19); frons with a median tubercle anterior to median ocellus. **Mesosoma:** notauli not distinct, broad, rugulose, and mesonotal lobes not well-defined (as in Fig. 11); scutellar furrow with 4 carinae; mesopleuron polished, minutely punctate; sternaulus foveolate, not broad or long; propodeum finely areolate-rugose, median depression weakly present. **Legs;** hind coxa rugulose, with distinct but fine carinae; tarsal claw with a very small lobe or basal tooth (as in Fig. 24). **Wings:** forewing length 4.4 mm; vein m-cu post furcal; vein 3RSa 1.7× length of r. **Metasoma:** (as in Fig. 3); ventral borders of first tergite joined completely along basal 1/2 of segment (as in Fig. 4); first tergite dorsally longitudinally costate, costae convergent posteriorly; ovipositor short, 1.5× longer than first tergite.

Variation of females.—Unknown.
Variation of males.—Unknown.
Cocoon.—Unknown.
Material examined.—**Holotype female:** COSTA RICA: San Jose Province: Zurqui de Moravia, 1600 m. I–II 1989, P. Hanson & I. Gauld. Deposited in RMSEL.

Distribution.—Known only from the holotype locality in San Jose Province.

Biology.—Unknown.

Comments.—This species has an unusual color pattern of dark brown and white patches, similar to the color pattern of *M. uno*, giving these two species a superficial similarity. Morphologically *M. dos* resembles *M. laphygmae*, as they share strongly twisted mandibles, completely joined ventral borders of the first tergite, large ocelli, short ovipositor, and a complete occipital carina. *Meteorus dos* can be further separated from this species by its very large eyes and median tubercle on the frons.

Etymology.—The specific epithet is an arbitrary combination of letters.

Meteorus laphygmae Viereck
(Fig. 13)

Meteorus laphygmae Viereck, 1913, Proc. U.S. Nat. Mus. 44:560.

Diagnosis of females.—**Body color:** yellow. **Body length:** 3.6–5.4 mm. **Head:** antenna with 31–34 flagellomeres; flagellar length/width ratios as follows: F1 = 5.0, F2 = 5.0, F3 = 2.7, F27 = 1.5, F28 = 1.5, F29 = 1.0, F30 = 1.3, F31 = 2.0; head 1.2× wider than high, head height 1.5× eye height, eyes large and protuberant; nearly parallel in anterior view; maximum face width 1.1× minimum face width; minimum face width = clypeus width; malar space length 0.8–1.2× mandible width basally; ocelli large, OCOD 1.0–1.4× OCD; mandible strongly twisted (as in Fig. 9); occipital carina complete (as in Fig. 19). **Mesosoma:** notauli not distinct, broad, rugulose, and mesonotal lobes not well-defined (as in Fig. 11); scutellar furrow with 3 carinae; mesopleuron polished, minutely punctate; sternaulus rugulose to rugose, broad and long (as in Fig. 13); propodeum rugose (as in Fig. 16) to areolate-rugose, median depression present, sometimes weak. **Legs:** hind coxa rugulose; tarsal claw with a small lobe, strongly curved. **Wings:** forewing length 3.2–4.7 mm; vein m-cu antefurcal or interstitial; vein 3RSa 1.0–0.4× length of r. **Metasoma:** (as in Fig.

3); ventral borders of first tergite joined completely along basal ½ of segment (as in Fig. 4); first tergite dorsally longitudinally costate, costae convergent posteriorly; ovipositor short, sometimes thick at base, 1.6–1.8× longer than first tergite.

Variation of males.—34 flagellomeres; eyes smaller, head height 1.9× eye height; maximum face width = minimum face width; propleura darker, propodeum brown dorsally, hind leg with tibia and tarsus darker, first tergite of metasoma brown apically..

Cocoon.—No reared specimens were examined from Costa Rica.

Material examined.—**COSTA RICA: Guanacaste Province:** 5 females, Hacienda El Vieja, Filadelfia, sugarcane, 110 m, V 1989, M. Garcia; 3 females, 1 male, [ACG, Sector Cacao] Volcan Cacao, Cerro Pedregal, 1000 m, II–IV 1989, I. Gauld & D. Janzen; 4 females, 3 males, Sotobosque, W side Volcan Cacao, 1100 m, II 1989, I. Gauld. Deposited in INBio, UCR, RMSEL. **Limon Province:** 1 female, Los Diamantes, Guapiles, 200m, 20/V/1988, col. Paul Hanson. Deposited in INBio, UCR, RMSEL.

Distribution.—In Costa Rica known from Guanacaste and Limon Provinces. Previously recorded from Venezuela, Colombia, and North America, and introduced into Hawai'i (Shenefelt 1969).

Biology.—Unknown.

Comments.—*Meteorus laphygmae* shares with *M. dos* and *M. alejandromasisi* the following combination of characters: strongly twisted mandibles, completely joined ventral borders of the first tergite, large ocelli, and a short ovipositor. *Meteorus laphygmae* can be separated from these species by a complete occipital carina and a longer malar space.

Meteorus mariamartae Zitani, new species

Holotype female.—**Body color:** orange-brown except head dark brown, antenna brown except F1–F3 white and with white annulus F9–F16; legs yellow; metasoma slightly paler than mesosoma. **Body length:** 2.5 mm. **Head:** antenna with 20 flagellomeres; flagellar length/width ratios as follows: F1 = 5.0, F2 = 5.0, F3 = 4.0, F16 = 2.0, F17 = 2.0, F18 = 2.0, F19 = 2.0, F20 = 3.0; antenna slightly tapered basally; head 1.4× wider than high, head height 1.5× eye height; eye large, convergent in anterior view; maximum face width 1.6× minimum face width; minimum face width 0.7× clypeus width; malar space short, malar space length 0.6× mandible width basally; ocelli small, OCOD 3.0× OCD; mandible not twisted; occipital carina complete (as in Fig. 19). **Mesosoma:** notauli finely areolate, distinctly linear, converging posteriorly in a distinct v-shape, and mesonotal lobes well-defined; scutellar furrow with one median carina; mesopleuron polished, smooth and shining; sternaulus foveolate, not broad (as in Fig. 14); propodeum carinate, with a distinct median and transverse carina creating very large, defined areolae (as in Fig. 18); median depression absent. **Legs:** hind coxa rugulose; tarsal claws simple (as in Fig. 20). **Wings:** fore wing length 1.9 mm; vein m-cu antefurcal; vein 3RSa 4.0× length of r. **Metasoma:** ventral borders of first tergite joined almost completely beneath, open basally for a short distance; first tergite dorsal surface rugulose and without any indication of costae; ovipositor long, 3.2× longer than first tergite.

Variation of paratype females.—Body color dark brown; dorsal surface of first tergite sometimes with very faint costae laterally.

Variation of males.—Unknown.

Cocoon.—Unknown.

Material examined.—Holotype **female: COSTA RICA: Puntarenas Province:** P[arque].N[acional]. Corcovado, Est. Sirena, 50 m, x–xii 1990. Deposited in RMSEL. **Paratypes: Guanacaste Province:** 1 female, [ACG, Sector Cacao, Estacion Cacao =] Estac. Mengo, SW Volcan Cacao, 1100 m, 1988–1989. **Puntarenas Province:**

2 females, same data as holotype; 1 female, Rancho Quemado, 200 m Peninsula de Osa, Dic 1992, M. Segura, L-S 292500, 511000. Deposited in INBio, UCR, RMSEL.

Distribution.—Known only from the holotype and paratype localities in Guanacaste and Puntarenas Provinces.

Biology.—Unknown.

Comments.—*Meteorus mariamartae* closely resembles *M. yamijuanum*, and *M. megalops.* These species have untwisted mandibles and a carinate propodeum (with large, defined areolae). *Meteorus mariamartae* can be distinguished from these other two species by its smaller eyes, unique notauli (converging posteriorly in a distinct V-shape), and small body size.

Etymology.—This species is named in honor of Srta. Maria Marta Chavarria Diaz in recognition of her unflagging support for the concept of biodiversity conservation throughout the history of the ACG and INBio.

Meteorus megalops Zitani, new species
(Figs. 12, 18, 20)

Holotype female.—**Body color:** Dark brown except; antenna brown with white annulus F13–F19; mesosoma with fore and mid coxae pale yellow; metasoma with first tergite below basally and apically, tergite 2+3 pale yellow for basal ¾. **Body length:** 5.4 mm. **Head:** antenna filiform with 25 flagellomeres; flagellar length/width ratios as follows: F1 = 5.0, F2 = 4.0, F3 = 3.0, F21 = 1.5, F22 = 1.5, F23 = 1.5, F24 = 1.0, F25 2.0x; head 1.3× wider than high, head height 1.4× eye height; eye large, strongly convergent in anterior view, bulging anteriorly and laterally; maximum face width 1.7× minimum face width; minimum face width 0.7× clypeus width; malar space short, malar space length 0.5× mandible width basally; ocelli small, OCOD 2.0× OCD; mandible not twisted; occipital carina complete (as in Fig. 19). **Mesosoma:** notauli distinct, foveolate, and mesonotal lobes well-defined (Fig. 12); scutellar furrow with a median carina, 2 lateral carinae weakly present; mesopleuron smooth, polished; sternaulus foveolate (as in Fig. 14); propodeum carinate, with a distinct median and transverse carina creating very large, defined areolae (Fig. 18); median depression absent. **Legs:** hind coxa polished, punctate; tarsal claws simple (Fig. 20). **Wings:** forewing length 4.8 mm; vein m-cu antefurcal; r 0.6× length of 3RSa; second submarginal cell slightly narrowed anteriorly. **Metasoma:** ventral borders of first tergite separated basally, joined apically; first tergite dorsally longitudinally costate; ovipositor long, thick at base, 3.6× longer than first tergite.

Variation of paratype females.—Mesopleuron reddish-orange ventrally; 24 flagellomeres, annulus on F9-F14;

Variation of paratype males.—29 flagellomeres; antennae without annulus, completely brown; eyes not so large and bulging.

Cocoon.—Unknown.

Material examined.—**Holotype female: COSTA RICA: San Jose Province:** Zurqui de Moravia, 1600 m, X–XII, 1989, col. Paul Hanson. Deposited in RMSEL. **Paratypes: COSTA RICA: Guanacaste Province:** 1 female, [ACG, Sector Pitilla] Est. Pitilla, 700 m, 9 km S. Sta. Cecilia, P.N. Guanacaste, C. Moraga, 31 mar–15 abr 1992, L-N 330200.380200. **Puntarenas Province:** 3 females, 8 males, San Vito, Estac. Biol. Las Alturas, 1500 m, vi. 1992, traps #1 & #2, Malaise, Paul Hanson; 1 female, San Vito, Estac. Biol. Las Alturas, 1500 m, v. 1992, in the forest, Malaise, Paul Hanson; 1 female, San Vito, Estac. Biol. Las Alturas, 1500 m, v. 1992, forest border, Malaise, Paul Hanson; 1 female, San Vito, Estac. Biol. Las Alturas, 1500 m, vi. 1992, Malaise, Paul Hanson; 1 female, Est. Biol. Las Alturas, 1500 m, Coto Brus, M.A. Zumbado, Nov 1991, L-S-322500,591300; 1 female, Est. Biol. Las Alturas, 1500 m, Coto Brus, F. Arayo, 23 mar a 2 may 1992, L-S-322500,591300; 2 females, Est. La Casona, 1520 m, Res. Biol. Monteverde, Ago 1992,

N. Obando L-N 253250,449700; **San Jose Province:** 1 female, Zurqui de Moravia, 1600 m IV/1989, col. Paul Hanson. Deposited in INBio, UCR, RMSEL.

Distribution.—Known only from the holotype and paratype localities in Guanacaste, Puntarenas, and San Jose Provinces in Costa Rica.

Biology.—Unknown.

Comments.—*Meteorus megalops* very closely resembles *M. mariamartae* and *M. yamijuanum*. These 3 species share in common untwisted mandibles and a carinate propodeum (with large, defined areolae, Fig. 18). *Meteorus megalops* is distinctive because of its huge, bulging, convergent eyes, longer antennae, and large body size.

Etymology.—From Greek meaning "large eyes."

Meteorus micrommatus Zitani, new species

Holotype female.—**Body color:** head black, antennae dark brown; mesosoma orange-brown except propleura dark brown; fore leg with coxa yellow, femur, tibia and tarsus brown; middle leg with coxa yellow, femur, tibia, tarsus brown; hind leg brown; wings dark; metasoma dark brown except first tergite orange basally, brown apically; tergite 2+3 yellow basally. **Body length:** 4.6 mm. **Head:** antennae broken, at least 22 flagellomeres; flagellar length/width ratios as follows: F1 = 3.0, F2 = 3.0, F3 = 4.0; head 1.2× wider than high, head height 1.9× eye height, eye small, nearly parallel in anterior view; maximum face width 1.1× minimum face width; minimum face width 1.2× clypeus width; malar space length long, 1.1× mandible width basally; ocelli small, OCOD 3.3× OCD; mandible moderately twisted, broad at base (as in Fig. 10); occipital carina complete (as in Fig. 19). **Mesosoma:** notauli distinct, foveolate, converging posteriorly in a depressed rugose area with 4 distinct carinae, and mesonotal lobes well-defined; scutellar furrow with 3 carinae; sternaulus distinct but not broad (as in Fig. 14); mesopleuron polished; propodeum areolate-rugose, median depression absent. **Legs:** hind coxa polished, punctate; tarsal claws simple. **Wings:** fore wing length 3.5 mm; vein m-cu antefurcal; vein 3RSa = length of r. **Metasoma:** ventral borders of first tergite separated but nearly touching apically; dorsal surface of first tergite with lateral costae, rugulose medially; ovipositor short, 1.4× longer than first tergite.

Variation of paratype females.—Mesosoma brown; body entirely dark brown; 29 flagellomeres.

Variation of males.—Unknown.

Cocoon.—Unknown.

Material examined.—**Holotype female: COSTA RICA: Puntarenas Province:** Fca. Cafrosa, 1300 m, Est. Las Mellizas, P. Internac. La Amistad, M. Ramirez, Jul 1991, L-S-316100, 596100, INBIO CR1000 624079. Deposited in RMSEL. **Paratypes: Guanacaste Province:** 1 female, [ACG, Sector Cacao] Est. Cacao, 1000–1400 m, Lado SO Vol. Cacao, C. Chaves, Ago 1991, L-N-32300, 375700, INBIO CR1000 571335; **Puntarenas Province:** 1 female, Est. La Casona, 1520 m, Res. Biol. Monteverde, J.A. Ugalde, Jul 1991, L-N-253250, 449700, INBIO CR1000 551283; 1 female, Est. Biol. Las Alturas, 1500m, Coto Brus, F. Araya, 23 mar a 2 may 1992, L-S 322500, 591300, INBIO CR1000 792767. Deposited in INBio, UCR, RMSEL.

Distribution.—Known only from the holotype and paratype localities in Guanacaste and Puntarenas Provinces.

Biology.—Unknown.

Comments.—*Meteorus micrommatus* is unusual in that although it lacks dorsopes, the ventral borders of the first tergite are very slightly separated. It shares with *M. coffeatus* moderately twisted mandibles but can easily be distinguished by its very small (head height 1.9× eye height) parallel eyes.

Etymology.—From Greek meaning "small eyes."

Meteorus papiliovorus Zitani
(Fig. 28)

Meteorus papiliovorus Zitani 1997:181. See Zitani et al. (1997) for a species diagnosis. No new material has been examined.

Meteorus pseudodimidiatus Zitani, new species
(Figs. 5, 15, 24)

Holotype female.—Body color: Dark brown except yellow around ventral borders of eyes, face yellow; pronotum with yellow spot ventrally, mesopleuron yellow on ventral ½; legs light brown; metasoma with T 2+3 white on basal ½, brown apically; T 4, 5 brown, white posteriorly and ventrally. Body length: 4.3 mm. Head: antenna with 29 flagellomeres; flagellar length/width ratios as follows: F1 = 4.5, F2 = 4.0, F3 = 3.5, F25 = 2.0, F26 = 1.5, F27 = 1.5, F28 = 1.5, F29 = 2.0; head 1.1× wider than high, head height 1.8× eye height; eye small, convergent in anterior view; maximum face width 1.5× minimum face width; minimum face width = clypeus width; malar space length 1.5× mandible width basally; ocelli small, OCOD 2.0× OCD; mandible strongly twisted. Mesosoma: notauli distinct and mesonotal lobes well-defined (as in Fig. 12); scutellar furrow with a median carina; sternaulus foveolate, not broad or long (as in Fig. 14); propodeum finely rugose, with a weak median carina (Fig. 15), median depression absent. Legs: hind coxa rugulose; tarsal claw with a small lobe or basal tooth (Fig. 24). Wings: forewing length 4.1 mm; vein m-cu post furcal; r 0.4× length of 3RSa. Metasoma: (Fig. 5); ventral borders of first tergite joined for only a short distance (as in Fig. 6); first tergite dorsally longitudinally costate; ovipositor short, 1.3× longer than first tergite.

Variation of paratype females.—30 flagellomeres.

Variation of males.—Unknown.

Cocoon.—Unknown.

Material examined.—Holotype female: COSTA RICA: Heredia Province: Vara Blanca, Finca Georgina, 2100 m, i–ii 1990, P. Hanson. Deposited in RMSEL. Paratypes: Heredia Province: 1 female, Vara Blanca, Finca Georgina, 2100 m, iii–iv 1990, P. Hanson; 1 female, Vara Blanca, Finca Georgina, 2100 m, vi–viii 1990, P. Hanson. San Jose Province: 1 female, 16km S. Empalme, 2600 m, III-IV 1989, P. Hanson & I. Gauld; 3 females, Cerro Muerte, 20 km S. Empalme, 2800 m, xi 88-i 1989, P. Hanson. Deposited in INBio, UCR, RMSEL.

Distribution.—Known only from the holotype and paratype localities in Heredia and San Jose Provinces.

Biology.—Based on the holotype and paratype localities M. pseudodimidiatus occurs at high elevations. The paratype record on Cerro de la Muerte, at 2800 m, is the highest elevation record for the known Costa Rican Meteorus.

Comments.—M. pseudodimidiatus is based on 7 female specimens and there is almost no morphological variation in the type specimens. This species is very similar to M. dimidiatus, and can be separated by the shorter length of the ovipositor and small size of the eyes.

Etymology.—Derived from Greek meaning "false dimidiatus" in reference to the many morphological similarities between this species and M. dimidiatus.

Meteorus rogerblancoi Zitani, new species
(Figs. 3–4, 9, 11, 16, 19)

Holotype female.—Body color: Very dark brown except antennae with white annulus F23–28; face light brown, orange around eyes; mesonotum yellow medially, scutellar disc yellow; pronotum white ventrally; propleura white; mesopleuron white medially; metapleura white; fore coxa white, leg light brown; mid coxa white, leg light brown; hind coxa white anteriorly, leg brown; first tergite white basally; T 2+3 white medially; metasoma white apically and ventrally. Body length: 4.3 mm. Head: antenna with 28 flagello-

meres; flagellar length/width ratios as follows: F1 = 3.5, F2 = 3.5, F3 = 2.5, F24 = 1.0, F25 = 1.0, F26 = 1.0, F27 = 1.0, F28 = 1.5; head 1.2× wider than high, head height 1.6× eye height, eye small, nearly parallel in anterior view; maximum face width 1.2× minimum face width; minimum face width = clypeus width; malar space length 1.5× mandible width basally; ocelli small, OCOD 1.50× OCD; occipital carina complete (fig. 19); mandible strongly twisted, and frons with faint horizontal carinae, clypeus rugulose (Fig. 9). **Mesosoma:** notauli not distinct, broad, rugulose, and mesonotal lobes not well-defined (Fig. 11); scutellar furrow with one distinct median carina, 4 lateral carinae weakly present; mesopleuron polished, punctate; sternaulus shallow but not broad or long; propodeum rugose (Fig. 16); median depression weakly present. **Legs:** hind coxa rugulose; tarsal claw with a small lobe, strongly curved. **Wings:** forewing length 4.0 mm; vein m-cu interstitial; vein 3RSa 2.0× length of r. **Metasoma:** (Fig. 3); ventral borders of first tergite joined completely along basal ½ of segment (Fig. 4); first tergite with longitudinal costae convergent ventrally; ovipositor short, 1.9× longer than first tergite.

Variation of paratype females.—Head completely yellowish; pronotum and mesopleuron completely white; body length 4.1–4.3 mm; 28–32 flagellomeres; maximum face width = minimum face width; fore wing vein m-cu postfurcal; ovipositor 2.0× length of first tergite.

Variation of paratype males.—Overall body color darker; 31 flagellomeres, annulus F27-F31, yellowish; head height 1.7× eye height.

Cocoon.—Unknown.

Material examined.—**Holotype female:** COSTA RICA: **Puntarenas Province:** San Vito, Estac. Biol. Las Alturas, 1750 m, IX–XI 1992, P. Hanson. Deposited in RMSEL. **Paratypes: Puntarenas Province:** San Vito, Estac. Biol. Las Alturas, 1500 m, P. Hanson; 9 females, 30 males, xi. 1991; 5 fe-

males, 16 males, xii 1991; 3 females, 20 males, i. 1992; 4 males, ii. 1992; 9 females, 21 males, forest border, v. 1992; 19 males, in the forest v. 1992; 6 females, 35 males, traps #1 & #2, Malaise, vi. 1992; 1 male, vi–vii 1992; 2 female, 8 males, same data as holotype; 5 females, 1 male, 1700 m, ii–iv, 1993. **San Jose Province:** 1 female, Zurqui de Moravia, 1600 m, vii. 1992, P. Hanson. Deposited in INBio, UCR, RMSEL.

Distribution.—Known only from the holotype and paratype localities at Biological Station Las Alturas, Puntarenas Province, and Zurqui de Moravia, San Jose Province.

Biology.—Unknown.

Comments.—*Meteorus rogerblancoi* shares with *M. uno* strongly twisted mandibles, completely joined borders of the first tergite, and small ocelli but can easily be separated from this species by its complete occipital carina. This is the most numerous of the species collected from Malaise traps, with nearly 200 individuals trapped at Biological Station Las Alturas during 1991–1993, and one individual from Zurqui de Moravia.

Etymology.—This species is named in honor of Sr. Roger Blanco in recognition of his tenacious and omnipresent guardianship of the coordination of the ACG Research Program, from its inception in 1990 to the present.

Meteorus rubens (Nees von Esenbeck)

For most of this century New World specimens of *M. rubens* were treated under the name *Meteorus vulgaris* (Cresson) (Muesebeck 1923) and *Meteorus leviventris* (Wesmael) (Shenefelt 1969; Marsh 1979). The correct taxonomic status of *M. rubens* was clarified by Huddleston (1980). This species was redescribed by Huddleston (1980) and Maetô (1990a), and the Costa Rican specimens do not differ from these descriptions.

Material examined.—**COSTA RICA: Guanacaste Province:** 5 females, 3 males, ACG, Sector Orosi, Est. Maritza, reared

from Megalopygidae, larva coll. 10 March, wasps eclosed 23 March 1992, Janzen & Hallwachs 92-SRNP-549. Deposited in IN-Bio, UCR, RMSEL.

Cocoon.—Brown, wooly, ovoid; length 3.9–4.7 mm, 1.7–1.9 mm wide medially; in mass of 30 (not all adults eclosed) cocoons, most terminating in a nipple-like projection.

Distribution.—In Costa Rica known only from the ACG, Guanacaste Province.

Biology.—30 wasp larvae emerged from a last instar megalopygid larva feeding on *Ardisia revoluta* Kunth (Myrsinaceae). The host larva was collected on 10 March 1992, the wasps pupated on 19 March, and the wasps eclosed 23 March 1992 (only 8 adults eclosed).

Comments.—*Meteorus rubens* is a widespread species, Holarctic in distribution, and also recorded from Mexico and Brazil (Shenefelt 1969).

Meteorus rubens shares with *M. dimidiatus* and *M. pseudodimidiatus* strongly twisted mandibles and ventral borders of first tergite not joined completely. *Meteorus rubens* can easily be separated from these species by its indistinct and broad notauli, and poorly defined mesonotal lobes. This is the first record of any species of *Meteorus* being reared from a megalopygid.

Meteorus sterictae Zitani, new species

Holotype female.—**Body color:** yellow except antennae brown; propodeum brown dorso-medially; hind leg with femur brown apically, tibia and tarsus brown; first tergite dark brown. **Body length:** 4.6 mm. **Head:** antenna with 28 flagellomeres; flagellar length/width ratios as follows: F1 = 3.6, F2 = 3.2, F3 = 2.3, F24 = 3.0, F25 = 2.0, F26 = 3.0, F27 = 2.0, F28 3.0; head 1.1× wider than high, head height 1.5× eye height; eyes large, nearly parallel in anterior view; maximum face width 1.3× minimum face width; minimum face width 1.1× clypeus width; malar space length 0.7× mandible width basally; ocelli large, OCOD = OCD; face punctate, with

faint transverse carinae near base of antennae; clypeus rugulose; mandible strongly twisted (as in Fig. 9); occipital carina complete (as in Fig. 19). **Mesosoma:** notauli not distinct, broad, rugulose, and mesonotal lobes not well-defined (as in Fig. 11); mesoscutum polished, punctate laterally; scutellar furrow with 3 distinct carinae; mesopleuron polished, punctate; sternaulus rugose, broad and long (as in Fig. 13); propodeum areolate-rugose, median depression present. **Legs:** hind coxa rugulose; tarsal claw lobed, strongly curved (as in Fig. 22). **Wings:** forewing length 3.4 mm; vein m-cu antefurcal; 3RSa 1.6× length of r; **Metasoma:** (as in Fig. 3); ventral borders joined completely along basal ½ of segment (as in Fig. 4); first tergite with dorsal, lateral, longitudinal costae which converge posteriorly, medially rugulose; ovipositor long, 3.0× longer than first tergite.

Variation of paratype female.—yellow areas may be orange; body length 3.9 mm; forewing length 3.3 mm; forewing vein 3RSa 2.0× length of vein r; ovipositor 3.4× longer than first tergite

Variation of paratype males.—body color as in females and propodeum almost completely brown; 29 flagellomeres; body length 3.8 mm; head height 1.8× eye height; malar space length 1.5× basal width of mandible.

Cocoon.—Brown, ovoid; length 4.6 mm, 1.9 mm wide medially; apparently not attached to substrate.

Material examined.—Holotype female: COSTA RICA: Guanacaste Province: ACG, [Sector] Santa Rosa, dry forest, reared from *Stericta albifasciata* (Druce) larva, 1996, Janzen & Hallwachs voucher 96-SRNP-9074. Deposited in RMSEL. Paratypes: Guanacaste Province: 1 male, same data as holotype; 1 female, same data as holotype except Janzen & Hallwachs voucher 96-SRNP-9103; 1 male with cocoon, same data as holotype except Janzen & Hallwachs voucher 96-SRNP-9102. Deposited in RMSEL.

Distribution.—Known only from the holotype and paratype localities in the dry forest of the ACG, Guanacaste Province, Costa Rica.

Biology.—*Meteorus sterictae* attacks a pyralid, *Stericta albifasciata*, which is a gregarious webber on *Ocotea veraguensis* (Meisn.) Mez in the Santa Rosa dry forest. *Meteorus sterictae* is solitary; each wasp emerged from a single last instar larva.

Comments.—*Meteorus sterictae* resembles *M. camilocamargoi* and *M. desmiae*, by sharing the following characters: strongly twisted mandibles, completely joined ventral borders of the first tergite, large ocelli, long ovipositor, and lobed tarsal claws. However, *M. sterictae* can be distinguished from these two species by its laterally flattened first tergite, rugulose sculpturing on the dorsal surface of the first tergite, and smaller eyes. The rugulose sculpturing may give the false appearance of dorsopes.

Etymology.—This species is named after the genus of the pyralid caterpillar it attacks, *Stericta*.

Meteorus uno Zitani, new species

Holotype female.—**Body color:** dark brown except head orange, area between ocelli black; pronotum orange dorsally, white ventrally; mesonotum orange; propodeum white laterally and posteriorly; fore and mid legs pale yellow; first tergite white basally; metasoma white laterally and ventrally; wings dark, infused with brown pigment. **Body length:** 4.3 mm. **Head:** antenna with 28 flagellomeres; flagellar length/width ratios as follows: F1 = 2.7, F2 = 2.3, F3 = 2.0, F24 = 1.5, F25 = 1.5, F26 = 3.0, F27 = 2.0, F28 = 3.0; head 1.2× wider than high, head height 1.6× eye height; eye small but protuberant, nearly parallel in anterior view; maximum face width 1.2× minimum face width; minimum face width 1.5× clypeus width; malar space length 1.7× mandible width basally; ocelli small, OCOD 1.5× OCD; mandible strongly twisted (as in

Fig. 9); occipital carina not complete, poorly defined medially (as in Fig. 21); vertex, in dorsal view, descending vertically behind lateral ocelli. **Mesosoma:** notauli rugulose, not distinct, and mesonotal lobes not well-defined; scutellar furrow with one median carina; mesopleuron polished, punctate; sternaulus rugulose, broad but not long; propodeum areolate-rugose, median depression absent. **Legs:** hind coxa polished, punctate; tarsal claw with a small lobe or basal tooth, strongly curved. **Wings:** forewing length 4.0 mm; vein m-cu post furcal; r 0.6× length of 3RSa. **Metasoma:** (as in Fig. 3); ventral borders of first tergite joined completely along basal ½ of segment (as in Fig. 4); first tergite dorsally longitudinally costate, costae slightly convergent posteriorly; ovipositor short, thick at base, 1.7× longer than first tergite.

Variation of females and males.—Unknown.

Cocoon.—Unknown.

Material examined.—**Holotype female: COSTA RICA: Puntarenas Province:** San Vito, Las Cruces, 1200msnm, VIII–IX 1988, Coll. P. Hanson. Deposited in RMSEL.

Distribution.—Known only from the holotype locality in Puntarenas Province.

Biology.—Unknown.

Comments.—*Meteorus uno* shares with *M. rogerblancoi* strongly twisted mandibles, completely joined borders of the first tergite, and small ocelli, but can easily be separated from this species by its incomplete occipital carina.

Etymology.—The specific epithet is an arbitrary combination of letters.

Meteorus yamijuanum Zitani, new species
(Fig. 14)

Holotype female.—**Body color:** body dark brown except antenna light brown; pronotum yellow anteriorly; propleuron yellow; legs yellow except prothoracic tarsus light brown; mesothoracic tibia and tarsus light brown; metathoracic tibia and tarsus

light brown; metasoma brown except first tergite yellow basally and apically, tergite 2+3 yellow basally. **Body length:** 3.5 mm. **Head:** antenna with 19 flagellomeres; flagellar length/width ratios as follows: F1 = 4.5, F2 = 3.5, F3 = 3.0, F15 = 2.0, F16 = 1.5, F17 = 1.5, F18 = 1.5, F19 = 3.0; head $1.1\times$ wider than high, head height $1.7\times$ eye height; eye small, not protuberant, strongly convergent in anterior view; maximum face width $1.8\times$ minimum face width; minimum face width $0.6\times$ clypeus width; malar space short, malar space length $0.5\times$ mandible width basally; ocelli small, OCOD $2.3\times$ OCD; face, clypeus polished, punctate; mandible not twisted; occipital carina complete (as in Fig. 19). **Mesosoma** notauli distinct, foveolate, and mesonotal lobes well-defined (as in Fig. 12); mesoscutum polished; scutellar furrow with a median carina; mesopleuron polished; sternaulus foveolate, not broad (Fig. 14); propodeum carinate, with a distinct median and transverse carina creating very large defined areolae (as in Fig. 18), median depression absent. **Legs:** hind coxa polished; tarsal claws simple. **Wings:** forewing length 3.1 mm; vein m-cu antefurcal; r $0.8\times$ length of 3RSa; second submarginal cell quadrate. **Metasoma:** ventral borders of first tergite separated basally, joined apically; first tergite polished with costae posteriorly; ovipositor $2.6\times$ longer than first tergite.

Variation of paratype females.—Body length 2.9–3.5 mm; 18 flagellomeres; ovipositor 2.6–3.0$\times$ length of first tergite.

Variation of males.—Unknown.

Cocoon.—Unknown.

Material examined.—**Holotype female: COSTA RICA: San Jose Province:** Zurqui de Moravia, 1600 m, vii 1990, Col Paul Hanson. Deposited in RMSEL. **Paratypes: Puntarenas Province:** 10 females, San Vito, Estac. Biol. Las Alturas, 1500 m, vi 1992, traps #1 & #2, Malaise, P. Hanson; 1 female, San Vito, Estac. Biol. Las Alturas, 1500 m, v 1992, forest border, Malaise, col. P. Hanson; 5 females, San Vito, Estac. Biol.

Las Alturas, 1500 m, v 1992, in the forest, Malaise, col. P. Hanson; **San Jose Province:** 1 female, Zurqui de Moravia, 1600 m, vii 1990, col. Paul Hanson. Deposited in INBio, UCR, RMSEL.

Distribution.—Known only from the holotype and paratype localities in Puntarenas and San Jose Provinces.

Biology.—Unknown.

Comments.—*Meteorus yamijuanum* closely resembles *M. mariamartae*, and *M. megalops*. These species have untwisted mandibles and a carinate propodeum (with large, defined areolae). *Meteorus yamijuanum* can be distinguished from these other two species by its smaller eyes and the condition of the notauli.

Etymology.—This species is named in honor of Yamilet Acosa and Juan Acosa, in recognition of their hospitality as caretakers of Pitilla Biological Station, ACG, Guanacaste Province in 1995 and 1996.

DISCUSSION

A close examination of *M. congregatus* revises our concept of *Meteorus*. ESEM images show that the ventral borders of the first metasomal tergite are partially fused (Fig. 7) or completely fused (Fig. 8). Previously the ventral borders of the first tergite in *Meteorus* have been known to be completely joined with a suture clearly visible (Muesebeck 1923; Huddleston 1980) (as in Fig. 4). This is the first documentation of the total fusion of the ventral borders of the first metasomal tergite in *Meteorus*. Also, *M. congregatus* is unusual in that this character varies within the species (Figs. 7–8).

The biological information for *M. congregatus, M. alejandromasisi,* and *M. rubens* is also of interest. Most meteorines are solitary (Shaw 1995). *Meteorus congregatus* is unusual in that it is highly gregarious (25–250 individuals per host larva). *Meteorus alejandromasisi* is also gregarious (4–13 individuals per host larva). These rearings provide the first records of *Meteorus* attacking the sphingid genera *Manduca* and

Unzela, and the family Hesperiidae. Along with *M. papiliovorus,* *M. congregatus* and *M. alejandromasisi* suspend their cocoons from very short threads.

The new biological information presented here, combined with what is known about *M. papiliovorus,* provides a basis for speculation about a possible phylogeny of *Meteorus.* Species of *Meteorus* attacking concealed coleopteran larvae form unsuspended cocoons in the protected environment of the host, and these species have been hypothesized to be relatively primitive (Maetô 1990b). Species that suspend their cocoons also attack exposed hosts, and given that this suspended cocoon makes the parasitoid less accessible to potential enemies (Shaw and Huddleston 1991) it can be regarded as an adaptation to attacking exposed hosts. It follows that species that form a suspended cocoon are derived with respect to the more primitive species that form unsuspended cocoons in the host's pupation chamber.

Multiple egg-laying gregarious parasitism probably evolved from solitary parasitism in the Hymenoptera (Hanson and Gauld 1995). Gregariousness in *Meteorus* is presumed to be derived from solitary parasitism. Gregarious species such as *M. papiliovorus,* *M. congregatus,* and *M. alejandromasisi* may have secondarily lost their longer cocoon threads. In addition to the short cocoon threads, these three species have cocoons that terminate with a distinct nipple-like projection. Based on observations of photographs of a highly gregarious African species that forms a very organized cocoon mass, that species also has cocoons that terminate in a nipple-like projection. These gregarious species with this unique cocoon shape are hypothesized to be derived, and probably form a monophyletic group.

Of the 4 new species with host associations (*M. desmiae,* *M. camilocamargoi,* *M. alejandromasisi,* and *M. sterictae*), only one individual (a female of *M. desmiae*) was found in the examined Costa Rican Mal-

aise trap material. This suggests that there may be quite a few more species of *Meteorus* in Costa Rica, and that host rearing, or some other method of trapping, will be necessary to find them.

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The Species of *Asaphes* Walker from America North of Mexico, with Remarks on Extralimital Distributions and Taxa (Hymenoptera: Chalcidoidea, Pteromalidae)

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Abstract.—The species of *Asaphes* Walker (Pteromalidae: Asaphinae) are reviewed for the world and revised for America north of Mexico. Six species are recognized as valid in the region: *Asaphes brevipetiolatus* n. sp. (Canada, USA, Finland), *A. californicus* Girault, *A. hirsutus* n. sp. (Canada, USA, Mexico, Austria, Czech Republic, Finland, Greenland, Norway, Russia, Sweden), *A. petiolatus* Zetterstedt, *A. suspensus* (Nees), and *A. vulgaris* Walker. *Asaphes petiolatus* (revised status) is removed from synonymy under *A. vulgaris*. *Asaphes indicus* (Bhatnagar), described from India, is removed from synonymy under *A. vulgaris* and along with *A. rufipes* Brues, *A. lucens* (Provancher), *A. fletcheri* (Crawford), and *A. americanus* Girault is synonymized under *A. suspensus* (new synonymies). A lectotype is designated for *A. americanus*. *Asaphes huebrichi* (Brèthes) and *A. bonariensis* (Brèthes), described from Argentina and previously synonymized under *A. fletcheri* and *A. lucens*, respectively, are treated as *nomina inquirenda*. A key is given to distinguish males and females of the species in the region; diagnostic features are illustrated using scanning electron micrographs. Distribution and host data are summarized for each species in the Nearctic region, including records of *A. brevipetiolatus* parasitizing *Choristoneura fumiferana* (Clemens) (spruce budworm) and *Neodiprion abietis* (Harris) (balsam fir sawfly), likely as a hyperparasite. Remarks are also given on extralimital distributions of world species and generic composition of the subfamily, including the existence of an undescribed genus of Asaphinae in the Neotropical region, the likelihood of at least three undescribed species of *Asaphes* in regions other than the Nearctic, and the likelihood that most or all records of *A. suspensus* and *A. vulgaris* from the Neotropical region, and of *A. vulgaris* from at least the Afrotropical region of Africa, are misidentifications.

Species of *Asaphes* Walker are known from all continents except Antarctica and usually are considered to be exclusively hyperparasites of aphids. Graham (1969) revised the western European species and Kamijo and Takada (1973) revised the Japanese species. Two species were recognized from each area, *A. suspensus* (Nees) and *A. vulgaris* Walker from western Europe, and *A. suspensus* and *A. pubescens* Kamijo & Takada from Japan. Burks (1979) catalogued four species from America north of Mexico, *A. californicus* Girault, *A. lucens* (Provancher), *A. rufipes* Brues, and *A. vulgaris*, though Graham (1969) had previously suggested that *A. lucens*

might prove to be a synonym of *A. suspensus* and Peck (1951, 1963), Graham (1969), and Burks (1979) all questioned the presence of *A. vulgaris* in North America. The only other currently recognized valid name of *Asaphes* is *A. aphidi* (Risbec), which was described from Madagascar by Risbec (1959). Though Bouček (1976) clarified the generic placement of this species he stated that further study was required to determine whether it was a good species or a synonym of one of what was then thought to be two cosmopolitan species, *A. suspensus* and *A. vulgaris*. All other names described from other regions, including India and South America, were

synonymized under *A. suspensus* or *A. vulgaris*. The purpose of this study was to clarify the species composition and host relationships of *Asaphes* in America north of Mexico. To do so, other genera of Asaphinae and *Asaphes* from other regions were examined and this has resulted in remarks being included on extralimital distributions and taxa. The discovery that *A. petiolatus* was incorrectly synonymized under *A. vulgaris* and that other species in Europe, North America, and elsewhere exist that are similar to *A. vulgaris* or *A. suspensus* suggest that all currently accepted synonyms of these names should be reexamined.

Unlike in most pteromalids, males of most species of *Asaphes* are more readily identified to species than are females, particularly by differences in the antennal scape. Also important for differentiating species, in either sex, are setal pattern of the forewing (setation of basal cell and structure of speculum), presence or absence of setae on the metapleuron, sculpture of the frenum, and color pattern of the legs. Although females of *A. brevipetiolatus* n. sp. are distinguished by head structure, females of all the other species can only be identified correctly by using combinations of the above features because of overlap in character states. Further, different species, or even opposite sexes of different species, can be collected or reared at the same place, time, and even from the same host. Consequently, it is easy to misidentify some specimens, particularly females or poorly preserved and mounted individuals.

MATERIALS AND METHODS

Terms and abreviations used for structures follow Gibson (1997), with the following clarifications: 'scutellum' is used for that part of the scutellum anterior to the frenum (Fig. 50); the 'disc' of the forewing is the entire membranous region beyond the basal setal line (Fig. 68); and the 'funicle' is composed of all flagellar segments basal to the club (Fig. 19), including the basal-most ring-like segment, which is designated as fu_1 (Figs. 19, 20). Head width is maximum width measured in dorsal view; head height is maximum height excluding the mandibles measured in lateral view; measurements of eye length and malar space are maximum lengths in lateral view with both end-points equally in focus; petiole width is maximum width behind the anterior flange and petiole length is maximum length from the anterior flange to the abruptly declined posterior edge. In order to obtain the accurate measurements and observations of structure and sculpture necessary to correctly identify specimens, glare from incandescent light sources must be reduced by using flourescent light or by placing some light-diffusing material, such as a piece of translucent tracing acetate, close to the specimen (see Goulet and Mason, 1993: 60). Color of the coxae is not included as part of the leg color pattern because the coxae can be yellowish or brownish in teneral specimens. However, color of the trochanter is important and sometimes differs from the trochantellus so that it is important that these two structures be differentiated.

Diagnoses of females and males are based on Nearctic specimens, with additional variability based on specimens from other regions included in brackets or discussed under 'Remarks'. The distribution listed and mapped for each species is based only on specimens examined, not literature records. Exact locality and other label and museum data are given only for the two newly described species and the two relatively uncommon species in North America, *A. petiolatus* and *A. vulgaris*. However, in order to facilitate future studies in other regions, all countries from which extralimital specimens were seen are listed under 'Distribution', along with acronyms of collections containing the specimens. Extralimital distributions listed for *A. petiolatus*, *A. suspensus*, and *A.*

vulgaris are not exhaustive because no attempt was made to examine collections extensively in other than the Nearctic region. Unless stated otherwise, listed specimens, including paratypes of the two new species, are in the CNCI. Acronyms for the museums from which material for this study was examined are listed in acknowledgments. Label collection data has been standardized to a single format, with any additional explanatory data given in brackets. Some records from Canada have an F.I.S. number, which refers to the Forest Insect Survey of the Canadian Forest Service; localities from Finland often have two sets of numbers separated by a colon, which is a uniform grid reference (Grid 27°E) explained in Heikinheimo and Raatikainen (1981). Locality records from Canada are listed by province from west to east and alphabetically by state for USA. Locality records for Finland, Norway and Sweden are ordered by biological province listed south to north and west to east; abbreviations used on the labels for each province are included in brackets. The numerical codes included as part of the label data of specimens reared in Sweden by Gärdenfors are partly explained in Gärdenfors (1986: 21).

Aphidae (Homoptera) nomenclature is based on Eastop and Hille Ris Lambers (1976). Invalid combinations as given on labels of paratypic material are not italicized when given in association with the valid combination. Mackauer (1968) is used for nomenclature of Aphidiinae (Hymenoptera: Braconidae). The publications of A.A. Girault are numbered according to the bibliography of Dahms (1978).

Specimens for scanning electron microscopy (SEM) were prepared following Bolte (1996). The SEM micrograph negatives were scanned into a computer with a 35mm scanner, digitized, enhanced, and the final plates compiled and labelled using Adobe Photoshop℗. Distribution maps were generated using Quickmap ℗. Only those localities whose position could

be determined unequivocally were mapped so that the maps generally are less comprehensive than the listed records.

ASAPHINAE

Pteromalidae, Miscogasterinae, Asaphini Ashmead 1904: 328; Peck 1951: 536; Peck 1963: 601; Peck et al. 1964: 36.

Pteromalidae, Asaphinae; Graham 1969: 77; Burks 1979: 785; De Santis 1979: 125; Dzhanokmen 1987: 112; Bouček 1988: 343.

Diagnosis.—Head with occipital carina (Figs. 13–17) and genal carina (Figs. 8, 10, 12); left mandible bidentate and right mandible tridentate (Fig. 18) (except *Ausasaphes*). Antenna inserted conspicuously below middle of face, dorsal margin of torulus slightly above to distinctly below lower orbit (Figs. 1, 3, 5, 7, 9, 11) (except *Ausasaphes*), 13-segmented with 1–3 basal flagellar segments ring-like and/or without longitudinal sensilla (Figs. 19–30). Pronotum in dorsal view transverse-rectangular and convexly rounded into neck (shape not evident in Figs. 43–48 because of view). Mesoscutum (Figs. 43–48) with complete, sulcate notauli; axillae not advanced anterior to base of scutellum. Forewing of fully winged individuals (some *Ausasaphes* brachypterous) with marginal and submarginal veins separated by very short hyaline region, with relatively long stigmal and postmarginal veins, and with marginal vein at most 2.4 times as long as stigmal vein. Metasoma with transverse to elongate, tubular, sculptured petiole (Figs. 43–48).

Asaphes Walker

Asaphes Walker 1834: 151. Type species: *Asaphes vulgaris* Walker; by monotypy.
Isocratus Förster 1856: 53, 58. Unjustified replacement name according to Gahan and Fagan 1923: 18; incorrectly considered as preoccupied by *Asaphus* Brongniart.
Notopodion Dahlbom 1857: 295. Type species: *Asaphes vulgaris* Walker; subsequently designated by Graham 1990: 200. Synonymy by Graham 1990: 200.

Parectroma Brèthes 1913: 91. Type species: *Parectroma huebrichi* Brèthes; by original designation. Synonymy by De Santis 1960: 113.

Diagnosis.—Body black or, more commonly, dark with obscure to bright metallic green luster on head and mesosoma. Head with broad, shallow scrobal depression occupying most of region between eyes and anterior ocellus, and smoothly rounded into parascrobal regions (Figs. 1–12). Clypeus distinctly delineated by sutures and at least slightly convex (Figs. 4, 6). Eye superficially bare or sparsely setose (Figs. 1–16). Flagellum (Figs. 19–42) with fu_1 ring-like; fu_2 ring-like to longer than wide but without longitudinal sensilla; fu_3 with longitudinal sensilla. Pronotum about half as long as mesoscutum (length not evident in Figs. 43–48 because of view), evenly setose and with very fine to distinct net-like engraved sculpture except along posterior margin. Mesoscutum (Figs. 43–48) setose and sculptured like pronotum except lateral lobes usually broadly bare and sometimes smooth medially; axillae widely separated; scutoscutellar suture deeply sulcate along anterior margin of scutellum and for short distance along anteromedial margins of axillae (Figs. 43–48); scutellum bare at least posteromedially, with bare frenum delineated by variedly distinct transverse sulcus (Figs. 50, 52, 54); prepectus bare (Figs. 61, 63); mesopleuron with shiny, characteristically shaped femoral depression that includes abrupt or carinate anterior margin, deep transepisternal pit posteromedially, and arcuate transepisternal sulcus between pit and anterobasal edge of mesocoxa (Figs. 61, 63). Metanotum with three or more long, curved, paramedial setae directed toward median (Figs. 43–48); metapleuron with supracoxal flange and with two or more carinae at least on flange (Figs. 64–66); metacoxa conspicuously setose dorsobasally (Figs. 55–66). Propodeum coarsely, irregularly sculptured, without complete median carina though

often with variedly distinct, inverted Y-shaped carina, and with long white setae lateral to each spiracle (Figs. 43–48). Forewing with marginal vein relatively short, at most 0.3 length of submarginal vein, subequal in length or shorter than stigmal vein and shorter than postmarginal vein. Petiole at least two-thirds as long as propodeum, tubular but divided into dorsal and ventral parts by lateral sulcus (Figs. 63–66), dorsally reticulate and usually with irregular longitudinal carinae or stronger parallel keels (Figs. 43–48, 55–60), ventrally concave (Figs. 75, 76), and with anterior margin carinate (Figs. 43–48, 55–60). Gaster (Fig. 74) with terga low convex, non-collapsing, and mostly smooth and shiny, at most with very fine micropunctulate or coriaceous sculpture on Gt_3–Gt_7; Gt_1 and Gt_2 occupying at least half length of metasoma; Gt_1 basally with at most 4 setae dorsolaterally near petiole (Figs. 43–48, 55–60); Gs_1 concave basolaterally for reception of posterolateral margin of petiole and with $\wedge$-or $\cap$-shaped, often longitudinally carinate, basomedian projection (Figs. 75, 77, 78).

Discussion.—Asaphinae was first established as the tribe Asaphini in the pteromalid subfamily Miscogasterinae by Ashmead (1904). The group has been recognized as a subfamily of Pteromalidae since Graham (1969). Graham (1969: 78) stated that "the group appears to me distinct enough to be regarded, at least provisionally, as a subfamily," but he did not list any features that he considered differential and simply keyed out assigned genera in three places in his key to pteromalid subfamilies. He classified three genera in Asaphinae, *Asaphes*, *Hyperimerus* Girault, and *Bairamlia* Waterston, and tentatively proposed that *Bairamlia* Waterston (1929) was a junior synonym of *Parasaphodes* Schulz (1906) (Graham 1969: 84). However, Bouček (1988) not only treated *Parasaphodes* as a valid genus, he established the new subfamily Parasaphodinae for it. Bouček (1988) also removed *Bairamlia*

from Asaphinae, stating (p. 343) that it "seems to have closer relation with the current Miscogasterinae," and assigned two additional genera to the subfamily, *Ausasaphes* Bouček and *Enoggera* Girault. In addition to keying out assigned genera in two places in his key to genera Bouček (1988: 343) listed several features that "seem to be of major importance" for the subfamily. In the course of this study we saw specimens (CNCI) of an undetermined number of species from Central and South America that appear to belong to a fifth, undescribed genus that should be classified in Asaphinae.

It is beyond the scope of this study to determine the validity or limits of the subfamily in Pteromalidae or to resolve the relationships of the genera currently assigned to Asaphinae. The diagnoses given above are based on examination of the four currently assigned genera and the undescribed genus from the Neotropical region. *Asaphes* is distinguished from the other four genera by one apparent autapomorphy, the presence of long, paramedial, medially-directed setae on the metanotum (Figs. 43–48, 55–60). Other Asaphinae have the metanotum bare.

Both *Ausasaphes* and *Enoggera* are restricted to Australia and can be identified using the key provided by Bouček (1988). *Hyperimerus* was previously thought to be Holarctic, but during the course of this study we saw two females of a new species from Guatemala (CNCI) that is similar to *H. corvus* Girault and a single female (CNCI) from Thailand that represents another new species. *Asaphes* is the most widely distributed genus, though it likely was introduced into Australia by man (Bouček 1988). The keys of Graham (1969), Bouček and Rasplus (1991), or Bouček and Heydon (1997) can be used to differentiate *Asaphes* from *Hyperimerus* and from other pteromalid genera, though features used in all three keys require slight clarification. Graham (1969: 78) was inaccurate in stating that the gena of *Hyperimerus* is not bor-

dered by a sharp carina. Also, the petiole of *Asaphes* is transverse in some species though certainly it is much longer and more conspicuous than that of *Hyperimerus* (see Graham 1969: 78 and Bouček and Rasplus 1991: 30). The differentiating couplet for *Asaphes* in Bouček and Heydon (1997: 567) has to be modified with the discovery that some species have a distinctly sculptured frenum (Figs. 50, 52). *Asaphes* is further distinguished from *Hyperimerus* by having a setose metanotum (Figs. 43–60), the basal gastral tergum sparsely (Figs. 43–48, 55–60) rather than extensively setose near the petiole (Graham 1969), the prepectus bare (Figs. 61, 63) rather than setose, and the anterior margin of the femoral depression abruptly margined (Figs. 61, 63).

Species of what we consider to be the new Neotropical genus more closely resemble species of *Asaphes* than *Hyperimerus* because individuals have a long petiole and sparsely setose gaster. However, they are readily distinguished from species of *Asaphes* by a distinctly reticulate femoral depression, mostly smooth and shiny propodeum with a straight median carina, uniformly cylindrical and longitudinally carinate petiole, evenly convex and entirely or anteriorly longitudinally carinate first gastral sternum, and conspicuously setose eyes.

Biology.—Species of *Asaphes* have usually been considered to be hyperparasites of aphids (Homoptera: Aphididae), through the following primary parasites: Aphidiinae (Ichneumonoidea: Braconidae), Encyrtidae, and Aphelinidae (Chalcidoidea) (Hagen and van den Bosch 1968). However, there are a few published records of other Homoptera or predators of aphids as hosts. Lal (1934) reared a species identified as *A. vulgaris* from nymphs of the pear psylla, *Psylla pyricola* Förster (Homoptera: Psyllidae), in Scotland, and McMullen (1966) reared *A. suspensus* (misidentified as *A. vulgaris* in McMullen 1996, 1971, and in Philogíne and Chang 1978)

from *P. pyricola* in British Columbia, Canada. In both instances the *Asaphes* likely was a hyperparasite because also reared were *Prionomitus mitratus* Dalman (Encyrtidae) and *Trechnites insidiosus* (Crawford) (Encyrtidae), respectively. Brown and Clark (1960) reared three females of *A. brevipetiolatus* (as *Asaphes* sp.) from a puparium of *Neocnemodon coxalis* (Curran) (Diptera: Syrphidae), a predator of the balsam woolly aphid, *Adelges piceae* (Ratzeburg), likely as a hyperparasite because four specimens of *Syrphophagus quadrimaculatus* (Ashmead) (Encyrtidae) were reared from the same puparium. We have seen additional specimens of *A. brevipetiolatus* whose labels and host remains indicate they were reared from syrphid larvae, as well as rearings from the spruce budworm, *Choristoneura fumiferana* (Clemens) (Lepidoptera: Tortricidae), and the balsam fir sawfly, *Neodiprion abietis* (Harris) (Hymenoptera: Diprionidae). One specimen reared from *C. fumiferana* had an unidentified braconid cocoon associated, indicating that *A. brevipetiolatus* is a hyperparasite of the spruce budworm. Multiple specimens of *A. brevipetiolatus* associated with some rearings indicate that it is or can be a gregarious parasite.

Species of *Asaphes* are ectoparasites and except for *A. brevipetiolatus* apparently almost always solitary hyperparasites. Usually they are secondary hyperparasites, ovipositing into mature larvae, prepupae or pupae of the aphidiine, encyrtid, or aphelinid primary parasite within the aphid mummy. The primary parasite is almost immediately paralysed by a venom as part of oviposition and further devel-

opment is prevented regardless of the stage attacked (Sullivan 1972, Keller and Sullivan 1976, Bocchino and Sullivan 1981). Studies have also shown that species can be tertiary hyperparasites if the primary parasite has already been parasitized by some other secondary parasite, such as by species of Megaspilidae (Hymenoptera: Ceraphronoidea) or Charipidae (Hymenoptera: Cynipoidea) (Griswold 1929, Sullivan 1972, Carew and Sullivan 1993), or by another *Asaphes* (Levine and Sullivan 1983). Sullivan (1972) also showed for *A. californicus*, and Keller and Sullivan (1976) for *A. suspensus* (as *A. lucens*), that females will make multiple attacks and drillings of the same aphid mummy and frequently deposit more than one egg, though in all cases only a single adult emerged. However, superparasitism and multiparasitism are possible though probably very rare because Carew and Sullivan (1993) reared two dwarf female *A. suspensus* (as *A. lucens*) from one aphid mummy, and a dwarf male together or with another secondary parasite from another mummy.

Host feeding was demonstrated for *A. californicus* by Sullivan (1972), for *A. suspensus* by Keller and Sullivan (1976), and for *A. vulgaris* by Le Ralec (1995). A feeding tube is constructed prior to oviposition. Once feeding is completed the ovipositor is reinserted, the feeding tube broken by the ovipositor, and an egg deposited (Keller and Sullivan 1976). Griswold (1929) described and illustrated the immature stages. Mating habits are described by Griswold (1929) and Sekhar (1958).

KEY TO SPECIES OF *ASAPHES* WALKER FROM AMERICA NORTH OF MEXICO

1   Female 2
–   Male 7
2(1) Head in frontal view subquadrate with dorsal margin of torulus distinctly below lower
     orbit (Figs. 1, 2); malar space as long as width of eye or longer and at least 0.7 eye
     length (Figs. 1, 2); frenum with distinct net-like sculpture similar to that on scutellum
     (Figs. 49, 50, 55); forewing with very narrow speculum, the bare area closed basally

by setae and with line or lines of setae immediately behind submarginal vein on disc (Fig. 73) . . . . *Asaphes brevipetiolatus* n. sp.
– Head in frontal view transverse-subtriangular with dorsal margin of torulus about in line with lower orbit (Figs. 5–12); malar space at most about 0.8 width of eye and less than 0.65 eye length; frenum **usually** smooth and shiny except for longitudinal carinae near lateral margin (Figs. 56, 57, 59, 60); forewing sometimes with broad speculum and without setae near submarginal vein on disc (Figs. 68, 70) 3

3(2) Frenum with distinct, uniform, engraved net-like sculpture similar to scutellum (Figs. 51, 52); metapleuron bare (Fig. 65); petiole at most as long as wide and usually slightly though obviously transverse (Fig. 51); legs with at least trochanters and all but extreme apices of femora dark (trochantelli rarely yellowish); forewing with speculum basally closed by setae and with line or lines of setae immediately behind submarginal vein on disc (Fig. 72) . . . . *Asaphes petiolatus* Zetterstedt
– Frenum **usually** broadly smooth and shiny except for longitudinal carinae near lateral margins (Figs. 56, 59, 60), but if with obscure net-like sculpture paramedially and along posterior margin (Fig. 54) then metapleuron with at least some setae anteroventrally and often conspicuously setose (Figs. 61, 62); petiole usually at least slightly longer than wide except sometimes if metapleuron also setose (Figs. 44–48); legs usually entirely yellowish or at least with trochanters yellowish; forewing sometimes with broad, open speculum and without setae near submarginal vein on disc (Figs. 68, 70) 4

4(3) Metapleuron with at least several setae anteroventrally and usually more extensively setose (Figs. 61, 62); legs with trochanters dark, concolorous with femora; forewing with speculum basally closed by setae and with line or lines of setae immediately behind submarginal vein on disc (Fig. 71) . . . . *Asaphes hirsutus* n. sp.
– Metapleuron bare (Figs. 63–66) or at most with one or two short seta anteroventrally; legs usually with at least trochanters yellowish and often uniformly light colored, but if trochanters dark then speculum broad, open, and disc without setae near submarginal vein (Figs. 68, 70) 5

5(4) Speculum distinct, broad basally and narrowed toward stigmal vein, without setae near submarginal vein and immediately beyond basal setal line at least as wide as distance between first and third setal lines on disc (Fig. 70); head in dorsal view distinctly concave between inner orbits (Fig. 15); hind leg with trochanter and femur (except often trochantellus and apex) infuscate to black [east of Manitoba in Canada and northeastern seaboard states in USA] . . . . *Asaphes vulgaris* Walker
– Speculum variedly distinct, most often with line of setae behind submarginal vein separated from vein by distance at most equal to distance to next setal line (Fig. 67), but sometimes with relatively broad speculum basally closed by one or more setae (Fig. 68); head in dorsal view shallowly concave between inner orbits (Fig. 16); hind leg uniformly yellowish or with trochanter and trochantellus usually yellowish (very rarely black) in contrast to infuscate or black femur [transcontinental] 6

6(5) Legs more or less uniformly light-colored, yellow; forewing always with several setae close to submarginal vein on disc, hence speculum very poorly developed (Fig. 69). . . . . *Asaphes suspensus* Walker
– Legs with at least metafemur in part darker than light-colored metatrochanter unless metacoxa also light-colored, and then forewing with broad speculum except for one or two setae interrupting bare area (Fig. 68) . . . . *Asaphes californicus* Girault

7(1) Antenna with scape and pedicel yellowish, contrasting distinctly with dark flagellum; scape with ventral margin sinuate, protuberant ventrobasally and tapered apically (Figs. 31, 32); head with dorsal margin of torulus distinctly below lower orbit (Figs. 3, 4) . . . . *Asaphes brevipetiolatus* n. sp.
– Antenna more or less uniformly dark or with flagellum lighter in color; scape usually almost cylindrical or spindle-shaped (Figs. 34, 36, 38, 40, 42); head with dorsal margin of torulus almost in line with lower orbit (Figs. 5–12) 8

8(7)   Outer surface of scape with variously elongate-oval or lanceolate microsetose sensory region (Figs. 33, 34a); legs usually with at least metafemur distinctly darker than metatrochanter unless metacoxa also yellowish-brown .... *Asaphes californicus* Girault
   —   Outer surface of scape without distinct setal patch, at most with linear setal band along ventral margin (Fig. 40a); legs varied in color, but often uniformly yellowish or with trochanters similarly dark as femora 9

9(8)   Metapleuron with at least 3 setae in extreme anteroventral angle, and often much more extensively setose (Figs. 61, 62); forewing without distinct speculum, disc setose behind submarginal vein, the distance between vein and first setal line only slightly greater than distance between first and second setal lines; metafemur and metatrochanter usually dark; scape usually with slightly concave to flat ventral surface over at least apical two-thirds (Fig. 36a) .... *Asaphes hirsutus* n. sp.
   —   Metapleuron bare (Figs. 63–66); other features varied but usually either forewing with distinct speculum (Figs. 68, 70) or legs yellowish beyond coxae and scape without distinctly differentiated ventral surface 10

10(9)   Forewing disc with broad speculum narrowed toward stigmal vein, but over most of length width of bare band about equal to distance from first to third setal lines on dorsal surface of disc (Fig. 70); basal cell with single line of setae behind submarginal vein except apically near basal setal line (Fig. 70); legs often with at least metafemur dark; frenum smooth and shiny (Fig. 60); petiole at least 1.25 times as long as wide (Figs. 59, 60) .... *Asaphes vulgaris* (Walker)
   —   Forewing disc with at least 3 setae on dorsal surface separated from submarginal vein by distance about equal to width of vein or by distance between first and second setal lines (Figs. 69, 72); basal cell with more than one line of setae behind submarginal vein over most of length and often more or less uniformly setose (Figs. 69, 72); legs usually entirely yellowish; frenum sometimes with fine sculpture (Figs. 52, 58); petiole sometimes less than 1.2 times as long as wide (Fig. 58) 11

11(10) Legs entirely yellowish beyond coxae; frenum smooth and shiny (Fig. 59); petiole usually at least 1.2 times as long as wide (Fig. 59) .... *Asaphes suspensus* (Nees)
   —   Legs with trochanters, trochantelli and most of femora dark[2]; frenum with fine sculpture at least paramedially (Fig. 58); petiole at most 1.15 times as long as wide (Fig. 58) .... *Asaphes petiolatus* Zetterstedt

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[1] Females from western Europe sometimes with frenum quite broadly smooth with only very obscure sculpture.
[2] Some western European males with legs almost entirely yellow beyond coxae, see 'Recognition' for *A. petiolatus*.

Asaphes brevipetiolatus Gibson and Vikberg, new species
(Figs. 1–4, 13, 14, 19, 20, 31, 32, 43, 49, 50, 55, 64, 73)

Type material.—Holotype, female (CNCI, Type No. 22267): CANADA, New Brunswick, F'ton [Fredericton], em. June 23, 1966, R.C. Clark, AP.66-10-2, ex. Syrphidae. Allotype, male (CNCI): same data as holotype. Paratypes: **CANADA: Yukon Territory:** Ross River, 16.IV–31.VIII.84, S.&J. Peck, aspen willow river terrace (1 ♀, 2 ♂). **British Columbia:** Manning Provincial Park, 2 km N Blackwall Peak, 49°07'N 121°

45'W, 2000 m, 9.VII.86, H. Goulet, subalpine meadow (1 ♀). **Alberta:** Banff, 12.VIII.53, F.I.S. No. A803D, ex. syrphid, host prob. aphid (3 ♀, NFRC). Fort MacKay, 2.8 km N bridge, 2.IX.79, G.J. Hilchie & J. Ryan, mixconifer forest (2 ♀). Jasper Gate, 2.III.51, F.I.S. No A3125B, ex. syrphid, host prob. aphid (2 ♀, NFRC). Jasper National Park, Maligne Road, 7.VIII.50, F.I.S. No. A615A, ex. *Metasyrphus lapponicus* (3 ♀, NFRC). Obed, 21.VIII.50, F.I.S. No. A20H9C, ex. *Metasyrphus lapponicus* (4 ♀, NFRC). Rocky Mountain House, 23 mi. NW, 17.VIII.53, F.I.S. No. A781D, ex. syrphid, host prob. aphid (1 ♀, 1 ♂, NFRC). Seebe, 13.VI.68, ex. *Cronartium comandrae* (fungus), *Pinus contorta* var. *latifolia*, 688 1190 03. **Manitoba:** Picnic Bog, 6.VI.61,

F.I.S. (1 ♀, NFRC). Warkworth near Churchill, 29.VI.52, J.G. Chillcott (1 ♀). **Quebec:** Ct. Jetté, RIF '40, 5103B, em. 18.VIII, ex. Syrphidae sp.? (2 ♀). Forbes, 26.VI.52, L. Daviault, associated with *Choristoneura fumiferana*, rearing no. 20 (5 ♀). Laniel, 9.VIII.40, C.E. Atwood, experiment no. 12131-69, *Cacoecia fumiferana* (2 ♀). Montcalm, em. 19.VI.11 from sp. B [?] worm, parasite of *Tortris fumiferana* (1 ♂). **New Brunswick:** same data as holotype (2 ♀, 3 ♂; 1 ♀ and ♂ used for SEM). Fredericton, em. 8.VII.47, N.R. Brown, 18839-4d5, ex. *Neocnemodon coxalis* (8 ♀, 1 ♂). **Newfoundland and Labrador:** Gallants, 9.VII.57, 57-0016(01) B10 (4♀, AFRC), 14.VII.59, 59-6009(01) A1–A9 (1 ♀, 6 ♂), F.I.S., host: *Neodiprion abietis*. Uncertain locality (likely Newfoundland or New Brunswick): 23 [mi. ?] NW Rocky, 17.VIII.53, 53A781D, ex. syrphid (6 ♀, 8 ♂). **USA.** Alaska: Fairbanks, 23.VI.45, 45-19058, par. aphids on wild raspberry (1 ♀, USNM). **Colorado:** Green Mountain Falls, Canyon, 10.VIII.41, 10,000', H.H. Ross (1 ♀, INHS). **Idaho:** Bounds Creek, Fairfield, 5.IX.63, H. Flake & K. Lister, Hopk US no. 50-718a, host: attached pupae (Syrphidae) (8 ♀, USNM). **Maine:** Liberty, em. 8.VI.48, parasite 48-C11 syrphid fly, beaten ex. Fir (2 ♀, USNM). Megalloway, 23.VI.49, parasite 49-255, *Neodiprion abietis*, beaten ex. Fir (6 ♂, USNM). **Washington:** Yakima Co., Green Lake Road, 31.VIII.94, K.S. Pike, ex. *Blacus* sp. or ichneumonid, from *Cinara chinookiana* or unknown on *Abies lasiocarpa* (subalpine fir) (1 ♂, WSUC).

EXTRALIMITAL.—**FINLAND** (FENNIA, SUOMI). **Savonia australis** [= Sa, ES]: Ristiina, 6826:502, 29.VII.83, M. Koponen (1 ♂, DAZH). **Ostrobottnia borealis, N part** [= ObN]: Pello, Pentik, 7417:368, 28.VI.97, V. Vikberg (1 ♀, VVPC). **Kuusamo** [= Ks]: Kuusamo, 7358:596, 27.VI.82, M. Koponen (1 ♀, DAZH).

Etymology.—From the Latin *brevis*, short, and *petiolus*, stalk, in reference to the transverse petiole of this species.

Female.—Head and mesosoma black with obscure metallic green luster under some angles of light; legs entirely black or, more often, black or dark brown with extreme apex of femora, extreme base and apex of tibiae to entire tibiae, and tarsi lighter in color, rufous to yellowish. Head subquadrate in frontal view (Fig. 1), with at most 1.2 times height, and in lateral view lower face abruptly to almost right-angled relative to upper face (Fig. 2); interorbital region in dorsal view deeply, broadly concave (Fig. 13); gena as long as or slightly longer than eye width and at

least 0.72 eye length; dorsal margin of torulus distinctly below lower orbit (Figs. 1, 2). Antenna (Fig. 19) with pedicel length about 3 times greatest width; funicle with fu_1 ring-like, fu_2–fu_4 subquadrate (Fig. 20), and fu_5–fu_8 increasingly transverse. Mesoscutum (Fig. 43) with mesoscutal lateral lobes broadly bare medially, and with fine engraved net-like sculpture over bare area. Scutellum mostly bare except along extreme anterior and lateral margins (Fig. 43); frenum with distinct, uniform, engraved net-like sculpture similar to scutellum (Fig. 50). Metapleuron with at most 5 setae anteroventrally, these setae mostly in line along base of metapleural flange. Forewing with basal cell evenly setose (Fig. 73); disc with narrow speculum, the speculum closed basally by setae and with one or more lines of setae immediately behind submarginal vein (Fig. 73). Petiole in dorsal view distinctly transverse, length 1.4–1.7 times width, reticulate with irregular longitudinal carinae or stronger keels (Fig. 49).

Male.—Antenna with scape, pedicel and fu_1 yellow to yellowish-orange, contrasting distinctly in color with rest of dark flagellum; color pattern otherwise similar to female except head and mesosoma usually with more distinct metallic green luster; legs usually more extensively light-colored, but at least hind leg brownish basally, including trochanter. Scape (Figs. 31–32) with dorsal margin slightly convex, ventral margin sinuate so as to be broadest subbasally and tapered to apex; inner and outer surfaces uniformly setose and sculptured. Pedicel (Figs. 31–32) length about 3 times width and about 0.40–0.45 scape length. Flagellum length subequal to head width; funicle (Fig. 31) with all segments at least slightly transverse or with one or more of $fu_{3–5}$ quadrate to very slightly longer than wide. Structure otherwise similar to female except head in dorsal view with interorbital region even more deeply, broadly concave (Fig. 14); malar space only about 0.77–0.87 eye

width and 0.5–0.6 eye length; petiole usually only slightly transverse (Fig. 55); and sculpture of frenum often distinctly finer than on scutellum (Fig. 55). Setal pattern similar to female except metapleuron with at most 2 short setae.

Distribution.—Holarctic; in North America transcontinental within the Boreal region and extending south along the Cascade and Rocky Mountains into Colorado (Fig. 79).

Biology.—*Asaphes brevipetiolatus* is a parasite of *Neocnemodon coxalis* (Curran), *Metasyrphus lapponicus* (Zetterstedt) and possibly other Syrphidae (Diptera) based on associated host pupal remains and label data. The balsam fir sawfly is also indicated as a host because two cocoons of *Neodiprion abietis* (Harris), one with two emergence holes and the other torn in half, are preserved with specimens. Labels from three different rearings in Quebec indicate that *A. brevipetiolatus* is also a parasite of the spruce budworm, *Choristoneura fumiferana* (Clemens). Although there are no associated host pupae, one of the two Laniel specimens has an unidentified braconid cocoon preserved with it, indicating that *A. brevipetiolatus* could be a hyperparasite of the spruce budworm through braconid primary parasites. There is also a single record, based on label data, of the species parasitizing an unidentified aphid on wild raspberry, plus a rearing from either *Cinara chinookiana* Hottes or an unknown aphid via either *Blacus* sp. (Braconidae) or an unidentified ichneumonid.

More than one emergence hole in some syrphid puparia and one balsam fir sawfly cocoon, plus multiple-mounted specimens, labelling, or both, for these two hosts and two of the three spruce budworm records indicate that *A. brevipetiolatus* is often gregarious when parasitizing larger non-aphid hosts. It remains to be demonstrated more conclusively that the balsam fir sawfly and spruce budworm are more than just accidental hosts, and whether *A. brevipetiolatus* is a primary or hyperparasite of these two species. However, based on current evidence it seems likely that host acceptance for *A. brevipetiolatus* includes not only syrphid larvae but other relatively large, oblong, brownish pupae or cocoons on coniferous trees. This suggests an evolutionary progression in *Asaphes* from parasitism of hymenopterous primary parasites of aphids, to syrphid-larvae predators of aphids and their parasites, to other hosts that resemble syrphid larvae.

Remarks.—Males are easily distinguished by structure and color of their scape and pedicel, both are yellowish in distinct contrast to the flagellum beyond fu_1. Also, the pedicel is conspicuously long, almost half the length of the scape, and the scape is widened subbasally so that its ventral margin is sinuate (Figs. 31, 32).

Females are distinguished by a combination of features, including a sculptured frenum (Fig. 50), dark trochanters and trochantelli, closed speculum (Fig. 73), transverse petiole (Fig. 49), and unique head structure (Figs. 1, 2). Because the legs are almost uniformly dark basally, females most closely resemble those of *A. vulgaris*, *A. petiolatus* and *A. hirsutus*, but are distinguished from all three species by described head structure. Absence of a broad speculum further differentiates females from those of *A. vulgaris*. Those *A. brevipetiolatus* females with setae on the metapleuron are more likely to be mistaken for females of *A hirsutus*, particularly because some *A. hirsutus* females have a slightly transverse petiole (Fig. 53) and some have the frenum extensively, though finely sculptured. However, in *A. hirsutus* the frenum is always more or less broadly smooth immediately behind the frenal sulcus even though often sculptured posteriorly (Fig. 54). Only head structure readily differentiates females of *A. brevipetiolatus* and *A. petiolatus*.

Asaphes californicus **Girault**
(Figs. 7, 8, 21, 22, 33, 34, 44, 56, 63, 67, 68, 76)

Asaphes californicus Girault 1917[330]: 1. Type data: USA: California [Spreckels], [25] September [1916]; reared from [parasitized] *Aphis rumicis*; [Chittenden No. 1671]; C.F. Stahl [collector]. Sex described: female. Holotype by monotypy; USNM, type no. 21411.

Female.—Head and mesosoma dark with varying intensity of olive green metallic luster under some angles of light; legs with trochanters and trochantelli almost always uniformly yellowish to yellowish-brown, at least middle and hind femora black except often apically, and tibiae and tarsi usually yellowish to reddish-brown. Head transverse-triangular in frontal view (Fig. 7), width at least 1.25 times height, and in lateral view lower face evenly curved into upper face (Fig. 8); interorbital region in dorsal view relatively shallowly concave; gena length about 0.62–0.80 eye width and 0.50–0.65 eye length; dorsal margin of torulus approximately in line with lower orbit (Figs. 7, 8). Antenna (Figs. 21, 22) with pedicel length at most about 2.5 times width; funicle with fu$_1$ ring-like, fu$_2$–fu$_4$ quadrate to transverse, and fu$_5$–fu$_6$ increasingly transverse. Mesoscutum (Fig. 44) with lateral lobes broadly bare medially, and either smooth and shiny or with fine, engraved net-like sculpture over bare area. Scutellum (Fig. 44) mostly bare except along extreme anterior and lateral margins; frenum smooth and shiny except finely carinate laterally. Metapleuron bare. Forewing with basal cell evenly setose to bare except for single row of setae on dorsal surface (Fig. 68); disc often without distinct speculum, distance between either basal setal line or submarginal vein and first setal line on disc at most about equal to distance between first and third setal lines on disc (Fig. 67) or, if with large and conspicuous speculum, then bare region with at least 2 dorsal setae within bare region, the setae

usually separated from basal vein and/or submarginal vein by distance about equal to length of setae or less (Fig. 68). Petiole at least quadrate and usually slightly longer than wide, but less than 1.3 times as long as wide (Fig. 44), reticulate with irregular longitudinal carinae (Fig. 44) or stronger keels.

Male.—Color pattern similar to female except legs sometimes entirely yellow (more commonly with at least metafemur infuscate to black); antenna usually uniformly brown to black except sometimes apex of pedicel and fu$_1$ lighter in color. Scape (Figs. 33, 34) length about 3.5–5.0 times width, ovoid to spindle-shaped, with dorsal and ventral margins convex to subparallel over most of length; outer surface with subbasal, ovoid to elongate-lanceolate, microsetose sensory region (Figs. 33, 34a); inner surface with line of ventrally directed setae, often from along fine ridge, parallelling ventral margin of scape below midline and mediolongitudinal bare, smooth band (Fig. 34b). Combined length of pedicel and flagellum less than 2.5 times scape length (Fig. 33) and at most subequal in length to head width; funicle with all segments at least slightly transverse or with one or more of fu$_{2–5}$ quadrate to very slightly longer than wide. Structure and setal pattern otherwise similar to female except petiole always distinctly (about 1.25–1.80 times) longer than wide (Fig. 56) and sometimes entirely reticulate without longitudinal carinae.

Distribution.—Restricted to western North America within the Nearctic region, except for one anomalous record from Georgia (see further under 'Remarks') (Fig. 82). **CANADA.** Yukon Territory, British Columbia, Alberta. **USA.** Alaska, Arizona, California, Colorado, ? Georgia, Idaho, Kansas, New Mexico, Nevada, Oregon, Washington, Utah. EXTRALIMITAL. **MEXICO** (BMNH: ♀, ♂; CNCI: ♀, ♂; EMEC: ♀), **ARGENTINA** (MLPA: ♀, ♂; TAMU: ♀, ♂); **BOLIVIA** (USNM: ♀),

Table 1. Host information for *Asaphes californicus* based on observed specimens; a question mark follows rearings or identifications indicated as questionable on the labels. Unless otherwise footnoted, all 'aphid or other hosts' are Homoptera (Aphidoidea: Aphididae) and all 'associated primary hosts' are Hymenoptera (Braconidae: Aphidiinae).

Aphid or other Hosts	Associated Primary Hosts	Localities	Museum Acronyms
	Acanthocaudus sp. ?	WA	WSUC
	Aphidius sp.	CA	USNM, UCRC
	A. alius Muesebeck	CA	UCRC
	A. nigripes Ashmead	CA	UCRC
	A. smithi Sharma & Subba Rao	CA	USNM, EMEC
	Diaeretus sp.	CA	UCRC
	Ephedrus sp.	CA	EMEC
	Lysiphlebus (Adialytus) salicaphis (Fitch)	CA	EMEC
	L. (Phlebus) testaceipes (Cresson)	CA	UCRC
	Pauesia californicus (Ashmead)	CA	USNM, EMEC
	Praon sp.	CA	UCRC
	T. (Trioxys) complanatus Quilis	CA	EMEC
	T. (Trioxys) curvicaudus Mackauer	CA	EMEC
Acyrthosiphon lactucae (Passerin)	*Praon* sp.	WA	WSUC
A. pisum (Harris)	*Aphidius* sps., *A. ervi* Haliday, *A. smithi* Sharma & Subba Rao	CA, OR, WA	UCRC, EMEC, USNM, WSUC
Amphorophora rubi (Kaltenbach)	*Praon pequodorum* Viereck	WA	WSUC
Aphis sp.		CA	EMEC, UCRC
A. ceanothi Clarke		WA	WSUC
A. fabae Scopoli	*Lysiphlebus* sp.	WA	WSUC
A. gossypii Glover	*Aphidius* sp.; *Lysiphlebus (Phlebus) testaceipes* (Cresson)	CA, NM	EMEC, UCRC, USNM
A. hederae pseudohederae Theobald	*Lysiphlebus (Phlebus) testaceipes* (Cresson)	CA	UCRC
A. helianthi Monell	*Ephedrus californicus* Baker; *Lysiphlebus (Phlebus) testaceipes* (Cresson); *Praon* sp.	WA	WSUC
A. holodisci Robinson	*Alloxysta* sp.	WA	WSUC
A. rumicis L.		CA	USNM
A. sambuci L.		WA	WSUC
A. spiraecola Patch		WA	WSUC
A. varians Patch		WA	WSUC
Aphthargelia symphoricarpi (Thomas)	*Lysiphlebus (Phlebus) testaceipes* (Cresson); *Praon* sp.	WA	WSUC
Brachycaudus cardui (L.)		WA	WSUC
B. helichrysi (Kaltenbach)		CA	EMEC
B. tragopogonis (Kaltenbach)		WA	WSUC
Brachycorynella asparagi (Mordvilko)	*Diaeretiella rapae* (M'Intosh)	WA	WSUC
Braggia sp.	*Lysiphlebus (Phlebus) testaceipes* (Cresson)	WA	WSUC
B. eriogoni (Cowen)		WA	WSUC
Brevicoryne brassicae (L.)	*Diaeretiella rapae* (M'Intosh)	CA, OR, WA	EMEC, OSUC, WSUC
Capitophorus elaeagni (del Guercio)		WA	WSUC
Cavariella aegopodii (Scopoli)	*Aphidus salicis* Haliday	CA, WA	CASC, WSUC
C. pastinacae (L.)	*Aphidus salicis* Haliday	WA	WSUC

Table 1. Continued.

Aphid or other Hosts	Associated Primary Hosts	Localities	Museum Acronyms
Chaetosiphon (*Pentatrichopus*) *fragaraefolii* (Cockerell)	*Aphidius* sp.	CA	UCRC, EMEC
Chaitophorus populifolii (Essig)	*Ephedrus* sp.	WA	WSUC
Chaitophorus salicicola Essig		CA	EMEC, USNM
Cinara ponderosae (Williams)	*Pauesia* sp.	MT	WSUC
Diuraphis noxia (Mordvilko)	*Diaeretiella rapae* (M'Intosh)	WA	WSUC
Dysaphis (*Pomaphis*) *plantaginea* (Passerini)?	*Praon unicum* Smith	WA	WSUC
Elatobium abietinum (Walker)	*Aphidius* sp.	BC	UCRC, NFRC
Ericaphis gentneri (Mason)	*Alloxysta* sp.; *Praon unicum* Smith	WA	WSUC
Essigella sp.		CA	EMEC
E. californica (Essig)	*Diaeretus* sp.	CA	UCRC
E. pini Wilson	*Aphidius* sp.; *Diaeretus* sp.	CA	UCRC, USNM
Eucallipterus tiliae (L.)		CA	EMEC
Euceraphis punctipennis (Zetterstedt)	*Praon* sp.	CA	USNM
Flabellomicrosiphum knowltoni Smith?		WA	WSUC
Hayhurstia atriplicis (L.)	*Diaeretiella rapae* (M'Intosh)	WA	WSUC
Hyalopterus pruni (Geoffroy)	*Praon* sp.	CA	EMEC
Hyperomyzus (*Neonasonovia*) *nigricornis* (Knowlton)	*Praon* sp.	WA	WSUC
Illinoia sp.	*Alloxysta* sp.; *Aphidius* sp.	WA	WSUC
I. azaleae (Mason)		WA	WSUC
I. liriodendri (Monell)		CA	CNCI, EMEC
I. morrisoni (Swain)		CA	EMEC
I. simpsoni (MacGillivray)	*Praon* sp.	BC	EMEC
I. subviridis (MacDougall)		WA	WSUC
Macrosiphoniella ludovicianae (Oestlund)	*Aphidius* sp.	CA	UCRC
Macrosiphum sp.	*Aphidius* sp.; *Praon* sp.	BC, CA, WA	CNCI, EMEC, WSUC
M. clydesmithi Robinson	*Praon* sp.	WA	WSUC
M. creelii Davis		WA	WSUC
M. euphorbiae (Thomas)	*Alloxysta* sp.; *Aphelinus* sp.?; *Aphidius nigripes* Ashmead	CA	EMEC, UCRC
M. parvifolii Richards		BC	CNCI
M. rosae (L.)	*Aphelinus* sp.?; *Aphidius* sp., *A. alius* Muesebeck; *Praon* sp.	CA, WA	CASC, EMEC, UCRC, USNM, WSUC
Metopolophium dirhodum (Walker)		WA	WSUC
Microlophium carnosum (Buckton)	*Praon* sp.	WA	WSUC
Myzocallis sp.	*T.* (*Truxys*) *pallidus* (Haliday)	WA	WSUC
M. coryli (Goeze)	*T.* (*Truxys*) *pallidus* (Haliday)	WA	WSUC
Myzus (*Nectarosiphon*) *persicae* (Sulzer)	*Aphidius* sp., *A. matricariae* Haliday; *Diaeretus rapae* (M'Intosh); *Lysiphlebus* (*Phlebus*) *testaceipes* (Cresson); *Praon* sp., *P. unicum* Smith	AB, CA, OR, WA	CNCI, EMEC, UCRC, USNM, WSUC
Nasonovia aquilegiae (Essig)		WA	WSUC

Table 1.   Continued.

Aphid or other Hosts	Associated Primary Hosts	Localities	Museum Acronyms
Obtusicauda sp.		WA	WSUC
O. artemisiphila (Knowlton & Allen) ?		WA	WSUC
O. coweni (Hunter)		WA	WSUC
O. filifoliae (Gillette & Palmer)?		WA	WSUC
Ovatus crataegarius (Walker)?		WA	WSUC
Phytomyza ilicis Curtis[2]		BC	CNCI
Phorodon humuli (Schrank)		WA	WSUC
Pseudoepameibaphis tridentatae (Wilson)	*T. (Trioxys) bonnevillensis* Smith	WA	WSUC
Rhodobium porosus (Sanderson)		CA	EMEC
Rhopalomyzus (Judenkoa) lonicerae (Siebold)	*Praon* sp.	WA	WSUC
Rhopalosiphum insertum (Walker)	*Praon unicum* Smith	WA	WSUC
R. maidis (Fitch)	*Lysiphlebus (Phlebus) testaceipes* (Cresson)	WA	WSUC
R. padi (L.)		WA	WSUC
Schizolachnus piniradiatae (Davidson)		CA	USNM
Sitobium avenae (Fab.)	*Aphidius* sps., *A. avenaphis* (Fitch)	OR, WA	OSUC, WSUC
S. pteridis (Wilson)		BC, CA, OR	EMEC, UCRC
Spilococcus implicatus Ferris[3]		CA	EMEC
Therioaphis riehmi (Börner)	*Praon americanum* (Ashmead)	CA	UCRC
T. trifolii (Monell)	*Praon exoletum palitans* Muesebeck; *Trioxys (Trioxys) complanatus* Quilis	CA	UCRC, USNM
Thripsaphis sp.	*Praon* sp.	WA	WSUC
Uroleucon (Lambersius) katonkae (Hottes)		CA	EMEC
U. russellae (Hille Ris Lambers)		WA	WSUC
Wahlgreniella nervata (Gillette)	*Praon* sp.	WA	WSUC

[1] Chalcidoidea (Aphelinidae).
[2] Diptera (Agromyzidae).
[3] Coccoidea (Pseudococcidae).

CHILE (ANIC: ♀; BMNH: ♀, ♂; CNCI: ♀; EMEC: ♀; TAMU: ♀, ♂; UCDC: ♀, ♂; **COLOMBIA** (CNCI: ♀), **COSTA RICA** (CNCI: ♀, ♂), **DOMINICAN REPUBLIC** (CNCI: ♀, ♂), **ECUADOR** (CNCI: ♀), **GUATEMALA** (CNCI: ♀, ♂), **URUGUAY** (USNM: ♀), **VENEZUELA** (CNCI: ♀).

Biology.—Nearctic specimens with host data indicate that *A. californicus* is strictly a hyperparasite of aphids through aphi-diine and aphelinid primary parasites, though there are two anomalous records from *Phytomyza ilicis* Curtis and *Spilococcus implicatus* Ferris (Table 1).

Type material examined.—The holotype consists of a point-mounted specimen and, in the general collection, a slide with one hind leg and both antennae. The holotype otherwise has the head, right pair of wings, and right front leg missing.

Remarks.—We are uncertain both as to the limits of morphological variation and the true range of *A. californicus* because there may well be more than one species represented within a species complex in the New World. Our concept of *A. californicus* is influenced largely by the males, which have a more or less well developed, but usually elongate-lanceolate or oval, sensory region on the outer surface of the scape (Fig. 34a). Apparently the region is always setose but the setae are not always distinct because of what appears to be an exudate covering the area in some specimens. Also, the more elongate spindle-shaped is the scape, the less obvious is the line of setae on its inner surface (Fig. 34b) because the line is closer to the ventral margin. At least within the Nearctic region, females seem to have quite a stable leg color pattern, with at least the hind leg having yellowish trochanters in contrast to darker femora. The size of the speculum varies considerably, some individuals have a broad bare band like *A. vulgaris* (Fig. 68), others have the disc almost uniformly setose (Fig. 67), and others have intermediate states. Males and females from the Nearctic region, like other species recognized from the Northern Hemisphere, also consistently have a distinctly sulcate, crenulate frenal groove (Figs. 44, 56). Because males sometimes have the femora entirely yellow or only inconspicuously infuscate they can easily be mistaken for males of *A. suspensus* if structure of the scape is not examined carefully. A difference in antennal color often suffices to differentiate unmounted males in ethanol. Males of *A. californicus* have uniformly brown antennae, whereas males of *A. suspensus* have the flagellum yellowish or at least distinctly lighter than the scape.

We have seen one anomalous female from Georgia (McIntosh Co., Sapelo Island, 28.IV–9.V.97, scrub sand dunes) (CNCI). Not only is this locality substantially outside the apparent range of *A. californicus*, the specimen has legs with the trochanters to femora almost uniformly dark (trochantelli yellowish-brown, similar in color to tibiae), which is an aberrant color pattern for the species. A basally closed and relatively narrow speculum indicates that this specimen does not belong to *A. vulgaris*, and it does not possess the distinguishing features of other Nearctic species whose females are characterized by dark legs. The only species of *Asaphes* otherwise known to occur in the southeastern USA is *Asaphes suspensus*, which has entirely yellow legs. Because it was collected in coastal Georgia it is possible that it represents an accidentally introduced species that is morphologically similar to *A. californicus*. However, until additional females with associated males can be collected and examined, we tentatively include the female in *A. californicus*. The outlier from Kansas (Wellington, USNM: 2 ♀, 3 ♂) is typical of the species and definitively identified.

We have seen mostly females of *Asaphes* from the Neotropical region, but included are specimens from the countries listed above that either greatly increase limits of variation for *A. californicus*, *A. suspensus* and *A. vulgaris*, or that represent additional species that are very similar to these species. Some females look superficially like *A. suspensus* females because they have entirely yellow legs (sometimes also with the coxae brownish rather than dark with metallic luster). Others are similar to *A. vulgaris* females because they have the trochanters, trochantelli and femora, and sometimes also the tibiae and tarsi similarly dark. These, and other females having a color pattern more typical of *A. californicus*, can also have different combinations of the following features: speculum usually similarly broad as for *A. vulgaris*, though sometimes with 1–3 setae somewhere within the bare band; frenal groove often poorly developed, indicated only by a faint transverse line or if distinctly sulcate then not distinctly crenulate; mesonotum usually shiny with dis-

tinct metallic sheen, very finely net-like coriaceous with bare region of mesoscutal lateral lobe smooth; petiole often obviously elongate, 1.25–1.60 times as long as wide; petiole with strong longitudinal carinae and irregular surface sculpture to evenly, finely, longitudinally striate-reticulate without longitudinal carinae. Females with entirely yellow legs tend to have a shorter petiole with distinct carinae, and always a broad speculum that distinguishes them from *A. suspensus* females. Females with dark legs tend to have a more elongate petiole and/or one that is evenly sculptured without or with only obscure carinae, and often with three or more setae within or basally closing an otherwise broad speculum. Both color forms usually also have a non-crenulate frenal groove. Finally, all males seen from South America, including all those associated with any of the different female color forms, have a scape similar in structure to *A. californicus*, including a varied sensory region on the outer surface. Because of what currently appears to be a continuum of states in females and the presence of some sort of sensory region on the scape of all males we are uncertain of species limits in the Neotropical region. However, we have not seen any *Asaphes* from America south of Mexico that we believe belong to *A. suspensus* or *A. vulgaris* (see respective sections for these two species).

In addition to the New World we have seen males with an elongate sensory region on the outer surface of the scape from the Oriental region [India (CNCI), Taiwan (UCRC)] and the Palaearctic region [Iran (TAMU), Morocco (UCRC), Turkey (UCRC)]. The males from India and Taiwan appear to belong to an undescribed species based on a much longer flagellum—the combined length of the flagellum and pedicel in these specimens is more than 2.5 times the length of the scape and distinctly longer (more than 1.2 times) than the width of the head, and all but the apical one or two segments are monili-

form to slightly longer than wide. Males, and associated females, have yellowish or at least lighter-colored trochanters contrasting with variedly infuscate or dark femora, a coloration similar to that in *A. californicus*. The females could be mistaken for those of *A. vulgaris* but both females and males have the speculum closed basally by setae or have a few setae within the speculum. Those males from Iran, Morocco and Turkey with an elongate sensory region on the outer surface of the scape are otherwise very similar to males of *A. suspensus*, including having a similar forewing setal pattern, entirely yellowish legs, and short antenna with the pedicel and flagellum, just the pedicel, or only the apex of the pedicel yellowish. Further, some males from Iran were reared along with typical males of *A. suspensus*. We could not find differences in associated females. It is unknown whether the sensory region on the scape of some males in the middle east and northern Africa indicates a separate species or whether scape structure is more variable for *A. suspensus* in these regions.

Asaphes hirsutus Gibson and Vikberg, new species
(Figs. 5, 6, 17, 18, 23, 24, 35, 36, 45, 53, 54, 57, 61, 62, 71, 74)

Type material.—Holotype, female (CNCI, Type No. 22266): CANADA, British Columbia, Cassiar Highway, Boyar Lake to Stikene River, 6.VIII.1988, S.&J. Peck, day car netting boreal forest. *Allotype*, male (CNCI): same data as holotype. *Paratypes:* **CANADA. Yukon Territory:** Dempster Hwy., 28.VI–2.VIII.82, D.M. Wood (2 ♀, 1 ♂). Heynes Junction 10, Dezadeash Lake, 700–900 m, 2.VIII.89, S.&J. Peck, car netting boreal dry forest (1 ♀). Herschel Island, 16–24, 26.VII.71, W.R.M. Mason (1 ♀, 1 ♂). Ross River, 16.VI–31.VIII.84, S.&J. Peck (3 ♀, 1 UCDC). **Northwest Territories:** Banks Island, Masik River, 10.VII.68, W.M. Mason (1 ♀). Salmita Mines, 64°05'N 111°15'W, 18.VI.53, J.G. Chillcott (1 ♀). **British Columbia:** same data as holotype (11 ♀, 5 ♂). Anahim Lake to Redstone, 1000–1500 m, 17.VII.88, S.&J. Peck, car netting pine sand land (2 ♀, 3 ♂). Charlie Lake, 25.VIII.80, R.J. Cannings (1 ♀, SMDV). Manning Provincial Park, 2 km N Blackwall Peak, 49°07'N 121°45'W, 2000 m, 9.VII.96, H. Goulet, subalpine

meadow (1 ♂). McLeod Lake, 12.VII.66, #P66–7–12a, P.A. Rauch, *Castilleia* (1 ♂, EMEC); #F66-7-12e, F.G. Andrews, *Castilleia* (1 ♂, EMEC). Manning Provincial Park, 1400m, 12–14.VII.88, H. Goulet (2 ♀). Mt. Revelstoke, 51°02′N 118° 05′W, 1800m, 30.VII.86, H. Goulet (1 ♂). Mt. Seymour, N Vancouver, 790 m, 17.V.73, J.R. Vockeroth (1 ♂). Ocean Falls, 13.VII.60, E.I. Schlinger, 60-7-28P, secondary parasite reared from *Aphidius* sp., host aphid *Neomyzaphis abietina* (4 ♀, 4 ♂, UCRC). Squamish, Diamond Head Trail, 4600′, 10, 11, 29, 30.VIII.53, W.R.M. Mason (8 ♀, 2 ♂). Summerland, 5.V1.59, R.E. Leech (1 ♂). Terrace, 18.VI.60, J.G. Chillcott (1 ♀). Vancouver Island, Forbidden Plateau, W of Courtenay, 1.VII.66, #F66-6-29b, on *Olopanax horridum* (1 ♀, 1 ♂, EMEC), #F66-7-1b, ex. aphids on *Achlys triphylla* (1 ♀, 1 ♂, EMEC); #F66-7-1e, ex. Macrosiphini on *Vaccinium ovalifolium* (1 ♀, EMEC), #F66-7-1f, 2 mi. NW of Courtenay, on manzita-like Ericaceae (2 ♀, EMEC), F.G. Andrews. Vancouver Island, 12 mi. E Port Alberni, 30.VI.66, P. Rauch, P66-6-30A, *Woodwardia* sp., *Macrosiphum pteridis* (1 ♀, 1 ♂, EMEC). Winfield, 20.III.54, F.I.S. no. 541, *Pinus ponderosa* cone (1 ♂). **Alberta:** Aspen Beach, 25.VIII. 44, O. Peck (1 ♂). Edmonton, 11, 16, 22, 23, 24.V.46, 27.V.46, 2, 6, 17.VI.46, W.R.M. Mason (10 ♀, 8 ♂). 24.IX.86, Jorgensen & Anderson (5 ♂). Fortress Mountain, 6 km S, 51°52′N 115°10′, 1700 m, 21.VI.86, H. Goulet (2 ♀). Fort McMurray, 30.VI.53, G.E. Ball (1 ♀). Seebe, reared from duff layer under *Pinus contorta* var *latifolia*, em. 11.I.71, L.S. Skaley (2 ♂, NFRC). W Waterton Lake National Park, 49°05′N 113°52′W, 1300 m, 6.VII.91 (1 ♀), 3 km E Cameron Lake, 49°03′N 114°01′W, 1650 m, 13–14.VII.91 (1 ♂), H. Goulet. **Saskatchewan:** Prince Albert National Park, 23.VII.54, ex. *Cinara hottesi* (G. P.). *Picea mariana* (1 ♀). Snowden, 26.VII.44, O. Peck (1 ♀). **Manitoba:** Winnipeg, coll. 31, 31–114, em. 28.VIII.50, F.G. Wylie (1 ♀, EDUM). **Quebec:** Chimo, 17–18.VIII.59, W.R.M. Mason (2 ♀, 4 ♂). Great Whale River, 11.VII, 31.VIII.49, J.R. Vockeroth (2 ♀). 8.VIII.59, sand dunes, W.R.M. Mason (1 ♂). Louvicourt, 16 km S, km 473.5, 17.VI.85, H. Goulet & D.R. Smith (6 ♀, 5 ♂). Parc de la Gaspésie, Mont Jacques-Cartier, 29.IX.91, C. Isabel, zone subalpine, sphaigne humide et krumholz (1 ♀). Mont Saint Marie, Low, 1800′, 20.IX.65, J.R. Vockeroth (1 ♂). Québec City area, 29.VIII.88, reared ex. mummy *Aphidius nigripes* in potato field (1 ♀). St. Gedeon, 26.VIII.7e, Remaudière, ex. *Calaphus* on *Betula* (3 ♂, BMNH). Ste-Catherine (de Portneuf), 5.VIII.87 (2 ♀), 18.VIII.87 (1 ♀), J. Brodeur. **New Brunswick:** Fredericton, 9.VIII.50, *Myzus persicae* on potato (1 ♂), 24.VIII.50, *Macrosiphum solanifolii* on potato (1 ♀), B.P. Spicer; 4.X.50, J.B. Adams, *Eulachnus agilis* on Scotch pine (1 ♂). Kouchibouguac National Park, 17.VII.77, I. Smith (1 ♀); 20.IX.77, S.J. Miller (1 ♀). St. John Co., Mary Pitcher Lake, IV.97, R'rd D. O'Shea, aphid on *Picea glauca* needle (1 ♀). **Prince Edward Island:** Harrington, 23–29.VIII.86, M.E. Smith, in potato field (1

♀). **Nova Scotia:** Coldbrook, 2, 7, 16, 30.X.63, H.B. Specht, host *Acyrthosiphum pisum* (Harris) on alfalfa (1 ♀, 5 ♂). Mantua, 23.X.63, H.B. Specht, host *Acyrthosiphum pisum* (Harris) on alfalfa (1 ♀). **Newfoundland and Labrador:** Junction Pond, Notre Dame Cp., 19.VII.61, C.P. Alexander (1 ♀, USNM). Labrador, Goose Bay, 7.VII.52 (1 ♀).

USA. Alaska: Bering Sea, St. Paul Island, T. Kincaid (1 ♀, USNM), 16.VIII.15, G.D. Hanna (1 ♀, USNM). Cape Thompson, 25.VII.61, R. Madge (1 ♀). Cartwell, Denali Highway Route #8, mi. 85–130, 24.VII.84, S.&J. Peck (9, 7 ♂). Cold Bay, 163° W, 26.VII.52, W.R. Mason, on tundra (1 ♀). Colorado Creek, 60°40′N 149°30′W, 9.VII.94, ex. aphid mummies on *Alnus* sp., D. Collet (1 ♀, DCPC). Dave's Creek, 60°30′N 149°45′W, 3.IX.94, swept from *Salix barclayi*, D. Collet (3 ♂, DCPC). Deering, 8–19.VIII.68, J. Matthews (1 ♀). Isabel Pass, mi. 206, Richardson Hwy, 2900′, 17.VII.62, P.J. Skitsko (1 ♀). Kasilof, 60°15′N 151°15′W, 27.VI.94 (2 ♀, 2 ♂, DCPC), 30.VII.94 (2 ♀, DCPC), ex. aphid mummies on *Salix barclayi*, D. Collet. Kenai Peninsula, trail to Bryan glacier, vicinity Portage Glacier, 22.VII.78, P. H. Arnaud, Jr. (1 ♀, CASC). King Salmon, Naknek River, 15.VII.52, W.R. Mason (1 ♀). Kotzebue., 420, 14.VIII.58, Lindroth (1 ♀). Matanuska, 6.X.45, J.G. Chamberlin (2 ♀, USNM). Steese Highway, mi. 96.4, 4.IX.48, G. Jefferson (1 ♀, USNM). Soldotna, 60°30′N 151°00′W, 16.VII.95, ex. aphid mummies on *Betula*, D. Collet (2 ♀, DCPC). Sterling, in front of Collet house, 60°30′N 150°45′W, 23.VII.94 (1 ♀, DCPC), 31.VII.94 (1 ♂, DCPC), ex. aphid mummies on *Salix barclayi*, D. Collet; Gann site, 60°30′N 150°45′W, 4.V.93, swept from *Salix barclayi* (1 ♀, DCPC), 3.V.93, swept from *Betula nana* (1 ♀, DCPC), D. Collet. Unalakeet, 27.VI.61, B.S. Hemming (1 ♀); 15.VII.61, R. Madge (1 ♀). Unknown locality, 15.VIII.94, D. Collet (1 ♀, DCPC). **Arizona:** Cochise Co., Chiricahua Mountains, Rustler Park, 8000′, 15.VIII.82, G.A.P. Gibson (2 ♀); 12 km S Sierra Vista, Ramsey Canyon, 1700 m, 1986, B.V. Brown (5 ♂). Tucson Co., Catalina Mountains, Mt. Lemmon, Crystal Springs Canyon, 8000′, 11.VII.90, L. Masner (1 ♀). **California:** Glenn Co., Mendocino National Park, Plaskett Meadows, 7000′, 28.VI.81, J.B. Whitfield (1 ♀, EMEC). Lake Tahoe, Pope Beach, 26.IX.75, E.C. Toftner & R.O. Schuster (1 ♀). Nevada Co., Sagehen Creek, 1.VII.70, *Salix*, E.E. Grissell (1 ♂, UCDC). Yosemite National Park, near Dog Lake, em 26.V.59, ex. *Essigella* mummy, *Pinus contorta* var. *murrayana* Englm. (4 ♀, UCRC); near Gaylor Lakes, X.59, *Pinus contorta* var. *murrayana* Englm. (1 ♂, UCRC). **Colorado:** Boulder Co., Chataqua Pk. W Boulder, 4.VI.90, S.L. Heydon (1 ♀, UCDC). Echo Lake, Mt. Evans, 10600′, 8.VII.61, S.M. Clark (2 ♂). Estes Park, 11.VIII.53, R.R. Dreisbach (1 ♀, USNM). Fort Collins, 86 km W, 4.VIII.92, R.B. Penfield, Hopkins US no. 36751-V-198, *Arceuthobium cyanocarpum* (1 ♂, USNM). New Castle, Hopkins US no. 34211-K, lot

no. 47-946, *Picea engelmanni* (1 ♀, USNM). Pitkin Co., 10.5 km SE Aspen, 2900m, 9.VII.92, S.L. Heydon (2 ♂, UCDC). **Idaho:** Clarkia, 24.V.60, R.E. Denton, Hopkins US no. 20366, *Pinus monticola* foliage (1 ♂, USNM). Shoshone Co., Thompson Pass Summit, 29.VII.95, K.S. Pike, ex. *Aphidius polygonaphis* or *Praon humulaphidis* from *Illinoia* sp. on *Vaccinium* sp. (1 ♀, WSUC). **Maine:** Aroostook Co., 9.VI, 10, 21, 31.VII, 4, 10.IX.58, ex. *Macrosiphum solanifolii* (3 ♀, 4 ♂, USNM). **New Hampshire:** Mount Washington, 4.VIII.50, S. Ristich (1 ♀); 1676m, 20.VIII.81, H. Goulet (1 ♀); Alpine Garden, 5200–5600', 7.VIII.54, Becker, Monroe & Mason (1 ♀, 1 ♂); Cow Pasture, 5700', 2.VIII.54, Becker, Monroe & Mason (1 ♀); Lakes of the Clouds, 5000', 3, 9.VIII.54, Becker, Monroe & Mason (2 ♀, 1 ♂); Tuckerman's Ravine, 31.VII.54, Becker, Monroe & Mason (1 ♂). **New Mexico:** Lincoln National Forest, Karr Canyon, 28.VII.77, L. Masner (1 ♀, 1 ♂). Otero Co., 2 mi N Cloudcroft, 5.VI.80, S.L. Heydon (1 ♀, UCDC). Valencia Co., 20 mi. W Los Lunas, Corritzo Arroyo, 1–23.VIII.77, S.&J. Peck (1 ♀ Oregon: Klamath Co., Sprague River, Hwy 87, Collier, 2.VII.85, D.G. Denning (1 ♂). **Washington:** Benton Co., WSU-Prosser Roza Unit, 27.VI.94, K.S. Pike, ex. *Aphidius ervi* from *Sitobion avenae* on *Triticum aestivum* (wheat) (1 ♂, WSUC). Clallam Co., 10 mi. E Pysht, 26.VI.66, #C66-6-26a, D. Calvert (1 ♀, 1 ♂, EMEC); Lake Ozette, 24.VII.90, J.D. Pinto (1 ♂). King Co., Stampede Pass lookout point, 8.VIII.96, K.S. Pike, unknown on *Rhododendron albiflorum* (white-flowered azalea) (1 ♀, WSUC). Kittikas Co., Lost Lake, 6.VIII.97, K.S. Pike, ex. *Aphidius* sp. from *Illinoia* sp. on *Lonicera involucrata* (black twinberry) (2 ♀, WSUC); Manashtash Cr., mile 8, 16.VIII.96, K.S. Pike, ex. *Alloxysta* sp. or *Aphidius ohioensis* or *Dendrocerus* sp. or *Ephedrus californicus* from *Macrosiphum creelii* on *Vicia* sp. (vetch) (2 ♀, WSUC); Manashtash Cr., mile12, 25.VI.97, K.S. Pike, ex. *Alloxysta* or *Aphelinus* on *Lonicera involucrata* (1 ♀, WSUC); 2 mi E. of Quartz Mtn, 25.VI.96, K.S. Pike, ex. *Aphidius* sp. or *Praon* sp. from unknown aphid on *Rubus lasiococcus* (dwarf bramble)(1 ♀). Lewis Co., Rainier National Park, Tipsoo Lake, 11.IX.96, K.S. Pike from *Macrosiphum* sp. on *Rhododendron albiflorum* (white-flowered azalea) (1 ♀, WSUC). Mount Baker, 2.VIII.86, 1700 m, H. Goulet (2 ♀). Mount Rainier National Park, Van Trump Park, 1500–1800 m, 29.VII.85, L. Masner (8 ♀, 17 ♂). Pierce Co., Mount Rainier National Park, Chinook Pass, 8.IX.95, K.S. Pike, unknown on *Spiraea densiflora* (1 ♀, 1 ♂, WSUC). Wenatchee, 22.VII.83, D. Carroll, host *Schizaphis graminum* via *Praon* sp. on *Agropyron repens* (1 ♀, Carroll); near bridge, 17.VII.82, D. Carroll, host *Rhopalosiphum insertum* via *Praon unicum* on *Crataegus douglasii* (1 ♀, Carroll). Yakima Co., 15 mi. E of Chinook Pass, 11.IX.96, K.S. Pike, free flying parasitoids on *Achlys triphylla* (vanilla-leaf) (1♀, 1 ♂, WSUC); Green Lake, 20.VII.94, K.S. Pike, ex. *Alloxysta* sp. or *Monoctonus* sp. from *Illinoia* sp. on *Rhododendron al-*

bifolorum (white-flowered azalea) (2 ♀, WSUC); Green Lake Road, 31.VIII.94, K.S. Pike, ex. *Blacus* sp. or ichneumonid, from *Cinara chinookiana* or unknown on *Abies lasiocarpa* (subalpine fir) (5 ♀, WSUC); trail, 1.5 mi. from Rd1010, 14.IX.95, K.S. Pike, ex. *Alloxysta* sp. or *Lysiphlebus testaceipes* from *Aphis fabae* on *Cirsium vulgare* (bull thistle) (13 ♀, 10 ♂, WSUC); Yakima Indian Reservation, Howard Lake, 19.IX.95, K.S. Pike, ex. *Aphidius polygonaphis* or *Praon* sp. from *Sitobion* sp. on *Pteridium aquilinum* (2 ♀, WSUC). **Wyoming:** Bighorn Co., Northern Bighorn Mountains, Sheep Mountain, 2800 m, 22.VII.88, H. Goulet (1 ♂).

EXTRALIMITAL—*Neotropical:* **MEXICO.** Rio Frio, 3150 m, 8.V.79, G. Remaudière, ex. *Macrosiphum* on *Euphorbia peplus* (5 ♀, 4 ♂ glued on 6 cards along with specimens of *A. californicus*, BMNH). *Palaearctic:* **AUSTRIA.** Dolomiten, S.-Tirol, Platzwiese, 200 m, Dürrnstein Geb., 1968, Schimitschek, ex. *Pauesia similis* Sta. in *Cinara cembrae* (1 ♀, BMNH). **CZECH REPUBLIC. Bohemia:** Studnice, nr Jablonec nad Nisou, 860m, 28.VI.63, V. Martinek (1 ♀). Teplice, Nove Mesto, 850m, 2.VII.63 (1 ♂), 12.VII.63 (1 ♂), 30.VII.63 (2 ♂), V. Martinek. **FINLAND** (FENNIA, SUOMI). **Karelia borealis** [= Kb]: Eno, Ahveninen, 698:65, 22.VIII.68, V. Vikberg (1 ♀, VVPC). **Ostrobottnia media** [= Om, KP]: Kestilä, 7135:461, 29.VII.84, M. Koponen (1 ♀, DAZH). **Ostrobottnia borealis, N part** [= ObN, PP]: Ranua, 7312:479, 20.VII.80, M. Koponen (1 ♀, DAZH). Rovaniemi, 737:44, 16.VIII.80, J. Halme (5 ♀, 1 ♂, DAZH). **Kuusamo** [= Ks]: Kuusamo, 735:61, 2.VII.79, V. Vikberg (3 ♂, VVPC); 7366:603, 26.VI.79 (1 ♀), 30.VI.79 (4 ♀, 3 ♂), 26.VI.82 (1 ♀), M. Koponen (DAZH). **Lapponia kemensis, E part** [= LkE, KemL]: Sodankylä, 7481:467, 11.VIII.83 (1 ♂), 7582:516, 6.VII.89 (1 ♀), M. Koponen (DAZH). **Lapponia kemensis, W part** [= LkW]: Kolari, 7501:382, 6.VII.97, M. Koponen (2 ♀, 1 ♂, DAZH), 7504:379, 4.VII.97, K. Silvonen (1 ♀, DAZH); Kolari, Ylläs, 7502:380, 29.VI.97, V. Vikberg (1 ♀, VVPC); Kolari, Ylläs, Varkaankuru, 7502:382, V. Vikberg (1 ♀, VVPC). Muonio, Olostunturi, 7541:366, 28.VI.97, V. Vikberg (1 ♀, VVPC). **Lapponia enontekiensis** [= Le, EnL]: Hetta, 759:36, 3, 4.VII.82, V. Vikberg (2 ♀, VVPC). Karesuvanto, 760:31, 29.VI.82, V. Vikberg (1 ♀, VVPC); 7605:313, 29.VI.82 M. Koponen (2 ♀, DAZH). Kilpisjärvi, Pien Malla, 2.VII.50, W. Hellén (1 ♀, UZMH); region subalpina, 767:25, 17.VI.71, V. Vikberg (1 ♀, VVPC); Siilastupa, 1.VII.50 (1 ♂, UZMH), 10–19.VII.50 (1 ♀, UZMH), W. Hellén. Ropinsalmi, 2.VII.82, Y. Zhongqi (1 ♀, DAZH). **Lapponia inarensis** [= Li, InL]: Inari, 7591:478, 1.VII.89 (1 ♀), 7617:521, 6.VII.89 (2 ♀, 2 ♂), 7664:504, 12.VIII.83 (2 ♀), 7615:517, 4.VII.89 (2 ♀), M. Koponen (DAZH); Inari, kk [= kirkonkylä = 'church village'], 24.VI.60 (1 ♀), 28.VI.60 (1 ♀), 29.VI.50 (1 ♀), V. Vikberg (VVPC); Inari, Kaunispää, 154/80, 759:50, 12.VIII.80 (1 ♀, 1 ♂), 159:51, 11.VIII.80 (1 ♀), 159:51, 15.VIII.80 (2 ♂), J. Halme (DAZH); Inari, Opukasjärvi, 772:55, 4.VII.60, V. Vikberg (1 ♀, VVPC). Utsjoki,

7741:500, 13.VIII.83, M. Koponen (1 ♀, DAZH); Uts-joki, kk [= kirkonkylä = 'church village'], 775:50, 4.VI.60 (1 ♀), 6.VI.60 (2 ♀, 1 ♂), 11.VI.60 (1 ♀), 16.VI.60 (4 ♀, 4 ♂), 18.VI.60 (1 ♀, 3 ♂), 19.VI.60 (2 ♀), 22.VI.60 (2 ♀), 29.VI.60 (2 ♀), V. Vikberg (VVPC); Utsjoki, Karigasniemi, 770:46, 30.VI.60, V. Vikberg (1 ♀, VVPC). **NORWAY**. Oppland [= O]: Dovre, Fokstua, 13.VII.53, W. Hellén (1 ♀, UZMH). **RUSSIA**. **Khabarovsk Kray**: Ochotsk [= Okhotsk], 1841, F. Sahlb. [= Sahlberg] (1 ♀, UZMH). **Kamchatka Oblast**: N. Kuril Islands, 5.VIII.64, aphid on *Salix* (3 ♂, ZMAS). **Murmansk Oblast**: Yläluostari, VIII.30, W. Hellén (1 ♀, UZMH). **SWEDEN** (SUECIA). **Norrbotten** [= Nb.]: Boden, Trehörningen, RN 1783/7326 810722–22 [*Equisetum silvaticum*; *Sitobion equiseti*; *Aphidius picipes*], U. Gärdenfors (1 ♀, MZLU). Luleå, Lulviken, RN 1793/7286 810721–30, [*Ephedrus* mummy on needle of *Pinus sylvestris* on ground] (1 ♀, MZLU), RN 1793/7286 810721-11, [*Wahlgreniella vaccinii*; *Praon myzophagum*, plus *Ephedrus plagiator*, plus *Aphidius* sp.; *Aphelinus* sp.] (2 ♀, 1 ♂, MZLU). U. Gärdenfors. Luleå, Svartöstaden, RN 1794/7288 800807-08, [*Epilobium angustifolium*; *Macrosiphum rosae*; *Aphidius* sp., plus *Ephedrus* sp.], U. Gärdenfors (1 ♀, MZLU). överkalix, RN 1815/7376 810722-08, [*Rosa* sp.; *Macrosiphum rosae*; *Praon* sp.] (1 ♂, MZLU), RN 1815/7376 810722-02, [*Lonicera* sp. culture; *Rhopalomyzus lonicerae*; *Ephedrus* sp.] (3 ♀, 8 ♂, MZLU), U. Gärdenfors. **Torne Lappmark** [= Lpl.]: Abisko, 15.VIII.51, J.R. Vockeroth (1 ♀).

Etymology.—From the Latin *hirsutus*, hairy, in reference to the partially setose metapleuron.

Female.—Head and mesosoma dark, usually with obscure metallic green luster under some angles of light; legs entirely dark or with at least coxae, trochanters and most of femora dark, the trochantelli sometimes, femora apically, and tibiae and tarsi often yellowish or distinctly lighter in color than rest of legs. Head transverse-subtriangular in frontal view (Fig. 5), width at least 1.25 times height, and in lateral view lower face evenly curved into upper face (Fig. 6); interorbital region in dorsal view relatively shallowly concave (Fig. 17); gena length about 0.64–0.82 eye width and 0.53–0.66 eye length; dorsal margin of torulus approximately in line with lower orbit (Figs. 5, 6). Antenna (Figs. 23–24) with pedicel length about 2.5–3.0 times greatest width; funicle with fu$_1$ transverse, fu$_2$–fu$_6$ transverse to very

slightly longer than wide (fu$_5$–fu$_5$ or fu$_6$ usually more or less moniliform), fu-quadrate to slightly transverse, and fu$_8$ transverse. Mesoscutum (Fig. 45) with lateral lobes broadly bare medially, and with fine engraved net-like sculpture over at least posterior half of bare area. Scutellum (Fig. 45) mostly bare except along extreme anterior and lateral margins; frenum broadly smooth and shiny or with lateral longitudinal rugae continued narrowly along posterior margin and with fine, engraved, net-like sculpture except for anteromedial smooth region (Figs. 53, 54). Metapleuron with at least a few setae in anteroventral angle and often extensively setose (Figs. 61, 62). Forewing with basal cell often evenly setose (Fig. 71) but at least setose apically and with one or more lines of setae along length; disc either without evident speculum (Fig. 71) or speculum narrow, closed basally by setae and with line or lines of setae close to submarginal vein. Petiole in dorsal view slightly transverse to longer than wide, length 0.8–1.2 times width, reticulate with irregular longitudinal carina or stronger keels (Figs. 45, 53).

Male.—Color pattern similar to female except legs sometimes more extensively light-colored, rarely almost uniformly yellow beyond coxae, antenna uniformly dark. Scape (Figs. 35, 36) length about 3.7–4.5 times greatest width, often widest subbasally but at least slightly tapered to apex, and in lateral view inner surface evenly setose but with flat to slightly concave ventrally or externally angled, sparsely setose or bare and shiny, surface over at least apical two-thirds (Fig. 36a). Pedicel (Figs. 35, 36) length about 2–2.25 times width and about 0.36–0.47 scape length. Combined length of pedicel and flagellum less than 2.5 times scape length, and flagellum at most as long as width of head; funicle (Fig. 35) with all segments slightly to distinctly transverse or with one or more of fu$_{2-6}$ slightly longer than wide,

quadrate, or moniliform (segments increasingly more transverse apically). Structure otherwise similar to female except petiole always at least slightly longer than wide, about 1.1–1.66 times as long as wide (Fig. 57). Setal patterns similar to female except more commonly with only a few setae in anteroventral angle of metapleuron.

Distribution.—Holarctic; in North America transcontinental across the Boreal region and extending south within and west of the Rocky Mountains in the USA (Fig. 80) and into Mexico along the Sierra Madre Occidental.

Biology.—All host records indicate that *A. hirsutus* is a hyperparasite of aphids, including: *Acyrthosiphon pisum* (Harris), *Aphis fabae* Scopoli, *Calaphis* sp., *Cinara cembrae* (Seitner), *Cinara chinookiana* Hottes ?, *Cinara hottesi* (Gillette & Palmer), *Elatobium abietinum* (Walker), *Essigella* sp., *Eulachnus agilis* (Kaltenbach), *Illinoia* sp., *Macrosiphum creelii* Davis, *Macrosiphum euphorbiae* (Thomas), *Myzus persicae* (Sulzer), *Rhopalosiphum insertum* (Walker), *Sitobion avenae* (Fabricius), *Sitobion pteridis* (Wilson), and *Schizaphis graminum* (Rondani). Label data also indicate species of *Praon* and *Aphidius* (Braconidae), and possibly *Alloxysta*, *Blacus*, *Lysiphlebus*, *Ephedrus*, *Monoctonus* (Braconidae) and *Dendrocerus* (Megaspilidae) as host primary parasites.

Remarks.—In addition to the paratypic material listed above, in 1984 the junior author examined two females and two males of *A. hirsutus* from the Greenland Hymenoptera Collection of the Zoological Museum, University of Copenhagen, Denmark. Lundbeck (1897) collected these specimens in 1889 from Arsuk and Sermiligârssuk fjord (= Sermiliarsuk) in southwestern Greenland. The four specimens had 1955 determination labels by O. Bakkendorf, as *A. vulgaris*. At the time of preparation of this manuscript these specimens could not be located in the museum (N. Kristensen, pers. comm.). However, they formed the basis for the literature records of *A. vulgaris* in Greenland cited in Bakkendorf (1955). It is possible that all records of *A. vulgaris* from Greenland are based on misidentifications of *A. hirsutus*.

The setose metapleuron (Figs. 61, 62) readily distinguishes most males and females of *A. hirsutus* from most other species of *Asaphes* in the Nearctic region. Those specimens with only a few setae within the anteroventral angle of the metapleuron are very similar to individuals of *A. petiolatus* but females of *A. petiolatus*, at least in the Nearctic region, have a distinctly sculptured frenum (Fig. 52). In addition to the absence of any setae on the metapleuron, males of *A. petiolatus* also have a slightly different structure of the scape. In lateral view the scape is more elongate-slender, without a distinct ventrally or externally angled surface but with a longitudinal, bare, shiny band on the inner surface, at least in larger specimens (*cf.* Figs. 36, 38). Some *A. brevipetiolatus* females also have setae on the metapleuron but are distinguished from *A. hirsutus* females by head structure. The combination of almost uniformly setose forewing and dark trochanters will differentiate females from those of *A. vulgaris* and *A. californicus*, respectively. Because of its setose metapleuron, setose forewings, and relatively dark legs, *A. hirsutus* is also very similar to the Japanese species *A. pubescens* Kamijo and Takada, but is distinguished by having the mesoscutal lateral lobes broadly bare medially (Fig. 45) rather than evenly setose. We saw three females from Nepal (CNCI) with the metapleuron entirely setose, which closely resemble *A. pubescens* because they have the mesonotal lateral lobes evenly setose. These specimens likely belong to an undescribed species because the flagellar segments, including fu_2, are all at least slightly transverse.

Asaphes petiolatus Zetterstedt, revised status

(Figs. 25, 26, 37, 38, 46, 51, 52, 58, 65, 72, 75)

Asaphes petiolatus Zetterstedt 1838: 423. Type data: Lapponia [Swedish Lapland]: Wittangi.

Sex described: female. Holotype by monotypy; MZLU.

Female.—Head and mesosoma black with obscure metallic green luster under some angles of light [some western European females with distinct metallic green luster]; legs entirely black or, more often, black to dark brown with extreme apex of femora, extreme base and apex of tibiae to entire tibiae, and tarsi lighter in color, rufous to yellowish. Head transverse-subtriangular in frontal view, width at least 1.25 times height, and in lateral view lower face evenly curved into upper face; interorbital region in dorsal view relatively shallowly concave; gena length about 0.72–0.85 eye width and 0.57–0.65 eye length; dorsal margin of torulus approximately in line with lower orbit. Antenna (Figs. 25, 26) with pedicel length about 2.0–2.5 times greatest width; funicle with fu$_1$ ring-like, fu$_2$ quadrate to slightly longer than wide, fu$_3$–fu$_5$ or fu$_3$–fu$_6$ subquadrate, but at least fu$_7$ and fu$_8$ transverse. Mesoscutum (Fig. 46) with lateral lobes broadly bare medially, and with fine engraved net-like sculpture over bare area. Scutellum mostly bare except along extreme anterior and lateral margins (Fig. 46); frenum with distinct, uniform, engraved net-like sculpture similar to scutellum (Figs. 51, 52) [some specimens from western Europe with frenum medially or mostly shiny and smooth except for very fine and obscure net-like sculpture]. Metapleuron bare (Fig. 65). Forewing with basal cell evenly setose (Fig. 72); disc with speculum closed basally by setae and with line or lines of setae close to submarginal vein (Fig. 72). Petiole in dorsal view variedly distinctly, almost always definitely transverse (Fig. 51), width 1.15–1.3 times length, reticulate with irregular longitudinal carinae or stronger keels.

Male.—Color pattern similar to female [western European specimens sometimes with head and mesosoma having distinct metallic green luster; legs usually more extensively light-colored, sometimes almost entirely yellow except metafemur partly infuscate]; antenna uniformly dark. Scape (Figs. 37, 38) length about 4.5–5.5 times greatest width, spindle-shaped with ventral and dorsal margins symmetrically tapered to apex; in lateral view with flat ventral surface differentiated only near pedicel, and at least larger individuals with elongate, bare, smooth band over most of inner surface (Fig. 38b). Pedicel length about 2.0–2.5 times width and about 0.36–0.42 scape length (Figs. 37, 38). Combined length of pedicel and flagellum less than 2.5 times scape length, and flagellum length slightly less than head width; funicle (Fig. 37) with at least fu$_4$ and fu$_5$ subquadrate to moniliform, and sometimes with fu$_2$ longer than wide and fu$_{3-5}$ subquadrate to moniliform. Structure otherwise similar to female except malar space about 0.62–0.74 eye width and about 0.51–0.54 eye length; petiole subquadrate to definitely longer than wide, but length less than 1.25 times width (Fig. 58). Setal patterns similar to female.

Distribution.—Holarctic; in North America restricted to the Boreal region (Fig. 79) and not commonly collected. **CANADA. Northwest Territories:** Kovaluk River [69°11′N 131°W], 2–6.VIII.71, W.R.M. Mason (1 ♀). **British Columbia:** Upper Carmanah Valley, UTM 10U CJ 801991, 28.VII.92, N. Winchester (2 ♂, PFRC). **Alberta:** Edmonton, 10.IX.86, A.T. Finnamore (1 ♀); 24.IX.86, Jorgensen & Andrews (1 ♂, used for SEM). **Saskatchewan:** Prince Albert National Park, 23.VII.54, ex. *Cinara hottesi* (G. & P.) (2 ♀, 1 used for SEM). Hudson Bay, 15.IX.59, J.R. Vockeroth (2 ♂). **Manitoba:** Warkworth Creek near Churchill, 21.VI.52, J.G. Chillcott (1 ♀). **Ontario:** Wawa, 2.VII.57, Forest Insect Survey record no. 710 (1 ♀). **Quebec:** Lac Brule, 7.VIII.45, O. Peck (1 ♀). **USA. Alaska:** Sterling, in front of Collet house, 60°30′N 150°45′W, 3.VIII.94, ex. aphid mummies on *Picea glauca*, D. Collet (1 ♀, DCPC). EXTRALIMITAL. **FIN-**

LAND (DAZH, VVPC), **ITALY** (BMNH),
SWEDEN (CNCI, MZLU), **SWITZER-
LAND** (BMNH).

Biology.—Apparently a hyperparasite of
aphids in North America, including *Cinara
hottesi* (Gillette & Palmer).

Type material examined.—The holotype
female of *A. petiolatus* is glued by its me-
tasoma to the side of a pin that also bears
the holotype of *Pteromalus violaceus* Zetter-
stedt (see Graham 1969: 81). It is entire,
except for the right antenna beyond the
pedicel, and has the following features:
frenum almost entirely coriaceous except
for narrow median smooth band that does
not quite extend to the posterior margin
of the frenum; speculum closed basally by
setae with four, almost evenly spaced,
setae behind the submarginal vein that are
separated from the vein by a distance less
than the length of a seta; petiole about 1.2
times as wide as long; and head and me-
sosoma with only relatively obscure me-
tallic green luster under some angles of
light.

Remarks.—We have seen too few speci-
mens of this species to estimate limits of
variation reliably, both within the Nearctic
region and across its known range. All
Nearctic females seen had the frenum dis-
tinctly sculptured whereas some females
from western Europe have a shiny, only
very finely and obscurely sculptured fre-
num. Males from both regions have the
frenum quite shiny, smooth medially
though finely sculptured paramedially.
Such males from the Nearctic had only
very obscure metallic green luster and
dark legs, whereas those from western Eu-
rope were distinctly metallic green and
had the legs almost entirely yellow except
for a partly infuscate metatrochanter and/
or metafemur. These males could easily be
mistaken for males of *A. suspensus* because
of their indistinct speculum and shallowly
concave interorbital region, but the anten-
na is uniformly dark and the scape and
basal flagellar segments are more elongate
than for males of *A. suspensus* (*cf.* Figs. 37,

39). Most males and females of *A. petiola-
tus*, particularly those with the frenum
more or less smooth and shiny medially,
are more likely to be mistaken for those of
A. vulgaris. However, in addition to hav-
ing a narrow, closed speculum, *A. petiola-
tus* also has the interorbital region more
shallowly concave (*cf.* Fig. 17) and usually
has an obviously shorter petiole than *A.
vulgaris* (*cf.* Figs. 58, 60). In both species
the petiole of the female is shorter relative
to the male so that females of *A. petiolatus*
usually have an obviously transverse pet-
iole (Fig. 46) whereas *A. vulgaris* females
have the petiole at least quadrate and al-
most always slightly to distinctly longer
than wide (Fig. 48). Males of *A. petiolatus*
usually have a subquadrate to only slight-
ly elongate petiole (Fig. 58), whereas
males of *A. vulgaris* have a more obviously
elongate petiole (Fig. 60). However, in
both cases the most elongate petioles of
specimens assigned to *A. petiolatus* ap-
proach the least elongate petioles of spec-
imens assigned to *A. vulgaris* based on
forewing setal pattern. Structures of the
scape are also similar. Males of *A. vulgaris*
do not have a distinct bare band on the
inner surface of the scape (*cf.* Figs. 38b,
42b), but because of poor preservation of
specimens we are uncertain whether this
feature is characteristic of and distinct for
all *A. petiolatus* males. Except for the ab-
sence of any metapleural setae, males of
A. petiolatus are also quite similar to males
of *A. hirsutus*. The slight differences in de-
scribed scape structure of the two species
help to differentiate those males of *A. hir-
sutus* that have only a few inconspicuous
setae (see 'Remarks' for *A. hirsutus*). Only
head structure reliably distinguishes fe-
males of *A. petiolatus* and *A. brevipetiolatus*.

Asaphes suspensus (Nees)
(Figs. 9, 10, 16, 27, 28, 39, 40, 47, 59, 66,
69, 77, 78)

Chrysolampus suspensus Nees 1834: 127. Type
data: Germany: Sickershusi province, 2 July
1813; reared from *Aphidii rosarum*. Female de-

scribed. Lectotype designated by Graham 1969: 82; Hope Entomological Collection, Oxford, England.

Chrysolampus altiventris Nees 1834: 127. Type data: Germany: Sickershausen [female: 21 April 1811; male: 17 September]. Both sexes described. Syntypes, lost. Synonymy by Graham, 1969: 82.

Pteromalus petioliventris Zetterstedt 1838: 429. Type data: Lapponia [Swedish Lapland] between Karesuando and Kengis in August. Described questionably as male [Graham, 1969: 82 erroneously stated that it was described as a female]. Holotype male by monotypy; MZLU. Synonymy by Graham, 1969: 82.

? *Colax aphidii* Curtis 1842: 60. Unknown type status, lost. Tentative synonymy by Graham 1969: 82, based on original description.

Chrysolampus aphidiphagus Ratzeburg 1844: 181. Holotype, lost. Synonymy by Graham 1969: 82, based on original description; incorrectly synonymized with *A. vulgaris* by Kurdjumov 1913: 24.

Chrysolampus aphidicola Rondani 1848: 19–21. Type data: reared from an aphid [*Aphis rosae*]. Female described. Lectotype designated by Bouček 1974: 244; Museo Zoologico 'La Specola', Florence, Italy. Synonymy by Bouček 1974: 244, 275; incorrectly synonymized with *A. vulgaris* by Delucchi 1955: 174.

Euplectrus lucens Provancher 1887: 207. Type data: Canada: Quebec, Cap Rouge; Ontario, Ottawa. Female described. Lectotype designated by Gahan and Rohwer 1917: 399; Université Laval Insect Collection, Quebéc City, Canada, type no. 1369. **New synonymy.**

Asaphes rufipes Brues 1908: 160. Type data: USA: Massachusetts, Forest Hills, 30.X.1908, P. Hayhurst; reared from *Aphis*, probably *A. atriplicis* L., on *Chenopodium album*. Female described. Holotype by original designation; MCPM. **New synonymy.**

Megorismus Fletcheri Crawford 1909: 98. Type data: Ottawa [15 Aug.] Canada [emerged]; bred from [ex.] *Nectarophora pisi*; Arthur Gibson collector. Both sexes described. Holotype female by original designation; USNM, type no. 12197. Previous synonymy with *A. lucens* by Burks, 1964: 1258. **New synonymy.**

Asaphes americana Girault 1914[219]: 114. Type data: USA: Iowa, Hampton, June 1912, R.L. Webster, exp. 101. Female described. Lec-

totype female hereby designated; USNM, type no. 15655. Previous synonymy with *A. fletcheri* by Burks, 1958: 74 and with *A. lucens* by Burks, 1964: 1258. **New synonymy.**

Pachycrepoides indicus Bhatnagar 1951: 160–163. Type data: India: Chaubattia (U.P.), 15.V.1946, Z.A. Siddiqi; reared from *Aphis helichrysi* Kalt. Female described. Holotype by monotypy; type depository unknown. Tentative synonymy with *A. vulgaris* by Bouček et al. 1978: 437, based on original description and illustrations. **New synonymy.**

? *Asaphes sawraji* Sharma & Subba Rao 1958: 181–183. Type data: India: Kalka, Punjab; reared from *Acyrthosiphon* (*Macrosiphon*) *pisi* on the garden pea, *Lathyrus odoratus* L. Both sexes described. Unknown type status; IARI. Synonymy by Bouček et al. 1978: 436–437.

Pachyneuron uniarticulata Mani & Saraswat 1974: 96–98. Type data: India: Northwest Himalayas, Dalhousie (Ahla catchment area), M.K. Kamath, 25.V.1971. Female described. Holotype by original designation; USNM. Synonymy by Bouček et al. 1978: 436–437.

Asaphes vulgaris; McMullen 1966: 236, 239; McMullen 1971: 34; Philogene and Chang 1978: 54; Batulla and Robinson 1985: 36. Misidentifications of *A. suspensus*.

Female.—Head and mesosoma with metallic green luster under some angles of light, and usually bright metallic; legs usually uniformly light-colored, yellowish to yellowish-orange, but femora sometimes darker, yellowish-brown, medially. Head transverse-subtriangular in frontal view (Fig. 9), width at least 1.25 times height, and in lateral view lower face evenly curved into upper face; interorbital region in dorsal view shallowly concave (Fig. 16); gena length about 0.6–0.72 eye width and 0.5–0.65 eye length; dorsal margin of torulus approximately in line with lower orbit (Figs. 9, 10). Antenna (Figs. 27, 28) with pedicel length at most about twice width; funicle with fu_1 strongly transverse, fu_2 ring-like, and usually all segments at least slightly transverse, but fu_1–fu_6 sometimes moniliform. Mesoscutum (Fig. 47) with lateral lobes broadly bare medially, and with finely engraved

Table 2. Host information for *Asaphes suspensus* based on observed specimens; a question mark follows rearings or identifications indicated as questionable on the labels. Unless otherwise footnoted, all 'aphid or other hosts' are Homoptera (Aphidoidea: Aphididae) and all 'associated primary hosts' are Hymenoptera (Braconidae: Aphidiinae).

Aphid or other Hosts	Associated Primary Hosts	Localities	Museum Acronyms
	Aphelinus semiflavus[1] Howard	OH	USNM
	Aphelinus sp.[3]	OH	USNM
	Aphidius sp.	CA, NY	CUIC, USNM
	A. smithi Sharma & Subba Rao	CA	EMEC
	Ephedrus incompletus Provancher	VA	USNM
	Praon aguti Smith	CA	EMEC
	P. exoletum palitans Muesebeck	CA	EMEC, USNM
	T. (Trioxys) complanatus Quilis	CA	EMEC
	T. (Trioxys) pallidus (Haliday)	CA	EMEC
Acaudus convolvuli Nevsky ?		NB	CNCI
Acyrthosiphon lactucae (Passerini)	*Praon* sp.	WA	WSUC
A. pisum (Harris)	*Aphidius* sp., *A. ervi* Haliday; *Praon* sp.	CA, IL, MB, NB, NS, OH, ON, OR, WA	CNCI, EDUM, EMEC, INHS, OSUC, USNM, WSUC
Amphorophora rubi (Kaltenbach) ?		WA	WSUC
Aphis atriplicis (L.)		MA	CUIC
A. brassicae L.		CA, IA, KS	USNM
A. craccivora Koch	*Lysiphlebus (Phlebus) testaceipes* (Cresson)	WA	WSUC
A. fabae Scopoli	*Lysiphlebus* sp.	WA	WSUC
A. gossypii Glover		CA, DC	UCRC, USNM
A. helianthi Monell	*Praon* sp., *P. unicum* Smith	WA	WSUC
A. holodisci Robinson		WA	WSUC
A. illinoisensis Shimer		DE	USNM
A. nasturtii Kaltenbach		ON	CNCI
A. rumicis L.		AB, CA, NB	CNCI, USNM
A. spiraecola Patch ?	*Alloxysta* sp.	WA, WV	USNM, WSUC
A. vitis Scopoli		KS	USNM
Aphthargelia symphoricarpi (Thomas)	*Lysiphlebus (Phlebus) testaceipes* (Cresson)	WA	WSUC
Brachycaudus helichrysi (Kaltenbach)	*Praon* sp.	WA	WSUC
B. (Appelia) tragopogonis (Kaltenbach)		WA	WSUC
Brachycornella asparagi (Modviko)	*Diaeretiella rapae* (M'Intosh)	WA	WSUC
Braggia sp.		WA	WSUC
Brevicoryne brassicae (L.)	*Aphidius ervi* Haliday; *Diaeretiella rapae* (M'Intosh)	CA, MD, WA, WI	EMEC, USNM, WSUC
Calaphis betulaecolens (Fitch)		NB	CNCI
Cavariella aegopodii (Scopoli)	*Aphidius salicis* Haliday	NB, WA	CNCI, WSUC
Chaitophorus salicicola Essig		CA	USNM
Chaetosiphon (Pentatrichopus) fragaefolii (Cockerell)		CA	UCRC
Chromaphis juglandicola (Kaltenbach) ?	*T. (Trioxys) pallidus* (Haliday)	WA	WSUC

Table 2.   Continued.

Aphid or other Hosts	Associated Primary Hosts	Localities	Museum Acronyms
Diuraphis noxia (Mordvilko)	*Aphidius ervi* Halliday; *Diaeretiella rapae* (M'Intosh)	TX, WA	TAMU, WSUC
Dysaphis (*Pomaphis*) *plantaginea* (Passerini)	*Praon sp., P. unicum* Smith	WA	WSUC
Elatobium abietinum (Walker)		BC	NFRC
Ericaphis gentneri (Mason)	*Praon unicum* Smith	WA	WSUC
Eriosoma americanum (Riley)		SK	CNCI
E. lanuginosum (Hartig)	*Aphelinus mali* (Haldeman)[1]	NY	USNM
Eucallipterus tiliae (L.)		CA	CNCI
Euceraphis punctipennis (Zetterstedt)		CA	USNM
Hayhurstia atriplicis (L.)		WA	WSUC
Hyalopterus pruni (Geoffroy)		CA	EMEC
Hyperomyzus lactucae (L.)		NB, WA	CNCI, WSUC
Hyperomyzus (*Neonasonovia*) *nigricornis* (Knowlton)	*Praon sp.*	WA	WSUC
Illinoia sp.	*Alloxysta sp.*	WA	WSUC
I. liriodendri (Monell)		CA, DC	EMEC, USNM
I. spiraeae (MacGillivary)		ME, WA	USNM, WSUC
Lipaphis erysimi (Kaltenbach)		CA, OK	CNCI, EMEC
Liosomaphis berberidis (Kaltenbach)		NB	CNCI
Macrosiphoniella ludovicianae (Oestlund)	*Praon sp.*	WA	WSUC
Macrosiphum sp.	*Aphidius sp.; Praon sp.*	NB, OH, ON, WA	CNCI, USNM
M. creelii Davis		WA	WSUC
M. euphorbiae (Thomas)	*Praon sp.*	DC, ME, NB, NJ, WA, WI	CNCI, USNM, UWEM, WSUC
M. rosae (L.)	*Aphidius sp.*	CA	CASC, UCRC
Malacosoma sp.[2]		BC	CNCI
Metopolophium dirhodum (Walker)	*Praon sp.*	WA	WSUC
Monellia caryae (Monell)	*Trioxys sp.*	WA	WSUC
Myzaphis rosarum (Kaltenbach)		DC	USNM
Myzus (*Nectarosiphon*) *persicae* (Sulzer)	*Aphidius sp.; Diaeretiella rapae* (M'Intosh); *Praon sp., P. unicum* Smith	CA, MD, MN, NB, OH, WA	CNCI, EMEC, UCRC, USNM, WSUC
Nasonovia (*Kakimia*) *sp.*		WA	WSUC
Nearctaphis bakeri Cowen	*Praon unicum* Smith	WA	WSUC
Obtusicauda coweni (Palmer)		WA	WSUC
Ovatus crataegarius (Walker) ?		WA	WSUC
Paraphis juglandis (Goeze)	*T.* (*Trioxys*) *pallidus* (Haliday)	WA	WSUC
Periphyllus lyropictus (Kessler)	*Euaphidius setiger* Mackauer	WA	WSUC
P. negundinis (Thomas)		NB	CNCI
Phorodon humuli (Schrank)	*Praon unicum* Smith	WA	WSUC
Pleotrichophous sp. ?		WA	WSUC
Psylla pyricola Förster[1]		BC, ON	CNCI

Table 2. Continued.

Aphid or other Hosts	Associated Primary Hosts	Localities	Museum Acronyms
Rhadobium porosus (Sanderson)		NB	CNCI
Rhopalomyzus (Judenkoa) lonicerae (Siebold)	Praon sp.	WA	WSUC
Rhopalosiphoninus (Myzosiphon) solani (Thomas)		NB	CNCI
Rhopalosiphum sp.		ON	CNCI
R. cerasifoliae (Fitch)	Lysiphlebus (Phlebus) testaceipes (Cresson)	WA	WSUC
R. insertum (Walker)	Lysiphlebus (Phlebus) testaceipes (Cresson); Praon unicum Smith	WA	WSUC
R. maidis Fitch	Alloxysta sp.	MN, WA	USNM, WSUC
R. padi (L.)	Diaeretiella rapae (M'Intosh); Lysiphlebus (Phlebus) testaceipes (Cresson)	WA	WSUC
Schizaphis graminum (Rondani)		IL, SK	CNCI, INHS
Sipha (Rungsia) maydis Passerini		ON	CNCI
Siphocoryne sp.		DC	USNM
Sitobion avenae (Fab.)	Aphidius sps.; Diaeretiella rapae (M'Intosh); Praon sp.	OR, WA	OSUC, WSUC
Therioaphis trifolii (Monell)	Aphelinus semiflavus Howard[1]	CA, WA	EMEC, WSUC
Thripsaphis sp.	Praon sp.	WA	WSUC
Uroleucon sp.	Alloxysta sp.; Praon sp.	WA	WSUC
U. ambrosiae (Thomas)	Aphidius polygonaphis Fitch ?	MD, ON	CNCI, USNM
U. (Lambersius) madia Swain		NB, NJ, ON	CNCI, USNM
U. sonchi (L.) ?		WA	WSUC
Wahlgreniella nervata (Gillette)	Praon sp.	WA	WSUC

[1] Chalcidoidea (Aphelinidae).
[2] From "egg mass", but likely some aphid with the egg mass.
[3] Homoptera (Psyllidae).

or subeffaced net-like sculpture over bare area. Scutellum mostly bare except along extreme anterior and lateral margins (Fig. 47); frenum smooth and shiny except finely carinate laterally. Metapleuron bare (Fig. 65). Forewing with at least two rows of setae in basal cell (Fig. 69); disc with very narrow speculum, its dorsal surface with at least three setae close to submarginal vein (within distance equal to or less than length of setae) (Fig. 69). Petiole (Fig. 47) length at least slightly greater than width (up to about 1.25 times), and strongly carinate with reticulate or subeffaced sculpture between carinae.

Male.—Color pattern similar to female;

antenna rarely uniformly dark brown, much more commonly with flagellum and usually pedicel yellowish or at least distinctly lighter brown than dark scape. Scape (Figs. 39, 40) robust-subcylindrical, length about 4–5 times width, with dorsal and ventral margins subparallel, and usually with obscure linear or very narrow ventrally or externally angled, flat, microsetose sensory strip (Fig. 40a); inner surface low convex to flat, smooth, shiny and sparsely setose (Fig. 40b); outer surface (Fig. 40a) more distinctly convex. Combined length of pedicel and flagellum less than 2.5 times scape length and shorter than head width; funicle (Fig. 39) with all

segments at least slightly transverse. Setal pattern similar to female except metapleuron rarely with one short setae directed ventrally toward metacoxa. Structure similar to female, with petiole always at least slightly longer than wide (up to about 1.35 times) (Fig. 59).

Distribution.—A naturally occurring Holarctic species (see also under 'Remarks'). In North America distributed throughout the Nearctic region (Fig. 81) and extending south into Mexico. The absence of observed specimens from the states and provinces listed below undoubtedly reflects artifacts of collection (except possibly for Newfoundland and Labrador). **CANADA:** all territories and provinces except Yukon, and Newfoundland and Labrador. **USA:** all states except Alabama, Louisiana, New Jersey, North Dakota, Rhode Island, and Vermont. EXTRALIMITAL. *Neotropical:* **MEXICO** (CNCI). *Palaearctic:* **AZORES** (USNM), **CANARY ISLANDS** (CNCI), **CZECH REPUBLIC** (CNCI), **DENMARK** (CNCI), **FINLAND** (CNCI, DAZH, VVPC), **FRANCE** (BMNH, CNCI, EMEC, UCRC, USNM), **GERMANY** (CNCI), **GREAT BRITAIN** (BMNH, EMEC), **HUNGARY** (CNCI), **ICELAND** (GNME, LUND, ZMCU), **IRAN** (ANIC, BMNH, CNCI, UCRC), **ISRAEL** (EMEC), **ITALY** (BMNH, CNCI, UCRC), **JAPAN** (CNCI, EMEC, UCRC, USNM), **SOUTH KOREA** (UCRC), **MADEIRA ISLANDS** (BMNH), ? **MOROCCO** (UCRC), **NETHERLANDS** (TAMU), **PEOPLE'S REPUBLIC OF CHINA** (CNCI, TAMU), **POLAND** (TAMU), **PORTUGAL** (BMNH), **SPAIN** (CNCI, UCRC), **SWEDEN** (BMNH, CNCI, MZLU), ? **TURKEY** (UCRC), **UKRAINE** (USNM). *Oriental:* **INDIA** (CNCI, UCRC), **NEPAL** (CNCI), **PAKISTAN** (UCRC).

Biology.—Specimens with host data from the Nearctic region indicate that *A. suspensus* is usually a hyperparasite of aphids through aphidiine and aphelinid primary parasites, and rarely also a parasite of *Psylla* (Homoptera: Psyllidae) (Ta-

ble 2). One record from a lepidopteran egg mass is undoubtedly erroneous.

Synonymy and type material examined.— *Asaphes suspensus* was generally considered to be a synonym of *A. vulgaris* until Graham (1969) reestablished the name as valid. Our synonymy of *A. rufipes* with *A. suspensus* is based on Graham's (1969) concept and examination of the holotype of *A. rufipes*. It is glued to a point and is entire, though the right wings are glued over the metasoma and the body is otherwise covered by a film of glue except for one antenna, about the dorsal half of the head and the dorsal surface of the mesosoma. The specimen is labelled as from "Boston Mass." rather than "Forest Hills," which was given in the original description, and has the additional labels "3671," "27315," "TYPE," "Asaphes rufipes Brues," "Holotype Asaphes rufipes Brues, V. Vikberg 1986," "Asaphes suspensus (Nees) det. V. Vikberg 1986."

The holotype female of *A. fletcheri* is point-mounted and entire. It has a hand written label with "Megorismus fletcheri Cwfd. ♀ type" and a red "Holotype" label. There are also 5 ♀ and 1 ♂ labelled as paratypes in the USNM as well as 5 ♀ labelled as paratypes in the CNCI. All specimens are labelled identically except for type labels. Because Crawford explicitly referred to 'paratypes' in the original description we consider the female labelled originally as 'Type' to be the holotype by original designation. The holotype is point-mounted and entire.

The type series of *A. americanus* consists of 4 ♀ and 1 ♂ syntypes on five slides. The Hampton female from experiment 102 is labelled as 'Type', the male from experiment 101 as 'Allotype', and the other three females as 'Paratypes'. However, in the original description Girault referred to all specimens as 'Types'. We hereby designate the Hampton female from experiment 101 as lectotype and the other four specimens as paralectotypes. The female originally labelled as type is not selected

as lectotype because the cover slip over the specimen is crushed.

Bouček et al. (1978) transferred *Pachycrepoides indicus* Bhatnager to *Asaphes* based on the original description and accompanying illustrations, and tentatively synonymized the name under *A. vulgaris* with the statement "judging from some points as e.g. head from above rectangular." We agree with the generic placement, but the original description states "Legs except the three coxae which are black, rest of legs are light yellowish-brown." This statement leads us to believe the name is a junior synonym of *A. suspensus*.

Remarks.—Females of *A. suspensus* are recognized by the combination of entirely yellowish legs and relatively narrow speculum with at least three setae very close to the submarginal vein (Fig. 69). Because of color variation, without associated males it is sometimes very difficult to distinguish females of *A. suspensus* and *A. californicus* in western North America. Males of *A. californicus* and *A. vulgaris* can have entirely yellowish legs, but structure of the scape distinguishes males of *A. californicus* and a broad speculum distinguishes males of *A. vulgaris*. Males of these last two species usually also have uniformly brown antennae (see under *A. californicus*).

Asaphes suspensus is undoubtedly widespread throughout the Palaearctic region from western Europe to Japan, much more so than is indicated by the relatively few countries listed above or in Graham (1969). Bakkendorf (1955), and probably based on him Graham (1969), reported *A. vulgaris* from Iceland. The junior author examined 3 females identified as *A. vulgaris* by Bakkendorf in 1955 (GNME), which were specimens of *A. suspensus*. *Asaphes suspensus* was also reported from southern Iceland and the Westman Islands by Lindroth et al. (1973). Because all specimens of *Asaphes* that we have seen from Iceland are *A. suspensus* it seems likely that this is the only species occurring in Iceland.

Farooqi and Subba Rao (1986) list *A. suspensus* from India and Pakistan, which we confirm. De Santis (1967, 1979) and De Santis and Fidalgo (1994) also recorded *A. suspensus* (as *A. lucens* and *A. rufipes*) within the Neotropical region as far south as Chile and Argentina. We saw specimens from La Plata and Jujuy, Argentina (MLPA) that were identified as *A. fletcheri* and *A. rufipes* by De Santis, but which fit within our concept of the *californicus*-complex. As discussed in the respective section for *A. californicus*, we suspect that most if not all records of *A. suspensus* south of Mexico result from misidentification of the *californicus*-complex.

Asaphes vulgaris Walker
(Figs. 11, 12, 15, 29, 30, 41, 41, 48, 60, 70)

Asaphes vulgaris Walker 1834: 152. Both sexes described. Lectotype female designated by Graham 1969: 80–81; BMNH.

Eurytoma aenea Nees 1834: 42. Type data: Germany: Sickershausen, 11 June 1813. Female described. Holotype by monotypy, lost. Synonymy by Walker 1846: 23.

Chrysolampus aeneus Ratzeburg 1848: 185. Female described. Holotype by monotypy, ? lost (see Graham 1969: 81). Synonymy by Reinhard 1857: 76.

Chrysolampus aphidophila Rondani 1848: 21–22. Female described. Lectotype designated by Bouček 1974: 244; Museo Zoologico "La Specola," Florence, Itatly. Synonymy by Bouček 1974: 244, 275.

Female.—Head and mesosoma dark with variedly distinct olive green metallic luster under some angles of light; legs mostly dark, at least middle and hind legs with trochanters infuscate to black [light-colored in some regions of western Europe] and femora black except apically, trochantelli often much lighter to yellowish, and tibia and tarsus usually yellowish. Head transverse-subtriangular in frontal view (Fig. 11), width at least 1.25 times height, and in lateral view lower face evenly curved into upper face (Fig. 12); interorbital region in dorsal view relatively

deeply concave (Fig. 15); gena length about 0.57–0.67 eye width and 0.5–0.6 eye length; dorsal margin of torulus approximately in line with lower orbit (Figs. 11, 12). Antenna (Figs. 29, 30) with pedicel length 1.65–2.3 times greatest width; funicle (Fig. 29) with fu₁ ring-like, fu₂–fu₄ quadrate to transverse (Fig. 30), and fu₅–fu₈ increasingly transverse. Mesoscutum (Fig. 48) with lateral lobes broadly bare medially, and with fine but distinct, engraved net-like sculpture over bare area. Scutellum mostly bare except along extreme anterior and lateral margins (Fig. 48); frenum smooth and shiny except finely carinate laterally. Metapleuron at most with one or two short setae directed ventrally toward metacoxa. Forewing with basal cell usually almost bare or with only single row of setae on dorsal surface (Fig. 70) except apically; disc with broad speculum, dorsal surface without setae near submarginal vein and with distance between basal setal line and first setal line on disc about equal to distance between first and fourth setal lines on disc (Fig. 70) (note: ventral surface of wing can have a few setae on bare band closer to submarginal vein). Petiole at least as long as usually slightly longer than wide (up to 1.2 times), entirely or mostly reticulate with at most few irregular carinae (Fig. 48) to strongly carinate with subeffaced sculpture between carinae.

Male.—Color pattern similar to female except legs usually more extensively yellowish, with trochanters and trochantelli usually yellowish and often legs mostly or entirely yellow; antenna uniformly brown to black except possibly apex of pedicel and fu₁ lighter in color. Scape (Figs. 41, 42) elongate-subcylindrical or spindle-shaped, length about 5–6 times width, with dorsal and ventral margins subparallel; outer surface with shorter setae along line ventrally but without well defined microsetose area or smooth band (Fig. 42a); inner surface with sparse setae (Fig. 42b). Combined length of pedicel and flagellum less than 2.5 times scape length and subequal in length to head width; funicle (Fig. 35) usually with all or most segments slightly to distinctly transverse, but at least fu₁ distinctly transverse, fu₂ transverse to quadrate, fu₃ and fu₄ transverse to slightly longer than wide, fu₅ and fu₆ transverse to quadrate, and fu₇–₈ distinctly transverse. Setal pattern and structure otherwise similar to female except petiole longer, length 1.25–1.60 times width (Fig. 60).

Distribution.—True world distribution is uncertain because of remaining taxonomic problems in differentiating the species (see under 'Remarks'). In North America *A. vulgaris* is restricted to eastern Canada and northeastern USA (Fig. 82). Based on this distribution and no collection records seen prior to 1953 it is probable that the species it is not naturally Holarctic but was introduced accidentally from Europe. Literature records from California and other western North American localities are based on misidentifications, probably mostly of *A. californicus*. At least some literature records from eastern North American localities are probably also based on misidentifications. **CANADA. Ontario:** Rondeau Provincial Park, 9–26.VI.80, H. Goulet (1 ♀). **Quebec:** Québec city, 27.VII.86, J. Brodeur, ex. *Aphidius nigripes* from *Macrosiphum euphorbiae* (1 ♀, 2 ♂). **Nova Scotia:** Aylesford, 24.VII.63, H. Specht, host *Acyrthosiphum pisum* (1 ♀). Centerville, 15.VIII, 9.IX.63, R. Foley, (4 ♀, 1 ♂); Coldbrook, 30.IX., 7, 10, 16, 21.X.63 (6 ♀, 3 ♂), Coldwell near Canard, 8, 23.VIII.63 (1 ♀, 1 ♂), Garland, 6.VIII.63 (1 ♂), Picketts Wharf near Canard, 2.VII.63 (2 ♀, 1 ♂)—all H. B. Specht, host *Acyrthosiphum pisum* (Harris) on alfalfa or clover. Kentville, greenhouse, 28.II.68, H.B. Specht, host pea aphid (1 ♂). Lockport, 20.VII.58, J.R. Vockeroth (1 ♀). **Prince Edward Island:** N Tryon, 26.VI.91, M.E.M. Smith, in potato field (1 ♀, 1 ♂). **USA. Maine:** Aroostook Co., 1953, ex. *Macrosiphum solanifolii* (4 ♀, 3 ♂). **Massachusetts:** Amherst, Nadel, clover (1 ♀, USNM). EX-

TRALIMITAL. *Palaearctic:* **AUSTRIA** (CNCI), **CZECH REPUBLIC** (CNCI, UCRC), **DENMARK** (CNCI), **FINLAND** (DAZH, VVPC), **FRANCE** (CNCI, EMEC, UCRC, USNM), **GERMANY** (BMNH, CNCI, USNM), **GREAT BRITAIN** (ANIC, BMNH, CNCI, EMEC, USNM), **GREECE** (CNCI, TAMU, UCRC), **IRELAND** (CNCI), **ISRAEL** (UCRC, USNM), **ITALY** (CNCI, UCRC, USNM), **LEBANON** (UCRC), **MOROCCO** (UCRC), **SPAIN** (CNCI, UCDC, UCRC), **SWEDEN** (BMNH, CNCI, MZLU), **TURKEY** (UCRC, USNM). *Afrotropical:* ? **ERITREA** (UCRC), ? **ETHIOPIA** (CNCI), ? **SOUTH AFRICA** (CNCI, USNM), ? **ZIMBABWE** (CNCI). *Australasian:* **AUSTRALIA** (Tasmania) (ANIC, BMNH), **NEW ZEALAND** (CNCI, EMEC).

Biology.—Host records based on examined specimens indicate that in North America *A. vulgaris* is a hyperparasite of aphids, including *Acyrthosiphon pisum* (Harris) and *Macrosiphum euphorbiae* (Thomas) through aphidiines, including *Aphidius nigripes* (Ashmead). Most of the unsubstantiated aphid host records from western North American localities given in Peck (1963) likely refer to *A. californicus,* whereas non-aphid hosts other than Syrphidae likely are erroneous.

Remarks.—Females of *A. vulgaris* are distinguished by a combination of features, but primarily by their broad, distinct speculum (Fig. 70), dark trochanters (at least in the Nearctic region), and relatively deeply concave interorbital region (Fig. 15). Females of *A. californicus* with a broad speculum could be confused with *A. vulgaris* females, but ranges of the two species apparently do not overlap in the New World (Fig. 82). Further, Nearctic *A. californicus* females have more or less uniformly light-colored trochanters and trochantelli, whereas the trochanters and trochantelli are dark in *A. vulgaris* or at least the trochanters are distinctly darker than the trochantelli, more similar in color to the femora. Some females of *A. vulgaris* from western Europe have both the tro-

chanters and trochantelli yellowish in distinct contrast to dark femora, but their broad speculum readily differentiates these from other known species in western Europe. All specimens tentatively identified as *A. vulgaris* from the Afrotropical region also have yellow trochanters and trochantelli plus a broad speculum. Only one male was seen from Zimbabwe but a series of both sexes were seen from Ethiopia, Eritrea and South Africa. The African males have scapes with a variedly distinct, flat, densely setose, sometimes laterally margined ventral surface. The scapes of most specimens are also distinctly shorter and more robust (more similar to *A. suspensus, cf.* Fig. 39) than the relatively elongate-slender, shinier, and much more sparsely setose scape of *A. vulgaris* males from North America or Europe (Fig. 41). Further, both sexes of the African specimens appear to have the interorbital region more shallowly concave (*cf.* Figs. 16, 17 with Fig. 15), though this feature is variable and difficult to quantify. Only females were seen from Lebanon and Morocco. The Afrotropical specimens are tentatively identified as *A. vulgaris* for the purposes of this study, but a comprehensive study of *Asaphes* is required from throughout the Palaearctic region and Africa to determine character variation and species limits. It is very possible that specimens with dark femora and yellowish trochanters and trochantelli from at least the Afrotropical region of Africa belong to an undescribed species different from *A. vulgaris.*

Males of *A. vulgaris,* particularly from regions outside of the Nearctic, can have the legs entirely yellow but are differentiated from males of *A. suspensus* by their broad speculum and longer scape (*cf.* Figs. 39, 40), though the range of variation is greater than stated by Graham (1969) and the shortest scape of *A. vulgaris* males is similar in relative length to the longest *A. suspensus* scape. Separation from males of

other species is discussed under the respective section for these species.

De Santis (1967, 1979, 1980) listed *A. vulgaris* from San Vincente, Juan Fernández, Argentina, Brazil, and Chile. We saw specimens from La Plata (♀, ♂) and Jujuy (♀), Argentina (MLPA) that were identified by De Santis as *A. vulgaris*, and these fit within our concept of the *californicus*-complex from South America. We have not seen any specimen from the Neotropical region that we identify as *A. vulgaris* (see 'Remarks' for *A. californicus*) and it is likely that most or all records of *A. vulgaris* from South America are based on misidentifications (see also 'Remarks' for *A. suspensus*). Records of *A. vulgaris* from Greenland may also be based on misidentifications of *A. hirsutus* (see 'Remarks' for *A. hirsutus*).

Nomina inquirenda

Parectroma hübrichi Brèthes 1913: 91–92. Type data: Argentina: Rosario (J. Hübrich) and Buenos Aires (A. Zotta). Female described. Syntypes [Rosario female examined]; MLPA. Synonymized with *A. fletcheri* by De Santis 1960: 114.

Pachycrepoideus bonariensis Brèthes 1916: 427. Type data: Argentina: Buenos Aires, 5.XI. 1915. Female described. Holotype by monotypy. Synonymized with *A. lucens* by De Santis 1967: 189.

Remarks.—De Santis (1960, 1967) synonymized, respectively, *A. huebrichi* (Brèthes, 1913) under *A. fletcheri* (Crawford, 1909) and *A. bonariensis* (Brèthes, 1916) under *A. lucens* (Provancher, 1887). Burks (1964) synonymized *A. fletcheri* under *A. lucens*, which in this paper we synonymize under *A. suspensus* (Nees, 1834). We examined the 'Rosario' female syntype of *A. huebrichi*. It is mounted laterally on a slide, is crushed, and otherwise is poorly preserved. The petiole is quadrate, although this appearance may partly be because it is flattened somewhat by the cover slip. The specimen also has uniformly yellowish legs, which led De Santis to synony-

mize the name under *A. fletcheri*. However, one forewing remains attached and although it lies over the hind wing a broad speculum is visible. Because of the absence of a row of setae immediately behind the submarginal vein on the disc we do not consider that *A. huebrichi* is synonymous with *A. suspensus*. The specimen has brownish coxae, a feature that we have observed only in some females from South America with uniformly yellowish legs and a broad speculum, which we currently include in the *californicus*-complex from South America (see 'Remarks' for *A. californicus*). At this time we do not formally synonymize the names *A. huebrichi*, *A. bonariensis*, and *A. californicus*. Formal synonymy of either *A. huebrichi* (1913) or *A. bonariensis* (1916) with *A. californicus* (1917) would result in *A. californicus* becoming the junior synonym. Our study of Neotropical material has been insufficient to confidently resolve the limits of variation and number of species of *Asaphes* occurring in the Neotropical region. For reasons of stability we do not consider it appropriate to make formal nomenclatural changes until concepts of species are better resolved and topotypic material of *A. huebrichi* and *A. bonariensis* can be studied. For this reason we treat these names as *nomina inquirenda*.

ACKNOWLEDGMENTS

Figs 1–6. Head. 1 and 2, *Asaphes breupetiolatus* (♀); 3 and 4, *A. breupetiolatus* (♂); 5 and 6, *A. hirsutus* (♀) (abbreviation: cly = clypeus, scale bars = microns)
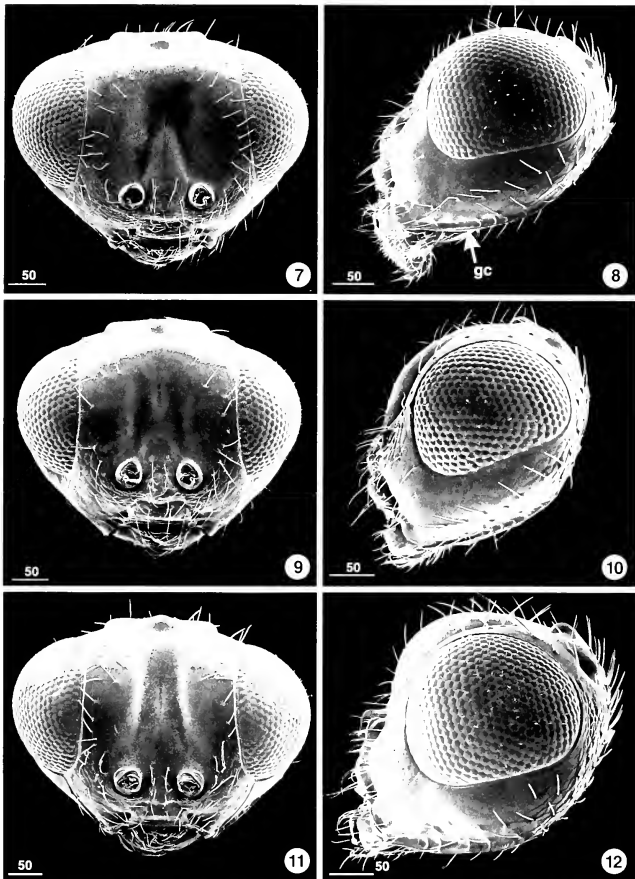
Figs. 7–12. Head (♀). 7 and 8, *Asaphes californicus*. 9 and 10, *A. suspensus*. 11 and 12, *A. vulgaris* (abbreviation gc = genal carina, scale bars = microns)
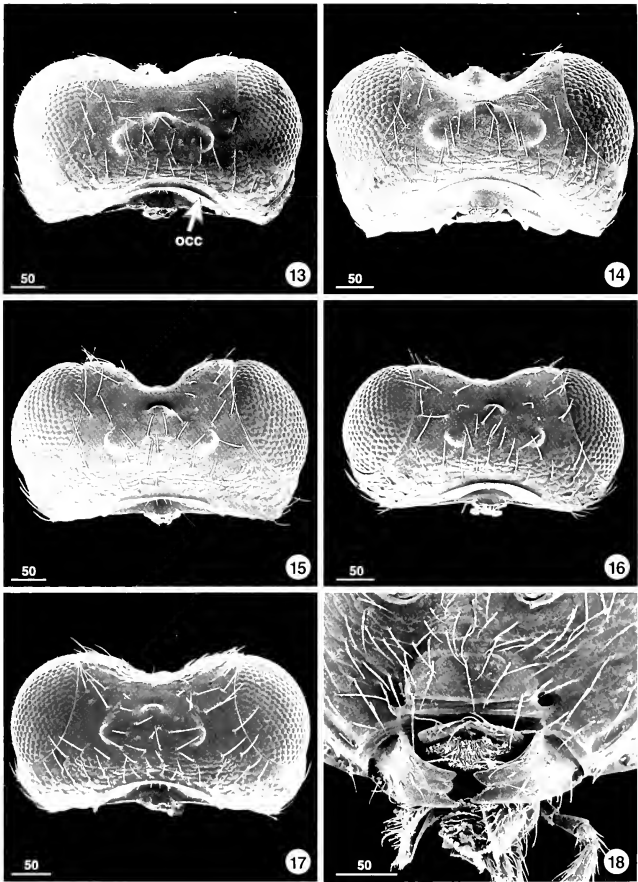
Figs. 13–18. 13–17. Head, dorsal. 13, *Asaphes brevipetiolatus* (♀). 14, *A. brevipetiolatus* (♂). 15, *A. vulgaris* (♀). 16, *A. suspensus* (♀). 17, *A. hirsutus* (♀). 18. Clypeus and mandibles, *A. hirsutus* (♀). (abbreviation: occ = occipital carina; scale bars = microns)
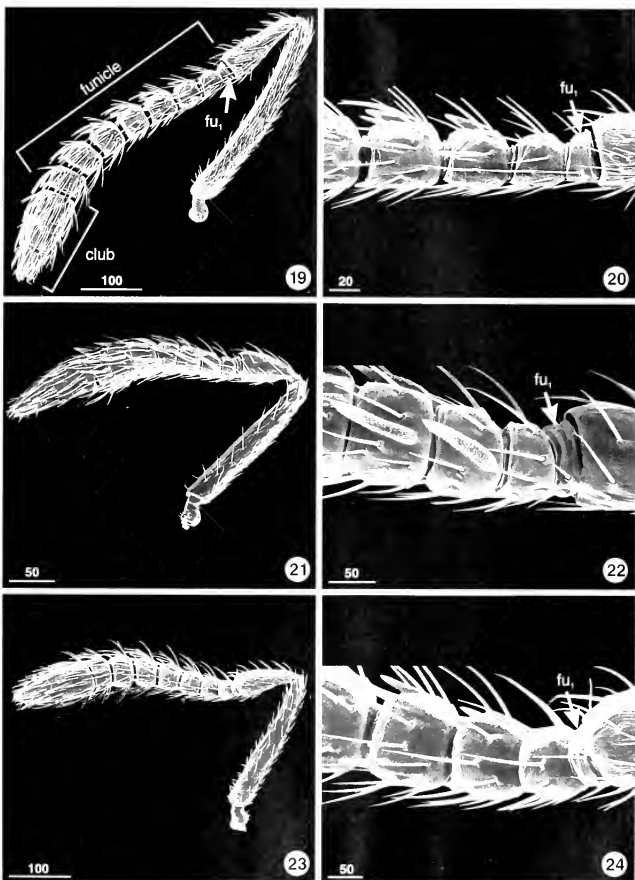
Figs. 19–24. 19 and 20, *Aphis bios* *oxystoma* (♀): 19, antenna; 20, basal 4 flagellar segments. 21 and 22, *A. calderanus* (♀): 21, antenna; 22, basal 4 flagellar segments. 23 and 24, *A. lineata* (♀): 23, antenna; 24, basal 4 flagellar segments (abbreviation: fu = first funicular segment; scale bars = microns).
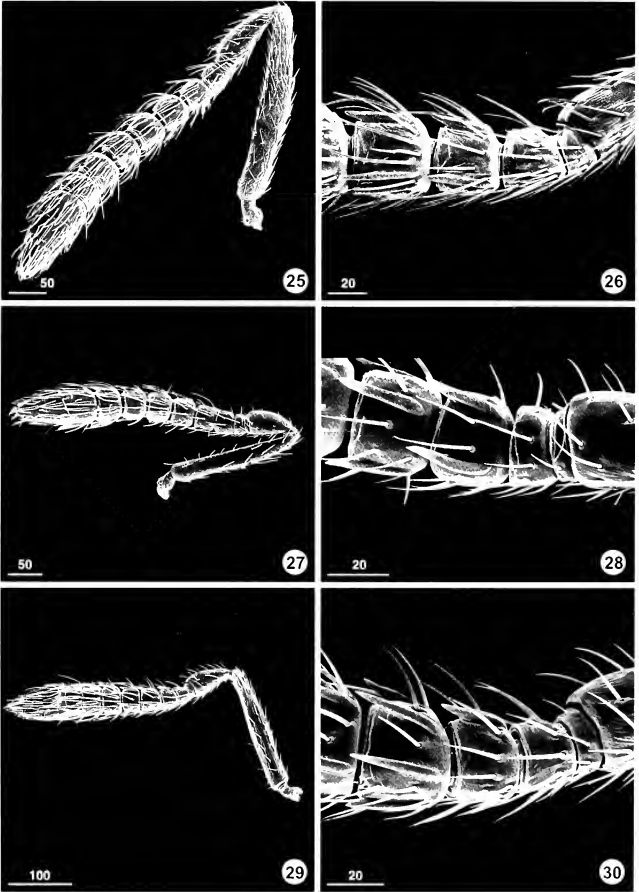
Figs 25–30. 25 and 26. *Asaphes petiolatus* (♀). 25, antenna. 26, basal 4 flagellar segments. 27 and 28. *A. suspensus* (♀). 27, antenna. 28, basal 4 flagellar segments. 29 and 30. *A. vulgaris* (♀). 29, antenna. 30, basal 4 flagellar segments (scale bars = microns)

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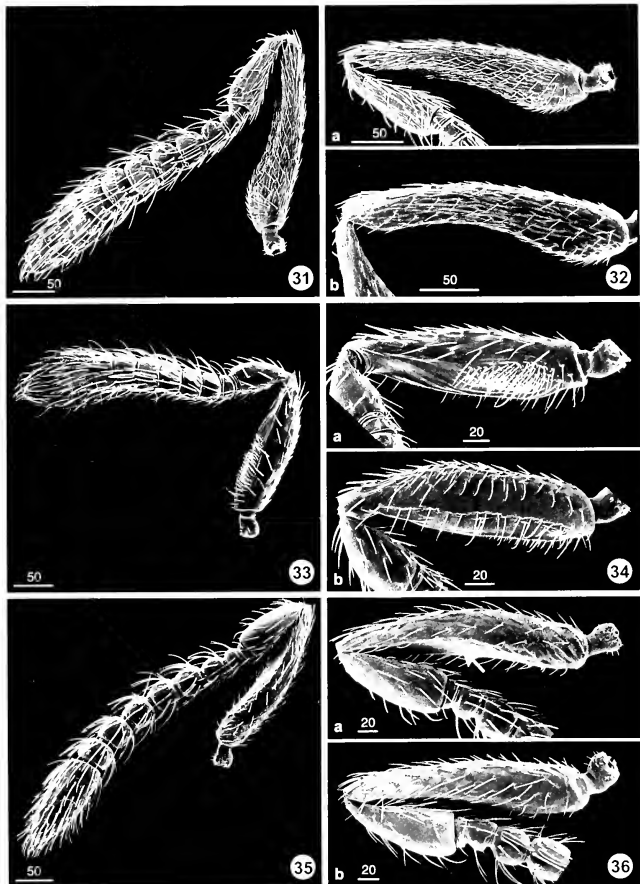
Figs 31–36 31 and 32. *Asaphes brevipetiolatus* (♀). 31, antenna; 32, scape—a, outer view; b, inner view 33 and 34 *A. californicus* (♀). 33, antenna; 34, scape—a, outer view; b, inner view 35 and 36 *A. hirsutus* (♀). 35, antenna; 36, scape—a, outer view (arrow points to flat surface); b, inner view (scale bars = microns)
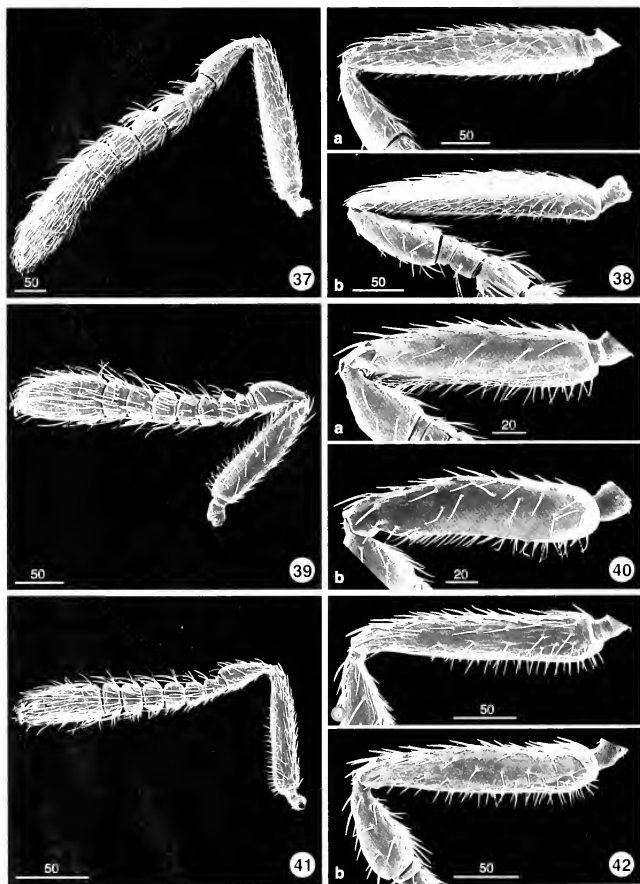
Figs. 37–42. 37 and 38. *Isaphes petiolatus* (♀). 37, antenna. 38, scape: a, outer view; b, inner view. 39 and 40. *A. steponus* (♀). 39, antenna. 40, scape: a, outer view; b, inner view. 41 and 42. *A. vulgaris* (♀). 41, antenna. 42, scape: a, outer view; b, inner view. (scale bars = microns)
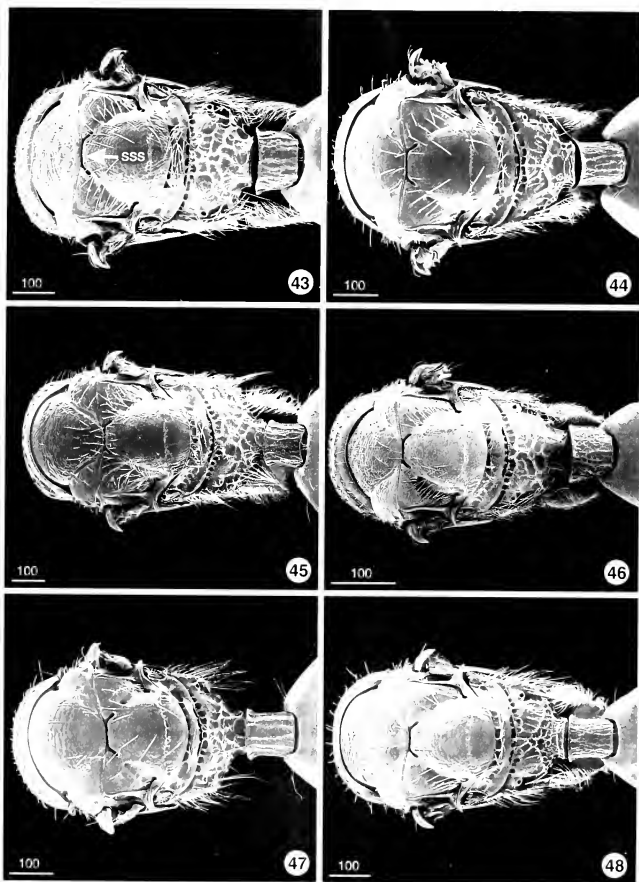
Figs. 43–48. Mesosoma, dorsal (.). 43, *Asapla obscapitolatus*. 44, *A. califorinicus*. 45, *A. tessatus*. 46, *A. apitolatus*. 47, *A. suspensus*. 48, *A. vulgaris*. (abbreviation sss = scutoscutellar suture. scale bars = microns).
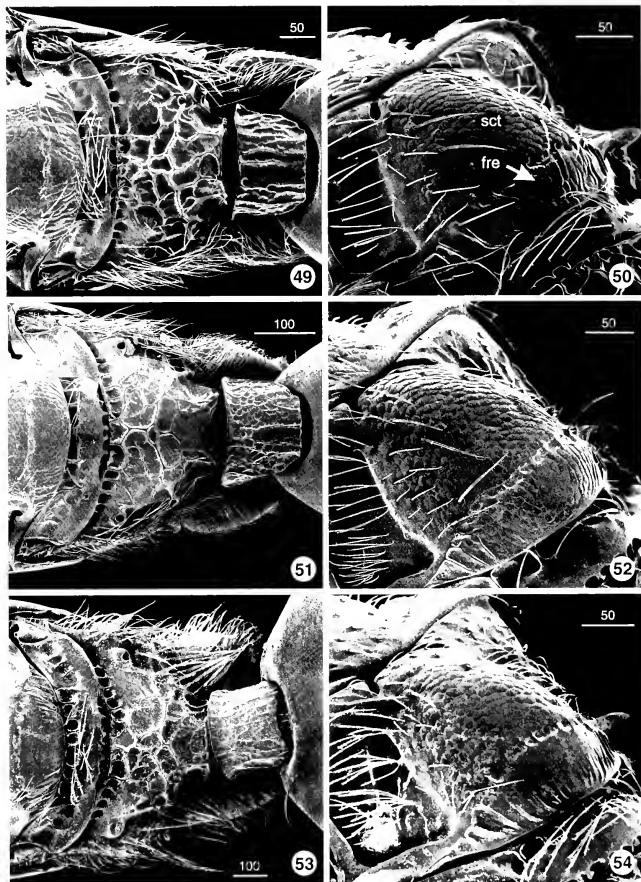
Figs 49–54. 49 and 50. *Asaphes brevipetiolatus* (♀). 49, trenum to petiole; 50, sculpture of scutellum and trenum. 51 and 52. *A. petiolatus* (♀). 51, trenum to petiole; 52, sculpture of scutellum and trenum. 53 and 54. *A. hirsutus* (♀). 53, trenum to petiole; 54, sculpture of scutellum and trenum. (abbreviations: tre = trenum, sct = scutellum, scale bars = microns)
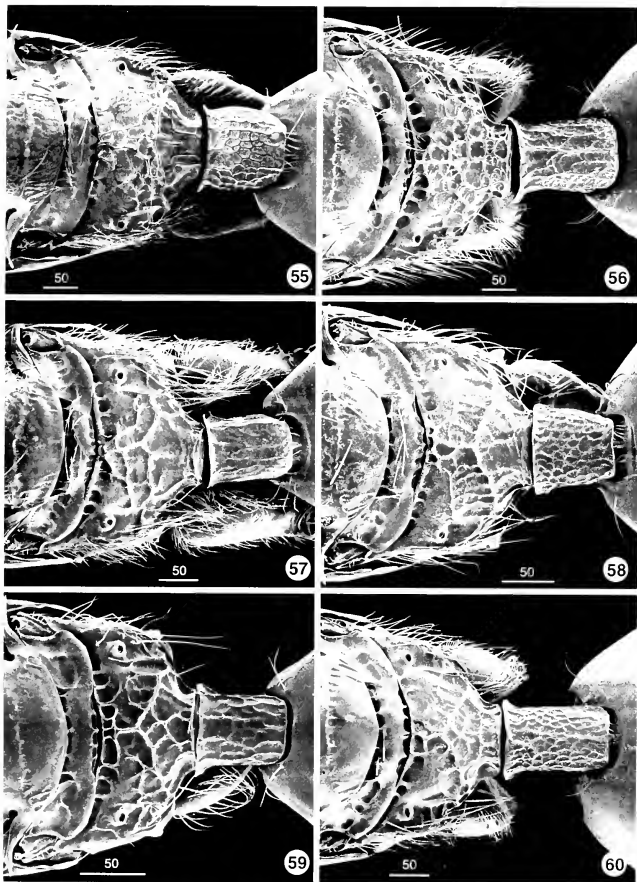
Figs. 55–60. Frenum to petiole (×): 55, *A. brevipetiolatus*; 56, *A. californicus*; 57, *A. insatus*; 58, *A. petiolatus*; 59, *A. suspensus*; 60, *A. vulgaris* (scale bars = microns)
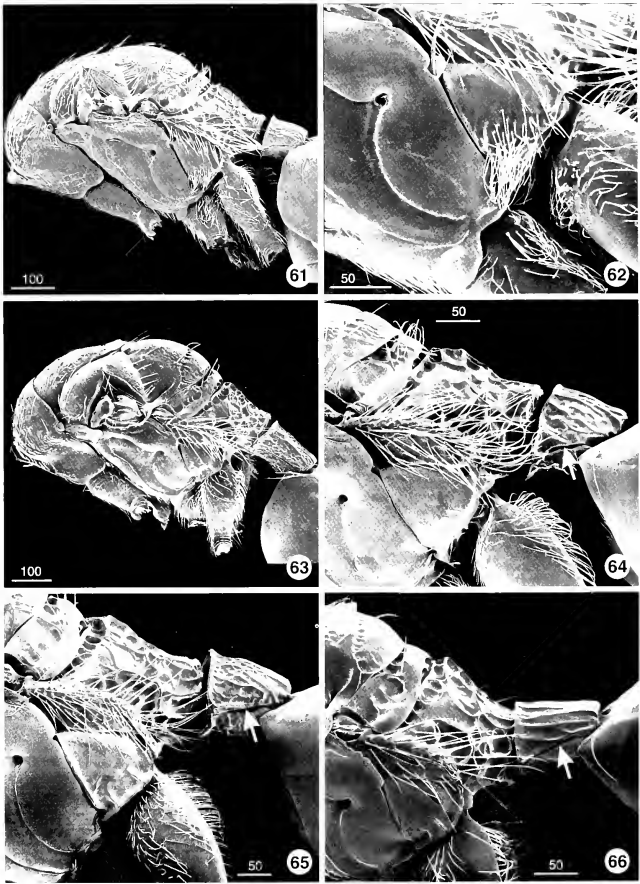
Figs. 61–66. 61 and 62. *Asaphes husutus* (♀): 61, lateral mesosoma (♀); 62, metapleuron (♂). 63. *A. californicus* lateral mesosoma (♂). 64–66. Metathorax to petiole, lateral (♀) (arrow points to lateral sulcus of petiole): 64, *A. breupetiolatus*, 65, *A. petiolatus*, 66, *A. suspensus* (scale bars = microns)
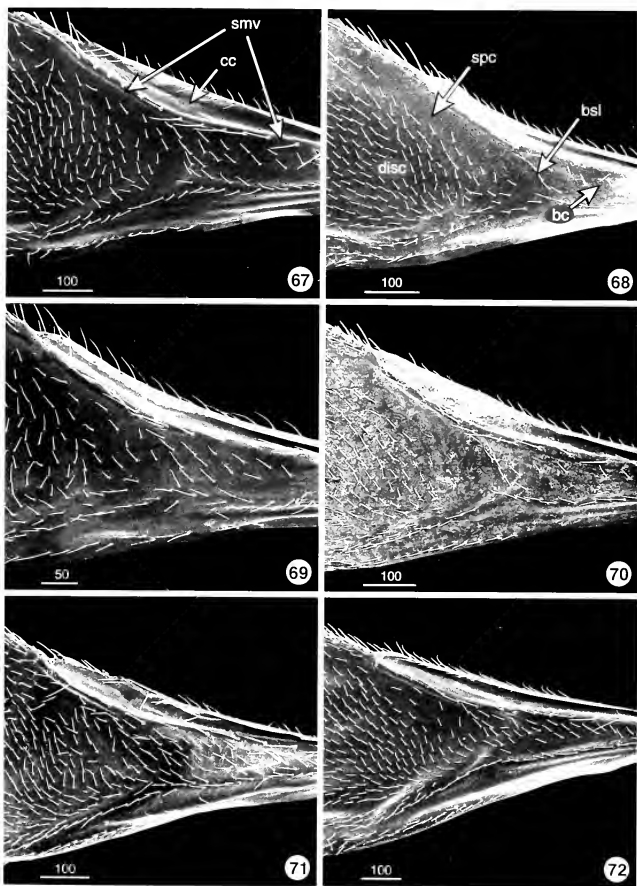
Figs 67–72. Forewing (♀). 67 and 68, *Asaphes californicus*. 69, *A. suspensus*. 70, *A. vulgaris*. 71, *A. hirsutus*. 72, *A. petiolatus* (abbreviations: bc basal cell, bsl basal setal line, cc costal cell, smv submarginal vein, spc speculum, scale bars microns).
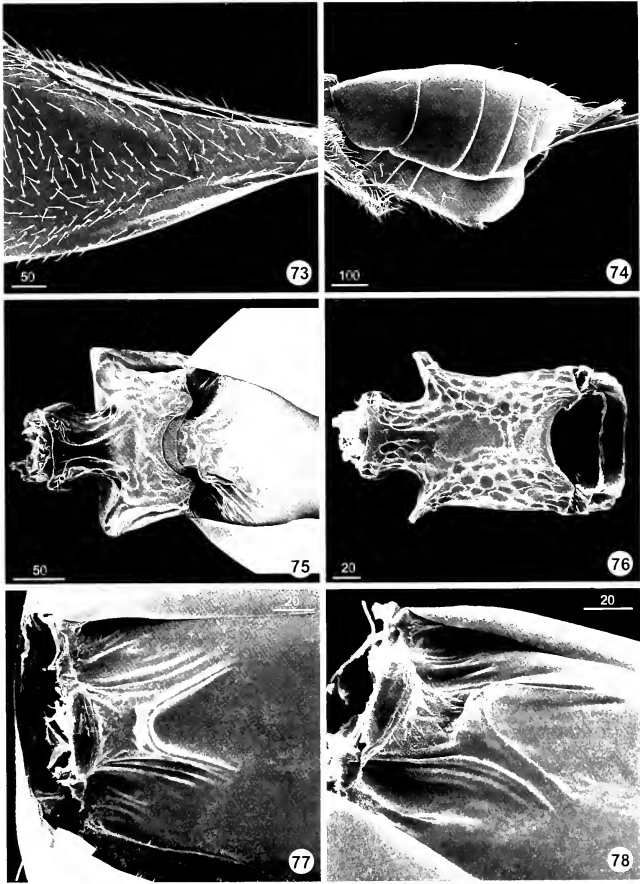
Figs. 73–78.   73. Forewing: *Asaphes brevipetiolatus* (♀). 74. Gaster: *A. hirsutus* (♀). 75. Petiole and base of gaster, ventral view: *A. petiolatus* (♀). 76. Petiole, ventral view: *A. californicus* (♀). 77 and 78. *A. suspensus*, base of gaster (♀): 77, ventral view; 78, ventrolateral view. (scale bars = microns)
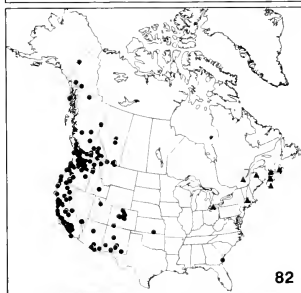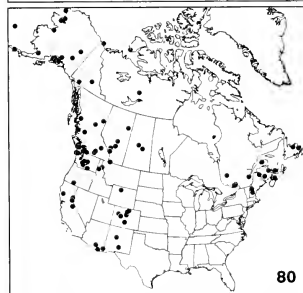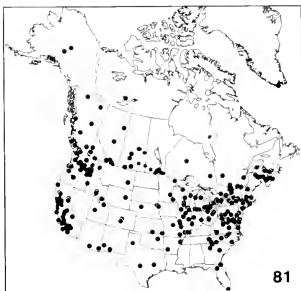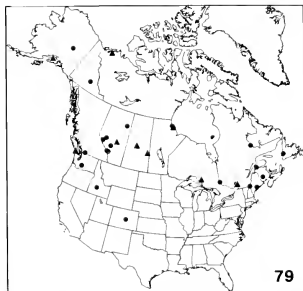
Figs. 79–80. Nearctic distribution: 79, *Asaphes brevipetiolatus* (●) and *Asaphes petiolatus* (▲). 80. *Asaphes hirsutus*.

Figs. 81–82. Nearctic distribution: 81, *Asaphes suspensus*. 82, *Asaphes californicus* (●) and *A. vulgaris* (▲).

MZLU Museum of Zoology, Lund University, Lund, Sweden (R. Danielsson, U. Gärdenfors).

NFRC Northern Forest Research Centre, Canadian Forest Service, Edmonton, AB (D. Williams).

PFRC Pacific Forestry Research Centre, Canadian Forest Service, Victoria, BC (L. Humble).

OSUC Collection of Insects and Spiders, Ohio State University, Columbus, OH (A. Sharkov).

OSUO Department of Entomology Collection, Oregon State University, Corvallis, OR (D.C. Darling).

SMDV Spencer Museum, Department of Zoology, University of British Columbia, Vancouver, BC (K. Needham).

TAMU Department of Entomology, Texas A&M University, College Station, TX (J. Woolley, E. Riley).

UCDC The Bohart Museum, University of California, Davis, CA (S. Heydon).

UCRC UCR Entomological Training and Research Collection, University of California, Riverside, CA (S. Triapitsyn).

USNM United States National Entomological Collection, U.S. National Museum of Natural History, Washington, DC (E.E. Grissell).

UZMH Zoological Museum, University of Helsinki, Helsinki, Finland (A. Albrecht, M. Koponen).

VVPC Veli Vikberg personal collection, Turenki, Finland (V. Vikberg).

WSUC James Entomological Collection, Department of Entomology Collection, Washington State University, Pullman, WA (K.S. Pike), and Tree Fruit Research Center, Washington State University, Wenatchee, WA (D. Carroll).

ZMAS Zoological Museum, Academy of Sciences, Saint Petersburg, Russia (V.A. Trjapitzin).

ZMUC Zoological Museum, University of Copenhagen, Copenhagen, Denmark (B. Petersen).

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Worker Versus Sexual, and Sex Ratio Investments in the Social Wasp *Vespula vulgaris* (L.) (Hymenoptera: Vespinae) in England

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Abstract.—An attempt has been made to quantify the relative investment in workers versus sexuals, and queens versus males in *Vespula vulgaris* (L.). In particular I have investigated MacNair's hypothesis that the queen invests equally in queen and male eggs, and that her investment stops after she has laid her eggs. The dry weights and calorific values of the workers, autumn queens, and small-cell, and large-cell, reared males were determined. The lipid content of the autumn queens was 39.9%, and the crop-solid of males was 34.5%, of their dry weight. The seasonal change in worker dry weight was related to the varying work loads of the workers. A simulation model using the compartmental system approach was used to estimate the number of workers, queens and males produced by a successful colony. Investment in workers, either as dry weight or calorific equivalent units, represented nearly 50% of the total colony investment. This is considered a relatively high investment and can be related to the delay of sexual production. Males and queens are produced in about equal numbers but, in terms of dry weight or calorific equivalent units, there is a bias toward queen production. Workers were found to be selectively destroying male brood probably derived from queen eggs. MacNair's hypothesis could not be supported.

In England the annual life-history of *Vespula vulgaris* (Linn.) starts with the emergence of the males and new queens from the mature colonies in the autumn. The sexuals remain in the colonies for a few days before leaving on their mating flights. After a short time the fertilised queens enter over-wintering sites while the males die. When the queens emerge in the spring they each search for a nest site, build a queen-nest and, by early June, rear the first workers. The workers take over the jobs of building the nest and looking after the brood from the queen which continues to lay eggs. At first, the workers build small cells (small-cell colony) in which more workers and, later, males are reared. From the beginning of August, the workers build large cells (large-cell colony) in which the queens and sometimes males are reared. The colony with its queen and workers usually dies by the

end of October or early November (Archer 1981a, 1984).

With the emergence of the new queens, brood in the small cells is neglected and not well fed (Montagner 1966). The neglected larvae and sealed brood are frequently pulled out of their cells by the workers and dropped some distance from the nest. This destruction of brood has been frequently recorded (Duncan 1939, Spradbery 1973, Archer 1981a, Greene 1991). The neglected brood also are eaten by dipterous larvae, e.g. *Volucella* sp. (Archer 1981a).

The above life-history in which the reproductive females fly away from their natal colonies and found new colonies independently is called 'Alate Dispersing' (Nonacs 1993). All alate dispersing colonies must make two investment decisions. The first is concerned with the proportion of resources devoted either to the produc-

tion of the workers or to the sexuals. The second is concerned with the proportion of resources devoted to either male or queen production (Nonacs 1993).

The first decision is a process of maximising sexual production. Sexual production could be delayed by the production of more workers for colony maintenance with the trade-off consequence of ensuring a greater future sexual production. Brian (1965) produced a general model of colonial growth which showed that queen production increases with increased investment in workers. Pamilo (1991) developed models for perennial colonies, finding that greater investment in worker production was related to a smaller chance of queens founding new colonies and the old colonies surviving. With the annual colonies of *V. vulgaris*, the old colonies do not survive and the queens have a very small chance of founding new colonies (Archer 1984) so worker production relative to sexual production should be higher. The timing of the switch from worker to sexual production varies between the species of vespine social wasps (Archer 1980, 1981a).

The second decision concerning proportional investments in males and queens focuses on the queen-worker conflict due to asymmetrical genetical relationships (Trivers and Hare 1976, Benford 1978, MacNair 1978, Nonacs 1986, Boomsma 1989, Ratnieks and Reeve 1992). A wide range of variation in sex investment ratios has been found (Crozier and Pamilo 1996), often due to multiple mating by queens and worker reproduction in queenright colonies (Trivers and Hare 1976, Benford 1978).

Usually sex ratio investment is measured by determining the dry weight production of queens and males (Trivers and Hare 1976, Crozier and Pamilo 1996). In a vespine colony with a singly-mated queen and no worker reproduction, it is expected that queens will adjust the sex ratio investment to give equal dry weights of queens and males. Workers, because of

asymmetrical genetical relationships, will increase the investments in queens to three times that of males. If the queen has mated with more than one male and/or there is worker reproduction, the sex ratio investment of the queen is unchanged, but the workers will increase their investment in the males, although investment in queens will still be greater.

MacNair (1978) argued that queen investment stops after the eggs are laid: further investment is then carried out by the workers. Thus the queen should distribute her parental investment equally between queen and male eggs to produce a primary sex ratio of 1:1. For workers to skew the investment towards queens, they should try to prevent the queen from laying male eggs or destroy the brood derived from the male eggs of the queen.

The queens have larger bodies in which to carry sufficient fat bodies to enable them to over-winter. The males do not over-winter but die soon after mating, or attempting to mate, for which purpose a smaller body seems adequate. Thus the departure from equal investment in queen and male eggs by the queen to a relatively greater queen investment does not necessarily imply the workers have succeeded in altering the sex ratio investment of the queen. To demonstrate that workers have succeeded in producing a relatively greater investment in queens, it is necessary to show that male brood derived from queen eggs have been destroyed.

Ideally, the determination of worker and sexual production should be carried out directly by visual observations on colonies under natural conditions. This is difficult to achieve since colonies of *V. vulgaris* are surrounded by envelopes, are often underground, and the workers are aggressive when disturbed during investigations. Visual observations on healthy colonies maintained in an observation box have so far been restricted to one comb, the lowest comb of the nest (Potter 1964).

However, indirect methods can be used

to estimate the production of workers and sexuals. Colonies can be collected throughout the year and counts made of the brood and adults present. At the end of the last larval stage the gut contents are evacuated to form the black meconium at the bottom of the cell. Counts of these meconia can be used as an estimate of the number of adults reared. Since a meconium is only evidence that a larva has pupated, the result could be an over-estimate if incipient adults died during the pupal stage. In addition, the meconial remains do not reveal the sex or caste of the former occupants of the cells. Thus precise counts of worker and sexual production cannot be made from collected colonies, although counts of meconia and queen and male sealed brood can give a first approximation (Archer 1993).

To improve the accuracy of estimating worker and sexual production a simulation model of a successful colony, i.e. one that rears many queens, has been developed (Archer 1981a, 1981b). The simulation model not only used the data from 198 collected colonies of *V. vulgaris* but also laboratory observations on the length of life of the brood stages and adult workers. The model incorporates meconial information for adult production, and rates of cell building, brood stage addition and adult appearance estimated from the collected data. Brood neglect and mortality were incorporated into the model to come into effect when adult and brood stages became too numerous in comparison with the data from collected colonies. The model achieves greater realism at the expense of complexity, with the use of 253 parameters and variables. To handle such a complex model the compartmental system approach (Odum 1971) was used.

In this paper, I will try to determine the extent of any destruction of queen-derived male brood to test the proposal of MacNair (1978), and derive estimates of the production of workers, males and queens to determine the relative importance of

worker production, and the relative investment in males and queens.

METHODS

Sources of, and treatment of workers.— Workers were bait-trapped during 1970 at Averhams Plantation, between Flaxton and Claxton, about 12 kilometres to the north-east of York, England. Averhams Plantation was an open site with a dense herb layer and recently planted conifers. The trapping station consisted of 16 sub-stations arranged in a square (4 × 4) with two traps at each sub-station. The traps were attached to canes about 70cm above the ground. Each trap consisted of a white polythene container (75mm deep, 75mm diameter) with a 10mm diameter hole in the lid, and contained a jam solution with added yeast. The fermenting jam solution was changed once every two weeks and the catch of workers collected once a week. Trapping was continuous from July until October. The workers were preserved in 70% ethanol.

Samples of 50 workers from each weekly catch were dried to constant weight in an air oven at 60°C. During July and October when the number of workers trapped were smaller all workers were dried. Each weekly sample of dried workers was weighed to 0.1mg. The weekly dry weight was divided by the number of workers in the sample to give the mean worker dry weight.

Workers from seven colonies were collected during late June and preserved by deep-freezing. Later the dry weights of these workers were obtained as previously described except that workers were weighed individually so a standard deviation could be calculated.

Correction for dry weight of workers due to 70% ethanol preservation.—To determine if ethanol-preserved workers lost dry weight, samples of 50 or 55 workers from three colonies were preserved in 70% ethanol and by deep-freezing. After about six months of such preservation dry weights

were obtained as previously described. Ethanol preserved workers showed a loss of dry weight compared with deep-frozen preserved workers from all three colonies. The percentage dry weight loss was 20.5%.

Sources of, and treatment of queens.—Autumn queens with fully developed fat bodies were collected from four colonies. From three colonies 172 queens were preserved by deep-freezing and from one colony 47 queens were preserved in 70% ethanol. Dry weights were obtained as previously described for workers except that queens were weighed individually. Dry weight loss from ethanol preservation was found to be 11.4% based on queens collected from one colony when 55 queens were preserved in 70% ethanol and 63 by deep-freezing.

Sources of, and treatment of males.—Males with full crops were collected from a colony which was rearing males both in the small and large cells. All 102 males were preserved in 70% ethanol. Dry weights were obtained as previously described for workers except that males were weighed individually. The dry weights of the males showed a bimodal distribution indicating a weight difference between males reared in the small and large cells. A method given by Lewis and Taylor (1967) was used to separate the 56 small-cell and 46 large-cell reared males.

Males with full crops were collected from three colonies which had reared males only in the small cells. From the three colonies 146 males were preserved by deep-freezing. Dry weights were obtained as previously described for workers except that males were weighed individually.

Dry weight loss from ethanol preservation was found to be 37.7% based on males collected from three colonies when 201 males were preserved in 70% ethanol and 146 by deep-freezing.

Lipid determinations.—Samples of workers, autumn queens and males were pre-served by deep freezing and extracted in the Soxhlet apparatus using trichlorethylene as a solvent. Extraction was continued until constant weight was obtained. Nine queens were extracted individually, 27 males in batches of threes, and 74 workers from three colonies in colony batches.

Male crop content determinations.—When males left their natal colonies in the autumn their crops were found to contain a clear viscous fluid. From one colony 50 males were collected and preserved by deep freezing. Their crop fluid was collected by cutting the gaster away from the rest of the body and gently squeezing the gaster so that the crop fluid could be absorbed by a known dry weight of filter paper. The filter paper with its absorbed crop fluids were dried in an air oven at 60°C to constant weight. All weightings were made to 0.1mg. Some general biochemical tests were performed on the crop fluid.

Ash content of workers, autumn queens and males.—A sample of 22 autumn queens was collected, preserved by deep-freezing, and dried by freeze-drying. Samples of 74 workers and 27 males were obtained from the lipid-extracted individuals. The samples were heated in a furnace at 500°C for three hours and the residue ash weighed to 0.1mg.

Calorific determinations.—Samples of workers, autumn queens with fat bodies and males with full crops were preserved by deep freezing, dried by freeze-drying and their calorific values determined with the aid of a Phillipson Oxygen Microbomb Calorimeter (Phillipson 1964).

Due to the high lipid content of the autumn queens oil was lost when the animal tissue was pelleted in preparation for bomb calorimetry. Attempts to bomb non-pelleted material as suggested by Woodland *et al.* (1968) and Howell and Fisher (1977) failed because oil was lost from the sample and found at the bottom of the bomb. The lipids were extracted, as pre-
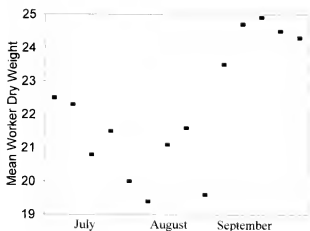
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Mean Worker Dry Weight

July   August   September

Fig. 1. Mean worker dry weight (mg) versus date for *Vespula vulgaris*.

Table 1. The mean dry weights of workers of *Vespula vulgaris* from late July colonies.

Date	No workers	Mean dry weight (mg)	Standard deviation
17	13	25.1	3.93
20	14	22.0	4.11
29	33	21.2	5.24
30	15	24.6	5.59
30	34	21.9	5.09
30	35	24.4	5.66

viously described, and the calorific determinations made on the remaining tissues.

Difficulties sometimes were experienced when freeze-drying males in that the viscous contents of the crops would not freeze-dry but rather exploded out of the male into the freeze-drying equipment. Calorific determinations were made on crop-extracted males, as previously described, and on males with crop fluids where freeze-drying was satisfactorily completed.

Simulation model of colonial determination.—The development of a simulation model is given in Archer (1981a). The model was developed on the DEC system-10 computer at the University of York, England. Recently the model has been transferred to a Personal Computer.

RESULTS

Seasonal variation of worker weights.—The seasonal change in the dry weights of workers from the bait traps is shown in Fig. 1. These dry weights have been corrected for dry weight loss during ethanol preservation. From a high mean dry weight during early July there is a decrease to a low value during August, followed by an increase during the first half of September, after which there is a slight decrease during late September and October.

The mean dry weights of the workers from the late June colonies are given in Table 1. The mean dry weight from the seven colonies is 23.3mg which is slightly higher than the value for early July (Fig. 1).

Lipid content of workers, autumn queens and males.—The lipid content of the workers is given in Table 2. The higher lipid content corresponds to the higher mean dry body weight found during September.

The mean lipid content of a male was 7.4mg (range 4.1–9.1) representing 10.3% of the mean dry body weight.

The mean lipid content of a queen was 65.0mg (s.d. 8.2) representing 39.9% of mean dry body weight.

Male crop fluid.—The mean dry weight of the crop fluid was 32.3mg (s.d. 9.98) which represented 60.5% of the wet weight of the crop fluid. The mean dry weight of the crop fluid represented 34.5% of the mean dry body weight. The dry weight of the crop fluid of each male was positively correlated with its dry body weight (n = 50, r = 0.57, p < 0.001).

The crop fluid gave a positive result with two general carbohydrate tests: (a)

Table 2. The lipid content of adult workers of *Vespula vulgaris*.

Date	No workers	Lipid extracted (mg)	% lipid of dry body weight
20 Jul.	20	23.0	5.7
26 Aug.	25	16.7	3.1
23 Sep.	29	95.5	10.1

Table 3. The mean dry weight of autumn queens of *Vespula vulgaris*.

Date	No. queens	Mean dry weight (mg)	Standard deviation
12 Sep.	22	163.7	11.18
20 Sep.	47	167.1*	11.75
9 Oct.	59	167.6	10.43
31 Oct.	91	155.3	8.43

* Corrected for 70% ethanol preservation.

Table 4. The mean dry weight of small-cell reared males of *Vespula vulgaris*.

Date	No. males	Mean dry weight (mg)	Standard deviation
12 Sep.	50	81.1	14.3
16 Sep.	56	87.3*	14.7
23 Sep.	50	96.3	23.0
31 Oct.	46	74.0	13.9

* Corrected for 70% ethanol preservation.

alcoholic thymol and conc. hydrochloric acid and (b) alcoholic alpha-naphol and concentrated sulphuric acid. A positive reaction also was obtained with Benedict's reagent indicating the presence of reducing sugar.

Queen dry weight.—The mean dry weights of autumn queens with fat bodies are given in Table 3. The closeness of the deep-freeze and corrected ethanol-preserved queens gives confidence in the use of the correction factor. The mean of the four samples is 163.4mg. Since these autumn queens consisted of 39.9% lipid content the mean dry weight would be made up 65.2mg lipid and 98.2mg non-lipid substances. The dry weight of lipid of each queen was positively correlated with its dry body weight (n = 19, r = 0.79, p < 0.0001).

Male dry weight.—The mean dry weights of males reared in the small cells are given in Table 4. The closeness of the deep-freeze and corrected ethanol-preserved males gives confidence in the use of the correction factor. The dry weight of the four samples is 84.7mg. Since the crop solid consisted of 34.5% of the body dry weight, the mean dry weight would be made up of 29.2mg crop solid and 55.5mg for the rest of the body.

The mean dry weight of males reared in large cells was 130.7mg. This dry weight has been corrected for dry weight loss during ethanol preservation. Assuming 34.5% of this dry weight was crop solid, the mean dry weight would be made up

of 45.1mg crop solid and 85.6mg for the rest of the body.

Calorific determinations.—The ash content of the adults was so low that it was unlikely to complicate the calorific determination. The ash percentage of mean dry weight for autumn queens was 2.8%, for males 2.9% and for workers 2.5%.

The mean calorific values of lipid-extracted queens, males and workers are given in Table 5. Assuming the calorific equivalent of queen lipid to be 9.2 cal/mg (Sawicka-Kapusta 1975) and knowing the lipid percentage of mean dry body weight then the calorific value of the total dry body weight of the queen would be 6.627 cal/mg dry weight.

Knowing the mean calorific values of crop-extracted males and males with crops (Table 5), it can be calculated that the crop solid has a calorific value of 4.232 cal/mg dry weight. Such a calorific value indicates that the crop solid was a protein or carbohydrate rather than a lipid substance. Earlier results showed that the

Table 5. Calorific values of autumn queens, males and workers of *Vespula vulgaris*.

	Sample size	Cal/mg dry weight	Standard deviation
Queen (lipid extracted)	10	4.820	0.085
Male (crop extracted)	10	5.201	0.149
Male (with crop)	10	4.872	0.142
Worker — 17 Jun.	10	5.092	0.122
Worker — 28 Jul.	10	5.273	0.147
Worker — 24 Sep.	10	5.220	0.109
Worker — combined	30	5.195	0.145

Table 6. The number, biomass (dry weight) and calorific equivalent of queens, queen lipid, males, male crop content and workers produced in a simulation colony of *Vespula vulgaris*.

	Number	Biomass (mg)	Calorific equivalent (cal)
Workers	10,248	217,072.3	1,127,690.6
Males			
Small cells	763	64,626.1	314,858.4
Large cells	261	34,112.7	166,197.1
Total	1,024	98,738.8	481,055.5
Crop solids		34,064.9	144,162.6
Queens	969	158,334.6	1,049,283.4
Lipid		62,985.0	579,462.0
Total	12,241	474,145.7	2,658,029.5

crop solid is a carbohydrate, probably reducing sugar.

Since the calorific values of workers varies little from samples collected during June, July and September a combined value has been calculated (Table 5).

The mean calorific values for workers and crop-extracted males are similar, but less than the mean calorific value of autumn queens because of the high lipid content of queens. The low mean calorific value of males is due to the high carbohydrate content of the crop. The lipid-extracted queens have a lower mean calorific value than the workers and crop-extracted males, as these workers and males have some lipid in their bodies.

Production estimates of a successful colony.—The number, biomass and calorific equivalents of the workers, males and queens produced in the simulation model are given in Table 6. The biomass and calorific equivalents of the males and queens were calculated by multiplying the number of males and queens produced by the model by the appropriate mean dry weight and calorific values. The crop solid of the males represents 30.0% of their calorific equivalent and the lipid of the queens 55.2% of their calorific equivalent.

Since the dry weight of workers varies during the development of the colony

Table 7. The dry weights of workers of *Vespula vulgaris* during the seasonal development of a colony derived from Fig. 1 and Spradbery (1972).

Date	Dry weight (mg)
6 Jun.	11.75 (Spradbery)
16 Jun.	11.75 (Spradbery)
6 Jul.	22.4
11 Aug.	19.5
14 Sep.	24.9
5 Oct.	24.3

(Fig. 1), it is necessary to know the dry weight of the workers on the days that they emerged as adults. These emergence dry weights were assumed to be those of the collected workers, half the length of worker life before the date on which the workers were collected (Archer 1981a). The model calculated the number of adult workers produced each day which was multiplied by the appropriate mean dry weight derived from Fig. 1 and given in Table 7. Increases and decreases in mean dry weight were assumed to be linear. The total worker dry weight produced could be multiplied by worker mean calorific value to give the total calorific equivalent.

The relative investment in workers, males and queens of a successful colony is given in Table 8. Just over five workers are needed to rear each sexual, but because sexuals are heavier than workers a greater biomass or calorific equivalent of sexuals is produced than for workers. Workers represent 45.8% by dry weight and 42.4% by calorific equivalent of the total production of the colony.

Slightly more males than queens are

Table 8. The relative investment in workers, males and queens in a simulation model of a successful colony of *Vespula vulgaris*.

	Number	Biomass (dry weight)	Calorific equivalent
Sexuals: Workers	1:5.14	1:0.84	1:0.74
Queens: Workers	1:10.58	1:1.37	1:1.07
Queens: Males	1:1.06	1:0.62	1:0.46

reared, but, because queens are heavier and of higher calorific value, the sex ratio investment changes markedly in favour of the queens. Because the males have higher metabolic rates than queens, the energetic cost ratio (Boomsma 1989, Bourke and Franks 1995) can be used. The sex ratio investment then becomes one queen to 0.72 male, still indicating an investment in favour of queens.

DISCUSSION

Worker dry weight.—A similar seasonal change in the dry weight of workers of *V. vulgaris* from early July until October (Fig. 1) was found by Spradbery (1972) in England and by Malham (1996) in New Zealand for the equivalent season. Spradbery (1972) also found a very low worker dry weight during June (Table 7): these were queen-reared workers. Brian and Brian (1952) also found that queen-reared workers of *Dolichovespula sylvestris* (Scopoli) had low weights.

Malham (1996) found that in areas where insecticide had been used to drastically reduce the number of workers, the dry weight of workers during March (equivalent to September in England, Fig. 1) was markedly higher than in untreated areas. This difference was less pronounced earlier in the season and had disappeared by the end of the season. Malham (1996) attributed the difference to food availability. In treated areas, relatively more food would be available per forager, so larvae would receive more food and produce workers of a heavier weight.

The low worker dry weight during August (equivalent to February in New Zealand) varied from 12–13mg (Malham 1996) to 17.4mg (Spradbery 1972) and 19.5mg in the present study. The high worker dry weight during September (equivalent to March in New Zealand) varied from 17–20mg (Malham 1996) to 20.8mg (Spradbery 1972) and 24.9mg in the present study. Following Malham (1996) these variabilities in dry weights could be due

to shortages in food supply as forager density increases.

The variation in worker dry weight also can be related to variation of the work load on workers. The work load will depend on the number of larvae to feed (larva/worker ratio), the number of cells to build, and the amount of soil to be excavated to make the cavity for the nest. Time spent in excavation and building could reduce the time available to feed the larvae.

The low weights of queen-reared workers could be a consequence of very high larvae per queen ratio, up to 30 larvae per queen, and high cell building rates, in excess of two cells per day (Archer, unpublished).

The relatively rapid increase in worker dry weight by late June until early July could be a consequence of workers aiding the queen in brood rearing. At this time the larva/worker ratio rapidly decreases to about 3–4 and the cell building rate to about one cell per worker per day (Archer 1981a).

The decline in worker dry weight from early July until August coincides with the development of the small-cell colony during which a large worker population is reared (Archer 1981a). Workers sampled during August had the lowest lipid content (Table 2). Despite the exponential growth of the small-cell colony, the work load on workers continues to decrease with larva/worker ratio decreasing to about one, and cell building rate per day per worker approaching zero. However the amount of excavation greatly increases and over 90% of the outgoing workers from a colony may be carrying earth particles (Archer, unpublished).

The increase in dry weight from August until September coincides with the development of the large-cell colony when the future sexuals are reared. Workers sampled during September also had the highest lipid content (Table 2). During this time the worker load remains low. Larva/worker ratio remains at about one, and

large cell building rate per worker per day is very low at about 0.04 (Archer 1981a). Soil excavation continues but usually less than 20% of outgoing foragers are carrying earth particles (Archer, unpublished).

Queen dry weight.—Spradbery (1973) and Harris and Beggs (1995) found that nearly 40% of the dry weight of autumn queens is lipid, which is similar to the value given earlier in this paper. The same authors found that the lipid was used as a food source of which about three-quarters was used during the over-wintering period. By dissecting queens of *Vespa affinis* (Linn.) from southern Japan, Martin (1993) found that the contents of the fat bodies were used up during the over-wintering period of four to five months.

Harris and Beggs (1995) found the mean dry weight of autumn queens from New Zealand was 121.7mg (range 108.0–154.5), which about 26% lower than the mean weight reported in the current study. They suggested the low weight of autumn queens was because the fat bodies of the queens had not reached their maximum level of lipid storage. The low weight of queens also could be a consequence of the very high colony densities: up to 33 colonies per hectare found in New Zealand, compared with up to about two colonies per hectare in England (Edwards 1980). At lower colony densities relatively more food resources might be available for queen rearing.

Male dry weight.—By measuring the wing length of males of *Vespa crabro* Linn., Potter (1964) also found a bimodal distribution of male size. Measurements were carried out on callow adults found in their cells. He also recorded that males of some colonies of *V. vulgaris* showed a bimodal size distribution but gave no numerical details. Potter's observations support the interpretation of the bimodal size distribution of males presented in this paper.

The carbohydrate food reserve found in the crops of the males seems to be a new observation. The function of this food re-serve would be to provide a readily available source of energy needed by the males when flying around their mating circuits (Edwards 1980).

Worker-sexual ratio investment.—Investment in workers represents nearly 50% of the total biomass investment of a colony (Table 8). By reference to Pamilo (1991, Table 2) the investment in the workers can be considered to be relatively high. This large investment in workers can be related to the delay of sexual production until September in *V. vulgaris*, with the consequence of a larger output of queens (Brian 1983). Sexual production in *Dolichovespula sylvestris* (Scopoli) occurs earlier, during July, so this species has a relatively smaller investment in workers, and also a smaller output of queens (Edwards 1980).

Sex ratio investment.—The more-or-less equal production of queens and males in *V. vulgaris* (Table 8) seems rather surprising since at the sealed brood stage, the number of males is usually twice the number of queens (Archer 1981a, Greene 1991). However, Archer (1981b) found that 45% of large-cell male sealed brood was destroyed, and observed large-cell male sealed brood and mature larvae were carried away from the colonies by the workers. If these large-cell sealed brood are included in the calculation of the primary sex ratio, the ratio becomes one queen to 1.28 males.

The simulation model allows for this destruction of large-cell larvae and sealed brood, as well as for the neglect and destruction of small-cell larvae and sealed brood. The output of the model indicates that 18.4% small-cell larvae and sealed brood will be neglected and destroyed. Since this destruction occurs in the later part of colonial development, most of the destroyed small-cell brood will be males (Archer 1981a). Thus the primary sex ratio would be even more biased towards the males.

The interpretation of the above observations and calculations would indicate

that the queen is not laying an equal number of male and queen eggs as MacNair (1978) suggested. Since males are smaller than queens, the queen would seem to be laying relatively more male eggs so that the investment in adult queens and males eventually becomes equal.

It is possible that the extra male eggs are derived from the workers and the destruction of the male brood an example of worker policing against male production by other workers (Ratnieks 1988), which is predicted when the queen mates with more than two males. Multiple matings by queens of *V. vulgaris* are highly likely (Page 1986). However, Ross 1986 and Bourke 1988, failed to find evidence of *Vespula* workers laying eggs in queenright colonies.

The workers would appear to be destroying male brood so as to bias investment towards the queens. However the sex-ratio investment does not reach three queens for every male (Table 8) probably because of multiple mating by the queen (Page 1986).

The destruction of males by the workers does not take place until the male brood has reached the mature larval and sealed brood stages. Thus, the queen would seem to be able to disguise the sex of her offspring during the egg and early larval stages. MacNair (1978) proposed that there would be an evolutionary race between the queens and workers, with genes selected which favour the disguise of the sex of the brood, followed by genes which enable the disguise to be penetrated. The evolutionary race seems to have reached an equilibrium with detection occurring at the late larval and sealed brood stages after the workers have made a considerable investment in rearing males.

Brood destruction.—Brood neglect and destruction has been linked to the death or physiological breakdown of the queen, leading to the disintegration of the social life of the colony (Spradbery 1973). However, the queen brood are not neglected but well fed (Montagner 1963), and selective destruction of male brood occurs in the large cells (Archer 1981b).

One consequence of the loss of queen influence is the appearance of a dominance struggle among the workers (Montagner 1966), whose ovaries start developing (Greene 1991). Workers with developed ovaries lay eggs destined to become males, although due to the lateness of the season it is unlikely these males will be reared, or if reared, will successfully mate (Ross 1985). Probably the capacity of workers to rear males from worker eggs is an adaptive response to the premature death or physiological breakdown of the queen (Ross 1985). About 28% of the colonies surviving until at least September (Archer, unpublished) are unsuccessful in producing many queens (Archer 1981b), but nevertheless rear males in the small cells. Many of these males could be derived from worker eggs.

In conclusion the outcomes of the two investment decisions of successful colonies of *V. vulgaris* have been found as follows. The first decision of the trade-off between worker production for colony maintenance and sexual production is to delay sexual production in order to produce more workers and hence to produce relatively more sexuals. In the second decision, there is a bias towards queen production at the expense of male production. This bias depends on worker action in the destruction of male brood probably derived from queen eggs.

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Response of *Glyptapanteles militaris* (Walsh) (Hymenoptera: Braconidae), a Larval Parasitoid of the Armyworm, *Mythimna unipuncta* (Haworth) (Lepidoptera: Noctuidae), to Different Temperatures

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Abstract.—The effect of four different temperatures (15, 20 25 and 30°C), on biological parameters of the Azorean population of *Glyptapanteles militaris* (Walsh) was studied, using *Mythimna unipuncta* (Haworth) as the host. Thirteen biological parameters of the host-parasitoid interaction were analysed: percentage of hosts that died without producing parasitoids; percentage of larvae parasitized from which parasitoids emerged; percentage of hosts surviving to pupate after the parasitoid's sting; egg-larval development time; pupal period; total developmental time; adult longevity; total number of larvae per host; number of larval parasitoids that fail to emerge from each host; mean number of parasitoids that emerged from host larva but failed to spin a cocoon; mean number of cocoons per host; parasitoid sex-ratio; and finally emergence rate of adult parasitoid progeny. The percentage of hosts that died without producing parasitoids increased with increasing temperature. Developmental times significantly decreased with increasing temperature. The mean number of cocoons per host; mean number of parasitoids that emerged from each host larva but failed to spin a cocoon; and total number of larvae per host were higher when the temperature was lower. Parasitoid sex ratio and emergence rate of adult progeny were not affected by the temperatures tested.

Mythimna unipuncta (Haworth) is the most important pest in Azorean pastures. Serious population explosions that require the use of pesticides often occur (Tavares 1992). *Glyptapanteles militaris* (Walsh) is a larval parasitoid of the armyworm in all islands of the Archipelago (Oliveira 1996). It is desirable to increase the natural population of *G. militaris* by field releases of wasps produced in the laboratory, during the first generation of *M. unipuncta*.

One of the most important abiotic factors that affect insects is temperature. In parasitoids this can influence development, fecundity, mortality, sex ratio, coloration and other characteristics in various species (Kaya and Tanada 1969; Yu and Luck 1988; Klein 1988; Lysyk and Nealis 1988; Spivac *et al.* 1992).

Temperature increases, within a favour-able range, will speed up insect metabolism and consequently increase the rate of development. Each species and each stage in the life history may develop at its own rate (Sedlacek *et al.* 1990, Spivac *et al.* 1992, Gullan and Cranston 1994).

A previous study of the effect of two different temperatures on the biological parameters of *G. militaris* was performed by Oliveira (1991, 1992). In the present study, we analyse the effect of two extreme temperatures (15 and 30°C) and two intermediate temperatures (20 and 25°C), on some biological parameters of the Azorean population of *G. militaris* using *M. unipuncta* as host.

MATERIAL AND METHODS

Glyptapanteles militaris used in this experiment emerged from naturally parasit-

ized *M. unipuncta* larvae, collected in pastures of São Miguel island. Groups of one hundred cocoons were placed in 400 ml glass vials until adult females were removed for experiments. Adults were supplied with honey solution (10%). We used as hosts *M. unipuncta* larvae from laboratory cultures, established from eggs laid by field-collected females.

On the third day after adult parasitoid emergence, one isolated female wasp was allowed to parasitize one isolated third instar larva of *M. unipuncta*. After the first sting, the host was removed from the parasitoid and individually kept, until emergence of the parasitoids, in a plastic container (4.5 × 3cm). Each host larva was supplied with a small piece (1cm^3) of artificial diet every two days as described by Poitout and Bues (1970) and modified by Oliveira (1991). After parasitization, each group of fifty parasitized host larvae were kept at a different temperature (15±0.5°C, 20±0.5°C, 25±0.5°C and 30±0.5°C), under 75±0.5% R.H. and 16:8 [L:D] photoperiod.

After larval parasitoid emergence and construction of the cocoons, each group was maintained in a plastic container (4.5 × 3cm) with a hole covered by nylon tissue. Emerged adults were kept in the same conditions and were supplied with honey solution (10%) until their death.

Thirteen biological parameters of the host-parasitoid interaction were analysed: percentage of larvae parasitized from which parasitoids emerged; percentage of dead hosts; percentage of hosts surviving to pupate after the parasitoid's sting; egg-larval development time; pupal period; total developmental time; adult longevity; total number of larvae per host; number of larval parasitoids that fail to emerge from each host; mean number of parasitoids that emerged from host larva but failed to spin a cocoon; mean number of cocoons per host; parasitoid sex-ratio (percentage of females); and finally emergence rate of adult progeny.

The first three parameters were ana-
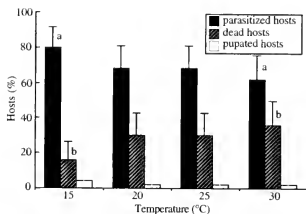
Fig. 1. Percentages of pupated, dead and parasitized larvae of *Mythimna unipuncta*, at four different temperatures (±standard error). A test for multiple comparison of proportions was used. Each column that is followed by a different letter is significantly different (p < 0.05).

lysed by a test for multiple comparisons of proportions (Zar 1996), and the others parameters were analysed by non-parametric "Kruskal-Wallis" and Multiple Comparison tests (p < 0.05) (Scherrer 1984) to compare the results obtained from different temperatures. To compare the effect of temperature on all studied parameters, a discriminant factorial analysis (Thioulouse 1989), was performed.

RESULTS AND DISCUSSION

Parasitized larvae of *M. unipuncta* were able to develop normally at the four different temperatures, with high percentages of hosts that were successfully parasitized and producing parasite progeny (Fig. 1). However the percentage of parasitized larvae from which parasitoids emerged differed significantly between 15 and 30°C (t = 1.983, p < 0.05), achieving maximum values at 15°C.

The percentage of hosts that died before emergence of the parasitoids increased with temperature. It was least at 15°C, intermediete and similar at 20 and 25°C, and most at 30°C (Fig. 1). A significant difference was observed for the percentage of dead hosts at 15 and 30°C (t = 2.280, p < 0.05). The percentage of surviving hosts after they had been stung by the parasit-

Table 1. Mean (±standard deviation) days of egg-larval development time in *Mythimna unipuncta* (D1), pupal period (D2), and the total developmental time (D1 + D2) of *Glyptapanteles militaris*, at four different temperatures.

Temperature °C	N	D1 x̄ ± sd	N	D2 x̄ ± sd	N	D1 + D2 x̄ ± sd
15	40	37.50 ± 4.90a	40	18.25 ± 1.89a	40	55.75 ± 5.87a
20	34	19.00 ± 2.89b	33	07.27 ± 1.15b	33	26.18 ± 3.07b
25	34	13.56 ± 2.14c	31	05.84 ± 0.69c	31	19.36 ± 2.32c
30	31	11.90 ± 2.01c	20	05.45 ± 1.47c	20	17.15 ± 2.01c
H value		118.495		96.684		108.677
P value		<0.0001		<0.0001		<0.0001

Kruskal-Wallis H and P values and Multiple Comparisons test. Means in each column that are followed by a different letter are significantly different (p < 0.05).

oid was very low (2–4 %) and therefore they were not statistically analysed.

The relation between temperature and rate of development of poikilotherms is an important aspect of ecological studies and basic to the development of pest management strategies (Lysyk and Nealis 1988). According to several authors, the period between parasitization and parasitoid emergence decreases with increasing temperature (Nealis and Fraser 1988; Gould and Elkinton 1990; Allen and Keller 1991; Tillman and Powell 1991). A similar result was obtained in this study with *G. militaris* and *M. unipuncta*. We divided the total development period in two parts: egg-larval development time, and pupal development (strictly, duration of the cocooned stages). We found similar results for both periods (Table 1), and significant differences were observed between the different temperatures with only one exception (25 and 30°C).

Temperature significantly affected the longevity of adult *G. militaris* obtained in this study except between 20 and 25°C. A similar result was obtained by Allen and Keller (1991) in a study of *Cotesia urabae* Austin and Allen reared from *Uraba lugens* Walker. The maximum longevity of *G. militaris* was obtained at 15°C (8.1 days) and the minimum was at 30°C (2.3 days). At the intermediate two temperatures we obtained 2.9 days. Comparing these values with the 16 days of maximum longev-

ity previously observed by Oliveira (1996), we conclude that our results are very low and they may be due to abiotic conditions, such as an insufficient level of ventilation in climatic chambers.

The temperature established during the development time of *G. militaris* can affect the mean number of cocoons found per host, the mean number of parasitoids that emerged from the host larva but failed to spin a cocoon, and the total number of discernable parasitoid larvae. The mean number of cocoons per host decreased with increasing temperature. A significant difference was observed between 30°C and 15 and 20°C (Table 2). Similar results were reported by Oliveira Filho and Foerster (1986) with "*Apanteles*" *muesebecki* Blanchard parasitising *Pseudaletia sequax* Franclemont. The mean number of parasitoid larvae that emerged from the host but then failed to spin a cocoon was relatively small in each case; the differences found (Table 2), are, though statistically significant, hard to explain in view of the non-linearity of the result and they may not really be informative. The number of parasitoid larvae that failed to leave the host larva was similar at the four temperatures tested (Table 2). The total number of larvae per host decreased with increasing temperature (Table 2). A significant difference was found between the result obtained at 30°C and the other three temperatures.

Table 2. Mean (±standard deviation) number of *Glyptapanteles militaris* cocoons, the number of larvae that failed to spin a cocoon, and that failed to emerge from the host of *Mythimna unipuncta*, at four different temperatures.

Temperature °C	N	N° cocoons/host x̄ ± sd	Par. larvae not pupated x̄ ± sd	Par. larvae not emerged x̄ ± sd	Total larvae x̄ ± sd
15	40	55.40 ± 38.24ab	8.50 ± 13.06ab	10.00 ± 16.46a	73.95 ± 31.43a
20	34	50.41 ± 28.71b	2.50 ± 04.86a	8.91 ± 14.83a	61.82 ± 29.25a
25	34	35.12 ± 27.81bc	8.94 ± 13.55ab	12.24 ± 21.84a	56.29 ± 29.21a
30	31	19.42 ± 16.29c	5.55 ± 04.25b	9.19 ± 12.33a	34.16 ± 21.49b
H value		27.36	12.84	3.20	30.19
P value		<0.0001	0.0050	0.3616	<0.0001

Kruskal-Wallis H and P values and Multiple Comparisons test. Means in each column that are followed by a different letter are significantly different (p < 0.05).

The sex ratios (percentage of females) were lower than 19%, in all cases (Table 3). No significant differences as a function of temperature were found. Similar results were obtained by Kolodny-Hirsch (1988) in his study of *Cotesia melanoscela* (Ratzburg) and the host *Lymantria dispar* (L.). In all laboratory cultures of the Azorean *G. militaris* population we systematically obtained low sex ratios (Oliveira 1991, 1992, 1996), when compared with the observed sex ratio of natural populations, usually between 48 and 78% (Oliveira 1991, 1996). This is due to a high percentage of the females that oviposit failing to produce female progeny, indicating a high level of unmated females under laboratory conditions. This is an important aspect that will require to be overcome, if we want to do

mass releases of *G. militaris* to control *M. unipuncta.*

The adult emergence rates were not very high, always less than 71%, but no significant differences were observed between temperatures (Table 3). However, an interesting result was observed at 30°C with a high number of adults dying before complete emergence from the cocoons.

To compare the effect of the different temperatures on all parameters a discriminant factorial analysis was performed. This analysis demonstrated: 1) a superposition of the values obtained at 25 and 30°C; 2) a light separation at 20°C; 3) a complete separation of the results at 15°C (Fig. 2). The parameters that had most influence on this separation were the egg-larval development time, the pupal period, adult longevity, and the number of cocoons per host.

Finally, these results confirm that *G. militaris* is very well adapted to the climatic conditions of the Azores, since the parasitoid develops better between 15 and 20°C than at 25 and 30°C, and the temperatures found on the Azores pastures range between 13 and 23°C during the period of highest activity of the parasitoid.

ACKNOWLEDGMENTS

Table 3. *Glyptapanteles militaris* sex-ratio (percentage of females) and adult emergence rates (±standard deviation), at four different temperatures.

Tempera-ture °C	Sex ratio		% Emergence	
	N	x̄ ± sd	N	x̄ ± sd
15	40	0.19 ± 0.29	40	70.90 ± 21.80
20	33	0.16 ± 0.23	34	63.00 ± 25.60
25	31	0.18 ± 0.25	34	70.30 ± 25.80
30	21	0.13 ± 0.22	31	49.80 ± 40.70
H value		0.595		5.012
P value		0.8976		0.1709

Kruskal-Wallis H and P values (p > 0.05).
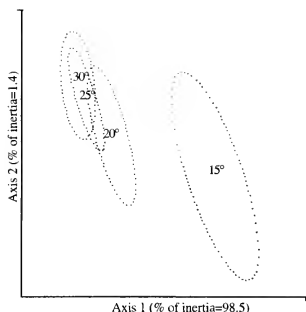
Fig 2. Discriminant factorial analysis performed with nine biological parameters of *Glyptapanteles militaris*: egg-larval development time, pupal period, adult longevity, mean number of cocoons per host, mean number of parasitoids that emerged from host larva but failed to spin a cocoon, mean number of larval parasitoids that failed to emerge from each host, total number of larvae per host, parasitoid sex ratio, and emergence rate of adult progeny.

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Response of *Pithecellobium tortum* Martius (Leguminosae) Seeds to the Attack of the Phytophagous Braconid *Allorhogas dyspistus* Marsh (Hymenoptera: Braconidae)

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Abstract.—This work describes morphological changes on the seeds of *Pithecellobium tortum* caused by the braconid *Allorhogas dyspistus*, at Restinga (Costal scrub) of Barra de Maricá, Rio de Janeiro State, Brazil. This species was shown to be a gall maker on *P. Tortum* seeds whose galls result from the proliferation of parenchymatous cells near the tegument but not of the seed coat cells. Its impact on the host plant consists of decreases in plant reproductive potential not only by directly reducing seed viability, but also by contributing to seed mortality via the adult emergence hole which allows invasion by pathogenic micro-organisms. The braconid's way of eating the seed, keeping itself in a chamber apart from the seed embryo, which remains alive and therefore demanding nutrients, accords it the profile of a "manipulative parasite" in the sense of Weis & Abrahamson (1986).

Signs of insect herbivory on plants vary greatly. Some are simple feeding marks left on the host plant which normally do not involve any apparent morphological response. Other signs, however, are very complex, resulting from a noticeable morphological and / or physiological response of the plant. This response may be defensive, pathological or one which benefits the herbivore (Price 1980, Weis & Abrahamson 1986). Herbivores that are capable of manipulating the response of their host plant for their own benefit have been called "manipulative parasites" (Weis & Abrahamson 1986). Gall makers induce the development of localised growing structures resulting from the abnormal increase in number and / or size of plant cells (Darlington 1975). Normally, the galls are induced in undifferentiated tissues, which have their development manipulated

(Weis *et al.* 1988). The gall phenotype is the result of two genotypes: the one of the gall maker, responsible for the stimulus, and the other of the plant, which produces the reaction (Abrahamson & Weis 1987). From an evolutionary perspective, gall morphology is the product of natural selection on the insect stimulating the development of a structure for protection and nutrition and on the plant resisting or trying to avoid the insect stimulus (Weis *et al.* 1988).

Most of the known entomogenous galls are induced by Diptera (especially Cecidomyiidae), Hymenoptera, Homoptera and Thysanoptera (Meyer 1987; Shorthouse and Rohfritsch 1992). Within the Hymenoptera the Cynipidae is the most important family, but there are also records for Tenthredinidae, Eurytomidae, Eulophidae, Pteromalidae and Tanaostig-

matidae (Fernandes 1987). Guimarães (1957) reared *Allorhogas muesebecki* Guimarães from *Anemopaegma mirandum* Alph. DC. (Bignoniaceae) galls. Because this braconid was the only species to emerge the author concluded that this was the gall inducer. Since the first record of a phytophagous braconid (Macêdo & Monteiro 1989) and its specific description by Marsh (1991) as *Allorhogas dyspistus*, Infante *et al.* (1995) redescribed *Monitoriella elongata* Hedqvist and recorded it as a new case of phytophagy within the Braconidae. This species, like *A. dyspistus*, belongs to the Doryctinae, a group which, according to Wharton (1993), should be searched for more cases of phytophagy. Ramirez & Marsh (1996) described two new *Psenobolus* species (Braconidae: Doryctinae) which appear to develop as inquilines on plant tissue in fig flowers after their pollination by Agaonidae wasps. More recently, Austin & Dangerfield (1998) recorded the biology of *Mesostoa kerri* Austin and Wharton, a member of the endemic Australian subfamily Mesostoinae, as a new case of galling Braconidae.

Pithecellobium tortum Martius (Leguminosae) seeds are enclosed in fruits containing about 30 seeds side by side. They are attacked by the braconid *Allorhogas dyspistus* Marsh, which oviposits directly into immature seeds, when abundant endosperm and a small embryo are still present. After oviposition by the braconid the seed divides internally and externally, resulting in an intact region, joined to the funicle, where the seed embryo is usually found (Macêdo & Monteiro 1989). In many cases this region of the seed continues growing even after the adult insect has emerged. More than one *A. dyspistus* can be found in a single seed. In these cases, more than one division occurs and still a single intact region within the seed embryo is found. The main purpose of this study is to describe and discuss the morphological seed changes caused by *Allorhogas dyspistus* in *Pithecellobium tortum* and

to evaluate this impact of the insect on the host plant.

MATERIALS AND METHODS

All seeds were collected at Restinga (Coastal scrub) de Barra de Maricá (22°57'S and 12° 52'W), Maricá county, Rio de Janeiro state, Brazil.

To investigate seed tissue morphology, intact and attacked seeds were collected during June 1994, and fixed in 70% alcohol. Seeds were then laid in 10% ethylenediamine for one week, as suggested by Carlquist (1982) to soften them. After washing in distilled water three times for a 2 hours period each time, the seeds were dehydrated in ethanolic series and then embedded in paraffin wax following Johansen (1940). Longitudinal serial 15 μm sections were obtained with a rotary microtome and stained with basic blue astrafucsin (Roeser 1962).

In 1994, a further sample of 2990 seeds from 150 fruits obtained from five *P. tortum* individuals were collected and dissected in order to evaluate the rate of *A. dyspistus* attack and to check if the attacked seeds died or continued development until complete maturation. In 1995, 327 fruits from 12 plant individuals were also collected and dissected to evaluated *A. dyspistus* seed attack rate.

At the end of the 1995 fruiting season in June, mature fruits of *P. tortum* were collected from their parent plant and from the ground. Attacked and non-attacked seeds were then obtained to perform the tetrazolium viability test (Delouche *et al.* 1962). This test was performed immediately after the collection of seeds from the plant and from the ground, and also after three and eight months of laboratory storage at room temperature for seeds collected from the ground. All tested seeds were cut lengthwise and one half of each seed was completely immersed in 0.5% chloride of 2,3,5-triphenyl tetrazolium solution and the other half boiled before being submitted to this tetrazolium test of viability.
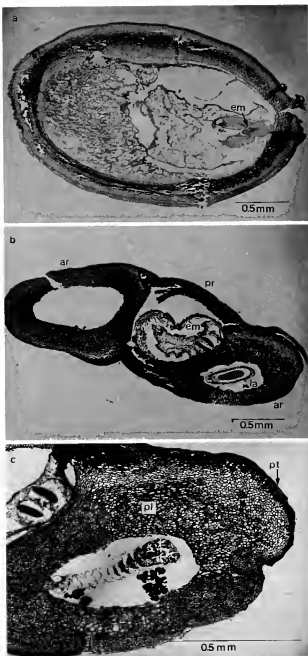
Fig. 1. Longitudinal sections of *Pithecellobium tortum* seeds. a) Non-attacked seed with its embryo (em); b) seed attacked by two *Allorhogas dyspistus* individuals, showing two attacked regions (ar); a larva (la) can be observed in one of them. The embryo (em) is present at the center in the preserved region (pr); c) an attacked region showing the seed coat palisade tissue (pt) which does not cover all of the region involving the larva. Note the thicker parenchymatous layer (pl).

This procedure was necessary in order to eliminate the possibility that the red coloration of the embryo was due to reduced ions and not to hydrogenases produced during the respiration process of the living

embryo. If the dead boiled embryo coloured, the test would be invalid. All beakers were kept in darkness at room temperature and the result checked after 12 hours.

RESULTS

Comparison between non-attacked (Fig. 1a) and attacked (Fig. 1b) seeds shows that the tissue associated with *A. dyspistus* larvae probably results from the proliferation of the fundamental parenchymatous cells near the inside tegument. The gall, the region resulting from tissue proliferation, keeps the insect larva apart from the seed embryo through a clear division of the seed. The seed coat does not cover the entire proliferated region where the braconid larva is found (Fig. 1c). This can also be seen by the naked eye because the texture of this attacked region is clearly different from that where the embryo is found.

Allorhogas dyspistus attacked 55.85% of the dissected seeds. In all, only 6.1%, out of 1670 attacked seeds appeared healthy after insect emergence or death. All other attacked seeds died mainly because of contamination, probably fungus, which probably entered the seed through the *A. dyspistus* or its parasitoid exit holes.

All mature attacked and non-attacked seeds collected from the plant itself were viable according to the tetrazolium test, as well as all mature non-attacked seeds collected from the ground (Table 1). A smaller proportion of attacked seeds were viable in the three-months stored group and an even smaller proportion of the attacked seeds were viable in the eight-months stored group. It is worth noting that in all groups the embryos from the intact seeds exhibited a clearly darker pink coloration in comparison with the viable embryos from the attacked seeds. No boiled seeds were coloured thus validating the above results.

Allorhogas dyspistus seed attack reached more than 70% in five out of the 12 plants

Table 1. Percentage of viable seeds according to tetrazolium test of attacked and non-attacked seeds under four situations of collection and storage. The number of tested seeds is in parentheses.

Collection / situation of the tested seeds	Non-attacked seeds	Attacked seeds
From ground / immediately after collection	100 (50)	100 (22)
Ground / immediately after collection	100 (25)	100 (18)
Ground / after three months of storage	100 (20)	73 (15)
Ground / after eight months of storage	100 (6)	18 (11)

Table 2. Numbers of seeds collected (N), attacked seeds and percentage of seed attack by *Allorhogas dyspistus* on each of the 12 plant individuals sampled in 1995.

Plant	N seeds	Attacked seeds	% attack *A. dyspistus*
1	359	41	11.42
2	288	33	11.46
3	386	130	33.68
4	339	83	24.48
5	252	26	10.32
6	365	290	79.45
7	394	274	69.54
8	558	39	6.99
9	385	307	79.74
10	468	436	93.16
11	436	435	99.77
12	338	337	99.70

studied and in two of these the rates were very near 100% (Table 2).

DISCUSSION

Clear cell proliferation, characteristic of the process of gall formation, indicates that *A. dyspistus* induces galls in *P. tortum* immature seeds. This kind of gall is, according to Gagné (1994), a simple gall, which does not differ from the normal plant tissue except for cell proliferation. This is very different from most of the complex galls (*sensu* Gagné 1994) on plant vegetative parts (*e.g.* Redfern & Askew 1992). *Monitoriella elongata* (Infante *et al.* 1995) and *Mesostoa kerri* (Austin and Dangerfield 1998), are two Braconidae leaf gallers whose galls are apparently as complex as any Cecidomyiidae leaf gall and quite different from the simple galls of *A. dyspistus*. As seeds are attacked when immature and still in the process of development, meristematic tissue is available, and this is where galls are primarily produced (Mani 1964, Bronner 1977). Quicke (1997) points out that there is growing evidence that at least seed predation actually involves the stimulation of proliferation of some plant cells, that is, a kind of incipient gall formation or simple gall (*sensu* Gagné 1994).

Other insect groups which develop inside seeds, such as Bruchidae (Coleoptera), do not promote any similar response

and most of them feed upon embryo and cotyledons (Southgate 1979). Even *Rinochenus stigma* (L.) (Coleoptera; Curculionidae), which eats the cotyledons but not the embryo of *Hymenaea* (Leguminosae) seeds, does not induce any kind of seed division (T.M. Lewinsohn pers. com.).

The way of attack by the braconid leaving the seed embryo region intact may be considered a way of maintaining nutrient demand by the living seed and therefore for the insect, which could not survive otherwise. The aggregated pattern of *A. dyspistus* occurrence in the fruits (M.V. Macêdo, pers. obs.) could, if the seeds died, cause selective abortion of most attacked fruits, as in *Cassia grandis* L. (Leguminosae) attacked by bruchids (Janzen 1971). This negative effect for the insect is more evident in younger fruits (Stephenson 1981). Thus, *A. dyspistus* may be considered a manipulative parasite of *P. tortum* immature seeds (*sensu* Weis & Abrahamson 1986).

It is clear that the potential negative effect is very high where reproductive tissue is attacked (Abrahamson & Weis 1987). Reduction of *P. tortum* seed viability over time is a clear effect of *A. dyspistus* attack (Table 1). Furthermore, the capability of germination of attacked living seeds still

remains to be tested. The tetrazolium test only proved that attacked seeds are alive; these seeds, however, could have lower chances of germination and establishment, as may be suggested by attacked seeds having a lower degree of respiratory activity which was shown by their lighter coloration in the test. Moreover, *A. dyspistus* exit holes seem to serve as a communicating channel between the seed and the external environment, which makes it possible for micro-organisms to enter and eventually kill most of the attacked seeds.

This work shows that, directly or indirectly, *A. dyspistus* considerably reduces plant fitness, and, because the species may attack up to 100% of the seeds in a plant, it can be considered a good example of a galler that imposes high negative effects on its host plant. We suggest that the galler's behaviour of maintaining the seed embryo alive while feeding upon seed tissue may avoid abortion of immature seeds increasing the galler's chances of survival.

ACKNOWLEDGMENTS

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Morphological Caste Differences in the Neotropical Swarm-founding Polistine Wasps IV: *Pseudopolybia vespiceps*, with Preliminary Considerations on the Role of Intermediate Females in the Social Organization of the Epiponini (Hymenoptera, Vespidae)

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Abstract.—The measurements of 22 body parts and counts of hamulus number for 300 wasps from a colony of *Pseudopolybia vespiceps* evidenced the occurrence of three types of females, i.e., queens (inseminated egg-layers), workers (uninseminated, non egg-layers), and intermediates (with well developed ovaries but uninseminated). Caste-linked aspects in this species are, thus, complex. Queens (Q) and workers (W) differed in only two characters (basal width of the second gastral tergite and hamulus number) (Bonferroni-test, $p < 0.05$), so, these castes can be considered as morphometrically similar. On the other hand, intermediates (I) were significantly larger than queens and workers in some body parts ($p < 0.05$). Canonical discriminant analysis revealed that Mahalanobis distances (D^2) between Q/W, Q/I and I/W were very small, 0.99, 1.51 and 1.12, respectively. In spite of this, color patterns of head and gastral parts separate queens and workers very well. In such aspects intermediates combine queen-worker similarities.

In social insects, approaches related to caste differences constitute a form of evidencing queen-worker specializations. To study the diversity of such aspects, the swarm-founding polistine wasps are very helpful because the castal differences so far known can be arranged along a spectrum ranging from taxa in which queens and workers are externally similar, to others with fairly distinct caste attributes. Despite occurence of transitional steps (e.g. *Protopolybia exigua* cf. Simões 1977; Noll et al. 1996), our previous serial papers showed two contrasting cases: queen dwarfism, as promoted by the prevalence of smaller body parts in queens relatively to workers (*Apoica flavissima* and *Polybia dimidiata*: Shima et al. 1994 and Shima et al. 1996a, respectively), and queens larger

than workers in most of the morphological characters (*Protonectarina sylveirae*: Shima et al., 1996b). Moreover, the taxa under such opposite trends showed also different color patterns allied to conspicuous external morphological peculiarities. However, the most pronounced dimorphism among polistine wasps has been found in some *Agelaia* (*Stelopolybia* auct.) species, such as, *A. flavipennis* (Evans & West-Eberhard 1970); *A. areata* (Jeanne and Fagen 1974; Jeanne 1980 1991), *A. pallipes* and *A. multipicta* (Noll et al. 1997) and *A. vicina* (Sakagami et al. 1996; Baio et al. in press).

The genus *Pseudopolybia* is poorly known. Indeed, only some details on nest architecture and fragmentary morphometric features had so far been reported by Richards

(1978, and references therein), before the recent paper on *Ps. difficilis* (Jeanne 1996). Contrary to those taxa previously studied in our serial papers, *Ps. vespiceps* shows no clear-cut morphological caste dimorphism. In addition, *Ps. vespiceps* evidenced the occurrence of intermediate females which are characterized by the combination of well developed ovaries and the absence of insemination (Richards & Richards 1951). Although the bionomic importance of such females remains largely speculative, their significance in the colonial socio-economics is apparently relevant because Naumann (1970), Simões (1977) and M. V. Baio (unpubl.) have found out that intermediates in *Protopolybia acutiscutis* (cited as *P. pumila*) and *P. exigua exigua*, frequently laid eggs which were primarily eaten by the layer herself. Based on the morphometric analysis adopted in our serial work, this paper deals with caste differences and related aspects in *Pseudopolybia vespiceps testacea* Ducke.

MATERIAL AND METHODS

A mature colony (A) of *Pseudopolybia vespiceps testacea*, from which a small number of individuals escaped during collection, was taken on 20 January 1975 in Ribeirão Preto, São Paulo State, southeastern Brazil. The 603 collected wasps, all of which were females, were fixed in Dietrich's solution and then kept in 70% ethanol until dissection. From this sample, 300 wasps were randomly chosen for examination. In order to detect caste differences the following 22 external body parts were measured and the number of hamuli was counted for each specimen under a binocular microscope: (1) head width (HW), (2) head length (HL), (3) and (4) maximum and minimum interorbital distances (IDx, IDm), respectively, (5) gena width (GW), (6) eye width (EW), (7) pronotal width (PW), (8), (9) length and width of mesoscutum (MSL and MSW), respectively, (10) mesoscutellar length (MTL), (11) metanotal length (MNL), (12) mesosomal height (MSH), (13) alitrunk length (AL), (14) propodeum length (PL), (15) length of gastral tergite I (T_1L), (16), (17) basal and apical heights of T_1 (T_1BH, T_1AH), respectively, (18), (19) basal and apical widths of gastral tergite II (T_2BW, T_2AW), respectively, (20), (21) length and height of T_2 (T_2L, T_2H), respectively, and (22) partial length of the forewing (WL) (See Fig. 2 in Shima et al. 1994). In addition, color patterns and other morphological peculiarities were examined. The numerical data were statistically analyzed in relation to ovarian and spermathecal conditions.

The statistical analyses including the canonical discriminant analysis (CDA: Rao 1973) and Mahalanobis's distances (Anderson 1968) through CDA were performed with the SAS Program Package at the Computer Center of Kyoto University. Afterwards, a second colony (B) was collected on February 3, 1995 in Pedregulho, São Paulo State. The illustrations (Fig. 1A, B, C, and D) pertain to this colony.

RESULTS

Nest architecture and colony composition.—Both nests (A,B) were found in shady places at about 3 m high aboveground and both were hung from terminal small branches, of which ramifications pierced the outer envelope at upper parts, but not the combs. In shape (ellipsoidal), size (17.0 cm high, 12 cm ø) and number of combs (8 and 7, respectively) both nests were very similar and so these features may represent the size reached by the mature colonies of *Ps. vespiceps* (Fig. 1). The multilayered greyish envelope covered combs entirely. It had several, sometimes indistinct, vertical rows formed by several pulp additions during construction (Fig. 1A–D). The nest top, which incorporated some twigs, was somewhat spongy, but latterally the envelope was formed by two to four layers of delicate and loose sheets (Fig. 1B). The nest entrance, which was large and devoid of special structures (Fig. 1C), was located at the lowermost part of
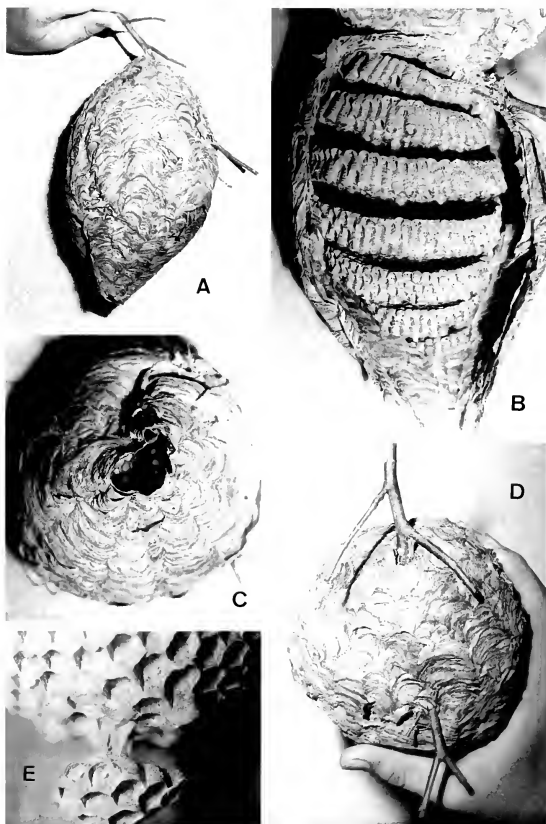
Fig. 1. Nest of *Pseudopolybia vespiceps*: A—held in the position as in nature; B—with the outer envelope removed partially; C—oriented as to exhibit an enlarged entrance and a part of the lower comb; D—seen from the top; E—lowermost combs and pedicel. A–D, nest 2; E, nest 1.

the nest. Each comb was hung below the other by a single centrally located paper pillar (1.0 cm long, 1.0 cm wide; Fig. 1E). The only exception was the uppermost comb which was attached to the substrate, a twig, by a row of 4 or 5 thin pillars. The first comb was solely supported by these pillars and, therefore, all combs hung from the upper one independently of the envelope. As recorded by Richards (1978) the general plan of *Pseudopolybia* nests is similar to *Vespula norwegica* of subfamily Vespinae. As stated above, colony A used in this study had 603 adult females (118 queens, 396 workers, 89 intermediates) and no males. The queen ratio (total queen number / total female number) was 0.196. Eight combs had 729 eggs, 584 larvae, 586 cocoons and 287 empty cells.

Ovarian development and insemination.— In the analyzed sample four types of ovary development were recognized (Fig. 2): type A (short ovarioles): A_1, thread-like with no sign of development (n = 60), A_2, slightly developed (n = 74) and A_3 (n = 10), more developed than A_2; type B (in developmental stages similar to type A, but with longer ovarioles); B_1, B_2, B_3 (n = 13, 33 and 7, respectively); type C (n = 44), moderately developed with a few (1 to 3) mature oocytes (mean 1.9, n = 85) and type D (n = 59), well developed with an average of 3.7 mature oocytes (range 1 to 7), n = 176. Since insemination was detected exclusively in females with type D ovaries, only these females are regarded as queens. All the others females were uninseminated, and those with type C (developed) ovaries were regarded as intermediates (sensu Richards and Richards 1951; Richards 1971). Conversely, females with A and B ovary types constitute the cohort of workers. Although measurements were not made, mature oocytes in the intermediates were clearly smaller than those in queens.

Ovariole length, wing-wear patterns and relative amount of fat tissue.—Mean ovariole length (MOL) was longer in queens

(8.52±0.46 mm, n = 46), followed by B typed workers (7.63±0.38 mm), intermediates (6.95±0.57 mm), and smallest in A typed workers (6.69±0.39 mm). These differences were statistically significant (ANOVA, p < 0.01, F = 0.242). Another interesting tendency was found connecting ovary development and amount of fat tissue. Indeed, individuals showing progressive kinds of ovary development presented also larger amounts of fat tissue. The culmination of such tendency was found in D typed females (queens) which showed higher amounts of fat reserve (grade IV, cf. captions in Fig. 3). Most uninseminated females (type A ovaries) had shorter ovarioles relative to the B typed ones, and both had little (I) or moderate (II) amounts of fat tissue. But, some uninseminated callow females, which were recognized by their pale and soft cuticle, had larger amounts of fat tissues also (grade IV). In this case, it seems that the mere presence of larger amounts of fat tissue is not conclusively connected to further queenhood. Indeed, extensive dissections in representatives of taxa with clear-cut caste differences suggest that callow stages of both castes invariably present conspicuous fat amounts (Noll unpubl.).

Figure 3 shows the relations between ovary development and wing-wear in the different kinds of Ps. vespiceps females. Grades of wing-wear showed relationship to the relative amount of fat tissues. Most analyzed females, including all queens, had fresh wings (pattern 0), while some workers and intermediates showed consistent wing-wear (patterns 1–3, Fig. 3). Wing-wear may indicate relative age progression and flight activities. The fact that all queens had fresh wings suggest their absence in extranidal tasks.

Morphometrics and hamulus number.— Differences of mean values of 24 characters measured or counted were tested in workers, queens and intermediates by Bonferroni-test (Table 1). Between workers and queens, significant differences were
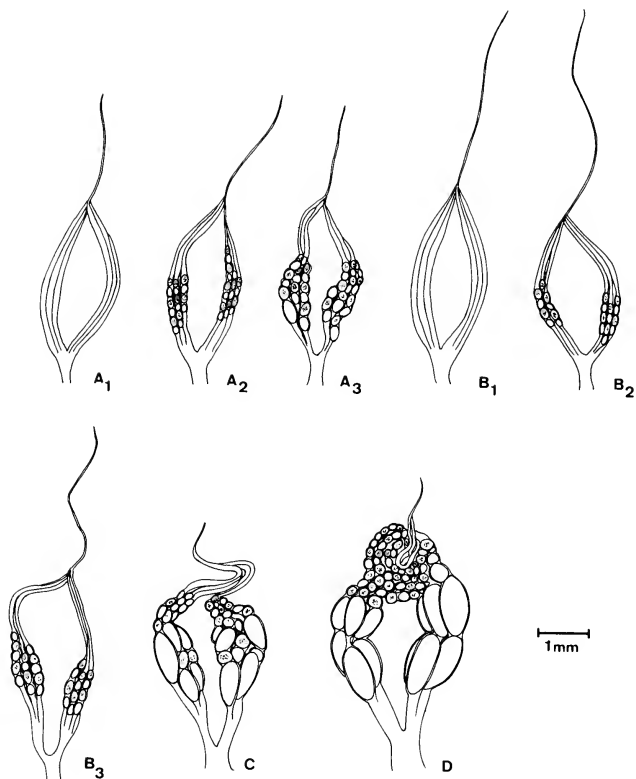
Fig. 2. Grades of ovarian development in *Pseudopolybia vespiceps*. Type A: short ovariole type. A₁-thread-like; A₂ and A₃-showing initial development of the oocytes); Type B: long ovaries type. B₁-thread-like as in A₁; B2 and B3-comparable to A₂ and A₃, respectively; Type C: moderately developed with a few mature oocytes; and Type D: well developed and bearing many mature oocytes. Other explanations, in the text.
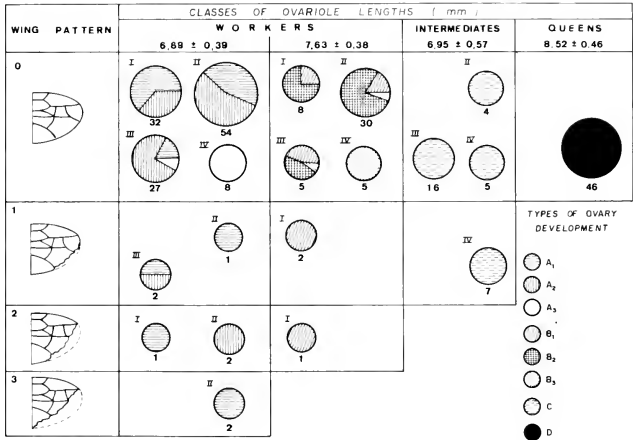
	CLASSES OF OVARIOLE LENGTHS (mm)					
WING PATTERN	WORKERS				INTERMEDIATES	QUEENS
	6.69 ± 0.39		7.63 ± 0.38		6.95 ± 0.57	8.52 ± 0.46

Fig. 3. Relationships between wing patterns (0 = fresh; 1–3 = worn in ascending order) and relative amounts of fat tissue (I = few; II = moderate; III = abundant; IV = much abundant). Number of individuals for each class of fat tissue is expressed by the size of circle, in which numbers of individuals of different ovarian types are shown.

detected only in T_2BW, being larger in workers, and NH, larger in queens (p < 0.05). Between queens and intermediates, means of five characters, i.e., HW and HL, Idx, T_2L, T_2BW and NH differed (p < 0.05). Values of all but one character (NH) were larger in the intermediates. Between intermediates and workers, differences were detected in four characters, HW, IDx, MSW and T_2H (p < 0.05), all of which were larger in intermediates. No significant difference was detected in AL, regarded as a reference length for comparing sizes, among the three classes of females. This implies that size differences are so small that virtually no size polymorphism exists in this species. But, it is noteworthy that the intermediates are larger in some characters than workers and even queens.

The results of the canonical discriminant analysis (CDA) based on 23 characters also show the absence of clear dimorphism between inseminated egg-layers (queens) and uninseminated non-egg-layers (workers) (Fig. 4). Queens and workers were plotted against scales of the CAN_1 and CAN_2 variables between −3.0 and 3.0 and −2.5 and 2.5, respectively. The distribution pattern of the intermediates was very peculiar because their plots showed a vertical distribution at the right side in the scatter diagram. Only one queen and one worker presented higher CAN_2 values than intermediates.

To calculate the CAN_1 and CAN_2 values the following equations were used (see table 1): $CAN_1 = −0.47$ (HW − 3.79) + 5.24 (HL − 3.04) − 0.36 (Idx − 3.17) − 5.13 (IDm − 1.81) + 0.53 (GW − 0.94) − 1.98

Table 1. Means and CAN_1 and CAN_2 values for 23 characters examined.

Characters	Means (mm) ± SD			CAN_1 values		CAN_2 values	
	Queens	Workers	Intermediates	Standardized	Raw	Standardized	Raw
HEAD							
HW**,¹	3.78 ± 0.07	3.82 ± 0.06	3.78 ± 0.08	−0.04	−0.47	0.67	8.86
HL**	3.02 ± 0.09	3.07 ± 0.08	3.04 ± 0.08	0.45	5.24	−0.41	−4.81
IDx*¹	3.17 ± 0.06	3.20 ± 0.08	3.17 ± 0.08	0.03	−0.36	−0.11	−1.51
IDm	1.81 ± 0.04	1.83 ± 0.05	1.81 ± 0.05	−0.24	−5.13	−0.24	−5.19
GW	0.94 ± 0.06	0.95 ± 0.05	0.94 ± 0.06	−0.03	0.53	0.09	1.53
EW	0.88 ± 0.06	0.88 ± 0.04	0.88 ± 0.06	−0.11	−1.98	−0.12	−2.30
MESOSOMA							
MSL	2.48 ± 0.06	2.49 ± 0.07	2.48 ± 0.07	−0.01	−0.12	0.22	3.36
MSW¹	2.50 ± 0.06	2.53 ± 0.06	2.50 ± 0.07	0.13	1.86	0.16	2.30
PW	3.20 ± 0.08	3.24 ± 0.07	3.21 ± 0.09	−0.09	1.02	0.15	1.75
MTL	1.14 ± 0.04	1.15 ± 0.04	1.13 ± 0.04	−0.10	2.35	0.25	6.10
MNL	0.66 ± 0.05	0.66 ± 0.05	0.65 ± 0.05	−0.30	−5.88	0.29	5.67
MSH	3.55 ± 0.13	3.57 ± 0.13	3.53 ± 0.14	−0.02	−0.14	0.19	1.41
AL	4.93 ± 0.12	4.95 ± 0.11	4.92 ± 0.13	−0.18	−1.47	0.05	0.40
METASOMA							
PL	1.44 ± 0.08	1.47 ± 0.08	1.44 ± 0.08	0.34	4.14	0.07	0.82
T_1L	2.10 ± 0.08	2.14 ± 0.08	2.12 ± 0.10	0.05	0.49	−0.07	−0.80
T_1BH	0.87 ± 0.09	0.86 ± 0.07	0.86 ± 0.08	−0.34	−4.12	−0.13	−1.58
T_1AH	1.53 ± 0.09	1.56 ± 0.10	1.55 ± 0.10	0.17	1.71	−0.15	−1.53
T_2L**	2.90 ± 0.13	2.97 ± 0.10	2.92 ± 0.13	0.32	2.44	−0.23	−1.78
T_2BW*,**	2.33 ± 0.11	2.42 ± 0.13	2.38 ± 0.14	0.56	4.21	−0.22	−1.62
T_2AW	3.68 ± 0.12	3.70 ± 0.15	3.67 ± 0.15	−0.31	−2.17	0.04	0.29
T_2H¹	3.19 ± 0.16	3.26 ± 0.14	3.14 ± 0.16	0.34	2.11	0.74	4.54
WING							
WL	5.09 ± 0.10	5.13 ± 0.10	5.10 ± 0.13	0.02	0.20	−0.42	−3.43
NH*,**	9.59 ± 0.89	9.07 ± 0.73	9.26 ± 0.84	−0.57	−0.57	0.04	0.04

Full names of characters are explained in the text (see Material and Methods).
*,**,¹ Mean significant differences between queens and workers, queens and intermediates and intermediates and workers, respectively (Bonferroni t-test, $p < 0.05$).

(EW − 0.88) − 0.12 (MSL − 2.48) + 1.86 (MSW − 2.51) + 1.02 (PW − 3.21) − 2.35 (MTL − 1.14) − 5.88 (MNL − 0.66) − 0.14 (MSH − 3.54) − 1.47 (AL − 4.92) + 4.14 (PL − 1.45) + 0.49 (T_1L − 2.12) − 4.12 (T_1BH − 0.86) + 1.71 (T_1AH − 1.55) + 2.44 (T_2L − 2.92) + 4.21 (T_2BW −2.37) − 2.17 (T_2AW − 3.68) + 2.11 (T_2H − 3.17) + 0.20 (WL − 5.10) − 0.67 (NH − 9.30)

CAN2 = 8.86 (HW − 3.79) − 4.81 (HL − 3.04) − 1.51 (IDx − 3.17) − 5.19 (IDm − 1.81) + 1.53 (GW − 0.94) − 2.30 (EW − 0.88) + 3.36 (MSL − 2.48) + 2.30 (MSW − 2.51) + 1.75 (PW − 3.21) + 6.10 (MTL − 1.14) + 5.67 (MNL − 0.66) + 1.41 (MSH − 3.54) + 0.40

(AL − 4.92) + 0.82 (PL − 1.45) − 0.80 (T1L − 2.12) − 1.58 (T1BH − 0.86) − 1.53 (T1AH − 1.55) − 1.78 (T2L − 2.92) − 1.62 (T2BW − 2.37) + 0.29 (T2AW − 3.68) + 4.54 (T2H − 3.17) − 3.43 (WL − 5.10) + 0.04 (NH − 9.30)

The most important variable to determine CAN1 was MNL. Some other variables, such as HL, IDm, T_2BW and T_1BH were also important. The most important variable to determine CAN_2 was HW. Mahalanobis's distances (D^2) between queens and workers, queens and intermediates and intermediates and workers were 0.99, 1.51 and 1.12, respectively, showing that, as
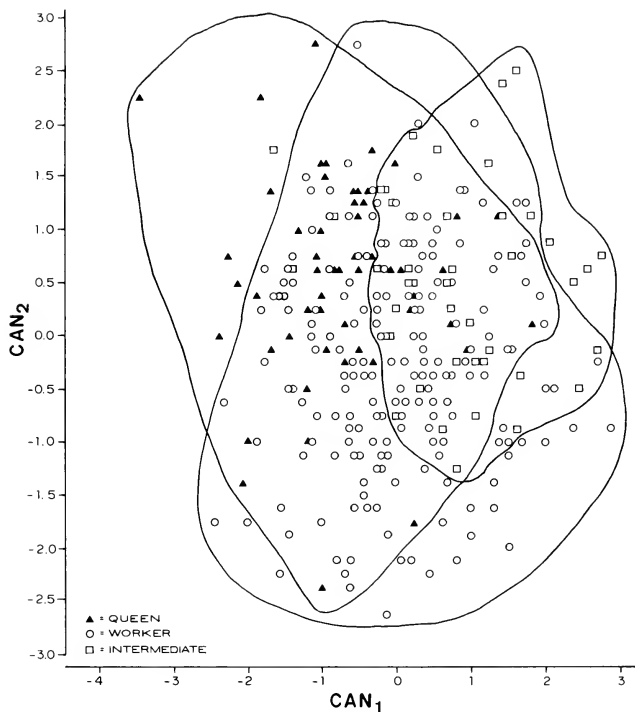
Fig. 4. Discrimination among queens, workers and intermediates of *Pseudopolybia vespiceps* by the canonical discriminant analysis based on 23 characters. Other explanations in the text.

expected from the result of basic statistics, queens are morphologically more similar to workers than to intermediates.

Aspects related to color patterns and external morphology.—Differences that were more conspicuous than morphometric characters were found in head, mesosoma and metasoma.

Head (Fig. 5): Workers heads are of various shapes. Despite sequentially continuous, these characteristics can be grouped into three major types, i.e., flat, ovate and pointed types (types I–III), and four color patterns (A_1 to A_4). A tendency was detected and it shows that the coloration of the flat head type is lighter than in the
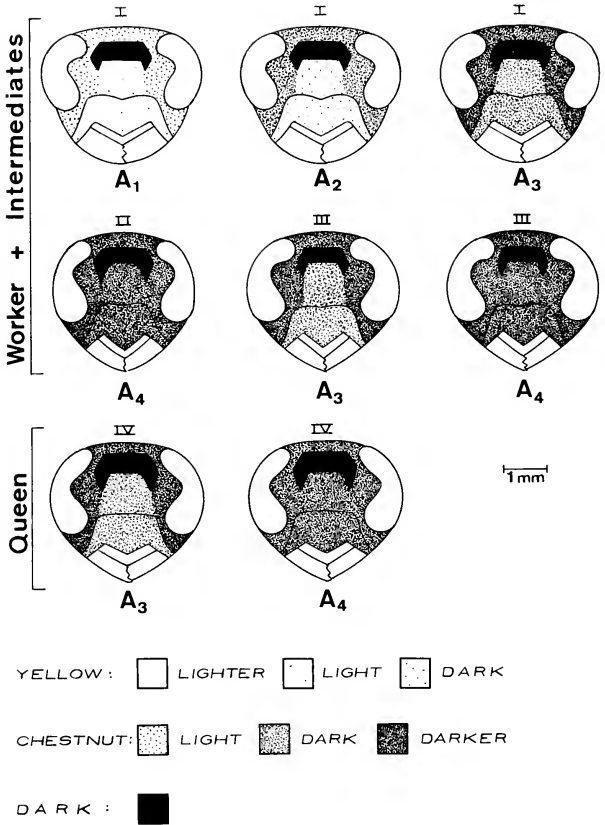
Fig. 5. Color patterns and shapes of head in queens, workers and intermediates of *Pseudopolybia vespiceps*. Color: A_1 to A_4; Shape: I. flattened; II. ovate; III. pointed; IV. ovate but more enlarged apically.

ovate and pointed head types. On the other hand, ovate head (type IV) characterizes the queens in which two color patterns (A_3, A_4) appear, and these are very similar to the workers darkest forms.

Mesosoma (Fig. 6): Workers present six mesosomal color forms ranging from light (B_1) to dark (B_6). Mesoscutellum of each type presents (or not, see type a, B_1) a pair of dark spots which vary in size and form (separated circles, ellipsoids partly fused) (e.g., types b–e, B_1). Except for type B_6, there are no double transverse bands on the mesoscutellum. On the other hand, queens present only one color form (B_7), but as workers, they present various spot types (a–e) on the mesoscutellum. In addition, a pair of arched transverse bands occur near the basal and apical margins of the mesoscutellum (apical bands are often lighter in color and more vestigial than basal ones). Such bands are seen through the transparent cuticle (Fig. 6, B_6 b–d, B_7 a–e). Despite color patterns overlap among the diverse types of females, mesoscutellar bands easily discriminated queens from workers. In intermediates, the patterns of the head and thorax were similar to workers including a tendency for the flat type of head (n = 30) and lighter colors (A_1, n = 9; A_2, n = 7; A_3, n = 14). Indeed, only one intermediate presented A_4 II pattern which is similar to queens. From 16 color patterns of the worker's thorax, 12 were similar to intermediates with higher frequency of B_1 b (12); B_1 e (7), B_5 e (8). Conversely, only B_1 a,c; B_3 b and B_4 e were not observed in such females.

Metasoma (Fig. 7): Three major color forms (G_1–G_3) occur, and each form has three to five color variations on T2 (C_1–C_{11}). Queens and intermediates present lighter gastral patterns (G_1 and C_1–C_4), among which C_3 is the most frequent (n = 28). Workers have darker gasters (G_2 and G_3, and C_2, C_5–C_{11}), among which C_5 and C_6 are the most frequent (n = 80 and 77, respectively). In intermediates, six forms occur (G_1, C_1–C_4, and G_2, C_5), with the high-

est frequency in C_2 (n = 18) and C_3 (n = 14). Although form C_2 is shared by all kinds of females, queens generally present lighter and enlarged gasters than workers.

DISCUSSION

Although caste differentiation in social wasps is most conspicuous in the Vespinae, especially *Vespula* (Blackith 1958; Spradbery 1972), certain swarm-founding polistine wasps have also evolved distinct size dimorphism. Such a fact was clearly stated long ago by von Ihering (1903), who described remarkable morphological caste differences in *Agelaia vicina*, but his results have been overlooked by modern specialists in spite of its citation by Richards and Richards (1951). Indeed, additional records on quite conspicuous caste differentiation in the Polistinae, analyzed either qualitatively and/or quantitatively by statistical methods, appeared only recently. Genera and species examined are: New World: *Agelaia flavipennis* (Evans and West-Eberhard 1970); *A. areata* (Jeanne and Fagen 1974); *Polybia emaciata* (Hebling and Letízio 1973); *Polybia dimidiata* (Maule-Rodrigues and Santos 1974; Shima et al. 1996a); *Apoica flavissima* (Shima et al. 1994); *A. pallens* (Jeanne et al. 1995); *Protonectarina sylveirae* (Shima et al. 1996b), *Pseudopolybia difficilis* (Jeanne 1996), and *Epipona guerini* (Hunt et al. 1996), and Old World genera: *Ropalidia montana* (Yamane et al. 1983); *R. bambusae* and *R. leopardi* (Kojima and Kojima 1994); *Polybioides tabidus* (Richards 1969; Turillazi et al. 1994), etc. In the Polistinae, according to Richards (1978) at least three patterns of caste differentiation are found: 1) Conspicuous size and allometric differences present, with queens larger than workers in the absence of intermediates (*Agelaia* spp: *A. areata*, Jeanne and Fagen 1974; *A. pallipes* and *A. multipicta*, Noll et al. 1997; *A. vicina*, Sakagami et al. 1996; *Protonectarina sylveirae*, Shima et al. 1996b; *Epipona guerini*, Hunt et al. 1996); 2) Conspicuous dimorphism present, with queens smaller than workers in most char-
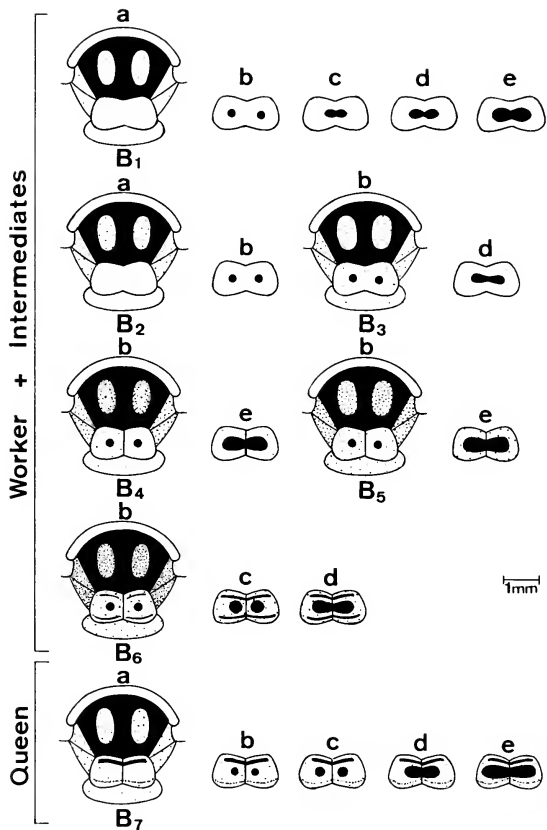
Fig. 6. Color patterns (B_1 to B_7) and mesoscutellar spots (a–e) in queens, workers and intermediates of *Pseudopolybia vespiceps*.
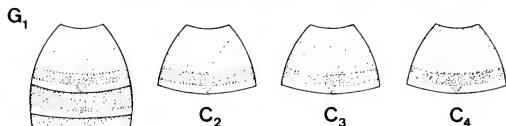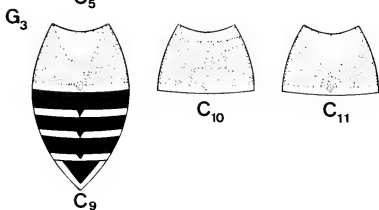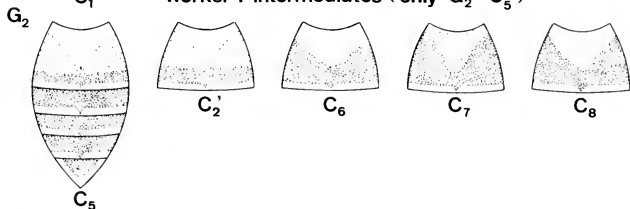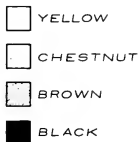
Fig. 7. Color patterns (G₁–G₃) in the gastral parts (C₁–C₁₁) of queens, workers and intermediates of *Pseudopolybia vespiceps*.

acters and intermediates absent (*Apoica flavissima*, Shima et al. 1994; *Polybia dimidiata*, Shima et al. 1996a); 3) Morphological differences slight or indistinct, and intermediates present (*Parachartergus smithii*, Mateus et al. 1997; *Protopolybia exigua*, Noll et al. 1996; and *Pseudopolybia vespiceps*, present work). However, in some groups, queens are significantly smaller than workers in some characters and larger in others (*Apoica pallens*, Jeanne et al. 1995; *Pseudopolybia difficilis*, Jeanne, 1996), and according to Jeanne et al. (1995) this is considered as non-size-based caste dimorphism probably due to a reprogrammation in growth parameters (Wheeler, 1991).

Differently from *Pseudopolybia difficilis*

(Jeanne 1996), *P. vespiceps* presented slight caste dimorphism between queens and workers. Most analyzed characters showed no differences between queens and workers. Such slight distinction is comparable to *Parachartergus smithii* (Mateus et al. 1997) and *Protopolybia exigua* (Noll et al. 1996). Using log-log plots of the most discriminant characters (Fig. 8) and considering three distinct groups (queens, workers and intermediates), queens presented a type of allometric growth (Fig. 8A) comparable to *Epipona guerini* (Hunt et al. 1996) while workers and intermediates presented non-allometric growth. However, disregarding intermediates (as done by Jeanne 1996 in *Ps. difficilis*) and considering only two groups, i.e. individuals with or without ovary development (Fig. 8B), *Pseudopolybia vespiceps* presented only non-allometric growth and such pattern is quite similar to that found in *Ps. difficilis* (Jeanne 1996). Such a fact is very important because origin and role of intermediates relies primarily on their careful detection according to taxa and colony cycle.

In addition to diverse degrees of caste differentiation in this subfamily, the occurrence of intermediates, brought about complexity in the caste problems. Richards (1971) assumed that their role is the production of either trophic eggs or males but, Forsyth (1978), West-Eberhard (1978) and Gastreich et al. (1993) considered them as young uninseminated queens. Richards (1971) and West-Eberhard (1978) considered that, in a general way, intermediates have ovary development related to queen number. That is, in the presence of a few queens they present larger ovaries and vice-versa. Intermediates are present in species with low caste dimorphism (Richards, 1978; Noll et al., 1996; Mateus et al., 1997; present paper). On the other hand, species with pronounced caste dimorphism as *Agelaia vicina* (Sakagami et al. 1996), *A. pallipes* and *A. multipicta* (Noll et al. 1997) and *Apoica flavissima* (Shima et

A

B
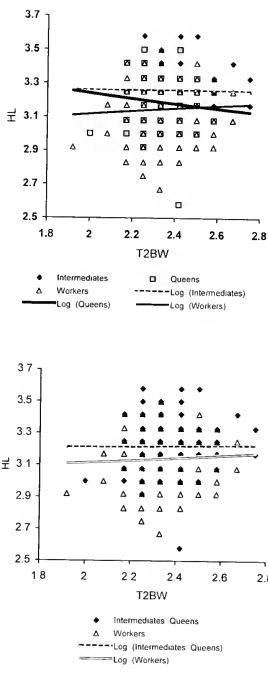
Fig. 8. Discrimination between queens, intermediates and workers of *Pseudopolybia vespiceps* using the log-log plots of basal width of tergite II (T_2BW) and head length (HL). A—Queens, workers and intermediates were separately plotted, B—Queens and intermediates were put together representing ovary-developed individuals and workers undeveloped-ovary individuals.

al. 1994) present sterile workers. However, uninseminated queens were found in *A. vicina* (Sakagami et al. 1996, Baio et al. in press.), *Polybia dimidiata* (Maule-Rodrigues & Santos 1974, Shima et al. 1996) and *Ro-*

& Santos 1974, Shima et al. 1996) and *Ropalidia marginata* (Chandrashekara & Gadagkar 1991), and so their contribution to male production seems likely. In a general sense, intermediate females have been recorded in several other taxa, e.g., *Polybia chrysothorax, P. jurinei, Parachartergus fraternus* and *Angiopolybia* spp. (Richards and Richards 1951); *Brachygastra scutellaris* (Carpenter and Ross 1984), *B. lecheguana* (Machado et al. 1988). But, most of these species must be reanalyzed with a standardized statistical method. Richards (1971, 1978) mentioned that the intermediates characterize taxa in which structural caste differences are absent. This is, however, only partly valid, because *P. dimidiata* (Shima et al. 1996a) albeit characterized by clear cut caste dimorphism with queens smaller than workers, have intermediates also. In addition, Naumann (1970) and Simões (1977) and M. V. Baio (unpubl.) discovered their occurrence in two taxa, *Protopolybia acutiscutis* (cited as *P. pumila*) and *P. exigua*, which bear quite clear intercaste morphological differences. The latter observations are very important because in both cases the eggs laid by the intermediates were invariably eaten by nearby mates, which suggests likely importance in colony socio-economics, and remarkable similarities to the system of worker's trophic eggs widespread in the stingless bees (Zucchi 1993 and ref. therein). By using basic and multivariate statistics, the present study revealed another important facet about intermediates. It is noteworthy that conspicuous morphometric differences between queens and workers were not detected in *Pseudopolybia vespiceps* whereas intermediates tended to be larger (significantly larger in some characters, such as HW and PW) than queens and workers. Such trend was also suggested by distribution of plots on CAN$_1$ and CAN$_2$ axes (Fig. 4) and Mahalanobis distances (1.51 for Q/I vs. 0.99 for Q/W). In contrast, intermediates were more similar to queens in gaster color than to workers (Fig. 5–7), while similar to workers in head color and mesoscutellar spots of the mesoscutellum.

Another interesting fact refers to head form since most intermediates had flattened head or queen-unlike head (Fig. 5), as also suggested by the significant differences in HW. Intermediates were also different in ovaries which were shorter and had eggs smaller than those in queens (Figs. 2, 3). As relative age estimated by wing-wear was apparently not related to ovarian development (Fig. 3), it may suggest that long ovaries did not develop from shorter ones. Indeed, older females (Fig. 3) presented both ovary lengths. So, intermediates are apparently uninseminated specialized females that have invariably shorter but developed ovaries. There is a possibility that their eggs are trophic, and invariably eaten as in the above mentioned *Protopolybia* species. In addition, they generally bear more abundant fat tissue than typical workers, and in some instances they may present as much fat tissue as true queens (Fig. 3, IV).

Colonies with intermediate females show curious combination of differences and similarities among the three types of females. These are probably related to the degree of caste differentiation: (1) species with intermediates more similar to workers usualy have clear-cut caste dimorphism (*Protopolybia exigua*, Simões 1977; *P. pumila* (= *acutiscutis*), Richards 1978; Naumann 1970); *P. sedula, Agelaia lobipleura melanogaster*, Richards 1978 and *Polybia emaciata*, Hebling and Letizio 1973); (2) species with intermediates more similar to queens have castes distinct in some characteristics (*Brachygastra bilineolata, Pseudopolybia compressa* morph *laticincta*, Richards 1978) or present clear-cut size dimorphism (*P. dimidiata*: Shima et al. 1996a) and (3) species with intermediates distinct in some characters can bear slight or no caste differences (*Pseudopolybia vespiceps*, present results, and *Belonogaster junceus*, Richards 1969) in which intermediates dif-

fered significantly from both castes in hamulus number (similar to *P. vespiceps*) and wing length, suggesting that these females are not merely queens or even ovary-developed workers (Richards, 1969).

In the studied case it is possible to consider intermediates by two ways: 1) Intermediates as young or uninseminated queens as pointed out by Forsyth (1978), West-Eberhard (1978) and Gastreich et al. (1993). In this case the pattern (Fig. 8B) is similar to that found in *Ps. difficilis* (Jeanne, 1996). 2) Specialized workers having a combination of queen and worker characters. In this case, intermediates have non-allometric growth but, queens presented allometric growth (Fig. 8A).

The present example shows how the caste system in neotropical swarm-founding polistine is complex and diverse. Moreover, the occurrence of intermediates in several polistine taxa turn the understanding of their social systems fascinating. The results at our hands suggest that the intermediates represent a specialized state. However, in the lack of substantial data a final conclusion has to be postponed.

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Priscomasaris namibiensis Gess, a New Genus and Species of Masarinae (Hymenoptera: Vespidae) from Namibia, Southern Africa, with a Discussion of its Position Within the Subfamily

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Abstract.—A new genus and species of Masarinae (Vespidae), *Priscomasaris namibiensis* Gess, is described from Namibia. Cladistic analysis of the Masarinae shows that *Priscomasaris* belongs within the tribe Masarini, in which it is the most plesiomorphic member, and that it represents a new subtribe, here named Priscomasarina, sister to the subtribes Paragiina and Masarina combined. The justification for Carpenter (1997) for recognising subtribes, that is to have a group name for the Australian masarines, remains untouched. *P. namibiensis* visits flowers of *Gisekia* and *Limeum* (Moluginaceae) and at pools lands on the water surface to drink.

The subject of this paper, an undescribed species of Masarinae, was discovered by the author and S.K.Gess while they were engaged in field studies in Namibia in March and April 1997. This wasp was widespread and abundant together with a species of *Jugurtia* Saussure of similar size and colouring. Its habit of alighting on water immediately attracted attention and distinguished it from the *Jugurtia* which, like all members of that genus, drinks at the water's edge.

Priscomasaris Gess, genus novum

Type species: *Priscomasaris namibiensis* Gess, sp. n.

Recognition.—*Priscomasaris namibiensis*, the only included species, is immediately recognisable by its very short tongue (glossa), the unique development of the scutellar (= axillary) processes, and the very shiny metasomal integument with a unique pattern of large pale spots situated posterolaterally on terga I-IV and posteromedially on terga II-V.

Description.—Head wider than long in frontal view. Clypeal dorsal margin straight, ventral margin broadly truncate. Eye with inner margin sinuous but smooth (like that of *Paragia* Shuckard lacking an interior emargination). Postocular and preoccipital carinae fused. Tempora at midheight slightly narrower than eye in lateral view at same level. Antenna in both sexes with ten flagellomeres and no club. Scape (with radicle) narrow and short, in male 2.3× and in female 3× as long as greatest width. Labrum width about half interantennal distance, ventral margin broadly rounded. Female mandible tridentate, that of male quadridentate. Glossa short, neither the section basal to the bifurcation nor the glossal lobes elongate, section basal to bifurcation slightly shorter than glossal lobe; paraglossa extending slightly beyond bifurcation. Length of extended tongue (measured from anterior edge of labrum to end of glossal lobes) equal to 0.07× body length. Acroglossal buttons present. Prementum whole, hypostomal bridge level, glossal sac absent. In both sexes maxillary palpus six-segmented, labial palpus four-segmented.

Propleuron neither grooved nor depressed, nor medially diverging dorsomedially to form a fossa. Pronotum ventro-laterally with an inconspicuous groove, pretegular area non-carinate. Tegula subtriangular, about as wide as long.

Scutellum triangular, roundly pointed posteriorly; antero-lateral angle conspicuously produced backward into an outwardly convex and apically pointed process, superficially reminiscent of the similar looking process (parategula) arising from the postero-lateral mesoscutal angle of some Eumeninae. Propodeum dorso-laterally produced into short, posteriorly directed spine.

Forewing not longitudinally folded when at rest. Marginal cell truncate basally, slightly wider basally than apically, 2r-rs straight basal to insertion of RS, with proximally tubular but distally merely pigmented appendix. Two submarginal cells present. CuA2 and A meeting at a near right angle, a stub of free apical section of A present. First discal cell longer than subbasal cell. Junction of RS and M slightly thickened. Prestigma short, about one quarter length of pterostigma. Cu-a situated shortly distad of fork of M and CuA.

Hindwing CuA diverging from M+CuA basad of insertion of cu-a; cu-a inserting on CuA and aligned with A; free apical section of A absent. Jugal lobe present but only about one quarter length of subbasal cell. Pre-axillary excision evanescent.

Male front trochanter without process; female front tarsal setae straight; middle coxa narrow; middle tibia with two spurs; hind coxa non-carinate; claws of all legs toothed.

Metasomal tergum I and sternum I separate. Metasomal segments after II non-retractile. Male genitalia with sharply pointed parameral spines, volsella separate from paramere.

Relationships.—The determination of the phylogenetic position of *Priscomasaris* would have been greatly facilitated had it been possible to add its character states to the data matrix used by Carpenter to generate his cladogram of the masarine genera (Carpenter 1993: Fig. 7.4). This was not possible to do as the characters and data

matrix used in generating the cladogram have not been published.

As *Priscomasaris* has many plesiomorphic characters, the present analysis confines comparison to the basal taxa of Carpenter's cladogram. [See also cladogram of Australian Masarinae (Carpenter 1997: Fig. 17).] These taxa are the Gayellini (only characters common to *Gayella* Spinola and *Paramasaris* Cameron are used), *Paragia* Shuckard, the basal member of the Australian Masarini (= subtribe Paragiina (Carpenter 1997)) and *Ceramius* Latreille, the basal representative of the remaining Masarini (*sensu* Carpenter) (= subtribe Masarina, the sister-group of the Paragiina (Carpenter 1997)). The use of *Paragia* and *Ceramius* is adequately justified as these two genera exhibit all the groundplan conditions for each of their respective subtribes for all of the characters considered in the analysis. *Euparagia* Cresson is included as the outgroup.

The characters considered, mostly drawn from Carpenter (1982, 1993 and 1997), some with modification, are:

Forewing

1. Marginal cell: not narrower basally than apically (0); 2r-rs curving basal to insertion of RS so that it is narrower (1).
   The basally sinuously narrowed marginal cell is a synapomorphy of Paragiina (Carpenter 1997).

2. Submarginal cell number: three (0); two (1).
   Two submarginal cells is a synapomorphy of Masarini (Carpenter 1982).

3. CuA2 and A: angled where meeting (0); rounded together (1).
   The apically smoothly rounded subdiscal cell is a synapomorphy of Paragiina (Carpenter 1997).

4. First discal cell: shorter than subbasal cell (0); as long or longer than subbasal cell (1). The short discal cell in Gayellini is considered a reversion from the state

of an elongate discal cell in other Vespidae and is thus an autapomorphy of Gayellini (Carpenter 1989).

Hindwing

5. CuA: diverging from M+CuA slightly distad of the insertion of cu-a or at the insertion of cu-a (0); distal to the insertion of cu-a at a distance much greater than the length of cu-a (1); basad to the insertion of cu-a (2). Nonadditive.

Divergence slightly distad of the insertion of cu-a or at the insertion of cu-a, as in *Euparagia*, is considered to be the plesiomorphic condition for Vespidae; divergence distal to the insertion of cu-a as in Gayellini appears to be a reversion to the plesiomorphic condition for aculeates and is an autapomorphy of Gayellini; and divergence basad to the insertion of cu-a is a synapomorphy of Masarini (Carpenter 1982).

6. Cu-a: transverse (0); inserted on CuA and aligned with A (1).

In the primitive state for aculeates, cu-a is transverse as in *Euparagia* and Gayellini. Derived states are to have cu-a inserted on CuA and either aligned with A (as in Masarini) or strongly angled with A (as for example in Eumeninae) (Carpenter 1982).

7. Free apical section of A: present (0); absent (1).

Loss of the apical section of A is synapomorphic for Masarini (Carpenter 1982).

Head

8. Clypeal dorsal margin: straight (0); bisinuate (1).

The dorsally bisinuate clypeus is an autapomorphy of Gayellini (Carpenter 1982).

9. Ocular emargination: present (0); absent (1).

Though relatively uncommon in aculeates, emarginate eyes are characteristic of Vespidae and absence of emargination within the Masarinae is interpreted as derived (Carpenter 1997). Loss of eye emargination, stated by Carpenter to be a fundamental autapomorphy of *Paragia*, is shared with *Priscomasaris*.

10. Number of male antennal articles: 13 (0); 12 (1).

Primitively, aculeate male antennae are composed of 13 articles. Reduction to 12 articles, as in Masarini, is apomorphic (Carpenter 1982).

Mouthparts

11. Labrum: narrow (0); broad (1).

A narrow labrum represents the ground-plan condition of Vespidae, while a broad labrum, resembling the plesiomorphic aculeate condition, is derived (Carpenter 1982).

12. Female mandibles: quadridentate (0); tridentate (1); bidentate (2). Nonadditive.

13. Distal section of glossal lobes: without processes (0); each with two rows of processes but these not together forming a tube (1); each with two rows of flattened overlapping (imbricate) processes curved such that their tips come together forming a tube (2). Nonadditive.

14. Unbranched basal section of glossa: shorter than paraglossae (0); longer than paraglossae (1).

Elongation of the unbranched basal section of the glossa beyond the level of the tips of the paraglossae is a synapomorphy for Masarina (Carpenter 1997).

Mesosoma

15. Pretegular carina: present (0); absent (1).

Polarity as in Carpenter (1997, character 17).

16. Propodeal spiracle: lateral (0); more or less dorsal (1).

Polarity as in Carpenter (1997, character 24).

Fig. 1. Cladogram showing the position of *Priscomasaris* relative to Gayellini, and to *Paragia* and *Ceramius*, the basal members respectively of Carpenter's subtribes Paragiina and Masarina of the Masarini.

17. Male foretrochanter: without process (0); with process (1).
Polarity as in Carpenter (1997, character 27).

The distribution of the 17 polarized characters is given below:

Euparagia	00010 00000 02000 00	
Gayellini	00001 00100 00001 00	
Priscomasaris	01012 11011 11101 00	
Paragia	11112 11011 11200 11	
Ceramius	01012 11001 11210 01	

A cladistic analysis using Hennig86 computer program (Ferris 1988) produces one cladogram with a length of 22 steps, consistency index of 0.90 and retention index of 0.81 (Fig. 1).

This analysis demonstrates that *Priscomasaris* belongs to the Masarini as it has the characters identified by Carpenter (1982, 1993) as supporting the monophyly of this tribe: forewing with two submarginal cells; hindwing with cu-a inserting on CuA and aligned with A; CuA diverging from M+CuA basad of insertion of cu-a; loss of free abscissa of A; labrum broad; male antennae 12-segmented. It, however, shows that *Priscomasaris* does not belong within either Paragiina, as represented by *Paragia*, or Masarina, as represented by *Ceramius*, being more primitive than either. The glossa is very short and exhibits no elongation of either the glossal lobes or the section basal to their bifurcation. These two means of elongating the tongue have

been shown by Carpenter (1996: 390) to define major lineages, of *Paragia* (and *Metaparagia* Meade-Waldo), and of *Ceramius* (and the remaining Masarini). Whereas the difference between *Priscomasaris* and *Paragia* with regard to glossal length may not be very obvious, differences in the distal section of the glossal lobes are very apparent. In *Priscomasaris* each glossal lobe has two rows of flattened processes forming a sponge-like extension; in *Paragia* and *Ceramius* the flattened processes are overlapping (imbricate) and are curved such that their tips come together to form a tube.

Priscomasaris shares with Carpenter's subtribe Masarina a plesiomorphic forewing venation: a basally truncate marginal cell with 2r-rs straight basal to insertion of RS, and CuA2 and A angled where meeting, clearly distinguishing it from the genera of Carpenter's subtribe Paragiina which show a derived, synapomorphic condition (see Carpenter 1996: 393).

The absence of a pretegular carina, an apomorphy according to Carpenter, distinguishes *Priscomasaris* from both *Paragia* and *Ceramius*.

The unique scutellar (= axillary) processes constitute an autapomorphy of *Priscomasaris*.

Clearly, if subtribes are to be maintained, the discovery of *Priscomasaris* necessitates the recognition of a third subtribe, the sister-group of Paragiina and Masarina combined. This subtribe can appropriately be named Priscomasarina. The justification by Carpenter (1997) for recognising subtribes, that is to have a group name for the Australian masarines, remains untouched.

Etymology.—The name *Priscomasaris* is derived from the Latin adjective *priscus* meaning ancient, antique, belonging to old times, and *Masaris*, the type genus of the subfamily Masarinae. It is intended to indicate its primitive nature.
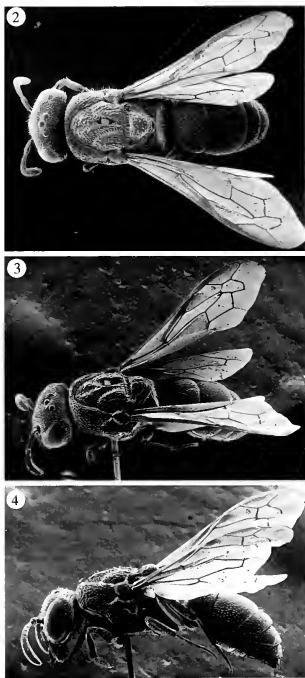
Figs. 2–4.   *Priscomasaris namibiensis*, female habitus. 2, dorsal; 3, dorso-lateral; and 4, lateral views (× 7.5).

Priscomasaris namibiensis
Gess, species nova
(Figs. 2–9)

Female.—(Figs. 2–8). Black. The following are white: rarely small spot on each side of frons near top of inner orbit; rarely small spot dorsally behind eye; usually short transverse marking medially on pronotum; usually small spot on humeral angle; large oval spot on prepectus; rarely

small streak medially on mesoscutum between notauli; usually part or whole of scutellar processes; propodeal spines and area at their base; large suboval posterolateral spots on terga I–IV; postero-medial spot (of varying size and present in only ca. 40% of individuals) on tergum I; large postero-medial spots on terga II–V. The following are reddish: mandible (except extreme base and apical teeth); clypeus along ventral margin; labrum; labial and maxillary palpi; most of pronotum (except for black ventral margin and, if present, white markings); variously developed diffuse markings on mesoscutum—small streak (if not yellow) medially between notauli and two pairs of spots flanking the notauli antero-laterally and postero-laterally; tegula; scutellar processes (if not yellow); scutellar disk; rarely diffuse area next to yellow markings at base of propodeal spines; most of terga I and II (other than white spots); rarely diffuse transverse posterior bands (between white spots) on terga III–V; tergum VI; most of sternum II (other than anterior transverse groove); diffuse transverse posterior bands on sterna III–V; apex of sternum VI; diffuse areas on all coxae and trochanters, distal half to three-quarters of femora, and entire tibiae and tarsi. Wings lightly infuscated, anterior half of marginal cell somewhat darker.

Pilosity pale; moderately dense, fine and semidecumbent on clypeus and lower half of frons; sparse, coarse and erect on upper half of frons, vertex, dorsal surface of pronotum, mesoscutum and scutellum; sparse, fine and erect on metasoma (especially on terga I and II).

Punctures of central part of clypeal disk, most of frons and all of vertex coarse, separated by shiny, unsculptured interstices; widest interstices, subequal to puncture diameter, on upper frons and vertex; punctures at base and sides of clypeus and between and around antennal sockets finer and closer. Punctures on dorsal surface of pronotum, mesoscutum, mesopleuron
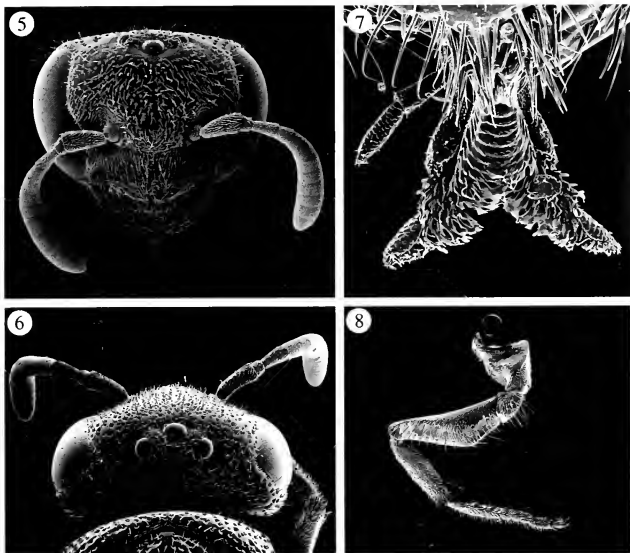
Figs. 5–8. *Priscomasaris namibiensis.* 5, Frontal view of head of female (× 25). 6, Dorsal view of head of female (× 25). 7, Glossa of female (× 150). 8, Front leg of female (× 25).

and scutellum similar to those on vertex or coarser (particularly on mesoscutum), separated by shiny unsculptured interstices subequal to puncture diameter or wider (on mesopleuron). Punctures of metasoma smaller and more widely separated (particularly on tergum II), interspaces unsculptured, strikingly shiny.

Length 7.8–8.2 mm (average of 5: 7.9 mm); length of front wing 5.6–5.9 mm (average of 5: 5.7 mm); hamuli 9–12.

Head (Figs. 5 and 6) noticeably wider (1.25×) than long in frontal view. Eye in frontal view markedly convex; inner margin smoothly sinuous, non-emarginate. Clypeus evenly convex, wider (1.4×) than

long; ventral margin broad, subtruncate, minimally curved; junction of ventral and lateral margins rounded. Antennal sockets separated by 3× their diameter; interocular distance at level of sockets 2.25× length of scape (with radicle); length of scape (with radicle) 3× greatest width, equal to 1.5× of combined length of pedicel and flagellomere I; flagellomeres I–X, respectively, with the following relative lengths (and breadths) [length of flagellomere I = 1.0]: 1.0 (0.50), 0.64 (0.54), 0.50 (0.57), 0.50 (0.71), 0.50 (0.79), 0.50 (0.86), 0.54 (0.86), 0.50 (0.86), 0.54 (0.86), 0.54 (0.86), 0.86 (tapering and end of segment narrowly rounded). POL: OOL = 1:1.1. Vertex be-

hind ocelli shallowly depressed in front of preoccipital carina. Glossa (Fig. 7).

Pronotum with carina running posteriorly from humeral angle and clearly separating dorso-lateral and ventro-lateral faces; with shallow groove ventro-laterally; pretegular area with no carina or groove, lobe slightly depressed. Mesoscutum with median line in anterior half and notauli deeply and widely depressed; notauli subtransversely carinate, especially posteriorly where concurrent; parapsidal lines distinct. Tegula subtriangular, about as wide as long. Mesopleuron anteriorly divided by sinuous carina into anteriorly and laterally facing surfaces; carinae prominent antero-ventrally, joining each other in front of coxae in wide, subtransverse curve; episternal scrobe unusually conspicuous. Scutellum triangular, posteriorly roundly pointed; antero-lateral angle conspicuously backwardly produced into outwardly convex and apically pointed process; pair of processes bracketing the basal three-eighths of the scutellum; basal quarter of scutellum a wide transverse furrow crossed by about twelve longitudinal carinae; posterior three-quarters of scutellum raised, markedly convex. Metanotum fully exposed over entire width, medially subvertical and slightly overhung by scutellum, laterally widened and excavated. Propodeum dorso-laterally produced into short, posteriorly directed spine.

Metasoma slightly constricted between terga I and II, widest across middle of tergum II and progressively narrowing posteriorly to rounded tergum VI. Tergum I 2.4× as wide as long; tergum II 1.6× as long as tergum I and 1.7× as wide as long; tergum I in posterior half with fine, impressed median line; terga I and II with fine but well defined longitudinal line above their lateral margins. Sternum II transversely grooved basally.

Front leg (Fig. 8); hind coxa non-carinate; tibiae of middle and hind legs on the exterior surface with scattered, small red-

1 mm
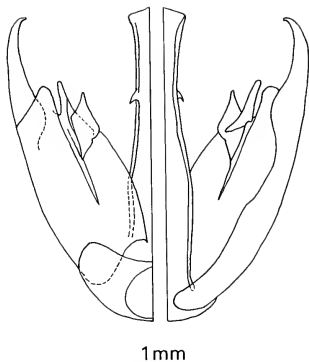
Fig. 9. *Priscomasaris namibiensis*. Male genitalia, ventral view on left, dorsal view on right.

dish peg-like setae (difficult to see amongst the longer pale hairs); middle tibia with two spurs; claws of all legs toothed.

Male.—(Fig. 9). Black. The following are yellowish-white: clypeal disk; large marking on mandible; small spot dorsally behind eye; broad transverse band on anterior aspect of pronotum; large suboval spot on prepectus; small streak medially on mesoscutum between notauli; rarely greater part of tegula; entire scutellar processes; in some individuals posterior half or less of scutellar disk; in some indiduals a small medial spot on metanotum; propodeal spines and area at their base; large suboval postero-lateral spots on terga I-IV and usually also on V and postero-medial spots on tergum I (usually), on terga II-V (always) and on terga VI and VII (usually); generally a complete or partially complete dorsal streak on front tibia and rarely diffuse dorsal markings on middle and hind tibiae. The following are reddish: mandible subapically; narrow streak along ventral margin of clypeus; labial

and maxillary palpi; side of pronotum; tegula; anterior half to entire scutellar disk; usually diffuse area next to yellow markings at base of propodeal spines; most of terga I and II (other than for yellowish-white spots); usually diffuse transverse posterior bands (between yellowish-white spots) on terga III or IV-VI; most if not all of tergum VII; most of sternum II (other than for anterior transverse groove); diffuse posterior bands on sterna III-VII; entire sternum VIII; legs as in female.

Length 6.9–7.8 mm (average of 5: 7.3 mm); length of front wing 5.3–5.9 mm (average of 5: 5.6 mm); hamuli 10–11.

In general facies similar to the female, the chief differences being as follow. Head width relative to head length even greater (1.33×). Mandible quadridentate. Antennal sockets separated by 1.9× their diameter; interocular distance at level of sockets 1.85× length of scape (with radicle). Antenna longer; scape (with radicle) 2.3× as long as greatest width and 1.4× as long as combined length of pedicel and flagellomere I; flagellomeres I–X, respectively, with the following relative lengths (and breadths) [length of flagellomere I = 1.0]: 1.0 (0.5), 0.69 (0.59), 0.66 (0.66), 0.63 (0.75), 0.63 (0.81), 0.56 (0.81), 0.56 (0.81), 0.56 (0.81), 0.56 (0.78), 0.86 (tapering and end of segment narrowly rounded). Tergum VII subtruncate with hind margin rounded laterally. Apical sternum with hind margin truncate, deeply, narrowly emarginate medially.

Front trochanter and metasomal sterna without any processes.

Genitalia (Fig. 9).

Material examined.—Holotype: female, Namibia: between Palm and Khorixas (20.17S 14.05E), 31.iii.1997 (F. W. and S. K. Gess) (on pink flowers of *Gisekia africana* (Lour.) Kuntze, Moluginaceae) [Albany Museum, Grahamstown]. Paratypes (216 females, 7 males): Namibia: between Palm and Khorixas (20.17S 14.05E), 31.iii.1997 (F. W. and S. K. Gess), 3 females, 5 males

(2 males on pink flowers of *Gisekia africana* (Lour.) Kuntze, Moluginaceae, 3 females and 3 males on white flowers of *Limeum argute-carinatum* Wawra & Peyr., Moluginaceae); 15.5 km W Khorixas (20.26S 14.54E), 1.iv.1997 (F. W. and S. K. Gess), 8 females (on water); between Khorixas and Uis (20.31S 14.56E), 1.iv.1997 (F. W. and S. K. Gess), 2 males (on small white flowers of *Limeum myosotis* H. Walter, Moluginaceae); 43 km S Mariental (24.58S 17.55E), 4.iv.1997 (F. W. and S. K. Gess), 154 females (on water and flying about above water of pool); 97 km S Mariental (25.24S 17.54E), 4.iv.1997 (F. W. and S. K. Gess), 47 females (on water and flying about above water of pool); 161 km S Mariental, Tses (25.53S 18.07E), 4.iv.1997 (F. W. and S. K. Gess), 3 females (on water); same locality, 17.iv.1998 (F. W. and S. K. Gess), 1 female (on water) [Albany Museum, Grahamstown; Namibian National Insect Collection, Windhoek; South African Museum, Cape Town; American Museum of Natural History, New York; California Academy of Sciences, San Francisco; and Natural History Museum, London].

Distribution.—The species appears to be widely distributed in Namibia, the present records covering six degrees of latitude (20–26S).

Behaviour.—Females visit pools of water in drainage channels and river beds in order to obtain water, presumably for use in nest construction. When filling their crops they alight on the water surface in the manner of some species of *Ceramius, Paragia, Metaparagia confluens* (Snelling), and *M. nocatunga* (Richards) (see Gess 1996: 67–76). When observed at pools, this behaviour, together with the habit of holding the wings erect whilst imbibing water, immediately distinguishes *P. namibiensis* from similarly sized and coloured species of *Jugurtia* Saussure, which alight on the saturated soil at the water's edge and lower their wings. Where common, females "swarm" in the air above water.

Both sexes forage on the small shallow

flowers of species of *Gisekia* and *Limeum* (Moluginaceae), for which their short tongues are adequate.

Nesting has not been observed.

Etymology.—The name *namibiensis*, an adjective, is derived from Namibia and refers to the provenance of the species.

ACKNOWLEDGMENTS

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EDITOR'S NOTE

Submission of Manuscripts

With this issue, we return to the former procedure of submitting manuscripts directly to the Editor. There has been a slight change in my address, so please use the following:

Dr. E. Eric Grissell
Systematic Entomology Laboratory, USDA
% National Museum of Natural History
Washington, DC 20560-0168

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General Policy. The *Journal of Hymenoptera Research* invites papers of high scientific quality reporting comprehensive research on all aspects of Hymenoptera, including biology, behavior, ecology, systematics, taxonomy, genetics, and morphology. Taxonomic papers describing single species are unlikely to be accepted unless a strong case is evident, such as importance in economic entomology or with concurrent biology or ecology. Manuscript length generally should not exceed 50 typed pages; however, no upper limit on length has been set for papers of exceptional quality and importance, including taxonomic monographs at generic or higher level.

All papers will be reviewed by at least two referees. The referees will be chosen by the appropriate subject editor. However, it would be helpful if authors would submit the names of two persons who are competent to review the manuscript.

The language of publication is English. Summaries in other languages are acceptable.

The deadline for receipt of manuscripts is 1 October (for the April issue) and 1 April (for the October issue).

Format and Preparation. Three copies of each manuscript, including copies of illustrations, should be submitted on letter size or A4 paper, double spaced, with at least 25 mm margins on all sides. On the upper left of the title page give name, address and telephone and fax numbers of the author to whom all correspondence is to be sent.

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References in the text should be (Smith 1999), without a comma, or Smith (1999). Two articles by a single author should be (Smith 1999a, 1999b) or Smith (1999a, 1999b). For multiple authors, use the word "and," not the symbol "&" (Smith and Jones 1999). For papers in press, use "in press," not the expected publication date. The Literature Cited section should include all papers referred to in the paper. Journal names should be spelled out completely and in italics.

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INTERNATIONAL SOCIETY OF HYMENOPTERISTS

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**Please see inside back cover of this issue for information regarding
preparation of manuscripts.**

This issue was mailed 3 May 1999

A Key to World Species of Scolebythidae (Hymenoptera: Chrysidoidea), with Description of a New Species of *Dominibythus* from Brazil

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Abstract.—**Dominibythus strictus** sp. n. from Brazil, the first extant species of the genus, is described and illustrated. Additional specimens of the rarely collected *Clystopsenella longiventris* Kieffer 1911 are examined and the species variation analyzed. A world key to the fossil and extant species of Scolebythidae is given.

Scolebythidae is a family of Aculeata with five monotypic genera. Evans (1963) proposed this family based on *Clystopsenella* Kieffer 1911, from Brazil, a genus transferred from the Bethylidae, and on *Scolebythus* Evans 1963, from Madagascar. Nagy (1975) added the third genus, *Ycaploca*, from South Africa and Australia describing the first male of Scolebythidae. Day (1977) described and illustrated the male genitalia of *Clystopsenella*. Evans et al. (1979) reanalyzed *Scolebythus* with description of the male and sting apparatus.

All extant species are exclusive austral, but Prentice et al. (1996) described two fossil genera, *Libanobythus* and *Dominibythus*, from Lebanese and Dominican amber.

Biological data on the species suggest that the species of Scolebythidae are possibly gregarious ectoparasitoids of wood-boring beetle larvae (Evans 1963, Nagy 1975, Day 1977, Evans et al. 1979), but Gauld (1995) pointed out that all published information is questionable.

In this paper, *Dominibythus strictus* sp. n. from Brazil is described and illustrated,

and new taxonomic data are provided for *Clystopsenella longiventris* Kieffer 1911. A world key to the fossil and extant species of this family is given.

The examined material used in the present paper was provided by Canadian National Collection of Insects, Canada (CNCI, J. T. Huber); Universidade Federal do Paraná, Brazil (DZPR, K. Zanol); and Instituto Brasileiro de Geografia e Estatística, Brasília, Brazil (IBGE, B. Dias).

Abbreviations for the main measurements used in this study are as follow: LH, length of head; WH, width of head; WF, width of frons; HE, height of eye; OOL, ocello-ocular line; WOT, width of the ocellar triangle, including the ocelli; DAO, diameter of anterior ocellus; VOL, vertex-ocular line; LFW, length of forewing.

The nomenclature of the integument follows Eady (1968) for the term coriaceous and Harris (1979) for the other textures. Terminology generally follows Evans (1963), and the terminology of wing cells and veins follows Gauld and Bolton (1988).

KEY TO FOSSIL AND EXTANT SPECIES OF WORLD SCOLEBYTHIDAE

1. Mesoscutum with notaulus absent or at least incomplete; prosternum large, its width at least 2.5 × length of propleuron; forewing with three closed cells, Rs vein shorter than stigma (***Dominibythus***) 2

– Mesoscutum with complete notaulus; prosternum smaller than above, its width at most 2
  × length of propleuron; forewing with five or six closed cells, Rs vein much longer than
  stigma 3

2. Frons with an arched prominence; eye forming the widest part of head; notaulus present
   anteriorly; occipital carina present dorsally; width of prosternum 2.5 × length of proplue-
   ron; Cu vein nebulous . . . . **Dominibythus inopinatus** Prentice and Poinar

– Frons without prominence; gena forming the widest part of head; notaulus absent; occipital
  carina absent dorsally; width of prosternum 2.8 × length of propleuron; Cu vein as a short
  stub . . . . **Dominibythus strictus** Azevedo, **new species**

3. Pronotal disc enlarged, 1.57 × longer than mesoscutum; parapsidal furrows absent; fore-
   wing without metacarpus, with five closed cells, marginal cell opened; tibial spur formula
   1,1,1 . . . . **Lybanobythus milkii** Prentice & Poinar

– Pronotal disc shorter than mesoscutum, about 0.6–0.7 × longer than mesoscutum; parap-
  sidal furrows present; forewing with metacarpus, with six closed cells, marginal cell closed;
  tibial spur formula 1,2,2 4

4. Frons with a median prominence between antennal sockets; malar space virtually nonex-
   istent; forewing with submarginal cell longer than marginal, extending beyond the basal
   half of marginal cell . . . . **Ycaploca evansi** Nagy

– Frons without median prominence between antennal sockets; malar space short; forewing
  with submarginal cell slightly shorter than marginal, not extending beyond the basal half
  of marginal cell 5

5. Occipital carina absent; malar space well over half as long as basal width of mandible;
   apex of marginal cell arched away from anterior margin of forewing; posterior area of
   metasomal sternite V with two groups of appressed and dense setae . . . .
   . . . . **Clystopsenella longiventris** Kieffer

– Occipital carina present; malar space short, less than half as long as basal width of man-
  dible; apex of marginal cell on anterior margin of forewing; posterior area of metasomal
  sternite V without special groups of setae . . . . **Scolebythus madecassus** Evans

## Dominibythus strictus Azevedo, new species
(Figs. 1–7)

Description of female holotype: length of body 3.93 mm; LFW 2.25 mm.

Color: body castaneous, head and mesosoma slightly darker; vertex with two lighter streaks starting on the crest and extending between the ocellar triangle and eye; malar space, antenna, midtibia and tarsi slightly lighter than head; wings hyaline, veins castaneous.

Pubescence: very sparse and long overall; setae short and dense on antenna, some erect; setae noticeably longer on hindtibia; nearly absent at dorsum of gastral tergites, and concentrated at posterior half in gastral sternites.

Head (Figs. 1–2): mandible wholly directed downward slightly, with two sharp apical teeth (Fig. 3), and with a shallow suture below upper tooth. Clypeus extremely short, median lobe angulate, without median carina. Antenna short, nearly reaching the pronotum; first four antennal segments in a ratio of about 7:4:1:2, flagellomere IX 1.2 × as long as thick, sensillae circular. Head slightly narrower below. Antennal sockets separated by less than their own diameters. Frons weakly coriaceous, with a very small number of small and shallow punctures; frontal carina low and short. Malar space broad, 1.0 × the basal width of mandible. LH 1.27 × WH; WF 0.5 × WH; WF 0.85 × HE; ocellar triangle very compact, OOL 1.45 × WOT and situated on an imaginary line between eye tops, its frontal angle obtuse; posterior ocelli distant from vertex crest by 2.94 × DAO. Eye subtriangular, with rounded corners; gena forming widest part of head.
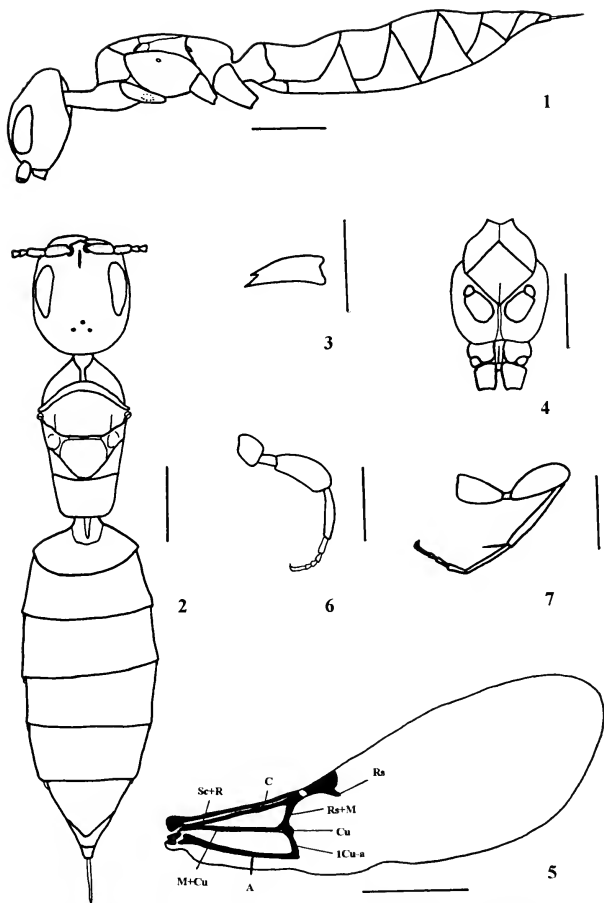
Figs. 1–7. *Dominibythus strictus.* 1. Body, lateral. 2. Body, dorsal. 3. Mandible, frontal. 4. Mesosoma, ventral. 5. Forewing. 6. Foreleg, lateral. 7. Hindleg, lateral. Scale bars = 0.5 mm.

Vertex rounded, VOL 0.73 × HE; sides of head straight and subparallel and slightly convergent below. Occipital carina weak, present only ventrally. Palpal formula 6:4, segment I–III of labial palpi and segments I–IV of maxillary palpi flattened.

Mesosoma (Figs. 1–2, 4): thorax weakly coriaceous. Pronotal disc very short, 0.4 × length of mesoscutum; anterior margin of pronotum evenly convex in dorsal view. Mesoscutum without notauli; parapsidal furrows well-impressed, absent on the anterior half of mesoscutum, paralleled by an outer carina. Scutellum long, only slightly shorter than mesoscutum, prescutellar sulcus narrow posterad laterally, crossing entire anterior margin. Metanotum very narrow medially. Propodeal disc 0.56 × as long as wide; anterior margin of propodeum with a transverse carina, posterior half of median propodeal line with a shallow groove; spiracle laterad, declivity without carinae. Propleuron very large, produced strongly forward. Prosternum very long, its width 2.8 × the length of propleuron, and 3 × longer than forefemur. Mesopleuron with a scrobal pit above midheight. Mesosterna separated by a wide longitudinal groove. Metasternum narrow, separating the base of midcoxa. Legs without spines. Forewing (Fig. 5) with only costal, basal and first discal cells, stigma wide, 0.63 × as long as wide; Rs vein very short, 0.37 × the length of stigma; 1cu-a vein nearly vertical; Rs+M vein reaching Sc+R vein far from stigma; Cu vein as a very short stub. Hindwing with anal lobe distinct. Forefemur 3 × as long as thick (Fig. 6). Hindtibia longer than hindfemur. Hindcoxae closely set. Basitarsus of hindleg very long, longer than half length of hindtibia and longer than remaining tarsomeres together (Fig. 7). Tibial spur formula 1:1:1. Claws simple and arched, dilated basally.

Metasoma (Figs. 1–2): coriaceous, wider than both mesosoma and head. Tergite VII with anterior margin deeply concavous. Gonostylus 0.28 × the length of sting.

Sting and lancets without teeth; bulbous little dilated; sting 0.63 mm long.

Material examined: 1 female holotype BRAZIL, Distrito Federal, Brasília, Roncador Ecological Station, shrub savanna; 12.ix.1979–21.x.1982; window trap; J. Dalmáceo col. (IBGE). Paratypes, 17 females BRAZIL, 16 females Distrito Federal, same data as holotype except places savanna grassland, shrub savanna, and swamp, and data 12.ix.1979–21.x.1982 (IBGE); 1 female Rio de Janeiro, Rio de Janeiro, Corcovado; i.1960; Seabra & Alvarenga col. (DZPR).

Variation: body wholly dark castaneous, clypeus distinctly lighter than head; specimen from Rio de Janeiro with clypeus projecting with a distinctly wider median lobe; WH 1.17–1.20 × LH; WF 0.45–0.55 × WH; WF 0.85–0.96 × HE; OOL 1.2–1.44 × WOT; posterior ocelli distant from the vertex crest 2.78–3.52 × DAO; VOL 0.68–0.8 × HE; parapsidal furrows not paralleled by outer carina.

Remarks: *Dominibythus* was first described from a fossil of Late Eocene to Late Oligocene Dominican amber (Prentice et al. 1990). *Dominibythus strictus* sp. n. is the first living species of the genus. It may be identified as *Dominibythus* by the 3 closed cells of the forewing. *Dominibythus strictus* differs from *D. inopinatus* by the absence of a frontal prominence, absence of occipital carina dorsally and notauli, and presence of a tubular apical abscissa of the Cu vein, although extremely short, as a stub, while Cu vein in *D. inopinatus* is entire nebulous. The color pattern of the malar space and the lighter streaks on the vertex of *D. strictus* resembles that of *Clystopsenella longiventris*.

Etymology: The name refers to the short Rs vein of the forewing.

Clystopsenella longiventris Kieffer

This species is first recorded for Bahia and Minas Gerais. The specimens are about 8 mm long and the light color streaks on the vertex are very weak or nearly absent;

mandible and malar space distinctly lighter than head, legs lighter than mesosoma; WH 1.06–1.10 × LH; WF 0.61–0.65 × WH; WF 1.10–1.29 × HE; OOL 0.85–0.86 × WOT; posterior ocelli distant from the vertex crest 4.0–5.4 × DAO; VOL 0.54–0.61 × HE; pronotal disc about 0.51 × the mesoscutum length; notauli and parapsidal furrows complete or nearly so; propodeal disc about 0.5 × as long as wide.

New material examined: 8 females BRAZIL, 1 female, Bahia, Encruzilhada; xi.1974; M. Alvarenga col. (CNCI); 4 females Minas Gerais, Pedra Azul; xi.1974; M. Alvarenga col. (CNCI); 2 females Distrito Federal, Brasília, Roncador Ecological Station, shrub savanna; 23.i.1982 and 7.iv.1983; window trap; J. Dalmáceo col. (IBGE); 1 female São Paulo, Mogi-guaçu, Campiminas Farm; 3.i.1970; J. M. & G. R. Campbell col. (CNCI).

Distribution: Brazil (Bahia, Minas Gerais, Distrito Federal, São Paulo, Mato Grosso de Sul, Santa Catarina). Gauld (1995) commented that there are a few undescribed species of *Clystopsenella* in museum collections from Neotropics and Australia, and one or, possibly two species in Costa Rica.

ACKNOWLEDGMENTS

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Functional Morphology of the Hind Tibial Spurs of the Cicada Killer (*Sphecius speciosus* Drury) (Hymenoptera: Sphecidae)

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Abstract.—The functional morphology of the hind tibial spurs in female cicada killers is examined in relation to digging. The spurs are controlled by a passive mechanical system using the corium; when the tarsus is flexed, the spurs are extended. The spurs resist extension, but not flexion. Videography demonstrated that the hind legs are used in burrow excavation to clear soil from the path of the wasp and that the position of the legs makes use of the spurs' resistance to extension. Spur function is not consistent with use during prey carriage, which should cause the spurs to lie flat. Enlarged spurs may have evolved from smaller structures used in grooming, and may reduce the energetic and temporal costs of burrowing.

The bodies of winged insects function in both aerial and terrestrial locomotion, which may present conflicting selection pressures on morphology. For example, flight performance may be improved by increasing the ratio of flight muscle mass to body mass (Marden 1987) at the expense of legs or associated muscles, but terrestrial locomotion would be adversely affected. Many insects also dig or burrow, which increases selection pressure for enhancement of the structures associated with the terrestrial mode. Although fossorial adaptation is relatively well understood in vertebrates (Hildebrand 1985), little of the function of specific adaptations of insects to fossorial life has been demonstrated. The Hymenoptera are generally excellent flyers, but many also dig burrows for nests. Therefore, they can be used to show how animals well adapted to flight handle the requirements of burrowing.

Various morphological modifications for fossorial life, such as foretarsal rakes,

have been described in wasps (Bohart and Menke 1976), but their function has not been ascertained. An exception is provided by Gorb (1996), who examined pretarsal anatomy and function in a variety of insects. Fossorial species, such as the sphecid *Bembix rostrata* L., have a large unguitractor with well-developed microtrichia for the production of strong frictional forces with the substrate.

Cicada killers (*Sphecius speciosus* Drury) are the largest (by mass) North American sphecid (Horn 1976), and they are superb flyers. Relative to other Hymenoptera, they have a high ratio of flight muscle to body mass, resulting in a high degree of maneuverability. Females weigh nearly one gram in body mass, which allows them to carry cicadas (*Tibicen* spp.) heavier than themselves (Coelho 1997). Metabolic rate during hovering is high (Joos and Casey 1992), and body temperature during flight is elevated and nearly constant (J.R. Coelho, pers. obs.).

Female cicada killers also dig extensive burrows. A cicada killer may move up to 1000 times her body mass in dry soil while excavating her burrow (J.R. Coelho and

[1] To whom all correspondence should be addressed.

A.J. Ross, pers. obs.). The opening of the burrow is elevated in comparison to the rest of the burrow, and a large tumulus accumulates outside the entrance. The entrance tends to run at a 35–45° angle downward and then becomes more level (Evans 1966). The burrow branches into an average of 15.8 cells (Dambach and Good 1943), which are used to store paralyzed cicadas. The female lays one egg per cell. On average, cells may vary in diameter from 2 to 3 cm. Burrows vary in length from 30 cm to over 100 cm (Evans 1966). After provisioning the cell, the female cicada killer places a wall of dirt across the entrance. A variety of burrow architectures, as determined by excavation, are depicted by Riley (1892) and Evans (1966). After the main burrow is dug, the dirt from new cells is apparently used to plug old ones, although soil may be added to the tumulus as new cells are excavated.

The digging method uses a variety of body parts and behaviors. The cicada killer uses her mouthparts to loosen compact soil to begin excavating. She uses her fore legs to rapidly rake the dirt under and behind her body. Finally, she uses her hind legs to push the soil behind her as she backs out of the burrow (Frost 1942; Dambach and Good 1943; Evans and West Eberhard 1970). The latter behavior results in the formation of a prominent trough through the tumulus leading away from the burrow entrance (Dambach and Good 1943; Evans 1966).

Cicada killer females have a pair of enlarged spurs on the distal end of the hind tibia (see Evans [1966] for line drawings). Males have similar spurs which, by comparison, are much reduced (Dambach and Good 1943). While the presence of such spurs in bees and wasps has been a useful taxonomic tool (Eickwort and Fischer 1963), their functional significance has rarely been addressed (except by Cane [1979]). Some suggest that the spurs of female *S. speciosus* are used to support the cicada during prey carriage (Howes 1919;

Evans 1962), but our preliminary observations suggest that they are used to move soil during burrow excavation.

Hildebrand (1985) lists five requirements of a fossorial animal to loosen and move resistant material: a digging tool, the capacity to produce and transmit large forces, a transport mechanism for soil, passive resistance to various loads, and the ability to sustain activity. The cicada killer hind leg functions as part of the transport mechanism for soil, and we hypothesize that the spurs are morphological adaptations for that mechanism.

In this study we investigate the functional morphology of the hind tibial spurs in female cicada killers. Their mechanism of action is demonstrated, and their potential function relative to digging and prey carriage is examined.

MATERIALS AND METHODS

Origin of specimens.—Live cicada killers were obtained from local nesting aggregations in McDonough County, Illinois; and the legs of freshly killed individuals were used in all experiments. Unless otherwise mentioned, all data are reported as mean ± SEM (N).

Dissection.—We first investigated the mechanism for movement of the spurs. Under a dissecting microscope, a section of the exoskeleton was removed from the tibia near the tibiotarsal joint. Muscle tissue was examined for any connection to the spurs or to the corium, the unsclerotized conjunctival membrane which forms the distal end of the tibia and from which the spurs arise.

Mechanical linkage.—Five hind legs were obtained. When the tarsus of each was manually flexed, the spurs extended. Similarly, when the tarsus was extended, the spurs became flexed. The corium was severed by making an incision perpendicular to a line between the spurs and tarsus using a 30-ga syringe needle. The tarsus was flexed and extended again and the results were recorded.
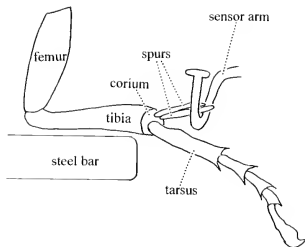
Fig. 1. Apparatus used to measure the force produced by the spurs. The spurs were extended by lowering the steel bar, to which the tibia was glued. The stationary force transducer measured the force exerted by the spurs during extension. To measure the force exerted during flexion, a similar set-up (not shown) was used, except that the sensor arm was placed above the spurs, and the steel bar was raised.

Having found that tarsal flexion causes spur extension, we measured the force generated by the spurs when they were extended in this manner. The tibia of an intact hind leg was glued to a steel bar. The tarsus was manually extended at different angles to the tibia, causing the spurs to extend. The spurs were oriented just below and perpendicular to the sensor arm of an optical force transducer (Narcosystems type A), which was calibrated with weights of known mass and connected to a physiograph (Narcosystems MK-III). The force exerted by the spurs was measured at tibia-to-tarsus angles of 180, 135, and 90° and recorded by the physiograph.

Force-displacement curves.—To determine the direction in which the spurs were capable of resisting force, the hind leg of a female wasp was removed and the tibia was glued to a steel bar with the spurs facing upward. To measure the effect of extension, spurs were placed on top of and perpendicular to the sensor arm of a force transducer connected to a physiograph (Fig. 1). An adjustable ringstand was calibrated so that fractions of a rotation of the knurled adjustment ring could be used to move the bar known vertical distances. The angle between the spurs and the tibia was gradually increased by moving the bar downward in 0.07-mm increments. Measurements were taken until the ends of the spurs slipped off the force transducer. At this point the force was maximal, but the spurs had not yet broken. In this way, the resistant force exerted by the spurs when they were extended to various degrees was recorded by the physiograph.

To measure the effects of flexion, the spurs were extended fully, then placed just below and perpendicular to the axis of the force transducer. The bar was moved upward in 0.07-mm increments until the spurs laid flat against the tarsus. Hence, the force exerted by the spurs in resistance to varying degrees of flexion was recorded by the physiograph.

Videography.—Cicada killers were recorded with a Sony VHS-C videotape recorder while digging. Burrow entrances were plugged with a small amount of soil to induce digging in most cases, but spontaneous digging was also recorded. The tapes were replayed using slow motion to examine and describe aspects of digging behavior in detail.

RESULTS

Dissections.—Of the 10 hind legs dissected, no muscle or tendon attachment to the spurs or corium was found. The tarsus was traversed by a single tendon arising from the pretarsal muscles in the femur and tibia, an arrangement essentially identical to that described for honey bees (Snodgrass, 1956).

Mechanical linkage.—When the tarsus was manipulated and the corium was intact, tarsal flexion caused spur extension, and tarsal extension caused spur flexion in every case. The spurs always moved in one plane and resisted lateral movements. After the corium was severed, the spurs
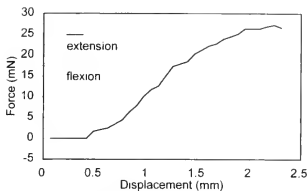
Fig. 2. Representative force-displacement curves for extension and flexion of the female cicada killer hind-tibial spurs.

no longer moved when the tarsus was manipulated.

When the tarsus was held at increasing angles relative to the tibia, the force produced by the extension of the spurs increased. When the tarsus was held at 180° to the tibia, no measurable force was detected. When the tarsus was held at 135°, an average force of 0.315 ± 0.041(7) mN was detected. Finally, when the angle was decreased to 90°, an average force of 0.615 ± 0.055(7) mN was produced.

Force-displacement curves.—Fig. 2 demonstrates that as the spurs are displaced, the force resisting extension increases linearly at first, then levels off near the maximum, while the force resisting flexion remains constant at zero until the spurs lie flat and touch the tarsus. Extension produced a maximum force of 21.68 ± 2.13(8) mN, which is eight times greater than the maximum force resulting from flexion, 2.64 ± 1.04(8) mN.

Video records.—Review of videotaped digging behavior in slow motion demonstrated how the female cicada killer uses the hind legs to move soil. A wasp broke off bits of soil from the burrow wall using the mandibles and threw them posteriorly under the body using rapid motions of the fore legs. She then backed out of the burrow, alternately thrusting her hind legs in arcs that began in a posterior direction and ended in a lateral direction, removing dirt from her path. Both front and rear

pairs of legs operated simultaneously, with fore leg raking being repeated during the recovery stroke of each hind leg. The tibiotarsal angle was near 90° at the beginning of the thrusting motion when the leg was cocked, then the angle increased as the leg was extended.

DISCUSSION

In dissections of the cicada killer hind tibia, no muscles or tendons were found leading to the spurs or corium. The spurs were extended with increasing force as the tarsus was flexed at increasing angles, suggesting that the spurs are not under direct muscular control, but that their degree of extension depends instead upon the angle of the tibiotarsal joint. When the corium was severed, the spurs no longer moved when the tarsus was manipulated. The corium, a flexible, unsclerotized conjunctival membrane, connects the tarsus and spurs. When the tarsus is flexed, it pulls on the lateral margin of the corium, which, in turn, pulls on the medial bases of the spurs, causing them to extend. When the corium is severed, this mechanical linkage is broken. Hence, the spurs are controlled by a passive mechanical system using the corium, as suggested by Cane (1979).

The spur extension system generates a very small force, less than 1 mN, which is sufficient to extend the spurs, but likely to be of little use otherwise. Hence, resistant forces determine what tasks can be accomplished by the spurs. The spurs produced a substantial resistant force to being extended outward, but not to being flexed inward (whereupon they simply fold flat against the tarsus). Only behaviors which flex the tibiotarsal joint, using the spurs' resistance to extension, are likely to effectively use the action of the spurs.

Hymenopteran hind tibial spurs are commonly used in grooming the contra-lateral hind leg (Farish 1972, Cane 1979), and we observed this behavior in captive cicada killers. The tibiotarsal joint is flexed

and brought under the body to the contra-lateral leg, where vertical motions up and down the second leg, held between the two spurs, occur (J.R. Coelho, pers. obs.). Known as L_3-L_3 grooming, this behavior occurs in all 15 superfamilies of bees and wasps tested by Farish (1972). Our data suggest that the downstroke is the most useful in L_3-L_3 grooming, as it is the power stroke, where the spurs' resistance to extension would be used. The upstroke is simply a return stroke. Although the spurs may be used to groom the ipsilateral wing (Farish 1972), we did not observe this behavior in cicada killers.

The utility of hind tibial spurs for L_3-L_3 grooming suggests that the spurs evolved from smaller setae, but it does not adequately explain their exaggerated size in female *Sphecius*. It seems unlikely that the grooming requirements of the female cicada killer would be so much greater than that of a male, or of other Hymenoptera, that such elaborate structures would evolve.

Howes (1919) suggests that the spurs of female *S. speciosus* are used to support the cicada during flight as "she squeezes [the spurs] against the cicada's sides and thus secures her burden during the overland journey to the burrow." When the spurs were removed from one wasp, the next cicada was carried in a more vertical position (Howes 1919). While Howes' (1919) single anecdotal observation weakly supports his suggestion that the spurs have a role in prey carriage, we do not believe the spurs can function in the manner suggested. The hind legs wrap around the cicada at high tibiotarsal angles (J.R. Coelho pers. obs.); therefore, the spurs would not be extended. If squeezed against the sides of the cicada, the spurs will lie flat against the tarsus, as they have almost no capacity to resist flexion.

In reviewing videotaped bouts of digging, we noted that although cicada killers are capable of buzzing to produce a powerful vibration (Coelho 1998), and many Hymenoptera use vibration to loosen soil (Spangler 1973), cicada killers did not buzz while digging. The compact soil was chewed from the walls of the burrow using the mandibles, and the fore legs were used in rapid motions to rake the loose particles below and behind the wasp. Hence, cicada killers are "rakers" in that they use the fore legs as rakes to move soil (Evans and West Eberhard 1970). Spines on the tarsus of the fore leg of *S. speciosus* form a pecten (rake), which is believed to augment the efficiency of raking (Evans 1966, Evans and West Eberhard 1970). Although raking moves the soil beyond the posterior margin of the animal, it does not necessarily clear it from the burrow or its entrance. As a unique type of "pusher," the female cicada killer uses the hind legs, as opposed to the abdomen, to move soil out of the burrow and beyond (Evans and West Eberhard 1970). She backs out of the burrow, thrusting each hind leg first posteriorly then laterally, removing soil from her path. The tibiotarsal angle appears to be low (near 90°) at the beginning of the motion when the leg is cocked, which extended the spurs. The path of the hind leg during the power stroke caused the spurs to be pushed against the soil in the direction of extension.

Hence, the high resistive force of the spurs is used to move additional dirt, thus increasing the efficacy of digging. Since little force is required for flexion, the spurs would not hinder the recovery stroke to complete the motion. This effect is similar to that of the "oars" of aquatic insects as they swim through the water (Gullan and Cranston 1994). When the spurs are fully extended, the effective surface area of the hind leg is substantially increased. Numerous setae on the tibia and tarsus probably also contribute to the effective surface area, which presumably allows the female to move more soil per stroke than she could otherwise, increasing the energetic efficiency of digging.

The resulting energy savings could be

used to dig more extensive burrows, to forage for additional cicadas, or for other fitness-enhancing activities. However, perhaps time is more limiting than energy. With an average lifespan of 13 days (Hastings 1989), they have little time to waste on burrow construction. Observations suggest that they carry out much of their digging at night (Dambach and Good 1943), which would avoid temporal conflicts with their strictly diurnal foraging bouts. Preliminary data from our laboratory (J.R. Coelho and A.J. Ross, pers. obs.) suggest that digging rates of cicada killers are consistent with completing a burrow in one night, as suggested by Dambach and Good (1943).

Hymenoptera tend to have long, thin, and even delicate legs, while a transport mechanism for soil should be large, broad, firm, and thick (Hildebrand 1985) as it is in mole crickets (*Gryllotalpa*), cicada nymphs (*Magicicada*) and certain scarab beetles (*Canthon*) (Gullan and Cranston, 1994). Evans (1966) states that the cicada killers' use of hind legs to move soil is "unusual among digger wasps," and Pate (1936) mentions the spurs as taxonomically important structural features of the genus *Sphecius*. The large hind tibial spurs of cicada killers appear to have been enhanced to function in digging while retaining their original function of grooming. Enlarged spurs appear to be an imperfect solution to the problem of fossorial adaptation in comparison to the highly derived morphology of fully fossorial insects. Nonetheless, cicada killers clearly are accomplished burrowers in addition to being excellent flyers. The spurs are light-weight and collapsible, which may make them a suitable compromise between the demands of different locomotory habits.

ACKNOWLEDGMENTS

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Biology and Systematics of New World *Heterospilus* (Hymenoptera: Braconidae) Attacking Pemphredoninae (Hymenoptera: Sphecidae)

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Abstract.—Four new species of the braconid genus *Heterospilus* are described from Brazil and Costa Rica and a key to the five species known to attack crabronid wasps of the genera *Microstigmus* and *Spilomena* is presented. Biological notes are given for the hosts and the parasitoids and comments on their relationships are also offered.

The genus *Heterospilus* Haliday is one of the largest of the family Braconidae with an estimated 500 or more species in the New World, most of which are undescribed. The genus belongs to the subfamily Doryctinae characterized by a circular opening present between the clypeus and mandibles (oral cavity) and a row of stout spines along the anterior edge of the fore tibia. It can be distinguished from most other braconid genera by the reduction or absence of fore wing vein 2RS and can be identified by the key to genera in Marsh (1997).

We have very little information about the biology of species in the genus *Heterospilus*, which are, as far as known, idiobiont ectoparasitoids (Shaw and Huddleston 1991). Most records suggest parasitism of wood boring Coleoptera, especially Scolytidae, but a few species have been reared from stem boring Lepidoptera and one species from stem boring Symphyta. However, in an unusual host association, one species has been described from nests of the crabronid wasp genus *Microstigmus* Ducke (Richards 1935; Matthews 1968).

Recently, one of us (GARM) reared several species of *Heterospilus* from nests of species of *Microstigmus* and *Spilomena* Shuckard that were being studied in Brazil and Costa Rica. The purpose of this paper is to provide descriptions of four new species of *Heterospilus* and present a brief discussion of the biologies of the hosts and parasitoids.

BIOLOGICAL NOTES

The genus *Microstigmus* constitutes a distinctive group of crabronid wasps, in particular because of the social behavior and the elaborate suspended nests found in several of its species (Matthews 1968; Richards 1972; West-Eberhard 1977; Matthews 1991; Melo in press). *Microstigmus* together with *Arpactophilus* Smith, *Spilomena* and *Xysma* Pate form the subtribe Spilomenina of the Pemphredonini (Menke 1989). Melo (1994) presented evidence that *Microstigmus* is closely related to a group of species within *Spilomena* containing *S. alini* Antropov, *S. kimseyi* Antropov and other related undescribed species. The use also of *S. alini* as host by *Heterospilus*,

reported here for the first time, therefore should not be considered unexpected. *Heterospilus* has not been found parasitizing other species of Neotropical *Spilomena* whose nests have been studied (Melo unpubl.).

Very little is known about the biology of *Heterospilus* attacking *Microstigmus* wasps. The only available information is provided by Matthews (1968, 1991), Richards (1972) and Melo and Campos (1993). Matthews (1968, 1991) reported on some aspects of the biology of *H. microstigmi* Richards parasitizing *M. comes* Krombein, and Melo and Campos (1993) reported *M. myersi* Turner being parasitized by a new, undescribed species of *Heterospilus*, here named *H. matthewsi*, new species.

Parasitoid females have never been found inside the host nests and apparently always lay eggs directly from the outside. The positive correlation between the length of the parasitoid ovipositor and the thickness of the host nest wall found among the different species of *Heterospilus* (see below) provides additional evidence for this behavior. Matthews (1968) observed females of *H. microstigmi* crawling over nests of *M. comes* and inserting their ovipositors repeatedly into the nest. He was not able to ascertain if these insertions represented only probing or repeated ovipositions. However, considering that only one egg or small parasitoid larva has been found on each of the attacked host immatures and that in most *Microstigmus* nests no more than one immature in the appropriate stage is likely to be found, these insertions may be only for probing or for stinging and paralysis of the host larva.

Only host pre-pupae seem to be attacked, since eggs and small larvae of *Heterospilus* have been found only on immatures at this stage. The pre-pupal stage in *Microstigmus* is relatively short because these wasps are not known to enter diapause, although data on the duration of this stage is lacking. The egg is laid directly on the surface of the integument of the host larva. Parasitized larvae seem to have their development interrupted which as probably caused by pre-oviposition stinging. In their Table 1, Melo and Matthews (1997) gave a record of a small parasitic larva, attributed by them to *Heterospilus*, on a male pupa of *Microstigmus flavus* Melo and Matthews (this record was erroneously printed as associated with nest 308 instead of nest 303). Since no adult *Heterospilus* has been reared from nests of this species of *Microstigmus*, it is possible that this larva represents another species of parasitoid (the only record of an unidentified Chalcididae attacking *Microstigmus* was obtained from this species), and not the result of exceptional behavior by a female *Heterospilus*.

The length of the female ovipositor is clearly correlated with the thickness of the host nest wall or the distance of the brood cells from the nest outer surface. The longest ovipositors are found in *H. richardsi*, new species, a species attacking *Spilomena alini* and an undescribed species of *Microstigmus*. In both host species, the brood cells are usually situated deep inside the nests (see account under *H. richardsi*). The second longest ovipositors are found in females of *H. matthewsi*, new species, a species associated with *M. myersi*. The thickness of the nest walls in *M. myersi* is quite variable (Melo and Campos 1993). This variation seems to be related to the nest age, with young nests having thinner walls and older nests tending to have an extra covering layer of dirt particles. The females of the other *Heterospilus* species have shorter ovipositors and attack *Microstigmus* species whose nest walls are relatively thin.

Matthews (1991) found a strong correlation between the number of brood cells in nests of *M. comes* and frequency of parasitism by *H. microstigmi*; almost all parasitized nests had eight or more cells. He explained this pattern also in terms of the relation between the length of the parasit-

oid ovipositor and the thickness of the host nest walls. Cells in nests with few cells tend to be centrally placed and to have thick walls, and therefore are out of reach for the short ovipositor of females of *H. microstigmi*. New cells are sequentially added toward the periphery of the nest and as their number increases, the outer wall of the nest becomes thinner, making the cells more accessible to the parasitoid's ovipositor. Except for silk secreted by females, addition of new construction material to the nest as it grows, a behavior observed for example in *M. meyersi* (Melo and Campos 1993), does not occur in *M. comes* (Matthews and Starr 1984), the new cells being added by stretching the nest walls and holding the newly created pockets (future cells) with silk.

One would expect females of *Heterospilus* to have an ovipositor long enough to cope with this kind of variation in wall thickness of the host's nests, since a long ovipositor could reach deep cells as well as those closer to the nest surface. However, considering the situation found in *H. microstigmi* this does not seem to be the case. Apparently these parasitic wasps are under strong selective pressure to have the length of their ovipositor matching very closely the average depth of the majority of their host's cells. As more material becomes available, it would be interesting to investigate the amount of intraspecific variation in ovipositor length.

Cocoon spinning by larvae of *Heterospilus* also varies among the species described here. Matthews (1968) mentioned that *H. microstigmi* spins an opaque white cocoon, usually near the bottom of the host cell. Melo and Campos (1993) observed that larvae of *H. matthewsi* spin very rigid cocoons, which adults of *H. myersi* are apparently unable to open. Cells of *M. myersi* successfully parasitized by *H. matthewsi* become useless after emergence of the adult parasitoid. The larvae of *H. richardsi* spin cocoons somewhat thicker than those of *H. microstigmi*, but much thinner than in *H. matthewsi*. On the other hand, mature larvae and pupae of *H. brasilophagous*, new species, and *H. arleiophagous*, new species, were not encased by any sort of conspicuous cocoons. This apparent absence of cocoon spinning behavior needs confirmation, however, because cells of *Microstigmus* are lined with silk and it would have been easy to overlook a very loose cocoon adhered to the cell walls. Newly emerged adults of *Heterospilus* leave their host's nests directly to the outside by chewing a hole in the nest wall, without passing through the nest entrance. In active nests, these emergence holes are sealed later on with silk and particles by the *Microstigmus* females.

Body color also varies in an interesting way among the present species of *Heterospilus*. Species of *Heterospilus* attacking *Microstigmus* with a predominately black integument (including *S. alini*) also have a dark body color, whereas species associated with light colored *Microstigmus* (predominately or entirely yellow) have a light body color. The significance of this variation in body color is unknown.

The species of *Heterospilus* show a high degree of specificity regarding their hosts. Four of the present species are associated with only one species of *Microstigmus* (*H. matthewsi*, *H. arleiophagus*, *H. brasilophagus*) or at most with a group of closely related species (*H. microstigmi*). Only *H. richardsi* is known to attack hosts in different groups, but even in this case the two hosts nest in the same type of habitat. Most of the material used in the present study was collected by the second author while studying the biology of *Microstigmus* and *Spilomena* wasps in the region of Viçosa (Minas Gerais, southeastern Brazil). Except for *H. microstigmi*, the remaining four species coexist sympatrically in this locality. The hosts of *H. microstigmi*, *Microstigmus* species in the group *theridii*, are known only from the Amazon basin and Central America. Judging from this degree of specificity, additional collecting will

probably reveal twice as many species of *Heterospilus* attacking these crabronid wasps.

Additional biological notes are included with the descriptions of the *Heterospilus* species presented below.

TAXONOMY OF *HETEROSPILUS*

Although the genus *Heterospilus* is large and badly in need of study for the entire Western Hemisphere, preliminary study indicates there will be many distinct spe-

cies groups. The species in this study fall in a group with the following characters: vertex, mesonotum and mesopleuron coriaceous (Figs. 9–11); flagellum unicolored without white band or tip; metasoma tergum 2+3 with two transverse scrobiculate grooves which enclose a slightly raised median area (Figs. 6–8, see arrow on Fig. 6). The following key is based heavily on characters found in the female although it will work with most males also. The identification of males is best done by associated rearings.


KEY TO *HETEROSPILUS* SPECIES PARASITIC ON *MICROSTIGMUS* AND *SPILOMENA*

1. Body of both sexes entirely brown 2
   – Body of both sexes honey yellow, metanotum and metasomal terga occasionally marked with brown 3
2(1). Ovipositor of female equal to or longer than metasoma; fore wing with vein 3RSa longer than r-m (Fig. 1); hind femur yellow or at most yellowish-brown . . . .
   . . . . **richardsi** Marsh and Melo, new species
   – Ovipositor ½ to ⅓ length of metasoma; vein 3RSa equal to r-m (Fig. 2); hind femur brown on apical ¾, yellow on basal ¼ . . . . **matthewsi** Marsh and Melo, new species
3(1). Antennal flagellum yellow, first flagellomere longer than second; forewing vein 3RSa longer than r-m (Fig. 5); ovipositor of female usually equal to length of second and third metasomal terga combined . . . . **microstigmi** Richards
   – Antennal flagellum black, first flagellomere usually equal to second; forewing vein 3RSa equal to or shorter than r-m; ovipositor usually equal to length of first metasomal tergum   4
4(3). Fore wing vein 3RSa equal to vein r-m (Fig. 4); median transverse area of metasomal terga 2+3 (between transverse scrobiculate grooves) coriaceous medially, striate laterally
   . . . . **brasilophagus** Marsh and Melo, new species
   – Fore wing vein 3RSa shorter than vein r-m (Fig. 3); median transverse area of metasomal terga 2+3 entirely coriaceous . . . . **arleiophagus** Marsh and Melo, new species

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Heterospilus arleiophagus Marsh and Melo, new species
(Fig. 3)

Female.—**Body color:** head yellow, palpi light yellow, antennal flagellum black, first flagellomere yellow at base, pedicel black, scape yellow with black longitudinal stripe on outer edge; mesosoma yellow, metanotum, sides of scutellum and propodeum occasionally black; legs yellow, wings slightly dusky, veins brown; metasoma yellow, first tergum occasionally marked with brown laterally, terga 2–

4 marked with brown medially. **Body length:** 2.5 mm. **Head:** vertex and frons weakly coriaceous, face and temple smooth; 26–27 antennomeres, first flagellomere equal in length to second; malar space about ½ eye height. **Mesosoma:** pronotum coriaceous dorsally with median scrobiculate groove; mesonotal lobes coriaceous, median lobe with median longitudinal depression, notauli scrobiculate and meeting in a wide rugulose area nearly as wide as scutellum; scutellum coriaceous; mesopleuron coriaceous, sternaulus short and weakly scrobiculate; propo-
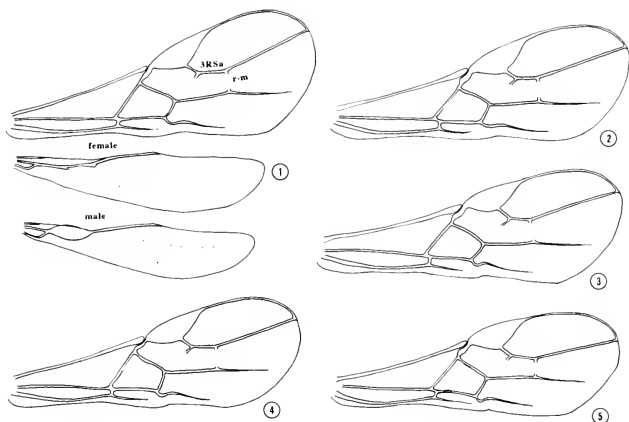
Figs. 1–5. Wings of *Heterospilus* species.: 1, *richardsi*, new species; 2, *matthewsi*, new species; 3, *arleiophagus*, new species; 4, *brasilophagus*, new species; 5, *microstigmi* Richards.

deum rugose with small basal lateral coriaceous spots. **Legs:** fore tibia with row of 4–6 short spines. **Wings:** fore wing vein 3RSa shorter than vein r-m (Fig. 3). **Metasoma:** first tergum slightly longer than apical width, carinate rugulose, raised median area not set off by carinae; second tergum carinate, transverse median area between two transverse scrobiculate grooves entirely coriaceous; third tergum coriaceous; remainder of terga weakly coriaceous; ovipositor as long as first metasomal tergum.

Male.—Agrees with description of female except as follows: scape usually entirely yellow; hind wing with oblong stigma at base (as in Fig. 1).

Holotype.—Female: BRAZIL, Viçosa, MG, January 28, 1990, G. A. R. Melo, collected in nest of *Microstigmus arlei*, nest 330. Deposited in the Museu de Zoologia, Universidade de São Paulo, Brazil.

Paratypes.—BRAZIL: 2 females, 1 male,

same data as holotype with additional dates of August 7, 1990 and February 2, 1992, nests 330, 367, 368, 603. Deposited in the Museu de Zoologia, Universidade de São Paulo, Brazil.

Biology.—Reared from nests of *Microstigmus arlei* Richards. This *Microstigmus* species makes suspended petiolated nests. The nests have been found attached only to surfaces other than plant leaves, like inclined tree trunks or branches, earth bank walls, and structural timber of exposed roofs of huts; the nests reported by Richards (1972) were hanging from the face of a rock. Cocoons have not been observed for this species.

Etymology.—The species name is based on the host wasp.

Heterospilus brasilophagus Marsh and Melo, new species
(Fig. 4)

Female.—**Body color**: head yellow, palpi light yellow, antennal flagellum black,

first flagellomere yellow at base, pedicel black, scape yellow with black longitudinal stripe on outer edge; mesosoma yellow, metanotum, sides of scutellum and scutellar sulcus black; legs yellow; wings slightly dusky, veins brown; metasoma yellow, terga 2–3 marked with brown. **Body length:** 2.5 mm. **Head:** vertex and frons weakly coriaceous, face and temple smooth; 26–27 antennomeres, first flagellomere equal in length to second; malar space about ½ eye height. **Mesosoma:** pronotum coriaceous dorsally with median scrobiculate groove; mesonotal lobes coriaceous, median lobe with median longitudinal depression, notauli scrobiculate and meeting in a wide longitudinal carinate area nearly as wide as scutellum; scutellum coriaceous; mesopleuron coriaceous, sternaulus short and weakly scrobiculate; propodeum rugose with small basal lateral coriaceous spots. **Legs:** fore tibia with row of 4–6 short spines. **Wings:** fore wing vein 3RSa usually as long as r-m (Fig. 4). **Metasoma:** first tergum slightly longer than apical width, carinate rugulose, raised median area not set off by carinae; second tergum carinate, transverse median area between two transverse scrobiculate grooves coriaceous, striate laterally; third tergum coriaceous; remainder of terga weakly coriaceous; ovipositor as long as first metasomal tergum.

Male.—Essentially as in female; hind wing with oblong stigma at base; with 25–27 antennomeres.

Holotype.—Female: BRAZIL, Viçosa, MG, February 15, 1992, G.A.R. Melo, collected in nest of *Microstigmus brasiliensis*, nest 582. Deposited in the Museu de Zoologia, Universidade de São Paulo, Brazil.

Paratypes.—BRAZIL: 5 males, same data as holotype with additional date of July 25, 1992, nests 579, 580, 619. Deposited in the Museu de Zoologia, Universidade de São Paulo, Brazil.

Biology.—Reared from nests of *Microstigmus brasiliensis* Melo. This *Microstigmus* species builds the type of pendulous nests

considered typical for this genus (see Richards 1972, West-Eberhard 1977); its nests were described and illustrated in Melo (1992).

Etymology.—The species name is based on the host wasp.

Heterospilus matthewsi Marsh and Melo, new species
(Figs. 2, 6)

Female.—**Body color:** head brown, palpi yellow; scape yellow with brown longitudinal strip laterally, pedicel brown, flagellum dark brown; mesosoma and metasoma dark brown; legs yellow, hind femur brown on apical ¾; wings hyaline, veins light brown, tegula yellow. **Body length:** 3 mm. **Head:** vertex and frons finely coriaceous, temple smooth, face smooth with fine striations laterally; 26–28 antennomeres; malar space about ⅓ eye height; maxillary palpus longer than fore tarsus. **Mesosoma:** pronotum coriaceous and shining dorsally with median scrobiculate groove; mesonotal lobes finely coriaceous, median lobe with median longitudinal depression, scutellum finely coriaceous and shining; mesopleuron coriaceous, sternaulus short and weakly scrobiculate; propodeum rugose, median rugae more distinct indicating vague areola, small basal lateral coriaceous spots. **Legs:** fore tibia with row of 4–5 short spines on anterior edge. **Wings:** fore wing with vein 3RSa equal in length to or slightly longer than vein r-m (Fig. 2). **Metasoma** (Fig.6): first tergum slightly longer than apical width, carinate rugulose, median raised area set off by complete distinct longitudinal carinae; second tergum weakly carinate coriaceous, ending in distinct transverse scrobiculate groove; third tergum with second transverse scrobiculate groove which meets first groove at sides, tergum carinate coriaceous before this groove and beyond to end of tergum; remainder of terga finely coriaceous and shining; ovipositor ⅓ to ½ length of metasoma.

Male.—Essentially as in female; hind wing with oblong stigma at base.

Holotype.—Female: BRAZIL, Viçosa, MG, February 10, 1992, G. A. R. Melo, collected in nest of *Microstigmus myersi*, nest 586. Deposited in the Museu de Zoologia, Universidade de São Paulo, Brazil.

Paratypes.—BRAZIL: 3 females, 2 males, same data as holotype with additional dates of March 16, 1992, July 31, 1992, January 28, 1990, nests 585, 586, 610, 620, 637; 1 female, Vargem Alta, ES, September 4, 1992, J. N. C. Louzada, collected in nest of *Microstigmus myersi*, nest 637; 1 male, Belo Horizonte, MG, July 18, 1992, J. N. C. Louzada, collected in nest of *Microstigmus myersi*. Deposited in the Museu de Zoologia, Universidade de São Paulo, Brazil.

Biology.—Reared from the nests of *Microstigmus myersi* Turner. Some aspects of the biology of *H. matthewsi* were presented in Melo and Campos (1993); this species was referred to as *Heterospilus* sp. in their paper. The rigid cocoons spun by its larvae set *H. matthewsi* apart from other *Heterospilus* attacking *Microstigmus*, whose larvae spin only a thin cocoon or no cocoon at all. It would be interesting to investigate the significance of these rigid cocoons.

Distribution.—Known only from Brazil.

Etymology.—Named for R. W. Matthews who gave the first complete description of the biology of *Heterospilus microstigmi* (see Matthews 1968).

Heterospilus microstigmi Richards
(Figs. 5, 7, 9–11)

Heterospilus microstigmi Richards 1935:131. Holotype female, deposited in The Natural History Museum, London.

Female.—**Body color:** head, mesosoma and metasoma yellow or honey-yellow, mesonotal lobes, metanotum, propodeum dorsally, and metasomal terga 1–4 often marked with brown; antenna varying from entirely brown to scape, pedicel and basal flagellomeres yellow, apical flagellomeres brown; legs yellow; wings hyaline or slightly dusky, veins light brown, tegula yellow. **Body length:** 2.5–3.0 mm. **Head:** vertex and frons finely coriaceous (Fig. 11), face and temple smooth; 24–28 antennomeres; malar space about ⅓ eye height; maxillary palpus longer than fore tarsus. **Mesosoma** (Figs. 9, 10): pronotum coriaceous and shining dorsally with median scrobiculate groove; mesonotal lobes finely coriaceous, median lobe with median longitudinal depression, scutellum finely coriaceous; mesopleuron coriaceous, sternaulus short and weakly scrobiculate; propodeum rugose, median rugae more distinct indicating vague areola, small basal lateral coriaceous spots. **Legs:** fore tibia with row of 4–5 short spines on anterior edge. **Wings:** fore wing with vein 3RSa about equal in length to vein r-m (Fig. 5). **Metasoma** (Fig. 7): first tergum slightly longer than apical width, carinate rugulose, median raised area set off by short indistinct basal carinae; second tergum carinate rugulose, ending in distinct transverse scrobiculate groove; third tergum with second transverse scrobiculate groove which meets first groove at sides, tergum carinate rugulose before this groove, strongly coriaceous beyond to end of tergum; remainder of terga coriaceous; ovipositor ⅓ to ¼ length of metasoma.

Male.—Essentially as in female; hind wing with oblong stigma at base.

Distribution.—Trinidad, Costa Rica, Brazil. For this study we have seen 23 specimens from the following localities in Brazil: Manaus, AM; Beruri, AM; Viçosa, MG; Mato Grosso.

Biology.—Previously reared from nests of *Microstigmus theridii* Ducke and *M. comes* Krombein (Richards 1935; Matthews 1968, 1991). Specimens from this study have been reared from nests of species of the *M. theridii* group which includes *M. comes* (nests 442, 443, 447, 531). This species group is restricted to northern South America and Central America (Melo unpubl.)
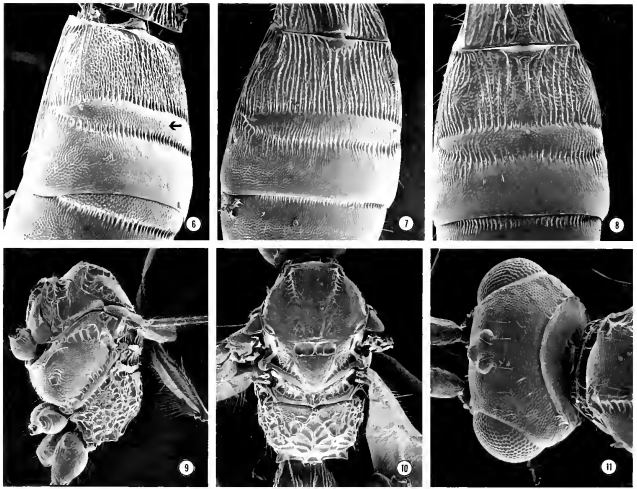
Figs. 6–11. Body parts of *Heterospilus* species: 6, metasoma, *matthewsi*, new species (arrow points to raised median area mentioned in the descriptions); 7, metasoma, *microstigmi* Richards; 8, metasoma, *richardsi*, new species; 9, mesosoma, lateral view, *microstigmi*; 10, mesosoma, dorsal view, *microstigmi*; 11, vertex, *microstigmi*.

Heterospilus richardsi Marsh and Melo, new species
(Figs. 1, 8)

Female.—**Body color:** head brown, face light brown, palpi yellow; scape yellow with brown longitudinal strip laterally, pedicel brown, flagellum dark brown; mesosoma and metasoma dark brown; legs yellow; wings hyaline, veins light brown, tegula yellow. **Body length:** 3 mm. **Head:** vertex and frons finely coriaceous, temple smooth, face smooth with fine striations laterally; 24–26 antennomeres; malar space about ⅓ eye height; maxillary palpus longer than fore tarsus. **Mesosoma:** pronotum coriaceous and shining dorsally with median scrobiculate groove; mesonotal lobes finely coriaceous, median lobe with median longitudinal depression, scu-tellum smooth and shining; mesopleuron coriaceous, sternaulus short and weakly scrobiculate; propodeum rugose, median rugae more distinct indicating vague areola, small basal lateral coriaceous spots. **Legs:** fore tibia with row of 4–5 short spines on anterior edge. **Wings:** fore wing with vein 3RSa longer than vein r-m (Fig. 1). **Metasoma** (Fig. 8): first tergum slightly longer than apical width, carinate rugulose, median raised area set off by short indistinct basal carinae; second tergum carinate rugulose, ending in distinct transverse scrobiculate groove; third tergum with second transverse scrobiculate groove which meets first groove at sides, tergum carinate rugulose before this groove, smooth beyond to end of tergum; remainder of terga smooth and shining;

ovipositor as long as or longer than metasoma.

Male.—Essentially as in female except as follows; scape usually entirely yellow; hind wing with oblong stigma at base.

Holotype.—Female: BRAZIL, Araponga, MG, March 22, 1992, G. A. R. Melo, collected in *Spilomena alini* nest. Deposited in the Museu de Zoologia, Universidade de São Paulo, Brazil.

Paratypes.—BRAZIL: 1 female, 1 male, same data as holotype; 1 male, Viçosa, MG, April 26, 1989, collected in nest of *Spilomena alini*. COSTA RICA: 3 females, 2 males, Heredia, Estacion Biol. La Selva, 10°25'N, 84°0'W, 80m, June 14, 1996, reared from nests of *Microstigmus* sp., nests 677, 680, GAR Melo. Deposited in the Museu de Zoologia, Universidade de São Paulo, Brazil and the national Museum of Natural History, Washington, DC.

Biology.—Reared from the nests of *Spilomena alini* Antropov in Brazil and an undescribed species of *Microstigmus* from Costa Rica closely related to *M. xanthosceles* Melo and Matthews. *Spilomena alini* excavates its nests in earth bank walls and in small soil clumps hanging from rootlets in banks (Carvalho and Zucchi 1989; Melo unpubl.; see Fig. 1 in Melo and Campos (1993) for an illustration of this kind of habitat). Some nests have also been found inside abandoned mud cells of eumenine wasps hanging from roots in banks (in this case, the nest tunnels and cells were dug in the loose detritus filling up the mud cells). *Heterospilus richardsi* was reared only from nests of *S. alini* built in soil clumps. In these nests, some of the host cells are close to the surface, especially in the smaller clumps, and therefore within reach of the parasitoid ovipositor. Nests built within bank walls are apparently protected from parasitism by *Heterospilus.*

The nests of the second host of *H. richardsi, Microstigmus* sp., are small to medium bags (3–12 mm long) built on hanging rootlets in earth banks or in tree trunks. The external walls of the nest are made of soil particles (for nests in banks) or particles of dead wood (nests in tree trunks) aggregated with silk from the female's silk glands. The central part of the nest has a sponge-like appearance and is formed by anastomosing pillars and channels; except in the upper part of the nest, this central portion is not in contact with the external walls. The brood cells are located in the central portion. It seems that only small nests, in which the cells are relatively close to the nest surface, are subject to parasitism by *Heterospilus.* One female and one male of *H. richardsi* were reared from a nest with six *Microstigmus* females (nest 677), while two females and one male were reared from a nest with only one *Microstigmus* female (nest 680). Four additional nests, containing four, five, 11 and 27 adult *Microstigmus* respectively, produced no *Heterospilus.*

Distribution.—Brazil, Costa Rica.

Etymology.—Named for O. W. Richards who described the first species of *Heterospilus* reared from *Microstigmus* wasps.

Heterospilus species

We have seen one female (nest 598) reared from the nests of an apparently undescribed species of *Microstigmus* species from the *bicolor* group in Viçosa. As in several other species of the group (West-Eberhard 1977), this *Microstigmus* species feeds its larvae progressively with Cicadellidae nymphs. This single female *Heterospilus* is similar to *microstigmi* but differs in having the body somewhat more coarsely coriaceous or punctate and darker wings. More specimens are needed to determine if it is a variation of *microstigmi* or another species.

Also, we have seen one badly damaged female specimen and one male specimen (nest 403) reared from *Microstigmus leuderwaldti* species group in Manaus, northern Brazil. These specimens are similar to *microstigmi* but are darker than identified members of that species. Exact placement

of these must wait until more undamaged specimens are collected.

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Cretaceous Digger Wasps of the New Genus *Bestiola* Pulawski and Rasnitsyn (Hymenoptera: Sphecidae: Angarosphecinae)

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Abstract.—The new genus *Bestiola* **Pulawski and Rasnitsyn**, characterized by a unique wing venation, is described for the following four new species from the Lower Cretaceous: *hispanica* **Martínez Delclòs and Rasnitsyn** (type species) from northeastern Spain, *communis* **Pulawski and Rasnitsyn** from central Mongolia, *subpetiolata* **Pulawski and Rasnitsyn** from central Mongolia, and *tenuipes* **Pulawski and Rasnitsyn** from Eastern Siberia. The genus is assigned to Angarosphecinae Rasnitsyn, 1975, new status by Rasnitsyn, which is treated as a paraphyletic Lower Cretaceous subfamily of Sphecidae. The family name Baissodidae Rasnitsyn, 1975, is synonymized with Angarosphecidae Rasnitsyn, 1975, by Rasnitsyn.

Sphecid wasps of the archaic subfamily Angarosphecinae (= Baissodinae) are the most abundant taxa among the Early Cretaceous Hymenoptera, particularly in the middle interval of that epoch, probably after Berriasian and before Albian, 140–113 myr before present (Rasnitsyn et al. 1998). Only a fraction of the material accumulated in the collections has been described (Evans 1969; Rasnitsyn 1975, 1986, 1990; Hong 1984; Zhang 1985, 1992; Darling and Sharkey 1990; Jarzembowski 1991; Ansorge 1993; Ren et al. 1995; Rasnitsyn et al. 1998). The Early Cretaceous fossils described here originate from three distant areas of Eurasia (central Mongolia, Eastern Siberia, and Spain), but have a unique wing venation and are all approximately the same age.

Most of the specimens examined were collected in Bon Tsagan, Central Mongolia, a rich fossil site 5–8 km north of Bon Tsagan Nuur (= Bon Tsagan Lake), in Bayanhongor Aymag (= Region). Specimens were impressed in marl of the Khurilt rock unit, Bon Tsagan Series (Sinitza

1993), possibly of Aptian age (Ponomarenko 1990). This hymenopteran assemblage is related to the Wealden Supergroup of the Southern England (Valanginian to Barremian: Rasnitsyn et al. 1998).

Siberian material was collected in two localities east of Lake Baikal. One is Baissa, a riverside outcrop on the left bank of the Vitim River, 3 km downstream of the former lodge Baissa and 45 air km upstream of the Romanovka Village, Buryat Republic. The fossils, impressed in marl of the Zaza Formation, are related to the Purbeck of South England (Berriasian), based on their hymenopteran assemblages (Rasnitsyn et al. 1998). The other Siberian locality, Semyon, is at Semyon Creek, 3.5 km SW of Elizavetino Village, west of Chita, Chita Oblast'. The age of insectiferous mudstones, disputable within the Early Cretaceous, is correlated either with Baissa (Zherikhin 1978) or with Bon-Tsagan (Dmitriev and Zherikhin 1988).

The Spanish specimen originates from the Montsec Range, central Lerida Province, and comes from lithographic lime-

stones named La Pedrera de Meià, located 5 km W of Santa Maria de Meià in La Noguera comarca, possibly of Berriassian-Valanginian age (Martínez-Delclòs 1995).

The following morphological structures, variously termed in the literature, are here defined or redefined as follows for clarity and convenience sake:

– mesosoma: thorax and propodeum combined;
– metasoma: abdomen excluding the propodeum (= gaster of Bohart and Menke 1976);
– metapostnotum: propodeal enclosure of Bohart and Menke 1976;
– spiracular lobe (as in Rasnitsyn 1988): pronotal lobe of Bohart and Menke 1976;
– adlateral lines: parapsidal line of Bohart and Menke (1976); we prefer this term to avoid confusion, as parapsidal lines of other entomologists correspond to notauli of most hymenopterists;
– cell 1+2r: submarginal cell I of Bohart and Menke (1976);
– 3r: marginal cell of Bohart and Menke (1976);
– 2rm and 3rm: submarginal cells II and III of Bohart and Menke (1976);
– 1mcu and 2 mcu: discoidal cells I and II of Bohart and Menke (1976);
– crossveins 2r-m and 3r-m: distal margins of 2rm and 3rm, respectively (as in Richards, 1956, and Gauld and Bolton, 1988), and corresponding to 1r-m and 2r-m of Bohart and Menke (1976); unlike the latter two authors, we call 1r-m the vein that extends from cell 1+2r to cell 1mcu (i.e., the vein that separates the basal cell from cell 2rm) in the xyelid genus *Pleroneura*;
– vein 1RS: a veinlet between basal cell (= medial cell of Bohart and Menke, 1976) and cell 1+2r;
– vein 2RS: a veinlet between cells 1+2r and 2rm;
– vein 2r-rs: a veinlet between cells 1+2r and 3r, called 2r by Bohart and Menke, 1976.

The abbreviation PIN stands for the Paleontological Institute, Russian Academy of Sciences, Moscow, Russia.

TAXONOMY

Family Sphecidae Latreille

Subfamily Angarosphecinae Rasnitsyn, new status

Angarosphecidae Rasnitsyn 1975:109. Type genus: *Angarosphex* Rasnitsyn 1975:110.
Baissodidae Rasnitsyn:1975:122. Type genus: *Baissodes* Rasnitsyn 1975:123. **New synonym** by Rasnitsyn.

Angarosphecinae are archaic Mesozoic wasps that lack the synapomorphies of any extant sphecid subfamily. They may be paraphyletic with respect to other Apoidea because they are not defined by any synapomorphy. They are treated here as a subfamily of Sphecidae because there is evidence in some specimens of two unique synapomorphies of Apoidea (they also lack any synapomorphy that would ally them with any other Aculeata). In particular, *Pompilopterus corpus* Rasnitsyn and Jarzembowski has an elongate spiracular lobe, pronotum thickened preapically, and an enlarged metapostnotum (Rasnitsyn, Jarzembowski, Ross 1998, Fig. 36), and *Angarosphex myrmicopterus* Rasnitsyn has an enlarged metapostnotum (Rasnitsyn 1980, Fig. 172). A large metapostnotum is also found in *Bestiola tenuipes* (Fig. 7). None of the Angarosphecinae has plumose setae or enlarged hindbasitarsi typical of bees. The form of the adlateral line of *Bestiola* and other Angarosphecidae differs from that of all extant Apoidea in that it extends to the posterior margin of the mesoscutum, as pointed out to us by M. A. Prentice (oral communication). This indicates that Angarosphecinae very probably represent the most basal lineage of known Apoidea.

Rasnitsyn (1975) recognized Baissodidae based on the presence of a unique median scutal sulcus believed to be lacking in all other non-bethyloid Aculeata (in-

cluding Angarosphecidae). Subsequently, he (Rasnitsyn 1980) included *Angarosphex* in the Sphecidae and hypothesized that the Baissodidae were sphecid ancestors. However, *?Angarosphex pallidus* Rasnitsyn, 1986, from the lowermost Lower Cretaceous of Mongolia, combines the wing venation of *Angarosphex* with the presence of a median scutal sulcus, although the latter is only slightly indicated. Because of this combination, Baissodidae are here synonymized with Angarosphecidae.

Bestiola Pulawski et Rasnitsyn, new genus

Name derivation.—Bestiola, Latin for small beast. Gender feminine.

Type species.—*Bestiola hispanica* Martínez Delclòs et Rasnitsyn, new species, Lower Cretaceous of Spain.

Recognition.—*Bestiola* is easily recognized by its unique wing venation (Figs 1–8). It has three radiomedial cells, and cell 2rm receives veins 1m-cu and 2m-cu (= both recurrent veins). The combination of three unusual features differentiates it from all other sphecid genera with these characteristics, both extinct and extant: 1. cell 3rm broader on the costal side than on the anal side (as in the North American genus *Xenosphex* and some *Palarus*); 2. crossvein 3r-m joining RS near the distal end of the latter (as in the North American genus *Eucerceris* and some *Palarus*); and 3. crossvein 2r-m equidistant from 2m-cu and 3r-m or closer to the latter (as in the Old World *Tachysphex brevipennis* Mercet, and several other Larrini and some *Diploplectron* approach this condition).

Description.—Size medium to large, length of forewing 5–15 mm. Antenna with no conspicuous modifications, at least basal flagellomeres longer than wide (all flagellomeres in most species). Occipital carina almost circular, reaching hypostomal carina. Ocelli not modified, distant from eye. Pronotum short, wide, thickened preapically, separated from mesonotum by a groove (Fig. 8). Mesoscutum

without median scutal sulcus, with long notauli and adlateral lines; mesopleuron with episternal and scrobal sulci, hypersternaulus, and possibly omaulus. Metanotum short, metapostnotum long, truncated, with median line. Propodeal spiracle elongate, slit-like. Forewing: pterostigma well defined; basal vein distant from pterostigma, evenly arched; cell 3r acuminate at wing foremargin; crossvein 2r-rs longer than width of pterostigma; 2r-m sinuate or arching outwardly, closer to 2r-rs than to 3r-m on RS, equidistant from 2m-cu and 3r-m on M or closer to the latter; 3r-m straight or arching outwardly; 1m-cu received near base of cell 2rm; M sharply angled at 2m-cu; cu-a interstitial with M or narrowly postfurcal. Hindwing venation complete, cu-a meeting Cu well beyond M+Cu fork. Fore and midfemora with well-defined, narrow trochantellus (hindleg condition unknown), but no obvious specializations. Metasoma rounded basally (neither petiolate nor pedunculate).

Composition.—Four species from the Lower Cretaceous of Spain, Eastern Siberia, and Mongolia, as described hereafter.

Taxonomic position.—*Bestiola* is a member of Aculeata s. s. (= Vespoidea + Apoidea) as evidenced by its sexually dimorphic antennal flagellum of 10 (female) and 11 articles (male). Unlike all Chrysidoidea, it possesses a complete set of forewing and hindwing cells. It belongs to Apoidea because it shares two unique synapomorphies of the superfamily: an elongate metapostnotum and a pronotum thickened preapically. The genus belongs to Sphecidae because it lacks the enlarged hindbasitarsus and plumose body setae of Apidae s. l. The genus shares with most other Angarosphecinae the position of 1m-cu which inserts near the RS+M fork. This feature occurs elsewhere only in some other Apoidea. The genus also lacks any synapomorphy that would place it in any extant sphecid subfamily and so we attribute it to Angarosphecinae.

KEY TO SPECIES OF *BESTIOLA*

1. Forewing cell 2rm conspicuously narrowing anterad, its costal margin markedly shorter than crossvein 2r-rs; the latter emerging shortly after pterostigma's midlength (Fig. 8) . . . .
. . . . **Bestiola subpetiolata Pulawski and Rasnitsyn, new species**
– Forewing cell 2rm moderately narrowing anterad, its costal margin about as long as crossvein 2r-rs; the latter emerging markedly beyond pterostigma's midlength 2
2. Forewing length 5 mm; crossvein 2r-rs markedly shorter than 2RS (Fig. 1); hindfemur and gastral terga with pale spots (Fig. 1); metasoma conspicuously setose (Fig. 1) . . . .
. . . . **Bestiola hispanica Martínez Delclòs and Rasnitsyn, new species**
– Forewing length 11.0–14.5 mm; crossvein 2r-rs longer to minimally shorter than 2RS (Figs. 2–7); hindfemur and gastral terga without pale spots (Figs. 2–7); metasoma not setose or less conspicuously setose (Fig. 5) 3
3. Head, wing veins, and legs except coxae light; forefemur slightly more elongate (Fig. 7)
. . . . **Bestiola tenuipes Pulawski and Rasnitsyn, new species**
– Head, wing veins, and legs dark; forefemur slightly stouter (Figs. 2, 3) . . . .
. . . . **Bestiola communis Pulawski and Rasnitsyn, new species**

Bestiola hispanica Martínez Delclòs and Rasnitsyn, sp. n.
(Fig. 1)

Name derivation.—Hispanica, Latin for Spanish.

Recognition.—*Bestiola hispanica* differs from its congeners by its small size (forewing length 5 mm rather than 11.0–14.5 mm), crossvein 2r-rs markedly shorter than 2RS (longer to minimally shorter in the other species), the presence of pale spots on the hindfemur and gastral terga, and a conspicuously setose metasoma.

Description.—Female unknown, male: Fig. 1. Body dark (including wing veins), but hindfemur with pale spot posteroapically and terga I–IV each with a pair of preapical spots. Head and metasoma conspicuously setose. Flagellomeres nearly equal in width, longer than wide, becoming shorter toward apex. Head relatively small, narrowing toward mouthparts; gena somewhat inflated; malar space half length of eye; clypeal free margin projecting mesally; hindocellus separated from eye by about its own diameter. Forewing: posterior pterostigmal margin straight; 2r-rs joining pterostigma near the latter's apex, about as long as costal margin of cell 2rm and half as long as 2RS; 3r-m straight;

costal margin of cell 2rm about twice as long as anal margin; cu-a almost interstitial with M+Cu fork. Hindwing with long row of hamuli (10 preserved) and cu-a angling at Cu. Legs not elongate; hindfemur as long as head width, moderately thick subbasally, not attenuated apically, its dorsal margin convex except subapically, ventral margin almost straight (ventral margin slightly convex on right femur, probably due to fossil compression). Hindtibia 1.25 times as long as femur, with no spines but with one spur. Hindtarsus slightly longer than tibia, basitarsus longer than tarsomeres II–IV combined. Apical gastral segments and genitalia not preserved. Body length ca 9 mm, distance from forewing base to apex of cell 3rm 5.1 mm.

Material examined.—Holotype (LP92/SC/3662): male, Spain: Lerida Province: La Pedrera de Meià 5 km W Santa Maria de Meià (Institut d'Estudis Ilerdencs, Lerida, Spain).

Bestiola communis Pulawski et Rasnitsyn, new species
(Figs. 2–6)

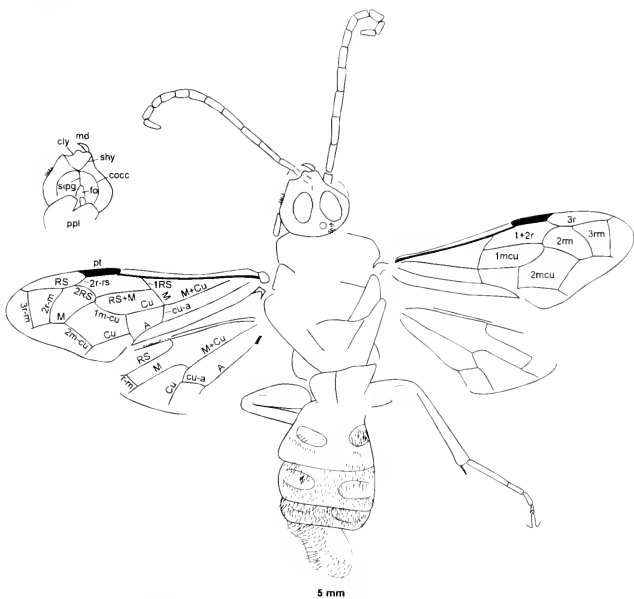*Name derivation.*—Communis, Latin for common.

Fig. 1. *Bestiola hispanica* Martinez-Delclòs and Rasnitsyn, new species, holotype: cly—clypeus; cocc—occipital carina; f—femur; fo—occipital foramen; md—mandible; ppl—propleuron; shy—hypostomal suture; sipg—interpostgenal suture.

Recognition.—The following combination of characters is unique to *Bestiola communis*: forewing length 11.0–14.5 mm (5 mm in *hispanica*); costal margin of cell 2rm about as long as crossvein 2r-rs (markedly shorter in *subpetiolata*); 2r-rs longer to minimally shorter than 2RS (markedly shorter in *hispanica*), emerging markedly beyond pterostigma's midlength (near pterostigma's midlength in *subpetiolata*); hindfemur and gastral terga without pale spots (with pale spots in *hispanica*); and forefemur not elongate (slightly elongate in *tenuipes*, compare Figs. 2 and 3 and 7). Unlike *tenuipes*, the body of *communis* is all dark, including the wing veins.

Description.—Female (Fig. 2), sex unknown in remaining specimens (Figs. 3–6). Body and appendages uniformly dark, metasoma inconspicuously setose (Fig. 5). Scape about as long as midflagellar articles; pedicel transverse; flagellomeres more than twice as long as wide, flagellomere I almost as long as II and III combined, following ones gradually shorter and thinner toward antennal apex, apical
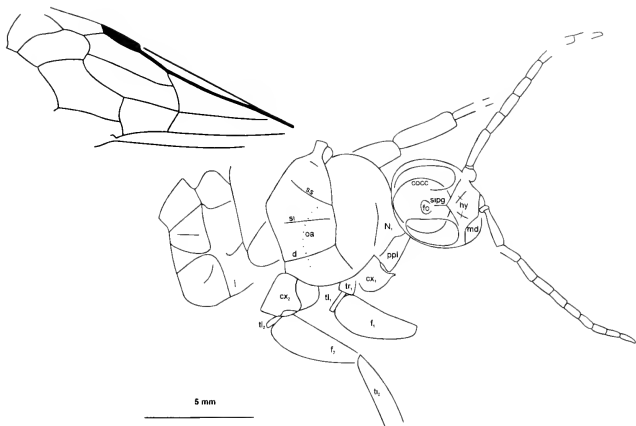
Fig. 2. *Bestiola communis* Pulawski and Rasnitsyn, new species, holotype: d—discrimen (interpleural suture); hy—hypostoma; hys—hypersternaulus or signum?; N1—pronotum; oa—omaulus; ss—scrobal suture; tl—trochantellus; tr—trochanter; other abbreviations as in Fig. 1.

flagellomere almost 3 times as long as wide. Head nearly circular in front view; eyes elongate, widest below midheight, with inner margin concave; malar space present; anterior clypeal margin protruding into wide medial lobe that is shallowly emarginate apically. Notauli and adlateral lines complete or nearly so. Mesopleuron with long, almost straight scrobal sulcus and hypersternaulus, possibly also with omaulus. Wing venation as in *hispanica* except 2r-rs subequal in length to 2RS and 3r-m arched. Fore- and midfemora thickest subbasally, narrow apically, with dorsal margin straight and ventral convex; forefemur as long as head width, midfemur slightly longer; fore- and possibly midtibiae shorter than respective femora. Metasoma missing in type series but present in specimen PIN 3559/4526 (that is excluded from type series). Forewing length 13.0–14.5 mm (11.0 mm in the specimen

PIN, 3559/4526 not included into the type series, Fig. 5).

Material examined.—Holotype: Central Mongolia, Bon-Tsagan, bed 87/8 (PIN. 3559/4525, incomplete female specimen with propodeum, hindlegs and metasoma missing).

Paratypes: same locality and bed (PIN, 3559/4528, incomplete specimen with most of antennae and legs, part of thorax and all metasoma missing; PIN, 3559/ 4530, two damaged wings mixed with other insect remains in vertebrate dropping).

Excluded from type series but possibly conspecific: same locality and bed (PIN, 3559/4526, a somewhat damaged specimen: Fig. 5); Eastern Siberia, Semyon (PIN, 2385/2392, an isolated wing with venation nearly identical to those of *communis* and *tenuipes*, and attributed to the
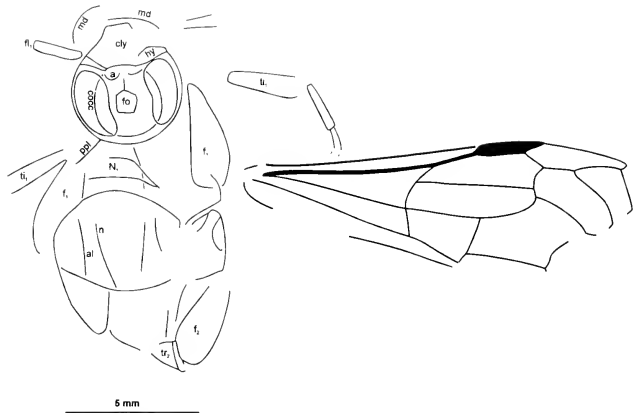
Fig. 3. *Bestiola communis* Pulawski and Rasnitsyn, new species, paratype PIN, 3559/4528: a—antennal foramen; al—adlateral line; h—hypostome; n—notaulus; otherwise as in Figs. 1, 2.

former because of its dark wing veins; Fig. 6).

Bestiola tenuipes Pulawski et Rasnitsyn, new species
(Fig. 7)

Name derivation.—Tenuipes, from the Latin words tenuis, thin, and pes, leg; with reference to the elongate forefemur.

Recognition.—The wing venation of *B. tenuipes* is as in *communis*, but the head, wing veins, and legs are light rather than

Fig. 4. *Bestiola communis* Pulawski and Rasnitsyn, new species, paratype, PIN, 3559/4530.

dark. Also, the forefemur is slightly longer (compare Figs. 7 with 2 and 3), although this difference is difficult to quantify. See Recognition of *communis* for differences with *hispanica* and *subpetiolata*.

Description.—Male (Fig. 7). Female unknown. Antenna and mesosoma (possibly in part) dark, metasoma infuscated toward apex, otherwise coloration light (including wing venation). Thorax with well-defined although shallow punctures that are about 1 diameter apart, and with moderately short and moderately dense setae. Basal flagellomeres unrecognizable, remaining flagellomeres 2.0–2.5 times as long as wide, gradually becoming shorter and thinner toward apex. Adlateral line of mesoscutum complete; scutellum wide, elongate; metascutellum contrastingly short; metapostnotum trapezoia, with basal impression, median longitudinal line, and rounded posterior angles. Propodeal spiracle elongate, narrow, slightly bent S-like. Wing venation
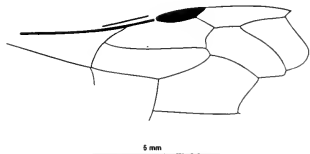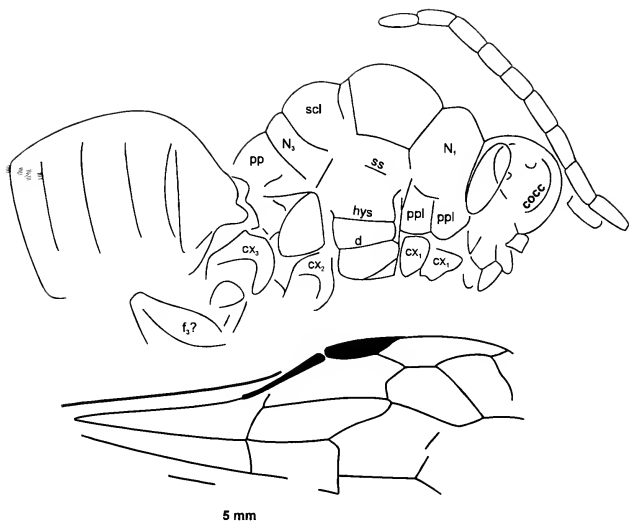
Fig. 5. *Bestiola* ? *communis* Pulawski and Rasnitsyn, new species, PIN, 3559/4526; N3—metanotum; pp—propodeum; scl—scutellum; other abbreviations as in Figs. 1–3.

as in *communis*. Legs relatively long, fore-femur slightly longer than head width, with dorsal margin straight and ventral margin convex; hindfemur elongate, almost symmetrical, attenuated apically, both dorsal and ventral margins straight (except basally); midtarsus markedly longer than midfemur; midbasitarsus shorter

Fig. 6. *Bestiola* ? *communis* Pulawski and Rasnitsyn, new species, PIN, 2385/2392.

than three following tarsomeres combined. Genitalia elongate, ovoid, with smooth contour, with gonostyle apex narrow rounded. Body length 21 mm as preserved, forewing length 11.5 mm.

Material examined.—Holotype: Russia: Eastern Siberia: Baissa, bed 31 (PIN, 3064/2055, incompletely preserved male).

Bestiola subpetiolata Pulawski et Rasnitsyn, new species
(Fig. 8)

Name derivation.—From the Latin petiolus, little foot, stalk, stem; and the prefix sub-, Latin for under, somewhat, less than; with reference to the shape of forewing cell 2rm.
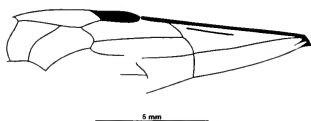
Recognition.—The following details of

Fig. 7. *Bestiola tenuipes* Pulawski and Rasnitsyn, new species, holotype: pN3—metapostnotum; sp—propodeal spiracle; other symbols as in Figs. 1–5.
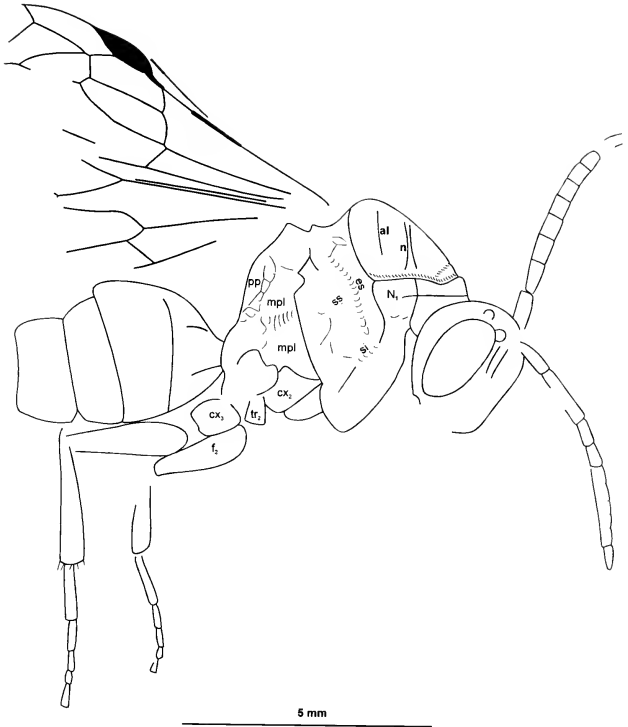
Fig. 8. *Bestiola subpetiolata* Pulawski and Rasnitsyn, new species, holotype: es—episternal suture; mpl—metapleura; other abbreviations as in Figs. 1–7.

the forewing venation distinguish *subpetiolata* from all of its congeners: vein 2r-rs meeting pterostigma near the latter's midlength, costal margin of cell 2rm markedly shorter than 2r-rs, and anterior end of vein cu-a closer to wing base than M+Cu fork. In addition, subapical flagellomeres ap-

pear to be only slightly longer than wide, thus markedly shorter than in other *Bestiola*.

Description.—Sex unknown (Fig. 8). Body moderately dark (including wing veins) but antennal apex, tarsi (except hindbasitarsus basally), and metasoma

light. Metasoma at least partly setose (setae preserved only along hind margin of last preserved tergum). Length of basal flagellomeres about 3 times width, subapical ones probably subquadrate. Eye large, elongate, almost symmetrical. Malar space probably short. Pronotum short, spiracular lobe not elongate. Mesoscutum: notauli and adlateral lines complete or nearly so. Mesopleuron with complete, crenulate episternal sulcus; and with anteriorly crenulate hypersternaulus. Metapleuron wide, crossed by subhorizontal sulcus. Other thoracic structures unrecognizable due to deformation. Forewing vein 2r-rs meeting pterostigma near the latter's midlength, meeting RS near 2rm (longer than costal margin of cell 2rm), 2rm weakly arching, 3r-m straight, anterior end of cu-a slightly closer to wing base than M+Cu fork. Hindwing vein cu-a meeting M relatively close to M+Cu fork. Midfemur: dorsal margin straight, ventral margin convex. Hindfemur about as long as head height, widest subbasally, attenuated apically, with dorsal margin concave in apical half and ventral margin straight except basally. Midtibia slightly shorter, hindtibia slightly longer, than respective femur. Mid- and hindtarsi longer than respective tibiae, respective basitarsi slightly shorter than following 3 tarsomeres combined. Metasoma somewhat attenuated basally, with apex missing, but probably shorter than head and thorax combined. Body length, as preserved, 10 mm, forewing length 7.0 mm

Material examined.—Holotype: Central Mongolia, Bon-Tsagan, bed 87/8 (PIN, 3559/4529, incomplete, rather poorly preserved specimen with somewhat crumpled thorax).

ACKNOWLEDGMENTS

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Ultrastructure of Imaginal Spermatozoa of Sawflies (Hymenoptera: Symphyta)

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Abstract.—We present the first ultrastructural study of sperm from representatives of three superfamilies of sawflies (Hymenoptera: Symphyta): *Xyela julii* (Xyeloidea), *Cephalcia arvensis* (Pamphiloidea) and *Tremex* sp. (Siricoidea), with particular attention being paid to characters that may be phylogenetically informative. Differences in the location of the centriolar adjunct, particularly in relation to the mitochondrial derivatives, would suggest *Cephalcia* has a better claim than *Xyela* as having sperm that may be representative of a common ancestral form. The centriolar adjunct of *Cephalcia* overlies both mitochondrial derivatives symmetrically, as found in ants and bees, whereas in *Tremex*, which its sperm otherwise closely resemble, the centriolar adjunct is located asymmetrically, abutting a single mitochondrial derivative and thus offsetting the pair of mitochondrial derivatives longitudinally. *Xyela* has radically different sperm in terms of size and both the arrangement and appearance of the organelles, especially acrosomal substructure and lack of an acrosomal rod.

Very little is known about sperm ultrastructure among the Hymenoptera compared with most other insect orders (Phillips 1970; Jamieson 1987; Quicke 1997), and most of the studies that do exist deal largely with common aculeates such as bees and ants (e.g. Dallai and Afzelius. 1990; Wheeler and Krutzsch. 1992). However, an initial study of the spermatozoa of some species (Quicke *et al.* 1992) revealed a considerable number of ultrastructural features that differ between taxa, raising the possibility that such variation might provide new phylogenetic indicators, as has been possible in many other groups of insects (Jamieson 1987). The phytophagous sawflies (Symphyta) constitute a relatively underived basal grade within the order of Hymenoptera. As such they are important for our understanding of the relationships and development of both the social species of the Aculeata (ants, wasps and bees) and members of the paraphyletic group of the ten or eleven currently recognised, extant superfamilies

generally referred to as the 'Parasitica'. This is especially so, since the sister group for the Hymenoptera is not at all certain at present (Whiting *et al.* 1997), and so it is not possible to make use of outgroup comparison to determine the ancestral sperm morphology of the order (Watrous and Wheeler 1981). Groundplan sperm ultrastructure may therefore be determined best by considering the sperm of those extant taxa (i.e. the sawflies) which represent the most basal hymenopteran lineages (Gibson 1993; Yeates 1995). The only previous work on sawfly sperm ultrastructure (Quicke *et al.* 1992) presented data for only two of the six symphytan superfamilies, the Tenthredinoidea and the Cephoidea. We have therefore examined sperm ultrastructure, and in particular that of cell organelles, in detail in representatives of three further superfamilies, the Xyeloidea, Pamphiloidea and Siricoidea, leaving only the rare, through interesting, Orussoidea unstudied. Two of the superfamilies examined here, the Xyeloidea represented

by *Xyela julii* (Brébisson) and the Pamphi-loidea, represented by the pamphiliid, *Cephalcia arvensis* Panzer have usually been considered to be among the most primitive of sawflies. In contrast, the Siricoidea represented by *Tremex* sp., are close to the origin of the Apocrita (Rasnitsyn 1980, 1988; Heraty *et al.* 1994; Vilhelmsen 1997). The results are discussed in terms of the likely plesiomorphic states for various subcellular features in the Hymenoptera.

MATERIALS AND METHODS

Testes were obtained from adult males of *Xyela julii, Cephalcia arvensis* and *Tremex* sp., which had been maintained on dilute honey solution for a maximum of 3 days. *Xyela* were collected as adults in Silwood Park, Berkshire, U.K., the *Cephalcia* were reared from larvae collected in Italy and the *Tremex* were collected as adults in California and couriered to the U.K. for preparation.

Light microscopy.—Vas deferentia and testes were dissected from living sawflies in insect saline and teased apart on a clean microscope slide. After a few minutes to allow the sperm/spermatodesmata to swim free of the disrupted tissue, the slides were dried on an hot plate at c. 80°C. The smear was then flooded with double-filtered, 0.1% w/w toluidine blue in 1% w/w aqueous sodium borate and stained at 80°C until crystallisation of the stain had started. Following washing in distilled water they were permanently stored dry.

Transmission electron microscopy.—Genitalia were dissected out under 2% glutaraldehyde in phosphate buffered saline (pH 7.2), and fixed for two hours. Tissue was transferred to 2% osmium tetroxide in cacodylate buffer (pH 7.2) for 2 hr. After another buffer wash, tissue pieces were dehydrated to 50% ethanol and then further fixed with saturated uranyl acetate in 50% ethanol prior to complete dehydration, embedding in Epon resin and polymerisation overnight. Silver sections were picked-up on to high resolution grids, stained with uranyl acetate and lead.

RESULTS

Woodwasps of the superfamily Siricoidea are considered to be amongst the most advanced of the sawflies, sharing a number of derived morphological features with the Apocrita (Vilhelmsen 1997). As has been reported previously for other sawflies (Quicke *et al.* 1992), the mature sperm of siricid, *Tremex*, stored within the vas deferens and seminal vesicles are present in spermatodesmata bundles (Fig. 1), though by the time they reach the spermatheca of the females they have broken up completely and only isolated sperm are present (Naito, personal communication). In our preparation of *Tremex* from male seminal vesicles, a small proportion of isolated sperm were also present but it is not clear whether they were the result of spermatodesmata fragmentation upon fixation or whether they indicate a normal pretransfer phenomenon.

The sperm heads are inserted throughout the fairly electron-dense and elongate cap of the spermatodesmata, with those sperm located more centrally being inserted more anteriorly (Figs 1, 2). As a result, many different levels of sperm are evident in a single transverse section of each spermatodesmata (Fig. 2). It is therefore possible, in the same transverse section, to locate adjacent sperm sectioned through acrosome and acrosomal rod (perforatorium), through the nucleus, the basal body with centriolar adjunct, and through the axoneme with mitochondrial derivatives. Also, in transverse section, the acrosome is clearly seen to have a membrane around both the outside and around the invaginated portion of the structure (Fig. 4c). Between the acrosomal membrane and the plasma membrane is an electron dense region extending from the acrosomal membrane (Fig. 4c, *arrowheads*). This may be comparable to the material reported to surround the acrosome in other sperma-
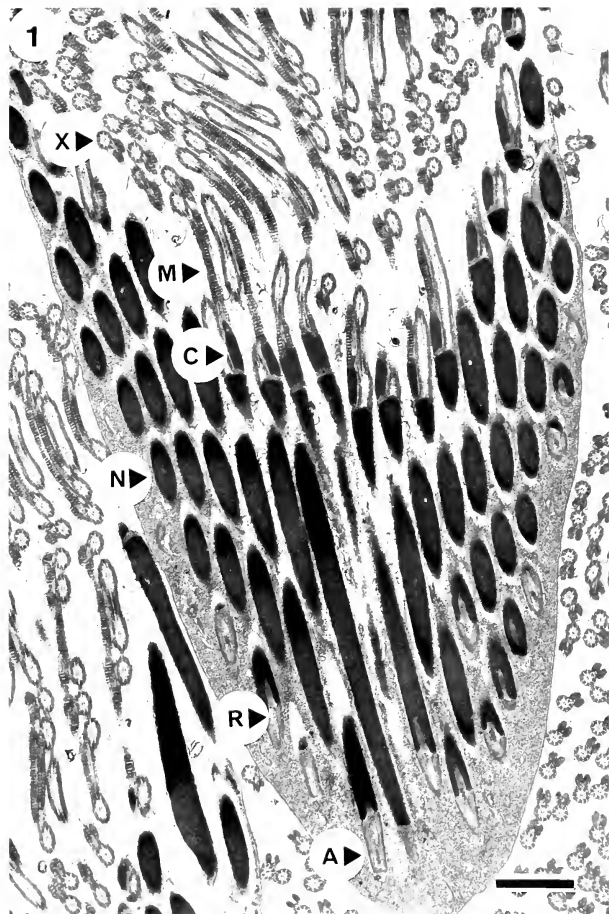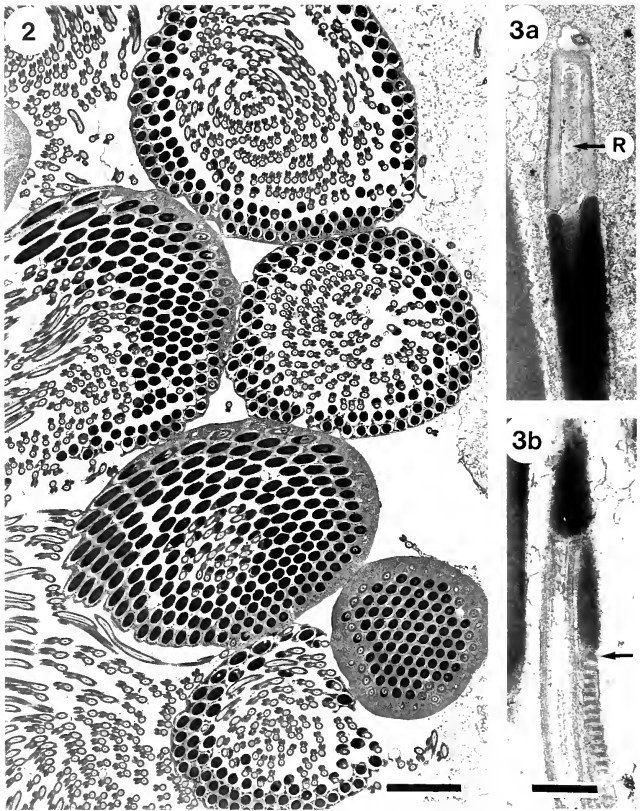
Fig. 1. Longitudinal section of a spermatodesmatum in the imaginal testes of the sawfly, *Tremex* (Siricoidea). A, acrosome; C, centriolar adjunct; M, mitochondrial derivative; N, nucleus; R, acrosomal rod; X, axoneme. Scale bar = 1.0 μm.

Figs. 2–3.   Features of spermatodesmata and sperm in the imaginal testes of the sawfly, *Tremex* (Siricoidea). 2, transverse sections through several spermatodesmata at different levels showing that the more centrally located spermatozoa have their heads inserted more anteriorly; 3, nuclear-associated organelles showing in 3a, the insertion of the acrosomal rod (R) into the anterior of the nucleus (note also the small anterior sac at the head of the acrosome), and 3b, the position of the centriolar adjunct (arrowed) in relation to the nucleus and striated mitochondrial derivative. Scale bars: 2 – 2.0 μm; 3 = 0.5 μm.
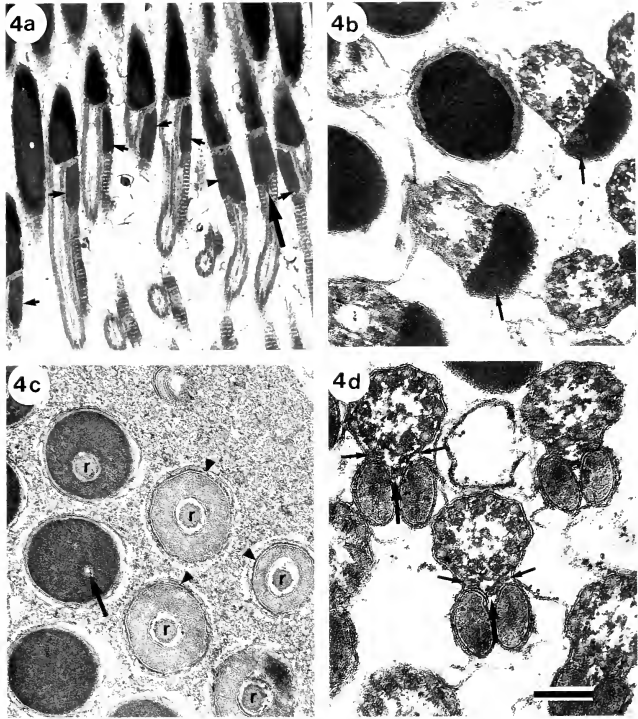
Fig. 4. Organelles of *Tremex* sperm (Siricoidea) seen in tranverse and oblique section: 4a, showing the centriolar adjuncts (small arrows) of a number of spermatozoa, and in the section indicated by the large arrow the centriolar adjunct can be seen to make contact with both mitochondrial derivatives; 4b, section at the level of the centriolar adjunct (arrowed) where it occupies all the extra-axonemal area; 4c, sections through anterior of nucleus and acrosome showing the acrosomal rod (r) fitting tightly into the nucleus but loosely in the subacrosomal space (note: the clear membranes surrounding acrosome and nucleus but not the rod; granular material between acrosomal and plasma membranes (arrowheads); putative nuclear 'pore' (large arrow)); 4d, axoneme with small deltoid bodies (small arrows) and central rod (large arrows) (note also mitochondrial derivatives with distinct membrane and internal structure). Scale bar: 4a = 0.66 µm; 4b,c = 0.25 µm; 4d = 0.2 µm.
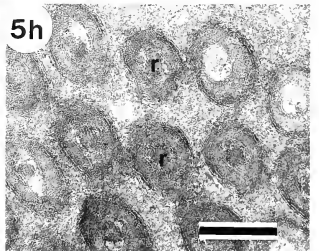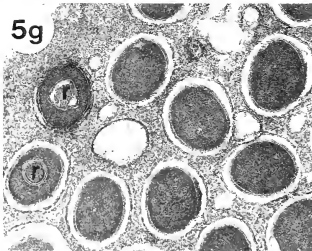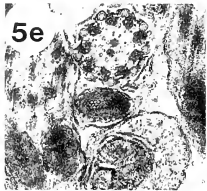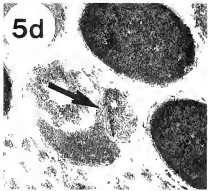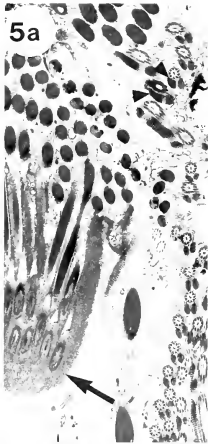
tozoa (Quicke *et al.* 1992), although the latter structures are larger and have a sub-layered appearance in at least some taxa.

In longitudinal section (Fig. 3), the acrosome of *Tremex* can be seen to have a large sub-acrosomal space (Fig. 3a) which is partly occupied by the acrosomal rod. This rod extends into the nucleus for almost the same length again as it does into the acrosome. Unlike the nucleus and acrosome, the rod is not membrane bound, but where the rod is inserted into the nucleus there is no surrounding space, giving the impression that the rod is being held by the nucleus. The plasma membrane surrounding the acrosome extends slightly anteriorly to produce a small extra-acrosomal space. A membrane bound area found within the nucleus (Fig. 4c, *arrow*) may represent a longitudinally running pore. The nucleus (Fig. 3b) is abutted posteriorly by the axoneme at the level of the latter's basal body, where the axoneme lacks the central pair of microtubules. A large centriolar adjunct is present, and this in turn contacts the mitochondrial derivatives which have very clearly defined membrane bound cristae (Fig. 3b, *arrow*). There is at least one membrane separating the centriolar adjunct from the nuclear membrane. The exact arrangement of the centriolar adjunct and nucleus, and in particular, how the centriolar adjunct contacts the nucleus, is not always obvious. In many insect spermatozoa this has given rise to confused interpretations of the

structure, even to suggestions that the centriolar adjunct is absent. From the present study, the relationship becomes clear at higher magnification where several spermatozoa lie in close proximity (Fig. 4). The centriolar adjunct (Fig. 4a, *arrows*) contacts two equally sized mitochondrial derivatives, and can be seen to extend some way in between the two, forming what appear in transverse sections, tail-like structures (Fig. 4a, *large arrow*). The mitochondrial derivatives are thus intimately connected to the centriolar adjunct. In transverse section, certainly at the level of the basal body, this produces an arrangement where the centriolar adjunct and basal body occupy most of the area of section; an appearance which could be mistakenly interpreted as there being an extension of the nucleus overlying the axoneme (Fig. 4b).

Although the acrosome is smaller in diameter than the nucleus, there is not a great discrepancy. The axoneme itself has the 9+9+2 arrangement (Fig. 4d) common to Hymenoptera; 9 outer single accessory tubules, 9 doublets and 2 central single microtubules. Intertubular material is abundant with radial spokes (Afzelius rays) and indications of the inner and outer dynein arms. Two deltoid bodies, (also referred to as triangular rods, (Lensky *et al.* 1979) are present, but they are not large. Between the two bodies, and the two mitochondrial derivatives (Fig. 4d) is a single central rod, as previously report-

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Fig. 5. Cell ultrastructure of *Cephalcia* sperm (Pamphilioidea): 5a, spermatadesmata with surrounding cap material (arrowed); 5b, centriolar adjunct (small arrow) abuts nucleus at membranous complex, extending beyond the level of the basal body (arrowhead) to abut a mitochondrial derivative (large arrow); 5c, showing that the centriolar adjunct does not overly both mitochondrial derivatives with one of the two derivatives (arrowed) abutting the nucleus at the region of the membranous complex; 5d, transverse section at level of basal body showing that the centriolar adjunct extends to partially enclose the parallel mitochondrial derivative (arrowed); 5e, transverse section through axoneme showing only a single mitochondrial derivative posteriorly near the tail piece; 5f, transverse section through midregion of axoneme with two mitochondrial derivatives (note distinct sub-structure at periphery of each mitochondrial derivative); 5g, transverse sections showing acrosomal rod (r) insertions into the nucleus; 5h, transverse sections showing insertion of acrosomal rod (r) into the acrosome. Scale bar: a = 1.3 μm; b = 0.5 μm; c, d = 0.42 μm; e = 0.3 μm; f = 0.27 μm; g = 0.7 μm; h = 0.57 μm.
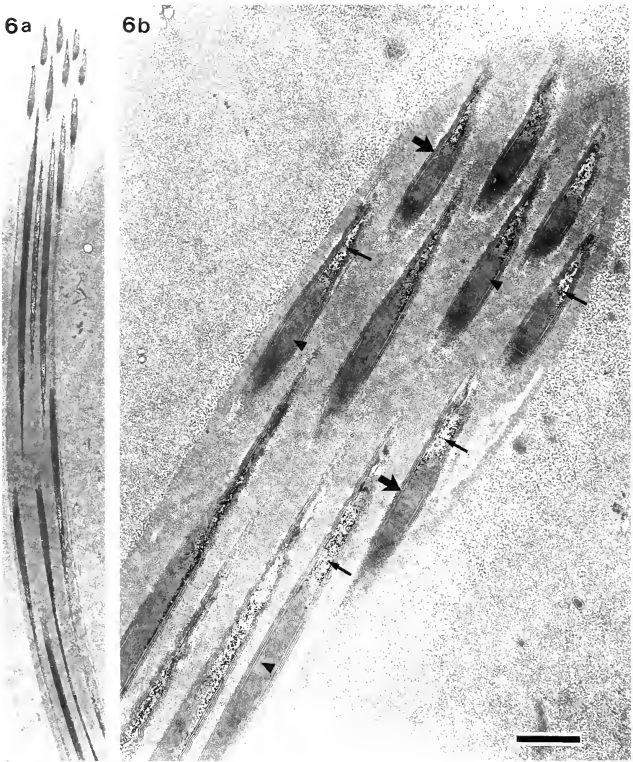
Fig. 6. Spermatatodesmata of *Xyela* (Xyeloidea): 6a, showing the extended length of the spermatodesmatal cap; 6b, showing the distinctive arrangement of the acrosome at the region of insertion into the cap with particulate material (small arrows), distinct periodicity in the core material (arrowheads; appears like longitudinal striations), and multilayered membrane coat to the acrosome (large arrows). Scale bar: a = 2.5 μm; b = 0.66 μm.

ed in ant spermatozoa (Wheeler *et al.* 1990). A tail piece is found where the axoneme has no associated mitochondrial derivatives.

Of the more basally derived sawfly superfamilies investigated, the Pamphilioidea (*Cephalcia*) represents a slightly more advanced evolutionary lineage than the Xyeloidea although it was once included in the same family. The spermatozoa of *Cephalcia* are arranged in spermatodesmata (Fig. 5a) and have heads (nucleus plus acrosome) approximately 28μm long, and tail, 75μm long. Ultrastructurally, they are very similar to those of *Tremex*, especially in terms of the size of the acrosomal rod, its position within the subacrosomal space (Fig. 5h), and its insertion into the nucleus (Fig. 5g). The most noticeable difference between the two is in the position of the centriolar adjunct. In *Cephalcia* the centriolar adjunct can be seen to run parallel to one to the pair of mitochondrial derivatives (Fig. 5b), rather than overlying both as in *Tremex*, as is evident in the region where one of the mitochondrial derivatives is found to abut the nucleus (Fig. 5c, *arrow*). For part of its length (at the level of the basal body) the centriolar adjunct contacts and even partially encloses the single mitochondrial derivative that lies parallel to it (Fig. 5d, *large arrow*). Possibly as a result of this arrangement, a region occurs at the posterior part of the sperm, where there is only a single mitochondrial derivative lying next to the axoneme (Fig 5e); here there is also only a single deltoid body, as opposed to the two found in normal section (Fig 5f). Similarly at the level of the centriolar adjunct the single mitochondrial derivative has only a single deltoid body. The axoneme is again similar to that of *Tremex* in the arrangement of elements. The ray material is particularly evident, with Afzelius rays having distinct spoke heads, and with distinct electron-opaque granules between the peripheral singlets (Bairati and Baccetti 1965).

Xyela spermatozoa, although present in spermatodesmata (Fig. 6), differ in a number of ways from those of both other sawflies described here as well as from the tenthredinoids described by Quicke *et al.* (1992). The spermatozoa are extremely long with the head (=nucleus plus acrosome) being approximately 60μm long, and the tail 150 μm long (Fig. 6a). This elongation compared with sperm of other sawflies, at all levels, viz. the acrosome, nucleus and tail, is also apparent in longitudinal section. At the anterior end the acrosomes can be seen to be asymmetrical and pointed, containing two types of material: an irregularly granular material and a core material that has an almost crystalline periodicity, aligned parallel to the long axis of the spermatozoa. In transverse section (Fig. 7) the most prominent of the features is an enlargement of one of the mitochondrial derivatives to a diameter greater than that of the axoneme (Fig. 7a), with a concomitant enlargement of that mitochondrial derivative's deltoid body (Fig. 7a, *right arrowhead*). This displaces the other mitochondrial derivative which, together with its deltoid body, now occupies an area approximately equivalent to the other, larger, deltoid body alone.

In *Xyela*, it is not immediately apparent if there is a centriolar adjunct. In some transverse sections, at the position of the smaller mitochondrial derivative/deltoid body a darker structure is present (Fig. 7b, *arrows*). This does not seem to be simply a denser mitochondrial derivative because it lacks a deltoid body and generally the two occur together (in shape it is actually closer to a deltoid body). In longitudinal section (Fig. 7c) a structure abutting on to the smaller mitochondrial derivative can be found. This closely resembles the situation in *Cephalcia*. The structure does not however extend to the nucleus like the other centriolar adjuncts found. Instead, at the region of the basal body, identifiable by the absence of the central pair of mi-
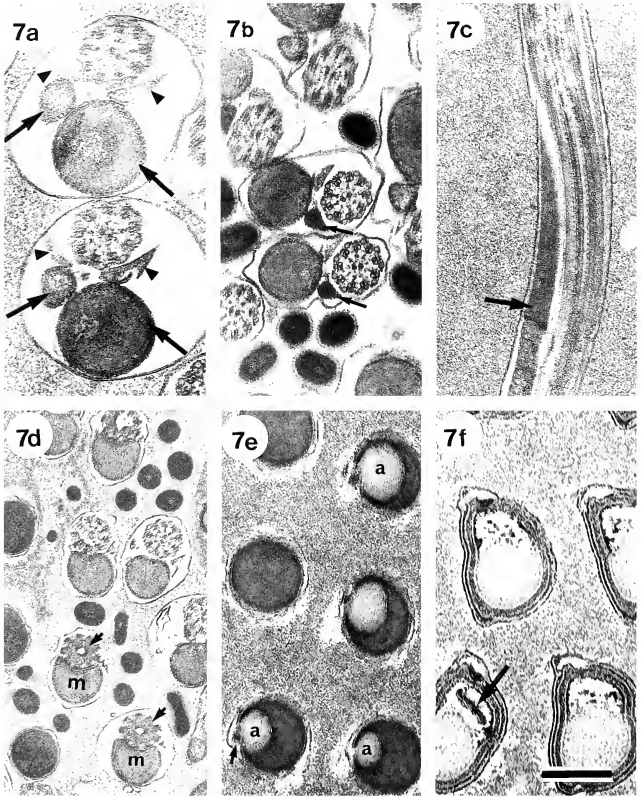
Fig. 7. Organelles of *Xyela* spermatozoa (Xyeloidea): 7a, asymmetric mitochondrial derivatives (arrows) and well-developed deltoid bodies (arrowheads); 7b, in one region the smaller mitochondrial derivative is replaced by a darker structure similar to a centriolar adjunct (arrows) (note also the numerous, smaller nuclear-like cross sections, smaller than other readily identified nuclei); 7c, longitudinal section showing a centriolar adjunct-like body (arrow) that abuts the smaller mitochondrial derivative; 7d, transverse section at the level of the basal body (arrows) showing that the centriolar adjunct-like organelle and the smaller of the two mitochondrial derivatives are both absent, and that the larger mitochondrial derivative (m) partially covers the basal body; 7e, showing asymmetric insertion of a cone of acrosomal (a) material into the nucleus isolating a

crotubules, the larger mitochondrial derivative wraps round to partially enclose the basal body and the smaller mitochondrial derivative/deltoid body is absent (Fig. 7d). If there is a centriolar adjunct, then how it terminates anteriorly and its relationship with the nucleus remains unclear. The nucleus itself appears similar to those of the other sawflies in density and membrane organisation at the level of the spermatodesmata. However, perhaps in accord with its greater length, there appears to be an area, posterior to its insertion into the cap of the spermatodesmata, that has a relatively smaller diameter and where it is significantly smaller than the tail region with its enlarged mitochondrial derivative (Fig. 7b, d).

In *Xyela* the interface of the acrosome with the nucleus also appears different. There is no discernible rod. Instead acrosomes, which have a distinct, paracrystalline substructure, contact the nucleus and may even be partially enclosed by it (Fig. 7e). This insertion is displaced to one side, and this asymmetry is also present in the acrosome itself (Fig. 7f). A ridge runs down one side of the acrosome (Fig. 7f, *arrow*). Spermatozoa are orientated within the spermatodesmata so that the ridges all point in the same direction. Interestingly, this is also the same side of the spermatozoon that the acrosome inserts into the anterior of the nucleus, although at this point the acrosomal material appears to have lost the ridge, and the acrosome at this level only shows the core of 'periodic material'. The ridge itself contains the particulate matter. In some areas the granules surround membranes resembling the multilayered coated complex that surrounds the acrosome itself. There is also an extension of the outer layers of this coat to form a small ridge to one side of the acrosome. This position of this smaller ridge is again consistent amongst the spermatozoa.

DISCUSSION

At least with regard to the ultrastructure of the spermatozoa, *Cephalcia* appears to have a better claim than *Xyela* as having sperm that may be representative of a common ancestral form. *Cephalcia* sperm are very similar to those of *Tremex*. It is mainly in the positioning of the centriolar adjunct that *Cephalcia* varies from *Tremex*, having an asymmetric location overlying only one mitochondrial derivative. *Tremex* by comparison has a centriolar adjunct overlying both mitochondrial derivatives. The arrangement of the centriolar adjunct might seem to have possible usage as a phylogenetic indicator. Unfortunately the arrangement of this organelle has often been poorly understood (e.g. Wilkes and Lee 1965), and so it is difficult to draw any conclusion from all previously reported works. From studies of bee sperm Jamieson (1987) concluded that in bees the centriolar adjunct also lies between the nucleus and one of the mitochondrial derivatives. Recently we have described the ultrastructure of the parasitic braconid wasp, *Aleiodes*, which appears to have relatively underived sperm (Quicke *et al.* 1992; Newman and Quicke 1998). The ultrastructure of individual *Aleiodes* spermatozoa closely resembles both *Tremex* and *Cephalcia*. The mitochondrial derivatives are similarly sized and the acrosomal rod is similarly positioned. The centriolar adjunct is, however, asymmetric and hence similar to *Cephalcia*. Given the primitive status proposed for *Cephalcia* this might be considered to be the archetype arrangement retained through evolution.

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small amount of membrane bound nuclear material (arrowed); 7f, showing the periodic appearance of the acrosome within the multilayered coat and membrane material (arrowed). Scale bar: a = 0.27 μm; b, c = 0.5 μm; d = 0.6 μm; e = 0.5 μm; f = 0.25 μm.

The case of *Tremex*, with symmetric centriolar adjunct overlying both mitochondrial derivatives, would have to be considered as an apomorphic development. However, it is not clear at present which of the arrangements of the centriolar adjunct represents the groundplan for either the Hymenoptera as a whole or for any of the major lineages within it, and more careful study is necessary.

As was made clear in the results, the positioning of the centriolar adjunct is not clear in *Xyela*. It appears to be asymmetric, but unlike the arrangement in other sawflies it does not appear to abut the nucleus. *Xyela* has sperm with a structure that is extremely divergent in a number of other ways; the shape and arrangement of the acrosome, the apparent absence of the acrosomal rod and the size difference in the two mitochondrial derivatives. It seems likely that these must represent a response to selective pressures subsequent to the divergence of both the other sawflies and the main body of the order of Hymenoptera.

The presence of an asymmetric centriolar adjunct in *Cephalcia* appears to cause the mitochondrial derivatives to be offset longitudinally, and this may explain why some sections through the posterior part of the spermatozoa have only a single mitochondrial derivative (e.g. Fig. 5e). Where there is only one mitochondrial derivative the deltoid body is also absent suggesting they may be a good marker for mitochondrial derivative identification.

From the present observations, it seems probable that the identification of the coat material surrounding the acrosome in many taxa may be incorrect. In the Hymenoptera, this material has been referred to as extracellular matrix (Quicke *et al.* 1992) and in some insect orders (e.g. Orthoptera) it has been reported that extracellular matrix granules accumulate around the plasma membrane of the acrosome to form an extracellular cap (Szöllösi 1974). However, these structures are

often highly complex, with layered or repeated substructure (see for example, Fig. 6b in Quicke *et al.* 1992), and it is not immediately clear how such a structure could be secreted if extracellular; the possibility that they are produced by the epithelia of a deferent duct cannot be excluded. Many plasma membranes possess a glycocalyx which comprises the carbohydrate portion of integral membrane glycoproteins and glycolipids together with associated glycosamminoglycans and proteoglycans, and these carbohydrates extend from the plasma membrane into the extracellular space. Where organelle membranes become glycosilated, as in the case of secretory granules that will eventually fuse with a plasma membrane, the coated face of the membrane that opposes the interior of the organelle is the one that will, upon fusion, face the extracellular space. In the sawflies investigated here, it is clear that the coat lies between two membranes, and is not extracellular as previously reported. An intracellular origin for this structure would at least allow a more conventional, although as yet, completely unrecognised, mechanism for its production.

ACKNOWLEDGMENTS

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A Review of the Old World Genus *Fopius* Wharton (Hymenoptera: Braconidae: Opiinae), with Description of Two New Species Reared from Fruit-infesting Tephritidae (Diptera)

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Abstract.—Two new species of the Old World genus *Fopius* are described: *ceratitivorus* from Kenya and *schlingeri* from Queensland, Australia. Both species were reared from fruit-infesting Tephritidae; *ceratitivorus* from *Ceratitis* and *schlingeri* from *Bactrocera*. Details are provided on differentiation of the known species of *Fopius*, with discussion of their hosts, host specificity, and distribution. The parasitoids of fruit-infesting tephritids from Kenya are closely related to those from Madagascar.

The most recent comprehensive classification of the Opiinae is the three-volume monograph published by Fischer (1972, 1977, 1987). This collective work established a basis for more intense scrutiny of the Opiinae, resulting in several subsequent modifications and additions to the classification, including the description of the Old World genus *Fopius* (Wharton 1987, van Achterberg and Maetô 1990). The numerous name changes affecting opiine parasitoids of fruit-infesting Tephritidae were recently reviewed by Wharton (1997b), who also provided suggestions for delineation of species groups within the genus *Fopius*. Additional changes in nomenclature, some of these affecting opiine parasitoids of tephritids, were published by van Achterberg and Salvo (1997) and Quicke et al. (1997). Keys to most of the species of *Fopius* can be found in Wharton and Gilstrap (1983) and Fischer (1987), with both works treating the species under the generic name *Biosteres*. Palacio et al. (1992) provide additional information on separation of males and immatures of two sympatric species.

All opiine braconids reared to date are koinobiont endoparasitoids of cyclorrhaphous Diptera, and all emerge from the puparium of their hosts. Hosts are known for one-third of the approximately 1500 described species, with most of these records pertaining to Agromyzidae and Tephritidae. All reared species of *Fopius* are parasitoids of Tephritidae. Summaries of the literature on hosts and biology of the opiine parasitoids of Tephritidae can be found in Fischer (1972, 1977, 1987), Clausen (1978), Wharton and Marsh (1978), Wharton and Gilstrap (1983), Gilstrap and Hart (1987), Wharton (1989, 1997a, b), Messing (1996), Sivinski (1996), and Sivinski et al. (1997).

The primary purpose of the work presented here is to facilitate on-going studies in biological control by providing names for two recently discovered, undescribed species. Both species are of interest with respect to tephritid biological control because of their potential for attacking eggs or early instars, and one of these is a native parasitoid of the Mediterranean fruit fly, *Ceratitis capitata* (Wiedemann). The use of parasitic Hymenoptera for the biological control of tephritid pests has received considerable attention in recent years (Knipling 1992, Waterhouse 1993, Head-

rick and Goeden 1996, Purcell, 1998), and there are active programs currently underway in several countries.

MATERIALS AND METHODS

With the exception of C. Granger's type material from the Paris Museum and a single, swept specimen of *Fopius schlingeri*, n. sp., all material used in the descriptions of the new species was reared from fruit in association with various fruit-infesting Tephritidae. In some cases, parasitoids were reared from bulk fruit samples, with unconfirmed host associations. Most of the material, however, was reared from isolated puparia. In several of the rearings for *Fopius ceratitivorus*, n. sp., puparia were individually isolated prior to emergence. Though this procedure decreases the percent emergence (due primarily to desiccation and/or physical damage), it enables correct association of the wasp with the host from which it was reared.

Specimens of the newly described species have been deposited in the following institutions: University of Queensland, Brisbane (UQBA), Australian National Insect Collection, Canberra (ANIC), Texas A&M University, College Station (TAMU), Bernice P. Bishop Museum, Honolulu (BPBM), Hawaii Department of Agriculture, Honolulu (HDA), Queensland Department of Primary Industries, Indooroopilly (QDPI), Nationaal Natuurhistorisch Museum, Leiden (RMNH), The Natural History Museum, London (BMNH), National Museum of Kenya, Nairobi, International Centre of Insect Physiology and Ecology, Nairobi (ICIPE), and U.S. National Museum of Natural History, Washington, D. C. (USNM).

Descriptive terminology follows Wharton (1987, 1988, 1997b) and Sharkey and Wharton (1997), and is based largely on the works of Fischer (1972). A tabular summary is presented rather than a dichotomous key to facilitate assessment of relationships and point out gaps in our knowledge.

IDENTIFICATION, RELATIONSHIPS, HOSTS, AND DISTRIBUTION PATTERNS

The tephritid parasitoids in the genus *Fopius* are readily distinguished from other opiines by the possession of crenulate notauli extending posteriorly to the mesonotal midpit, an oblique ridge ventral-laterally on the propleuron, a short second submarginal cell (3RSa ≤ 2RS), and a long ovipositor (1.3–4.5 × longer than mesosoma). Character states useful for identifying species with known tephritid host records are provided in Table 1, and the characters themselves are discussed below. Eight closely related species for which host records are lacking have also been included in the table. The table is deemed more informative than a dichotomous key because it provides preliminary data for phylogenetic analysis, which is beyond the scope and purpose of the present work, as well as providing supplemental characters for assistance in identification. More than half of the species in Table 1 (including several of the tephritid parasitoids) are known only from the type or the type plus a few other specimens. Additional collecting is essential before progress can be made in our understanding of these species. Individual species and species groups are treated further following discussion of the characters.

Character 1.—Striate sculpture on the second and third metasomal terga. 0 = striae absent; 1 = striae present on tergum 2 only; 2 = striae present on tergum 2 and at least base of tergum 3. For most species, assignment of either character state 0 or character state 1 is unambiguous. *Fopius deeralensis* (Fullaway), however, has weak striae on tergum 2, and the sculpture is not always readily visible (see diagnosis following description of *F. schlingeri*, n. sp.). *Fopius skinneri* (Fullaway), from the Philippines, is the only species in which striae are usually

Table 1. Matrix of coded character states for species in the genus *Fopius* (see text for character definition).

	1	2	3	4	5	6	7	8	9	10	11	12	13	14
denticulifer (van Achterberg & Maetô)	0	0	0	2	5	1	0	0	3	1	0	4	4.1–4.6	0
marangensis (Fischer)	0	0	0	2	5	1	0	0	2b	1	?	4	1.7	?
taiwanicus (Fischer)	0	0	0	2	5	1	0	0	2b	1	?	4	~3.0	0
ruficornis (Granger)	0	1	0	1,2	3	1	0	0	1	2	0	2	1.5	0
rubrithorax (Granger)	0	1	0	1	2	0	1	1	1	0	1	0	1.3	1
bevisi (Brues)	0	0	1	1	1	0	1	1	0	0	1	0	2.2–2.3	1
desideratus (Bridwell)	0	0	1	1	1	0	1	1	0	0,1	1	0	3.0–3.2	1
niger (Széplgeti)	0	0	1	1	1	0	1	1	0	1	0,1	0	2.6–2.7	1
ottotomoanus (Fullaway)	0	0	1	1	1	0	1	1	0	1	1	0	2.8	1
rufotestaceus (Granger)	0	0	1	1	1	0	1	1	1	0	0,1	0	2.0–2.3	1
alternatus (Tobias)	1	0	0	0	0	0	?	0	3	1	?	2	~1.25	?
arisanus (Sonan)	1	0	0	0	0	0	0	0	2	0,1	0	3	2.5–2.8	0
carpomyiae (Silvestri)	1	0	0	0	0	0	0	0	2a	0	1	2	1.5–1.7	0
myolejae (Tobias)	1	0	0	0	0	0	?	0	3	1	?	2	~2.0	?
persulcatus (Silvestri)	1	0	0	0	0	?	0	0	2a	0	?	3	?	?
skinneri (Fullaway)	2	0	0	0	0	0	0	0	2b	1	0	3?	~2.65	0
vandenboschi (Fullaway)	1	0	0	0	0	0	0	0	2b	0,1	0	2	2.5–2.7	0
ceratitivorus n. sp.	0	0	0	0	5	0	0	0	0	0	0,1	2	1.7–1.9	0
longicauda (Granger)	0	0	0	0	0	0	0	0	1	0	0	2	2.6	1
pyknothorax (Fischer)	0	0	0?	?	?	?	?	0,1	0	1	?	?	?	?
silvestrii (Wharton)	0	0	0	0	0	0	0	0	0	0	1	0	2.5–2.6	0
deeralensis (Fullaway)	1	0	0	0,2	5	0	0	0	4	0	0	1	3	1
schlingeri n. sp.	0	0	0	0	5	0	0	0	4	0	0	3	2.3–2.5	1
caudatus (Széplgeti)	0	0	0	1	4	0	0	0,1	0	1	1	3	2	1

present on tergum 3, though the sculpturing on tergum 3 is usually not extensive.

Character 2.—Occipital carina. 0 = present laterally; 1 = completely absent. The occipital carina is absent mid-dorsally in *Fopius*, but present laterally in nearly all species. There is also some variation among species in the height of the occipital carina, as exemplified by the two species described below, and this variation may eventually prove useful in demonstrating character state transformations leading to complete loss of the occipital carina.

Character 3.—Setal pattern on the ovipositor sheath. 0 = two or more rows of densely spaced setae; 1 = setae sparse, at most with a row of long, moderately sparse setae basally and short, widely spaced setae apically. This coding is useful for segregating groups of species, but oversimplifies the complexity of the character states that may eventually be

useful for delineation of additional species. Setal rows are difficult to count, however, and many of the specimens examined were in such poor condition that it could not be determined if setae were sparsely arranged or merely broken off. Of the species coded 0 in Table 1, setal density was greatest in *F. denticulifer* (van Achterberg and Maetô) and least in *F. schlingeri*, n. sp. and *F. rubrithorax* (Granger).

Character 4.—Ventral margin of clypeus. 0 = thin, sharp, and evenly convex, without median projection; 1 = somewhat thickened medially, and slightly protruding, with labrum sometimes partially exposed; 2 = with median, ventrally-directed, tooth-like (i. e. pointed) projection (clypeus completely occludes labrum). Differences between states 0 and 1 may not be apparent without dissection to reveal the thickened margin. The tooth-like projection is very small in *deeralensis,* and the margin thinner than

in members of the *F. marangensis* (Fischer) species group, as reflected by its coding in Table 1.

Character 5.—Pattern of sculpture and setae on frons. 0 = densely setose and punctate, the punctures tending to coalesce to some degree, giving the appearance of transversely rugulose lines (Fig. 4), midline longitudinally rugose; 1 = transversely striate and impunctate over middle half of frons, with deep, widely spaced punctures laterally; 2 = laterally as in state 1, but largely unsculptured medially (at most with a few, irregular, very weak wrinkles), midline with sharp carina basally; 3 = smooth, impunctate, depressed along midline; 4 = broad, transverse band of deep punctures extending from ocelli to eye, otherwise smooth; 5 = densely setose and punctate, the punctures discrete, with no indication of rugosities as in state 0; for state 5, the punctures are very densely spaced in *marangensis*, *F. taiwanicus* (Fischer) and *denticulifer*, less so in *deeralensis* and *schlingeri*, and least in *ceratitivorus* (where they are virtually absent basal-laterally).

Character 6.—Postpetiole carina. 0 = well developed; 1 = weak to absent.

Character 7.—Relative length of first two flagellomeres. 0 = first flagellomere about same length as second (ratio varying from 0.9–1.1); 1 = first flagellomere distinctly shorter than second (0.8 × length or less).

Character 8.—Shape of petiole. 0 = petiole length equal to or shorter than apical width, strongly widening apically; 1 = petiole appearing more parallel-sided, with length distinctly greater (at least 1.3 times) than apical width. The petiole of *F. caudatus* (Szépligeti) is somewhat intermediate, as reflected by its coding in Table 1. The petiole is not necessarily more parallel-sided in state 1 than in state 0 (width at apex may be twice width at base in both), but appears to be so because the petiole is longer in state 1.

Character 9.—Geographic distribution. 0 = continental Africa; 1 = Madagascar; 2 = southern Asia (2a = India; 2b = southeast Asia, including Indonesia, Philippines, and Taiwan); 3 = Japan, eastern Russia; 4 = northeastern Australia. Distribution patterns given here do not reflect the successful introductions of *F. arisanus* (Sonan) and *F. vandenboschi* (Fullaway) to Hawaii and *arisanus* to Central America.

Character 10.—Color of mesosoma. 0 = largely pale (red, orange, yellow, or brownish-white); 1 = dark black to brown; 2 = pale with large black spots on mesoscutum and mesopleuron. Assessment of coloration is somewhat problematic due to postmortem changes, especially in shades of red, yellow, and orange. Also, there is almost a complete continuum in shades of red from pale through nearly black (*skinneri* is dark reddish-brown). Two of the species for which there is abundant material (e. g. *arisanus* and *vandenboschi*) are color-variable.

Character 11.—Dorsal carinae of petiole. 0 = dorsal carinae extending posteriorly beyond spiracle for at least a short distance as a distinctly elevated ridge; 1 = dorsal carinae not extending past spiracle as a distinctly elevated ridge. At least three species are variable in this feature, as reflected by the coding in Table 1.

Character 12.—Configuration of ovipositor tip. 0 = distinct double node dorsally; 1 = weak node or swelling dorsally; 2 = parallel-sided at apex, with little or no node; 3 = strongly tapered apically to a fine, smooth point, narrowest subapically; 4 = strongly tapered apically as in state 3, but with tip flattened dorsal-ventrally. States 1 and 2 merely represent different degrees of development of a transverse ridge near the tip of the ovipositor; and states 3 and 4 represent

conditions for which it is hypothesized here that nodes and/or transverse ridges have been lost. Detailed SEM work is still needed to elucidate these character states for many of the species.

Character 13.—Approximate ovipositor length. Values given are total ovipositor length divided by length of mesosoma. Accurate measurement of ovipositor length often requires dissection, which was not possible for some of the species.

Character 14.—Mesopleural setae. 0 = at least some setae present on mesopleuron dorsal to the speculum (the dorsal-posterior section of the mesopleuron); 1 = setae completely absent above speculum.

Table 1 has been arranged to facilitate identification of both species and species groups. Several of the species groups are quite distinctive and thus readily recognizable (Wharton 1997b), and these will be treated first in the following discussion. Since the focus of this paper is on parasitoids of fruit-infesting Tephritidae, *F. ruficornis* (Granger) and the *marangensis* species group are not further discussed because there are no host records and the species are readily identified using Table 1.

The *desideratus* species group of *Fopius* consists of *bevisi* (Brues), *desideratus* (Bridwell), *niger* (Szépligeti), *ottotomoanus* (Fullaway), and *rufotestaceus* (Granger). As noted by Wharton and Gilstrap (1983), the species of the *desideratus* group are very similar to one another. For example, *rufotestaceus* is virtually identical to *bevisi*, but has the mesosoma red rather than yellow or yellow-orange. Unfortunately, few specimens have been available for study of intraspecific variation in the color patterns currently used to differentiate the species of this group. There are published host records (summarized by Wharton and Gilstrap 1983) for all but *rufotestaceus*. Most of the specimens examined were reared from *Dacus* infesting Cucurbita-

ceae. Both *desideratus* and *ottotomoanus* have been recorded from undetermined species of *Dacus* in cucurbits (Bridwell 1919, Fullaway 1957), and *niger* was reared from *D. humeralis* Bezzi (Wharton and Gilstrap 1983). The few remaining published records (Bridwell 1919, Clausen et al. 1965) are from *Ceratitis anonae* Graham on *Myrianthus arboreus* (specimens of *desideratus*) and *Trirhithrum queritum* Munro on *Strychnos usambarensis* (a specimen tentatively identified as *bevisi*). All members of this species group have large, sub-apical nodes on the ovipositor. Based on comparisons of ovipositor morphology with species of known biology in the related genus *Diachasmimorpha* Ashmead, it is suggested here that members of the *desideratus* group attack late instar larvae of their hosts. Members of this group are known from Cameroon, Kenya, Nigeria, Tanzania, South Africa, and Madagascar, and undoubtedly occur throughout sub-saharan Africa. *Fopius rubrithorax* (Granger) is very similar to the other species mentioned here, despite the reduced sculpture on the frons and a slightly more setose ovipositor sheath; and I therefore place it as a basal member of this group. This placement assumes that both the reduced setal pattern on the ovipositor sheath and the pattern of sculpture on the frons of the five other species of the *desideratus* group are derived relative to the conditions in *rubrithorax*; this remains to be tested in a more rigorous fashion.

The *persulcatus* species group of *Fopius*, characterized largely by striate sculpture on the second metasomal tergum, consists of *alternatae* (Tobias), *arisanus* (Sonan), *carpomyiae* (Silvestri), *myolejae* (Tobias), *persulcatus* (Silvestri), *skinneri* (Fullaway), and *vandenboschi* (Fullaway). The species are very similar to one another, but differ primarily in coloration, length of ovipositor, and configuration of the ovipositor tip. Following their successful introduction to Hawaii during the biological control program against oriental fruit fly (Clausen et

al. 1965), *arisanus* and *vandenboschi* were intensively studied, and much is now known about their biology (with most of the early literature on *arisanus* published under the name *Opius oophilus* Fullaway). In their native range, centered around Malaysia and Indonesia, both are parasitoids of tephritids in the dacine genus *Bactrocera* Macquart. Unlike *skinneri*, neither is attracted to cucurbit-infesting flies. Other than the original host records little is known about the other species in this species group, including *skinneri*. Data on *persulcatus* (type material reared from *B. caryeae* Kapoor) are particularly problematic because of widespread confusion regarding the identity of this species during the Hawaiian oriental fruit fly program, and the subsequent description of several subspecies (Fischer 1965). The other species (viz. *carpomyiae*, *myolejae*, and *alternatae*) have been reared, respectively, from trypetine tephritids in the genera *Carpomya* Costa, *Myoleja* Rondani, and *Rhagoletis* Loew. Based on the similarities in the shape of the ovipositor tip, all species in this species group preferentially attack either the egg or early instar larva of their host (though all eventually emerge from the puparium). This biology, however, has only been confirmed for *arisanus* (attacking eggs) and *vandenboschi* (attacking primarily first instars). The species of this group are known from Pakistan and India east through Indonesia and north through Taiwan, Japan, and far eastern Russia.

Wharton (1997b) delimited a *silvestrii* species group containing *longicauda* (Granger), *pyknothorax* (Fischer), and *silvestrii* (Wharton). One of the species described below, *ceratitivorus*, also belongs here. This group is currently defined largely by the absence of features that define the three species groups already mentioned: the clypeus lacks a median tooth on the ventral margin, the setae on the ovipositor sheath are not reduced, and the second metasomal tergum is unsculptured. Reduction of features on the dorsal

valve of the ovipositor suggests either a sister group relationship to the *persulcatus* species group or a parallel loss relative to the *desideratus* species group, but this hypothesis needs to be tested more rigorously. Both *silvestrii* and *ceratitivorus* have been reared from ceratitine tephritids infesting coffee, and *silvestrii* has also been reared from *Dacus bivittatus* (Bigot) infesting squash (Steck et al. 1986, Wharton 1987). Other members of this group have not been reared. Members of the *silvestrii* species group have much the same distribution pattern as those of the *desideratus* species group, and are differentiated from one another largely by color (*silvestrii* and *pyknothrorax* are dark, *longicauda* and *ceratitivorus* are pale) and ovipositor length.

The remaining three species, *caudatus*, *deeralensis*, and *schlingeri*, do not readily cluster into distinctive species groups. Identification of *deeralensis* and *schlingeri* is discussed below under the diagnosis following the description of *schlingeri*; *caudatus* is readily separated from all other species of *Fopius* by the distinctive band of setae and punctures on the frons. Both *deeralensis* and *schlingeri* are from Queensland, where (as noted below under the description of *schlingeri* and in Clausen et al. 1965) they have been reared from various species of *Bactrocera* in a variety of host fruits. *Fopius caudatus* has thus far been reared exclusively from ceratitines (Steck et al. 1986). It is known from tropical regions of both eastern and western Africa, where it has been reared from coffee berries containing the ceratitines *Trirhithrum coffeae* Bezzi, *C. anonae* and *C. capitata* as well as from other fruits containing *anonae*. Specific host records for *caudatus* need confirmation, in part because of earlier confusion regarding its identity (Wharton 1987). This species resembles members of the *desideratus* species group in the morphology of the clypeus and petiole, but has a distinctly different ovipositor (strongly narrowed, suggesting oviposition in the host egg) as well as several fea-

tures unusual for members of the genus *Fopius* (Wharton 1997b).

A few generalizations can be made about hosts and distribution patterns, even though our current knowledge is somewhat limited. Rearing records from within their native ranges (Clausen et al. 1965, Steck et al. 1986) suggest that the 16 species for which we have host records are restricted to fruit-infesting tephritids, but that there are different levels of specificity. Some are currently known only from a single host, others (e. g. *caudatus* on ceratitines) have only been reared from a narrow group of hosts, and several have been reared from hosts in two or three different tribes. Most of the known hosts belong to the tribes Ceratitini and Dacini, both in the tephritid subfamily Dacinae (White and Elson-Harris 1992). Except where they have been introduced for biological control, members of the *persulcatus* group occur outside the range of fruit-infesting Ceratitini, and several of them have been reared from Trypetini in the tephritid subfamily Trypetinae. Where introduced outside their native range for biological control, *arisanus* and *vandenboschi* have been able to attack other fruit-infesting tephritids (Clausen et al. 1965, Wharton et al. 1981). Yet, while some of the species of *Diachasmimorpha* Viereck introduced to Hawaii to control fruit-infesting Tephritidae occasionally attack gall-making (but not flower-infesting) Tephritidae, *arisanus* and *vandenboschi* do not (Duan et al. 1996).

The genus *Fopius* provides evidence for a close relationship between the fauna of Madagascar and that of adjacent regions of continental Africa (as do its host tephritids). Although a few of the Madagascar elements (notably *rubrithorax* and especially *ruficornis*) are unique in several respects, both *rufotestaceus* and *longicauda* have their closest known relatives (*bevisi* and *ceratitivorus* respectively) on the adjacent mainland.

DESCRIPTIONS

Fopius ceratitivorus Wharton, new species
(Figs. 1, 2, 7, 8, 10, 11, 13–15, 21)

Female.—**Head:** 1.55–1.75 (m=1.65±.07) times broader than long; 1.25–1.35 times broader than mesoscutum; face distinctly punctate throughout, pattern variable but spacing between most punctures about equal to diameter of punctures; setae short, somewhat decumbent; midridge low, polished, more prominent dorsally, extending between antennal bases (toruli) as a low, flat ridge; distance between toruli greater than distance from torulus to eye; frons longitudinally rugulose along midline, highly polished and weakly depressed basally on either side of rugulose midline, deeply punctate elsewhere, the patch of punctures on each side anteriorad ocelli usually more densely spaced, occasionally with punctures coalescent, ocellar triangle almost completely margined by a crenulate sulcus. Occipital carina in lateral view extending dorsally from base of mandible to a point just below top of eye. Clypeus in profile slightly bulging dorsomedially; ventral margin of clypeus thin and evenly convex, not thickened medially; setae on clypeus very sparse, at least twice length of those in middle of face, weakly directed ventrally; clypeus completely concealing labrum when mandibles closed. Eye (at 50×) apparently bare, large, 2.85–3.8 (m=3.2±0.3) times longer temple; temples very weakly receding in dorsal view; width of head at temples slightly less than width at eyes. Antenna 31–37 segmented; roughly 3.0–3.1 times longer than mesosoma; first flagellomere 0.9–0.95 times length of second. Maxillary palps longer than height of head. **Mesosoma:** 1.25–1.35 (m=1.3±0.05) times longer than high, 1.55–1.7 (m=1.65±0.05) times longer than broad. Median lobe of mesoscutum with 2 parallel, rugosopunctate, longitudinal grooves extending more than half length of median lobe, median lobe otherwise setose, with
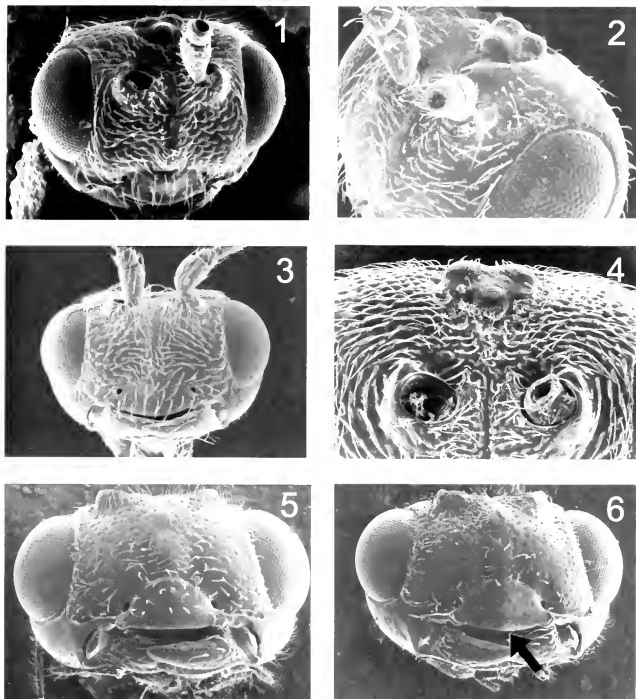
Figs. 1-6. Heads of *Fopius* spp.: 1 and 2, *ceratitivorus* frons and face; 3, *schlingeri* face and clypeus; 4, *arisanus* frons; 5, *schlingeri* face and clypeus; 6, *deeralensis* face and clypeus (most setae broken), arrow = median projection on ventral margin of clypeus.

scattered, deep punctures; lateral lobes bare and impunctate medially, with numerous, relatively long, inwardly directed setae around margins; notauli broadening posteriorly, distinctly crenulate throughout, with pits usually becoming elongate posteromedially where the ridges between the pits form a small strigose area; space between strigose area and scutellar sulcus with scattered, deep punctures, posteromedian area either broadly and very shallowly depressed or with a shallow, more discrete midpit. Scutellar sulcus broader medially than laterally, the posterior margin with a distinct median excavation; number of longitudinal ridges in sulcus

variable. Metanotum with relatively low median ridge. Propodeum finely, densely rugose, the sculpture without obvious pattern; elevated median longitudinal carina usually distinct only on anterior 0.25–0.35; propodeum laterally not separated from metapleuron by a well-defined pleural carina, the demarcation represented only by the transition to the weakly sculptured dorsal portion of the metapleuron. Sternaulus broad, deep, crenulate throughout, extending posteriorly roughly 0.7 times distance from anterior margin of mesopleuron to mid coxa; crenulate sculpture extending dorsally along anterior margin of mesopleuron through subalar depression; posterior margin crenulate ventrad speculum, but with unsculptured sulcus dorsally; mesopleural disc setose throughout; postpectal carina present, but variously developed. **Wing**: Stigma 2.7–2.9 (m=2.85±0.1) times longer than wide, with r arising slightly distad its midpoint; 2RS weakly sinuate, 1.2–1.45 (m=1.3±0.05) times longer than 3RSa; 3RSa 1.55–2.5 (m=2.1±0.3) times longer than r; 3RSb ending slightly but distinctly anteriorad wing tip; (RS+M)a sinuate; (RS+M)b present, m-cu nearly always arising distinctly basad 2RS; 1cu-a inclivous, usually postfocal relative to 1M but varying from interstitial to postfocal by 0.4 times its length. Hind wing m-cu reclivous, straight or very weakly recurved near wing margin, extending to wing margin or nearly so as well-developed, deeply impressed crease, usually weakly pigmented anteriorly. **Metasoma**: Petiole 0.95–1.05 (m=1.0±0.05) times longer than apical width, apex 1.80–2.15 (m=1.95±0.1) times wider than base; densely and finely striate; dorsal carinae well-developed over basal two-thirds, weaker posteriorly but distinct to posterior margin, carinae very weakly converging, with distance between carinae at posterior margin roughly equal to distance to lateral margin; dorsope present but not extending basally as a deep pit. Metasoma unsculptured beyond petiole. Hypopygium strongly narrowed and

pointed posteriorly but short, not greatly attenuate. Ovipositor tip weakly narrowed apically, without distinct dorsal node or carina but with weak ventral serrations; 1.65–1.95 (m=1.8±0.1) times longer than mesosoma; ovipositor sheath densely setose with multiple rows of at least 30 setae each, the number of rows difficult to distinguish because of density of setae; sheath 1.35–1.55 (m=1.45±0.05) times longer than mesosoma. **Color**: Pale, yellow to orange, the exact hue dependent largely on manner of preservation; ovipositor sheath, veins, and stigma brown; antenna brown, with scape, pedicel, and basal flagellomeres usually yellow to orange medially. Wings hyaline.

Male.—As in female except eye 2.9±0.25 times longer than temple; antenna 30–35 segmented; petiole narrowed at apex, 1.1–1.25 (m=1.15±0.05) times longer than apical width, apex 1.6–1.95 (m=1.75±0.1) times wider than base; dorsope less distinct. **Length**: 2.0–3.4 (♀) and 1.85–2.9 (♂) mm.

Hosts.—This species has been reared from isolated puparia of fruit-infesting Tephritidae attacking coffee in central Kenya. It has also been reared from bulk samples of coffee. The tephritids from these samples, in order of abundance, were *Ceratitis capitata*, *C. rosa* Karsch, and *Trirhithrum coffeae*. All are members of the tribe Ceratitini, subtribe Ceratitina.

Material examined.—Holotype female, "Kenya: Ruiru C. R. F. 17.IX.1996 ex: tephritid on coffee berries Ref. No. CB03" Deposited in Kenya National Museum, Nairobi. Paratypes (BMNH, BPBM, RMNH, HDA, ICIPE, TAMU, USNM): 5♀, 7♂, "Kenya: Nairobi 20.v.1997 ex: *Ceratitis capitata*, coffee M. Ramadan & R. Messing"; 33♀, 25♀, "Kenya E. Province, Mbeere Distr Mbeti south Rurima 30.iv.97 ICIPE Fruitfly Project ex Fruitfly on Coffee berries"; 1♀, 1♂, "Kenya: Ruiru 15mi NNE Nairobi 10.iv.1995 ex: coffee No. CB05 ICIPE Collections"; 1♀, "Kenya: Western Prov. Koru iv.1995 ex. Coffea caneophora CAB Collections" and, 1♂
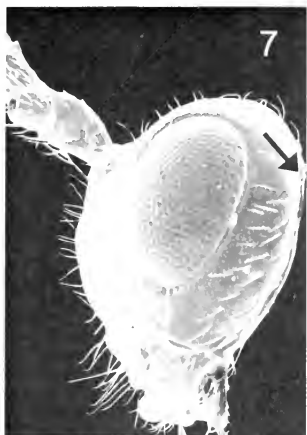
Figs. 7-10. *Tapus* spp.: 7, *ceratiticornis* head, arrows — top of occipital carina and mid-dorsal elevation of clypeus; 8 and 10, *ceratiticornis* dorsal view of mesosoma; 9, *schlingeri* dorsal view of mesosoma

"Kenya: E. Province Mbeere District Rurima Farm 0°38'29"S, 37°29'49"E 3.x.1997 ex tephritid in coffee Wharton, Kimani, Overholt." This species is known only from central Kenya.

Diagnosis.—This species closely resembles *longicauda*, known only from Madagascar. The two species are similarly colored, have a densely punctate frons, densely setose ovipositor sheath, and identical configuration of the clypeus. *Fopius ceratitivorus* differs from *longicauda* primarily in the possession of a shorter ovipositor (sheaths at least 2 times longer than mesosoma in *longicauda*). The median lobe of the mesoscutum and the junction of the notauli (Fig. 10) are also more heavily sculptured in *ceratitivorus* than in *longicauda*, and hind wing m-cu is straighter. Both *ceratitivorus* and *longicauda* differ from other Old World species of *Fopius* either in coloration, sculpture of the frons, length of ovipositor, and/or shape of the clypeus and its relative degree of concealment of the labrum. From other orange opiines reared from tephritids in coffee in Kenya, *ceratitivorus* may be readily distinguished by the short second submarginal cell with fore wing m-cu distinctly separated from 2RS (Fig. 21) and by the completely sculptured notauli.

Discussion.—I place *ceratitivorus* in the *silvestrii* species group of *Fopius* (Wharton 1997b). The ovipositor tip of *ceratitivorus*, though narrowed, does not have exactly the same morphology as found in *arisanus* and *schlingeri* n. sp. Thus, females probably do not oviposit in host eggs, but based on the shape of the ovipositor tip, they may attack early instars. The same may be true of *longicauda*, the holotype of which appears to have a similar ovipositor.

A weak negative correlation was observed between body length and relative length of the ovipositor, but the sample size (N=10) was too small to confirm this apparent trend.

Fopius schlingeri Wharton, new species
(Figs. 3, 5, 9, 12, 16, 18–20)

Female.—**Head:** 1.55–1.65 (m=1.6±.05) times broader than long; 1.3–1.4 (m=1.35±.05) times broader than mesoscutum; face distinctly punctate throughout, pattern variable but spacing between most punctures distinctly greater than diameter of punctures; setae short, somewhat decumbent; midridge low, polished, narrower dorsally, extending between toruli; distance between toruli varying from slightly to distinctly greater than distance from torulus to eye; frons with polished, weakly elevated, crenulately margined, triangular projection extending from median ocellus at least half distance to torulus; frons otherwise punctate, the punctures anteriorad ocellar field dense, with spacing between punctures about equal to diameter of punctures; ocellar triangle margined at least in part by an impressed line. Occipital carina in lateral view extending dorsally from base of mandible to about middle of eye. Clypeus in profile weakly to distinctly bulging dorsomedially; ventral margin of clypeus thin and weakly but evenly convex, not thickened medially nor with median projection; setae on clypeus sparse, about twice length of those on face, weakly directed ventrally; ventral margin of clypeus not sufficiently convex to completely conceal labrum when mandibles closed. Eye usually with 1–4 minute setae visible in dorsal view, very large, 5.3–7.5 (m=6.45±0.75) times longer than temple; temples weakly receding in dorsal view; width of head at temples about 0.9 times width at eyes. Antenna 41–47 segmented; roughly 3.5 times longer than mesosoma; first flagellomere equal in length to second. Length of maxillary palps equal to height of head. **Mesosoma:** 1.25–1.35 (m=1.3) times longer than high, 1.75–1.80 times longer than broad. Median lobe of mesoscutum with 2 parallel, unsculptured, longitudinal grooves extending more than half length
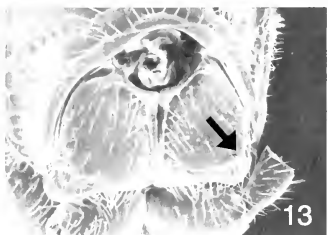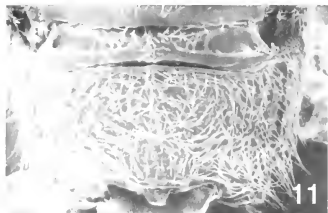
Figs. 11–16. *Topus* spp. 11, *ceratiicornis* propodeum; 12, *schlingeri* propodeum; 13 and 14, *ceratiicornis* propleuron, arrow = oblique carina; 15, *ceratiicornis* petiole; 16, *schlingeri* petiole

Figs. 17 and 18.   Ovipositors of *Fopus* spp: 17, *deeralensis*; 18, *schlingeri*.

of median lobe, median lobe otherwise se-
tose with numerous, very fine, widely
spaced punctures; lateral lobes with nu-
merous, relatively long setae around mar-
gins and more sparsely scattered setae me-
dially; notauli distinctly crenulate though-
out, meeting posteriorly in a clearly de-
fined midpit that often extends narrowly
to posterior margin. Scutellar sulcus par-
allel sided or nearly so, usually with 3
well-developed longitudinal carinae plus
several additional weaker ones. Metano-
tum with distinctly elevated median
flange posteriorly. Propodeum densely ru-
gose, the sculpture largely without obvi-
ous pattern though elevated median lon-
gitudinal carina distinct on anterior 0.25,
and posterior 0.25 often with remnants of
the parallel ridges from a median areola;
propodeum laterally not separated from
metapleuron by a well-defined pleural ca-

rina, the demarcation represented only by
the transition to the weakly sculptured
dorsal portion of the metapleuron. Ster-
naulus broad, deep, crenulate throughout,
extending posteriorly roughly 0.7 times
the distance from anterior margin of me-
sopleuron to mid coxa; crenulate sculpture
extending dorsally along anterior margin
of mesopleuron throughout subalar de-
pression; posterior margin crenulate ven-
trad speculum, with unsculptured sulcus
dorsally; mesopleural disc setose; postpec-
tal carina well developed medially. **Wing:**
Stigma 2.6–3.0 (m=2.8±0.15) times longer
than wide, with r arising slightly distad its
midpoint; 2RS nearly as sinuate as
(RS+M)a, 1.15–1.3 (m=1.25±.05) times
longer than 3RSa; 3RSa 1.7–2.25
(m=1.9±0.2) times longer than r; 3RSb
ending nearly at wing tip; (RS+M)a sin-
uate; (RS+M)b present and fairly long,

roughly 0.25 times length of m-cu; 1cu-a inclivous, usually slightly postfurcal relative to 1M but varying from nearly interstitial to postfurcal by 0.5 times its length. Hind wing m-cu strongly reclivous, distinctly recurved near wing margin, extending to wing margin or nearly so as a deeply impressed, completely pigmented crease. **Metasoma**: Length of petiole 0.85–0.95 (m=0.9±0.05) times width at apex; apex 2.3–2.5 (m=2.4±0.1) times wider than base; moderately and somewhat irregularly striate posteriorly; dorsal carinae well-developed over basal two-thirds, weaker posteriorly, often indistinct at posterior margin, parallel to very weakly converging posteriorly; dorsope weakly developed. Metasoma unsculptured beyond petiole. Hypopygium strongly narrowed and distinctly pointed at extreme posterior end, but short, not greatly attenuate, length along midline about 0.55 times width at base. Ovipositor tip strongly narrowed subapically, without dorsal node or carina, ventral serrations indistinct to absent; 2.3–2.55 (m=2.4±0.1) times longer than mesosoma; ovipositor sheath moderately setose with 3 rows of setae, two of which have 30–35 setae per row with the third row more sparsely setose, distinct tuft of longer setae at apex, sheath 2.0–2.25 (m=2.09±0.1) times longer than mesosoma. **Color**: Orange; propleuron and propodeum often paler, at least in part, sometimes nearly white; ovipositor sheath, hind tarsi, flagellum, and sometimes pedicel dorsally brown to light brown; base of arolium dark brown. Wings weakly to distinctly infumate: more noticeably infumate in larger specimens.

Male.—As in female except eye distinctly smaller, 4.4–5.85 (m=5.15±0.5) times longer than temple; petiole narrower at apex with length equal to apical width and apex 1.95–2.25 (m=2.15) times wider than at base. **Length**: 3.05–4.9 mm.

Hosts.—This species has been reared from guava (Myrtaceae) infested with *Bactrocera tryoni* (Froggatt), *Rauwenhoffia lei-*

chardtii (Annonaceae) infested with *B. halfordiae* (Tryon) and *B. neohumeralis* (Hardy), *Syzygium bamagense* (Myrtaceae) infested with *B. rufofuscula* (Drew and Hancock), and *Fagraea cambagei* (Loganiaceae) infested with *B. peninsularis* (Drew and Hardy). It thus appears to be able to attack several species of *Bactrocera* (Tribe Dacini) developing in the fruit of at least three plant families.

Material examined.—Holotype female, "Australia: QLD Mt. Glorious 26.i.1994 G. Quimio MG9413 ex: Rauwenhoffia leichardtii fruit containing Bactrocera halfordiae and B. neohumeralis" Deposited in ANIC. Paratypes (ANIC, BMNH, QDPI, TAMU, UQBA, USNM): 17♀, 17♂, same data as holotype; 2♀, 2♂, "Nambour Qld 24.iv.95 Guava G. Quimio"; 2♀, 1♂, same data except 29.v.95; 1♀, "Australia: QLD Wongabel 6 km S Atherton 1-28-1990 R. Wharton; 1♀, "Malanda NQ 22.xi.1987 M. Elson-Harris Ex Dacus rufofusculus 249"; 2♀, "Sydney, N.S.W., 28-6.1954 G. J. Snowball" one of these with an additional label "37/54" and the other "51/54". Additional material (not paratypes): 11♀, 3♂, Australia, North Queensland, Balinda, 10.vi.1993 from fruits of *Fagraea cambagei* infested with *Bactrocera peninsularis*. This species is known only from the eastern coast of Australia.

Diagnosis.—As with *ceratitivorus*, *schlingeri* also closely resembles the Madagascar species *longicauda*. The latter has a smaller eye (slightly less than 4 times longer than temple), somewhat more densely setose ovipositor sheath, a smaller gap between clypeus and mandibles when mandibles closed, and the distal portion of the ovipositor is parallel-sided rather than subapically narrowed relative to *schlingeri*. Of the species known from Queensland, *schlingeri* most closely resembles *deeralensis*. The latter has the ventral margin of the clypeus distinctly pointed midventrally (Fig. 6, with mid-ventral projection more distinct when head rotated forward), a distinct subapical ridge on the ovipositor
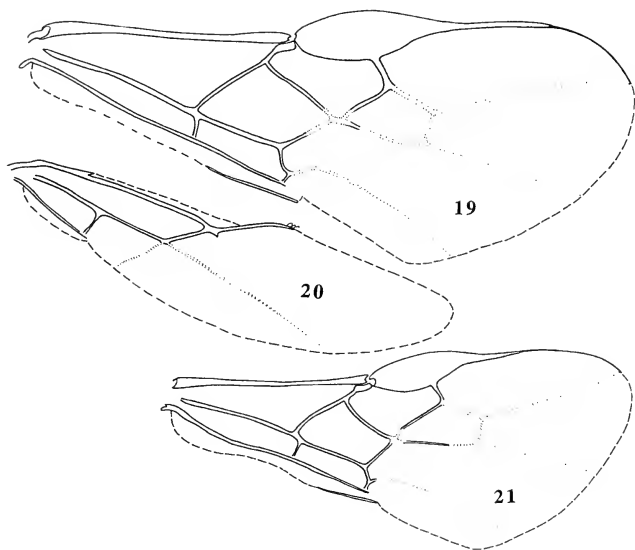
Figs. 19–21.   Wings of *Fopius* spp.: 19 and 20, *schlingeri* fore and hind wing; 21, *ceratitivorus* fore wing.

(Fig. 17), and the second metasomal tergum is usually weakly striate, at least basally.

Discussion.—Wharton (1997b) observed that the hypopygium is strongly attenuate in many of the parasitoids of fruit-infesting Tephritidae. He also noted in his redescription of *Fopius* that the hypopygium varies from weakly to strongly produced posteromedially. Though distinctly narrowed and projecting posteriorly in both *ceratitivorus* and *schlingeri*, the hypopygium is much less strongly produced than it is in members of the *Fopius marangensis* species group or in other fruit-infesting tephritid parasitoids such as the members of the *Diachasmimorpha longicaudata* (Ashmead) species group or the species of *Psyt-*

talia. Fischer (1987) includes species with a partially visible labrum in *Diachasma* Foerster. Wharton (1997b) briefly discussed variation in this character in *Fopius* and other genera, noting that some of the "variation" can be attributed to angle of view or the degree to which the mandibles are closed on any given specimen (compare Figs. 3 and 5). Nevertheless, there are slight differences among species of *Fopius* in the exposure of the labrum, and *schlingeri* provides a good example of a species with a partially exposed labrum (in contrast to the completely concealed labrum of *ceratitivorus*). The ovipositor in *schlingeri* (Fig. 18) is virtually identical in form to that of *arisanus*, strongly suggesting a biology similar to the latter in which the

parasitoid oviposits into the egg of its host. Field observations kindly supplied by Greg Quimio of the University of Queensland support this.

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New Genera and Species of Brachycistidine Wasps from Southwestern North America (Hymenoptera: Tiphiidae: Brachycistidinae)

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Abstract.—The new genera *Brachymaya, Paraquemaya* and *Sedomaya* are described from southwestern Arizona, Baja California and Sonora Mexico, and Imperial Co., California. *Brachymaya* is based on the new species *mexicana. Paraquemaya* is based on the new species *pallida*, and *Sedomaya* is based on the new species *glamisensis*. Three other new species of *Paraquemaya* are also described: *bitincta, maxima*, and *bajaensis*.

Until recently (Kimsey and Wasbauer 1998) the subfamily Brachycistidinae had not received taxonomic attention in nearly three decades. The last major revisions of any kind of members of this group were published by Mickel and Krombein (1942) and later by Wasbauer (1958, 1966 and 1968). Studies of unidentified male brachycistidines, which have accumulated in collections in the past 30 years, have revealed a variety of new taxa.

Six of these undescribed species had a combination of features, which did not fit any of the current generic groupings. Preliminary cladistic analyses of the Brachycistidinae indicated the need to describe three new genera for these species. Each of these genera is characterized by a unique combination of apomorphic features, which occur in other brachycistidine genera in various combinations. They include a tailed antennal socket, external mandibular carina, stridulatory structure on the forecoxa, an elongate digitus, changes in the position of the carina enclosing the oral fossa, loss of the hindcoxal carina, loss of the basolateral carinae on the first gastral tergum, and highly reduced wing venation. The first of these genera, *Paraquemaya*, has a large number

of primitive features, although it is still more highly derived than *Quemaya*. *Paraquemaya* has the following apomorphic characteristics: a tailed antennal socket, presence of a mandibular carina, an elongate digitus and hindwing venation similar to that seen in *Brachycistellus* and *Hadrocistis*. The second new genus, *Brachymaya*, appears to be most closely related to *Brachycistina* and *Hadrocistis*, based on the slender, ecarinate mandible and lack of the dorsal carina on the hindcoxa. Finally, the third genus, *Sedomaya*, belongs to a group of genera with the stridulatory structure on the forecoxa and the first gastral sternum with a short medial carina. This group also includes *Brachycistis, Brachycistellus* and *Colocistis.*

As with many of the brachycistidine genera the undoubtedly wingless, and probably nocturnal, females are unknown. Although a number of genera have been described based only on females (Mickel and Krombein 1942) the taxonomy of the Brachycistidinae is essentially based on the males. None of the female-based genera described by Mickel and Krombein (1942) are known to occur in the same region as the taxa described below (Fig. 1), although this is no guarantee that there is
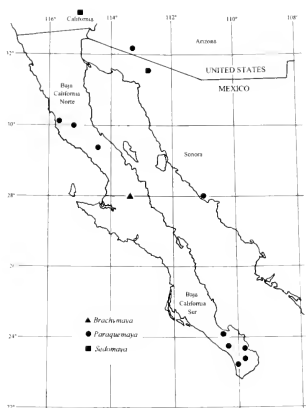
Fig. 1. Distribution map showing collection localities of the brachycistidine genera *Brachymaya, Paraquemaya* and *Sedomaya*.

no geographic overlap. In addition, the genera described by Mickel and Krombein are relatively large, ranging in length from 5–12 mm. The females of the new genera described below should be small, about 2–3 mm in length, roughly the size of female *Quemaya*, which are also as yet undescribed. Female brachycistidines described thus far are considerably larger than the females of *Brachymaya, Paraquemaya* and *Sedomaya* should be based on the male to female body size ratio seen in species where both sexes have been described. Additionally, no hosts are known for any of the new species described below. Description of these new genera is essential to enable us to finalize phylogenetic analyses of the subfamily Brachycistidinae.

MATERIALS

Specimens used in this study came from the Bohart Museum of Entomology, University of California, Davis, S. L. Heydon

(DAVIS); California Academy of Sciences, San Francisco, N. Penny (SAN FRANCISCO); Los Angeles County Museum, California, R. R. Snelling (LOS ANGELES); University of California, Riverside, S. Frommer, S. Triapitsyn (RIVERSIDE), and the personal collection of M. S. Wasbauer. Type repositories are indicated by the capitalized name given in parentheses.

Brachymaya Kimsey and Wasbauer, new genus
(Figs. 2, 6, 18, 19)

Description of male.—Face (Fig. 6): Mandible with two apical teeth and without longitudinal carina on external surface; palpi long, extending well outside of oral fossa, maxillary palpus 6-segmented; labial palpus 4-segmented; inner eye margin converging medially; flagellomeres somewhat arcuate, particularly apical articles; antennal carina greatly thickened into ventral subtriangular process, with tail-like carinule; gular suture with large subtruncate swelling near mandible; clypeus medially evenly convex, apical margin without ventral bevel; forecoxa without stridulatory patch; scrobal pit small and circular; propodeum without longitudinal groove on dorsal surface and without transverse carina; metasternum without medial ridge terminating in two lobes near hindcoxal base; hindcoxa without ventral or dorsal longitudinal carinae; wings (Fig. 2): forewing with one large rhomboid second submarginal cell, and smaller second submarginal cell, marginal cell nearly parallel-sided, R1 barely visible and bending away from the costal margin toward the stigma, one discoidal cell, one subdiscoidal cell; hindwing M vein diverging from Cu + M after cross vein cu-a; gastral segment I, tergum with well-developed lateral carina at base, sternum without longitudinal carina extending from base; epipygium delimited by small sublateral welt, apex truncate or somewhat short and apically rounded; genital capsule (Figs. 18, 19): paramere slender

and tapering dorsally; volsella with small submedial lobe externally, inner surface with several rows of denticles; digitus elongate terminating in acutely pointed lobe.

Distribution.—This genus is known only from the vicinity of San Augustine, BCN, Mexico.

Etymology.—The name is intended as a nonsense combination of letters, taken from *Brachycistis* and *Quemaya*, and is assumed to be feminine.

Type species.—*Brachymaya mexicana* n. sp.

Discussion.—*Brachymaya* is somewhat similar to *Brachycistina* and *Hadrocistis*. All three genera are characterized by having a slender mandible, with subsidiary dentition reduced to one or two very small teeth, and the hindcoxa lacking a dorsobasal carina. As with most brachycistidine genera Brachymaya has the digitus elongate and pointed. However, *Brachymaya* has the antennal socket subtended by a large triangular enlargement of the carina and the gular carina is dilated, forming a truncate projection near the mandibular base. In addition, the wing venation is reduced, with one discoidal and one submarginal cell.

Brachymaya mexicana Kimsey and Wasbauer, new species
(Figs. 2, 6, 8, 19)

Description of male.—Body length 5–6 mm; face (Fig. 6); clypeus evenly convex medially, apical truncation 0.9–1.0 midocellus diameters wide; interantennal distance 0.7–0.8 midocellus diameters wide; distance between midocellus and nearest eye margin 1.4–1.5 midocellus diameters; flagellomeres I–II 2.2–2.4 times as long as broad; facial and thoracic punctures small, shallow and widely spaced, 4–6 puncture diameters apart; forewing with two submarginal cells (Fig. 2); abdominal segments appearing impuncate, integument finely shagreened; genital capsule (Figs. 18, 19). Head dark brown; thorax and legs

pale yellowish brown; abdomen darker brown; forewing venation yellow, except stigma brown; hindwing venation yellow; wing membrane faintly yellow tinted.

Type material.—Holotype male: Mexico: BCN, San Augustine, 20 Oct. 1956, R. Mattoni (LOS ANGELES). Paratypes: three—same data as holotype (LOS ANGELES, DAVIS); one—3 mi. s. San Augustine, 14 June 1973, J. Doyen (DAVIS).
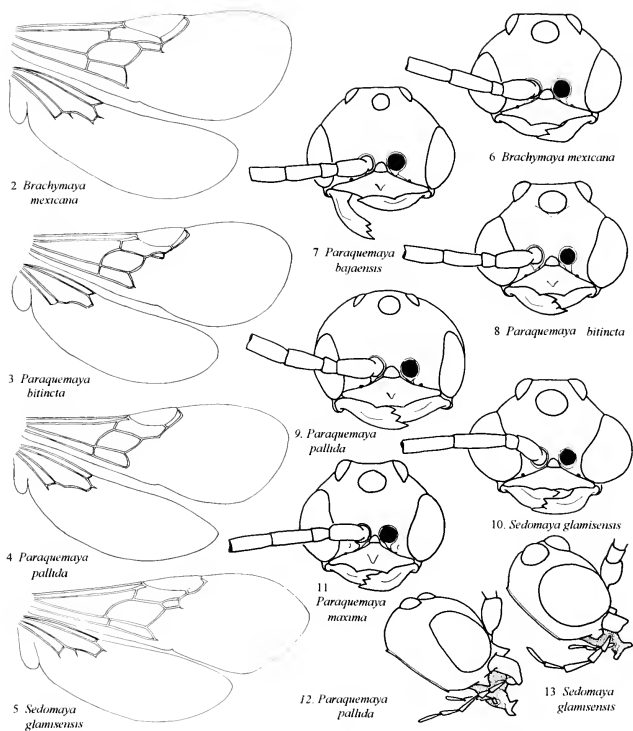
Etymology.—This species is named after the country of collection.

Discussion.—Although there are currently no other species placed in this genus, species distinctions probably include proportions of the flagellomeres, ocellocular distances, punctation and coloration of the wing veins.

Paraquemaya Kimsey and Wasbauer, new genus
(Figs. 3, 4, 7–9, 11, 12, 14–17)

Description of male.—Face (Figs. 7–9): Mandible with three apical teeth and longitudinal carina on external surface; palpi long, extending well outside of oral fossa, maxillary palpus 6-segmented; labial palpus 4-segmented; flagellomeres somewhat arcuate; antennal carina slightly thickened ventrally, but without tail-like carinule; gular carina with tooth-like projection near mandible (Fig. 12); forecoxa without stridulatory structure; scrobal pit small and circular; propodeum with longitudinal groove on dorsal surface and no transverse carina; metasternum with medial ridge terminating in two small lobes near hindcoxal base; hindcoxa without ventral or dorsal longitudinal carinae; wings (Figs. 3, 4): forewing with one large rhomboid submarginal cell, and smaller second submarginal cell in several species, marginal cell nearly parallel-sided, R1 barely visible and bending away from the costal margin toward the stigma, one discoidal cell, one subdiscoidal cell; hindwing M vein diverging from Cu + M after cross vein cu-a; gastral segment I, tergum with well-developed lateral carina at base, vis-

2 *Brachymaya mexicana*

3 *Paraquemaya bitincta*

4 *Paraquemaya pallida*

5 *Sedomaya glamisensis*

6 *Brachymaya mexicana*

7 *Paraquemaya bajaensis*

8 *Paraquemaya bitincta*

9. *Paraquemaya pallida*

10. *Sedomaya glamisensis*

11 *Paraquemaya maxima*

12. *Paraquemaya pallida*

13 *Sedomaya glamisensis*

Figs. 2–13. Figs. 2–5. Fore and hindwing of males. Figs. 6–11. Front view of male face, with right antenna removed. Figs. 12, 13. Side view of male head.

ible in most specimens, sternum with short longitudinal carina extending from base; epipygium delimited by small sublateral welt, apex truncate or somewhat rounded; genital capsule (Figs. 14–17): parameres slender and tapering apically; volsella with small rounded submedial lobe, inner margin with small denticles; digitus elongate and awl-shaped.

Distribution.—This genus occurs in southern Arizona and Baja California, Mexico.

Etymology.—The generic name refers to the superficial similarity, because of their

small size, to species of *Quemaya*; feminine.

Discussion.—Although *Paraquemaya* resembles *Quemaya* in terms of its reduced wing venation and small size, it shares the majority of characteristics with more derived brachycistidine genera including *Brachycistis* and *Brachycistellus*. Features shared with these genera include the elongate digitus, carinate mandible, unmodified palpi, basal gastral sternum with a medial carina, and basal tergum with a well-developed lateral carina adjacent to the petiolar insertion. The presence of a gular tooth is a characteristic shared with some species of *Brachycistis* and one *Quemaya* species. Additional diagnostic features include the lack of hindcoxal carinae, no forecoxal stridulatory structure and the configuration of the hindwing venation, which is very similar to that of *Hadrocistis* and *Brachycistellus*.

KEY TO THE SPECIES OF *PARAQUEMAYA* (MALES)

1. Forewing with two submarginal cells (Fig. 3); interantennal distance 0.5 midocellus diameter wide or less; body usually appearing bicolored with thorax paler than head and abdomen 2
 — Forewing with one submarginal cell (Fig. 4); interantennal distance more than 0.5 midocellus diameter; body concolorous 3
2. Shortest distance between midocellus and eye margin 1–1.2 midocellus diameters wide (Fig. 11); flagellomeres I and II subequal, 2.3–2.6× as long as broad . . *maxima* new species
 — Shortest distance between midocellus and eye margin 1.4–1.6 midocellus diameters wide (Fig. 8); flagellomere I shorter than II, 2.2–2.3 times as long as broad and II 2.3–2.5× as long as broad . . . . *bitincta* new species
3. Flagellomere I 2.0–2.2 times as long as broad (Fig. 9); flagellomere II 2.2–2.4× as long as broad; interantennal distance 0.6–0.8 midocellus diameters wide; shortest distance between midocellus and eye margin 1.8–2.0 midocellus diameters wide . . . . *pallida* new species
 — Flagellomere I 1.7–1.9× as long as broad (Fig. 7), flagellomere II length 2.0–2.2× breadth; interantennal distance 0.8–0.9 midocellus diameters wide; shortest distance between midocellus and eye margin 2.1–2.3 midocellus diameters wide . . . . *bajaensis* new species

Paraquemaya bajaensis Kimsey and Wasbauer, new species
(Fig. 7)

Description of male.—Body length 4 mm; face (Fig. 7); clypeus with narrowly acute medial projection, apical truncation 0.9 midocellus diameter wide; interantennal distance 0.8 midocellus diameter; distance between midocellus and nearest eye margin 2.3 midocellus diameters; flagellomere I twice as long as broad; flagellomere II length 2.4× breadth; facial and thoracic punctures small and widely spaced, 4–6 puncture diameters apart; forewing with one submarginal cell; abdominal segments appearing impunctate, integument finely s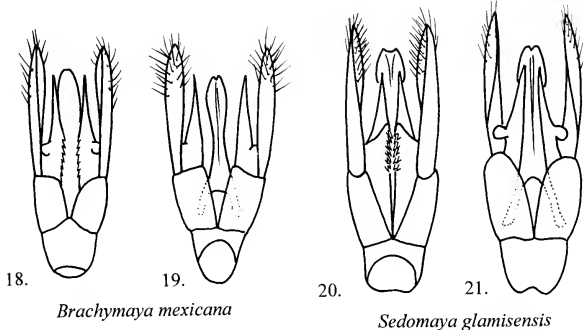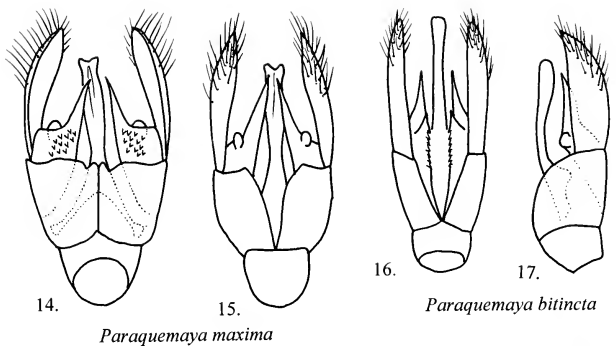hagreened. Body color dark brown; fore-wing venation light brown-tinted, except stigma darker brown; hindwing venation faintly brown-tinted; wing membrane untinted.

Type material.—Holotype male; Mexico, BCS, 14 mi s El Arco, 2 Nov. 1965, W. Ewart & R. Dickson (RIVERSIDE). Paratypes: 1 male same data as holotype, except 5 Nov. 1965; one male: BCN, El Consuelo, 0–50 ft. elev., 11 Sept. 1983, R. R. Snelling (DAVIS).

Etymology.—The name is derived from the region of collection, Baja California, Mexico.

Discussion.—This species most closely resembles *pallida*, as both have a single submarginal cell and the body color is

Figs. 14–21. Male genital capsule. Figs. 14, 16, 18, 20. Ventral view. Figs. 15, 19, 21. Dorsal view. Fig. 17. Lateral view.

concolorous. These two also have the widest ocellocular distance and widest interantennal distance. *P. bajaensis* has the smallest ocelli in the genus, with the midocellus separated from the eye margin by 2.3 midocellar diameters. This species also has the longest basal flagellomeres of any species of *Paraquemaya*.

Paraquemaya bitincta Kimsey and Wasbauer, new species
(Figs. 3, 8, 16, 17)

Description of male.—Body length 5 mm; face (Fig. 8); clypeus with narrowly acute medial projection, apical truncation 1 midocellus diameter wide; interantennal distance 0.3 midocellus diameter; distance

between midocellus and nearest eye margin 1.6 midocellus diameters; flagellomeres I and II subequal, length 2.3–2.4× breadth; facial and thoracic punctures small and widely spaced, 4–8 puncture diameters apart; forewing with two submarginal cells (Fig. 3); abdominal segments essentially impunctate, integument finely shagreened; genital capsule (Figs. 16, 17). Body color reddish brown, head and abdomen darker brown than thorax; forewing venation untinted, except stigma brown; hindwing venation untinted; wing membrane untinted.

Type material.—Holotype male: Arizona, Pima Co., Organ Pipe, 12 April 1947, A. L. Melander (RIVERSIDE). Three paratypes, same data as holotype (RIVERSIDE, DAVIS).

Etymology.—The name, *bitincta*, is derived from the two-tone brown color of the body.

Discussion.—This species can be distinguished from *pallida* and *bajaensis* by the presence of two submarginal cells. It can be separated from *maxima* by the smaller body size, shorter flagellomeres shorter, and greater distance between the eye and the midocellus.

Paraquemaya maxima Kimsey and Wasbauer, new species
(Figs. 11, 14, 15)

Description of male.—Body length 7 mm; face (Fig. 11); clypeus with acute, narrowly hooked medial projection, apical truncation 1 midocellus diameter wide; interantennal distance 0.5–0.6 midocellus diameters; distance between midocellus and nearest eye margin 0.1–1.1 midocellus diameters; flagellomeres I and II length 2.6× breadth; facial and thoracic punctures small and widely spaced, 4–6 puncture diameters apart; forewing with two submarginal cells; abdominal segment I with broad, shallow irregular punctures and shagreening; segments II–V with sparse shallow punctures, 4–6 puncture diameters apart; genital capsule (Figs. 14, 15).

Body color: head and abdomen brown, thorax lighter reddish brown; forewing venation pale brown-tinted, except stigma reddish brown; hindwing venation nearly colorless; wing membrane untinted.

Type material.—Holotype male: Mexico, Sonora, 22 km se Quitovac, 14 Nov. 1965, W. Edward & R. Dickson (RIVERSIDE). Two paratypes, same data as holotype (DAVIS, RIVERSIDE).

Etymology.—The name is based on the unusually large body size for this genus.

Discussion.—Other than the large body size of this species, the two submarginal cells and long flagellomeres will distinguish *maxima* from other species placed in *Paraquemaya*.

Paraquemaya pallida Kimsey and Wasbauer, new species
(Figs. 4, 9)

Description of male.—Body length 3.5–6.0 mm; face (Fig. 9); clypeus with small acute medial projection, apical truncation 1.0–1.3 midocellus diameters wide; interantennal distance 0.6–0.8 midocellus diameters; distance between midocellus and nearest eye margin 2.0–2.2 midocellus diameters; flagellomere I 2.0–2.2 times as long as broad; flagellomere II length 2.2–2.4× breadth; facial and thoracic punctures small and widely spaced, 3–5 puncture diameters apart; forewing with one submarginal cell (Fig. 4); abdominal segments with sparse shallow punctures, 2–4 puncture diameters apart. Body color pale reddish brown, rarely darker brown; forewing venation slightly brown-tinted, except stigma darker; hindwing venation untinted.

Type material.—Holotype male: MEXICO: Baja California Sur, 4 mi. wsw Miraflores, 23–24 April 1979, M. Wasbauer (DAVIS). Paratypes, 68 males (DAVIS, SAN FRANCISCO): 25—same data as holotype; four—El Salto, 8 mi ne Todos Santos, 9 Oct. 1983, D. Faulkner & F. Andrews; twenty-six—Los Barriles, 24 Mar.–5 April 1984, J. H. Lynch; two—Puerto Es-

condito, 10–14 July 1989, R. Shaver; one—BCN, Sierra Calamajué, 11 km e Chapala, 29°31'N 115°42'E, 23 Aug. 1994, S. Heydon; one—BCS: El Pescadero, Playa Los Cerritos, 16–17 April 1979, M. Wasbauer; one—BCS, 13 mi nw La Paz, 10 Nov. 1965, W. Ewart and R. Dicksen; one—Sonora, 14 mi w Guaymas, 13 Nov. 1965, Ewart and R. Dicksen.

Etymology.—The name, *pallida*, refers to the pale coloration of the male.

Discussion.—*Paraquemaya pallida* is characterized by having one submarginal cell, flagellomeres I and II subequal in length and about 2.2× as long as broad, and the midocellus separated from the eye by 2 midocellus diameters or slightly less.

Sedomaya Kimsey and Wasbauer, new genus
(Figs. 5, 10, 13, 20, 21)

Description of male.—Face (Fig. 10): mandible with three apical teeth and longitudinal carina on external surface; palpi long, extending well outside of oral fossa, maxillary palpus 6-segmented; labial palpus 4-segmented; eye strongly converging medially, inner eye margin slightly indented; flagellomeres somewhat arcuate, particularly apical articles; antennal carina slightly thickened ventrally, but without tail-like carinule; gular carina with large subtruncate swelling near mandible (Fig. 13); clypeus medially concave and slightly trilobate apically, apical margin with ventral bevel; forecoxa with small stridulatory patch; scrobal pit small and circular; propodeum with obsolescent longitudinal groove on dorsal surface and no transverse carina; metasternum with medial ridge terminating in two small lobes near hindcoxal base; hindcoxa with dorsal longitudinal carinae, without ventral one; wings (Fig. 5): forewing with one large rhomboid submarginal cell, and smaller second submarginal cell, marginal cell nearly parallel-sided, R1 barely visible and bending away from the costal margin toward the stigma, one discoidal cell, one

subdiscoidal cell; hindwing M vein diverging from M + Cu after cross vein cu-a; gastral segment l, tergum with well-developed lateral carina at base, visible in most specimens, sternum with short longitudinal carina extending from base; apical tergum evenly convex, apex truncate or somewhat rounded; short and apically rounded; genital capsule (Figs. 20, 21): paramere slender and tapering apically; volsella with rounded medial lobe, inner margin with numerous small denticles; digitus elongate and apically acute.

Distribution.—This genus is known only from the vicinity of Glamis, in the Algodones Dunes, Imperial Co., California.

Etymology.—The name is a nonsense combination of letters, and is assumed to be feminine.

Type species.—*Sedomaya glamisensis* n. sp.

Discussion.—No one genus appears to be the sister group of *Sedomaya*. It belongs to the group of genera characterized by the presence of a stridulatory structure on the forecoxae, elongate digitus and the first gastral sternum with a short longitudinal carina extending posteromedially from the base. *Sedomaya, Dolichetropis, Acanthetropis* and *Colocistis* all have a ventral clypeal bevel below the apex. However, unlike the latter three genera *Sedomaya* has highly reduced wing venation, having only two small forewing submarginal cells and one discoidal cell.

Sedomaya glamisensis Kimsey and Wasbauer, new species
(Figs. 5, 10, 13, 20, 21)

Description of male.—Body length 5–7 mm; face (Figs. 10, 13); clypeus medially convex, apex slightly trilobate with medial lobe projecting anteriorly in profile; apical truncation 0.9–1.0 midocellus diameters wide; interantennal distance 0.4–0.5 midocellus diameters; flagellomere l–II 2.9–3.1 times as long as broad; facial and thoracic punctures small, shallow and widely spaced, 4–6 puncture diameters apart; forewing with one submarginal cell (Fig.

5); abdominal segments appearing impunctate, integument finely shagreened; genital capsule (Figs. 20, 21). Body color pale reddish brown; fore and hindwing venation yellow; wing membrane slightly yellow tinted.

Type material.—Holotype male: California, Imperial Co., Glamis, 23 April 1972, M. Wasbauer, blacklight (DAVIS). Paratypes: twenty-five males (DAVIS); two—same data as holotype; twenty-two—3 mi n Glamis, 15–16 Sept. 1972, M. Wasbauer and A. Hardy; four—10 Sept 1974, M. Wasbauer and R. McMaster.

Etymology.—This species is named after the vicinity of the collection sites in and around Glamis, on the edge of the Algodones Dunes.

Discussion.—As with *Brachymaya mexicana*, species distinctions within this genus will probably be based on flagellar dimensions, the size of the midocellus and its distance to the ocular margin, other facial dimensions and perhaps the configuration of the clypeus.

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Deceptive Similarity in Army Ants of the Genus *Neivamyrmex* (Hymenoptera: Formicidae): Taxonomy, Distribution and Biology of *N. californicus* (Mayr) and *N. nigrescens* (Cresson)

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Abstract.—The army ant *Neivamyrmex californicus* (Mayr) is demonstrated to be a distinct species, endemic to California and adjacent Baja California, whose range overlaps that of *N. nigrescens* (Cresson), with which it has been previously confused. *N. nigrescens* is widespread throughout the southern Nearctic region, and shows extensive morphological variation in shape, size and sculpture. In the northwestern extremities of its range (i.e., north-central California, Nevada, Utah, and southwestern Colorado) *N. nigrescens* is convergently similar to *N. californicus* in certain aspects of worker morphology: workers lack the densely punctulate head sculpture typical of this species, and in their more shiny appearance they are superficially similar to workers of *N. californicus*. Many records of "*N. californicus*" (and the description of its supposed queen) actually refer to this shiny morph of *N. nigrescens*. That the shiny form is conspecific with, although partially differentiated from, other populations of *N. nigrescens* is indicated by the occurrence of intermediate populations in a relatively narrow transition zone in the San Gabriel Mountains of southern California. No intermediates have been observed between *N. nigrescens* and *N. californicus*. The latter species appears to be more closely related to *N. opacithorax* Emery than to *N. nigrescens*. In California *N. nigrescens* and *N. californicus* raid the nests of other ants, including *Messor andrei*, *Pheidole californica*, *P. hyatti*, *Solenopsis molesta*, and *Formica moki*. Field observations, combined with indirect evidence from the contents of ant nest middens, suggest considerable overlap in prey choice and habitat use. Both *N. nigrescens* and *N. californicus* are commonly sympatric in southern California (where *N. nigrescens* retains its distinctive granular-punctulate body sculpture), but less frequently so in northern California where they are more similar in appearance, and where *N. californicus* tends to be confined to more mesic, coastal areas than *N. nigrescens*.

Army ants in the genus *Neivamyrmex* are a frequent component of ant communities in tropical and warm temperate regions of the New World. The group has received considerable attention from taxonomists (e.g., Smith 1942; Borgmeier 1953, 1955, 1958; Watkins 1976, 1982, 1985), with the resulting recognition of about 120 species (Bolton 1995). Taxonomic problems persist, however, partly because many names are based on either workers or males only—and the names for the two castes are not yet cross-referenced and synonymized—but also because there is substantial and often confusing intraspecific variation in morphology (Smith 1942). Such variation is not unexpected

given that the reproductive females (queens) of these and other army ants are entirely wingless and have quite limited powers of dispersal (Gotwald 1995), a factor that favors population differentiation.

The present contribution is concerned with clarifying the taxonomy of *Neivamyrmex californicus* (Mayr) and several closely related species. Earlier treatments of these species are shown to be misleading. Simple morphometric analyses help to resolve and diagnose *N. californicus* and *N. nigrescens* (Cresson), two species whose taxonomic distinctness was previously called into question (Watkins 1985). Both these species—but especially *N. nigrescens*—show considerable variation in integu-

ment sculpture, and this phenomenon misled earlier investigators about species limits.

The range of *Neivamyrmex californicus* is more restricted than previously thought, the species being confined to the Californian floristic province (California and adjacent northern Baja California), where it is broadly sympatric with *N. nigrescens*. The latter is shown to be a highly polytypic species with an extensive transcontinental distribution.

MATERIALS AND METHODS

Specimens were examined in the following collections:

CASC   California Academy of Sciences, San Francisco, California, U. S. A.

CDAE   California Department of Food & Agriculture, Sacramento, California, U. S. A.

JTLC   John T. Longino Collection, Olympia, Washington, U. S. A.

LACM   Natural History Museum of Los Angeles County, Los Angeles, California, U. S. A.

MCZC   Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts, U. S. A.

MHNG   Muséum d'Histoire Naturelle, Geneva, Switzerland

NHMV   Naturhistorisches Museum, Vienna, Austria

RAJC   Robert A. Johnson Collection, Tempe, Arizona, U. S. A.

UCDC   Bohart Museum of Entomology, University of California, Davis, California, U. S. A.

USNM   National Museum of Natural History, Smithsonian Institution, Washington, D. C., U. S. A.

Other collections cited are:

ANSP   Academy of Natural Sciences, Philadelphia, U. S. A.

MCSN   Museo Civico di Storia Naturale, Genoa, Italy

The following measurements and indices were used for workers and queens. All measurements were taken at 50× magnification with a Wild M5A microscope and a pair of Nikon stage micrometers wired to a digital readout. Measurements were recorded to the nearest thousandth of a millimeter.

HW   Maximum width of head, measured in full-face (frontal) view

HL   Maximum length of head in frontal view, from the midpoint of a line drawn across the posterior margin to the anteriormost point on the clypeal margin. This *excludes* the thin, lamelliform clypeal apron, which projects forward from the clypeal margin and may be partly hidden by the mandibles.

MFC   Minimum distance between the frontal carinae

SL   Length of the scape, excluding the basal neck

WL   Weber's length: length of the mesosoma, as seen in lateral view, from the anterior pronotal margin (excluding the collar) to the posterior extremity of the metapleuron

PL   Length of the petiole, measured in lateral view along the long axis of the petiole, from the anterior margin (excluding the short peduncle) to the posterior extremity

PH   Petiole height, measured at right angles to PL, from the summit of the petiole to the petiolar venter, excluding the anteroventral tooth (if present)

DPW   Maximum dorsal width of the petiole, measured in dorsal view

PPW   Maximum dorsal width of the postpetiole, measured in dorsal view

MTL   Length of the metatibia, excluding the basal condyle (Fig. 3)

QGL   Length of the gaster (queen caste only), measured in lateral view from the posterior end of the gas-

ter to the anterior extremity of abdominal segment 3, excluding the helcium. This measurement was taken only on non-physogastric queens.

CI   Cephalic index: HW/HL
SI   Scape index: SL/HW
FCI   Frontal carinal index: MFC/HW
PLI   Petiole length index: PH/PL
PWI   Petiole width index: DPW/PL
MTI   Metatibial index: MTL/HW

Neivamyrmex californicus and allied species.

Among the North American army ants of the genus *Neivamyrmex* three species—*N. californicus*, *N. nigrescens* and *N. texanus*—can be diagnosed in the worker caste by having a mandible whose basal margin rounds gradually into masticatory margin, without an angular junction (Figs. 1, 4, 7). The species have many other traits in common, including: moderately large size (HW 0.60–1.42); well developed clypeal apron; relatively prominent ocellus-like eye with convex surface; weakly developed occipital lobes; lamellate and ventrally directed lower pronotal flange; petiole longer than high (PLI 0.68–0.96) and markedly longer than wide (PWI 0.52–0.74); and dense punctulate sculpture covering part of the body but without conspicuous overlying coarse impressions or rugae.

These taxa are part of a larger group of species, including *N. chamelensis* Watkins, *N. cornutus* Watkins, *N. manni* (Wheeler), *N. opacithorax* (Emery) and *N. sumichrasti* (Norton), that can be placed together, on the basis of similarities in worker morphology and male genitalia, in an assemblage of *Neivamyrmex* species termed

"Gruppe VI" by Borgmeier (1955: 490). Although the three species treated in this paper are evidently closely related, their exact phylogenetic relationship to one another and to these other taxa remains to be resolved.

List of species considered here, with known castes (w = worker, m = male, q = queen) and distribution:

californicus (Mayr 1870) (w)
    U. S. A.: California
    Mexico: Baja California
nigrescens (Cresson 1872) (w, q, m)
    U. S. A.: California, Nevada, Utah, Arizona, New Mexico, Colorado, and east-central United States
    Mexico: Baja California, Baja California Sur, Jalisco, Nayarit, Oaxaca, San Luis Potosí, Sonora, Tamaulipas
texanus Watkins 1972 (w, q, m)
    U. S. A.: Arizona, New Mexico, Colorado, and east-central United States
    Mexico: Chihuahua, Durango, Hidalgo, Jalisco, Nuevo León, San Luis Potosí, Sonora

SPECIES ACCOUNTS

### *Neivamyrmex californicus* (Mayr 1870)
(Figs. 1–3, 10)

Eciton californicum Mayr 1870: 969. Nineteen syntype workers, San Francisco (Schaufuss) (NHMV) [examined]. One syntype worker here designated **lectotype.**
*Eciton (Acamatus) californicum* Mayr; Emery 1894: 182.
Eciton (Acamatus) californicum var. *obscura* Forel 1914: 265. Two syntype workers, Vista, California (E. Hindle) (MHNG) [examined]. One syntype worker here designated **lectotype.** Synonymy by Borgmeier 1955: 517; here confirmed.
Eciton (Neivamyrmex) californicum Mayr; Smith

→

Figs. 1–12. *Neivamyrmex* workers, full-face view of head (1, 4, 7), lateral view of mesosoma, petiole and postpetiole (2, 5, 8), lateral view of metatibia (3, 6, 9), and dorsal view of propodeum, petiole and postpetiole (10–12). 1–3, 10: *N. californicus*, San Francisco, California, lectotype worker; 4–6, 11: *N. nigrescens*, shiny form, 2km SE Mt. Vaca, California; 7–9, 12: *N. nigrescens*, typical form with opaque head, Sevilleta NWR, New Mexico. Fig. 3 indicates measurement of MTL.
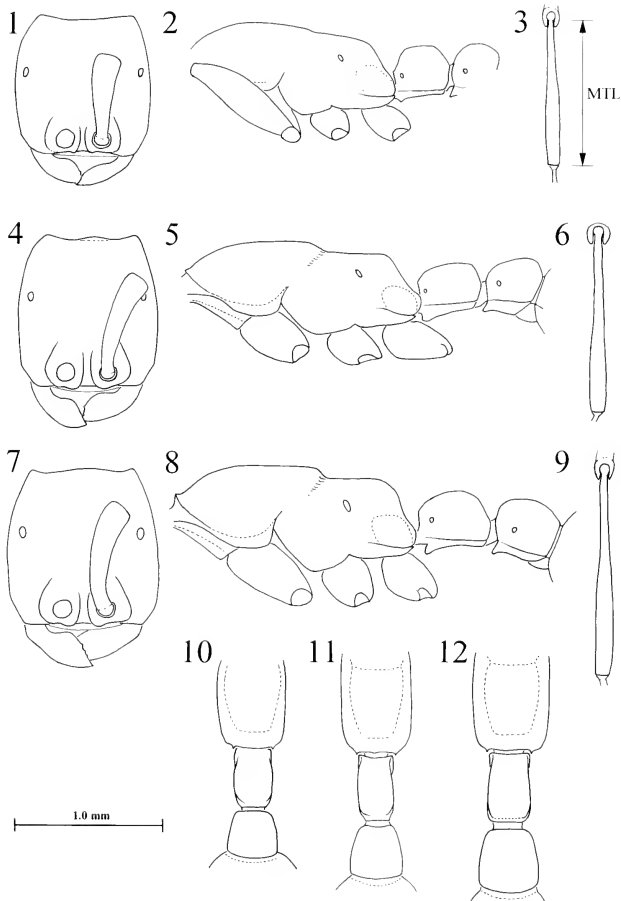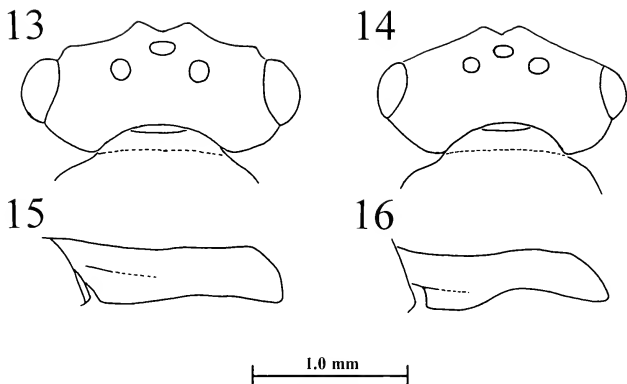
Figs. 13–16. Neivamyrmex males, dorsal view of head (13, 14) and lateral view of left paramere (15, 16). 13, 15: N. nigrescens, Ash Mountain Kaweah Power Stn.#3, Tulare Co., California; 14, 16: Neivamyrmex species, probably opacithorax, same locality.

1942: 560. First combination in subgenus Neivamyrmex, but the material examined and described by M. R. Smith was N. opacithorax not N. californicus.

Neivamyrmex californicus v. obscurus (Forel); Borgmeier 1953: 8.

Neivamyrmex californicus (Mayr); Borgmeier 1953: 11.

Neivamyrmex californicus (Mayr); Borgmeier 1955: 517.

Neivamyrmex californicus (Mayr); Watkins 1972: 363 (part). Description of queen (p. 364) is that of N. nigrescens, not N. californicus.

Neivamyrmex californicus (Mayr); Watkins 1985: 482 (part). Key (p. 482) and distribution map (figure 4, p. 500) refer partly to N. californicus and partly to N. nigrescens.

Worker measurements.—(n = 28). HW 0.63–1.10, HL 0.69–1.11, WL 1.03–1.67, MTL 0.68–1.18, CI 0.86–1.00, FCI 0.033–0.061, SI 0.68–0.80, MTI 1.05–1.14, PLI 0.78–0.88, PWI 0.62–0.73.

Worker description.—Body of moderate size (see HW, HL and MTL measurements) and somewhat compact (see plot of WL on HW; Figs. 19, 23); head broad, CI approaching 1.00 in largest workers, i.e., those in which HW and MTL > 1.00 mm; mandible with basal margin rounding gradually into masticatory margin (Fig. 1); masticatory margin with a small tooth at the terminus of this rounding, followed by 1–4 denticles (tending to increase in size), then a more prominent tooth midway along the margin; distal portion of masticatory margin generally edentate (a small denticle or two may follow the mid-point tooth) except for the acute apical tooth; anterior margin of torulus separated from anterior margin of clypeus (ignoring the thin diaphanous clypeal apron) by about 0.2× the diameter of the torulus; frontal carinae moderately well separated (MFC 0.022–0.061), diverging anteriorly, and protruding very slightly (largest workers) or not at all (most workers) beyond the anterior clypeal margin, when the head is seen in frontal view; anterior clypeal margin more or less straight (weakly convex

in smallest workers, and slightly concave in largest workers); clypeal apron relatively well developed, its anterior margin generally slightly convex or subangulate; clypeal apron extending anteromedially beyond the clypeal margin proper by a distance equal to 0.4–0.5× the torulus diameter; each compound eye consisting of a single convex ommatidium, breaking the surface of the head, its maximum diameter approximately 0.06–0.08 mm (6–10% of head width); scapes of moderate length, exceeding the eye when held back against the head (SI 0.68–0.80; SI2 0.67–0.75) (see also plot of SL on HW and SI on MTL; Figs. 18, 22, 26); posterior margin of head usually concave, in frontal view; occipital lobes weakly developed, not protruding conspicuously when the head is seen in frontal view; anterior pronotum descending gradually towards the collar, transverse ridge weakly developed; lower pronotal flange thin, lamellate, directed more or less ventrally; dorsal profile of mesosoma rather flat, and dorsal face of propodeum only slightly depressed below the level of the mesonotum (Fig. 2); dorsal face of propodeum rounding into, and subequal in length to, the declivitous face; latter flat to weakly concave, in profile; legs relatively short, MTL/HW (=MTI) < 1.15; petiole short, high, and with short vertical anterior face, followed by a more or less evenly convex dorsal surface (as seen in profile; Fig. 2), or with a slightly steeper posterodorsal than anterodorsal slope; in dorsal view, petiole subrectangular, but with somewhat convex sides, about 1.5 times longer than wide; anteroventral process of petiole a thickened transverse shelf, in lateral view appearing as a relatively small, blunt tooth directed anteroventrally; a similar, less protrusive structure at the anteroventral extremity of the postpetiole; in dorsal view postpetiole subtrapezoidal (Fig. 10), with straight, diverging sides, broadest posteriorly, and slightly broader than long. Upper surface of mandible finely and densely striate with scattered punctures, subopaque, lateral surface of mandible and area immediately preceding the masticatory margin smooth and shiny with scattered punctures. Head largely smooth and shining, with numerous piligerous punctures separated by several to many diameters; in larger workers (and in more southern populations) the punctures may be coarser and denser, and parts of the intervening shiny integument dulled very slightly by weak reticulation. Mesosoma densely punctulate, opaque, but in smaller workers the sculpture weakened laterally on the pronotum (which becomes finely reticulate and sublucid) and replaced by smooth shiny areas on the dorsum of the promesonotum. In workers of all sizes, including heavily sculptured large individuals, the center of the mesonotum is nearly always smooth and shiny, with a few larger piligerous punctures, and contrasts with the predominantly punctulate and opaque dorsal face of the propodeum (exceptions include some heavily sculptured workers from southern California in which the mesonotum center is weakly reticulate and sublucid, but still contrasts with the opaque dorsal surface of the propodeum; and small, shiny workers from northern California in which even the propodeum dorsum loses its punctulate sculpture centrally, so that contrast between the mesonotum and the propodeum is lessened). Petiole laterally reticulo-punctate and subopaque to sublucid, petiolar dorsum mostly shining, but with variable traces of punctulate reticulation; postpetiole and gaster smooth and shiny, with scattered piligerous punctures. Long, fine, golden pilosity conspicuous on body and appendages (scape, funiculus, legs), mostly suberect to subdecumbent. Body light castaneous brown to deep reddish-brown, tending towards a lighter yellow-brown on the postpetiole and gaster. Mandible medium to dark brown, usually contrasting somewhat with the lighter head color.

Queen.—Unknown. The "*N. californicus*" queen from Davis, California, described by Watkins (1972), is that of the shiny form of *N. nigrescens*. A single queen, in rather poor condition, from Monterey, California (31.v.1963; leg. Roy Johnson; USNM), could be either *N. opacithorax* or *N. californicus*. It is relatively small in size (HW 1.65, WL 2.68, MTL 1.33), with short scapes (SI 0.46), rounded occipital lobes, short legs (MTI 0.81), and a long gaster (QGL/WL = 2.34). The short appendages and elongate gaster are features that distinguish *N. opacithorax* queens from those of *N. nigrescens*, but they might also be characteristic of *N. californicus*. There are apparently no worker specimens associated with the Monterey queen, leaving its specific identity uncertain.

Male.—Unknown. In LACM and CASC there are a series of *Neivamyrmex* males, collected in California but unassociated with workers, that appear to be *N. opacithorax* on the basis of head shape and (especially) male genitalia (Figs. 14, 16). The proximal flange on the ventral margin of the paramere would seem to be particularly characteristic of that species. Nevertheless, until worker-associated males of *N. californicus* are discovered, one cannot exclude the possibility that some of these males (from Contra Costa and Tulare Counties) represent *N. californicus*.

Comments.—Workers of *N. californicus* can be distinguished from those of *N. nigrescens* by their more compact body, shorter legs and scapes, and broader head and petiole (Figs. 1–3). The simplest quantitative diagnostic is the metatibial index (MTI = MTL/HW) which ranges from 1.05 to 1.14 in *N. californicus* (n = 28) compared to 1.16 to 1.52 in *N. nigrescens* (n = 89). A bivariate plot of the relevant measurements (MTL and HW) demonstrates the distinction (Fig. 17). Other differences between *N. californicus* and *N. nigrescens* are captured by plots of scape length (SL) on head width (HW) and Weber's length (WL) on head width (Figs. 18, 19, 21, 22).

When samples from all populations of *N. nigrescens* are considered (i.e., including workers from the Southwest and from eastern United States) there is a slight overlap in the distribution of points (Figs. 18, 19); but when confining the comparisons to populations of *N. nigrescens* that are sympatric with *N. californicus* (i.e., populations from California) these and other bivariate plots produce non-overlapping clouds of points (see Figs. 21–28). Because of allometry, neither the cephalic index (CI = HW/HL) nor the scape index (SI = SL/HW) are diagnostic in themselves, but when plotted against the metatibia length (MTL) a sharp distinction is seen between the two species (Figs. 25–26). Thus, within a given size class (as measured by MTL) there is no overlap in CI or SI; but small workers of *N. californicus* have scape and cephalic indices that overlap with large workers of *N. nigrescens*.

Workers of *N. californicus* also have the dorsal face of the propodeum less depressed below the level of the mesonotum than in *N. nigrescens* (compare Figs. 2 and 5), and this difference is diagnostic. Less tangible are differences in body sculpture: the dense punctulate sculpture that is so prominent in most populations of *N. nigrescens* and that imparts a granular appearance to the head and mesosoma is much less developed in *N. californicus*, such that the head, mesonotum, and postpetiole are largely smooth and shiny (covered only with scattered piligerous punctures). But a reliance on sculptural differences led to the past confusion between these two species: populations of *N. nigrescens* that are broadly sympatric with *N. californicus* in central and northern California also have weakened body sculpture and are superficially similar to those of *N. californicus*. On average, *N. californicus* is still the shinier of the two (see distinctions in key couplet 9A below) but the differences are subtle. The contrasts in body shape and leg length documented
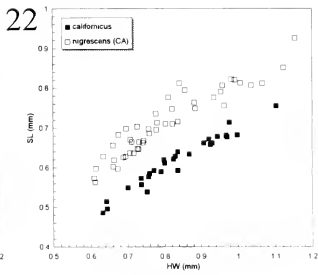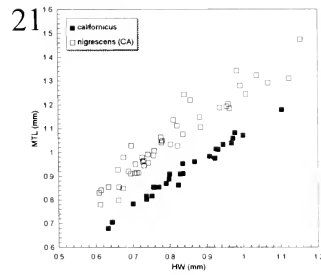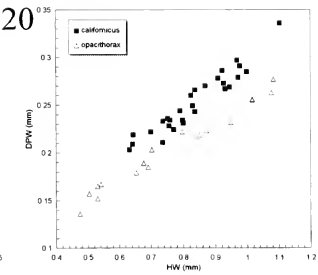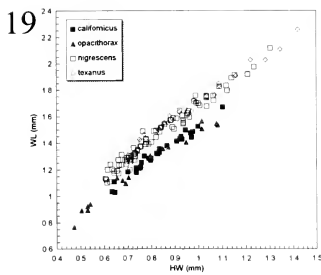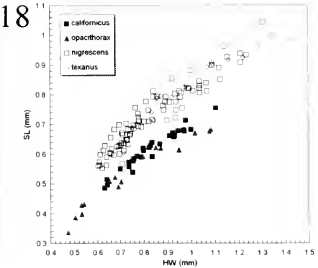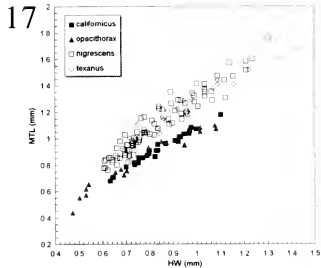
Figs. 17-22.   Bivariate plots of various metric measurements in workers of four species of *Neivamyrmex*.
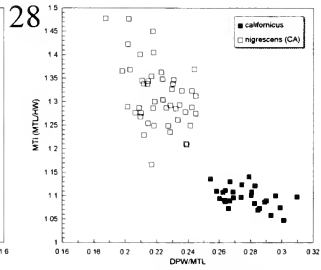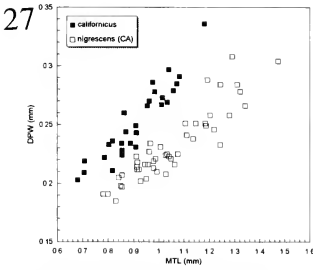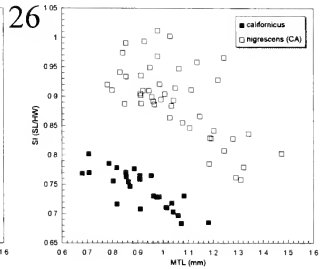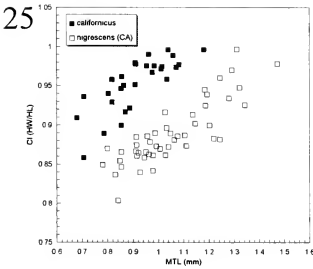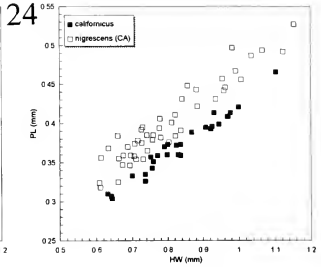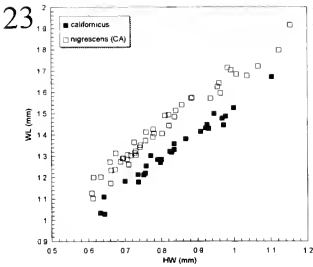
Figs. 23–28. Bivariate plots of metric measurements and indices in workers of *Neivamyrmex californicus* and *N. nigrescens* (California populations only).
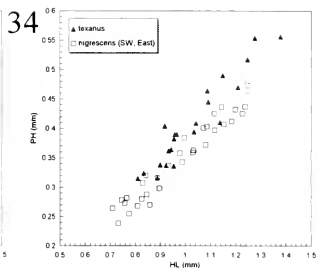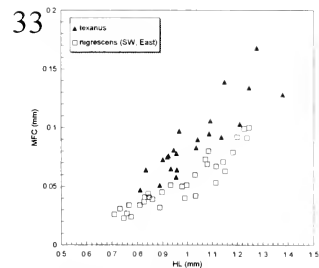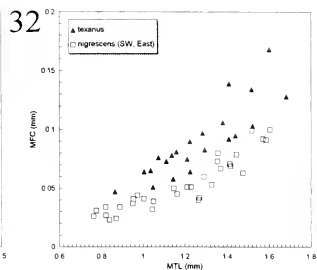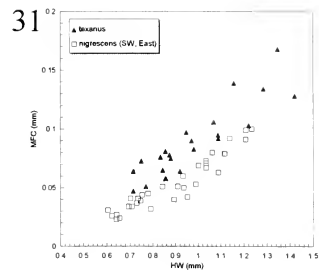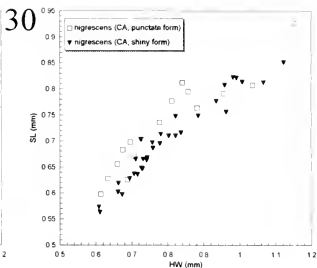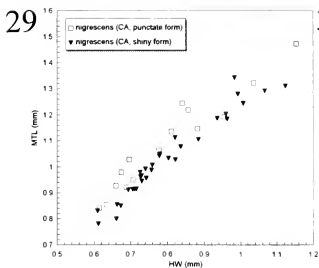
Figs. 29–34. Bivariate plots of metric measurements and indices in workers of *Neivamyrmex texanus* and various populations of *N. nigrescens*.

above are more reliable for distinguishing these two species.

N. californicus differs more obviously from *N. texanus*. Like *N. nigrescens*, workers of *N. texanus* have longer legs (MTI 1.18–1.48), longer scapes (SI2 0.75–0.89), and a more gracile body than those of *N. californicus*. They also average larger in size, have more widely separated frontal carinae (FCI 0.066–0.125 compared to 0.033–0.061 in *N. californicus*), and a consistently opaque, densely punctulate head and mesosoma such that they are unlikely to be confused with *N. californicus* workers. As far as known, the ranges of the two species do not overlap (Fig. 36).

The bivariate plots of measurements (Figs. 17–19) show that in many respects *N. californicus* is more similar to *N. opacithorax* than to *N. nigrescens* or *N. texanus*. *N. opacithorax* can be distinguished from *N. californicus* by the angular basal margin of the mandible; shorter clypeal apron; narrower petiole (Fig. 20); and different pattern of body sculpture (side of pronotum usually smooth and shiny, and contrasting with the rugulose-punctulate mesosoma dorsum).

Material examined.—(CASC, CDAE, JTLC, LACM, MCZC, MHNG, NHMV, RAJC, UCDC, USNM)

MEXICO **Baja California**: 28km E Ensenada, 750m (P. S. Ward).

UNITED STATES **California** *Contra Costa Co.:* 9km ENE Danville, 490m (P. S. Ward); *El Dorado Co.:* 14km NW Shingle Springs, 340m (P. S. Ward; G. C. Snelling); *Los Angeles Co.:* Arcadia (c.u.); La Verne (A. C. Oberle); Los Angeles (A. Mallis & J. Schwartz); *Monterey Co.:* Salinas (B. Oliver & J. Bunch); *Orange Co.:* Irvine Park (A. Mintzer); Laguna Hills (R. J. Hamton); Limestone Canyon, El Toro Rd., 1.8mi E Cooks Corner (A. Suarez); Tonner Canyon (W. P. Mackay); *Riverside Co.:* Riverside (K. Cooper; K. W. Cooper; E. I. Schlinger); Temecula (A. Suarez); *San Bernardino Co.:* Chino Hills State Park (G. C. Snelling *et al.*); Chino Hills State Park, 700 ft. (R. A. Johnson); *San Diego Co.:* 5mi. NE Poway, 600m (M. S. Trepanier); Camp Pendleton (J. H. Hunt); Chula Vista, E end, 160m (P. S. Ward); Chula Vista, 70m (A. Suarez); Elliott Reserve, 150m (A. Suarez); La Jolla (c.u.); Mt. Laguna, MSP site, 6050 ft. (J. H. Hunt); National City (K. Ross); San Diego (c.u.); Vista (E. Hindle); *San Francisco Co.:* San

Francisco (Schaufuss); *San Mateo Co.:* Jasper Ridge, 150m (K. G. Human; N. J. Sanders); *Santa Barbara Co.:* 9km N Goleta, 490m (P. S. Ward); Cachuma Saddle, 1100m (J. Longino); *Santa Clara Co.:* 11km S Palo Alto, 490m (P. S. Ward); *Santa Cruz Co.:* Santa Cruz (K. Brown).

Neivamyrmex nigrescens (Cresson 1972)
(Figs. 4–9, 11–12)

Labidus nigrescens Cresson 1872: 194. Holotype male, Bosque Co., Texas (Belfrage) (ANSP) [not examined].

Eciton nigrescens (Cresson); Dalla Torre 1893: 5.

Eciton (Acamatus) schmitti Emery 1894: 183. Syntype workers, Doniphan, Missouri (Pergande) (MSCN) [not examined], MCZC, USNM [examined]. Synonymy by M. R. Smith 1938: 160.

Eciton (Labidus) nigrescens (Cresson); Emery 1895: 258.

Eciton (Acamatus) nigrescens (Cresson); Emery 1900: 187.

Eciton sumichrasti; Wheeler (nec Norton) 1900: 564. Description of queen (as "*E. sumichrasti*").

Eciton (Neivamyrmex) nigrescens (Cresson); Smith 1942: 550 (part). Description of worker (part), queen and male.

Eciton (Neivamyrmex) californicum; Creighton (nec Mayr) 1950: 70 (part).

Neivamyrmex nigrescens (Cresson); Borgmeier 1953: 6.

Neivamyrmex nigrescens (Cresson); Borgmeier 1955: 494 (part). Description of worker (part) and queen. Male (p. 496) is that of *N. texanus* (Watkins 1972).

Neivamyrmex sp. c; Borgmeier 1955: 531. Description of male.

Neivamyrmex nigrescens (Cresson); Watkins 1972: 358.

Neivamyrmex californicus; Watkins (nec Mayr) 1972: 363 (part). Description of queen (as "*N. californicus*").

Neivamyrmex nigrescens (Cresson); Watkins 1985: 482.

Neivamyrmex californicus; Watkins (nec Mayr) 1985: 482 (part).

Worker measurements.—(n = 89). HW 0.60–1.31, HL 0.71–1.31, WL 1.10–2.12, MTL 0.76–1.76, CI 0.80–1.00, FCI 0.030–0.106, SI 0.75–1.01, MTI 1.16–1.52, PLI 0.68–0.91, PWI 0.52–0.71.

Worker diagnosis.—Moderately large body size (see HW, HL and MTL measurements); mandible with basal margin rounding gradually into masticatory margin (Figs. 4, 7); frontal carinae moderately well separated (MFC 0.021–0.138); clypeal apron well developed and, in all but the largest workers, produced anteromedially by an amount subequal to, or greater than, the minimum distance between the frontal carinae (MFC); scapes relatively long, SI > 0.69 (see also plot of SL on HW and SI on MTL; Figs. 18, 22, 26); occipital lobes weakly to moderately developed; anterior margin of pronotum with transverse ridge generally well developed; dorsal (= basal) face of propodeum conspicuously depressed below the level of the promesonotum (Figs. 5, 8), and rounding into the declivitous face, the latter more or less flat (or weakly concave) in profile; legs relatively long, MTL/HW (=MTI) > 1.15; petiole subrectangular, somewhat variable in shape (see PLI and PWI values), but always longer than high or wide (Figs. 5, 8, 11, 12). Head and mesosoma typically densely punctulate, and having an opaque, granular appearance; populations from northwestern portions of the species' range, however, have the sculpture much weakened such that the head is partly smooth and shining, with scattered piligerous punctures and variable amounts of finer reticulate sculpture that partly dulls the sheen; and in this "shiny morph" the mesosoma is partly sublucid, although with at least weak reticulate-punctulate sculpture on most surfaces. In all populations sculpture weakened on the surface of metapleural gland bulla, such that the lower half or more is smooth (or weakly reticulate) and conspicuously shiny. Petiole densely punctulate, subopaque, postpetiole tending to be more lightly sculptured. Body varying from light castaneous brown to dark reddish-brown, the postpetiole and gaster usually lighter than the rest of body.

Queen diagnosis.—Eye distinct, consisting of single convex ommatidium. Head as broad as, or slightly broader than, long (CI 0.96–1.02, n = 6). Occipital corners generally angular and projecting, but may be weakly angulate or rounded. Pronotum without posterior dorsolateral projection. Propodeum (and sometimes also mesonotum) with a median longitudinal impression. Metatibial index (MTI) 0.89–1.07 (n = 6). Petiole subquadrate, slightly broader than long (PWI approximately 1.1–1.2), with a vertical anterior face that rounds into a flat dorsal face, as seen in lateral view. Petiole width much less than the length of the metatibia, DPW/MTL 0.58–0.72 (n = 6). Length of gaster (non-physogastric) less than twice WL (QGL/WL = 1.70–1.90, n = 5).

Male diagnosis.—Mandibles broad, spatulate (not sickle-shaped). Ocelli moderate in size and separated from the upper margin of the compound eye by a distance greater than twice the diameter of the median ocellus. Prominent transverse swelling above antennal fossa, discerned most clearly in dorsal view (Fig. 13). Setae on venter of petiole typically short, whitish, and slanted posteroventrally, but in some western populations the setae are longer, golden, and suberect. Gaster typically black or blackish-brown, often reddish-brown in western populations. In profile, paramere (= stipes) linear subrectangular, with an oblique (anterodorsal to posteroventral) posterior margin, and a straight ventral margin, not produced anteroventrally (Fig. 15); posterodorsal extremity with a low, triangular projection (Watkins, 1985, Plate 9, fig. 4), tending to become obsolete in western populations (Fig. 15); volsella unforked, with long, slender upturned apex; aedeagus (=sagitta) with an apically upturned posteroventral process, just exceeding the posterodorsal process (in posterior reach).

Comments.—The characteristics that distinguish workers of *N. nigrescens* from those of *N. californicus* and *N. texanus* are discussed under those respective species.

N. nigrescens differs from *N. opacithorax* by the shape of the worker mandibles, by the heavier body sculpture, especially on the side of the pronotum, by the longer scapes, mesosoma and legs (Figs. 17–19), and by the more strongly convex profile of the promesonotum.

A remaining question concerns the status of the *nigrescens*-like populations with shiny worker heads, that are superficially similar to those of *N. californicus*. This "shiny morph" of *N. nigrescens* is found in north-central California, parts of the Great Basin, and in upper sections of the Colorado River drainage, while the more "typical" form, with densely punctulate and opaque worker head, is distributed widely from southern California, Arizona and adjacent regions of Mexico to southeastern United States (Fig. 37). What happens in zones of contact between the two forms? Records are too sparse to answer this question for the Colorado River basin, but collections from southern California reveal a zone of intergradation centered on the north side of the San Gabriel Mountains. In fact patterns of sculpturation are intermediate in samples taken from this region, so that the distinction between the two "forms" becomes quite arbitrary. For this reason it seems clear that they must be treated as conspecific, although the patterns of distribution are suggestive of a previous period of isolation followed by secondary contact and introgression.

Material examined.—(1) Typical form with opaque, densely punctulate head (CASC, CDAE, LACM, MCZC, RAJC, UCDC, USNM)

MEXICO **Baja California:** 28km E Ensenada, 750m (P. S. Ward); 31.7mi WNW Bahia de los Angeles (Hardy, Andrews & Giuliani); 6mi SE Laguna Chapala (A. E. Lewis); **Baja California Sur:** 12mi S Santa Rosalia (Michelbacher & Ross); 15mi S San Domingo (Ross & Bohart); 20mi W La Paz (E. L. Sleeper); 26km NW Santa Rosalia (R. A. Johnson); Coyote Cove, Conception Bay (Michelbacher & Ross); Isla San José, 1mi S Punta Colorada [as "Punta Colorado"] (J. T. Doyen); San Hilario (E. L. Sleeper); San Ignacio, 140m (M. Bennett); **Jalisco:** 3mi SE Plan de Barrancas (F. D.

Parker & L. A. Stange); **Nayarit:** *Islas Tres Marias:* Isla Cleofas (R. R. Snelling); Isla Magdalena (R. R. Snelling); **San Luis Potosi:** Cd. Valles, El Bañito (J. F. Watkins); **Sonora:** 2km N Bahía de la Cruz, Isla Tiburón, 10m (P. S. Ward); 2km SW Punta Narragansett, Isla Tiburón, 5m (P. S. Ward); 37mi N Hermosillo, 1700 ft. (R. R. Snelling); 5mi S Cananea (V. D. Roth); 8km N Desemboque de los Seris (R. A. Johnson); Los Horcones, Rte. 16, 4km E La Colorada (B. Bestelmayer); **Tamaulipas:** Cd. Victoria (J. F. Watkins).

UNITED STATES **Alabama:** *Dallas Co.:* Selma (W. H. Patton); *Jefferson Co.:* Birmingham (R. D. Jordan); *Lauderdale Co.:* Florence (W. Cloyd; F. Moore); *Lawrence Co.:* King Cove, Bankhead Natl. Forest (E. O. Wilson); *Mobile Co.:* Kushla (A. C. Sturtevant); Spring Hill [as "Springhill"] (W. S. Creighton); *Morgan Co.:* Decatur (Murphree); **Arizona:** *Cochise Co.:* 2mi NE Portal (G. D. Alpert); Chiricahua Mts. (W. & E. MacKay; J. F. Watkins); Chiricahua Mts., 5000 ft. (J. F. Watkins); Chiricahua Mts., 13mi NW jct. Rte. 80 on FSR 74, 5850 ft. (S. P. Cover); Chiricahua Mtns., Cave Creek Canyon, SW Res. Stn., 5400 ft. (S. P. Cover); Copper Canyon, 8.1mi SE Sunnyside, 5900–6000 ft. (R. R. Snelling); Copper Canyon, Huachuca Mtns., 22km SSW Sierra Vista, 1770m (S. G. Brady); Douglas (W. W. Jones); Huachuca Mts., Miller Canyon (A. E. Lewis); Miller Canyon, Huachuca Mtns., 6000 ft. (W. M. Wheeler); Palmerlee, Huachuca Mtns., 5300 ft. (W. M. Wheeler); Paradise Rd., 1.3mi W Portal Rd. Chiricahua Mts. (G. C. Snelling); Portal (Gotwald); Ramsey Canyon, Huachuca Mts. (W. S. Creighton); Ramsey Canyon, Huachuca Mts., 5800 ft. (W. M. Mann); SWRS, Portal, 5600 ft. (W. S. Creighton); Texas Pass, Dragoon [as "Dragon"] Mtns. (W. M. Wheeler); *Gila Co.:* Pinal Mts., 8000 ft. (R. A. Flock); Sierra Anchas, Hwy. 288 at Exp. Res. Stn., 4800 ft. (R. A. Johnson); *Maricopa Co.:* Four Peaks Wilderness, nr. Pidgeon Springs, 5600 ft. (R. A. Johnson); Mazatzal Mtns., on Four Peaks Rd., 10.3mi E Hwy. 87, 4000 ft. (R. A. Johnson); South Phoenix Park (P. S. Ward); *Mojave Co.:* Hualapai Mts., s. of Kingman, 1450m (E. I. Schlinger); *Pima Co.:* Baboquivari Mtns., Forestry Cabin, 3500 ft. (W. S. Creighton); Buehman Canyon, Santa Catalina Mts., 2900–3000 ft. (R. R. Snelling & G. C. Snelling); Santa Catalina Mts. (M. Chrisman); Tucson (R. H. Crandall); *Pinal Co.:* Oracle, 4500 ft. (W. M. Wheeler); *Santa Cruz Co.:* 6.7mi W I-19 on Ruby Rd. (G. C. Snelling); Bog Springs Cpgrd., Madera Canyon, Santa Rita Mts. (G. C. Snelling); Madera Canyon (R. H. Crandall); Madera Canyon, Santa Rita Mts. (R. H. Crandall); Nogales (Ehringer); Pajarito Mtns., Ruby Rd., 6.7mi W I-10, 4000 ft. (R. A. Johnson); Peña Blanca Lake (B. V. Brown & D. H. Feener); Ruby Rd., 7mi W Peña Blanca (G. C. Snelling); *Yavapai Co.:* 7.2mi E Chino Valley, 4600 ft. (R. A. Johnson); *Yuma Co.:* Burro Cyn., 2mi SE jct. 24, Kofa Game Refuge (P. Melhop & R. R. Snelling); **California:** *Los Angeles Co.:* Claremont (B. Crow); E fork, San Gabriel R., Angeles N. F.

(C. Ishida); Eaton Canyon (Sutton?); Eaton Canyon Pk. (R. H. Crandall); Jct. Angeles Crest & Angeles Forest Hwys. (G. C. Snelling); Millard Canyon, San Gabriel Mts. (R. H. Crandall); Placerita Canyon Park (F. T. Hovore); *Orange Co.*: Tonner Canyon (W. P. MacKay); *Riverside Co.*: Camino Rosales (A. Suarez); Margarita Summit (A. Suarez); near Perris (Mallis, Zschokke & Schwartz); Pinyon Flat, 1220m (P. S. Ward); Riverside (K. W. Cooper; M. E. Irwin); San Timoteo Cyn. (M. Wasbauer & A. Hardy); Temecula Cyn., Sta. Margarita R. (E. I. Schlinger); *San Bernardino Co.*: 2mi E Mentone (W. S. Creighton); Aliso Cr., Chino Hills State Park (M. Bennett *et al.*); Chino Hills State Park, 700 ft. (R. A. Johnson); *San Diego Co.*: 18km E Mt. Laguna, 300m (P. S. Ward); 5mi N Descanso, MSP primary site, 3000 ft. (J. H. Hunt); 5mi. E La Jolla (M. S. Trepanier); Chula Vista (E end), 160m (P. S. Ward); La Jolla (M. S. Trepanier); La Mesa (F. X. Williams); Nate Harrison Rd. nr. Mt. Palomar, 4800 ft. (E. I. Schlinger); nr. La Mesa (F. X. Williams); Point Loma (P. Leonard; A. Suarez); Ramona, 450m (M. S. Trepanier); San Diego (c.u.); **Colorado**: *Chaffee Co.*: Salida (c.u.); Salida, 7050 ft. (W. M. Wheeler); **Georgia**: *Jackson Co.*: Commerce (Vanderford); **Illinois**: *Adams Co.*: Quincy (T. E. Musselman); *Johnson Co.*: Ferne Clyffe St. Pk. (W. S. Creighton); **Iowa**: *Harrison Co.*: Little Sioux (W. F. Buren); *Woodbury Co.*: Sioux City (C. N. Ainslie; W. F. Buren); **Kansas**: *Douglas Co.*: Lawrence (F. X. Williams); Nat. Hist. Reser., Lawrence (C. W. Rettenmeyer); *Harvey Co.*: Sedgwick [as "Sedwick"] (A. J. McCurray); *Jefferson Co.*: Valley Falls (A. Mattis); *McPherson Co.*: McPherson (W. Knaus); *Pottawatomie Co.*: Onaga (F. F. Crevecoeur); *Riley Co.*: Jardine Terr. (J. F. Watkins); Manhattan (A. J. Mattis; R. C. Smith); no specific locality (F. Marlatt; J. B. Norton; J. F. Watkins); *Sedgwick Co.*: Wichita (J. R. Horton); **Kentucky**: *Marshall Co.*: Kentucky Dam (W. L. Brown); **Louisiana**: *Acadia Co.*: Crowley (C. E. Hood); *Beauregard Co.*: DeRidder (W. F. Buren); *East Baton Rouge Co.*: Baton Rouge (T. H. Jones); *Lafayette Co.*: Lafayette (E. S. Tucker); *Madison Co.*: Tallulah (McGehee); *Plaquemines Co.*: Buras (J. R. Horton); Naomi [as "Naomie"] (c.u.); *Rapides Co.*: Alexandria (E. S. Tucker); **Mississippi**: *Adams Co.*: Natchez (G. W. Alexander); *Clarke Co.*: Quitman (Murphree); *Clay Co.*: Cedar Bluff (c.u.); Cedar Bluff, Trimcane (G. W. Haug); *Harrison Co.*: Landon (Murphree); *Humphreys Co.*: Belzoni (Murphree); *Jones Co.*: Laurel (M. R. Smith); *Lowndes Co.*: Columbus (Murphree); *Monroe Co.*: Aberdeen (Murphree); Oktibbeha Co.: Maben (L. C. Murphree); Starkville (W. W. Lowe; M. R. Smith); State College [as "Agr. Col. Miss."] (M. R. Smith); *Stone Co.*: Bond (Murphree); Wiggins (Murphree); *Washington Co.*: Greenville (G. L. Snodgrass); **Missouri**: *Boone Co.*: Columbia (A. C. Cole; L. Haseman; M. Talbot); *Butler Co.*: Poplar Bluff (D. E. Read); *Cape Girardeau Co.*: Cape Girardeau (D. E. Read); *Cole Co.*: Jefferson City (A. C. Burrill); *Johnson Co.*: Knob Noster State Park

(M. B. & J. R. DuBois); *Ripley Co.*: Doniphan (Pergande); *St. Charles Co.*: St. Charles (M. Talbot); *St. Louis Co.*: Webster Groves [as "Webster Grove"] (G. Loeffel); **New Mexico**: *Colfax Co.*: Cimarron Canyon, Cimarron (A. C. Cole); *Dona Ana Co.*: 45km NE Las Cruces (W. MacKay); University Ranch (C. A. Kay); *Grant Co.*: 5km NW Silver City, 1900m (P. S. Ward); I-10, 3mi E Separ (R. A. Johnson); *Hidalgo Co.*: 4km N Rodeo, 1250m (P. S. Ward); San Simon Valley, 0.25mi W jct. Rte. 80 on Portal Rd. (NM533), 4250 ft. (K. Helms); San Simon Valley, 0.3mi NE jct. State Line Rd. & Rte. 533, 4250 ft. (S. P. Cover); San Simon Valley, 0.5mi W jct. Rte. 80 on Portal Rd. (NM533), 4250 ft. (D. Gordon); San Simon Valley, jct. State Line Rd. & Portal Rd. (NM533), 4250 ft. (S. P. Cover); *Santa Fe Co.*: Santa Fe (W. M. Mann); Santa Fe, 0.5mi N I-25 on Cerillos Rd., 6200 ft. (S. P. Cover); *Sierra Co.*: Hillsboro, 1600m (P. S. Ward); *Socorro Co.*: Sevilleta NWR (M. Kaspari); *Torrance Co.*: 10mi S Mountainair, 6650 ft. (A. C. Cole); *Union Co.*: Clayton (W. M. Wheeler); **North Carolina**: *Swain Co.*: Great Smoky Mts. Natl. Park, 5500 ft. (E. S. Ross); **Oklahoma**: *Cimarron Co.*: Kenton (T. H. Hubbell); *Kay Co.*: Ponca City (A. C. Burrill); **Tennessee**: *Chester Co.*: Henderson (Murphree); *Davidson Co.*: Nashville (W. S. Creighton; A. R. Laskey); near Nashville (L. Wesson); *Hawkins Co.*: Rogersville (W. S. Creighton); *Knox Co.*: Knoxville (A. C. Cole); *McMinn Co.*: Athens (Murphree); *Monroe Co.*: no specific locality (Jones); *Shelby Co.*: Memphis (Murphree); *Wayne Co.*: Clifton (Murphree); **Texas**: *Bell Co.*: Bowmer Ranch (J. F. Watkins); *Bexar Co.*: 20mi S San Antonio (E. S. Ross); San Antonio (E. S. Ross); *Calhoun Co.*: Port Lavaca (McGehee); *Dallas Co.*: Dallas (F. C. Bishop; E. W. Laake; W. D. Pierce; Vanderford); *Grimes Co.*: Shiro (W. Buren); *Hall Co.*: 6mi SE Turkey (C. W. O'Brien); *Harris Co.*: Houston (H. C. Millerider); *Jeff Davis Co.*: Fort Davis State Park (J. F. Watkins); *McLennan Co.*: Waco (R. S. Baldridge; J. F. Watkins); *Montgomery Co.*: Willis (J. C. Bridwell); *Travis Co.*: Austin (W. M. Wheeler); *Val Verde Co.*: Del Rio (c.u.); **West Virginia**: *Mason Co.*: West Columbia (Murphree).

(2) Form with shiny head (CASC, CDAE, JTLC, LACM, MCZC, UCDC, USNM)

UNITED STATES **California**: *Amador Co.*: 9km WNW Plymouth, 200m (P. S. Ward); *Colusa Co.*: 1km W Fouts Springs, 600m (P. S. Ward); *Contra Costa Co.*: Danville [as "Dannville"] (F. X. Williams); *El Dorado Co.*: 14km NW Shngle Springs, 340m (P. S. Ward); 9km SW Pilot Hill, 340m (P. S. Ward); *Kern Co.*: Lonetree Cyn., 6.8mi S jct. Randsburg [as "Randsbury"] Rd. & Hwy 14 (F Andrews & M. Wasbauer); *Lake Co.*: 14km ENE Lower Lake, 290m (P. S. Ward); 19km ESE Lower Lake, 700m (P. S. Ward); 20km ESE Lower Lake (B. L. Fisher); 6km NW Middletown, 490m (P. S. Ward); Nice-Bartlett Sprgs (A. Andrastalvy); *Los*

Angeles Co.: Los Angeles (A. Mallis); Pearblossom Hwy & Barrel Spr. Rd. (G. C. Snelling); *Mendocino Co.*: Hopland Field Stn., 240m (P. S. Ward); *Monterey Co.*: 10km SSW Jolon, Fort Hunter Liggett MR, 340m (P. S. Ward); 14km SW Jolon, Fort Hunter Liggett MR, 640m (P. S. Ward); 15km SW Jolon, Fort Hunter Liggett MR, 490m (P. S. Ward); Paraiso Springs (c.u.); *Napa Co.*: 5km ENE Rutherford, 120m (P. S. Ward); 5km W Oakville, 560m (P. S. Ward); N. side Howell Mtn., 3km NNE Angwin, 396m (H. B. Leech); *Placer Co.*: 2km E Colfax, 490m (P. S. Ward); *Riverside Co.*: Red Cloud Mine, Chuckwalla Mts., 2700 ft. (G. C. Snelling); *San Benito Co.*: 16.8mi N New Idria (A. J. Gilbert & N. Smith); *San Bernardino Co.*: Cima (c.u.); *San Luis Obispo Co.*: 19km SSE California Valley, Carrizo Plain Natural Area, 800m (P. S. Ward); 2.5mi. S Arroyo Grande (G. I. Stage); 20km ESE California Valley, Carrizo Plain Natural Area, 800m (P. S. Ward); *Santa Barbara Co.*: Arroyo Burro, 800m (J. Longino); Cachuma Saddle, 1100m (J. Longino); Cachuma Saddle, Los Padres N. F., 930m (P. S. Ward); N end Sedgwick Ranch, 610m (P. S. Ward); N end Sedgwick Ranch, 730m (P. S. Ward); near top of Las Cruces Mts (Heath); *Solano Co.*: 2km SE Mt. Vaca, 680m (P. S. Ward); Cold Canyon, 19km NNW Vacaville, 120m (D. M. Olson; P. S. Ward); Cold Canyon, 19km NNW Vacaville, 300m (P. S. Ward); Cold Canyon, 19km NNW Vacaville, 360m (P. S. Ward); Cold Canyon, 19km NNW Vacaville, 420m (P. S. Ward); Cold Canyon, 19km NNW Vacaville, 600m (P. S. Ward); Pleasants Ridge, 530m (P. S. Ward); *Sonoma Co.*: 1km NNE Sonoma, 170m (P. S. Ward); 3km N Sonoma, 290m (P. S. Ward); 8km NNW Cazadero, 300m (P. S. Ward); Pepperwood Ranch, 15km N Santa Rosa, 360m (P. S. Ward); *Stanislaus Co.*: Del Puerto Canyon, 18km WSW Patterson, 300m (P. S. Ward); *Tulare Co.*: Ash Mtn. Kwh Pwr Stn. #3 (J. A. Halstead); *Tuolumne Co.*: 2mi SE jct. Hwy. 49 & 120, 1840 ft. (G. C. Snelling); *Yolo Co.*: 6km SW Winters, 45m (D. A. Holway); 8km SE Davis, 10m (P. S. Ward); Davis (J. J. DuBois; A. Mallis); Woodland (E. I. Schlinger); **Colorado:** *Montezuma Co.*: Mesa Verde N. P., 6300 ft. (E. V. Gregg); **Nevada:** *Lyon Co.*: East Walker River, 26km SSE Yerington, 1460m (P. S. Ward); Weeks, 1280m (P. S. Ward); **Utah:** Millard Co.: White Sage Valley [as "White Valley"] (R. W. Fautin); *Washington Co.*: Springdale, 0.25mi S Zion Natl. Park (G. C. Snelling).

Note. Workers from sites in Los Angeles County, California are intermediate in sculpture between the two forms.

Neivamyrmex texanus Watkins 1972

Neivamyrmex texanus Watkins 1972: 353. Holotype male, Austin, Texas (W. M. Wheeler) (MCZC) [examined].

Neivamyrmex nigrescens; Watkins 1972: 358 (part).

Worker measurements.—(n = 22). HW 0.71–1.42, HL 0.81–1.38, WL 1.27–2.26, MTL 0.87–1.68, CI 0.83–1.06, FCI 0.066–0.125, SI 0.70–0.93, MTI 1.18–1.48, PLI 0.78–0.96, PWI 0.58–0.74.

Worker diagnosis.—Rather large body size (see HW, HL and MTL measurements); mandible with blunt basal tooth in largest workers, such a tooth becoming indistinct to absent in smallest workers; basal margin of mandible rounding into masticatory margin; frontal carinae well separated (MFC 0.047–0.168); clypeal apron conspicuous but less well developed than in *nigrescens*; scapes relatively long, SI > 0.69 (see also plot of SL on HW; Fig. 18); occipital lobes generally well developed; anterior margin of pronotum with transverse ridge well developed; dorsal face of propodeum conspicuously depressed below the level of the promesonotum, and forming a subangulate juncture with the declivitous face, the latter more or less concave in profile; legs relatively long, MTL/HW (=MTI) > 1.15; petiole subrectangular, variable in shape (see PLI and PWI values), always longer than high or wide, although generally shorter and higher than in *nigrescens*. Head, mesosoma, petiole and postpetiole densely punctulate, and having an opaque, granular appearance. Most of the surface of metapleural gland bulla densely punctulate and opaque, although sometimes with a very small, thin shiny strip immediately above the flange of the metapleural gland orifice. Body varying from dark reddish-brown to blackish-brown, the gaster and legs lighter.

Queen diagnosis.—Eye distinct, consisting of single convex ommatidium. Head slightly broader than long (CI 1.05–1.12, n = 5). Occipital corners rounded. Pronotum with a distinct posterior dorsolateral projection (Watkins, 1972, fig. 11). Mesonotum and propodeum without a median longitudinal impression, but propodeum with a shallow longitudinal concavity. Metatibial index (MTI) 0.81–0.90 (n = 5).

Petiole transverse, markedly broader than long (PWI approximately 1.2–1.7) in, in lateral view, with a single convex antero-dorsal face. Petiole width only slightly less than the length of the metatibia, DPW / MTL = 0.75–0.91 (n = 4). Length of gaster (non-physogastric) approximately twice WL (QGL/WL = 1.88–2.25, n = 3).

Male diagnosis.—Mandibles broad, spatulate (not sickle-shaped). Ocelli moderate in size and separated from the upper margin of the compound eye by a distance greater than twice the diameter of the median oecllus. No prominent transverse swelling above antennal fossa. Setae on venter of petiole long, golden, erect or suberect. Gaster reddish-brown. In profile, paramere (= stipes) slender, with a truncate posterior margin, and a tall, angular posterodorsal projection (Watkins 1985, Plate 9, fig. 5); volsella unforked, with long, slender upturned apex; aedeagus (=sagitta) with straight posteroventral process, just exceeding the posterodorsal process (in posterior reach).

Comments.—Despite the distinctive males and queens of this species, workers of *N. texanus* are difficult to distinguish from those of *N. nigrescens*. As Watkins (1972, 1985) noted, workers of *N. texanus* have the declivitous face of the propodeum slightly concave in profile (more or less straight in *N. nigrescens*), and forming a more distinctive angle with the dorsal face of the propodeum, but the difference is a subtle one. Workers of *N. texanus* also have the frontal carinae more widely separated than those of *N. nigrescens*, and plots of MFC (the minimum distance between the frontal carinae) against various measures of body size (e.g., HW, HL, MTL) reveal strong and almost diagnostic differences (Figs. 31–33), when considering those populations of *N. nigrescens* in the Southwest and eastern United States that are sympatric with *N. texanus*. Workers of *N. texanus* also tend to have a shorter, higher petiole than those of *N. nigrescens* (Fig. 34). Finally, the swelling of the

metapleural gland (bulla) is densely punctulate and more or less opaque over nearly all its surface in workers of *N. texanus*, while in *N. nigrescens* it presents a more shiny appearance. Differences between *N. texanus* and *N. californicus* have been considered under the latter species.

Material examined.—(CASC, LACM, MCZC, RAJC, UCDC, USNM)

MEXICO **Chihuahua:** Mpio. Riva Palacio, Bellavista (W. & E. MacKay); Mpio Chihuahua, 45km S Sueco (Carnada); **Durango:** 37mi W Durango (W. S. Creighton); **Hidalgo:** 5mi S Tizacuya (W. S. Ross); Guerrero Mill (W. M. Mann); Pachuca (W. M. Mann); San Miguel (W. M. Mann); **Jalisco:** Guadalajara (McClendon; W. M. Mann; Cadwallader); Japopan (Cadwallader); **Nuevo León:** Vallecillo (W. F. Buren); **Sonora:** 10mi S Agua Prieta (V. Roth); 26mi NW Bahia Kino (E. M. Fisher).

UNITED STATES **Arizona:** *Cochise Co.:* 5.8mi SE Sunnyside, 5700 ft. (R. R. Snelling); 8.1mi SE Sunnyside, 5950 ft. (R. R. Snelling); Chiricahua Mts., Rucker Camp, T19S R29E Sect.22 (W. MacKay); Douglas (W. W. Jones); Huachuca Mtns., 3mi SW Rte. 92 on Coronado Natl. Mon. Rd., 5100 ft. (S. P. Cover); Huachuca Mtns., 3mi S jct. Rt. 92 on rd. to Coronado Natl. Mon., 5100 ft. (S. P. Cover); Huachuca Mtns., Bear Creek, 19km SW Sierra Vista, 1640m (S. G. Brady); Palmerlee, Huachuca Mtns., 4500 ft. (W. M. Wheeler); San Bernardino Valley, 1mi NW jct. Rt. 80 on FSR 74 (Rucker Canyon Road), 4700 ft. (S. P. Cover); *Pima Co.:* 16mi W Tucson (S. Prchal; G. C. Snelling); Baboquivari Mtns, Brown Canyon (A. C. Cole); Baboquivari Mtns, Forestry Cabin, 3500 ft. (W. S. Creighton); Brown Canyon, Baboquivari Mtns. (Menke & Stange); Sabino Canyon (R. H. Crandall); Tucson Mtns. (F. R. Gehlbach); *Santa Cruz Co.:* Nogales (Buren); **Colorado:** *El Paso Co.:* Colorado Springs (J. G. Jack); Colorado Springs and vicinity (W. M. Wheeler); *Jefferson Co.:* Prospect Park (c.u.); **Florida:** *Alachua Co.:* 29°34.5′N, 82°29′W (R. W. Lundgren); Austin Carey Forest, Gainesville (G. B. Fairchild); Gainesville (T. H. Hubbell; A. Van Pelt); Pierce Homestead, Gainesville (W. R. Pierce); *Escambia Co.:* Pensacola (R. M. Lhamon); *Indian River Co.:* Sebastian (Nelson); *Leon Co.:* Woodville (D. E. Read); *Volusia Co.:* Daytona [Beach] (W. F. Buren); **New Mexico:** *Dona Ana Co.:* 45km NE Las Cruces (W. Mackay); *Eddy Co.:* Los Medanos, T22S R31E, Sect.15 (c.u.); *San Miguel Co.:* Las Vegas (W. M. Wheeler); **North Carolina:** *New Hanover Co.:* Wilmington (Vanderford); *Yancey Co.(?):* Black Mts. (c.u.); **South Carolina:** *Oconee Co.:* Clemson College (J. Berly & M. Smith); **Texas:** *Bexar Co.:* San Antonio (E. S. Ross); *Crockett Co.:* Ozona (A. C. Cole); *Jeff Davis Co.:* Fort Davis (T. W. Taylor); *Kimble Co.:* Junction (J. F. Watkins); *Llano Co.:* Llano (A. W. Morrill); *McLennan Co.:* Baylor Camp (J. F. Watkins); Waco (J.

Briga; S. Davis; S. Eldridge; F. R. Gehlbach; O. L. Nicholson; R. W. Plsek; C. A. Rhines; J. F. Watkins); *Taylor Co.*: Abilene rest stop (W. S. Creighton); *Travis Co.*: Austin (W. M. Wheeler); Austin, Brackenridge Field Lab (S. D. Porter); *Victoria Co.*: Victoria (c.u.); **Virginia**:

Chesterfield Co.: Warwick (Bond); *Essex Co.*: 1mi SE Dunnsville (D. R. Smith); *Henry Co.*: Chatmoss Plant, Martinsville (S. Schaeffer); *Louisa Co.*: 4mi S Cuckoo (J. Kloke & D. R. Smith); *Norfolk city*: Norfolk (Vanderford).

MODIFICATION OF EXISTING IDENTIFICATION KEYS

Couplets 5 and 9 of Watkins' (1985) worker key to the United States species of *Neivamyrmex* need modification to take into account the much greater intraspecific variability in body sculpture in *N. nigrescens*. In the updated portions of the key (below) I have also documented additional features of *N. texanus* and *N. opacithorax* which will facilitate their identification.

5 In lateral view declivitous face of propodeum slightly concave and forming a somewhat angular corner with the dorsal (basal) surface; frontal carinae well separated (MFC 0.05–0.17), as revealed in bivariate plots of MFC on various measures of body size (Figs. 31–33); petiole relatively short and high (Fig. 34); surface of most of the metapleural gland bulla densely punctulate and opaque, although sometimes with a very small, thin shiny strip immediately above the flange of the metapleural gland orifice . . . **N. texanus** Watkins
– Declivitous face of propodeum more or less straight in lateral view and forming a rounded angle with the dorsal (basal) surface; frontal carinae usually more closely contiguous (Figs. 31–33) and petiole height tending to be lower (Fig. 34); sculpture on surface of metapleural gland bulla becoming obsolete, such that the lower half or more is smooth (or weakly reticulate) and conspicuously shiny . . . . *N. nigrescens* (Cresson) (part)

9 Inner basal margin of mandible with a straight edge which forms an angular corner or small tooth at its juncture with the masticatory margin; side of pronotum usually smooth and shiny, and contrasting with the rugulose-punctulate sculpture that covers at least part of the mesosoma dorsum . . . . *N. opacithorax* (Emery)
– Inner basal margin of mandible with a convex edge which curves into the masticatory margin without forming an angular corner (Fig. 1); pronotal sculpture variable, but side of pronotum usually at least weakly reticulate-punctulate rather than exhibiting a smooth, shiny surface that contrasts with the sculptured mesosoma dorsum 9A
9A Body, scapes and legs shorter, head broader; MTI 1.05–1.14; see also plots of MTL on HW, SL on HW, WL on HW, CI on MTL and SI on MTL (Figs. 17–19, 21–23, 25, 26); dorsal surface of propodeum only slightly depressed below the level of the mesonotum (Fig. 2); dorsum of postpetiole and (typically) center of mesonotum smooth and shining, with scattered piligerous punctures but little or no trace of reticulation or punctulae . . . . *N. californicus* (Mayr)
– Body, scapes and legs longer; MTI 1.16–1.52; see also Figs. 17–19, 21–23, 25, 26; dorsal surface of propodeum conspicuously depressed below the level of the mesonotum (Fig. 5); postpetiole and mesonotum varying from opaque to sublucid, with traces of reticulation or punctulae usually evident . . . . *N. nigrescens* (Cresson) (part)

In the key to United States *Neivamyrmex* based on queens (Watkins 1972: 350–351) "*californicus*" in couplet 7 should be replaced with "*nigrescens* (part)". The queen of *N. californicus* is not yet definitively known (see discussion above, under that species).

Couplet 8 of Watkins' (1982) key to Mexican species of *Neivamyrmex* can be modified as follows to incorporate *N. californicus* and the more recently described *N. chamelensis* Watkins (1986). The treatment of *N. nigrescens* requires no change since the shiny form of *N. nigrescens* is not known to occur in Mexico.

8 Head and gaster of smaller workers blackish brown or reddish brown with a black overcast, mesosoma reddish brown without a blackish overcast; dorsum of promesonotum

slightly convex, and dorsum of propodeum as short or shorter than the node of petiole in lateral view . . . . *N. manni* (Wheeler)

– Head and mesosoma same color (reddish brown), gaster slightly lighter; posterior one-half of promesonotum flattened; dorsum of propodeum variable in length 8A

8A Dorsal face of propodeum shorter than the declivitous face, and conspicuously depressed below the level of the promesonotum, at least in larger workers (Watkins 1986, fig. 2); postpetiole as long as petiole . . . . *N. chamelensis* Watkins

– Dorsal face of propodeum as long as, or longer than, the declivitous face, and not conspicuously depressed below the level of the promesonotum (Fig. 2); postpetiole shorter than petiole 8B

8B Inner basal margin of mandible with a straight edge which forms an angular corner or small tooth at its juncture with the masticatory margin; clypeal apron short, extending anteriorly by a distance equal to about 0.2–0.4 times the diameter of the torulus; petiole relatively narrow (Fig. 20); side of pronotum usually smooth and shiny, and contrasting with the rugulose-punctulate sculpture that covers at least part of the mesosoma dorsum . . . . *N. opacithorax* (Emery)

– Inner basal margin of mandible with a convex edge which curves into the masticatory margin without forming an angular corner (Fig. 1); clypeal apron longer, extending anteriorly by a distance equal to about 0.4–0.5 times the diameter of the torulus; petiole broader (Fig. 20); pronotal sculpture variable, but side of pronotum usually at least weakly reticulate-punctulate rather than exhibiting a smooth, shiny surface that contrasts with the sculptured mesosoma dorsum . . . . *N. californicus* (Mayr)

## BIOLOGICAL OBSERVATIONS

Habitat Preferences

Although *N. nigrescens* and *N. californicus* are probably not sister taxa (see below) they appear to have similar ecological preferences in California. In southern California and northern Baja California, where morphological differences between the two species are greatest, their geographical distributions overlap broadly (Figs. 35, 36) and they occur together in such habitats as chaparral, coastal sage scrub and oak woodland. In northern California workers of *N. nigrescens* are more difficult to distinguish from those of *N. californicus*, due to convergence in body sculpture. In this region the two species are less frequently sympatric. *N. californicus* tends to be confined to more mesic, coastal locations than *N. nigrescens*, although the habitats occupied are similar: oak woodland, riparian woodland, chaparral and grassland. An exception to this is the occurrence of *N. californicus* at a xe-

ric inland site in the Sierra Nevada foothills (14km NW Shingle Springs, El Dorado County) where it co-occurs with *N. nigrescens* and *N. opacithorax* in a distinctive chaparral vegetation on gabbro soil. It was the sympatric association at this locality that alerted me to the distinction between true *N. californicus* and the "shiny morph" of *N. nigrescens*. The gabbro site has a number of rare plant species (Hunter and Horenstein 1992) and *N. californicus* likewise gives the impression of being an isolated, relic population here (the northern-most point in Fig. 36).

Throughout California both *N. californicus* and *N. nigrescens* are limited to low elevations, essentially below the coniferous forest zones. Most recorded populations come from locations below 1500m (*N. californicus*: sea level to 1840m; *N. nigrescens*: sea level to 1460m).

Outside the range of *N. californicus*, populations of *N. nigrescens* show a wide latitude of habitat choice, being found in scrubland, grassland and canyons of the

35

36

◆ *californicus*
■ *texanus*

■ *nigrescens*

37

38

■ *nigrescens* (s.s.)
◆*nigrescens* (shiny form)
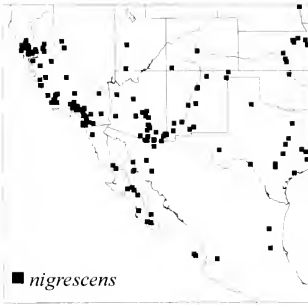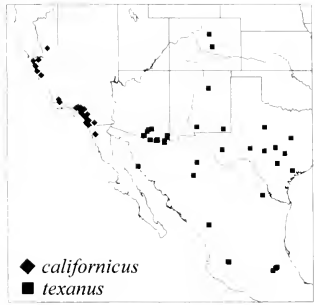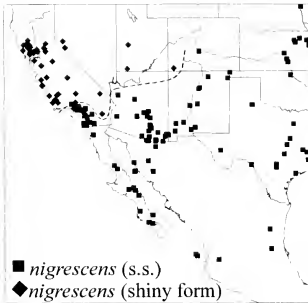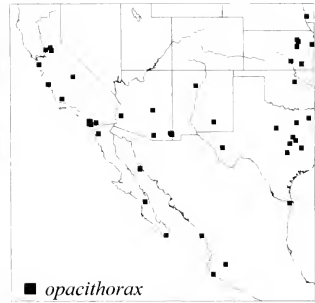
■ *opacithorax*

Figs. 35–38.   Known distributions in southwestern United States and Mexico of *Neivamyrmex nigrescens* (25), *N. californicus* and *N. texanus* (26), shiny and punctate forms of *N. nigrescens* (27), and *N. opacithorax* (28). *N. nigrescens*, *N. opacithorax* and *N. texanus* also occur in eastern United States (see Watkins 1985: 499–500).

Sonoran and Chihuahuan deserts, pine-oak-juniper woodland, prairie grassland, and eastern deciduous forest (Gregg 1963; Mirenda *et al.* 1980; Schneirla 1958; Smith 1942). It is perhaps unsurprising that over this broad range of ecological conditions the species displays considerable intraspecific variation in worker morphology.

Associations with *Messor andrei*

In California both *Neivamyrmex nigrescens* and *N. californicus* are often associated with nests of the common seed-harvesting ant, *Messor andrei* (Mayr). Indeed, one of the most efficient ways to determine the presence of these species at a locality is to examine the chaff piles of *Messer andrei*

nests. Such middens frequently contain the corpses of *Neivamyrmex* workers. There are several possible explanations for this.

First, *Messor andrei* workers appear to be efficient scavengers that collect dead and dying ants (of all kinds) and later discard the dried corpses in their middens. This is indicated by the fact that the remains of other ants, including species of *Camponotus, Crematogaster, Dorymyrmex, Forelius, Formica, Leptothorax, Monomorium, Pheidole, Prenolepis, Solenopsis* and *Stenamma*, are often encountered in *M. andrei* middens (Ward, pers. obs.).

Second, both *N. californicus* and *N. nigrescens* have been observed attacking nests of *Messor andrei*. In Amador County, California I observed nocturnal foraging columns of *N. nigrescens* workers entering two adjacent *M. andrei* nests—one containing a large *Messor* colony, the other a small incipient colony. The raid on the small nest was partially successfully, with *N. nigrescens* workers carrying off paralyzed *Messor* worker minims, although some *Messor* workers (and a dealate queen) escaped capture by climbing short grass stalks. No prey were observed to be taken from the larger nest, which contained normal-sized *Messor* workers. Mark Brown (1999) recorded *N. californicus* workers attacking *Messor andrei* nests at Jasper Ridge Preserve, near Stanford University. These raids on *Messor andrei* nests by *N. californicus* do not *N. nigrescens* do not appear to be especially effective, yet in the observed cases the army ants persisted in their assaults.

Third, the high frequency of *Neivamyrmex* worker corpses in *Messor* middens may reflect a tendency of *Neivamyrmex* colonies to temporarily occupy part of the underground chambers of the *Messor* nests, leading to an increased frequency of interactions between the two species. Some evidence for this comes from an observation that I made in early April 1984 near Rutherford, Napa County, northern California: a colony of *N. nigrescens*

("shiny form"), containing larvae, was located in wet but well-aerated soil immediately adjacent to an active *Messor andrei* nest. The *N. nigrescens* workers were emerging from the soil and slowly milling about on the ground surface during daylight hours, an unusual behavior but one which occurs in spring (March–May) in northern California before *N. nigrescens* begins its period of summer-active—and predominantly nocturnal—surface raiding. Thus, it appeared that this Rutherford colony of *N. nigrescens* had over-wintered in the soil in abandoned sections of the *Messor andrei* nest. Schneirla (1963) reported the use of pre-empted ant nests (species not specified) by over-wintering colonies of *N. nigrescens* in Arizona.

Interactions with Other California Ant Species

Other ants besides *Messor andrei* that are subject to raids by *Neivamyrmex nigrescens* in California include *Pheidole californica* Mayr, *P. hyatti*, *Solenopsis molesta* (Say) and *Formica moki* Wheeler (Ward, pers. obs.). Mallis (1938, 1941) reported *N. nigrescens* (misidentified as *N. californicus*) foraging nocturnally for insects attracted to street lamps on the Davis campus of the University of California, and attacking nests of the introduced ant, *Tetramorium caespitum* (Linnaeus). At the same location Mallis (1938) also recorded an altercation between *Neivamyrmex* and Argentine ants, *Linepithema humile* (Mayr), in which *Linepithema* emerged the victor. *L. humile* is now very abundant on the UC Davis campus and, during 17 years of observation here, I have seen no evidence that populations of *Neivamyrmex nigrescens* survive on campus, although the species occurs 8km southeast of Davis at a site not yet overrun by *Linepithema humile*. Work by Suarez *et al.* (1998) in southern California shows that *Neivamyrmex* species, including *N. nigrescens*, are among the first ant species to disappear from patches of remnant coastal sage scrub when *Linepithema humile* invades from adjacent urban habitat.

Table 1. Tests of nest evacuation response in potential prey of *Neivamyrmex*. Each test involved placement of one to several live *Neivamyrmex* workers at the nest entrance of an active test ant colony. All locations are in California.

Test species	Location	*Neivamyrmex* species (and source population)	Mass evacuation response?
Pheidole desertorum	Pinyon Flats	*nigrescens* (Pinyon Flats)	Yes
Pheidole hyatti	Carrizo Plain	*nigrescens* (Carrizo Plain)	Yes
Pheidole hyatti	Del Puerto Canyon	*nigrescens* (Cold Canyon)	Yes
Pheidole californica	Cold Canyon	*californicus* (El Dorado Co.)	Yes
Pheidole californica	Cold Canyon	*nigrescens* (Cold Canyon)	Yes
Pheidole californica	Davis	*nigrescens* (Cold Canyon)	Variable[a]
Pheidole californica	Davis	*nigrescens* (Carrizo Plain)	No
Pheidole californica	Del Puerto Canyon	*nigrescens* (Cold Canyon)	No
Pheidole californica	Ventura Co.	*nigrescens* (Carrizo Plain)	No
Pheidole californica	El Dorado Co.	*opacithorax* (El Dorado Co.)	No
Messor andrei	Cold Canyon	*nigrescens* (Cold Canyon)	No
Dorymyrmex bicolor	Pinyon Flats	*nigrescens* (Pinyon Flats)	No
Dorymyrmex insanus	Davis	*nigrescens* (Cold Canyon)	No

[a] Evacuation response seen in one of two trials.

Elsewhere, across its broad transcontinental distribution, *N. nigrescens* is reported to preferentially raid ant nests, especially those of *Pheidole* species (Mirenda *et al.* 1980), but also including colonies of *Aphaenogaster*, *Camponotus*, *Dorymyrmex*, *Formica*, *Leptothorax* and *Solenopsis* (LaMon and Topoff 1981; Mirenda *et al.* 1980; Schneirla 1958, 1963; Smith, 1927). Both ant brood, adult workers, and (when available) sexual alates are taken as prey, as are occasionally termites and non-social insects.

Less is known about the prey preferences of *Neivamyrmex californicus* but they appear to be similar to those of *N. nigrescens*. Mark Brown (1999) observed *N. californicus* attacking both *Messor andrei* and *Pheidole californica* colonies at Jasper Ridge. There is indirect evidence that *Solenopsis molesta* may be preyed upon. In a collection of dead *N. californicus* workers from a *Messor andrei* chaff pile at Jasper Ridge (collected by Nate Sanders) several individuals had dead workers of *Solenopsis molesta* attached (with closed mandibles) to legs and/or antennae. Dead workers of *N. californicus* (as well as those of *N. nigrescens*) have been found in the nest middens of *Pheidole hyatti* (Ward,

pers. obs.). This and certain other *Pheidole* species in California show an enemy-specific nest evacuation response to the presence of *N. californicus* and *N. nigrescens* workers.

Observations on this nest absconding behavior in California *Pheidole* are summarized in Table 1. A single *Neivamyrmex* worker, held with a pair of forceps at the nest entrance, can be sufficient to cause mass evacuation of workers and brood in *Pheidole californica*, *P. desertorum*, and *P. hyatti*. In *Pheidole californica* the response is not invariably observed, however (Table 1), and seems to vary with location, ambient conditions, and possibly as a function of previous experience (as documented for another prey species, *Aphaenogaster cockerelli* André (McDonald and Topoff 1986)). Similar nest evacuation behavior has been studied in Arizona populations of *Pheidole desertorum* and *P. hyatti* attacked by *N. nigrescens* (Droual 1983, 1984).

POPULATION DIFFERENTIATION AND BIOGEOGRAPHY

The taxonomic confusion surrounding *N. californicus* and *N. nigrescens* can be traced to undue reliance on superficial features of head sculpture, lack of attention

to other structural differences, and insufficient appreciation of the degree of variability in *N. nigrescens*. In *Neivamyrmex* and in all other genera of New World army ants (which together comprise the subfamily Ecitoninae) the queens are entirely wingless and have limited capacities for dispersal (Gotwald 1995). Because of the population viscosity associated with limited female movement—only partly mitigated by gene flow via dispersing, winged males—and perhaps also because of the lower effective population sizes achieved by these highly predacious (and hence higher trophic level) organisms, one *expects* conspecific allopatric populations of army ants to develop substantial differences. The prediction is borne out, at least among the more widespread species of ecitonine army ants, in which there exists a large amount of geographical variation (Borgmeier 1955, 1956). It seems desirable for taxonomists to be cautious in establishing new species of army ants especially when dealing with closely related allopatric populations. In the present paper I have refrained from giving a new name to the shiny form of *N. nigrescens*, because it is essentially allopatric to the more typical granulate-punctate *N. nigrescens*. The two are not known to both occur sympatrically *and* retain their distinctness; rather, in geographically intermediate localities (i.e., in the San Gabriel Mountains of southern California) we find morphologically transitional populations. A genetic analysis of the transition zone would be interesting, especially in view of its relative narrowness.

Thus, the distribution of the two forms of *N. nigrescens* (Figure 37) suggests a previous fragmentation of the range of *N. nigrescens*, and the consequent differentiation of populations but not to a degree sufficient to cause reproductive isolation. The Transverse Ranges of California and the upper Colorado River basin emerge as the probable sites of geographic barriers. The divergence between the common

ancestor of *N. nigrescens* (sensu lato) and *N. californicus* must have occurred considerably earlier. On the basis of structural similarities (Figs. 17–19) *N. californicus* actually appears to be more closely related to *N. opacithorax* than to *N. nigrescens*, with the latter species being more closely related to *N. texanus*. This hypothesis could be tested with the study of additional characters and (crucially) the inclusion of additional taxa from Mexico, especially *N. chamelensis*, *N. cornutus*, *N. manni*, and *N. sumichrasti*. The possibility that the widespread *N. nigrescens* is paraphyletic should also be considered.

A final point of biogeographic interest concerns the distribution limits of *Neivamyrmex californicus* (Fig. 36) and *N. opacithorax* (Fig. 38) in northern California. Both species appear to be restricted to areas east and south of the Sacramento River and the San Francisco/San Pablo Bays. This drainage system can be expected to be a significant barrier for dispersal in hymenopterans such as army ants whose reproductive females are wingless.

ACKNOWLEDGMENTS

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Revision of North American *Aleiodes* Wesmael (Part 5): The *melanopterus* (Erichson) Species-Group (Hymenoptera: Braconidae, Rogadinae)

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Abstract.—The *Aleiodes melanopterus* (Erichson) species-group is regarded as monophyletic based on the large oral opening and narrow clypeus. It is defined to include 13 Palaearctic and Neotropical species plus the following North American species: *mandibularis* **(Cresson) new combination**, *megastomus* **new species**, *melanopodus* **new species**, *mexicanus* Cresson, *miani* **new species**, and *politiceps* **(Gahan) new combination**. A key to the North American species of the *melanopterus* species-group is presented.

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 fifth in a series of planned papers 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 Shaw, 1998). The *melanopterus* (Erichson) group is moderate sized with species occurring in the Palaearctic, Nearctic and Neotropical Regions. This is a distinctive monophyletic group with all species having a large oral opening and narrow clypeus. Our definition of this species-group includes all species known to us worldwide. However, because our main 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, Sphingoidea and Papilionoidea (S. Shaw et al., 1997). Very little is known about the biology of the *melanopterus* species-group but the few records indicate parasitism of noctuid larvae. 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). We have host information for only one North American species, *politiceps* (Gahan), which has been reared from at least two species of noctuid 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 Wharton *et al.* (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 keys of Wharton *et al.* (1997). The species-groups of North American *Aleiodes* can be identified using the key provided in S. Shaw *et al.* (1997).

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) and agrees closely with that of Goulet and Huber (1993). 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: AEI (American Entomological Institute, Gainesville, FL), AMNH (American Museum of Natural History, New York, NY), ANSP (Academy of Natural Sciences, Philadelphia, PA), CNC (Canadian National Collection, Ottawa, Canada), CAS (California Academy of Sciences, San Francisco, CA), FSCA (Florida State Collection of Arthropods, Gainesville, FL), MCZ (Museum of Comparative Zoology, Harvard University, Cambridge, MA), MSU (Montana State University, Bozeman, MT), NCSU (North Carolina State University, Raleigh, NC), NNML (Nationaal Natuurhistorisch Museum, Leiden, The Netherlands), RMSEL (Rocky Mountain Systematic Entomology Laboratory, University of Wyoming, Laramie, WY), TAMU (Texas A&M University, College Station, TX), UCD (University of California, Davis, CA), USNM (National Museum of Natural History, Smithsonian Institution, Washington, DC).

ALEIODES MELANOPTERUS SPECIES-GROUP

Included species.—*miniatus* (Herrich-Schaeffer) 1838, new combination, Europe, North Africa; *melanopterus* (Erichson) 1848, new combination, South America; *aestuosus* (Reinhard) 1863, new combination, eastern Europe, Middle East; *mexicanus* Cresson 1869, Mexico, southern United States; *mandibularis* (Cresson) 1872, new combination, central United States; *krulikowskii* (Kokoujev) 1898, new combination, eastern Europe, Mongolia; *venustulus* (Kokoujev) 1905, new combination, eastern Europe; *lucidus* (Szépligeti) 1906, new combination, Bolivia; *politiceps* (Gahan) 1917, new combination, eastern United States, Central America; *wadai* (Watanabe) 1937, new combination, Japan; *agilis* (Telenga) 1941, new combination, eastern Europe; *desertus* (Telenga) 1941, new combination, eastern Europe; *fahringeri* (Telenga) 1941, new combination, Mongolia; *glaber* (Telenga) 1941, new combination, eastern Europe, Mongolia; *ruficeps* (Telenga) 1941, new combination, eastern Europe; *flavistigma* Shaw 1993, Brazil; *megastomus*, new species; *melanopodus*, new species; *miani*, new species.

Diagnostic characters.—Oral opening (Figs. 5–9) large and oval, width equal to or greater than height of face, clypeus very narrow; eyes and ocelli large, the ocellar diameter equal to or slighter greater than diameter of lateral ocellus; mesonotum and mesopleuron usually smooth and polished; hind wing vein RS straight, marginal cell gradually widening to wing apex (Figs. 1–4). A discussion of the phylogenetic relations of the species-groups of *Aleiodes* can be found in Fortier (1997).

Comments.—This is a moderately sized species-group associated with noctuids and distinguished by the large oval oral opening. The Neotropical species have been reviewed by Shaw (1993) where he placed them in the subgenus *Eucystomastax*. Although the name *melanopterus* used for this species-group is not the oldest name, it has been used previously by Shaw (1993) in his study of the Neotropical species and Fortier (1997) in his study of *Aleiodes* phylogeny. For this reason and

because the ICZN does not provide for the naming of species groups, we have decided to continue the usage of *melanopterus* in this paper.

KEY TO THE NORTH AMERICAN SPECIES OF THE *MELANOPTERUS* SPECIES-GROUP

1. Width of oral opening about equal to height of face (from clypeus to antennal sockets); malar space about equal to basal width of mandible (Figs. 8, 9) 2
– Width of oral opening greater than height of face; malar space much less than basal width of mandible (Figs. 5–7) 3
2(1). First and second metasomal terga strongly porcate (Fig. 11); fore wing vein 1CUa longer than 1cu-a, wings strongly infumated (Fig. 3) . . . . *politiceps* **(Gahan)**
– First and second metasomal terga weakly costate rugulose (Fig. 10); fore wing vein 1CUa equal in length to 1cu-a, wings hyaline or weakly infumated . . . .
. . . . *miani* **Marsh and Shaw, new species**
3(1). Body bicolored, at least legs black, differently colored from body 4
– Body unicolored, legs concolorus with rest of body 5
4(3). Head and legs entirely black . . . . *mexicanus* **Cresson**
– Head orange, femora, tibiae and tarsi only black . . . .
. . . . *melanopodus* **Marsh and Shaw, new species**
5(3). Fore wing vein 1CUa as long as or shorter than vein 1cu-a (Fig. 4); clypeus flat, narrow, without distinct apical border . . . . *megastomus* **Marsh and Shaw, new species**
– Fore wing vein 1CUa longer than 1cu-a (Fig. 1); clypeus protruding, with distinct apical carinate border . . . . *mandibularis* **(Cresson)**

Aleiodes mandibularis (Cresson), new combination
(Figs. 1, 6)

Rogas mandibularis Cresson 1872:188.

Diagnosis.—Body unicolored orange, antenna brown, wings hyaline or slightly dusky, veins brown; body length, 8.5–10.0 mm; 55–65 antennomeres; oral opening width greater than height of face (Fig. 6); malar space short, equal to or less than basal width of mandible; face costate, frons, vertex and temple smooth; ocelli small, diameter of lateral ocellus less than ocell-ocular distance; pronotum rugose medially; mesonotum, scutellum and mesopleuron punctate and shining, subalar sulcus and sternaulus weakly rugose; propodeum rugose, median carina complete; first, second and basal ½ of third metasomal terga costate-rugose, median carina complete to middle of third terga; fore wing vein 1cu-a beyond 1M by distance greater than length of 1cu-a, vein 1CUa

longer than 1cu-a (Fig. 1); hind wing marginal cell narrowest basally, gradually widening apically, vein RS straight, vein m-cu present (Fig. 1); tarsal claws strongly pectinate.

Type material examined.—Holotype male of *Rogas mandibularis* Cresson is not in the ANSP and apparently lost. A neotype has been selected as follows: male, TEXAS, Victoria, September 18, 1904. Deposited in USNM.

Distribution.—Scattered collections throughout central United States from Ohio south to Georgia, west to Nebraska and Texas.

Biology.—Host unknown.

Comments.—Although *mandibularis* is a large and distinctive species, it is not commonly collected. Superficially it resembles *politiceps* because of its large orange body, but the more greatly enlarged oral opening, robust mandibles, and hyaline wings will easily distinguish *mandibularis* from that species.
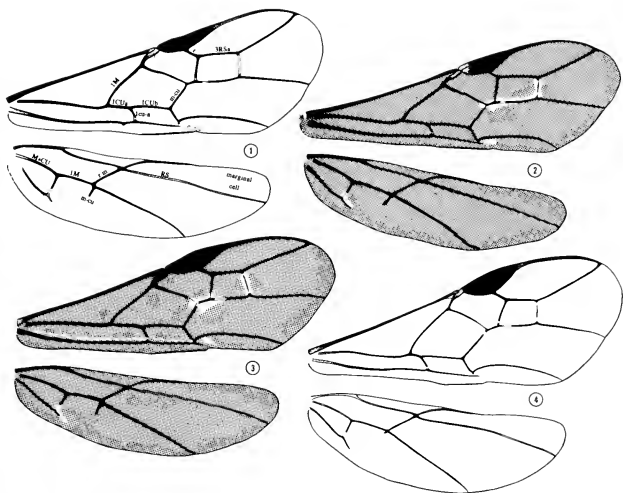
Figs. 1–4. Wings of *Aleiodes* species: 1, *mandibularis* (Cresson); 2, *melanopodus* n. sp.; 3, *politiceps* (Gahan); 4, *megastomus* n. sp.

Aleiodes megastomus Marsh and Shaw, new species
(Figs. 4, 5)

Female.—**Body color:** varying from dark honey yellow to dark brown or black, legs and mandibles always brown; wings hyaline, veins including stigma dark brown, stigma occasionally lighter brown or yellow. **Body length:** 7–9 mm; fore wing length, 7–9 mm. **Head** (Fig. 5): 57–61 antennomeres, flagellomeres beyond first slightly longer than wide, first flagellomere nearly twice as long as second; malar space short, $\frac{1}{5}$ eye height and $\frac{2}{3}$ basal width of mandible; temple $\frac{2}{3}$ eye width; occipital carina not meeting hypostomal carina; oral opening very wide and oval, width three times malar space and slightly greater than height of face; clypeus flat,

without distinct apical carinate border; ocelli large, greatest diameter of lateral ocellus slightly greater ($\frac{3}{5}$) than ocell-ocular distance; face rugulose, frequently with median longitudinal ridge below antennae; frons smooth, occasionally rugulose behind antennae; vertex punctate; temples punctate, rugulose near base of mandibles; maxillary palpus not swollen; mandibles large, when closed tips going well beyond middle of oral opening. **Mesosoma:** pronotum rugulose; mesonotum and scutellum smooth but often with conspicuous hair pits making it appear punctate; notauli weakly scrobiculate, meeting posteriorly in triangular rugose area; scutellar furrow wide, scrobiculate posteriorly, separated from mesonotum by transcutal ridge; mesopleuron smooth, subalar groove

scrobiculate; sternaulus absent; propodeum weakly rugulose dorsally, smooth laterally, propodeal carina present but often weak. **Legs:** tarsal claw weakly pectinate, with 3–4 short teeth near base; inner spur of hind tibia slightly less than half length of hind basitarsus; hind coxa rugulose dorsally. **Wings** (Fig. 4): hyaline; fore wing vein r ⅓ length of 3RSa and of m-cu, vein 1cu-a beyond 1M by distance less than length of 1cu-a, vein 1CUa about ¼ length of 1CUb, vein 1CUa about equal to 1cu-a; hind wing marginal cell gradually widening from about middle to wing margin, vein r-m equal to or slightly shorter than 1M, vein M+CU only slightly longer than 1M, vein m-cu present. **Metasoma:** first tergum weakly strigate with raised smooth triangular area at base, as long as apical width, basal width ⅓ apical width, median carina usually present, often weak and occasionally absent; second tergum weakly strigate, often smooth at apex, median carina weak and often absent; third and following terga smooth, third occasionally punctate at base, median carina absent on third tergum; ovipositor sheaths ¾ length of hind basitarsus.

Male.—Essentially as in female.

Holotype.—Female: CALIFORNIA, Corcoran, Kings County, March 10, 1965, F. H. Surber, light trap. Deposited in USNM.

Paratypes.—ARIZONA: 2 females, Nogales, January 30, 1954, March 9, 1961, A. C. Valcarce; 1 female, Prescott, April 22, 1936, Cby. and Bish.; 3 females, Tempe, February 5, 1923, February 8, 1926, E. V. Walter; 10 females, 5, males, Tuscon, January 27, 1935, February 4, 1935, December 10–20, 1939, January 8, 1940, January 26, 1953, R. H. Crandall, Hubbard, Samual Green, E. C. Narschall, Donald Foote, G. C. Butler, Bryant collectors, some at light; 1 female, Cameron, Coconimo Co., February 28, 1978, R. C. Miller; 1 female, Beaver Dam, Mojave Co., April 2, 1969, P. M. Marsh; 1 fenale, 1 male, Baboquivari Mtns., August 1, 1924, O. C. Poling. CALIFORNIA: 1 female, Manzanita Lake, Las-

sen Nat. Park, May 23, 1941, P. D. Hurd; 1 female, 1 male, May Lake, Yosemite Pk. July 26, 1948, H. K. Townes; 6 females, 5 males, 3 mi. SW Somerset, El Dorado Co., dates ranging from April 20, 1974 to May 20, 1978, R. Wharton; 2 females, 2 males, Thousand Palms, February 14–22, 1955, W.R.M. Mason, J.E.H. Martin; 1 female, Desert Hot Springs, February 14, 1965, J.E.H. Martin; 1 female, Wrightwood, San Bernardino Co., June 16, 1964, J. S. Buckett; 2 females, Quincy, Plumas Co., June 5, 1963, G. Jeskey; 1 female, McClure Vly., Kings Co., March 6, 1953, J. C. Hall; 1 female, Huntington Lake, June 26, 1961, A. T. McClay; 5 females, 1 male, Calaveras Co., 4.8 km S West Point, May 1–9, 1981, Stanley C. Williams; 1 female, Napa Co., N. side Howell Mtn., 2 mi NNE Angwin, 1300 ft., April 11, 1978, H. B. Leech; 1 female, Napa Co., 1 mi N. Angwin, May 9, 1964, H. B. Leech; 1 female, Nevada City, May 16, 1930, E. P. Van Duzee; 1 female, Fresno Co., Coalinga, Los Gatos Cn., March 17, 1931, E. P. Van Duzee; 1 female, Mt.. Diablo, April 23, 1939. IDAHO: 1 male, Murtaugh, May 27, 1931, D. E. Fox; 2 females, Lewiston, April 27, 1936, alt. 550 ft., R. E. Miller. KANSAS: 1, female, Manhattan, April 24, 1926, R. T. Cotton, at light. MONTANA: 1 female, Gallatin Co., May 8, 1932. NEVADA: 1 female, Reno, May 14, 1915; 1 female, Kyle Cyn., Chlstn, Mt., May 25, 1940, G. E Bohart. UTAH: 1 female, Blue Spruce Camp, 18 mi. N Escalante, Garfield Co., 8000 ft., July 30, 1965, F., P. & M. Rindge; 6 females, Richfield, May 22, 1929, May 28, 1930, light trap; 2 females, 1 male, Wellsville, May 17, 1961, G. E. Bohart; 1 female, Baker, S14,T13N,R69E, May 4, 1939, T. O. Thatcher. WASHINGTON: 3 females, 1 male, Yakima, June–September, March 30, 1932, at light, A. R. Rolfs; 1 male, Orville WYOMING: 2 females, Stratton Expt. Watershed, nr. Saratoga, May 16–17, 1972, June 4–8, 1972, J. M. Schmid; 26 females, 2 males, Albany Co., T15N R73W, 7500′, May 15, 1978, May 20, 1980, C. D. Ferris;

1 female, Carbon Co., 3 mi. N of WY 130W, between mi. 54 and 55, June 25–July 4, 1991, Malaise trap, Mian; 1 female, Fremont Co., Sinks Cyn., 12.1 mi. SW Lander, June 23, 1980, LT, Mike Pogue, Robert Lavigne; 2 females, 1 male, Albany Co., 1 mi. E Laramie, May 10–18, 1994, June 8, 1996, BLT 2217, Skyview Lane, 7465 ft., J. S. Nordin. SASKATCHEWAN: 1 female, Saskatoon, May 12, 1933, A. R. Brooks. Deposited in USNM, RMSEL, AMNH, TAMU, MCZ, MSU, CNC, CAS, UCD, NNML.

Distribution.—This species is common in western North America from Saskatchewan to New Mexico and west. The single specimen from Kansas is this species and with more collecting it probably will occur throughout the western half of North America.

Biology.—No host records are available. Many of the type series were collected at light or in light traps. The general habitus and color of this species is similar to species of *Homolobus* which frequent light traps.

Comments.—This species is similar to *mandibularis* because of the wide oral space. It differs in several characters: the ocellus of *megastomus* is larger than in *mandibularis*, the clypeus of *megastomus* is flat rather than protruding as in *mandibularis*, and vein 1cu-a in the fore wing of *megastomus* is closer to 1M than in *mandibularis*.

Etymology.—The specific name is from the Greek *megas* meaning large or great and *stoma* meaning mouth referring to the large wide oral space.

Aleiodes melanopodus Marsh and Shaw, new species
(Figs. 2, 7)

Female.—**Body color**: head, mesosoma, metasoma, coxae and trochanters orange; antenna, palpi, ovipositor sheaths, and legs beyond trochanters black, trochanter 2 sometimes dark; wings dusky. **Body length**: 8–9 mm, fore wing length, 7–8 mm. **Head** (Fig. 7): 53–58 antennomeres, first flagellomere twice as long as wide, flagellomeres 10–30 as wide as long; malar space short, ¼ eye height and ¾ basal width of mandible; temple bulging, about as wide as eye; occipital carina nearly meeting hypostomal carina; oral opening wide and oval, width 3.5 times malar space and about twice height of face; clypeus protruding; ocelli small, greatest diameter of lateral ocellus about ¾ ocellocular distance; face costate, with median longitudinal ridge below antennae; frons smooth, occasionally weakly rugulose behind antennae; vertex and temple smooth; maxillary palpus not swollen; mandibles large, when closed tips going beyond middle of oral space. **Mesosoma**: pronotum rugulose laterally; mesonotum and scutellum smooth and shining; notauli weakly scrobiculate, meeting posteriorly in triangular rugulose area with central longitudinal carina; mesopleuron smooth and shining, subalar sulcus rugulose, sternaulus short and wide, weakly scrobiculate; propodeum strongly rugose dorsally, smooth laterally with rugosities near hind coxa, median carina complete. **Legs**: tarsal claws strongly pectinate, with 6–8 teeth on entire inner surface of claw; hind coxa smooth dorsally. **Wings** (Fig. 2): fore wing vein r ⅓ length of 3RSa and ⅓ length of m-cu, vein 1cu-a beyond 1M by distance about twice length of 1cu-a, vein 1CUa about ⅞ length of 1CUb, vein 1CUa longer than 1cu-a; hind wing marginal cell gradually widening from about middle to wing margin, vein r-m about ¾ length of 1M, vein M+CU about 1.4 times longer than 1M, vein m-cu present. **Metasoma**: first tergum costate-rugose, length slightly less than apical width, median carina complete; second tergum costate-rugose, median carina strong on basal half; third tergum costate on basal ¾, median carina absent; fourth and following terga smooth, fourth weakly coriaceous on basal half; ovipositor sheaths about 1.5 times longer than hind basitarsus.
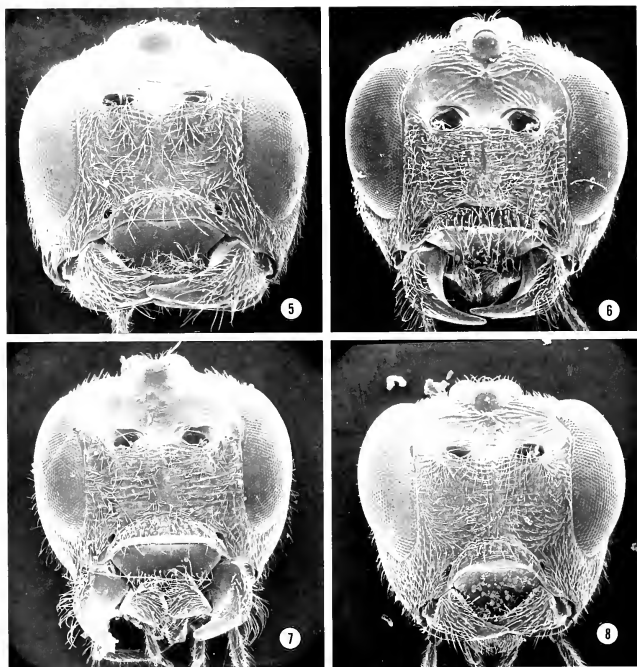
Figs. 5–8. Faces of *Alciodes* species: 5, *megastomus* n. sp.; 6, *mandibularis* (Cresson); 7, *melanopodus* n. sp.; 8, *miau* n. sp.

Male.—Essentially as in female.

Holotype.—Female: MARYLAND, Cabin John, (label actually states Washington, DC which is in error), September 24, 1922, H. S. Barber collector. Deposited in USNM.

Paratypes.—KENTUCKY: 1 female, 1 male, Golden Pond, October 1–8, 1964, September–October, 1965, S. G. Breeland. MARYLAND: 1 male, Cabin John, October 1, 1916, R. M. Fouts collector; 1 male,

Bethesda, September 23, 1914, R. C. Shannon collector; 1 female, Prince George's Co., Beltsville, September 19, 1964, Paul H. Arnaud, Jr.; 1 female, Riverdale, Prince George's Co., September 26, 1979, T. Waters; 1 female, Takoma Park, September 29, 1945, H. and M. Townes. LOUISIANA: 1 male, Sunshine, October 27, 1972, V. A. Brou. NORTH CAROLINA: 1 male, Wake Co., October 16, 1959; 1 female, Wake Co., October 3, 1959, O. F. Vargas; 1 male,

Clayton, Cent. Crops. Res. Sta., 1959, A. Saldarriaga; 1 male, Raleigh, October 3, 1959, L. Self; 1 female, Pender Co., October 9, 1954, D. A. Becker; 1 male, Wake Co., Raleigh, Centienial Campus, October 13, 1992, E. D. Karoly; 1 male, Wake Co., Raleigh, November 5, 1988, D. L. Moncol. VIRGINIA: 1 female, Richmond, collection Ashmead; 1 female, Falls Church, September 26 (no year), Banks collector. Deposited in USNM, RMSEL, MCZ, CAS, NCSU, FSCA, AEI.

Distribution.—Known from Maryland, Virginia, North Carolina, Kentucky and Louisiana.

Biology.—Unknown.

Comments.—This species is very similar to *mandibularis* by the shape of the mouth and the body color. It differs in having black legs, smaller ocelli, and longer ovipositor.

Etymology.—The specific name is from the Greek *melanos* meaning dark or black and the Greek *podos* meaning foot referring to the distinctive black legs.

Aleiodes mexicanus Cresson

Aleiodes mexicanus Cresson 1869:378.

Diagnosis.—Body bicolored, head, antenna, pronotum, propleuron and legs black, mesosoma and metasoma orange, wings dusky, veins brown, tegula orange; body length, 9 mm; 64 antennomeres; malar space very short, about ½ basal width of mandible; oral opening large, diameter 5 times malar space length and about equal to face height; ocelli large, ocellocular distance less than diameter of lateral ocellus; frons, vertex and temple smooth, face rugulose; mesonotum and mesopleuron smooth; propodeum with dorsal apical corners sharp, median carina complete; first, second and basal ¾ of third metasomal terga strigate, median carina complete of first and second terga which also have lateral carinate edges; fore wing vein 1cu-a beyond vein 1M by distance slightly greater than length of 1cu-a, vein 1CUa

slightly longer than 1cu-a; hind wing marginal cell narrowest at base, gradually widening to apex, vein RS straight; tarsal claws pectinate, with 4–6 slender spines.

Type material examined.—*Aleiodes mexicanus* Cresson, holotype female (not male as in original description), Mexico [ANSP].

Distribution.—In addition to Mexico, we have seen one specimen from Mississippi.

Biology.—Unknown.

Comments.—This species is distinctive by its color, short malar space and wide oral opening. The one specimen from Mississippi may be an accidental introduction and the establishment of this species in the U.S. needs to be confirmed by further collecting in the southern United States. Shaw (1993) provides a description and key to this species and other related Neotropical species.

Aleiodes miani Marsh and Shaw, new species
(Figs. 8, 10)

Female.—**Body color**: honey yellow except antenna, ocellar triangle, palpi, propleuron, mesosternum, metanotum, propodeum, basal half of first metasomal tergum, apex of all femora, fore and hind tibiae, apical half of hind tibia and all tarsi black, wings hyaline, veins dark brown, tegula yellow. **Body length**: 7.0–9.0 mm; fore wing length, 5.0–7.0 mm. **Head** (Fig. 8): eyes and ocelli not unusually large; 59–60 antennomeres, all flagellomeres beyond the first about as wide as long; malar space shorter than basal width of mandible and about ¼ eye height; temple broad, slightly less than eye width; occipital carina complete on vertex, not reaching hypostomal carina; oral opening large, circular, width greater than basal width of mandible and face height; clypeus narrow, not swollen; ocelli small, diameter of lateral ocellus slightly less than ocellocular distance; face, frons and malar space rugose, temple and vertex smooth except for hair pits; maxillary palpus not swollen;
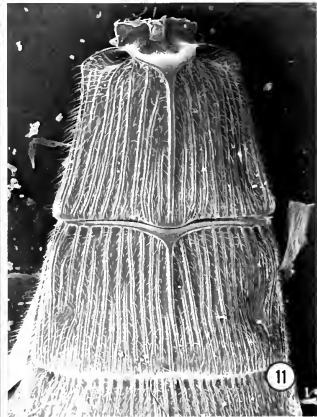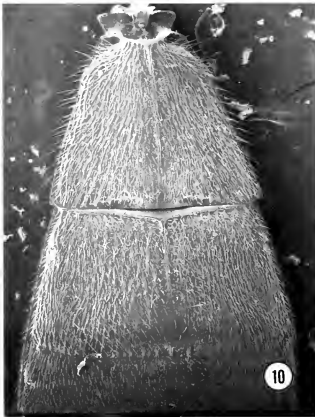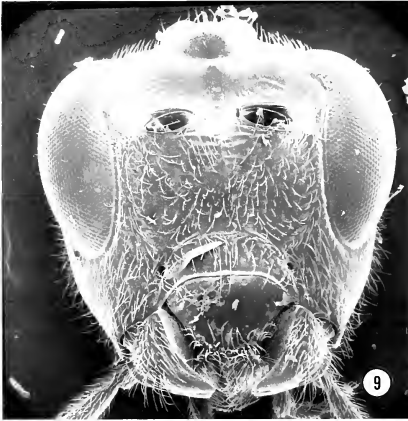
Figs 9–11. Morphological features of *Aleiodes* species: 9, face of *politiceps* (Gahan); 10, metasomal terga of *miani* n. sp.; 11, metasomal terga of *politiceps* (Gahan).

mandibles large, tips crossing when closed. **Mesosoma**: pronotum costate rugose laterally, costate ventrally; mesonotum and scutellum smooth except for hair pits, notauli weakly scrobiculate, meeting in shallow rugose area before scutellum; mesopleuron smooth, subalar sulcus rugose, sternaulus carinate; propodeum rugose dorsally, smooth laterally, median carina weak but complete. **Legs**: tarsal claws weakly pectinate; hind coxa punctate dorsally. **Wings**: fore wing vein r about ⅓ length of 3RSa and m-cu, vein 1cu-a beyond 1M by distance equal to length of 1cu-a, vein 1CUa about ¼ length of 1CUb; hind wing vein RS straight, marginal cell gradually broadening to apex, vein r-m shorter than 1M, vein M+CU slightly longer than 1M, vein m-cu weak and leaving 1M before junction of r-m. **Metasoma** (Fig. 10): first tergum costate rugose, apical width about equal to length, median carina complete; second tergum costate rugose, median carina not quite complete; third tergum costate rugose on basal half, coriaceous on apical half, median carina absent; remainder of terga coriaceous; ovipositor less than ½ length of hind basitarsus.

Male.—Essentially as in female except mesopleuron and pronotum nearly and first metasomal tergum entirely black.

Holotype.—Female: WYOMING, Carbon Co., ¾ mi. N of WY 130 W between mi. 56 & 55, mixed forest near water, Malaise, Mian, July 14–27, 1991. Deposited in RMSEL.

Paratypes.—WYOMING, 1 female, 4 males, same data as holotype with dates of June 25 through August 6, 1991. Deposited in USNM, RMSEL.

Distribution.—Known only from Wyoming.

Biology.—Unknown.

Comments.—This species is similar to *mandibularis* but can be distinguished by its different coloration with the black propodeum and first tergum and its smaller oral opening.

Etymology.—Named for Mian Inayatullah who collected the type series.

Aleiodes politiceps (Gahan), new combination
(Figs. 3, 9, 11)

Rogas politiceps Gahan 1917:206.

Diagnosis.—Body unicolored orange, antenna black, legs orange except apex of hind tibia and all tarsi black, wings black; body length, 7.0–9.0 mm; 60–65 antennomeres; malar space shorter than basal width of mandible; oral opening large (Fig. 9), diameter greater than malar space; ocell-ocular distance greater than diameter of lateral ocellus; head smooth and shining, face weakly costate; mesonotum, scutellum and mesopleuron smooth and shining, propodeum areolate-rugose, median carina complete; first, second and basal half of third metasomal terga strongly porcate (Fig. 11), median carina complete on first and second terga; fore wing vein 1cu-a beyond 1M by distance greater than length of 1cu-a (Fig. 3); hind wing marginal cell gradually widening, vein RS straight (Fig. 3); tarsal claws pectinate.

Type material examined.—*Rogas politiceps* Gahan, holotype female, Nashville, Tennessee (USNM).

Distribution.—Virginia south to Florida, west to Arkansas and Texas. Also recorded from San Jose, Costa Rica (new record), at an elevation of 1300m. Not yet recorded from other parts of Central America.

Biology.—The usual hosts appear to be moderately large noctuid larvae, including *Anicla infecta* (Ochs.) and *Pseudaletia unipuncta* (Haw.).

Comments.—This is one of the commonest large *Aleiodes* species occurring in the southern states. It is frequently taken in Malaise traps, and in large numbers at black lights. The entirely dark wings, bright orange body, and strongly porcate metasomal terga make this species quite distinctive. It is one of the few *Aleiodes* species that can be reliably identified even

without a microscope. The very coarse sculpture of metasomal terga is unique among the species covered in this study.

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Further Evidence of Male Antennal Glands in Aphelinidae: The Case of *Aphytis melinus* DeBach (Hymenoptera: Aphelinidae)

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Abstract.—Ultrastructural investigations of the elongated male club, antennomere 6, in *Aphytis melinus* DeBach have shown that a small oval ventral area, bearing numerous minute setae, is not a sensory complex but rather the release site of a glandular complex with unicellular unit type 1. This finding, combined with behavioral observations reported in the literature, strongly indicates that the secretion induces sex recognition during pre-coital phase. This morpho-functional interpretation is discussed in other aphelinids exhibiting similar structures on different antennomeres.

In the last few years, some peculiar antennal structures of parasitoid hymenopterans have received increasing interest, and have revealed new aspects for functional morphology, biosystematics, and phylogeny (Isidoro *et al.* 1996). In fact, the male antennae, which were previously believed to be only sensory appendages, have instead been demonstrated as also having a secretory function through epidermal glands involved in courtship behavior (Bin *et al.* 1997). The secretory function has been reported in families Eulophidae (Dahms 1984), Scelionidae (Bin and Vinson 1986), Platygastridae (Isidoro and Bin 1995), Ichneumonidae (Isidoro *et al.* 1997), Diapriidae (Romani *et al.* 1997; Sacchetti *et al.* 1997) and Eucoilidae (Isidoro *et al.* submitted).

Male antennal glands were reported for the first time in *Encarsia asterobemisiae* Viggiani et Mazzone (Pedata *et al.* 1995), a species supplied with two peculiar ventral features, respectively on antennomeres four and five, which likely appear to be used during pre- and post-coital phases (Viggiani and Laudonia 1989). In another aphelinid, *Aphytis melinus* DeBach, an important worldwide biocontrol agent of citrus scales, the courtship behavior was also described stressing the importance of antennation during the precoital phase (Gordh and DeBach 1978). The occurrence of this behavior, along with the presence of a "specialized sensory area" on the ventral side of the male elongated club, has prompted an ultrastructural study of this "small oval area or plate bearing numerous minute setae" (Rosen and DeBach 1979).

This study proves that in *A. melinus* such an area, present on A6 in the form of an elongated club, is the release site of adjacent integumentary glands. In addition, for the first time in hymenopterans, glands are reported on the apical antennomere.

MATERIALS AND METHODS

A colony of *A. melinus*, laboratory reared on *Aonidiella aurantii* (Maskell), was provided by the Entomology Department of the University of California (Riverside).

For scanning electron microscopy (SEM) observations, 10 males, newly emerged and anaesthetized in CO_2, were beheaded and immediately immersed in 50% ethanol water solution and kept overnight at 4°C. After dehydration in a graded ethanol series, the heads with antennae were critical point dried in a Balzers Union CPD

020 unit, gold coated in a Balzers Union SCD 040 unit, and finally examined with a Philips XL 30.

For transmission electron microscopy (TEM) observations, 10 males were anaesthetized in CO2 and immediately immersed in 2.5% glutaraldehyde in 0.1 M cacodylate buffer + 5% sucrose, pH 7.2–7.3. The apical antennomeres were detached to aid fixative penetration, and left at 4°C for 2h. After rinsing overnight in a cacodylate buffer, the specimens were postfixed in 1% osmium tetroxide at 4°C for 1h and rinsed in the same buffer. Dehydration in a graded ethanol series was followed by embedding in Epon-Araldite with propylene oxide as a bridging solvent. Thin sections were taken with a diamond knife on a L.K.B. "Nova" ultramicrotome, and mounted on collodium-coated 50 mesh grids. Finally, the sections were investigated with a Philips EM 400T, after staining with uranyl acetate (20 min, room temperature) and lead citrate (5 min, room temperature).

RESULTS

The geniculate antennae of male *A. melinus* consist of six antennomeres. The apical antennomere, A6 or club, is elongated and bears an oval area on the proximal ventral side which is the release site structure (RSS) of the integumentary glands (Fig 1a). This area is covered by minute, non-socketed microtrichia and bordered by one row of socketed trichoid sensilla (Fig 1b); while the former are not innervated the latter are provided of one mechanosensory neuron. SEM observations of the ventral side of A6 show the oval area slightly depressed and partially cut off from the surrounding club portion by indistinct grooves.

Serial longitudinal and cross sections of the apical antennomere reveal a well developed glandular epithelium adhering to the internal wall of the oval area (Fig 2a). This glandular complex consists of numerous, unicellular secretory units varying in size and shape. Each glandular cell has a large, round and regularly shaped nucleus which is often located in the basal part of the cell (Fig 2b). Chromatin is not abundant and most of it is apposed to the nuclear membrane. The perinuclear region of the cytoplasm contains mitochondria with conventional cristae and abundant free ribosomes while few signs of granular or smooth endoplasmic reticulum were observed. The basal plasma membrane of the cell has deep, irregular invaginations forming a lacunar system. The apical cell membrane is surrounded by densely packed microvilli, delimiting a narrow extracellular space. The cuticle associated with the glandular epithelium is pierced by numerous tiny pores randomly distributed. The secretory apparatus underneath each pore is formed by a spherical chamber, from which numerous cuticular filaments radiate (Fig 2c). These filaments, apparently a specialization of the external epicuticle, have a tubular structure and extend deeply in the extracellular space between the microvilli of the apical cell membrane.

DISCUSSION

The "small oval area or plate bearing numerous minute setae" on the ventral side of male club in *A. melinus* (Rosen and DeBach 1979) is not a "specialized sensory area" but the release site of epidermal glands. These glands are unicellular secretory units belonging to the type 1 gland cell (Noirot and Quennedey 1974, 1991; Quennedey 1998). The cytological features of the secretory cells do not allow us to attempt an interpretation on the nature of the secretion which in other hymenopterans acts on contact (Isidoro *et al.* 1996) or is volatile (Felicioli *et al.* 1998). The peculiar releasing apparatus consists of numerous pores so tiny that neither the external openings nor the material secreted can be seen with SEM, contrary to what has been reported for other parasitoids (Bin and Vinson 1986; Isidoro and Bin 1995). The
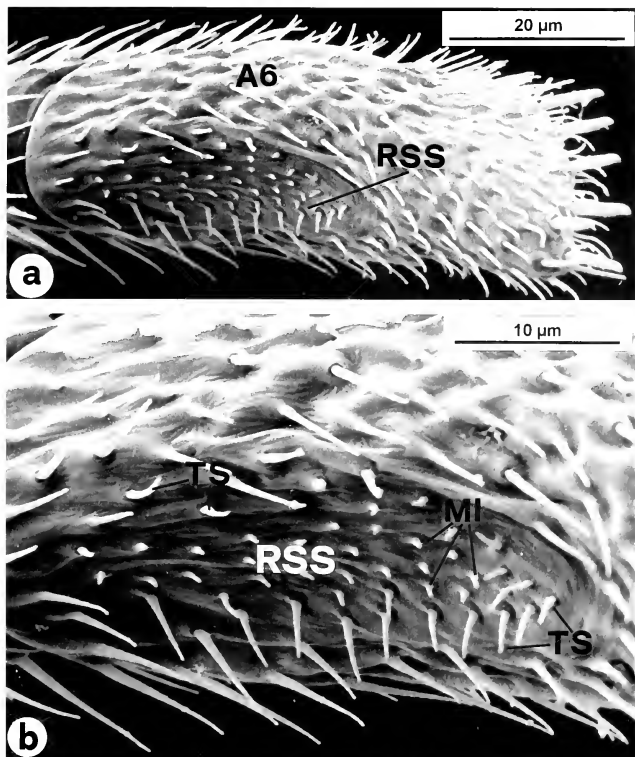
Fig. 1. *Aphytis melinus* male. a) ventro-lateral view of antennomere 6 (A6) showing the release site structure (RSS); b) detail of the RSS covered by numerous microtrichia (MI) and bordered by a single row of tactile setae (TS).

conceivable function of no-socketed microtrichia is that of increasing the release surface while that of socketed trichoid sensilla is that of perceiving tactile stimuli.

Encarsia asterobemisiae has two glandular complexes, respectively on A3 and A4, belonging to the same type 1 but different in cytological characteristics and release site
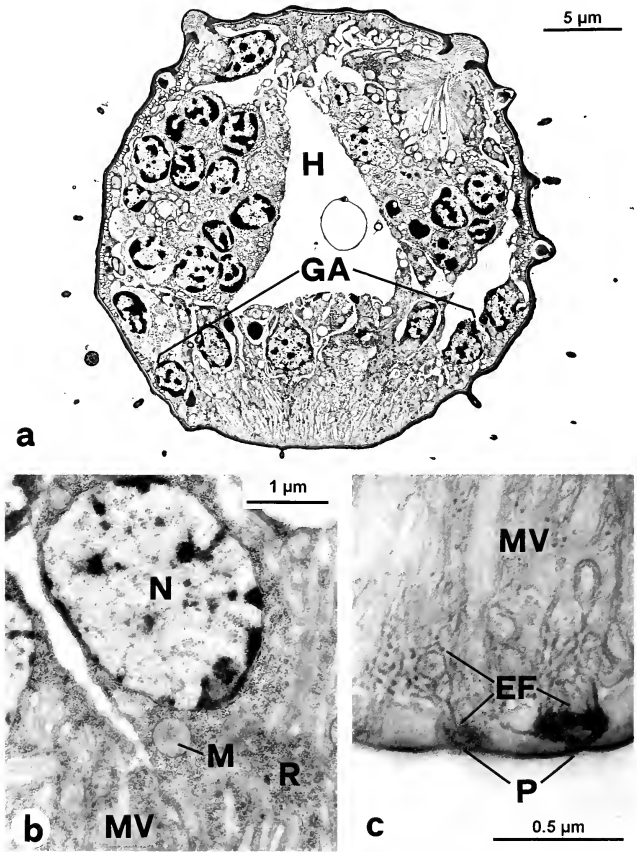
Fig. 2. *Aphytis melinus* male: a) cross section of antennomere 6 at about half level showing the extension of the glandular area (GA) on the ventral side; b) perinuclear detail of a secretory cell; c) apical detail of a secretory cell showing the tiny cuticular pores (P). N, nucleus; EF, epicuticular filaments; H, haemocele; M, mitochondrion; MV, microvilli; R, ribosomes.

features. This could indicate a difference in composition and role of the relative secretions (Pedata *et al.* 1995). From these two ascertained cases it appears that the so called sensorial complexes described in other aphelinids need to be investigated to define their real nature. Morphological and behavioral observations strongly suggest in fact that glands are present on different antennomeres involving the scape (A1), from one to 3 intermediate antennomeres (A3 to A5) or the apical antennomere (A6). Some examples are as follows:

On A1 of *Physcus testaceus* Masi there are special structures which could be related to a gland (Viggiani *et al.* 1986) and something similar occurs in *Pteroptryx chinensis* (Howard) (Viggiani and Ren 1993). Numerous species of *Encarsia* Foerster have one up to three antennomeres, A3–A5, which may or may not be noticeably enlarged, and ventrally provided of one specialized structure or two different ones. When two or more antennomeres are glanded the release sites are of two types; furthermore, one enlarged antennomere does not necessarily bear a specialized structure, as A3 in the case of *E. asterobemisiae* (Pedata *et al.* 1995). Therefore, some of the following examples having two or three enlarged antennomeres may need to be confirmed: A3 in *Encarsia albiscutellum* (Girault) (Viggiani 1985), A4 in *Encarsia aleurotubae* Viggiani, *E. herndoni* (Girault) (Viggiani 1987), A3–A4 in *Encarsia olivina* (Masi) (Viggiani and Mazzone 1982), *E. gigas* (Tchumakova), *E. opulenta* Silvestri and *E. perniciosi* (Tower) (Viggiani and Laudonia 1989), A3–A5 in *Encarsia antiopa* (Girault) (Viggiani 1985).

As regards the apical antennomere the A6 of several species of *Aphytis* Howard, as illustrated by Rosen and DeBach (1979), have external features similar to those described for *melinus*, and therefore could have glands: *A. cochereaui* DeBach and Rosen, *A. fabresi* DeBach and Rosen, *A. chilensis* Howard, *A. columbi* (Girault), *A. par-*

amaculicornis DeBach and Rosen, *A. diaspidis* (Howard), *A. lingnanensis* Compere, *A. roseni* DeBach and Gordh, *A. pilosus* DeBach and Rosen.

Behavioral observations indicate that the antennation mechanism during mating is different in species having one or two glanded antennomeres. While the single release site seems to be logically related to the pre-coital phase, e.g. triggering sex-recognition, female stimulation or female sedation (Gordh and DeBach 1978; Viggiani *et al.* 1986), the presence of a second and different release site has been observed in species performing also a post-coital phase, e.g. *E. asterobemisiae* (Pedata *et al.* 1995).

These chemo-physical mechanisms can only partially explain the sexual isolation since there also are other chemicals involved in mating behavior. In some species of *Aphytis* a female sex pheromone (Rao and DeBach 1969) and a male aphrodisiac pheromone (Khasimuddin and DeBach 1975), whose sources are as yet unknown (Gordh and DeBach 1978) have in fact been reported. In another aphelinid, *Aphelinus asychis* Walker, the mate finding is mediated by a female trail sex pheromone deposited in a yet unknown way on the substrate while walking (Fauvergue *et al.* 1995).

As it is being shown in other parasitoid groups (Bin *et al.* 1997; Isidoro *et al.* submitted) the glandular nature of the antennal structures provides a new perspective to define the sex selection strategies of aphelinids as well as additional characters for taxonomy and phylogeny.

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A New Species Group and Two New Species of *Euderomphale* Girault (Hymenoptera: Eulophidae) from North America

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Abstract.—Two new species of *Euderomphale*, E. sinuata and E. suzannae, are described from North America. These represent a distinct species group within the genus *Euderomphale*, which is here referred to as the *sinuata* group. E. sinuata is brachypterous, and this represents the first record of brachyptery in the Euderomphalini.

Euderomphale is a cosmopolitan genus containing parasitoids of whiteflies. Thirteen described species in this genus were listed by LaSalle and Schauff (1994). No comprehensive keys to species have been published, but there are keys to limited numbers of regional species (Erdös 1966, for Hungary; Huldén 1986, for Finland). *Euderomphale* belongs in the tribe Euderomphalini. This tribe, containing parasitoids of whiteflies, was treated at the world level by LaSalle and Schauff (1994), who presented keys to, diagnoses for, and support for the monophyly of seven included genera in two genus groups. The present paper describes two new species which represent a new species group within the genus *Euderomphale*, the *sinuata* group. *Euderomphale* is thus separated into two species groups: the *flavimedia* group (based on the valid name for the type species) contains 13 species (LaSalle and Schauff 1994), and the *sinuata* group contains the two species described in this paper. Biology for the two new species in the *sinuata* group is unknown, but it is presumed they are parasitoids of whiteflies like all other members of the Euderomphalini. E. *sinuata* is brachypterous, and this represents the first record of brachyptery in the Euderomphalini. It is also the first record of brachyptery in females of any Entedoninae, although brachyptery is known in males of *Microdonophagus woodleyi* Schauff (Schauff 1986). Kerrich (1973) reported the males of *Pediobius aracanae* Kerrich to be micropterous, although in this species the wing is only slightly reduced and does not have a highly modified shape.

KEY TO SPECIES GROUPS WITHIN *EUDEROMPHALE* AND SPECIES OF THE *SINUATA* GROUP (FEMALES)

1. Axilla smoothly rounded anteriorly (Fig. 4). Vertex smoothly rounded posteriorly (Fig. 4), with the lateral ocellus placed on the top of the head. Prepectus partially fused to mesopleuron anteriorly . . . . *flavimedia* group (discussed by LaSalle and Schauff 1994)
– Axilla sinuate and concave anteriorly (Figs. 1, 3). Vertex with a distinct transverse carina; lateral ocellus behind this carina (Figs. 1–3). Prepectus free, not fused to mesopleuron *sinuata* group 2
2. Brachypterous; wings short, not extending past first gastral tergite (Fig. 1), infumated. Axilla with anterior margin deepl concave, anteromedial lobe narrower and more distinct (cf. Figs. 1 and 3). Gaster uniformly dark brown . . . . *E. sinuata* LaSalle
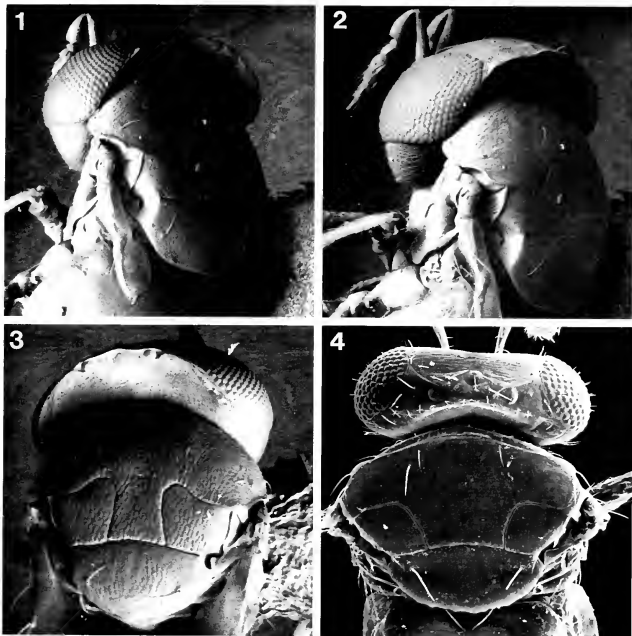
Figs. 1–4   *Euderomphale* species, head and mesosoma. 1–2. *Euderomphale sinuata*. 3. *Euderomphale suzannae* 4. *Euderomphale* sp. (*flavimedia* group).

– Not brachypterous; wings normal, extending to or slightly past apex of abdomen, hyaline or very lightly infumate. Axilla with anterior margin shallowly concave, anteromedial lobe wider and less distinct (cf. Figs. 1 and 3). Gaster yellow or pale brown, with several dark transverse stripes . . . . **E. suzannae** LaSalle

Characters for the *Euderomphale* genus group (within the Euderomphalini): Head usually smooth to lightly sculptured. Frontal suture, when present, placed just ventral to median ocellus. Vertexal suture present, either placed between the ocelli, or behind the ocelli. Malar sulcus usually present, although sometimes incomplete. Funicle with 1 or 2 segments. Dorsum of mesosoma more or less flattened and usually smooth to lightly sculptured, generally when distinct sculpture is present it is

incised. Midlobe of mesoscutum usually with only 1 or 2 pairs of setae. Scutellum distinctly wider than long, with 1 or 2 pairs of setae. Axilla either completely separated from mesoscutum by a complete suture, or partially fused to mesoscutum. Submarginal vein with one or two setae on dorsal surface. See LaSalle and Schauff (1994) for further discussion and illustration of these characters, and characters to define the Euderomphalini.

Characters for *Euderomphale*: Scrobal suture and frontal suture absent. Vertexal suture extending from the eye margin between the median and lateral ocelli. Malar sulcus present, although incomplete and extending away from the mouth margin (postero-laterally from the eye). Antenna with two funicular segments, although the first is reduced to not much larger than the size of an anellus (the small first funicular segment can generally be distinguished from an anellus by the presence of setae). Mesosoma always black, non-metallic, more or less flattened in lateral view, sculpture on dorsal surface usually either finely incised or smooth. Midlobe of mesoscutum generally with 2 pairs of setae near the anterior margin. Scutellum distinctly wider than long, and with two pairs of setae: a larger one near the middle of the scutellum and a smaller one at the posterior margin. Axilla large (as wide as long), and completely separated from mesoscutum by a sulcus. Dorsal surface of submarginal vein with 2 setae (a single seta in the brachypterous *sinuata*). See LaSalle and Schauff (1994) for further discussion and illustration of these characters.

Characters for the *flavimedia* species group in *Euderomphale*: Vertex smoothly rounded posteriorly. Axilla smoothly rounded anteriorly. Prepectus reduced and partially fused to the mesopleuron.

Characters for the *sinuata* species group in *Euderomphale*: Vertex with a distinct transverse carina; lateral ocelli placed posterior to this carina. Axilla sinuate and

concave anteriorly. Prepectus reduced (strongly so in *sinuata*) but separate, not fused to mesopleuron.

Euderomphale sinuata LaSalle, sp.n.
(Figs. 1–2)

Female.—Length 0.75 mm. Head and mesosoma black, gaster dark brown. Scape yellow, pedicel and flagellum brown. All coxae black; fore and middle femora and tibiae dark brown to black; hind femur brown to light brown, hind tibia brown basally, light brown apically; tarsi brown, with apical segment dark brown. Wings infumated. Head with delicate, small, regular incised sculpture. Vertexal suture present near the eye margin; joining or running just anterior to vertexal carina. Mesosoma with delicate, small, regular incised sculpture. Axilla with anterior margin distinctly concave, antero-medial lobe narrower and more distinct than in *suzannae*. Prepectus quite reduced, separate from the mesopleuron. Wings greatly reduced, not reaching apex of first gastral tergite. Forewing with a single strong seta on submarginal vein and another on marginal vein. Gaster with tergite 5 extending over the telescoped tergites 6 and 7 and short ovipositor.

Holotype female, USA, Florida, Levy Co., 5 km SW Archer, 2–15.ix.1987, FIT, turkey oak shrubs, BRC HYM. TEAM (Canadian National Collection, Ottawa).

Euderomphale suzannae LaSalle, sp.n.
(Fig. 3)

Female.—Length 0.90–0.95 mm. Head and mesosoma black, gaster yellow with transverse brown stripe on tergites 2–5, and a median longitudinal brown stripe on tergite 1. Scape yellow, pedicel and flagellum brown. Fore and middle coxae dark brown to black, hind coxa brown to light brown; fore femur dark brown; middle femur light brown, dark brown dorsoapically, hind femur yellow; fore tibia yellow to light brown, dark brown dorsally, middle tibia dark brown basally,

yellow to light brown apically, hind femur yellow to light brown; all tarsi yellow to light brown. Wings hyaline or very lightly infumated. Head with small, regular slightly raised sculpture (slightly stronger than in *sinuata*). Vertexal suture present near the eye margin; joining or running just anterior to vertexal carina. Mesosoma with small, regular incised sculpture (slightly stronger than in *sinuata*). Axilla with anterior margin moderately concave, anteromedial lobe broader and not as distinct as in *sinuata*. Prepectus moderately reduced, separate from the mesopleuron. Wings normal. Forewing with two strong setae on the submarginal vein. Gaster with last tergite not extending over the ovipositor.

Holotype female, USA, Missouri, Wayne Co., Williamsville, 10–26.vi.1987, MT, J. Becker (Canadian National Collection, Ottawa). Paratype female, USA, Missouri, Wayne Co., Williamsville, vii.1987, MT, J. Becker (Canadian National Collection, Ottawa).

Etymology.—Named for Suzanne Lewis.

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A New Genus and Two New Species of Brachypterous Lysiterminae (Braconidae)

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Abstract.—A new genus *Neolysitermus* gen. n. and two new species *N. turneri* sp. n. and *N. spinator* sp. n. (tribe Lysitermini), both from South Africa, are described and illustrated. These are the first brachypterous species belonging to the subfamily Lysiterminae.

Aptery and brachyptery are known in only a few subfamilies of Braconidae, including the Alysiinae, Aphidiinae, Blacinae, Doryctinae, Hormiinae, Masoninae, Pambolinae and Orgilinae. In the first of these, aptery is probably a result of their hosts dwelling within subterranean or filthy habitats and the associated difficulty in negotiating soil particles or costs of wing fouling, however, in the others, no obvious host habitat association is apparent, though many other brachypterous parasitoids are associated with stored products or with tree trunks/tall shrubs. The brachypterous and apterous braconids are more or less equally split between ecto- and endoparasitoids and between idiobiont and koinobiont taxa, suggesting that at least in this family when considered at subfamily level, brachyptery is not dependent upon major life history features. However, formal comparative analysis at species level will be required before firm conclusions can be reached.

The Lysiterminae have previously often been regarded as a tribe within either the Rogadinae, Exothecinae or the Hormiinae (van Achterberg 1976, 1982; Quicke & van Achterberg 1990; Wharton 1993; Beloko-

bylskij 1993) but was afforded subfamily status by van Achterberg (1993, 1995) and van Achterberg & Steiner (1996) because it shares no obvious synapomorphies with either Rogadinae s.s. or Hormiinae. This arrangement seems best at present since there is considerable doubt about the monophyly of the Hormiinae as treated (conservatively) by some workers (see for example, Whitfield & Wharton 1997). New molecular data, as well as the investigation of more character systems, will be required to resolve this (see Quicke *et al.* 1992; Belshaw *et al.* 1998).

No apterous or brachypterous species have previously been described in the Lysiterminae. Although little is known biologically about the Lysiterminae, they appear to have diverse host associations including being ectoparasitoids, or presumed ectoparasitoids, of bagworms (Psychidae) and web-feeders (Xyloryctidae = Stenomidae), and also apparently endoparasitoids of Orthoptera (Hedqvist 1963; Wharton 1993; van Achterberg & Steiner 1996). Interestingly, all of these hosts live in retreats involving silk.

The Lysiterminae Tobias, 1968 includes only seven genera in the Old World (van

Achterberg 1995; Belokobylskij 1995; van Achterberg & Steiner 1996). Unfortunately, differences between lysitermine genera mostly concern fore wing venation, though members of the subtribe Tritermina, with 2 genera (*Tritermus* van Achterberg and *Afrotritermus* Belokobylskij) differ from the other genera of Lysiterminae in having fused, and therefore immobile, 1st and 2nd metasomal tergites (Belokobylskij 1993). Because of the major reliance of lysitermine systematics on wing venation, interpreting the relationships of *Neolysitermus* gen. n., with its reduced wings, is not so straightforward. Apart from the reduced wings, *Neolysitermus* gen. n. has a distinct median emargination of the posterior margin of 3rd metasomal tergite—a character not known in any other species of Lysiterminae.

TERMINOLOGY AND COLLECTIONS

The wing venation terms used largely follow Tobias (1986). The following abbreviation are used: POL—postocellar line; OOL—ocular-ocellar line; Od—maximum diameter of lateral ocellus. Collections are abbreviated as follows: The Natural History Museum, London (BMNH); Zoological Institute, Russian Academy of Sciences, St. Petersburg, Russia (ZIP).

Neolysitermus Belokobylskij and Quicke, new genus

Type species: *Neolysitermus turneri* new species

Etymology.—From "neo" (new) and "*Lysitermus*" the genus of the subfamily Lysiterminae.

Diagnosis.—The position of this new genus is not clear. Differences between genera of the tribe Lysitermini are connected mostly with the venation of the fore wing, but species of *Neolysitermus* gen. n. have very short wings with reduced venation. This new genus differs from other genera

of Lysitermini (in addition to the very short wings) by the presence of distinct median emargination on the posterior margin of 3rd tergite, a character that is absent in all described species of this tribe.

Description.—Head weakly transverse (Figs 2, 11). Scapus (Fig. 4, 13) thick, with distinct round cut in outer apical side. Flagellum filiform. Apical flagellomere without apical spine. Maxillary palpi 6-segmented, labial palpi 4-segmented; 3rd labial segment distinctly shortened. Malar suture absent. Clypeus strongly convex (Figs 3, 12). Eyes glabrous. Occipital carina fused with hypostomal one higher mandibles. Hypostomal keel distinct. Ocelli small, forming an almost equilateral triangle. Mesosoma reduced, but with all sutures and depressions (Figs 7, 8, 16, 17). Propleura with longitudinal median carina on basal half. Pronotum with distinct lateral median corners (see Figs 8, 17). Notauli deep and wide. Lateral lobes of mesoscutum with oval depressions posterolaterally. Scutellum with high lateral carinae. Sternauli rather deep, wide, oblique, coarsely crenulate. Prepectal carina very strong. Postpectal carina absent. Metapleural flange long and narrow. Propodeal areola incomplete or absent. Fore wing very short and narrow, stylet-shaped or oval. Hind tibia and tarsus slender. Hind tibial spurs very short. Hind basitarsus 0.9–0.95 × as long as 2nd–5th segments combined. First and second metasomal tergites not fused, mobile (Figs 9, 10, 18, 19). Dorsope of first tergite small. Second suture deep. Dorsal carina of first tergite semicircularly united basally. Third tergite without spines and carina posteriorly, with deep and rather narrow median emargination, with small single tooth ventro-laterally (Figs 9, 18).

Distribution.—Afrotropical Region (South Africa).

KEY TO SPECIES OF *NEOLYSITERMUS*

1. Antenna 17-segmented; apical segment dark. Length of mesosoma 1.7–1.8 × height. Scutellum flat. Propodeum without lateral spines. Metasoma narrow, its length 2.3–2.4 × maximum width. First metasomal tergite longer, apically 1.2–1.3 × wider than long . . . .
. . . . *N. turneri* sp. n.

– Antenna 14-segmented; apical segment whitish. Length of mesosoma 1.3–1.4 × height. Scutellum strongly pointedly convex. Propodeum with distinct pointed lateral spines. Metasoma wide, its length twice maximum width. First metasomal tergite shorter, apically 1.7–1.8 × wider than long . . . . *N. spinator* sp. n.

### *Neolysitermus turneri* Belokobylskij and Quicke, new species

(Figs 1–10)

Holotype female.—"S. Africa. R.E. Turner. Brit. Mus. 1924–136", "Port St. John, Pondoland. 6–25. Feb. 1924" (BMNH).

Paratypes.—1 female, same data as holotype (BMNH); 1 female, "S. Africa. R.E. Turner. Brit. Mus. 1924–97", "Port St. John, Pondoland. Jan. 1924" (ZIP); 1 female, "S. Africa. R.E. Turner. Brit. Mus. 1924–109", "Port St. John, Pondoland. 29.I – 5.II.1924" (BMNH).

Description.—Female. Body length 1.8–2.3 mm. **Head:** 1.5–1.6 × wider than medially long; 1.7–1.8 × width of mesoscutum. Antennae 17-segmented. Scapus 1.5–1.6 × as long as wide. First flagellar segment 3.7–4.2 × longer than apically wide, slightly longer than 2nd segment. Penultimate segment 3 × as long as wide, 0.7 × as long as 1st flagellar segment, 0.9–1 × as long as apical segment. Temple roundly narrowed behind eyes. Transverse diameter of eye 1.4–1.6 × length of temple (dorsal view). POL 1.2–1.5 × Od, 0.3–0.4 × OOL. Antennal socket diameter 0.8–1 × distance between sockets, almost twice distance between socket and eye. Eye 1.2–1.3 × taller than broad. Cheek height 0.7–0.8 × height of eye, 1.6–1.7 × basal width of mandible. Face 1.2–1.4 × wider than eye height and 1.2 (wider than height of face and clypeus combined). Clypeus with distinct narrow flange along lower margin. Hypoclypeal depression oval, 0.7–0.8

× wider than distance from depression to eye. Head distinctly and roundly narrowed below eyes. **Mesosoma:** 1.7–1.8 × longer than high, almost twice longer than wide. Median lobe of mesoscutum with antero-lateral teeth. Prescutellar depression long, with median carina, granulose-crenulate, 0.5–0.6 × as long as scutellum. Scutellum rather flat. Subalar depression deep, narrow, crenulate. Mesopleura without median furrow. Propodeum without lateral spines. Fore wing stylet-shaped, 3.2–4.5 × longer than wide, 0.35–0.4 × length of mesosoma. Hind femur 4.5–5 × longer than wide. Hind tibia 0.8–0.85 × hind tibia. Second tarsal segment 0.3–0.35 × length of 1st segment, almost as long as 5th segment (excluding pretarsus). **Metasoma:** Convex and narrow, its length 2.3–2.4 × maximum width (on the level of middle of 2nd tergite), 1.4–1.5 × as long as mesosoma. First tergite distinctly and roundly narrowed towards base, rather long, its apical width 1.2–1.3 × length, 2.0–2.2 × its minimum width. Second tergite almost as long as basally wide, 0.8–0.9 × maximum width, 1.3–1.4 × length of 1st tergite, 0.8–0.9 × length of 3rd tergite. Third tergite regularly and almost linearly narrowed toward apex. Ovipositor sheath 0.5–0.6 × as long as metasoma, 0.8–0.9 × as long as mesosoma. **Sculpture and pubescence**: Head densely granulate, vertex strongly granulate and usually with fine rugae; face finely granulate. Mesothorax densely and entirely granulate. Propodeum with median carina, which is
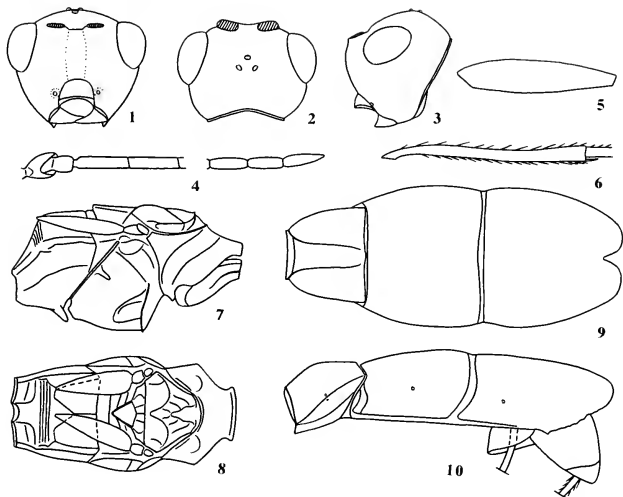
Figs. 1–10. *Neolysitermus turneri* gen. et sp. n.: 1—head, frontal view; 2—head, dorsal view; 3—head, lateral view; 4—basal and apical segments of antenna; 5—hind femur; 6—hind tibia; 7—thorax, lateral view; 8—thorax, dorsal view; 9—metasoma, dorsal view; 10—metasoma, lateral view.

1–1.4 × as long as furca; basolateral areas densely granulate; posterior half of propodeum transversely striate with dense granulation and 2 short submedian longitudinal carinae. Hind legs finely granulate. First to 3rd metasomal tergites strongly striate, with fine and dense transverse rugae between striae; striae at 2nd and 3rd tergites weakly convexly curved. Setae on dorsal side of hind tibia sparse, short and not erect. **Colour:** Body light reddish brown, sometimes dorsally darker. Head yellow. Antenna yellowish brown, submedially slightly darkened, 5–6 subapical segments whitish, apical segment dark. Palps pale yellow. Legs yellow.

Male.—Unknown.

Neolysitermus spinator Belokobylskij and Quicke, new species

(Figs 11–19)

Holotype female.—"S. Africa. R.E. Turner. Brit. Mus. 1924–136", "Port St. John, Pondoland. 6–25. Feb. 1924" (BMNH).

Paratypes.—1 female, same data as holotype (BMNH).

Description.—Female. Body length 1.8–2.1 mm. **Head:** 1.4–1.5 × wider than medially long; 1.6–1.9 × width of mesoscutum. Temple roundly narrowed behind eyes. Transverse diameter of eye 1.7–2 × length of temple (dorsal view). POL 1–1.3 × Od, 0.3–0.4 × OOL. Antennal socket diameter 1.5–2 × distance between sockets,
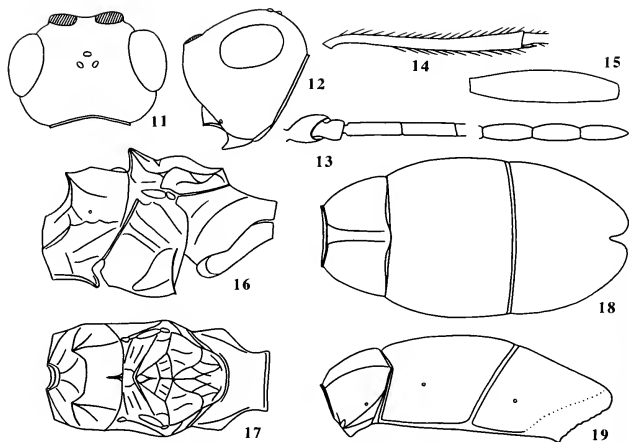
Figs. 11–19. *Neolysitermus spinator* gen. et sp. n.: 11—head, dorsal view; 12—head, lateral view; 13—basal and apical segments of antenna; 14—hind tibia; 15—hind femur; 16—thorax, lateral view; 17—thorax, dorsal view; 18—metasoma, dorsal view; 19—metasoma, lateral view.

almost 1.5 × distance between socket and eye. Eye 1.3–1.4 × as taller than broad. Cheek height 0.8 × height of eye, nearly twice basal width of mandible. Face 1.3 × wider than eye height and 1.25 × wider than height of face and clypeus combined. Clypeus with distinct narrow flange along lower margin. Head distinctly and roundly narrowed below eyes. Antennae 14-segmented. Scapus 1.5–1.6 × as long as wide. First flagellar segment 3.7–4.0 × longer than apically wide, 1–1.2 × as long as 2nd segment. Penultimate segment 2.5–2.7 × as long as wide, 0.8 × as long as 1st flagellar segment, as long as apical segment. **Mesosoma**: 1.3–1.4 × longer than high, 1.5–1.8 × longer than wide. Median lobe of mesoscutum with antero-lateral teeth. Prescutellar depression long, with median carina, granulose-crenulate, 0.6–0.7 × as long as scutellum. Scutellum strongly

pointedly convex. Subalar depression deep, narrow, granulose-crenulate. Mesopleura with fine oblique median furrow. Propodeum with distinct pointed lateral spines and mediobasal flat small lobe. Fore wing oval and short. Hind femur 4.5–5 × longer than wide. Hind tarsus 0.8 × length of hind tibia. Second tarsal segment 0.3 × as long as 1st segment, nearly as long as 5th segment (excluding pretarsus). **Metasoma**: Convex and wide, nearly twice longer than maximally wide (at level of middle of 2nd tergite), 1.7–1.9 × longer than mesosoma. First tergite distinctly and roundly narrowed towards base, short, its apical width 1.7–1.8 × length, 2.4 × its minimum width. Second tergite 0.9–1 × longer than basally wide, 0.8 × its maximum width, 1.7 × length of 1st tergite, as long as 3rd tergite. Third tergite regularly and roundly narrowed to-

ward apex. Ovipositor sheath 0.3–0.4 × as long as metasoma, 0.6–0.8 × as long as mesosoma. **Sculpture and pubescence:** Head largely densely granulate, vertex sometimes (paratype) with rugae, frons striate with granulation, face finely granulate. Mesothorax densely and almost entirely granulate. Propodeum with transverse median carina between spines; basolateral areas densely granulate; posterior half rugulose-striate, with fine granulation. Hind legs finely granulate. First to 3rd metasomal tergites strongly longitudinally striate, with fine and dense transverse rugae between striae; striae of 3rd tergite distinctly converging posteriorly. Setae on dorsal side of hind tibia sparse, short and not erect. **Colour:** Body light reddish brown, metasoma partly darker. Head yellow. Antenna yellowish brown, submedially slightly darkened, 5 distal segments whitish, apical segment dark. Palps pale yellow. Legs yellow.

Male.—Unknown.

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NOTE

New Host Record of a Ceraphronid (Hymenoptera) in Trichoptera Pupae

J. C. Luhman, R. W. Holzenthal, and J. K. Kjaerandsen

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Pupae of the microcaddisfly *Ochrotrichia moselyi* Flint (Trichoptera: Hydroptilidae) were collected in Costa Rica that contained pupae of *Aphanogmus* sp. (Hymenoptera: Ceraphronidae). The caddisflies were collected in Puntarenas Province, Bellavista River, ca. 1.5 km NW of Las Alturas, at 1400 m elevation (8.951°N, 82.846°W). Collections were made June 15–17, 1986. All material is housed in the University of Minnesota Insect Collection, St. Paul, Minnesota. Three collections in alcohol yielded one *Aphanogmus* pupa each. There were a total of 12 *Ochrotrichia moselyi* cocoons of which 3 contained *Aphanogmus* pupae, 6 contained eaten caddisfly pupae, and the remainder, developed caddisflies. The cocoons with the parasitoid pupae contained only the wings and cast larval skin of the caddisfly. There was one *Aphanogmus* per parasitized cocoon. Dr Paul Dessart, a ceraphronid specialist in Belgium, confirmed Luhman's identifications of the *Aphanogmus* in the cocoons and stated this to be a new ordinal and family host record for Ceraphronidae (pers. comm., 1996). Heretofore recorded hosts of Ceraphronidae included Diptera, Homoptera, Hymenoptera, Neuroptera, and Thysanoptera (Muesebeck 1979; Hanson and Gauld 1995).

The *Aphanogmus* were discovered inside the cocoons of *Ochrotichia moselyi*, but outside of the caddisfly pupa. Only the developed wings remained uneaten. The *Ochrotichia* cocoons may have been parasitized when exposed to the surface near the water substrate interface. *Ochrotichia* pupate within their larval cases in small clusters of individuals on the sides of rocks and boulders. During the dry season, pupae are often exposed or closer to the surface.

ACKNOWLEDGMENTS

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Reproductive Variability in *Pediobius alcaeus* (Walker) (Hymenoptera: Eulophidae), a Parasitoid of *Phyllonorycter* (Lepidoptera: Gracillariidae)

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Abstract.—Separate, but sympatric, sexual and asexual populations of *Pediobius alcaeus* (Walker) (Hymenoptera: Eulophidae), a parasitoid of leaf-mining *Phyllonorycter* species (Lepidoptera: Gracillariidae), are shown to exist and to be associated with hosts on different tree species in Britain.

Pediobius alcaeus (Walker) is a solitary koinobiont endoparasitoid of many species of *Phyllonorycter* mining the leaves of deciduous trees and shrubs (Askew & Shaw 1974, 1979). Eggs are laid inside third instar or older host larvae which continue to develop as far as the pupal stage before being killed, and the adult *P. alcaeus* emerge from the host pupae (Askew & Shaw 1979). In Britain, *Phyllonorycter* feeding on *Alnus glutinosa*, *Corylus avellana* and *Quercus* (both *petraea* and *robur*) seem to be particularly liable to attack from *P. alcaeus*, but the chalcidoid is also frequently associated with *Phyllonorycter* hosts on *Fagus sylvatica*, *Malus* spp. and *Carpinus betulus* (Askew 1994).

Our long-standing interest in chalcidoid parasitoids of leaf mining and other insects is, in part, manifested by a records database maintained by one of us (RRA), into which are entered all rearing records from our own field-work, from host collections made by others who submit parasitoids to us for identification, and from reared specimens we have otherwise seen (i.e. all records entering the database are of parasitoids identified by us). As they currently stand, our total records continue to indicate that *Pediobius alcaeus* is exclusively associated with *Phyllonorycter* species mining the leaves of deciduous trees

and shrubs. Our accumulated rearing records of *P. alcaeus* for which sex was scored are given in Table 1: an earlier, condensed compilation giving fewer data was published by Askew (1994), but the rearing records of *P. alcaeus* previously analysed by Askew & Shaw (1974) are not all included in Table 1 as not all of those samples were sexed. For most host species the rearing records of *P. alcaeus* presented in Table 1 come from numerous collections made over a wide geographical spread of localities in Britain and sometimes also continental Europe.

As was first noted by Askew (1975), samples of *P. alcaeus* originating from hosts on different tree genera have one of two distinct categories of sex ratio: either males are well-represented (35–48 per cent), or the sample is virtually unisexual with males comprising at most only about three per cent (Table 1, see also Askew 1994). Samples from *Alnus*, *Carpinus* and *Corylus* are sufficiently large to permit their categorization as host tree genera which support unisexual (female) populations of *P. alcaeus*, whilst bisexual populations are associated with *Betula*, *Fagus*, *Quercus*, *Malus*, *Sorbus* and probably *Acer*. Different *Phyllonorycter* species feeding on the same genus of host plants are attacked by *P. alcaeus* having the same

Table 1. Accumulated total rearing records of *Pediobius alcaeus* (Walker) of known sex (specimens all seen by the authors).

Host plant	*Phyllonorycter*	Country	P. alcaeus ♀♀	P. alcaeus ♂♂
Acer campestre	*sylvella* (Haworth)	Britain	1	0
A. platanoides	*platanoidella* (Joannis)	Britain	0	1
A. pseudoplatanus	*geniculella* (Ragonot)	Britain	1	0
Alnus glutinosa	*froelichiella* (Zeller)/*kleemanella* (Fabricius)	Britain	1	62
		Belgium	0	1
	rajella (Linnaeus)	Britain	0	21
		Netherlands	0	1
		Germany	1	780
	stettinensis (Nicelli)	Britain	0	4
		Germany	0	43
A. incana	*strigulatella* (Zeller)	Britain	0	20
		Germany	3	135
A. cordata	*rajella*	Britain	0	4
A. viridis	*alpina* (Frey)	Switzerland	0	1
Betula spp.	*ulmifoliella* (Hübner)	Britain	13	26
		Netherlands	3	4
Carpinus betulus	*quinnata* (Geoffroy)	Britain	6	219
		Netherlands	0	1
	tenerella (Joannis)	Britain	1	4
		Belgium	0	1
Corylus avellana	*coryli* (Nicelli)	Britain	0	58
		Belgium	0	9
		Netherlands	0	2
	nicellii (Stainton)	Britain	0	47
Crataegus monogyna	*oxyacanthae* (Frey)	Britain	0	1
Fagus sylvatica	*maestingella* (Müller)	Britain	83	107
		Netherlands	2	0
Malus domestica	*corylifoliella* (Hübner)	Britain	0	1
M. sylvestris	*blancardella* (Fabricius)	Britain	0	3
	cydoniella (Denis & Schiffermüller)	Britain	7	5
Quercus robur/petraea	*quercifoliella* (Zeller)/*harrisella* (Linnaeus)	Britain	110	155
		Netherlands	0	1
	lautella (Zeller)	Britain	10	21
		France	2	2
		Netherlands	2	0
	saportella (Duponchel)	Britain	0	1
Salix caprea	*salicicolella* (Sircom)	Britain	0	1
	species indet.	Britain	0	2
S. aurita	*viminiella* (Sircom)	Britain	0	1
Sorbus aucuparia	*sorbi* (Frey)	Britain	3	2
		Netherlands	1	0

type of sex ratio; further, our limited data indicate that the sex ratio type/host plant relationship probably remains constant across Europe. Careful comparison failed to reveal any consistent morphological differences between *P. alcaeus* from the unisexual and bisexual populations.

In this paper we report the results of sleeving experiments in which virgin female *P. alcaeus* from either the unisexual or bisexual populations were presented with developing leaf-mines on the parasitoids' own or on an alien host plant. The aims of this investigation were first, to establish the type of parthenogenetic reproduction employed by each of the two pop-

Table 2. Sleeves on *Quercus robur* and *Corylus avellana* into which *Phyllonorycter* species, and later virgin *Pediobius alcaeus* females from varying sources, were introduced. The number of moths and the number and sex of *P. alcaeus* reared in each sleeve are recorded.

Sleeve No	Host tree	*Phyllonorycter* species	*Pediobius +* no. & source	No. of moths reared	*P. alcaeus* reared
1	*Q. robur*	*quercifoliella*	1, ex *P. quercifoliella*	36	4 ♂ ♂
2	*Q. robur*	*quercifoliella*	1, ex *P. coryli*	40	34 ♀ ♀
3	*Q. robur*	*quercifoliella*	2, ex *Phyllonorycter* sp. underside miner on *Alnus glutinosa*	1	6 ♀ ♀
4	*C. avellana*	*coryli*	2, ex *P. coryli*	4	29 ♀ ♀
5	*C. avellana*	*coryli*	2, ex *P. coryli*	14	40 ♀ ♀
6	*C. avellana*	*nicellii*	2, ex *Phyllonorycter* sp. underside miner on *Alnus glutinosa*	14	23 ♀ ♀
7	*C. avellana*	*nicellii*	2, ex *P. coryli*	36	14 ♀ ♀

ulations, and second, to determine whether the host plant range of the unisexual population could be expanded under artificial rearing conditions.

METHODS

Seven muslin sleeves were fastened to branches of oak (*Quercus robur*) (sleeves 1–3) and hazel (*Corylus avellana*) (sleeves 4–7) in the period 21–25.v.1979. At the same time, or shortly afterwards, reared adult *Phyllonorycter* were introduced. The three *Quercus* sleeves each received two male and two female *P. quercifoliella* (an undersurface miner), whilst six male and three female *P. coryli* (an uppersurface miner) were put into sleeves 4 and 5, and four male and two female *P. nicellii* (an undersurface miner) were introduced to sleeves 6 and 7. Variation in the numbers of moths introduced was partly due to shortage of livestock, but was also experimental against the risk of overstocking sleeves (which might cause leaf abscission as the mines developed).

Virgin female *Pediobius alcaeus* were put in the sleeves during the period 22–25.vi.1979, at which time developing third and fourth instar mines could be seen in most sleeves. The *Pediobius* had been individually reared in tubes and came from three sources: *P. quercifoliella* mines on *Quercus*, *P. coryli* mines on *Corylus* and from undersurface leaf-mines, probably of

P. froelichiella, on *Alnus glutinosa*. One or two virgin *Pediobius* were introduced into each sleeve; their host origins are given in Table 2. Variation in stocking levels was entirely due to shortage of livestock. All host and parasitoid material came from sites in the vicinity of Reading, Berkshire where the experiments were performed.

The sleeves were brought indoors on 10.vii.1979 (sleeves 1–3), 13.vii.1979 (sleeves 4,5) or 1.viii.1979 (sleeves 6,7). All mature and most immature mines were removed and stored separately in plastic boxes for rearing adult insects. When emergence had finished, the numbers and sex of *Pediobius* and numbers of moths produced in each sleeve were recorded.

RESULTS

Despite sometimes heavy leaf abscission due to population explosions of enclosed aphids, mines matured in all sleeves, mostly in good numbers but rather sparsely in sleeve 3. The first *P. quercifoliella*, a leaf undersurface miner, and *P. coryli*, an uppersurface miner, emerged 12–14.vii.1979, whilst *P. nicellii*, another undersurface miner, emerged somewhat later about 2.viii.1979. *Pediobius* also commenced emergence about this latter date. Total emergences of *Pediobius* and moths are shown in Table 2.

DISCUSSION

Sleeve 1, the only sleeve holding *P. alcaeus* from a bisexual population, yielded only male *Pediobius*. This unequivocal result demonstrates that the bisexual population of *P. alcaeus* on *Quercus* produces males parthenogenetically by arrhenotoky, which is usual in haplodiploid Hymenoptera. In contrast the other sleeves, in which *Pediobius* from unisexual populations were introduced to their own or alien hosts, all produced only female *P. alcaeus*. This confirms that the populations which appear to be unisexual from rearing records (Table 1) are indeed thelytokous, and not the result of inseminated females exercising control over fertilisation of their eggs.

The successful parasitization of *P. quercifoliella* on *Quercus*, naturally a host of bisexual populations of the parasitoid, by *Pediobius* originating from unisexual populations on *Corylus* and *Alnus* (sleeves 2 and 3), shows that hosts on the parasitoid's 'wrong' host food-plant can support it under artificial rearing conditions. Also, less surprisingly, *Pediobius* from *Alnus* undersurface mines was reared through undersurface mines on *Corylus* (sleeve 6), and *Pediobius* from uppersurface leaf-mines on *Corylus* was reared through undersurface mines on the same tree (sleeve 7).

Populations of *P. alcaeus* therefore differ in their reproductive biology. The bisexual populations reproduce by haplodiploidy and only males result from unfertilised eggs (arrhenotokous parthenogenesis). Reproduction in the unisexual populations is thelytokous with females developing from unfertilised eggs. It is not clear whether the occasional males appearing in rearings of normally unisexual populations, as on *Alnus* and *Corylus* (Table 1), are the progeny of 'stray' bisexual females, in which case they would presumably be potentially reproductively functional in relation to the bisexual race, or whether they are

progeny of normally thelytokous females, in which case they may be entirely reproductively non-functional.

The situation in *Pediobius alcaeus* is similar in some respects to that pertaining in *Diplolepis spinosissimae* (Giraud) (Hym., Cynipidae) (Plantard *et al.* 1998). This rose gallwasp is thelytokous (up to 4 per cent males) in populations on the Atlantic coast of France, but in two inland populations males comprise 21 and 29 per cent of the populations. The thelytokous populations were found to be infected by the endo-symbiotic bacterium *Wolbachia* which prevents the formation of males. Bisexual populations of *D. spinosissimae* were free of *Wolbachia*. Whether or not a micro-organism is implicated in the thelytoky of *Pediobius alcaeus* remains to be determined, but even if this were to be the case, the apparent segregation of sexual and thelytokous populations onto different tree genera, which in *Pediobius alcaeus* occurs sympatrically and (certainly in Britain) consistently, would still require explanation.

ACKNOWLEDGMENTS

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The *Chilicola megalostigma* Species Group and Notes on Two Lost Types of *Chilicola* (Hymenoptera: Colletidae, Xeromelissinae)

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Abstract.—The three species of the *megalostigma* group of *Chilicola* (*Hylaeosoma*) are reviewed and a key for their separation is provided. *Chilicola* **(H.) stenocephala Brooks and Michener,** new species, is described from Amazonian Colombia. *Chilicola (H.) polita* Michener is recorded for the first time from Costa Rica. Lectotypes are designated for two Brazilian *Chilicola* species originally described as *Oediscelis huberi* Ducke and *O. minima* Ducke.

The xeromelissine genus *Chilicola* Spinola has been characterized by Toro and Moldenke (1979) and Michener (1994, 1995). It consists of small, slender, usually black bees superficially similar to species of *Hylaeus* in the subfamily Hylaeinae, but differing notably in the presence of a weak scopa on the posterior femora and tibiae, and on the first three metasomal sterna, the hairs on the second sternum being the best developed part of the scopa. *Chilicola* is particularly abundant and diverse in temperate South America (Chile, Argentina) but ranges north to central Mexico and to St. Vincent in the Lesser Antilles.

The subgenus *Hylaeosoma*, characterized by Michener (1994, 1995), occurs from Brazil to central Mexico. It consists of unusually slender species with a depression for the reception of the antennal scape above each antennal alveolus.

THE *CHILICOLA MEGALOSTIGMA* SPECIES GROUP

Within the subgenus *Hylaeosoma* there is a species-group consisting of very smooth, shiny species with a strong, flaring preoccipital carina. This group, here known as the *megalostigma* group, which was also characterized as Group B by Michener (1994:83), consists of *C. megalostigma* Ducke from northeastern Brazil, *C. polita* Michener from Mexico to Panama, and the new species described below from Colombia.

A hitherto unrecognized characteristic of the *megalostigma* group is the modified front tarsus of females, perhaps serving to pull pollen from minute, deep flowers or tubular anthers. The front tarsus of an ordinary species of *Hylaeosoma*, *Chilicola mexicana* Toro and Michener, is illustrated in Figure 1. Figures 2 to 4 show the front tarsi of the three species of the *megalostigma* group. All (including *C. mexicana*) are bristly, with strong curved bristles as well as straight ones, as shown in Figure 4. This vestiture is omitted in Figures 1 to 3. In females of the *megalostigma* group, the front basitarsus is shortened if one ignores the apical process, whereas the second segment is relatively large, compared to that of other species groups. More details are indicated in the figures and in the key to species, below.

Abbreviations used are the following: S, sternum; T, tergum. KSEM, Entomology Division, Snow Collections, University of Kansas Natural History Museum, Lawrence, Kansas, U.S.A. MPEG, Museu Paraense Emílio Goeldi, Belém, Pará, Brazil.

KEY TO THE SPECIES OF THE *MEGALOSTIGMA* GROUP OF *CHILICOLA*

1. Minimum distance between eyes about three-fourths of width of eye on same horizontal line seen from front (Fig. 8); malar area distinct, over half as long as wide (Fig. 9). First and second front tarsal segments of female each ending in long, down-curved, horn-like process with blunt apex (Fig. 4) . . . . *stenocephala* **Brooks & Michener**
– Minimum distance between eyes about equal to width of eye on same horizontal line seen from front; malar area short, less than half as long as wide. First and second front tarsal segments of female each ending in long process terminated by curved bristle 2
2. Frons with pit on frontal line above level of antennae, forming equilateral triangle with the two antennal sockets; first and second front tarsal segments of female each ending in long process terminated by curved bristle coarser than other tarsal bristles (Fig. 3) . . . . .
. . . . *megalostigma* **(Ducke)**
– Frons without pit on frontal line; first and second tarsal segments of female each with apical process ending with curved bristle similar to bristles elsewhere on tarsus . . . .
. . . . *polita* **Michener**

Figs. 1–4. Outer views of anterior tarsi of females of *Chilicola* (*Hylaeosoma*). All are bristly with both curved and relatively straight bristles and hairs, as shown in Figure 4. 1, *C. mexicana* Toro and Michener; 2, *C. polita* Michener; 3, *C. megalostigma* (Ducke); 4, *C. stenocephala* n. sp. In Figure 3 the bases of only two large setae are indicated arising from the apices of the processes of the first two tarsal segments of *C. megalostigma*. Comparable but seemingly more slender setae exist in *C. polita* (Fig. 2).

Chilicola (*Hylaeosoma*) *megalostigma* (Ducke)

Oe[discelis] megalostigma Ducke 1908:62; Ducke 1912:83.
Oediscelis megalostigma, Nascimento 1979:7.
C[hilicola] (H[ylaeosoma]) megalostigma, Michener 1994:87.

This species is known from the Serra de Baturité, 4°15′S, 39°05′W, altitude 700 m, in the state of Ceará, Brazil. Although on a mountain, this location in the xeric northeast of Brazil is a very different habitat from the moist forest areas where other species of this group are found. The specimens were taken by Ducke on the flowers of *Borreria verticillata* Mey. (Rubiaceae).

The lectotype, selected but not published by J. S. Moure and C. D. Michener, was designated (i.e., published) by Nascimento (1979); it is in MPEG. Lectoparatypes are in MPEG, KSEM, and presumably in the collection of Padre J. S. Moure, Universidade Federal do Paraná, Curitiba. Specimens are also in the Departamento de Zoologia, Universidade de São Paulo, São Paulo, Brazil.

A front tarsus from two different females was removed and examined in glycerin (and preserved in microvials on the pins). The apical processes of the first two

tarsal segments each ends in a curved bristle coarser than the other tarsal bristles. Bases of these bristles are shown in Figure 3. A bristle that is nearly as coarse, however, arises from the lower distal end of the third tarsal segment. These bristles are brittle, easily broken off so that they look like pegs even at a magnification of 80×.

Chilicola (Hylaeosoma) polita Michener

Chilicola (Hylaeosoma) polita Michener 1994:87.

Except for the characters indicated in the key to species, *C. polita* appears not to differ from *C. megalostigma*. When the front tarsus of the female is in its usual slightly down-curved position, the process of the basitarsus is appressed against the under side of the second segment and is unrecognizable, its hairs seemingly arising from the second segment. We recognized the process only when the tarsus was relaxed and bent under in a dissecting microscope (Fig. 2). We have not been able to examine the front tarsi of females of *C. polita* at high magnification in a liquid such as glycerin; there may be no consistent difference between *C. polita* and *C. megalostigma* in this structure (see key to species).

Chilicola polita is known from Veracruz and Oaxaca, Mexico, and Chiriquí Province, Panama. A new record is as follows: Costa Rica: San José Province, San Antonio de Escazú (Eberhardt's house) [9°55'N, 84°08'W], May 27, 1996, on *Cuphea* (G. Melo, collector). [See Addendum.]

The specimen from Costa Rica as well as the holotype from Veracruz are in KSEM.

Chilicola (Hylaeosoma) stenocephala Brooks and Michener, new species

In its elongate body form (Figs. 5, 6) this species resembles other species of *Hylaeosoma*, although the length is exaggerated by the long head which in all specimens available is directed forward in a prognathous position (Fig. 7), rather than being hypognathous as in most bees. Other species of the subgenus have a tendency to the same condition, especially in species with long heads. This is likely to be related to pushing down into small deep flowers or flower clusters. The key to species indicates some of the principal differences between *C. stenocephala* and its closest relatives, *C. megalocephala* and *polita*.

Male: Body length 6 mm. Coloration: Black, the following parts testaceous: longitudinal band on clypeus (yellowish), labrum, mandible, malar area (dark), anterior part of hypostomal area, antennal scape and pedicel, under side of flagellar segments 2 to 4 (sometimes dark brown), legs (femur, tibia and tarsus of posterior leg infuscated). The following transparent amber: posterior pronotal lobe, tegula, axillary sclerites of wings, apical margins of metasomal terga. Bases of T2 to T4 and metasomal sterna except S1 brown. Wings transparent with veins and stigma black. Body surface: Highly polished and shining, with widely separated, not sharply defined punctures, except propodeum; dorsal surface of propodeum with fine longitudinal, radiating striae; sides of propodeum lineolate with small punctures, rather dull; metasomal sterna lineolate. Hairs: Sparse, simple, erect, dark testaceous to dull whitish, notably long on metasoma, especially posteriorly; frons with V-shaped pattern of hairs, lower end between antennae, arms extending to upper part of frons (Fig. 8); pronotal lobe margined with short, appressed white hairs; propodeum with short, appressed white hairs that do not hide surface, except for hairless striate dorsal surface. Structure: Head elongate (Figs. 7, 8), proportions as shown in illustrations, paraocular area, with well developed depression for antennal scape extending upward toward ocellocular area (as in other *Hylaeosoma*); medial to depression a longitudinal, impunctate welt (white on left of Fig. 8) extending from antennal base to upper ocular tangent; first flagellar seg-
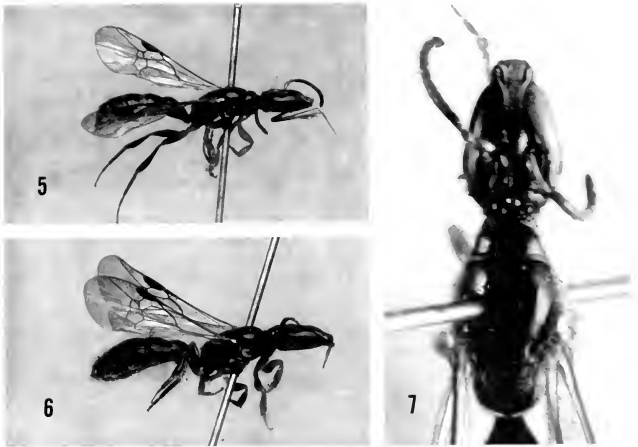
Figs. 5–7. *Chilicola (Hylaeosoma) stenocephala* n. sp. 5, male holotype; 6, female paratype; 7, dorsal view to show thorax, male.

ment shorter than pedicel, about 1.5 times as long as broad, segments 2 and 3 broader than long, remaining segments longer than broad, 11 over three times as long as broad; malar area about as long as wide (Fig. 9); ocelloccipital distance about two ocellar diameters measured to apex of high preoccipital carina; genal area above about as wide as eye seen from side, below tapering to vanishing point. Maxillary palpus about as long as prementum, nearly as long as head, first two segments short, remaining four segments long, straight, progressively slightly shortened toward apex, so that segment 3 is longest (also broadest). Pronotum with large dorsal surface (Figs. 5, 7) about on level with scutum which is over three times as long as mid-dorsal part of pronotum. Legs slender (Fig. 5). Wings as shown in Figure 5; apex of marginal cell minutely truncate. T1 longer than broad, in profile a slight

constriction between T1 and T2 (Fig. 5); T7 rather narrowly rounded at apex; posterior half of S6 with strongly elevated longitudinal ridge tapering posteriorly, ending in narrow, sharp, bristled apex (Figs. 10, 11). T7, T8 and genitalia as in Figures 12 to 14; genitalia with apices of gonoforceps much elongated and curved mesad, thus differing from those of the other species of this group (see Michener 1994, Fig. 10) as well as from all other *Chilicola* (see Toro and Moldenke 1979).

Female: As described for male except as follows: Clypeus black, without testaceous band; flagellum blackish; pronotal lobe dark brown; legs infuscated dark brown except trochanters testaceous; metasoma black, dark brown ventrally. Scopa of nearly erect whitish plumose hairs on S1 to S3, longest on S2. Scopal hairs of hind femur plumose, shorter than femoral diameter; hairs of hind tibia long and sim-
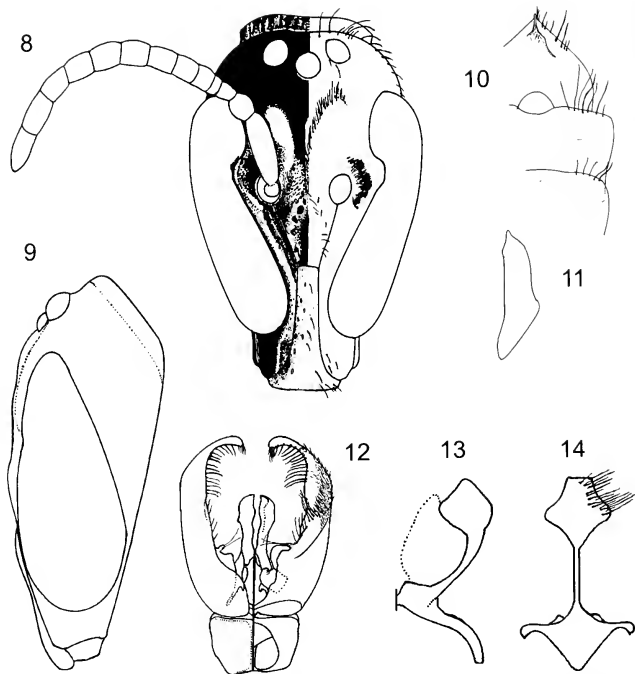
Figs. 8–14. Male of *Chilicola* (*Hylaeosoma*) *stenocephala* n. sp. 8, face, sculpturing on left, hairs on right; 9, side view of head; 10, S5 and S6; 11, side view of S6, ventral side to the left; 12, genitalia, dorsal on left; 13, S7, right hand half, ventral view; 14, S8, dotted line across extreme base represents actual condition of specimen; but the base has been drawn in what is presumably its undamaged shape.

ple. Flagellum short, segments broader than long except 8 and 9 which are slightly longer than broad and 10 which is about twice as long as broad; last two segments of maxillary palpus missing, probably broken off in the single specimen; anterior tarsus bristly, segments 1 and 2 with large, apical, down-curved processes lacking apical hairs or pegs (Fig. 4); T1 about as long as broad; apex of metasoma unmodified.

Holotype male and one male and one female paratype: Colombia: Amazonas: La Chorrera [0°44'S, 73°01'W], 24–31 August, 1976 (M Cooper). One additional male paratype, same data but 3 September,

1976. All bear the Natural History Museum (London) number BM 1976-727, and the specimens are in that Museum except one male paratype in KSEM.

NOTES ON TYPES

While on the subject of tropical species of *Chilicola*, it is appropriate to publish information on the types of two species that had been lost. In 1955 Padre J. S. Moure and C.D.M. remounted many specimens in the Ducke collection in the Museu Paraense Emílio Goeldi in Belém, Pará, Brazil (MPEG). Remounting was necessary because of corroded pins that broke at the levels of labels and inside of specimens, sometimes bursting them. Many species were represented by series of syntypes. We selected and labeled lectotypes and lectoparatypes. These were published, and thus formally designated, by Nascimento (1979) in his catalog of hymenopteran types in MPEG.

That catalog makes no mention of *Oediscelis huberi* Ducke and *O. minima* Ducke, although types of *O. megalostigma* Ducke and other species described by Ducke in the same paper were designated. The reason has only now become evident, since the lectotypes of *O. huberi* and *minima* were found by G. Melo in KSEM, where they must have been left by C.D.M. or by Padre Moure. They will be returned to MPEG. The following notations and lectotype designations are in the style of Nascimento's (1979) catalog of types.

Oediscelis huberi Ducke 1908:63.
    Lectótipo. Brasil: Ceará, Serra de Baturité [4°15′S, 39°05′W], 600 m, 3-VIII-08 (Ducke). (Des. Moure e Michener, 1955).

The headless female is badly mounted on a paper point. To judge by the wing venation this is a member of the subgenus *Hylaeosoma*, where it was placed by Michener (1995). The abundant punctures and unmodified front tarsus exclude it from the *megalostigma* group.

Oediscelis minima Ducke 1908:63.
    Lectótipo: Brasil: Ceará, Quixadá [04°58′S, 39°01′W], 4-VII-08 (Ducke). (Des. Moure e Michener 1955).

The specimen consists of a female head and anterior half of thorax, with one badly damaged forewing, but no other wings, badly mounted on a paper point. This species is a member of the subgenus *Prosopoides*, where it was placed by Michener (1995).

ACKNOWLEDGMENTS

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ADDENDUM

We have just received four specimens of *Chilicola* (*Hylaeosoma*) *polita* Michener that add substantially to its distribution as indicated in the body of this paper. The first two, listed below, are from the Centre for Land and Biological Resources, Ottawa, Ontario, Canada. The other two were received through Laurence Packer, York

University, North York, Ontario, Canada. The data are as follows (one specimen from each locality):

Guatemala: Zacapa, 3.5 km southeast of La Union, 1500 m altitude, 20–27 June 1993, in flight intercept trap (J. Ashe, R. Brooks).

Mexico: Chiapas: Pk. Lago Belgica, 14 June 1989, in flight intercept trap (H. Howden); Puebla: 22 km north of Xicotepec de Juarez, 1070 m altitude, 17 June 1983 (M. Kaulbars); Tamaulipas: Rancho del Cielo near Gomez Farias, 1000 m altitude, 7 Aug. 1983 (M. Kaulbars).

The last locality is the northernmost record for the genus *Chilicola*.

Descriptions of New Genera from Brazil in the Tribes Heterospilini and Spathiini With Similar Wing Venation (Hymenoptera: Braconidae, Doryctinae)

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Abstract.—Six new genera and 11 new species are described from Brazil. These new taxa all have wing venation similar to that found in the genus *Heterospilus*, with fore wing vein 2RS absent or weakly indicated. The new genera are placed in the tribes Heterospilini and Spathiini and a key to the New World genera of these tribes is given. The new taxa described are as follows: *Amazondoryctes* Barbalho and Penteado-Dias, n.gen., *A. bicolor* Barbalho and Penteado-Dias, n. sp., *A. ater* Barbalho and Penteado-Dias, n. sp.; *Cauchim* Barbalho and Penteado-Dias, n.gen., *C. carinatus* Barbalho and Penteado-Dias, n. sp., *C. erugosus* Barbalho and Penteado-Dias, n. sp.; *Heterospathius* Barbalho and Penteado-Dias, n.gen.; *H. belokobylskiji* Barbalho and Penteado-Dias, n. sp., *H. petiolatus* Barbalho and Penteado-Dias, n. sp., *H. silvaticus* Barbalho and Penteado-Dias, n. sp.; *Jataiella pilosa* Barbalho and Penteado-Dias, n.gen., n.sp.; *Leptodoryctes luizi* Barbalho and Penteado-Dias, n.gen., n.sp.; *Pioscelus austrinus* Marsh, n. sp.; *Spathiospilus brasiliensis* Marsh, n. gen., n. sp.

The subfamily Doryctinae is one of the most diverse groups in the Braconidae, especially in the Old and New World tropics. Recent studies by Marsh for the Neotropics (see for instance Marsh 1993) and Belokobyl'skij for the Old World tropics (see for instance Belokobyl'skij 1994a, b, 1995) have shown the incredible diversity at the generic level and have lead to revised concepts of previously described genera.

The genus *Heterospilus* was described by Haliday in 1836 and characterized by the absence of fore wing vein 2RS, thus the first and second submarginal cells are more or less confluent. In some cases, vein 2RS may be sclerotized but only appears as an infuscate line with no distinct vein edges such as a true tubular vein (see Mason 1986 for definition of wing vein types in braconids). This character was unique

for the Braconidae and for many years *Heterospilus* was the only genus known with such wing venation. Several more genera that were subsequently described with this type of wing venation have been synonymized with *Heterospilus* (Shenefelt and Marsh 1976; Belokobyl'skij 1992). Muesebeck and Walkley (1951) proposed the genus *Pioscelus* for two species which differed from the typical *Heterospilus* in other morphological characters. Hedqvist (1963) described the genus *Labania* which had this same wing venation; he placed it in the subfamily Hormiinae but stated that it had more affinities to the Doryctinae. The genus *Heterospilus* is a very large genus with about 500 species in the New World, most of which are undescribed. Thus, most doryctines with the fore wing vein 2RS absent have been placed in this genus.

Recent studies of the Neotropical fauna of the Doryctinae have revealed several forms with this wing venation but which differ in many distinct characters from typical *Heterospilus*. Until recently, these would have all been placed near *Heterospilus* in the tribe Heterospilini. However, some of these are more closely related to the genus *Spathius* Nees with its petiolate metasoma. These genera are properly placed in the tribe Spathiini as defined by Belokobyl'skij (1992). The genus *Labania* is placed in its own tribe, Labaniini, and is more closely related to the tribe Ecphylini.

The purpose of this paper is to provide descriptions of several new genera from Brazil in the tribes Heterospilini and Spathiini which have this characteristic wing venation. Keys to the New World genera are also provided. This is part of a long term program by the first author (SMB) to study the Doryctinae of Brazil.

MATERIALS AND METHODS

The subfamily Doryctinae can be identified using the keys provided by Wharton *et al.* 1997. The New World genera can be identified using the key provided by Marsh (1997) and a key to the tribes of Doryctinae is provided by Belokobyl'skij

(1992). Morphological and wing venation characters are based on Wharton *et al.* (1997). Taxonomic authority for the new genera and species described here is as indicated for each taxon. Abbreviations for institutions that provided specimens for this study and where type specimens are deposited are: DCBU, Departamento de Ecologia e Biologia Evolutiva da Universidade Federal de São Carlos, São Carlos, SP, Brazil; INPA, Instituto Nacional de Pesquisas da Amazônia, Manaus, Brazil; UFPR, Universidade Federal do Paraná, Brazil; USNM, National Museum of Natural History, Smithsonian Institution, Washington, DC.

TRIBE HETEROSPILINI FISCHER

This tribe is distinguished from the Spathiini by the following characters: metasoma not petiolate, the first metasomal tergum being usually broad and short with length not much longer than apical width; the acrosternite of the first metasomal segment short, less than $\frac{1}{5}$ length of the tergum and not fusing with the lateral margins (Fig. 13); dorsope on first metasomal tergum usually distinct and deep (see Belokobyl'skij 1992).

KEY TO THE NEW WORLD GENERA OF THE TRIBE HETEROSPILINI

1. Fore wing vein r-m absent (Figs. 4, 5) 2
–   Fore wing vein r-m present (Figs. 1–3) 3
2(1). Hind wing veins cu-a and m-cu present (Fig. 5) . . . .
    . . . . *Canchim* Barbalho and Penteado-Dias, new genus
–   Hind wing veins cu-a and m-cu absent (Fig. 4) . . . .
    . . . . *Leptodoryctes* Barbalho and Penteado-Dias, new genus
3(1). Hind coxa with a more or less distinct antero-ventral basal tubercle or tooth 4
–   Hind coxa round at base, without antero-ventral basal tubercle or tooth 5
4(3). Body densely covered with long white hair (Figs. 7–9) . . . .
    . . . . *Jataiella* Barbalho and Penteado-Dias, new genus
–   Body usually sparsely covered with short hair . . . . *Heterospilus* Haliday
5(3). Second metasomal tergum with two posteriorly converging grooves (Fig. 15) . . . .
    . . . . *Pioscelus* Muesebeck and Walkley
–   First and second metasomal terga with two median parallel carinae (Fig. 29) . . . .
    . . . . *Amazondoryctes* Barbalho and Penteado-Dias, new genus
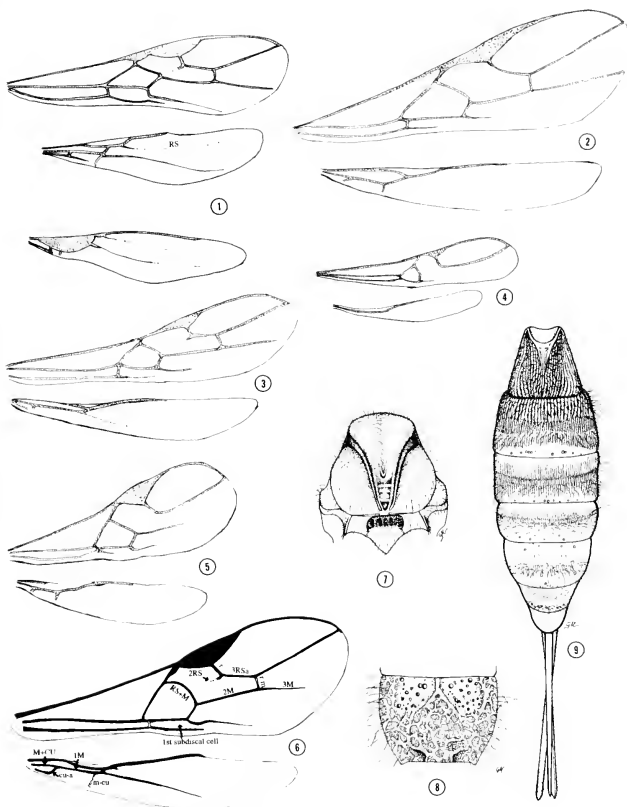
Figs. 1–9. Figs. 1–6, wings: 1, *Jataiella pilosa* n. sp.; 2, *Amazondoryctes ater* n. sp.; 3, *Heterospathius petiolatus* n. sp.; 4, *Leptodoryctes luizi* n. sp.; 5, *Canchim carinatus* n. sp.; 6, *Spathiospilus brasiliensis* n. sp. Figs. 7–9, *J. pilosa*: 7, mesonotum; 8, propodeum; 9, metasoma.

Amazondoryctes Barbalho and Penteado-Dias, new genus

Type species.—*Amazondoryctes bicolor* Barbalho and Penteado-Dias, new species.

Diagnosis.—Face striate; vertex, malar space and temples smooth and shining; frons smooth or slightly striate; pleuron with transverse carinae; pronotum weakly granulate with longitudinal scrobiculate groove; mesopleuron smooth; notauli distinctly scrobiculate; sternaulus complete; propodeum strongly areolate-rugose; hind coxa round at base, without basal tubercle; fore wing vein 2RS absent, first and second submarginal cells confluent, first subdiscal cell open at apex (Fig. 2); hind wing vein M+CU shorter than 1M; first, second and base of third metasomal terga striate, remaining terga slightly granulate, first and second terga with strong complete parallel carinae (Fig. 29).

Distribution.—Amazonas State of Brazil. One of us (PMM) has also seen an apparently undescribed species from Costa Rica.

Comments.—This genus is similar to *Pioscelus* and will run to that genus in the key provided by Marsh (1997) but is distinguished by the parallel, rather than diverging, carinae on the second metasomal carina.

Etymology.—The generic name is in reference to the locality of the two known species from Amazonia.

KEY TO SPECIES OF THE GENUS *AMAZONDORYCTES*

1. First and second metasomal terga striate, remaining terga smooth and shining; frons slightly excavated . . . . *A. bicolor* Barbalho and Pentado-Dias, new species
– First and second and basal half of third metasomal tergum striate; frons not excavated . . . . *A. ater* Barbalho and Penteado-Dias, new species

Amazondoryctes bicolor Barbalho and Penteado-Dias, new species
(Fig. 30)

Female holotype.—Head: circular; 28 antennomeres, first flagellomere shorter than scape plus pedicel; occipital carina meeting hypostomal carina; oral cavity small, diameter equal to malar space and ⅓ eye height; face striate, 1.2 times longer than eye height; vertex, frons, malar space and temples smooth and shining; frons slightly excavated. Mesosoma (Fig. 30): pleuron with transverse carinae; pronotum weakly granulate, with longitudinal scrobiculate groove; mesopleuron smooth; mesonotum angled and declivous anteriorly; notauli scrobiculate and meeting before scutellum in costate-rugose area; middle mesonotal lobe granulate basally, alveolate apically, lateral lobes granulate; sternaulus complete, weakly scrobiculate; metapleuron areolate; propodeum areolate with two longitudinal carinae laterally. Legs: fore tibia with single row of 8 spines on anterior edge; hind coxa without basal tubercle. Wings (as in Fig. 2): fore wing vein 2RS absent, first subdiscal cell open at apex, vein 2cu-a absent or represented by a fuscous spot; hind wing vein M+CU shorter than 1M, 1r-m more than half length of 1M, m-cu weak or absent. Metasoma: first and second terga striate, remaining terga weakly granulate; parallel median carinae on first and second terga complete and strong; ovipositor shorter than metasoma. Color: body and antenna dark brown, face yellowish, vertex dark brown, first metasomal tergum black, remaining terga brown, fore and middle legs yellow, hind coxa and femur brown, tibia yellow basally, brown apically, ovipositor sheaths yellow with black at apex,

wings slightly dusky. Body length: 3.1 mm.

Male.—Unknown.

Holotype female.—BRAZIL: Amazonas, Manaus, ZF3, Km 23, Fazenda Esteio Res. 1112, November 26, 1986, B. Klein col. Deposited in INPA.

Etymology.—The specific name is in reference to the bicolored body with the face yellow and mesosoma and metasoma dark brown or black.

Amazondoryctes ater Barbalho and Penteado-Dias, new species
(Figs. 2, 29)

Female holotype.—Agrees with the description of *A. bicolor* except as follows: 38 antennomeres; face with converging sculpture; frons not excavated, slightly striate and with rugose sculpture between toruli and eyes; eye height 2.4 times longer than diameter of oral cavity; first, second and basal half of third metasomal terga striate (Fig. 29); fore tibia with 3 rows of 22 strong spines; head and mesosoma entirely black, first and second metasomal terga black, remaining terga black on basal half, light brown on apical half; body length 4.6 mm.

Male.—Unknown.

Holotype female.—BRAZIL: Amazonas, Manaus, ZF3, Km23, Fazenda Esteio Res. 1208, February 9, 1985, B. Klein col. Deposited in INPA.

Paratypes.—BRAZIL: 1 female, Amazonas, Manaus, ZF3, Fazenda Esteio Res. 1112, February 9, 1985. Deposited in DCBU.

Etymology.—The specific name is in reference to the black color.

Canchim Barbalho and Penteado-Dias, new genus

Type species.—*Canchim carinatus* Barbalho and Penteado-Dias, new species.

Diagnosis.—Vertex and frons striate or smooth; face only slightly striate; temple and malar space smooth; mesonotum declivous anteriorly; notauli and sternaulus complete and scrobiculate; propodeum areolate-rugose; hind coxa rugose and with basal tubercle; fore tibia with row of 8 spines on anterior edge; fore wing veins r-m and 2RS both absent; hind wing vein M+CU slightly longer than 1M; first and at least basal half of second metasomal terga striate, terga beyond third smooth and shining.

Distribution.—São Paulo State of Brazil.

Comments.—This genus will run to *Heterospilus* in the key provided by Marsh (1997) but is distinguished by the absence of fore wing vein r-m, thus all submarginal cells are confluent.

Etymology.—The generic name is in reference to the localities for the known species, Fazenda Canchim, São Carlos, SP, Brazil.

KEY TO SPECIES OF THE GENUS *CANCHIM*

1. First, second and basal ⅓ of third metasomal terga striate; vertex and frons striate . . . . .
   . . . . **C. carinatus** Barbalho and Penteado-Dias, new species
 – First and basal ½ of second metasomal terga striate; vertex and frons often smooth . . . . .
   . . . . **C. erugosus** Barbalho and Penteado-Dias, new species

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Canchim carinatus Barbalho and Penteado-Dias, new species
(Figs. 5, 26–28)

Female.—Head (Fig. 28): occipital present and meeting hypostomal carina; ver-

tex and frons striate; face slightly striate; temple and malar space smooth; face height 1.4 times longer than eye height; eye width 2.2 times temple width; oral cavity about equal to malar space; 17 an-

tennomeres; first flagellomere equal to length of scape and pedicel. Mesosoma (Fig. 26): pronotum, mesopleuron and mesonotum granulate; mesonotum declivous anteriorly; notauli complete and scrobiculate; sternaulus scrobiculate, not complete; propodeum areolate-rugoae. Legs: hind coxa rugose, with basal tubercle; fore tibia with row of 8 short spines on anterior edge. Wings (Fig. 5): fore wing veins r-m and 2RS both absent, first subdiscal cell open at apex, vein 2cu-a absent; hind wing vein M+CU slightly shorter than 1M. Metasoma (Fig. 27): length of first metasomal tergum equal to apical width; first, second and basal third of third terga striate, remaining terga smooth and shining; ovipositor ¼ length of metasoma. Color: head light brown; mesosoma and metasoma dark brown; second tergum sometimes with triangular yellow spot at base; legs yellow; wings hyaline, veins brown. Body length 2 mm.

Male.—Unknown.

Holotype female.—BRAZIL: Fazenda Canchim, São Carlos, São Paulo State, October 9, 1996. Deposited in DCBU.

Paratypes.—BRAZIL: 2 females, same data as holotype except dates of June 27, 1985 and July 26, 1989. Deposited in DCBU.

Etymology.—The specific name is in reference to the sculpture of the head.

Canchim erugosus Barbalho and Penteado-Dias, new species
(Fig. 25)

Female.—Agrees with the description of *C. carinatus* except as follows: head smooth and shining, vertex slightly striate (Fig. 25); mesopleuron slightly granulate; first and basal ⅔ of second metasomal terga striate; ovipositor about ⅓ length of metasoma; body length 1.8 mm.

Male.—Unknown.

Holotype female.—BRAZIL: Fazenda Canchim, São Carlos, São Paulo State, April 25, 1985, A. S. Soares col. Deposited in DCBU.

Paratypes.—BRAZIL: 1 female, Telêmaco Borba, PR, September 1, 1986, PROFAUPAR (Levantamento da Fauna Entomológica do Estado do Paraná). Deposited in UFPR.

Etymology.—The specific name is in reference to the smooth head.

Jataiella Barbalho and Penteado-Dias, new genus

Type species.—*Jataiella pilosa* Barbalho and Penteado-Dias, new species.

Diagnosis.—Body densely covered with long white hair; face, temples and vertex smooth and shining; frons striate; pronotum striate laterally; propleuron and mesopleuron smooth; notauli deep, smooth and meeting in a triangular area sculptured (Fig. 7); sternaulus absent; hind coxa with a small rounded tubercle at base; fore wing vein 2RS absent except for short stub, first subdiscal cell open (Fig. 1); hind wing vein M+CU shorter than 1M, male with stigma in hind wing; first metasomal tergum (Fig. 9) slightly longer than apical width; metasomal terga 1–3 and base of 4 striate, remaining terga striate at base, granular at apex.

Distribution.—São Paulo State of Brazil.

Comments.—This genus is distinguished from other genera of Heterospilini by the very densely hairy body, which will separate it from *Heterospilus* in the key provided by Marsh (1997).

Etymology.—The generic name is in reference to the locality of the type species.

Jataiella pilosa Barbalho and Penteado-Dias, new species
(Figs. 1, 7–9)

Female holotype.—Head: densely hairy; occipital carina present and meeting hypostomal carina; face and vertex smooth and shining, frons striate; face height 1.7 times eye height; eye width 1.8 times temple width; malar space ⅓ oral cavity; first flagellomere equal to length of scape and pedicel combined. Mesosoma: densely hairy; pronotum striate laterally; propleu-

ron and mesopleuron smooth and shining; middle mesonotal lobe more elevated than lateral lobes, middle lobe with complete median longitudinal groove (Fig. 7); notauli deep, smooth, meeting before lateral lobes, middle lobe with complete median longitudinal groove (Fig. 7); notauli deep, smooth, meeting before scutellum in area with longitudinal carinae and few cross carinae (Fig. 7); sternaulus absent; propodeum rugose-areolate with two basal smooth areas (Fig. 8). Legs: hind coxa with small tubercle at base; fore tibia with row of 9 spines on anterior edge. Wings (Fig. 1): fore wing vein 2RS absent except for short stub, vein r-m present, first subdiscal cell open at apex; hind wing vein M+CU shorter than 1M, r-m less than half length of 1M. Metasoma (Fig. 9): first metasonal tergum 1.2 times longer than apical width; terga 1–3 and base of 4 striate, remaining terga striate at base, granular at apex; ovipositor about ⅔ length of metasoma. Color: body black, mesopleuron dark brown; wings infuscated. Body length: 5.6 mm.

Male.—Essentially as in female except as follows: propodeum smooth; all metasomal terga except apical one striate; stigma in hind wing (Fig. 1); only lower part of mesopleuron dark brown.

Holotype female.—BRAZIL: Rio Mogi-Guaçú, Luiz Antônio, São Paulo, November 26, 1993, L. A. Joaquim col. Deposited in DCBU.

Paratypes.—BRAZIL: 1 male, same data as holotype. Deposited in DCBU.

Leptodoryctes Barbalho and Penteado-Dias, new genus

Type species.—*Leptodoryctes luizi* Barbalho and Penteado-Dias, new species.

Diagnosis.—Head, pronotum, propleuron, mesopleuron and mesonotum smooth and shining; notauli meeting well before scutellum, sometimes incomplete; sternaulus complete and scrobiculate; propodeum rugulose; hind coxa round at base; fore wing veins 2RS, r-m, 2M and 3M absent, vein 2-1A also absent and, thus, first subdiscal cell absent; hind wing veins cu-a and m-cu absent; first metasomal tergum

weakly striate, remaining terga smooth and shining.

Distribution.—São Paulo, Amazonas and Rio de Janeiro States of Brazil.

Comments.—This genus is distinguished from most other braconids by the wing venation with the absence of several veins in both fore and hind wings. It can be definitely placed in the Doryctinae by the presence of a row of stout spines along the anterior edge of the fore tibia, presence of a flange at the apico-lateral corner of the propleuron, circular opening between clypeus and mandibles and presence of the occipital carina. The genus will not fit well in the key to genera provided by Marsh (1997) but would possible run to *Heterospilus* because of the absence of fore wing vein 2RS.

Etymology.—The generic name is from the Greek *leptos,* meaning slender, weak, in reference to the fragile appearance of this genus.

Leptodoryctes luizi Barbalho and Penteado-Dias, new species
(Figs. 4, 10–12, 31)

Female holotype.—Head (Fig. 12): completely smooth and shining; occipital carina present and meeting hypostomal carina; face height 2.3 times eye height; eye width equal to temple width; oral cavity diameter 1.2 times malar space. Mesosoma (Fig. 11): pronotum, propleuron, mesopleuron and mesonotum smooth and shining; notauli not complete, meeting well before scutellum; sternaulus complete and scrobiculate; propodeum rugose. Legs: hind coxa round at base; fore tibia with row of 8 spines on anterior edge. Wings (Fig. 4): fore wing veins 2RS, r-m, 2M and 3M absent, first subdiscal cell absent, vein 2-1A absent; hind wing veins cu-a and m-cu absent. Metasoma (Fig. 10): First metasomal tergum 3.2 times longer than apical width, weakly striate; remaining terga smooth and shining; ovipositor as long as entire body. Color: head, mesosoma, legs and first metasomal terga
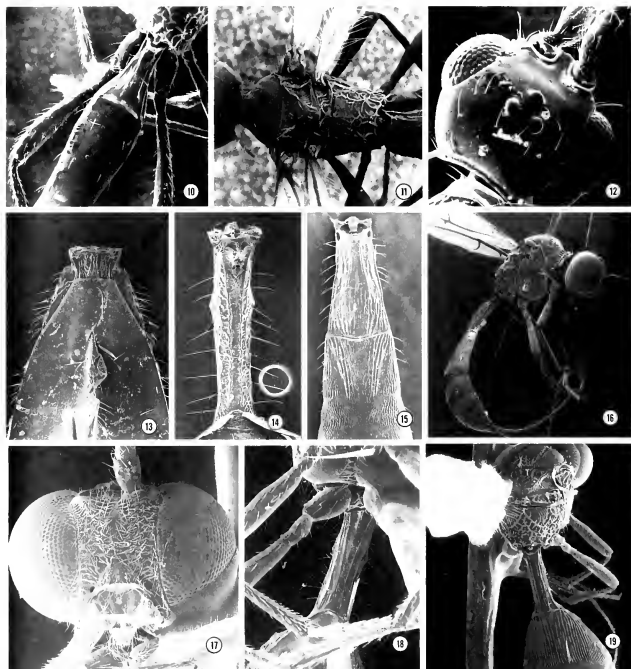
Figs. 10–19. Figs. 10–12, *Leptodorjctes luizi*: 10, metasoma; 11, mesosoma; 12, head. Fig. 13, *Heterospilus* sp., ventral view, first metasomal segment. Fig. 14, *Notospathius* sp., ventral view, first metasomal segment. Fig. 15, *Poscelus austrmus* n. sp., metasoma, dorsal view. Figs. 16–19, *Spathospilus brasiliensis*: 16, habitus; 17, face; 18, first metasomal segment, ventral view; 19, mesosoma and metasoma, dorsal view.

yellow, remaining terga and hind femur light brown; wings lightly infuscated. Body length: 1.6 mm.

Male.—Essentially as in female except as follows: head and mesosoma dark brown, metasoma light brown, legs yellow; fore wing vein 1A weak.

Holotype female.—BRAZIL: Amazonas,

Manaus, Reserva Ducke, September 6, 1993, M. T. Tavares, col. Deposited in DCBU.

Paratypes.—BRAZIL: 2 males, Ilha Grande, Rio de Janeiro, RJ, May 6, 1997, L. A. Joaquim, col.; 1 male, Estação Experimental de Ubatuba, SP, November 15, 1990, L. A. Joaquim, col. Deposited in DCBU.

Etymology.—This species is named after the collector and our friend Luiz Joaquim.

Pioscelus Muesebeck and Walkley

Pioscelus Muesebeck and Walkley, 1951: 180.

Pioscelus austrinus Marsh, new species
(Fig. 15)

Female.—Body color: head honey yellow; scape, pedicel and basal 3–6 flagellomeres honey yellow, remainder of flagellomeres brown; mesonotum brown, mesonotum and mesopleuron often light brown; fore and middle legs yellow, hind coxa except at apex and hind femur brown, apex of hind coxa, trochanters, tibia and tarsus yellow; metasoma brown, grooves on second metasomal tergum sometimes lighter; wings hyaline, veins including stigma light brown. Body size: 4.0 mm. Head: antenna with at least 19 antennomeres (broken in all females of type series), all flagellomeres at least 5 times longer than wide, first flagellomere very slightly shorter than second; vertex and temple smooth and shining; frons excavated, mostly smooth and shining but with a few striations medially; face rugulose and dull; eyes large, malar space about ⅓ eye height; ocelli small, ocell-ocular distance about twice diameter of lateral ocellus; occipital carina complete, reaching hypostomal carina. Mesosoma: pronotum coriaceous with median scrobiculate groove; mesonotum coriaceous, median lobe sharply declivous anteriorly with lateral corners broadly produced, notauli scrobiculate, meeting before scutellum in narrow longitudinally rugose-carinate area; mesopleuron smooth medially, subalar area broadly scrobiculate, sternaulus smooth, as long as mesopleuron; propodeum slightly longer than first metasomal tergum, not declivous apically, rugose-areolate laterally, rugose dorsally with basal lateral areas indistinct, coriaceous. Wings: fore wing vein 2RS weak or absent, at most indicated by weak infuscated line apically, vein 3RSa twice as long a vein r, first subdiscal cell open at apex, vein 2cu-a absent; hind wing vein cu-a present, vein M+CU about ½ length of 1M. Legs: hind coxa angled at base but without a distinct antero-ventral basal tubercle; hind femur short and swollen, about three times longer than wide. Metasoma (Fig. 15): first tergum with length about twice as long as apical width, strongly longitudinally carinate; second tergum with two converging grooves enclosing a basal semicircular carinate area, tergum carinate laterally; third tergum separated from second by transverse arcuate groove, carinate on basal ¾, coriaceous apically; remainder of terga coriaceous basally, smooth apically; ovipositor about ½ length of metasoma.

Male.—Essentially as in female; hind femur more greatly swollen, about twice as long as wide; hind wing without stigma.

Holotype female.—BRAZIL: Manaus, ZF3, Km23, Faz. Esteio, Res., 1208, B. Klein col., November 5, 1985. Deposited in INPA.

Paratypes.—BRAZIL: 2 females, same data as holotype, February 27, 1985, November 18, 1987; 1 female, Cerrado, Canchim, São Carlos, S.P., December 4, 1989, L. A. Joaquim, col.; 1 male, Mata Canchim, São Carlos, S.P., April 26, 1996, L. A. Joaquim, col. Deposited in DCBU.

Etymology.—The specific name is from the Latin *austrinus* meaning southern in reference to this species being the first one recorded from South America.

TRIBE SPATHIINI FOERSTER

This tribe is distinguished from the Heterospilini by the following characters: metasoma petiolate, first tergum usually long and narrow, acrosternite very long, at least ⅓ length but usually nearly as long as the tergum, fused with lateral margins (Figs. 14, 18); dorsope on first tergum weak or absent (see Belokobyl'skij 1992).

KEY TO THE NEW WORLD GENERA OF THE TRIBE SPATHIINI

1. Fore wing vein 2RS absent or not sclerotized (Figs. 3, 6) 2
 – Fore wing vein 2RS present and sclerotized 3
2(1). Eyes large, malar space very short or absent (Fig. 17); fore wing vein RS+M arched (Fig. 6); hind coxa with small but distinct antero-ventral basal tubercle ....
    .... *Spathiospilus* Marsh, new genus
 – Eyes smaller, malar space at least ⅓ eye height; fore wing vein RS+M not arched (Fig. 3); hind coxa without basal tubercle (Fig. 21) ....
    .... *Heterospathius* Barbalho and Penteado-Dias, new genus
3(1). Hind coxa round at base, without basal tubercle 4
 – Hind coxa with distinct basal tubercle or tooth at base 5
4(3). Hind wing vein m-cu curved toward wing apex, hind wing vein M+CU ⅔ length of vein 1M .... *Psenobolus* Reinhard
 – Hind wing vein m-cu curved toward wing base, hind wing vein M+CU ¼ length of vein 1M .... *Notiospathius* Matthews and Marsh
5(3). First metasomal tergum without triangle area at base .... *Spathius* Nees
 – First metasomal tergum with distinct triangular area at base 6
6(5). Fore wing vein m-cu asising distad of 2RS .... *Ptesimogaster* Marsh
 – Fore wing vein m-cu arising basad or directly in line with 2RS ....
    .... *Trigonophasmus* Enderlein

Heterospathius Barbalho and Penteado-Dias, new genus

Type species.—*Heterospathius petiolatus* Barbalho and Penteado-Dias, new species.

Diagnosis.—Diameter of oral cavity about equal to malar space; occipital carina meeting hypostomal carina; 25–35 antennomeres; mesonotum declivous anteriorly; notauli complete, scrobiculate; sternaulus complete, scrobiculate; propodeum horizontal for basal ¾, usually with two lateral longitudinal carinae; hind coxa without basal tubercle; fore wing vein 2RS absent, first subdiscal cell open at apex, vein 2cu-a absent, hind wing vein M+CU shorter than 1M, m-cu absent, r-m less than ½ length of 1M, no stigma in hind wing of male; first metasomal segment

long and slender, length at least 4 time apical width.

Distribution.—Amazonas, Pará, Rondônia and São Paulo States of Brazil. Also, one of us (PMM) has seen several undescribed species from Costa Rica, so the distribution of this genus is probably over Central and South America.

Comments.—This genus is similar to *Notiospathius* but is distinguished by the absence of vein 2RS in the fore wing; it will run to *Heterospilus* in the key provided by Marsh (1997) but is separated by the shape of the petiolate metasomal segment.

Etymology.—The generic name is in reference to the fore wing similarity to *Heterospilus* and the first metasomal segment similarity to *Notiospathius*.

KEY TO SPECIES OF THE GENUS *HETEROSPATHIUS*

1. Vertex and face strongly striate-rugose; ovipositor about 1.5 times longer than body (Fig. 24) .... *H. belokobylskiji* Barbalho and Penteado-Dias, new species
 – Vertex (Fig. 22) and face finely to weakly striate; ovipositor equal to or shorter than body 2
2(1). Ovipositor about ½ length of metasoma ....
    .... *H. petiolatus* Barbalho and Penteado-Dias, new species

– Ovipositor about equal to body length ....
.... *H. silvaticus* Barbalho and Penteado-Dias, new species

Heterospathius petiolatus Barbalho and Penteado-Dias, new species
(Figs. 3, 20–23)

Female holotype.—Head (Fig. 22): occipital carina meeting hypostomal carina; face and vertex striate; frons smooth; temple smooth and shining; face height 2.1 times eye height; face width 1.6–2.1 times eye width; diameter oral cavity about ⅓ eye height; eye width 1.4–1.7 times temple width; malar space about equal to diameter of oral cavity; 25 antennomeres, first flagellomere longer than scape and pedicel combined. Mesosoma (Fig. 20): pronotum rugulose-granulate; mesonotum declivous anteriorly; mesonotum rugulose-granulate; notauli scrobiculate, meeting at scutellum in triangular rugose area; mesopleuron granulate; sternaulus complete, scrobiculate; propodeum areolate-rugose, with distinct longitudinal carinae. Legs: fore tibia with single row of 7 spines on anterior edge; hind coxa (Fig. 21) rugose, without basal tubercle; first tarsomere of hind tarsus 2.3 times longer than second, second equal to length of third and fourth combined, fifth twice as long as fourth. Wings (Fig. 3): fore wing vein 2RS absent or represented by short stub, first subdiscal cell open at apex, vein 2cu-a absent; hind wing vein M+CU much shorter than 1M, r-m less than half length of 1M. Metasoma (Fig. 23): first tergum rugose, slender, length 5.7 times apical width, apical width equal to basal width; remaining terga smooth and shining; ovipositor about ½ length of metasoma. Color: head, mesosoma and first metasomal tergum dark yellow, remaining terga dark to light yellow; ovipositor light yellow with apex black; apical 6–12 flagellomeres white, remainder brown; wings slightly dusky, veins brown, stigma brown with white at basal third. Body length: 3.3 mm.

Variation in female.—Face occasionally weakly striate or granular, width 1.6–2.1 times eye width; eye width 1.4–1.7 times temple width; 20–32 antennomeres; fore tibia with row of 7–13 spines; metasoma with apical terga occasionally black; body length 1.5–3.7 mm.

Male.—Essentially as in female except as follows: 20–25 antennomeres, apical 2–6 flagellomeres white; diameter of oral cavity slightly greater than malar space; face width 1.5–1.9 times eye width; frons smooth or granulate; fore tibia with row of 7–13 spines; metasoma completely light yellow or with apical ¼ dark brown; no stigma in hind wing.

Holotype female.—BRAZIL: Amazonas, Manaus, ZF3, Fazenda Esteio, November, 1984. Deposited in INPA.

Paratypes.—BRAZIL: 2 females, 1 male, Rondônia, Ariquemes, Rio Ji, October 28, 1986, R. A. Rafael, col; 1 female, Fazenda Canchim, São Carlos, São Paulo state, April 30, 1987, L. A. Joaquim, col; 1 female, Rio Tocantins, Tucuruí, Para state, November, 22, 1989, N. Degullier, col.; 1 female, Santarém-Cucurunã, Para state, February, 1996, A. R. Lisboa col.; 2 females, Amazonas, Manaus, ZF3, Faz. Esteio, Res. 1301, January 22, 1986; January 29, 1986, B. Klein col.; 1 female, 1 male Amazonas, Manaus, ZF3, Faz. Esteio, Res. 1208, October 22, 1986, B. Klein col.; 1 female, Amazonas, Manaus, km 60, PDBFF/WWF, Res. 1210, November 8, 1984, B. Klein col.; 1 female, Rio Tocantins, Tucuruí, Para state; 2 females, Rio Branco, Acre state, October 25–November 8, 1991, F. Ramos, A. Henriques, I. Gorayeb & N. Bittencourt cols.; 1 male, Amazonas, Manaus, ZF3, Faz. Esteio, Res. 1113, January 30, 1986, B. Klein col.; 1 male, Manaus, ZF3, Faz. Esteio, Res. 1113, January 23, 1986, B. Klein col.; 2 males, Manaus, ZF3, Faz. Es-

Figs. 20–31. Fig. 20–23, *Heterospathius petiolatus* n. sp., 20, propodeum, 21, hind coxae; 22, vertex of head, 23, metasoma. Fig. 24, *Heterospathius belokobylskii* n. sp., metasoma. Fig. 25, *Canchim erugosus* n. sp., vertex of head. Figs. 26–28, *C. carinatus* n. sp., 26, mesopleuron, 27, metasoma, 28, vertex of head. Fig. 29, *Amazonodacnes ater* n. sp., metasoma. Fig. 30, *A. bicolor* n. sp., mesopleuron. Fig. 31, *Leptodacnes luizi* habitus.

teio, Res. 1208, November 20, 1984; October 17, 1984, B. Klein col.; Conceição do Araguaia, Para state, January 19–31, 1983, R. Nonato col. Deposited in DCBU, INPA, USNM.

Etymology.—The specific name is in reference to the petiolate metasoma.

Heterospathius belokobylskiji Barbalho and Penteado-Dias, new species
(Fig. 24)

Female.—Agrees with the description of *petiolatus* except as follows: 35–38 antennomeres, apical 12–13 flagellomeres white; face and vertex strongly striate-rugose, vertex occasionally strongly striate; frons striate; temples smooth; face height 1.6 times eye height; fore and mid granulate; propodeum without strong longitudinal carina; ovipositor 1.5 times longer than body (Fig. 24); body entirely brown; body length 5.5 mm.

Male.—Unknown.

Holotype female.—BRAZIL: Amazonas, Manaus, ZF3, Km32, Fazenda Esteio, January 1986, B. Klein col. Deposited in INPA.

Paratypes.—BRAZIL: 1 female, same data as holotype; 1 female, Pará, Santarém-Cucurunã, February, 1996, A. Penteado-Dias, col. Deposited in INPA, DCBU.

Etymology.—This species is named in honor of our colleague and fellow researcher on the Doryctinae, Sergey Belokobyl'skij, Zoological Institute, Russian Academy of Sciences, St. Petersburg, Russia.

Heterospathius silvaticus Barbalho and Penteado-Dias, new species

Female holotype.—Agrees with description of *petiolatus* except as follows: 27 antennomeres, apical 8 flagellomeres white; face striate; vertex only slightly striate; frons, temple and malar space smooth and shining; face width 2.2 times eye width; face height 1.7 times eye height; diameter of oral cavity slightly greater than malar space; no longitudinal carinae on propo-

deum; fore tibia with row of 7 spines on anterior adge; fore and middle coxa weakly striate; ovipositor about equal to body length; body length 2.8 mm.

Male.—Agrees with female except as follows: entire body light brown, propodeum dark brown.

Holotype female.—BRAZIL: Amazonas, Manaus, ZF3, Km23, Fazenda Esteio, November 8, 1984, B. Klein col. Deposited in INPA.

Paratypes.—BRAZIL: 1 male, Amazonas, São Gabriel da Cachoeira, April 29, 1982, J. A. Arias, col. Deposited in DCBU.

Etymology.—The specific name is from the Latin *silvaticus* meaning belonging to woods or trees in reference to the collection of this species in the jungle.

Spathiospilus Marsh, new genus

Type-species.—*Spathiospilus brasiliensis* Marsh, new species.

Diagnosis.—Cyclostome braconid, oral cavity circular, labrum concave; eyes large, malar space very small or absent; flagellomeres with double row of placodes separated by ridge around middle of flagellomere; mesonotum strongly declivous anteriorly; fore wing vein 2RS absent or weakly present apically near vein r, vein RS+M strongly arched, hind wing of male with stigma; for tibia with row of short stout spines along outer edge, hind coxa with small but distinct antero-ventral basal tubercle; metasoma petiolate, first tergum slender, parallel sided, rest of metasoma suddenly widened, acrosternum nearly as long as tergum and fused with tergum.

Distribution.—São Paulo State of Brazil. We have also seen one undescribed species from Panama.

Comments.—This genus is similar to *Heterospathius* in the Spathini by the absence of fore wing vein 2RS but distinguished by the strongly arched fore wing vein RS+M and the large eyes. In the key provided by Marsh (1997) it will run to *Heterospilus* but is distinguished by the long

and fused acrosternum of the first metasomal segment.

Etymology.—The generic name refers to the similarity to *Heterospilus* by the wing venation and to *Spathius* by the petiolate metasoma.

Spathiospilus brasiliensis Marsh, new species
(Figs. 6, 16–19)

Female.—Body color: head, mesosoma and metasoma reddish-brown, metasomal terga 2–5 sometimes infused with black; scape and pedicle yellow, flagellum yellow basally turning brown to apex; legs yellow; wings hyaline, veins yellow at base and apex, stigma and veins across middle of wing brown; ovipositor sheaths yellow, black at tip. Body size: 3–4 mm. Head (Fig. 17): 29–31 antennomeres, flagellomeres with two rows of placodes separated by ridge around middle of each flagellomere; eyes large, covering most of head; malar space extremely short or absent, lower margin of eye nearly touching base of mandible; face narrow, width less than length from clypeus to antennal sockets; oral cavity circular, diameter slightly greater than basal width of mandible; temple very narrow, about $\frac{1}{5}$ eye width; ocellocular distance shorter than diameter of lateral ocellus; face, frons and vertex rugulose-coriaceous, temple coriaceous; occipital carina scrobiculate along vertex and temple side. Mesosoma (Fig. 19): pronotum with scrobiculate grove across dorsal surface extending laterally on each side, bordered laterally by strong carina, dorsally coriaceous; mesonotum strongly declivous anteriorly, mesonotal lobes coriaceous, notauli scrobiculate, median lobe with short and wide carinate-rugulose area before scutellum and with median raised line extending to pronotum; scutellum coriaceous, bordered laterally by carina, scutellar sulcus deep with 5 cross carinae; mesopleuron coriaceous, subalar area rugose, sternaulus scrobiculate; propodeum strongly areolate-rugose apically

and laterally, with semicular coriaceous areas basolaterally bordered by distinct carinae. Wings (Fig. 6): fore wing vein r ½ length of 3RSa, vein RS+M strongly arched; hind wing vein RS absent, vein m-cu curved toward wing apex. Metasoma (Fig. 19): first tergum petiolate, parallel sided with apical and basal widths equal, longitudinally costate, weakly rugulose between costae; second tergum longitudinally costate, weakly rugulose between costae, triangular shaped with basal width abiut ½ apical width, weak line between second and third tergum; third tergum longitudinally costate on basal ⅔, coiraceous on apical ⅓; remainder of terga coriaceous; ovipositor about ⅗ length of metasoma.

Male.—Essentially as in female; 26 antennomeres; stigma present in hind wing.

Holotype Female.—BRAZIL: Rio Mogi Guaçu, Luís Antônio, S.P., February 18, 1988, L. A. Joaquim collector. Deposited in DCBU.

Paratypes.—BRAZIL: 1 female, 3 males, same data as holotype with additional dates of March 20–27, 1987; 1 female, Luís Antônio, S.P., Reserva Ecol. do Jataí, February 8, 1994, A. S. Soares collector; 1 female, Faz. Canchim, São Carlos, S.P., June 20, 1985, A. S. Soares collector. Deposited in USNM, DCBU.

Etymology.—The specific names is in reference to the localities of the types series from Brazil.

ACKNOWLEDGMENTS

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New Host and Distribution Records for *Leucospis* (Hymenoptera: Leucospidae) Associated Primarily with Nests of *Centris* (Hymenoptera: Anthophoridae) in the Dry Forests of Costa Rica

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Abstract.—A study conducted in the dry forests of Lomas Barbudal Biological Reserve, Guanacaste Province, Costa Rica, revealed new host records and elevation data for five species of *Leucospis*: *azteca, bulbiventris, cayennensis, egaia,* and *latifrons*. Four species of trap nesting *Centris* bees (Hymenoptera: Anthophoridae) were attacked, as well as at least 4 species of trap nesting bees in the family Megachilidae. Of 295 *Leucospis* wasps reared from these trap nesting bees, it was possible to associate 236 with hosts, 189 of which were from nests of *Centris bicornuta*. Elevational data and host species data are summarized for each *Leucospis* species reared, as well as sex ratios of reared material. Additional notes on biology and behavior are provided, along with a key to the five species reared from trap-nesting *Centris* bees in Costa Rica. The taxonomic status of *L. bulbiventris*, a sexually dimorphic species, is discussed relative to *L. manaica*.

Members of the family Leucospidae are among the largest species of Chalcidoidea, and all are parasitoids of solitary and subsocial aculeate bees and wasps. They drill through the hardened cell walls of their hosts' nests with their unusual ovipositors, and develop as ectoparasitoids. Excellent summaries of leucospid biology are provided by Clausen (1940), Habu (1962), and Bouček (1974). The family was revised on a world basis by Bouček (1974), who also summarized the known host data. Hosts were recorded for 32 of the 130 species of Leucospidae recognized by Bouček (1974). Prior to Bouček's (1974) revision, no species of leucospids had been recorded as parasitoids of *Centris* bees, though other anthophorids (notably species of *Xylocopa*) were known as hosts of at least three species of *Leucospis*. Subse-

quently, Chandler *et al.* (1985) reared two individuals of *L. cayennensis* Westwood from *Centris* in Minas Gerais, Brazil. Leucospids frequently parasitize megachilid bees in California (GWF, personal observations), and there are several published records of species of *Leucospis* attacking various megachilids (Bouček 1974, Burgis 1995).

Centris is a large genus of bees in the hymenopteran family Anthophoridae, with at least 32 species occurring in Costa Rica (Snelling, 1984). Their nesting habits are diverse. Some species make their nests in the ground while others utilize holes left in wood by other insects; some provision multiple cells per nest, others provision only one cell per nest. Aside from collecting pollen, all of them collect oil from plants that have oil producing flowers, and that oil is used in their nesting biology (Vinson *et al.* 1996).

Centris bees, because of their large size,

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are a readily observed component of the Mesoamerican dry forest habitat during the dry season. Trap-nests are very effective means of studying the activity of wood-cavity nesting species (Frankie *et al.* 1988, 1993, Vinson *et al.* 1996). In the area of this study, six species of *Centris* have been found to nest in tree holes, however only four of these are commonly found in the trap nests (Frankie *et al.* 1988). *Centris bicornuta* Mocsáry is one of the most abundant of the trap nesting species in this area (Frankie *et al.* 1988, 1993, 1997). A number of inquilines and parasitoids can be reared from trap-nests, and in the Guanacaste Province of Costa Rica, leucospids were one of the dominant parasitoids of some of the species of *Centris* being studied there. Below we record the first specific host associations for Leucospidae on *Centris* in Costa Rica.

MATERIALS AND METHODS

Study sites.—The study was conducted at the Lomas Barbudal Biological Reserve in the dry forest in Guanacaste Province, Costa Rica. Two bundles, each containing six block monitoring units (BMUs) (Frankie *et al.* 1993), were placed in dry forest sites at 100 m, 300 m, 600 m, and 800 m elevations in a transect extending from Hacienda Monteverde (at 100 m, 8 km NW Bagaces) northwards towards Volcan Rincón de la Vieja. All BMUs were hung at eye level on tree trunks in shaded locations, and were monitored at 14 day intervals throughout the dry season (late December to May). The 100 m site had a mixture of oak forest and riparian evergreen forest (Frankie *et al.* 1988), and had been disturbed by agricultural development. The 300–800 m sites were largely intact oak forest with several other scattered tree species. The oak species, *Quercus oleoides* Schlecht. & Cham., was the same at all four sites.

Trap nests.—The nesting activities of several species of *Centris* were monitored using BMUs. These BMUs consisted of 12

small wooden sticks (11.5 × 2.3 × 2 cm) with holes drilled in one end, bundled together to form a block. The wooden sticks (consisting of pine or two local hard wood species) were drilled lengthwise to a depth of between 7.0 to 11.0 cm depending on the hole sizes (diameters of 4.5, 6.5, 8, 9.5 and 11 mm were used). Two sticks representing each of the hole diameters, along with two additional sticks with a hole diameter of 8 mm, were bundled together using fine wire or twine. The 8 mm hole size was doubled as it is the hole size most commonly used by *Centris* bees (Frankie *et al.* 1988, 1993). Sticks were layered within the block so that a drilled end of a particular hole size always alternated with a non-drilled end, and small to large hole sizes descended from the top to bottom of a block.

Emergence.—Each BMU was numbered and identified as to location, altitude, and time and date of placement. Every 14 days the sticks with completed bee nests were replaced with a new stick of the same hole diameter and additional information was recorded on the removed stick, including date removed. Sticks with completed nests were placed in large wire baskets (~20 × 20 × 40 cm) made of 2.5 cm open mesh hardware cloth that prevented access by mammals, but not parasitoids. These baskets were hung from nails on nearby trees. During the wet season, glass scintillation vials were taped to the nest entrances to intercept any emergences. Emergences were monitored on a two week basis and parasitoid and host associations recorded. Data presented here were collected during four consecutive years (December 1993 to December 1997).

Behavior and development.—All observations on female wasp behavior were made at 100 m sites where 2–4 BMUs were continuously being monitored. Completed nests, 1 to 14 days old, were removed from BMUs, placed in baskets at these sites, and observed daily during daylight hours for 3 weeks. Each basket contained
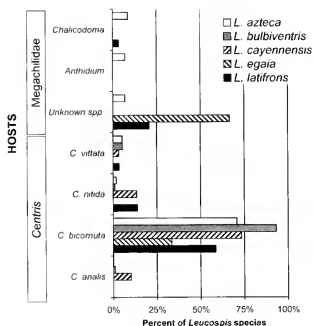
Fig. 1. Percent of each *Leucospis* species found on different hosts. Total for each *Leucospis* species across all hosts adds to 100%.

approximately 100 sticks arranged in three rows of two sticks deep so that each stick had at least one surface exposed. The number of leucospids searching or attempting to oviposit on nests was recorded until the experiment was terminated. One stick from each basket was removed daily during week 3 of the experiment, and opened to monitor bee development, and that of any present parasites, parasitoids, and diseases. This experiment was replicated 4 times.

Additional observations were made on 16 ovipositing female leucospids where, following completion of oviposition and departure of the leucospid, the exact drilling location was marked. The marked stick was then removed and dissected to determine the stage of the host attacked and the placement of the leucospid egg. Observations on oviposition behavior were also made on nests removed from BMUs and placed in baskets at the 100 m site.

Specimen repositories.—Voucher specimens for the *Centris* and megachilid bees are at University of California, Berkeley, and those for the *Leucospis* species are at

UC Berkeley and Texas A&M University (TAMU). Material for comparison, including primary types, was borrowed from the Philadelphia Academy of Natural Sciences (ANSP), the Natural History Museum, London (BMNH), and TAMU.

RESULTS AND DISCUSSION

Emergence data.—We reared 295 leucospids, representing five species, from at least seven species of wood-hole nesting bees in Guanacaste Province. Of 236 host bees, 189 were *Centris bicornuta* which was attacked by all five species of *Leucospis*: *L. azteca* Cresson, *L. bulbiventris* Cresson, *L. cayennensis* Westwood, *L. egaia* Walker, and *L. latifrons* Schletterer (Fig. 1). *Centris nitida* F. Smith and *C. vittata* Lepeletier each hosted four different species of *Leucospis* (Fig. 1). The most abundant leucospid in our samples was *L. bulbiventris* (56% of reared individuals) (Fig. 2). Discounting *L. egaia*, represented only by three reared individuals in our samples, all leucospids were more abundant at lower elevations (Fig. 3). *Leucospis azteca* and *L. cayennensis* were most abundant at the 100 m site; *L. bulbiventris* and *L. latifrons* were most abundant at the 300 m site (Fig. 3). In addition to *C. bicornuta*, *C. nitida*, and *C. vittata*, we also reared leucospids from *C. analis* F., undetermined species of *Chalicodoma* and *Anthidium* (Hymenoptera: Megachilidae), and at least two other undetermined species of megachilid bees, all from the trap nests described above.

The experimental environment employed in this study was artificial owing to the fact that the *Centris*-infested trap nests were highly accessible to leucospids by being clustered in baskets. The nests were thus at much higher densities than would be encountered in nature. In Costa Rican dry forests, *Centris* nests tend to be more widely dispersed, and the bees are not limited to nesting in holes in small sticks, where are maximally exposed for *Leucospis* oviposition. Therefore, the large number of leucospids recorded here is at

Frequency of Each *Leucospis* Species Reared
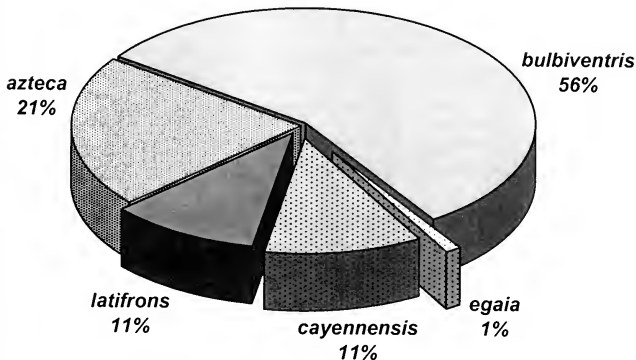
Fig. 2. Relative proportions of *Leucospis* species reared from trap nesting bees.

least in part a reflection of the experimental manipulations.

Observations on oviposition.—No female leucospids were observed around the wire baskets or on the sticks until nests were at least 3 weeks old (Fig. 4). Peak activity occurred towards the end of the third week, but since the experiment was terminated before all activity ceased, we lack data on how long nests remain attractive. Female leucospids fly up wind to the wire enclosures (100% N = 19), and ultimately land on one of the sticks containing bee nests. Generally, they walk the length of the stick slowly while alternately drumming the surface with their antennae. Prior to drilling, they stop to antennate the wood surface with both antennae held close together, then move forward half a body length to drill the antennated spot with the ovipositor.

Based on dissections of the 16 marked cells into which leucospids were observed ovipositing, female leucospids only attacked cells in which the mature larvae had at least begun to spin a cocoon. Leucospid eggs were always located inside the cocoons, either on the surface of a host larvae still finishing its cocoon (N = 1), a prepupa (N = 3), or a pupa (N = 12). Of the 18 other leucospid larvae or pupae recorded from randomly dissected nests, all were within the cocoon of a bee, indicating that either the bee is allowed to develop to a prepupa and spin a cocoon, or they are only parasitized following cocoon formation. The failure to find leucospid larvae on younger stages of bee larvae, and the delay in leucospid response to newly provisioned bee nests, suggests that these leucospids, at least, do not attack earlier stages of their hosts. Parasitized host larvae did not move, but it was not clear if they

Proportions of Four Species of
Leucospis Found at Different Elevations
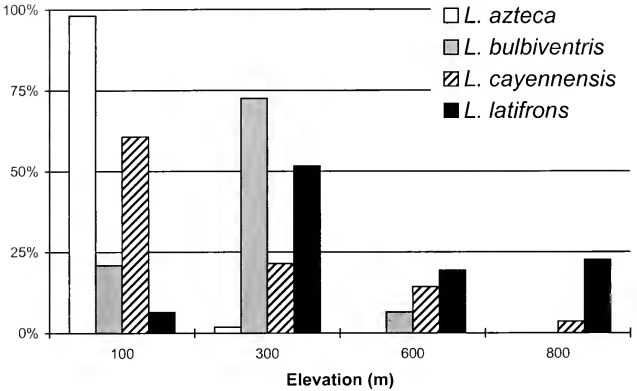
Fig. 3. Proportions of four species of *Leucospis* found at different elevations. Total for each *Leucospis* species across all elevations adds to 100%.

Average Number of *Leucospis* Attacks on Bee Nests

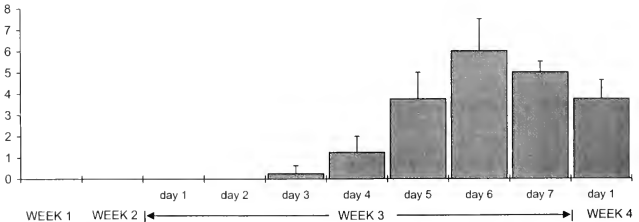Fig. 4. Behavioral observations. Number of *Leucospis* attacks on provisioned sticks observed over time. Nests at the beginning of week 1 were from 1 to 14 days old. Observations were not extended beyond the first day of week 4.

were paralyzed since larvae at this stage of development are lethargic.

There have been few prior studies in which more than one species of leucospid has been reared from a single host species. In addition to the five specific examples listed by Bouček (1974), RAW (unpublished) has collected both *L. histrio* Maindron and *L. moleyrei* Maindron from nests of a single species of *Xylocopa* in Papua New Guinea. The data presented here represent the first record, to our knowledge, of five leucospid species reared from a single host species. Further, we know of only one species of Leucospidae previously associated with *Centris* bees (Fritz and Genise 1980, De Santis 1983, Chandler *et al.* 1985).

Parasitoid identifications.—Preliminary identifications of the *Leucospis* species were greatly facilitated by the excellent detail provided in the monograph by Bouček (1974). In our attempt to confirm the identifications of these species, however, we uncovered several problems associated with the primary types. The holotypes of *bulbiventris* and *dubiosa* Cresson and lectotype of *azteca* should be in ANSP. They were all examined by Bouček, and the types returned as indicated by correspondence at ANSP. Despite considerable effort by D. Azuma, however, no leucospid primary types could be found, though several others should also be at ANSP.

The key presented here to the leucospids attacking *Centris* bees in dry forests of Costa Rica is adapted largely from this work, as is the terminology. The key has been greatly simplified for ease in identification of leucospids attacking *Centris* in dry forests of Costa Rica, and should only be used in this context (or for comparison with *Centris* parasitoids from dry forests elsewhere). There are several other species of *Leucospis* known from Mesoamerica, and Bouček's work should therefore be consulted for any species not reared from *Centris*, and for rigorous confirmation of suspect individuals.

KEY TO SPECIES OF *LEUCOSPIS* ASSOCIATED WITH *CENTRIS* BEES IN COSTA RICAN DRY FOREST HABITATS

1. Pronotum with a transverse, premarginal cross carina and/or narrow yellow stripe near posterior margin. Mandible with triangular indentation on mesal chewing edge (Fig. 5) .. 2
 – Pronotum without transverse, premarginal cross carina or narrow yellow stripe. Mandible with semicircular indentation on mesal, chewing edge (Fig. 6) ... **L. cayennensis Westwood**

2. Scutellum at least partly yellow 3
 – Scutellum completely without yellow coloration .... **L. bulbiventris Cresson**

3. Hind femur with fewer than 10 small teeth on ventral margin. Hind coxa with a slender tooth (spine) on its dorsal posterior edge (as in Figs. 8, 9) 4
 – Hind femur with more than 10 small teeth on ventral margin. Hind coxa with a thin, partially translucent lobe on dorsal-posterior edge (as in Fig. 7), never with a spine-like tooth .... **L. egaia Walker**

4. Setae on hind coxa converge towards center of depression (Fig. 8). Ovipositorial furrow on first metasomal tergum in the form of a simple, smooth, convex ridge down the midline (Fig. 11). Yellow coloration on scutellum restricted to posterior half, at least anterior half of scutellum black .... **L. latifrons Schletterer**
 – Setae on hind coxa nearly all pointing in the same direction, not converging towards the center (Fig. 9). Ovipositorial furrow on first metasomal tergum with a smooth, shiny, convex ridge down the midline, and concave slopes on either side of the ridge (Fig. 12). Nearly entire scutellum yellow or yellowish, with only anterior edge black ...... **L. azteca Cresson**
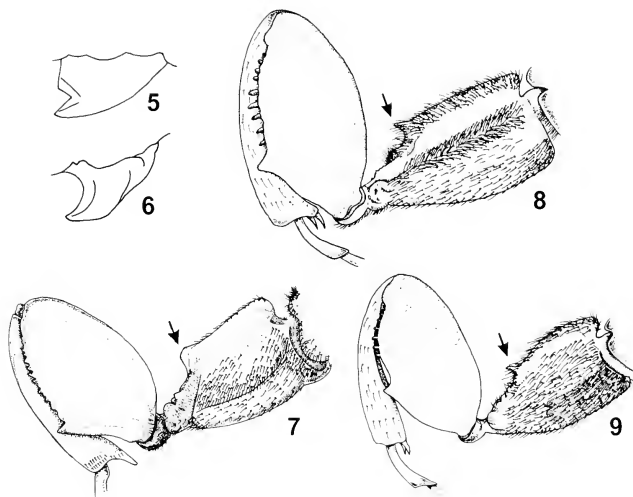
Figs. 5–9. Mandibles and hind legs of *Leucospis* species. 5. Mandible of *L. latifrons*, female. 6. Mandible of *L. cayennensis*, female. 7. Hind leg of *L. bulbiventris*, female. 8. Hind leg of *L. latifrons*, female. 9. Hind leg of *L. azteca*, female.

Leucospis azteca Cresson
(Figs. 9, 12)

Leucospis azteca, previously known only from the three specimens of the original type series, lacks obvious diagnostic features. It can be identified by the following combination of characters: mandible with triangular indentation (Fig. 5); pronotum with premarginal carina (a weak, transverse ridge within a yellow band that runs parallel and slightly anterior to the posterior margin of the pronotum), median lobe of metanotum (= dorsellum) coarsely sculptured, but without distinctly carinate lateral margins; hind tibia apically truncate; hind coxa regularly punctate and setose (as in Fig. 9); and ovipositorial furrow

as in Fig. 12. Bouček (1974) noted that *L. azteca* shared several features in common with both *L. latifrons* and *L. affinis* Say, and that the species had been variously confused in previous studies. *Leucospis latifrons* is readily identified by the pattern of dense pubescence on the hind coxa (compare Figs. 8 and 9), but one of the subspecies of *L. affinis* treated by Bouček, *L. a. dubiosa* Cresson, is particularly problematic as it is very similar to *L. azteca*. The apparent loss of the holotype of *L. dubiosa* and lectotype of *L. azteca* makes it even more difficult to separate *L. affinis* from *L. azteca*. Fortunately, the two other members of the original type series of *L. azteca* were located in ANSP. Structurally, both of
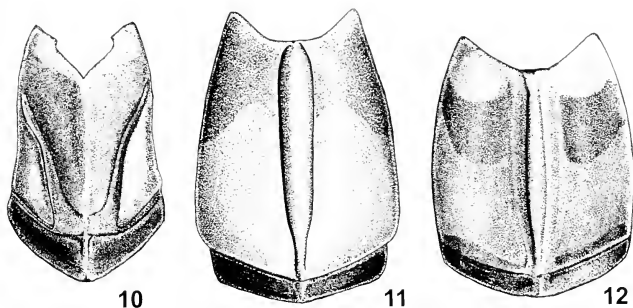
Figs. 10–12. Ovipositorial furrows on the first metasomal terga of *Leucospis* species. 10. *L. bulbiventris*, female. 11. *L. latifrons*, female. 12. *L. azteca*, female.

these agree very closely with our material, but there are some differences in color. This is particularly noticeable on the scutellum. In our material, the yellow coloration covers at least the posterior half of the scutellum, providing a readily observable field characteristic for separating this species from the otherwise similar *L. latifrons*. In both of the *L. azteca* paratypes, however, the scutellum is much less extensively yellow, and similar to our *latifrons* in this regard. Given this variation in color, we concur with Bouček (1974) that the differences in the ovipositorial furrow on the first metasomal tergum are important for distinguishing *L. affinis* from *L. azteca*, and it is on this basis that we have determined our material as *L. azteca*. In *L. azteca*, the furrow is generally not as deep as in *affinis* (a feature that is difficult to assess without side by side comparison), and scattered setae occur on the polished median ridge. In the specimens of *L. affinis* available to us from California and southern Texas, the median, polished ridge lacks setae (though these are abundant along the edge of the furrow). We have found that density of punctation on the

hind leg (a feature used by Bouček 1974) is too variable to be used for separation of *L. affinis*, *L. azteca*, and *L. latifrons* unless side by side comparison is possible with a good series of specimens representing all three species (which we were fortunate to have at our disposal).

The biology of this species was previously unknown. Our data suggest that it is a generalist, capable of attacking several different species. Of the 58 individuals for which we had host data, 41 came from *C. bicornuta*, 1 from *C. nitida*, 3 from *C. vittata*, 4 from *Anthidium*, 5 from *Chalicodoma*, and 4 from other undetermined species of Megachilidae. Unlike *L. latifrons*, *L. azteca* was confined to lower elevations. Of the 53 specimens for which we had altitudinal data, 98%, were reared from nests at 100 m, and only 2% from 300 m (Fig. 3). Of the 63 individuals we reared, only 17% were male, showing a strong female bias (Fig. 13). *Leucospis affinis* has been reared from a wide variety of megachilid bees, and could conceivably be found on the same hosts as *L. azteca* where their ranges overlap (e.g. in Mexico). As these species

are very difficult to separate, caution must be exercised when identifying them.

Leucospis bulbiventris Cresson
(Figs. 7, 10)

Leucospis bulbiventris is readily identifiable by the complete absence of yellow coloration on the scutellum, the shape of the ovipositorial furrow, which is exceptionally broad anteriorly (Fig. 10), the deep, triangular incision of the mandible (much deeper than in Fig. 5), and the shape of the hind coxa, which has a thin, partially translucent lobe on its dorsal posterior edge (Fig. 7). It is a large but slender species with a distinctly petiolate abdomen.

Leucospis bulbiventris was previously known only from the male holotype collected in Mexico. A second nominal species, *L. manaica* Roman, described from Brazil, has heretofore been known only from five females that are similar in many respects to the holotype of *L. bulbiventris* (Bouček 1974). We reared a good series of males and females, in several cases from the same host nest, enabling us to associate the sexes with certainty. Bouček (1974) was the first to suggest that perhaps *L. bulbiventris* and *L. manaica* represent different sexes of the same species. We confirm that the differences in setation and overall shape between *L. manaica* and *L. bulbiventris* noted by Bouček represent sexual dimorphism. Based on our rearings, we therefore strongly suspect that *L. manaica* and *L. bulbiventris* are the same; but because we do not have males from South America, and, more importantly, cannot locate the holotype of *L. bulbiventris*, we must unfortunately leave this problem unresolved. The name *bulbiventris* has priority over *manaica*, and since males from our material fit the description of *L. bulbiventris* provided by Bouček (1974), we have therefore used this name for our species.

No biological information has previously been published for either *L. bulbiventris* or *L. manaica*, nor have either of these been recorded before from Costa Rica. Of the 116 individuals for which we have host data, the majority (108) came from nests of *C. bicornuta*. The others were reared from *C. analis* (1), *C. nitida* (1), and *C. vittata* (6). Of 150 reared individuals for which we have elevation data, 21% were from 100 m, 73% from 300 m, and only 7% from nests at 600 m. None were found at 800 m (Fig. 3). Of 165 individuals reared, only 19% were males, showing a strong female bias (Fig. 13).

Leucospis cayennensis Westwood
(Fig. 6)

This is a widespread Neotropical species recorded from Mexico to Argentina as well as the Caribbean (Fidalgo 1980, De Santis 1983). It is readily identified by the semicircular indentation of the mandible (Fig. 6), the complete lack of a transverse premarginal carina on the pronotum, and the relatively smooth hind coxa (with dorsal two-thirds of the depression smooth, shiny, bare and impunctate).

Fritz and Genise (1980) were the first to record *Centris tarsata* Smith as a host of *L. cayennensis*, and this is the only specific host recorded to date (Chandler *et al.* 1985, De Santis 1983). In Fritz and Genise's (1980) study, *L. cayennensis* was reared from 14% of the *C. tarsata* cells in old, abandoned *Sceliphron asiaticum* (L.) nests. Our data show that *L. cayennensis* attacks at least four other species of *Centris* bees. Of the 30 individuals for which we have host data, 22 came from nests of *C. bicornuta*, 4 from *C. nitida*, 3 from *C. analis*, and 1 from *C. vittata*. *Leucospis cayennensis* was found at all four elevations sampled during this study, but seemed to have a preference for lower elevations. Approximately 61% of the individuals for which we have elevational data were reared from nests at 100 m, 21% from 300 m, 14% from 600 m, and 4% from 800 m (Fig. 3). Of 33 individuals collected, one third were males, showing a female sex bias (Fig. 13).

Sex Ratios for Reared *Leucospis* Species (N)
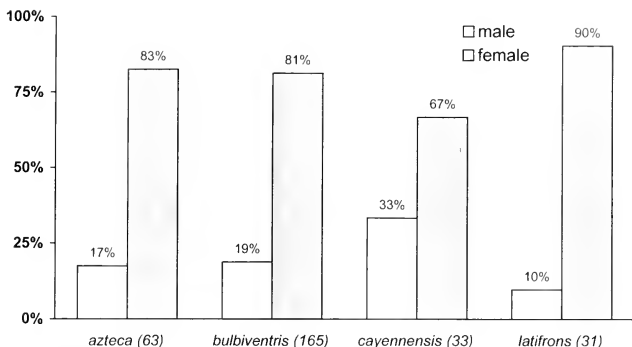
Fig. 13. Sex ratios of *Leucospis* species reared from trap-nesting hosts.

Leucospis egaia Walker

This species is similar in general appearance and coloration to *L. azteca* and *L. latifrons*, but has a carinately margined dorsellum, a more rounded, translucent lobe rather than a spinose tooth on the hind coxa, and an oblique rather than truncate margin to the hind tibia. No host records existed previously for *L. egaia* (Bouček 1974). We reared a male from *C. bicornuta* at 100 m, a male from a megachilid bee at 600 m, and a female from a megachilid bee at 600 m. Since only 3 individuals of this species were found, we cannot make general inferences about its biology.

Leucospis latifrons Schletterer
(Figs. 5, 8, 11)

This is another widespread Neotropical species, occurring from Mexico to Bolivia. It is readily identified by the arrangement of the dense patch of setae in the central depression of the hind coxa (Fig. 8). The color pattern on the scutellum was sufficiently stable in our material to use for separation of *L. azteca* from *L. latifrons* in the field. As noted above, however, these color patterns may vary from one locality to the next, and should be used cautiously for identification purposes. Hosts were previously unknown for *L. latifrons*. Of the 29 individuals for which we have rearing data, 17 came from *C. bicornuta*, 6 from megachilid bees, 4 from *C. nitida*, 1 from *C. vittata*, and 1 from *Chalicodoma*. Of the 32 individuals with altitudinal data, 6% came from nests at 100 m, 52% came from nests at 300 m, 19% from nests at 600 m, and 23% from nests at 800 m (Fig. 3). This species seems to be more of a generalist, able to adapt to a variety of hosts and elevations, with an apparent preference for habitats at 300 m. Although *L. latifrons* and *L. azteca* are extremely similar morphologically, the elevation data suggest a biological difference supporting Bouček's (1974) finding that they are two distinct species. Of 31 individuals reared, only 10% were male, showing a strong female bias, as in all the other species in our samples (Fig. 13).

ACKNOWLEDGMENTS

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The Taxonomy of Recent and Fossil Honey Bees (Hymenoptera: Apidae; *Apis*)

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Abstract.—An attempt is made to clarify the complicated and error fraught taxonomic history of the honey bees (genus *Apis* Linnaeus) by cataloguing the numerous names proposed for *Apis*. The 178 species- and 10 genus-group names (including those proposed herein) are brought for the first time into accord with the modern classification of the honey bees. The results of this synthesis reveal a number of names in current usage to be taxonomically confused. The authorship of the species *Apis koschevnikovi* is established as Enderlein and not Buttel-Reepen. The correct names for four subspecies of the Western honey bee, *A. mellifera*, are established as *A. mellifera remipes* Gerstäcker (not *A. mellifera armeniaca* Skorikov), *A. mellifera siciliana* Grassi (not *A. mellifera sicula* Montagano), *A. mellifera jemenitica* Ruttner (not *A. mellifera yemenitica* Ruttner), and *A. mellifera caucasia* Pollmann (not *A. mellifera caucasica* Gorbachev). The correct authorship of the subspecies *A. mellifera iberica* is established as Ruttner and not Goetze, of *A. mellifera syriaca* as Skorikov and not Buttel-Reepen, and of *A. mellifera intermissa* as Maa and not Buttel-Reepen. Three replacement names are proposed for preoccupied subspecific taxa: *A. mellifera artemisia* Engel (new name for *A. mellifera acervorum* Skorikov, *nec* Linnaeus), *A. mellifera iberiensis* Engel (new name for the aforementioned *A. mellifera iberica* Ruttner, *nec* Skorikov), and *A. mellifera sossimai* Engel (new name for *A. cerifera* Gerstäcker, *nec* Scopoli). The previously confused Himalayan honey bee (infrequently associated with *A. cerana skorikovi* Maa, *nomen nudum* or *A. cerana* "Himalaya race") is proposed and validated as *A. cerana skorikovi* Engel (new subspecies). Similarly the large black race of China (Aba race) is proposed as *A. cerana heimifeng* Engel (new subspecies). A lectotype and 11 paralectotypes are designated for *A. mellifera ruttneri* (by Sheppard *et al.*), a lectotype is designated for *A. koschevnikovi*, and a neotype is designated for *A. mellifera iberica* Ruttner. *Apis cuenoti* Théobald is **newly synonymized** under *A. henshawi* Cockerell, *A. mellifera rodopica* Petrov is **synonymized** with *A. mellifera macedonica* Ruttner, while *Hauffapis scheeri* Armbruster, *H. scharmanni* Armbruster, *H. scheeri gallauni* Armbruster, *H. scheeri rahdei* Armbruster, *H. scheuthlei seemanni* Armbruster, and *H. scheuthlei zeuneri* Armbruster are all synonymized under *A. armbrusteri* Zeuner (**new synonymies**). The name *A. vetustus* Engel for a fossil from the Oligocene of Europe is emended to *A. vetusta* Engel. All genus-group taxa are characterized on the basis of adult and larval morphology and ethology. Two new subgenera are proposed to accommodate fossil honey bee species: *Cascapis* **Engel** new subgenus (type: *A. armbrusteri* Zeuner) and *Priorapis* **Engel** new subgenus (type: *A. vetusta* Engel).

The honey bees (genus *Apis* Linnaeus) are the most famous of all insects owing to their import for the pollination of crops, their social organization, and the honey they produce. There has been a long association between *Apis* and man as is attested by the Paleolithic Araña Cave paintings near Valencia, Spain which depict early humans collecting honey combs. Similarly, the honey bees figure prominently in human cultures, mythologies, and religions (e.g., see Ransome 1937). Numerous world revisions have been attempted for the genus (Gerstäcker 1862, 1863, Smith 1865, Ashmead 1904, Buttel-Reepen 1906, Enderlein 1906, Skorikov

Table 1. Classificatory structure of major honey bee revisions since Gerstäcker (1862); living species only. Subspecies and varieties omitted so as to save space. Species are in alphabetical order and do not necessarily correspond in rows from one column to the next. I have replaced uses of *mellifica* by some of these authors with *mellifera*. Although Maa (1953) observes that Skorikov (1929b) recognized 14 species, the later author left one unnamed (the "Egyptian bee") and I have therefore listed only 13 here. G = genus, sg = subgenus.

Gerstäcker 1862	Smith 1865	Ashmead 1904	Buttel-Reepen 1906	Enderlein 1906	Skorikov 1929b	Maa 1953	Present author 1999
G. *Apis*	G. *Apis*	G. *Apis*	G. *Apis*	G. *Apis*	sg. *Apis*	sg. *Apis*	G. *Apis*
dorsata	*adansonii*	*cerana*	*dorsata*	*dorsata*	*adansonii*	*adansonii*	*cerana*
florea	*dorsata*	*indica*	*florea*	*florea*	*cerana*	*intermissa*	*koschevnikovi*
indica	*florea*	*mellifera*	*mellifera*	*indica*	*cypria*	*lamarckii*	*mellifera*
mellifera	*indica*	*nigritarum*		*mellifera*	*indica*	*meda*	*nigrocincta*
	mellifera	*nigrocincta*			*japonica*	*mellifera*	sg. *Megapis*
	nigrocincta	*unicolor*			*johni*	*remipes*	*dorsata*
	sinensis	G. *Megapis*			*meda*	*unicolor*	sg. *Micrapis*
	zonata	*dorsata*			*mellifera*	sg. *Sigmatapis*	*andreniformis*
		zonata			*remipes*	*cerana*	*florea*
		G. *Micrapis*			*syriaca*	*indica*	
		florea			*unicolor*	*javana*	
					sg. *Megapis*	*johni*	
	1871				*dorsata*	*koschevnikovi*	
	added:				sg. *Micrapis*	*lieftincki*	
	laboriosa				*florea*	*nigrocincta*	
						peroni	
						philippina	
						samarensis	
						vechti	
						G. *Megapis*	
						binghami	
						breviligula	
						dorsata	
						laboriosa	
						G. *Micrapis*	
						andreniformis	
						florea	

1929b, Maa 1953) as well as an unpublished faunal revision from Thailand (Malaipan 1972). Since the first detailed study by Gerstäcker (1862), anywhere from 3 to 24 species have been recognized while the four subgenera have at times been treated as distinct genera (Table 1). Despite the consistent and concentrated effort on *Apis* taxonomy for well over a century, a clear picture of the species and the numerous names associated with each has yet to be achieved. It is hoped that this paper (although mostly an exercise in "bookkeeping") will make a small step towards achieving these goals.

The primary objective of this paper has been to pull together the extensive literature pertaining to the taxonomy of honey bees and to associate the long lists of junior synonyms with their valid counterparts. The last catalogue of *Apis* names was undertaken by Maa (1953); however, his list of names contains a number of errors and his rather extreme classification is not easily reconcilable with current usage. Moreover, Maa did not treat the numerous fossil honey bees and at least 60 names have either been discovered or were proposed since his study (approximately one-third of the total number of names). Below I have compiled a listing of all names applied to honey bees, both liv-

ing and extinct. This compilation contains 178 species- and 10 genus-group names. Although Maa (op. cit.) and Ruttner (1988) noted that over 600 species-group names have been proposed for *Apis*, this does not mean that 600 names have been proposed for honey bees. Many of these names were proposed under a Linnean concept of the genus which included *all* bees. Thus, most of the 600+ names pertain to species now placed in other genera and families (e.g., *Anthophora*, *Bombus*, *Megachile*, *Trigona*, &c.). Interestingly most of the names applicable to honey bees have been proposed during this century. A breakdown of the list reveals eight names appearing between 1758 and 1799, 17 from 1800 through 1849, 26 between 1850 and 1899, 66 in the period 1900 to 1949, and 61 names between the years 1950 and 1999. Of these names 146 are applicable to the living species (90 associated with *Apis mellifera* alone!), 25 for the fossil species, and seven names are of dubious taxonomic status.

Included with this catalogue I have provided descriptions of all genus-group taxa now included in *Apis*, thereby adding to this work a subgeneric revision of the genus. Table 2 summarizes the hierarchical classification of *Apis* as it is proposed herein.

Phylogenetic studies on the genus have recently been undertaken by Alexander (1991a,b), Engel (1998a), and Engel and Schultz (1997: see also works cited therein). The current hypothesis of relationships among the subgenera and species is depicted in Figure 1 (modified from Engel 1998a). General works on honey bee anatomy, biology, behavioral ecology, and diversity have been presented by Snodgrass (1956), Winston (1987), Seeley (1985, 1995), and Smith (1991a) respectively. The distribution of the various species and subspecies has been thoroughly treated by Ruttner (1988, 1992), Otis (1996), and Hepburn and Radloff (1998). The position of the Apini among the other tribes of corbiculate

Table 2. Current hierarchical classification of the honey bees; tribe Apini Latreille (excluding infraspecific taxa). Daggers (†) indicate extinct taxa.

Genus *APIS* Linnaeus
subgenus *Apis* Linnaeus
cerana Fabricius
koschevnikovi Enderlein
mellifera Linnaeus
nigrocincta Smith
† subgenus *Cascapis* Engel
† *armbrusteri* Zeuner
subgenus *Megapis* Ashmead
dorsata Fabricius
subgenus *Micrapis* Ashmead
andreniformis Smith
florea Fabricius
† subgenus *Priorapis* Engel
† *vetusta* Engel
† subgenus *Synapis* Cockerell
† *henshawi* Cockerell
† *longtibia* Zhang
† *miocenica* Hong
† *petrefacta* (Říha)

bees has been considered most recently by Chavarría and Carpenter (1994), Engel (1998b, unpubl. data), Noll (1998, in prep.), and Schultz et al. (1999).

FORMAT

Standard formats for taxonomic histories are used. Comments provided for each taxon give information on the assignment of authorship to certain names, subspecific classifications, studies of the recognition of difficult taxa, and occasionally historical information on the biogeography or biology of the species. Several honey bee names were used in publications as *nomina nuda* and in those cases where no description was later provided they are indicated as such. However, whenever a name was later made available by an associated description I have only listed the publication making the name available under the rules of the I.C.Z.N. (1985) and not the original paper in which it appeared as a *nomen nudum*.

For those species in which subspecies are currently recognized (*A. cerana*, *A. dor-*

Fig. 1.   Phylogeny of the honey bees (genus *Apis* Linnaeus) with subgenera indicated (modified from Engel 1998a).

sata, and *A. mellifera*) I have associated each junior synonym with its corresponding subspecies. Names in brackets at the end of each entry indicate which subspecies the name corresponds to. In some cases (e.g., *nomina nuda*) this decision cannot always be made with certainty and so are accordingly noted with an interrogative mark.

Descriptions are provided for genus-group taxa and are based on information from all adult castes, the mature larva (of workers), and ethological information. Too little information exists at this time on *Apis* pupae to know whether additional character data can be gleaned from this life-stage. Characters given for workers also apply to drones and queens (except when indicated), although characters given for drones and queens do not necessarily occur in the worker caste. The abbreviations T1, T2, ..., T8 are used for the

corresponding metasomal terga (S for sternum).

Since the literature on honey bees is vast, some names may have been inadvertently overlooked. Researchers discovering names (*nomina nuda, nova, &c.*) omitted here or of earlier usage than the dates cited are urged to contact me and, if possible, to send a copy of the relevant paper(s). All in all, however, this list should prove a reasonable starting point for future research.

RECENT HONEY BEES

Genus *Apis* Linnaeus

Diagnosis.—Modified and updated from Michener (1990: as Apinae). WORKER: Labral apex gently and often weakly concave; labrum three to four times broader than long (median width). Malar space as long as, or longer than basal width of mandible. Mandible without dentition
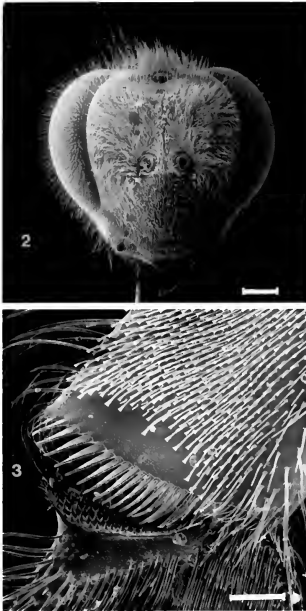
Figs. 2–3. Honey bee structural characteristics represented by *Apis* (*Apis*) *cerana* Fabricius. 2, Worker head (scale bar = 500 μm). 3, Inner surface of meta-tibia-metabasitarsus junction showing pollen press (auricle), rastellum, and absence of tibial spurs (scale bar = 200 μm).

(Fig. 2) (not so for queens or males). Hairs of compound eye long and erect (Fig. 2). Vertex extremely short, much less than ocellar diameter. Scutellum strongly convex and bulging, obscuring metanotum and basal area of propodeum. Basal area of propodeum extremely short and declivious. Mesocoxae nearly meeting medially. Strigilis with prong on anterior margin. Corbicula, rastellum, and auricle present (workers only). Metatibial spurs absent (Fig. 3); metatibia without penicillum; inner surface of metabasitarsus with setal comb rows (worker only: referred to as *brush combs* in Michener 1990). Claws cleft; arolia present. Distal wing venation strong and complete; 1r-m and 2r-m strongly angled respective to M (Fig. 3). Marginal cell long (Fig. 3) and bluntly rounded at apex, not gently tapering over its length. Jugal lobe present. Sting straight (worker only). DRONE: Mandible usually bidentate, frequently only weakly. Holoptic (compound eyes meeting at top of head). S8 reduced to transverse bar, without spiculum. Spatha and volsella absent. QUEEN: Mandible bidentate. Inner surface of metabasitarsus unmodified. Sting curved. MATURE LARVA: Without small dorsal tubercles on segments 1–4. Mandible weakly sclerotized, bluntly pointed, without concavity on inner surface. ETHOLOGY: Nest a vertical comb of cells made of wax. Dance language communication system present. Highly eusocial (with morphologically distinct castes). New colonies founded by fission and include the old queen. Brood and storage cells similar. Immatures progressively provisioned.

Biogeography.—Honey bees are predominantly a tropical group and arose in the Indo-Malayan region during the early Oligocene (Engel 1998a). The genus is native to Europe, Africa, Madagascar, Arabia, the Near East, as well as Central and Southern Asia inclusive of most Southeast Asian Islands. Honey bees are not native to the Australian or American continents having been moved to these regions by humans. Species radiated from southern Asia perhaps being limited only by temperature extremes. The clade of living species (subgenera *Apis*, *Megapis*, and *Micrapis*: Fig. 1) arose sometime in the latter half of the Miocene (Engel 1998a). The development of cavity-nesting behavior in the earliest Pliocene (perhaps in the latest Miocene) enabled at least two of the species, *A. cerana* and *A. mellifera*, to extend their ranges

into more temperate areas. In the case of *A. mellifera* this was into Europe and northwestern Asia while for *A. cerana* this was into northeastern China, and the eastern regions of the former Soviet Union. The fossil species were presumably open-nesting (refer to Engel 1998a for a cladistic reconstruction of this behavior) and the slightly warmer temperatures in the Miocene would have partly allowed species such as *A. armbusteri* to exist in Europe even in the absence of well developed thermoregulatory capabilities. As the temperatures continued to cool (e.g., by the Pliocene) open-nesting species would have been forced from these areas and the cavity-nesting species would be free to colonize.

Subgenus *Apis* Linnaeus

Apis Linnaeus 1758: 343, 574. Type species: *Apis mellifica* Linnaeus 1761 (= *Apis mellifera* Linnaeus 1758), designation of Latreille (1810). Michener 1944: 292. Maa 1953: 557. Michener 1990: 140.

Apicula Rafinesque 1814: 29. Unjustified replacement name for *Apis* Linnaeus 1758.

Apiarus Rafinesque 1815: 123. Unjustified replacement name for *Apis* Linnaeus 1758.

Apis (*Sigmatapis*) Maa 1953: 556. Type species: *Apis cerana* Fabricius 1793, original designation.

Diagnosis.—WORKER: Forewing length 7–10 mm. Basal vein frequently gently curved, strongly distad cu-a (Fig. 4). Angle of posteroapical margin of first submarginal cell less than 45°. Distal abscissa of vein M in hind wing variable (present [Fig. 5] or absent). DRONE: Hind basitarsus without thumb-like process. Vertical arm of T8 longer than horizontal arm; S7 and S8 fused mesally. Gonobase absent. Ventral gonocoxa membranous; dorsal gonocoxa reduced. Ventral cornua of endophallus recurved ventrally. MATURE LARVA: Labrum with peg-like setae restricted to apical surfaces and tubercles. Galea smaller than maxillary palpus. Labial palpus not spiculate. Epipharynx with

or without setae. Atrial inner walls smooth. ETHOLOGY: Nest constructed in a cavity. Dance language performed on vertical surface; wagging metasoma positioned parallel to dance surface; recruits positioned next to dancer's metasoma (within a near field sound range). Drone cell cap variable (present or absent).

Apis (*Apis*) *cerana* Fabricius

The Eastern *or* Asian Honey Bee

Apis cerana Fabricius 1793: 327. [*cerana* Fabricius]

Apis indica Fabricius 1798: 274. [*indica* Fabricius]

Apis socialis Latreille 1804a: 390. [*indica* Fabricius]

Apis peroni Latreille 1804b: 173. [? *indica* Fabricius: see treatment of *javana* subspecies]

Apis gronovii Guillou 1841: 323. [? *indica* Fabricius: see treatment of *javana* subspecies]

Apis perrottetii Guérin-Méneville 1844: 461. [*indica* Fabricius]

Apis delessertii Guérin-Méneville 1844: 461. [*indica* Fabricius]

Apis sinensis Smith 1865: 380. [*cerana* Fabricius]

Apis mellifica variety *japonica* Radoszkowski 1887: 436. [*japonica* Radoszkowski]

Apis delesserti Buttel-Reepen 1906: 168. Unjustified emendation. [*indica* Fabricius]

Apis indica variety *javana* Enderlein 1906: 337. [*javana* Enderlein]

Apis indrea Baldensperger 1928: 173. *Lapsus calami*. [*indica* Fabricius]

Apis johni Skorikov 1929b: 251. [*johni* Skorikov]

Apis indica philippina Skorikov 1929b: 252. [*indica* Fabricius]

Apis indica skorikovi Maa 1944: 4. *Nomen nudum*. [*skorikovi* Engel]

Apis mellifera gandhiana Muttoo 1951: 153. *Nomen nudum*. [*indica* Fabricius]

Apis (*Sigmatapis*) *lieftincki* Maa 1953: 572. [*johni* Skorikov]

Apis (*Sigmatapis*) *samarensis* Maa 1953: 580. [*indica* Fabricius]

Apis indica sinensis ussuriensis Goetze 1964: 26. *Nomen nudum*. Refer to comments under *A. mellifera*. [*cerana* Fabricius]

Apis cerana himalaya Smith 1991b: 154. *Nomen nudum* (see below). [*skorikovi* Engel]

Apis cerena Willis, Winston, and Honda 1992: 169. *Lapsus calami*. [*cerana* Fabricius]
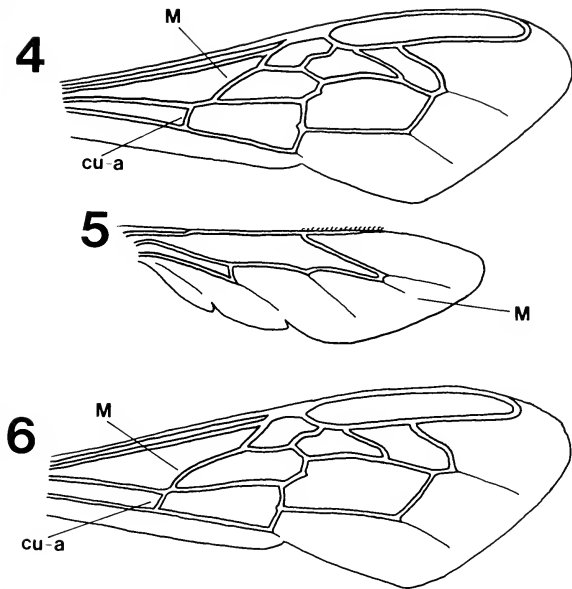
Figs. 4–6. Honey bee wing venation. 4, *Apis (Apis) cerana* Fabricius, worker, forewing. 5, *A. (A.) cerana*, worker, hind wing. 6, *A. (Synapis) henshawi* Cockerell, worker, forewing reconstruction. In the forewing M indicates an abscissa of vein M that is called the basal vein, while in the hind wing a distal abscissa is indicated which is referred to as the indica vein by some authors; cu-a is the cubital-anal crossvein, also called cu-v by some authors.

Apis nuluensis Tingek, Koeniger, and Koeniger 1996 [1997]: 116. [*nuluensis* Tingek et al.]

Apis cerana heimifeng Engel 1999: see below. [*heimifeng* Engel]

Apis cerana skorikovi Engel 1999: see below. [*skorikovi* Engel]

Comments.—The name *gandhiana* Muttoo (1951) was also used by Muttoo (1956) for an invalid variety of *A. cerana*. The name *nuluensis* was synonymized by myself in Schultz et al. (1999) and therefore appears here for the first time as a sub-specific entity of *A. cerana* (see treatment of subspecies below).

Distribution.—Refer to treatment of individual subspecies below.

Apis (Apis) koschevnikovi Enderlein, corrected authorship

The Sundaland Honey Bee

Apis mellifica indica variety *koschevnikovi* Buttel-Reepen 1906: 192. Unavailable (I.C.Z.N. 1985: Arts. 10c, 23j, and 50c).

Apis indica variety *koschevnikovi* Enderlein 1906: 335. First available usage.

Apis (Sigmatapis) vechti Maa 1953: 572.

Apis (Sigmatapis) vechti linda Maa 1953: 574.

Apis mellifica adansonii koschevnikovi Goetze 1964: 25. Unjustified emendation.

Comments.—The authorship of this name has almost universally been given to Buttel-Reepen who first proposed it in 1906. However, Buttel-Reepen used the name infrasubspecifically and thus according to the I.C.Z.N. (1985: Art. 10c) does not become available until it is first used as a species or subspecies, and then the authorship is assigned to the author who used the name in such a sense (Arts. 23j and 50c). Enderlein (1906) was the first to use the name *koschevnikovi* subspecifically and he must therefore be considered as the author.

This species was only recently reinstated although under the junior synonym *A. vechti* (Koeniger *et al.* 1988, Tingek *et al.* 1988). Ruttner *et al.* (1989) recognized that the correct name for this species was *A. koschevnikovi*. There are presently no subspecific forms recognized.

Distribution.—*Apis koschevnikovi* occurs on the Malay Peninsula, Borneo, Brunei, Java, Sabah, Sarawak, and Sumatra.

Lectotype.—Worker; BORNEO: Kinabalugebirge, John Worterstradt, L. [leg.]; now with an additional label reading, "Lectotype, *Apis koschevnikovi* Enderlein, desig. M. S. Engel" (deposited in the Museum für Naturkunde, Berlin). The original series of *A. koschevnikovi* used by Buttel-Reepen is located in the Museum für Naturkunde, Berlin. The type series consists of one worker from northern Borneo and eight labeled as from Cameroon. No *cerana*-like bees are natively known from the African continent, yet the specimens from "Cameroon" are clearly conspecific with the one from Borneo, and all correspond to the species widely recognized as *A. koschevnikovi* today. The specimens from Camaroon are very likely mislabeled; something even Buttel-Reepen

(1906) suspected. Although Maa (1953) chose Cameroon as the type locality, this cannot be considered a type fixation since there are eight specimens from this locality and none are labeled as the type (in fact, Maa admits having never seen any specimens of *A. koschevnikovi*). I therefore have selected the single specimen from Borneo to serve as the lectotype.

Apis (Apis) mellifera Linnaeus

The Western Honey Bee

Apis mellifera Linnaeus 1758: 576. [*mellifera* Linnaeus]

Apis mellifica Linnaeus 1761: 421. Unjustified emendation. [*mellifera* Linnaeus]

Apis gregaria Geoffroy 1762: 407. [*mellifera* Linnaeus]

Apis cerifera Scopoli 1770: 16. [*mellifera* Linnaeus]

Apis unicolor Latreille 1804b: 168. [*unicolor* Latreille]

Apis fasciata Latreille 1804b: 171. Preoccupied (*nec* Linnaeus 1767, Scopoli 1770). [*lamarckii* Cockerell]

Apis adansonii Latreille 1804b: 172. [*adansonii* Latreille]

Apis ligustica Spinola 1806: 35. [*ligustica* Spinola]

Apis capensis Eschscholtz 1822: 97. [*capensis* Eschscholtz]

Apis caffra Lepeletier de Saint Fargeau 1836: 402. Preoccupied (*nec* Linnaeus 1767). [*scutellata* Lepeletier de Saint Fargeau]

Apis scutellata Lepeletier de Saint Fargeau 1836: 404. [*scutellata* Lepeletier de Saint Fargeau]

Apis nigritarum Lepeletier de Saint Fargeau 1836: 406. [*adansonii* Latreille]

Apis daurica Fischer von Waldheim 1843: 1. [*mellifera* Linnaeus]

Apis mellifica variety *cecropia* Kiesenwetter 1860: 315. [*cecropia* Kiesenwetter]

Apis australis Kiesenwetter 1860: 317. Unjustified replacement name for *Apis ligustica* Spinola 1806. [*ligustica* Spinola]

Apis cecropia Gerstäcker 1862: 60. Preoccupied (*nec* Scopoli 1770). [*sossimai* Engel]

Apis mellifica variety *remipes* Gerstäcker 1862: 61. [*remipes* Gerstäcker]

Apis liguria Smith 1861b: 14. *Nomen nudum.* [? *ligustica* Spinola]

Apis mellifica germanica Pollmann 1879: 1. [*mellifera* Linnaeus]

Apis mellifica carnica Pollmann 1879: 45. [*carnica* Pollmann]

Apis mellifica hymettea Pollmann 1879: 50. Unjustified replacement name for *Apis mellifica carnica* Pollmann 1879. [*carnica* Pollmann]

Apis mellifica cypria Pollmann 1879: 52. [*cypria* Pollmann]

Apis siciliana Grassi 1881: 1. [*siciliana* Grassi]

Apis mellifica variety *nigrita* Lucas 1882: 62. [*mellifera* Linnaeus]

Apis mellifida Pollmann 1889: 90. *Lapsus calami.* [*mellifera* Linnaeus]

Apis mellifida [sic] variety *caucasia* Pollmann 1889: 90. [*caucasia* Pollmann]

Apis ligurica Dalla Torre 1896: 602. *Nomen nudum* (*nec* Tegetmeier 1859, 1860: see below). Corrected authorship. [*ligustica* Spinola]

Apis mellifera carniolica Koschevnikov 1900: 1. Unjustified emendation. [*carnica* Pollmann]

Apis mellifica cypriaca Koschevnikov 1900: 1. Unjustified emendation. [*cypria* Pollmann]

Apis mellifica mellifica variety *siziliana* Buttel-Reepen 1906: 168. Unjustified emendation. [*siciliana* Grassi]

Apis mellifica unicolor variety *syriaca* Buttel-Reepen 1906: 175. Unavailable (I.C.Z.N. 1985: Arts. 10c, 23j, 50c). [*syriaca* Skorikov]

Apis mellifica mellifica variety *lehzeni* Buttel-Reepen 1906: 184. Unavailable (I.C.Z.N. 1985: Arts. 10c, 23j, 50c). [*mellifera* Linnaeus]

Apis mellifica unicolor variety *intermissa* Buttel-Reepen 1906: 187. Unavailable (I.C.Z.N. 1985: Arts. 10c, 23j, 50c). [*intermissa* Maa]

Apis mellifica unicolor variety *friesci* Buttel-Reepen 1906: 188. Unavailable (I.C.Z.N. 1985: Arts. 10c, 23j, 50c). [*adansonii* Latreille]

Apis mellifera lamarckii Cockerell 1906: 166. Replacement name for *Apis fasciata* Latreille 1804b. [*lamarckii* Cockerell]

Apis mellefica Enderlein 1906: 331. *Lapsus calami.* [*mellifera* Linnaeus]

Apis mellifica unicolor variety *frisei* Enderlein 1906: 335. *Lapsus calami.* [*adansonii* Latreille]

Apis mellifera sicula Montagano 1911: 26. [*siciliana* Grassi]

Apis adamsoni Meunier 1915: 210. *Lapsus calami.* [*adansonii* Latreille]

Apis fuscata Meunier 1915: 210. *Lapsus calami.* [*lamarckii* Cockerell]

Apis mellifica kaffra Jack 1916: 397. *Lapsus calami.* [*scutellata* Lepeletier de Saint Fargeau]

Apis mellifera caucasica Gorbachev 1916: 39. Unjustified emendation. [*caucasia* Pollmann]

Apis mellifica variety *banatica* Grozdanic 1926: 57. [*carnica* Pollmann]

Apis fascrata Baldensperger 1928: 173. *Lapsus calami.* [*lamarckii* Cockerell]

Apis eurasiatica Skorikov 1929a: 14. Unjustified replacement name for *Apis mellifica* variety *remipes* Gerstäcker 1862. [*remipes* Gerstäcker]

Apis mellifera mellifera natio *tesquorum* Skorikov 1929a: 29. Unavailable (I.C.Z.N. 1985: Arts. 10c, 23j, 50c). [*artemisia* Engel]

Apis mellifera remipes natio *absuatna* Skorikov 1929a: 32. Unavailable (I.C.Z.N. 1985: Arts. 10c, 23j, 50c). [*remipes* Gerstäcker]

Apis mellifera remipes natio *siganica* Skorikov 1929a: 32. Unavailable (I.C.Z.N. 1985: Arts. 10c, 23j, 50c). [*remipes* Gerstäcker]

Apis mellifera remipes natio *georgica* Skorikov 1929a: 32. Proposed as new again in Skorikov (1929b). Unavailable (I.C.Z.N. 1985: Arts. 10c, 23j, 50c). [*remipes* Gerstäcker]

Apis meda Skorikov 1929b: 253. [*meda* Skorikov]

Apis mellifera natio *acervorum* Skorikov 1929b: 253. Preoccupied (*nec* Linnaeus 1758). [*artemisia* Engel]

Apis remipes transcaucasica Skorikov 1929b: 254. [*remipes* Gerstäcker]

Apis remipes transcaucasica natio *absuana* Skorikov 1929b: 254. *Lapsus calami.* [*remipes* Gerstäcker]

Apis remipes transcaucasica natio *iberica* Skorikov 1929b: 254. Unavailable (I.C.Z.N. 1985: Arts. 10c, 23j, 50c). [*remipes* Gerstäcker]

Apis remipes armeniaca Skorikov 1929b: 254. [*remipes* Gerstäcker]

Apis mellifera banata Skorikov 1929b: 263. Unjustified emendation. [*carnica* Pollmann]

Apis (Apis) syriaca Skorikov 1929b: pl. 1. First available usage. [*syriaca* Skorikov]

Apis mellifica variety *sahariensis* Baldensperger 1932: 829. [*sahariensis* Baldensperger]

Apis niger Baldensperger 1932: 830. *Nomen nudum.* [? *mellifera* Linnaeus]

Apis mellifera mingrelica Lavrezhin 1935: 656. *Nomen nudum.* [*remipes* Gerstäcker]

Apis mellifera taurica Alpatov 1935: 665. Proposed as new again in Alpatov (1938). [*taurica* Alpatov]

Apis (Apis) intermixsa Maa 1953: 591. First available usage [*intermissa* Maa].

Apis (Apis) mellifera anatoliaca Maa 1953: 599. [*anatoliaca* Maa]

Apis mellifera siriaca Kerr and Amaral 1960: 12. *Lapsus calami*. [*syriaca* Skorikov]

Apis mellifera monticola Smith 1961a: 258. Proposed as new again in Smith (1961b). [*monticola* Smith]

Apis mellifera litorea Smith 1961a: 259. Proposed as new again in Smith (1961b). [*litorea* Smith]

Apis mellifera lamarchii Smith 1961b: 148. *Lapsus calami*. [*lamarckii* Cockerell]

Apis millifica Goetze 1964: 9. *Lapsus calami*. [*mellifera* Linnaeus]

Apis mellifica intermissa tellica Goetze 1964: 25. *Nomen nudum*. See also below. [*intermissa* Maa]

Apis mellifica mellifica silvarum Goetze 1964: 26. *Nomen nudum*. See also below. [*mellifica* Linnaeus]

Apis mellifica lamarcki Ruttner 1968: 41. Unjustified emendation. [*lamarckii* Cockerell]

Apis mellifera adami Ruttner 1975: 271. Proposed as new again in Ruttner (1980) with the species called *mellifera*. [*adami* Ruttner]

Apis mellifera major Ruttner 1976a: 354. [*intermissa* Maa]

Apis mellifera nubica Ruttner 1976a: 359. [*jemenitica* Ruttner]

Apis mellifera littorea Ruttner 1976a: 361. *Lapsus calami*. [*litorea* Smith]

Apis mellifera jemenitica Ruttner 1976a: 366. [*jemenitica* Ruttner]

Apis mellifera carpatica Barac 1977: 270. [*carnica* Pollmann]

Apis mellifera anatolia Winston 1987: 12. *Lapsus calami*. [*anatoliaca* Maa]

Apis mellifera yemenitica Ruttner 1988: 212. Unjustified emendation. [*jemenitica* Ruttner]

Apis mellifera sudanensis Ruttner 1988: 214. *Nomen nudum* (see below). [*jemenitica* Ruttner]

Apis mellifera iberica Ruttner 1988: 236. Preoccupied (*nec* Skorikov 1929b, Goetze 1964: see treatment of *A. mellifera* subspecies below; corrected authorship. [*iberiensis* Engel]

Apis mellifera macedonica Ruttner 1988: 249. [*macedonica* Ruttner]

Apis mellifera logustica Kugler 1988: 268. *Lapsus calami*. [*ligustica* Spinola]

Apis mellifica rodopica Petrov 1991: 17. Proposed as new again in Petrov (1996). [*macedonica* Ruttner]

Apis millifica Willis, Winston, and Honda 1992: 169. *Lapsus calami*. [*mellifera* Linnaeus]

Apis mellifera Petrov 1993: 36. *Lapsus calami*. [*mellifera* Linnaeus]

Apis mellifica capratica Petrov 1996: 58. *Lapsus calami*. [*carnica* Pollmann]

Apis mellifera bandasii Radloff and Hepburn 1997: 57. *Nomen nudum* (see below). [*jemenitica* Ruttner]

Apis mellifera ruttneri Sheppard, Arias, Grech, and Meixner 1997 [1998]: 290. [*ruttneri* Sheppard *et al.*]

Apis mellifera artemisia Engel 1999: see below. Replacement name for *Apis mellifera acervorum* Skorikov 1929b (*nec* Linnaeus 1758). [*artemisia* Engel]

Apis mellifera iberiensis Engel 1999: see below. Replacement name for *Apis mellifera iberica* Ruttner 1988 (*nec* Skorikov 1929b). [*iberiensis* Engel]

Apis mellifera sossimai Engel 1999: see below. Replacement name for *Apis cerifera* Gerstäcker 1862 (*nec* Scopoli 1770). [*sossimai* Engel]

Comments.—The term "natio" as used by Skorikov (1929a, b) appears to be synonymous with "variety" as used by other authors.

Both Maa (1953) and Goetze (1964) include the name *A. domestica* Ray (1710) in their taxonomic treatment of the western honey bee. This is a pre-Linnean name and it is therefore excluded from zoölogical nomenclature (I.C.Z.N. 1985: Art. 3) and my treatment above.

It might be interpreted from my treatment of Pollmann's names above that *A. mellifida* as used by this author was not a *lapsus calami* but in actuality an unjustified emendation due to the fact that it appears to have been used twice (under *mellifida* and *mellifida caucasia*). This is not the case. The name *mellifida* was only used once in Pollmann's (1889) work in the proposal of the variety *caucasia*. It appears twice in my list since two taxonomic entities are involved in this one action by Pollmann; one as the *lapsus calami mellifida* and the second for the proposal of the variety (now subspecies) *caucasia*.

Maa (1953) and Dalla Torre (1896) both cite the name *A. ligurica* with one author attributing it to Tegetmeier (1859) and the other to that paper as well as to Tegetmeier (1860). Interestingly enough neither

of Tegetmeier's contributions use this name. Tegetmeier's 1859 paper, the purported first usage of the epithet, is merely an untitled note about an exhibition of *Apis* specimens at a meeting of the Entomological Society of London and simply reads, "Mr. Tegetmeier exhibited specimens of *Apis ligustica*, of which he had lately received living examples of the queen and workers from the Continent, where it is considered a more profitable species to the owner than the common honey bee; he hoped, during the next season, to test the correctness of this opinion." Tegetmeier (1860), a similarly untitled note from a societal meeting, is merely a follow up to his 1859 notice and uses the name *A. ligustica* as well (not *A. ligurica*). A perusal of other issues of the *Proceedings of the Entomological Society of London* failed to find any usage of *A. ligurica*, and it would therefore appear that the first appearance of such a name was in Dalla Torre's catalog (1896).

The name *mingrelica* was used by Lavrezhin (1935) and attributed to Skorikov (1929a); however, Skorikov did not propose such a specific epithet. Skorikov (1929a: 32, 41, 44) used the name

мингрельская

only in Russian and as part of a vernacular name (it even has a Russian adjectival ending which changes in the text as the case of the noun it modifies changes), never once proposing it as a latinized taxonomic entity with a description. The same can be said for several of the *nomina nuda* listed by Goetze (1964); these being *silvarum* attributed to Alpatov (1935), *tellica* attributed to Buttel-Reepen (1906), and *ussuriensis* attributed to Lawrjochin (1960). These names, as used by Goetze (op. cit.), are also excluded from nomenclature owing to the fact that they are infrasubspecific names proposed after 1960 (I.C.Z.N. 1985: Art. 1b and 45e–g).

Radloff and Hepburn (1997) employ the subspecific names *bandasii* (attributed to

Mogga) and *sudanensis* (attributed to Rashad) both of which are *nomina nuda*. I failed to find in publications of Rashad available to me any official proposal of a subspecies with the latinized name *sudanensis* that would satisfy the rules of nomenclature, although many of his papers mention the Sudanese bees as variable and distinctive (e.g., Rashad and El-Sarrag 1978). Ruttner (1988) also employs the name *sudanensis* (attributing it to an unpublished manuscript by Rashad) and thus it is a *nomen nudum* with Ruttner apparently being the correct author. The name *bandasii*, however, was proposed by Mogga (1988) and would meet the appropriate criteria except that this name was only treated in his unpublished Master's thesis, is therefore excluded from zoölogical nomenclature [I.C.Z.N., 1985: Art. 9(11)], and means that its use by Radloff and Hepburn (op. cit.) is a *nomen nudum*. Both of these names were once again used by Hepburn and Radloff (1998) although they were only mentioned as synonyms of *jemenitica* in their consideration of African races, a synonymy considered amply justified by both Ruttner (1988) and myself (above).

This seems an appropriate venue to comment on the apparent confusion of the valid name for this species. The persistent use of the unjustified replacement name *A. mellifica* by some modern authors is distressing and either demonstrates a general ignorance of taxonomic rules or a flagrant dismissal of the International Code of Zoölogical Nomenclature. Ignorance of the Code is understandable as not all biologists are intimately familiar, or even have an express need to be so familiar, with its rules and nuances. Dismissal of the Code is, however, a more serious situation. The criticism that the name *mellifica* is more descriptive than *mellifera* is beside the point and, if the argument of Benton (1904) is followed, vastly incorrect anyway. Suffice to say, the use of *A. mellifera* versus *A. mellifica* is not a matter of

personal choice. *Apis mellifera* is the *only* valid name for this species and authors should abide by this.

Distribution.—The western honey bee presumably arose in the Near East or Pontocaspian regions at some point during the early Pliocene. This species subsequently dispersed throughout Africa and Madagascar (entering via the Arabian Peninsula), into Europe, and into Northwestern Asia as far as the Russian Steppes. Localized adaptation gave rise to the numerous subspecies which are recognized today. Spread of this species elsewhere in the world has been through the action of human interference. Refer to treatment of individual subspecies for further details.

Apis mellifera was introduced into the New World by European settlers during their colonization of the western hemisphere. Although some early authors felt that that North American honey bees were specifically distinct from the European honey bees (e.g., Belknap 1792) it was quickly recognized by naturalists of the time that *Apis* was not native to the New World (e.g., Barton 1793), a belief confirmed by their discussions with the Native American populace. In fact, President Thomas Jefferson commented that the Native Americans referred to the honey bees as "the white man's fly" (Jefferson 1787) and signaled to them the advance of colonists. Early reports that honey bees occurred in the New World (Hernandez 1648) were based on misidentifications with species of *Melipona* (Gerstäcker 1863). Most early authors correctly referred to the transport of honey bee colonies from Europe by colonists (e.g., Josselyn 1674). Despite the arguments raging in the late 1700's over the "distinctiveness" and nativity of *A. mellifera* in the Americas, no names were proposed for them.

Apis (Apis) nigrocincta Smith
The Sulawesian Honey Bee

Apis nigrocincta Smith 1861a: 93.
Apis mellifica indica variety *picea* Buttel-Reepen 1906: 193. Unavailable (I.C.Z.N. 1985: Arts. 10c, 23j, 50c).
Apis (Sigmatapis) nigrocincta marginella Maa 1953: 575.

Comments.—Although I have previously been hesitant to recognize this species as distinct from *A. cerana* (e.g., Engel 1998a), I here correct this following the excellent work of Hadisoesilo *et al.* (1995), Hadisoesilo and Otis (1996, 1998), and Hadisoesilo (1997). The absence of a pore in the drone cell cap is a plesiomorphic feature of *Apis* in general and for the *cerana*-clade in particular (Fig. 1). *Apis nigrocincta* is the only member of the *cerana*-clade to lack this feature. The apomorphic presence of such a pore unites *A. cerana* and *A. koschevnikovi*. No subspecies are recognized in *A. nigrocincta*.

Distribution.—This species only occurs on the island of Sulawesi except in the extreme southwest corner in a lower elevation band from a bit northwest of Ujung Padang around to Bulukumba and beyond (G. W. Otis pers. comm.). Previous records of this species on Mindanao (Otis 1996, Damus and Otis 1997) are probably *A. cerana* as revealed by the development of the drone cell which had a hard cap with a pore (G. W. Otis pers. comm.), this being a feature of *A. cerana* and not *A. nigrocincta* (Hadisoesilo and Otis 1998). Populations of Mindanao are certainly distinctive from typical *A. cerana* and need to be investigated further.

Subgenus Megapis Ashmead

Megapis Ashmead 1904: 120. Type species: *Apis dorsata* Fabricius 1793, original designation. Maa 1953: 552.

Diagnosis.—WORKER: Forewing length 12–15 mm. Basal vein frequently gently curved, strongly distad cu-a (similar to Fig. 4). Angle of posteroapical margin of first submarginal cell less than 45°. Distal abscissa of vein M in hind wing present (similar to Fig. 4). DRONE: Hind basitarsus without thumb-like process. Vertical

arm of T8 as long as horizontal arm; S7 and S8 not fused mesally. Gonobase absent. Ventral gonocoxa membranous; dorsal gonocoxa reduced. Ventral cornua of endophallus not recurved ventrally. MATURE LARVA: Labrum with peg-like setae scattered over surface. Galea larger than maxillary palpus. Labial palpus spiculate. Epipharynx without setae. Atrial inner walls ridged. ETHOLOGY: Nest constructed in the open. Dance language performed on vertical surface; wagging metasoma held above dance surface; recruits potentially far from dancer's metasoma (potentially outside a near field sound range). Drone cell cap without pore.

Apis (Megapis) dorsata Fabricius
The Giant Honey Bee

Apis dorsata Fabricius 1793: 328. [*dorsata* Fabricius]

Apis nigripennis Latreille 1804b: 170. [*dorsata* Fabricius]

Apis bicolor Klug 1807: 264. Preoccupied (*nec* Fabricius 1781, Villers 1789). [*dorsata* Fabricius]

Apis testacea Smith 1858: 49. [*dorsata* Fabricius]

Apis zonata Smith 1859: 8. Preoccupied (*nec* Linnaeus 1758). [*binghami* Cockerell]

Apis laboriosa Smith *in* Moore *et al.* 1871: 249. [*laboriosa* Smith]

Apis testacca Smith 1871: 396. *Lapsis calami.* [*dorsata* Fabricius]

Megapis zonata (Smith); Ashmead 1904: 121. [*binghami* Cockerell]

Megapis dorsata (Smith); Ashmead 1904: 121. [*dorsata* Fabricius]

Apis dorsata binghami Cockerell 1906: 166. Replacement name for *Apis zonata* Smith 1859. [*binghami* Cockerell]

Apis binghami sladeni Cockerell 1914: 13. [*laboriosa* Smith]

Apis darsata Baldensperger 1928: 173. *Lapsus calami.* [*dorsata* Fabricius]

Apis himalayana Maa 1944: 4. *Nomen nudum.* [*laboriosa* Smith]

Megapis breviligula Maa 1953: 563. [*breviligula* (Maa)]

Megapis binghami (Cockerell); Maa 1953: 564. [*binghami* Cockerell]

Megapis laboriosa (Smith); Maa 1953: 570. [*laboriosa* Smith]

Apis dorsatao Ruttner 1988: 118. *Lapsus calami.* [*dorsata* Fabricius]

Apis labortiosa Willis, Winston, and Honda 1992: 169. *Lapsus calami.* [*laboriosa* Smith]

Distribution.—Refer to treatment of individual subspecies below.

Subgenus *Micrapis* Ashmead

Micrapis Ashmead 1904: 122. Type species: *Apis florea* Fabricius 1787, monobasic and original designation. Maa 1953: 557.

Diagnosis.—WORKER: Forewing length 6–7 mm. Basal vein frequently gently curved, strongly distad cu-a (similar to Fig. 4). Angle of posteroapical margin of first submarginal cell less than 45°. Distal abscissa of vein M in hind wing absent. DRONE: Hind basitarsus with thumb-like process. Vertical arm of T8 as long as horizontal arm; S7 and S8 not fused mesally. Gonobase represented by isolated fragments. Ventral gonocoxa sclerotized as transverse bar; dorsal gonocoxa not reduced. Ventral cornua of endophallus not recurved ventrally. MATURE LARVA: Labrum with peg-like setae scattered over surface. Galea larger than maxillary palpus. Labial palpus spiculate. Epipharynx with setae. Atrial inner walls ridged. ETHOLOGY: Nest constructed in the open. Dance language performed on horizontal surface; wagging metasoma held above dance surface; recruits potentially far from dancer's metasoma (potentially outside a near field sound range). Drone cell cap without pore.

Apis (Micrapis) andreniformis Smith
The Black Dwarf Honey Bee

Apis andreniformis Smith 1858: 49.

Apis florea andreniformis variety *sumatrana* Enderlein 1906: 339. Unavailable (I.C.Z.N. 1985: Arts. 10c, 23j, 50c).

Micrapis andreniformis (Smith); Maa 1953: 601.

Comments.—This species was reinstated just over a decade ago by Wu and Kuang (1986, 1987) with additional evidence for this decision provided by Wongsiri *et al.*

(1989). It's common name comes from the nearly black T1-2 while in *A. florea* these structures are reddish brown. No subspecies are recognized.

Distribution.—*Apis andreniformis* occurs as far north as southern-most Yunnan Province in China, south into Malaysia, eastward on the mainland to the coast of Vietnam, and westward as far as northwestern India along the eastern border of Nepal. Although specimens are not recorded from Bhutan, Cambodia, Myanmar, or Nepal the records of *A. andreniformis* in the Bengal, Sikkim, and Assam regions of India suggests that it will eventually be found in these countries (Otis 1996) unless it has since become locally extinct.

Apis (Micrapis) florea Fabricius

The Red Dwarf Honey Bee

Apis florea Fabricius 1787: 305.
Apis semirufa Hoffmannsegg 1818: 60.
Apis lobata Smith 1854: 416.
Apis floralis Horne and Smith 1870: 181. *Lapsus calami.*
Apis testacea Bingham 1898: 129. Preoccupied (*nec* Smith 1858).
Micrapis florea (Fabricius); Ashmead 1904: 122. [see Comments below]
Apis florea variety *rufiventris* Friese *in* Buttel-Reepen 1906: 167, 170.
Apis florea florea variety *fuscata* Enderlein 1906: 338. Unavailable (I.C.Z.N. 1985: Arts. 10c, 23j, 50c).
Apis nursei Cockerell 1911a: 319. Replacement name for *Apis testacea* Bingham 1898.
Apis florea nasicana Cockerell 1911b: 241.

Comments.—Although when proposing the genus *Micrapis* Ashmead (1904) did not explicitly transfer the type species, *A. florea*, into this genus (he still referred to the species as *A. florea* and not *Micrapis florea*) he is to be consider as having made the combination as the proposal of *Micrapis* was done prior to 1961 [I.C.Z.N. 1985: Art. 51c(ii)]. There are presently no subspecies recognized in *A. florea*.

Distribution.—This species is distributed from the eastern regions of the Arabian Peninsula, through southern Iran and Iraq to Pakistan and India as far north as the Himalayan uplift. The species extends eastward as far as Vietnam, north to Yunnan Province, China, and south into Indonesia. Refer to Otis (1996) for more precise locality records. *Apis florea* was introduced into Sudan a little over a decade ago from Pakistan and has become established (Lord and Nagi 1987, Mogga and Ruttner 1988).

SUBSPECIES

Owing to both the high visibility and dramatic geographic variation of the honey bees, the more common species have been heavily divided infraspecifically. Below I have attempted to outline the presently recognized subspecies. There are no valid subspecies of *A. andreniformis*, *A. florea*, *A. koschevnikovi*, or *A. nigrocincta* and I have not recognized any subspecies among the fossil forms. A few of the names treated below are used incorrectly under the rules of zoölogical nomenclature (I.C.Z.N. 1985) and are therefore treated in further detail, otherwise I have not given detailed taxonomic histories for each subspecies. I have tried to provide common names for these morphs as well as historical, geographical, or important biological comments for some taxa.

As far as I have been able to ascertain, holotypes or neotypes have not been designated for certain subspecies. This will be necessary to assure stability in nomenclature. The general problems with the recognition of subspecies have been discussed by several authors, the best critique being that by Wilson and Brown (1953). My recommendation is a complete cessation of proposals of new subspecies in *Apis* (primarily *A. mellifera*) until the taxonomy has been more thoroughly examined (something which I hope this paper will facilitate).

Apis (Apis) cerana Fabricius

The populations of *A. cerana* in the Philippines are somewhat distinctive (e.g., Ruttner 1988, Smith 1991b, Smith and Hagen 1996, Damus and Otis 1997) and could possibly be elevated to subspecific status. If this is done the name of this race would become *A. cerana philippina* Skorikov with *A. samarensis* Maa as a junior synonym.

1. *Apis cerana cerana* Fabricius: The Eastern Honey Bee

Distribution.—This subspecies occurs as far east as Afghanistan and south along the central deserts and mountain ranges. Along the Himalayan uplift in Tibet it is replaced by *A. cerana skorikovi* and further south in India it is replaced by *A. cerana indica*. The subspecies then ranges across most of central and southern China although not in the high regions of central China where the black bee (*A. cerana heimifeng*) occurs. *Apis cerana cerana* then ranges along the eastern edge of Asia up to Korea and the southern-most areas of the former Soviet Union (Ussuria) and south to the northern reaches of Vietnam.

2. *Apis cerana heimifeng* Engel, new subspecies: The Black Chinese Honey Bee

Apis cerana, Aba race, Peng *et al.* 1989: 15.

Diagnosis.—Distinguishable from typical *A. cerana cerana* in China by the dark brown to black scutellum and T3-4 (these are yellow in *A. cerana cerana*). In this respect it resembles the Tibetan Honey Bee, *A. cerana skorikovi*, from which it differs in the larger body size (body length 12.5–13.7 mm; forewing length 8.8–9.3 mm) and low tendency to swarm (very strong in *A. cerana skorikovi*). This is the largest *A. cerana* race in China and is a relatively dark bee (hence its common name) with a dark metasoma, scutellum, and legs. This dark coloration is partly owing to the very narrow to completely absent bands of orange on T3-5. Peng *et al.* (1989) provide several

morphometric measures for this bee (as "Aba race").

Distribution.—This is a distinctive race in central China and occurs in relatively high elevation areas (although certainly not at the highest points for this region) mostly near river valleys. Its general distribution is in northern Sichuan Province, southwestern Gansu Province, and eastern Qinghai Province.

Holotype.—Worker; CHINA: [Northern Sichuan Province], Nanping, 21 April 1920 (deposited in the American Museum of Natural History, New York).

Etymology.—The specific epithet is derived from the Mandarin words *hei* (meaning "dark") and *mifeng* (meaning "honey bee") and refers to the dark coloration of this race. The name is a noun in apposition.

3. *Apis cerana indica* Fabricius: The Indian Honey Bee

Distribution.—This race occurs through most of India except in the higher regions towards the north where it is replaced by *A. cerana cerana* or in Tibet by *A. cerana skorikovi*.

4. *Apis cerana japonica* Radoszkowski: The Japanese Honey Bee

Distribution.—This race occurs on the islands of Japan.

5. *Apis cerana javana* Enderlein: The Javanese Honey Bee

Comments.—The taxa described as *A. peroni* by Latreille (1804b) and *A. gronovii* by Guillou (1841) may be the same as Enderlein's *A. cerana javana*. Owing to this uncertainty I have for now retained *A. cerana javana* as the name of this taxon and considered *A. peroni* and *A. gronovii* to be *A. cerana indica*. Researchers, however, should be aware of this uncertainty and if the consubspecific nature of these taxa is confirmed in the future, then the name of the subspecies would have to be changed to *A. cerana peroni* with *gronovii* and *javana*

as junior synonyms. This situation was also noted by Maa (1953: 580). If this unfortunately turns out to be the case, then it would probably be advisable to petition the I.C.Z.N. to suppress *A. peroni* and *A. gronovii* in favor of *A. cerana javana* although such a case would not be a very strong one owing to the fact that *A. peroni* has been in use within the last 50 years (e.g., Maa 1953).

Distribution.—This subspecies is presently known from Java and as far east as Timor.

6. *Apis cerana johni* Skorikov: The Sumatran Honey Bee

Distribution.—This subspecies only occurs on the island of Sumatra.

7. *Apis cerana nuluensis* Tingek, Koeniger, and Koeniger: The Malaysian Mountain Honey Bee

Distribution.—This morph occurs in the mountains of Sabah, Malaysia. Otis (1996) provides details of various collection locales in Malaysia.

8. *Apis cerana skorikovi* Engel, new subspecies: The Himalayan Honey Bee

Apis cerana skorikovi Maa 1944: 4. *Nomen nudum.*
Apis cerana, Himalaya race, Ruttner 1988: 121, 158.
Apis cerana, Xizang race, Peng *et al.* 1989: 15.
Apis cerana himalaya Smith 1991b: 154. *Nomen nudum.*

Diagnosis.—This race is fairly gray in overall body coloration, some areas being slightly more yellow while others are closer to black (e.g., T4 is entirely black) and with paired yellow spots on S3. There are distinctive white hairs on the terga which contribute to the overall grayish appearance. *Apis cerana skorikovi*, like *A. cerana heimifeng*, also differs from *A. cerana cerana* (as well as *A. cerana indica* and other subspecies) in the dark scutellum and slightly larger size (body length around 12.2 mm; forewing length around 8.75 mm). Addi-

tional morphometric values are provided by Peng *et al.* (1989).

Comments.—The Himalayan race of *A. cerana* (sometimes called the Tibetan race) was referred to as *A. cerana skorikovi* by Maa (1944); however he never provided a description for this subspecies. Many authors have subsequently recognized this race as distinctive but never associated a name with the numerous descriptions simply referring to this taxon as the Tibetan honey bee (among other common names). Peng *et al.* (1989) have done the best to characterize and describe this taxon referring to it as the Xizang race (Xizang is Chinese for Tibet, sometimes spelled Sitsang). I here validate the name *A. cerana skorikovi* for this taxon, referring readers to the diagnosis provided above as well as the descriptive comments given by Peng *et al.* (1989: as "Xizang race") and Ruttner (1988: as *A. cerana* "Himalaya race"). Smith (1991b) referred to this race as *A. cerana himalaya* making a Latin name out of Ruttner's "*A. cerana* Himalaya race". Ruttner's name was not used as, nor intended as, a scientific name and *A. cerana himalaya* as used by Smith (1991b) is a *nomen nudum*.

Distribution.—This subspecies occurs along the Himalayan uplift at elevations of 1900–4000 meters.

Holotype.—Worker; NEPAL: Ko Pasi near Panauti, 19 March 1982, B. A. Underwood (deposited in the Cornell University Insect Collection, Ithaca).

Paratypes.—Three workers, same collection data as holotype, deposited in the same collection as the holotype; two workers, same collection data as holotype, deposited in the American Museum of Natural History, New York.

Etymology.—I have retained the specific epithet used by Maa (1944) for this race. The epithet is a patronymic honoring Dr. A. S. Skorikov who did much work on the classification of bees; honey bees and bumble bees in particular.

Apis (Apis) mellifera Linnaeus

The western honey bee, *A. mellifera*, is remarkable for its geographic variation and, for this reason, has been broken into a plethora of taxonomic entities over the past two centuries. In earlier studies these forms were often treated as distinct species; however, today they are recognized as subspecies of a single variable species.

1. *Apis mellifera adami* Ruttner: The Cretan Honey Bee

Comments.—No type has been designated for this race. Ruttner's specimens are among the collection of the Institut für Bienenkunde in Oberursel, Germany. A single worker from this material should be selected as the lectotype and the others designated as paralectotypes.

Distribution.—This race occurs on the island of Crete in the Mediterranean Sea.

2. *Apis mellifera adansonii* Latreille: The West African Honey Bee

Distribution.—This subspecies has a wide distribution in western Africa ranging from Niger in the north, east to Senegal, and as far south as Zaire.

3. *Apis mellifera anatoliaca* Maa: The Anatolian Honey Bee

Distribution.—This race occurs throughout Turkey, bordering with *A. mellifera macedonica* in the European portion of that country. In the east, *A. mellifera anatoliaca* borders with *A. mellifera caucasia* and *A. mellifera remipes* in the area of Azerbaijan, Armenia, and Georgia and with *A. mellifera meda* in the southeastern-most regions of Turkey.

4. *Apis mellifera artemisia* Engel, new name: The Russian Steppe Honey Bee

Apis mellifera mellifera natio *tesquorum* Skorikov 1929a: 29. Unavailable (I.C.Z.N. 1985: Arts. 10c, 23j, 50c).
Apis mellifera acervorum Skorikov 1929b: 253. Preoccupied (*nec* Linnaeus 1758).

Etymology.—Named for Artemis (Greek; Diana in Roman mythology), the goddess for whom the honey bee was a symbol and whose temple at Ephesus, the Artemisium, was listed by Callimachus of Cyrene and Philo of Byzantium as one of the seven wonders of the world.

Distribution.—This race occurs in the central Russian Steppes.

5. *Apis mellifera capensis* Eschscholtz: The Cape Honey Bee

Comments.—This subspecies is biologically distinctive for its ability to undergo parthenogenetic reproduction when deprived of a queen (Jack 1916, Anderson 1963, Ruttner 1977).

Distribution.—As is indicated by the name of this race, it occurs in the Cape region of South Africa.

6. *Apis mellifera carnica* Pollmann: The Carnolian Honey Bee

Distribution.—This European race occurs south of the Alps, east into northern Italy, and west into Yugoslavia and Romania.

7. *Apis mellifera caucasia* Pollmann, reinstated name: The Caucasian Honey Bee

Apis mellifida [sic] variety *caucasia* Pollmann 1889: 90.
Apis mellifera caucasica Gorbachev 1916: 39. Unjustified emendation.

Distribution.—This race occurs in the Caucasus Mountains. It is sometimes referred to as the "grey" Caucasian honey bee.

8. *Apis mellifera cecropia* Kiesenwetter: The Greek Honey Bee

Distribution.—This race occurs throughout most of Greece and surrounding Aegean islands. It borders *A. mellifera macedonica* in the northeast regions of Greece and *A. mellifera carnica* in the northwest corner of the country.

9. *Apis mellifera cypria* Pollmann: The Cyprian Honey Bee

Distribution.—This race is presently known only from the island of Cyprus.

10. *Apis mellifera iberiensis* Engel, new name: The Iberian Honey Bee

Apis mellifica intermissa iberica Goetze 1964: 25. Infrasubspecific name proposed after 1960 and therefore unavailable (I.C.Z.N. 1985: Art. 1b); preoccupied (*nec* Skorikov 1929b).

Apis mellifera iberica Ruttner 1988: 236. Corrected authorship (first available usage); preoccupied (*nec* Skorikov 1929b).

Comments.—Goetze (1964) proposed this form as a variety of the subspecies *intermissa*. Since this is a varietal name (i.e., infrasubspecific) proposed after 1960 it is unavailable and does not enter into zoölogical nomenclature (I.C.Z.N. 1985: Arts. 1b and 45e–g). The first correct application of this name as a subspecies was by Ruttner (1988) which thereby validates the name to that author. Unfortunately, a further complication arises as the name is a primary junior homonym of an available name proposed by Skorikov (1929b) for another type of honey bee from Azerbaijan. Since no type exists for Ruttner's subspecies I here designate a neotype for *A. mellifera iberica*, the name of which will be replaced by *A. mellifera iberiensis*.

Neotype.—Worker; SPAIN: Córdoba, Andalusia, September 1986, D. Smith and R. Hagen; now with additional labels reading "NEOTYPE, *Apis mellifera iberica* Ruttner, desig. M. S. Engel, 1999" and "*Apis mellifera iberiensis* Engel" (deposited in the Snow Entomological Collection, Natural History Museum, University of Kansas, Lawrence). Three additional workers, identical to the neotype, have also been deposited with the University of Kansas and the American Museum of Natural History, New York.

Etymology.—The new subspecific epithet refers to the distribution of this subspecies on the Iberian Peninsula.

Distribution.—This race natively occurs on the Iberian Peninsula in Europe. Colonies were transferred to the South American tropics several decades ago, prior to the introduction of *A. mellifera scutellata*, but populations never became established.

Two ecotypes of *A. mellifera iberiensis* occur in Spain as shown by Santiago *et al.* (1986) as well as two mitochondrial types as demonstrated by Smith *et al.* (1991) and Smith and Glenn (1995). The neotype selected above comes from the Córdoba populations sampled by Smith and Glenn (1995: their colony 1-1).

11. *Apis mellifera intermissa* Maa, corrected authorship: The Tellian Honey Bee

Comments.—As was noted in the taxonomic history of *A. mellifera*, the name *intermissa* as used by Buttel-Reepen (1906) is unavailable for the same reasons as presented for Buttel-Reepen's name *koschevnikovi* (see Comments for *A. koschevnikovi*). The name of this subspecies was first made available by Maa (1953).

Distribution.—This race has a tight distribution along the northern coast of Africa as far west as Morocco, into Tunisia in the east, but bordered by the Atlas range in the south.

12. *Apis mellifera jemenitica* Ruttner, reinstated name: The Arabian *or* Nubian Honey Bee

Apis mellifera nubica Ruttner 1976a: 359.

Apis mellifera jemenitica Ruttner 1976a: 366.

Apis mellifera yemenitica Ruttner 1988: 212. Unjustified emendation.

Apis mellifera sudanensis Ruttner 1988: 214. *Nomen nudum.* Corrected authorship.

Apis mellifera bandasii Radloff and Hepburn 1997: 57. *Nomen nudum.* Corrected authorship.

Comments.—Ruttner (1988) synonymized *A. mellifera jemenitica* with *A. mellifera nubica* and acting as first reviser (I.C.Z.N. 1985: Art. 24) gave *jemenitica* priority over *nubica*. In addition, the name *je-*

menitica was unnecessarily emended from its original spelling. The correct name of this taxon should be *A. mellifera jemenitica*, not *yemenitica*.

No type has been designated for this race. See comments under *A. mellifera adami* for location of Ruttner's original material.

Distribution.—This subspecies of small bees occurs in hot arid zones of eastern Africa and the Arabian Peninsula. Countries in which it occurs include Chad, Oman, Saudi Arabia, Somalia, Sudan, and Yemen.

13. *Apis mellifera lamarckii* Cockerell: The Egyptian Honey Bee

Distribution.—This honey bee race occurs in a narrow range along the Egyptian Nile Valley.

14. *Apis mellifera ligustica* Spinola: The Italian Honey Bee

Distribution.—This subspecies occurs along the Italian Peninsula although it has been commercially transported throughout the world. The bees currently distributed in Italy have hybridized much with *A. mellifera mellifera* and *A. mellifera carnica* in the north. In fact, untainted populations of *A. mellifera ligustica* appear to be confined to Kangaroo Island, Australia where they are being maintained as an unhybridized strain (Ruttner 1976b). I recently (January 1999) had the opportunity to visit Kangaroo Island and to see one of these colonies.

15. *Apis mellifera litorea* Smith: The East African Honey Bee

Comments.—This name was originally proposed by Smith (1961a) but was also proposed as new by Smith (1961b). No type appears to have been designated for this subspecies.

Distribution.—This subspecies is distributed along the eastern coast of tropical Africa occurring from Kenya (perhaps even

the southern-most portions of Somalia) south to Mozambique.

16. *Apis mellifera macedonica* Ruttner: The Macedonian Honey Bee

Apis mellifera macedonica Ruttner 1988: 249.
Apis mellifica rodopica Petrov 1991: 17. **New synonymy.**

Comments.—No type has been designated for this race. See comments under *A. mellifera adami* for location of Ruttner's original material. The name *rodopica* was proposed again as new by the same author five years later (Petrov 1996). There appears to have been no type designated for Petrov's race either.

Distribution.—This subspecies occurs as far north as southern Romania, east to Yugoslavia, and south to northern Greece where it borders *A. mellifera cecropia.* In the Carpathian Mountains and in Yugoslavia it borders *A. mellifera carnica.*

17. *Apis mellifera meda* Skorikov: The Median Honey Bee

Distribution.—This race is most common in Iran and Iraq but does range into southeastern Turkey and northern Syria.

18. *Apis mellifera mellifera* Linnaeus: The Western *or* European Honey Bee

Distribution.—This subspecies originally ranged throughout central Europe north of the Alps, as far south as southern France in the west, southern Sweden in the north, central Russia in the east, and on the British Isles. In the Ukraine there is a transition over the steppe region to *A. mellifera sossimai.*

19. *Apis mellifera monticola* Smith: The East African Mountain Honey Bee

Comments.—The name was first proposed by Smith (1961a) but was designated as new a second time in Smith (1961b). No type appears to have been designated for this subspecies.

Distribution.—This race occurs within the mountains of eastern Africa (e.g., in

Kenya and Tanzania). The occurrence of *A. mellifera monticola* in the mountains of Cameroon should be checked carefully.

20. *Apis mellifera remipes* Gerstäcker, reinstated name: The Yellow Armenian Honey Bee

Apis remipes Gerstäcker 1862: 61.
Apis mellifera armeniaca Skorikov 1929b: 254.

Comments.—The name *armeniaca* was subjectively chosen by Ruttner (1988: 192) over *remipes*. This decision is invalid because *remipes* has priority and the senior synonym must be recognized as the name for the subspecies.

Distribution.—This race occurs in Armenia and may be the same as *A. mellifera anatoliaca*, in which case Gerstäcker's name has priority for the subspecies.

21. *Apis mellifera ruttneri* Sheppard, Arias, Grech, and Meixner: The Maltese Honey Bee

Comments.—No type was originally designated for the subspecies but this is here corrected by the original authors thereby stabilizing the name of this taxon.

Lectotype.—Worker; MALTA: St. Julians, 10 August 1995, W. S. Sheppard; designation of W. S. Sheppard, M. C. Arias, A. Grech, and M. D. Meixner. The lectotype now bears a label indicating it as such and is deposited in the M. T. James Entomological Museum, Washington State University.

Paralectotypes.—Nine workers; same collection data as lectotype; deposited in the same collection as the lectotype. A further two paralectotype workers are deposited in the American Museum of Natural History, New York. All paralectotypes designated by W. S. Sheppard, M. C. Arias, A. Grech, and M. D. Meixner.

Distribution.—This race is only distributed on the island of Malta in the Mediterranean Sea.

22. *Apis mellifera saharensis* Baldensperger: The Saharan Honey Bee

Comments.—Ruttner (1988) attributed this name to Baldensperger (1923). He has, however, unfortunately confused recognition of the subspecific entity with taxonomic proposal of the subspecies. Although Baldensperger (1923) notes the distinctive character of the Saharan honey bees he does not provide a latinized name for them (in fact, nowhere in his work does he even mention the name *Apis*, let alone *saharensis*). Instead Baldensperger (1923) only uses the vernacular name "l'abeille saharienne". Thus, as far as I have been able to determine, the name is first made taxonomically available by Baldensperger in his later paper (1932) where he uses the latinized name (1932) and provides a diagnosis.

This is one of the races for which I know that no type was ever designated; however I have not been able to confirm whether any material survives of Baldensperger's original colony which he brought back to France. I have therefore hesitated to designate a neotype. This race is markedly lighter in coloration, particularly on T1-3, than the more common *A. mellifera intermissa* (which has a noticeably shiny, dark brown to black integument with more sparse pubescence). See Ruttner (1988) for further descriptive details. It is possible that this race is synonymous with *A. mellifera lamarckii* in which case the name *lamarckii* has priority for the subspecies. This possibility should be closely examined in the future.

Distribution.—This race, like *A. mellifera intermissa*, has a tight range in northwestern Africa. It occurs along the southern side of the Atlas range.

23. *Apis mellifera scutellata* Lepeletier de Saint Fargeau: The African Honey Bee

Comments.—This is the race introduced into Brazil in the 1950's which has capti-

vated the apicultural world as well the imagination of the public; popularly known as the "Africanized Honey Bee" or "Killer Bee". An account of the transport of African bees to Brazil and their accidental release is given by Kerr (1957, 1967: see also Michener 1975, Spivak *et al.* 1991, Taylor 1977, 1985 for information on the introduction, spread, and effect of this race in the western hemisphere and for direction to other literature sources).

Distribution.—This subspecies also has a large distribution in Africa and ranges from South Africa northward along the eastern half of the continent to about Somalia, it apparently does not occur along the eastern coastal plain where *A. mellifera litorea* is found.

24. *Apis mellifera siciliana* Grassi, reinstated name: The Sicilian Honey Bee

Apis siciliana Grassi 1881: 1.
Apis mellifica mellifica variety *siziliana* Buttel-Reepen 1906: 168. Unjustified emendation.
Apis sicula Montagano 1911: 26.

Comments.—Ruttner's (1988) arbitrary choice of the epithet *sicula* over *siciliana* for the Sicilian race of honey bees does not meet the criterion of priority and thus the name *siciliana* must be reinstated for this morph.

Distribution.—This subspecies occurs on the island of Sicily in the Mediterranean Sea.

25. *Apis mellifera sossimai* Engel, new name: The Ukrainian Honey Bee

Apis cerifera Gerstäcker 1862: 60. Preoccupied (*nec* Scopoli 1770).

Etymology.—The new specific epithet is derived from St. Sossima, patron saint of beekeeping in the Ukraine. St. Sossima may be a Christian version of the bee-god Zosim of some early pagan tribes of Russia.

Distribution.—This race occurs along the eastern borders of *A. mellifera carnica*'s range. It occurs mostly in the Ukraine and

easterly over to the northern regions of the Caucasus Mountains where it borders *A. mellifera caucasia.* South in the Crimea it is replaced by *A. mellifera taurica.*

26. *Apis mellifera syriaca* Skorikov, corrected authorship: The Syrian Honey Bee

Comments.—As was noted in the taxonomic history of *A. mellifera*, the name *syriaca* as used by Buttel-Reepen (1906) is unavailable for the same reasons as presented for Buttel-Reepen's name *koschevnikovi* (see Comments for *A. koschevnikovi*). The name of this subspecies was first made available by Skorikov (1929b).

Distribution.—*Apis mellifera syriaca* occurs along the eastern shores of the Mediterranean Sea; north from Syria to the Negev Desert in the south. It is sometimes known as the Palestine honey bee.

27. *Apis mellifera taurica* Alpatov: The Crimean Honey Bee

Distribution.—This race occurs along the north-central shores of the Black Sea; in the Crimea.

28. *Apis mellifera unicolor* Latreille: The Malagasy Honey Bee

Distribution.—The distribution of this race in Madagascar is discussed by Brooks and Michener (1988).

Apis (Megapis) dorsata Fabricius

Some authors prefer to recognize one or more of the *A. dorsata* races as distinct species. This is most often done with *A. dorsata laboriosa* followed by *A. dorsata breviligula* and to a much lesser degree with *A. dorsata binghami*.

1. *Apis dorsata binghami* Cockerell: The Giant Sulawesi Honey Bee

Distribution.—This race of giant honey bees occurs on the island of Sulawesi.

2. *Apis dorsata breviligula* (Maa): The Giant Philippine Honey Bee

Comments.—Since Maa (1953) originally proposed the name *breviligula* in the genus *Megapis* his name should be written in parentheses (I.C.Z.N. 1985: Art. 51c).

Distribution.—This morph of giant honey bees occurs in the Philippines. The species status of this race is oft argued based on nest site characteristics as reported by Morse and Laigo (1969: as *A. dorsata*) and Starr *et al.* (1987).

3. *Apis dorsata dorsata* Fabricius: The Common Giant Honey Bee

Distribution.—This subspecies has the largest distribution of the group; ranging from India, east to the coast of Vietnam, and into the southeast Asian islands where it is sometimes replaced by other subspecies (see accounts for *binghami* and *breviligula*).

4. *Apis dorsata laboriosa* Smith: The Giant Himalayan Honey Bee

Comments.—I currently do not recognize the subspecific form *laboriosa* as a separate species (see also Engel 1998a; but see Sakagami *et al.* 1980, Roubik *et al.* 1985, McEvoy and Underwood 1988, Underwood 1990a, b). Growing evidence, however, suggests that the distinction may be valid and my decision to place *laboriosa* within *dorsata* should be examined more closely. Sakagami *et al.* (1980) provided a detailed account of the morphology of *laboriosa* versus typical *dorsata*. Many of the characters they use to justify specific status are, however, quite variable (e.g., protuberance of the ocelli, general pubescence patterns, &c.) and across a large range of specimens blend naturally into one another except some measures of body size which I presently feel are more indicative of a subspecies rather than of a separate species. One character which appears to me to be somewhat reliable is the minute, broad medioapical extension of the grad-

ulus on S3 in *dorsata* while this is completely absent in *laboriosa*.

Distribution.—This subspecies is distributed at high altitudes (1,200 to 4,000 m) on the slopes of the mountains from northernmost India to the northernmost boundary of Laos. Further details of its distribution are provided by Otis (1996).

FOSSIL HONEY BEES

More paleontological work has focused on the honey bees than on any other group of bees. Recently I have treated some of these extinct species and attempted to place them into a phylogenetic framework with the living species (Engel 1998a: Fig. 1). Petrov (1992, 1997) also discussed *Apis* evolution with reference to the fossil record, in particular focusing on the origin of the Bulgarian honey bee (*A. mellifera rodopica* = *A. mellifera macedonica* in my system). Hong (1984) described a compression fossil from the Early Cretaceous of China as the oldest fossil bee and as a relative of *Apis*. Hong's *Palaeapis beiboziensis* is in actuality a sphecid wasp (Michener 1997, Engel 1998a) and has no bearing on apine evolution. Lastly, Nel *et al.* (1999) presented a small review of fossil *Apis* specimens but overlooked the species presented by myself, recent treatments of Apini (e.g., Michener 1990), as well as the numerous synonymies within the group, instead simply regurgitating the classification of Zeuner and Manning (1976) which is fraught with errors (e.g., refer to Engel 1998a). Nel *et al.* (op. cit.) have also followed Zeuner and Manning (1976) and other authors in over splitting "species" of honey bees based on minor morphometric differences in wing venation and size (e.g., their unnamed species A-J; Nel *et al.* 1999); characters which distinguish mere subspecies in *Apis* at best. These authors concluded (p. 31) that the fossil honey bees could not be studied from a phylogenetic perspective; however, such an attempt had already been successfully undertaken at least three times previously (e.g., Buttel-

Reepen 1906, Statz 1931, Engel 1998a). I am presently involved in a monographic study of the fossil bees, particularly those from Baltic amber, and cladistic analyses have been successfully completed for the living and fossil corbiculate bees, including Apini (Engel 1998b, in prep.).

In order to maintain the monophyly of the generally recognized subgenera (recent and fossil) it seems appropriate to propose two new subgenera thereby breaking up the paraphyletic subgenus *Synapis*. One of these new groups was called *Hauffapis* by Armbruster (1938), but he failed to designate a type species for the genus, thereby making this name unavailable according to the I.C.Z.N. (1985: Art. 13c) (see also discussions in Michener 1990, 1997). None of the fossil species belongs to the living subgenera *Apis*, *Megapis*, or *Micrapis*.

Subgenus *Cascapis* Engel, new subgenus

Hauffapis Armbruster 1938: 37. Unavailable as no type species was originally designated (I.C.Z.N. 1985: Art. 13c). See also Michener (1990, 1997).

Type species.—*Apis armbrusteri* Zeuner 1931.

Diagnosis.—WORKER: Basal vein gently curved, strongly distad cu-a (similar to Fig. 4). Angle of posteroapical margin of first submarginal cell greater than 45°. Distal abscissa of vein M in hind wing present (similar to Fig. 5). Drone, mature larva, queen, and ethology all unknown.

Etymology.—The new genus-group name is a combination of *cascus* (L. old) and *apis* (L. bee).

Comments.—The subsequent designation of *Hauffapis scheuthlei* by Zeuner and Manning (1976) as the type species was in the synonymy of *Hauffapis* with *Apis* and is therefore invalid (I.C.Z.N. 1985: Art. 11c) (see also Michener 1990).

Apis (Cascapis) armbrusteri Zeuner
Armbruster's Honey Bee

Apis armbrusteri Zeuner 1931: 292.
Hauffapis scheuthlei Armbruster 1938: 43.
Hauffapis scheeri Armbruster 1938: 43. **New synonymy.**
Hauffapis scharmanni Armbruster 1938: 44. **New synonymy.**
Hauffapis scheeri variety *gallauni* Armbruster 1938: 45. **New synonymy.**
Hauffapis scheeri variety *rahdei* Armbruster 1938: 45. **New synonymy.**
Hauffapis scheuthlei variety *seemanni* Armbruster 1938: 45. **New synonymy.**
Hauffapis scheuthlei variety *zeuneri* Armbruster 1938: 45. **New synonymy.**
Apis armbrusteri cheuthlei Hong and Miao 1992: 2. *Lapsus calami.*

Comments.—The species and subspecies of *Hauffapis* proposed by Armbruster (op. cit.) were all described from the Miocene of Randecker Maar and were based on minor wing variations. None of these variations justifies subspecific status even under the extreme criteria used for splitting morphs of extant species (e.g., *A. mellifera*). The species is presently known from the Miocene of Germany.

Subgenus *Synapis* Cockerell

Apis (Synapis) Cockerell 1907: 229. Type species: *Apis (Synapis) henshawi* Cockerell 1907, monobasic. Zeuner and Manning 1976: 240.

Diagnosis.—WORKER: Basal vein gently curved, only slightly distad cu-a (Fig. 6). Angle of posteroapical margin of first submarginal cell greater than 45°. Distal abscissa of vein M in hind wing present (as in Fig. 5). Drone, mature larva, queen, and ethology all unknown.

Apis (Synapis) henshawi Cockerell
Henshaw's Honey Bee

Apis (Synapis) henshawi Cockerell 1907: 229.
Apis dormitans Cockerell 1907: 228. Preoccupied (*nec* Heyden 1862).
Apis oligocenica Meunier 1915: 210.
Synapis dormitans (Cockerell); Statz 1931: 45.
Synapis henshawi (Cockerell); Statz 1931: 45.

Synapis kaschkei Statz 1931: 50.
Apis cuenoti Théobald 1937: 401. **New synonymy.**
Apis oligocaenica Goetze 1964: 9. Lapsus calami.
Apis henshawi Goetze 1964: 9. Lapsus calami.
Apis kaschki Goetze 1964: 9. Lapsus calami.
Apis henshawi dormiens Zeuner and Manning 1976: 241. Replacement name for Apis dormitans Cockerell 1907.
Apis henshawi kaschkei (Statz); Zeuner and Manning 1976: 243.
Apis aquisextana Nel, Martínez-Delclòs, Arillo, and Peñalver in Arillo et al. 1996: 60. Proposed as new again in Nel et al. (1999).

Comments.—This species is perhaps the most famous of the fossil honey bees. The type was redescribed and new synonymies presented by Engel (1998a). This species is from the Oligocene of Europe (in Germany, France, and Spain).

Apis (Synapis) longtibia Zhang
The Long-legged Honey Bee

Apis longtibia Zhang 1990: 85.

Comments.—Engel (1998a) gave some characters to support the recognition of this species, although far much work remains to be done on the fossil honey bees of Asia. This fossil is from the Miocene of Shandong Province, China.

Apis (Synapis) miocenica Hong
The Chinese Miocene Honey Bee

Apis miocenica Hong 1983: 10.
Apis fota Zhang 1989: 323.
Apis shandongica Zhang 1989: 325.

Comments.—This species was briefly treated by Engel (1998a) and reasons for the synonymy of A. fota and A. shandongica were given. The species is from the Miocene of Shandong Province, China.

Apis (Synapis) petrefacta (Říha)
The Petrified Honey Bee

Synapis petrefacta Říha 1973: 217.
Apis petrefacta (Říha); Engel 1998a: 275.

Comments.—A fossil form from Miocene strata of the Ceské Stredhorí Mountains of the Czech Republic.

Subgenus Priorapis Engel, new subgenus

Type species.—Apis vetusta Engel 1998a.
Diagnosis.—WORKER: Basal vein straight, confluent with cu-a. Angle of posteroapical margin of first submarginal cell greater than 45°. Distal abscissa of vein M in hind wing present. Drone, mature larva, queen, and ethology all unknown.

Etymology.—The new subgeneric name is derived from prior (L. earlier) and apis (L. bee).

Apis (Priorapis) vetusta Engel, emended name
The Aged Honey Bee

Apis vetustus Engel 1998a: 271.

Comments.—Through a lapse on my part I failed to adjust the gender of the specific epithet to match that of the genus (which is feminine). I here correct this error. The species occurred in the Oligocene of Germany.

NOMINA DUBIA AND UNASSOCIATED NOMINA NUDA
Apis aenigmatica Rayment, nomen dubium

Apis aenigmaticus Rayment 1925: 67.

Comments.—As pointed out by Cardale (1993), this name was based on the drawing of a comb and anecdotal reports of the insect in the absence of any specimens. Rayment (1935) gives another lively account of this elusive "species" which still had not been found at that time (nor has it been found since). See also discussion in Michener (1965: 232).

Apis catanensis Roussy, nomen dubium

Apis catanensis Roussy 1960: 8.
Apis catanensis avoli Roussy 1960: 8.

Comments.—Judging from the original

description, which is exceedingly incomplete, this may not be a honey bee at all. The subspecific name *avolii* is unnecessary and invalid since no subspecific forms were recognized; besides, any subspecies based on the type specimen would have to take the nominate specific epithet and would therefore become *A. catanensis catanensis*, with *A. catanensis avolii* being an invalid synonym. This is reportedly a fossil species from Miocene Sicilian amber.

Apis melisuga Zeuner and Manning, nomen dubium

"Apidae" *melisuga* Handlirsch 1907: 893. Unavailable (I.C.Z.N. 1985: Art. 11h[iii]).
Apis melisuga Zeuner and Manning 1976: 248.

Comments.—The original proposal of this epithet by the great paleoentomologist Anton Handlirsch (1907) was not in accord with the principles of zoölogical nomenclature and is therefore unavailable under Article 11h (iii) (I.C.Z.N. 1985). Zeuner and Manning (1976) made the name available through their monograph by publishing this name in combination with a genus-group name and a diagnosis; although these authors attributed the name to Handlirsch. Neither Prof. Zeuner nor Dr. Manning had seen the type and their diagnosis of the species was a mere regurgitation of Handlirsch's original descriptive comments that the specimen resembled *A. mellifera*. In the absence of the type (which is presumably lost) and any real character information it is impossible to confidently place this as a species of *Apis*. The specimen was reportedly from the Miocene of Italy. Refer to Engel (1998a) for a more thorough treatment of this name.

Apis postadamitica Buttel-Reepen, nomen nudum

Apis postadamitica Buttel-Reepen 1906: 163.

Comments.—Buttel-Reepen (op. cit.) considered this as the hypothetical direct ancestor of *A. mellifera* and postulated its occurrence in the Pliocene. No specimen for this species exists, and it was a mere hypothesis of Buttel-Reepen's that this species existed and would someday be discovered. The fact that this name is for a hypothetical taxon means that it is also excluded from zoölogical nomenclature (I.C.Z.N. 1985: Art. 1b).

Apis styriaca Pongrácz, nomen nudum

Apis styriaca Pongrácz 1931: 105.

Comments.—A supposed fossil species from the Miocene of Germany represented by a wing fragment. No description or figure was provided and the whereabouts of this material is unknown.

Apis trigona Rayment, nomen nudum

Apis trigona Rayment 1925: 69. Preoccupied (*nec* Schrank 1798).

Comments.—The decision to place this as a *nomen nudum* was made by Cardale (1993) and is followed here.

HONEY BEE *VERSUS* HONEYBEE

In closing I should like to make a brief comment on common names for this group of bees. The great arthropod morphologist Robert E. Snodgrass presented a short discussion on the common name for honey bees in the preface to his work concerning the anatomy of *A. mellifera* (Snodgrass 1956). His brief discussion advocating the use of the two word common name (*honey bee*) over a single word (*honeybee*) does not appear to have been widely accepted since apiculturists still commonly use "honeybee." Although there are no absolute rules for the use of this and other common names, I agree with Snodgrass' preference for a two word name and the logic by which he justified this position. Since I cannot hope to word his position more eloquently, I quote here his short argument: "Regardless of dictionaries, we have in entomology a rule for insect common names that can be followed. It says: If the insect is what the

name implies, write the two words separately; otherwise run them together. Thus we have such names as *house fly*, *blow fly*, and *robber fly* contrasted with *dragonfly*, *caddicefly*, and *butterfly*, because the later are not flies, just as an *aphislion* is not a lion and a *silverfish* is not a fish. The honey bee is an insect and is preëminently a bee; 'honeybee' is equivalent to 'Johnsmith.'"

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Ultrastructure of Spermatozoa in *Leptopilina* (Hymenoptera: Cynipoidea: Eucoilidae)

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Abstract.—The mature spermatozoa of the eucoilid wasp, *Leptopilina heterotoma* (Thomson), is characterised by a solid corkscrew-shaped nucleus with a posteriorly directed flange that is unique, not only among other reported Hymenoptera, but among all insect sperm previously investigated. *Leptopilina* spermatozoa are further characterised by possession of a complex acrosomal structure, asymmetric mitochondrial derivatives and a centriolar adjunct interposed between the smaller mitochondrial derivative and the nucleus. Because of their uniqueness, *Leptopilina* sperm offer little insight into the relationship between the eucoilids and other members of the Cynipoidea, or the relationships of the Cynipoidea to the rest of the Hymenoptera.

The Hymenoptera is one of the largest orders of insects, but despite this there have been remarkably few studies of hymenopteran sperm ultrastructure, and particularly among the parasitic taxa considering their diversity and species richness (Baccetti 1972; Jamieson 1987; Newman and Quicke, in press). The sperm of some social taxa such as ants and bees (Hoage and Kessel 1968; Lensky et al. 1979; Thompson and Blum 1967; Wheeler et al. 1990; Dallai and Afzelius 1990), and a few Chalcidoidea among the 'Parasitica' (Wilkes and Lee 1965; Lingmei and Dunsu 1987) are relatively well described, but there are still a number of superfamilies and many families for which there is very little spermatological information. Sperm structure in the superfamily Cynipoidea, for example, is known only through one investigation of a member of the family Figitidae (Quicke et al. 1992). The relationship of the Cynipoidea to the other apocritan (wasp-waisted) Hymenoptera is not well understood. They have been considered as being related to the Chalcidoidea

(Königsmann 1977), but also to Diapriidae (Proctotrupoidea *sensu lato*) (Rasnitsyn 1988; Ronquist 1994, 1995) and to Roproniidae + Vanhorniidae (Proctotrupoidea *sensu stricto*) (Dowton and Austin 1994). Greater knowledge of the sperm structure of other cynipoids may therefore shed new light on the relationships of this superfamily to the other Hymenoptera.

The present paper deals with the sperm of another member of the superfamily Cynipoidea, *Leptopilina heterotoma* (Thomson) (Quicke 1997), a koinobiont endoparasitoid of *Drosophila* larvae. This is the first member of its family, the Eucoilidae, whose sperm morphology has been investigated. It has a solid-corkscrew nucleus, that is not only different to that of the only other cynipoid so far described, but is unlike any other Hymenopteran sperm previously reported.

MATERIAL AND METHODS

Testes and vas deferens from freshly eclosed adult males of *Leptopilina heterotoma*, kept in culture on their host (*Drosophi-*
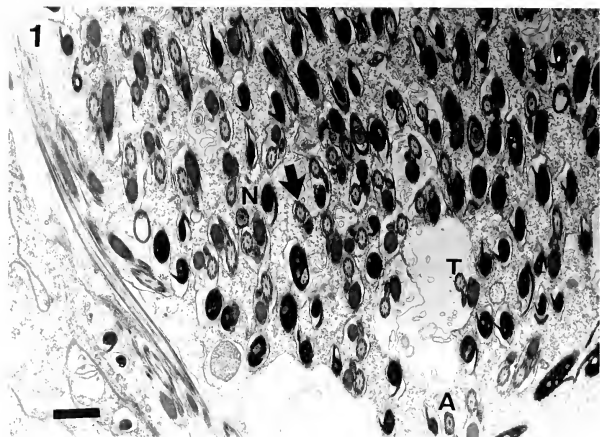
Fig. 1. Low power view of sectioned vas deferens of *Leptopilina heterotoma* with sections through acrosome (A), nucleus (N) and tail piece (T) including some with only one mitochondrial derivative (arrowed) (scale bar = 1 μm).

la melanogaster) were studied. Preparation was based on the protocol used by Newman and Quicke (1998). The tissues were dissected under 2% glutaraldehyde in phosphate buffered saline (0.1 M; pH 7.2), fixed for two hours, then transferred to 2% osmium tetroxide in cacodylate buffer (0.1 M; pH 7.2) for a further 2 hr fixation. After two buffer washes, tissue was dehydrated to 50% ethanol and then contrasted with a saturated solution of uranyl acetate in 50% ethanol prior to complete dehydration, embedding in Epon resin and polymerisation overnight. Large silver sections were picked up on high resolution grids and contrasted with uranyl acetate and lead citrate.

RESULTS

The mature sperm of *Leptopilina heterotoma* exhibit many of the structures described for other parasitic wasps, e.g. cristate mitochondrial derivatives, deltoid bodies and an axoneme with 9+9+2 arrangement of microtubules (Fig. 1). However, they also have several features different from previously reported examples. The acrosome is a much more complicated structure than any yet described, forming part of an acrosomal complex (Fig. 2 arrow). Posteriorly the acrosomal rod (perforatorium) lies to one side of the nucleus and is not held tightly there. The anterior portion of the acrosomal rod protrudes

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Figs. 2–5. Features of *Leptopilina heterotoma* sperm: 2, longitudinal section with acrosomal complex surrounded by extracellular cap (arrowed) and showing alternating protuberances from the nucleus which are the result of sectioning through the spiral ridge (scale bar = 1 μm); 3, high power oblique section through
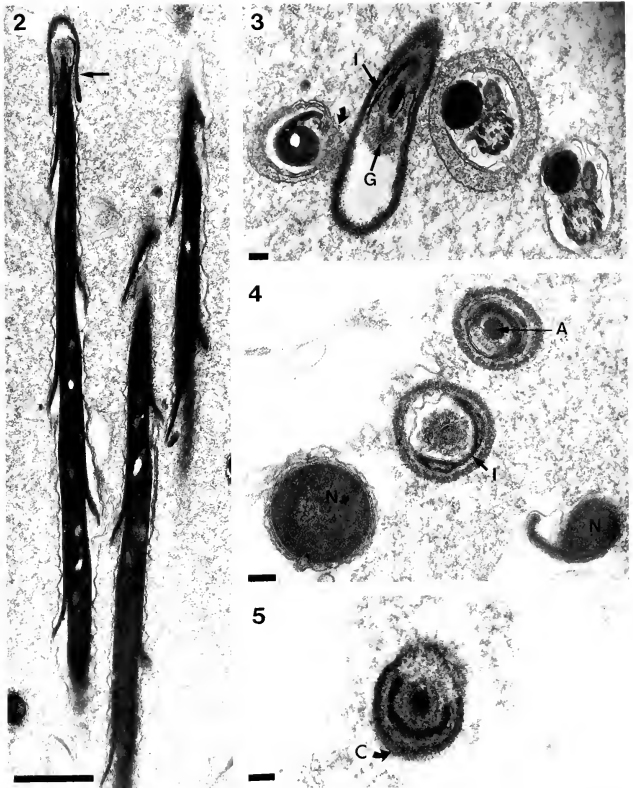
acrosomal complex illustrating the extracellular cap, acrosomal rod, inner sheath (I), granular mass (G), granular extracellular cap surrounding anterior part of nucleus (curved arrow, left hand section) [note also more posterior section to right of middle which still has cytoplasm indicative of immature sperm] (scale bar = 100 µm); 4, transverse sections through nucleus (N) showing (lower right section) comma-shaped profile characteristic of anterior and medial part, and (left section) round profile towards posterior; acrosomal complex(middle two sections), showing asymmetric electron dense inner sheath of acrosome (I) and acrosomal rod (A) (scale bar = 100 µm); 5, transverse section through acrosomal complex at level of acrosomal rod, illustrating that the inner sheath does not completely enclose the granular material of the sub-acrosomal space, and showing denser structure of extracellular cap (C) adjacent to inner sheath (scale bar = 100 µm)

into a mass of fine fibrous material which partially fills the sub-acrosomal space (Figs. 2–5). The true acrosome, that is the portion derived from the acrosomal vesicle, has a conical shape. This forms a membrane-bound inner sheath below the true cell plasma membrane (Fig. 3). The acrosomal contents are asymmetrically distributed around the fibrous material. Thus, posteriorly, in section, (Fig. 4, *upper profile*) there is almost a complete ring of material, whereas more anteriorly (Fig. 4, *middle profile*), on one side of the acrosomal complex the acrosomal contents are absent and only the membrane is found. Surrounding this acrosomal complex is an extracellular cap (Figs. 2 and 5). In longitudinal section this cap covers, and completely encloses, the anterior of the nucleus (Figs. 2, 3 *curved arrow*).

It is in the structure of the nucleus that the main difference between the sperm of *Leptopilina* and those of other hymenopterans studied to date is found. In most transverse nuclear sections, there is a protuberance, giving the nucleus a comma-shaped profile (Figs. 1, 3, 4). In longitudinal section, these protuberances alternate along either side of the nucleus for most of its length (Fig. 2). Posteriorly the nucleus abuts the axoneme at the area of the basal body (Fig. 6), where the nucleus overlaps the larger of two mitochondrial derivatives for a short distance (Fig. 6 *open arrow*). In transverse section (Fig. 7, *arrow*) an electron dense line is found that may be a continuation of a similar structure found at the interface of the axoneme and the nucleus. Next to the axoneme, and also abutting the nucleus, is a large electron-dense centriolar adjunct (Fig. 8, *open arrow*). Posteriorly, this centriolar adjunct contacts the smaller of the two mitochondrial derivatives (Fig. 9). The positioning of these structures is such that at the region of overlap it is possible to obtain oblique sections with centriolar adjunct, mitochondrial derivative and nucleus all present (Fig. 10). Closely apposed to the mitochondrial derivatives are the two deltoid bodies (also called triangular rods; Lensky et al. 1979). Although membranous, their derivation is not clear, but they are probably associated with the mitochondrial derivatives because they are also of different sizes (Fig. 11, *arrows*). This offsetting of the mitochondrial derivatives probably results in the tail piece of the wasp spermatozoon only containing a single (small) mitochondrial derivative.

Observations of living sperm expressed from the vas deferens into saline showed (× 400; phase contrast) that the nucleus is a straight, rigid-appearing structure which appears to rotate around its long axis as because waves that we believe correspond to the nuclear ridges described here can be seen passing posteriorly along them.

DISCUSSION

The most probable interpretation of the nuclear structure, as derived from longitudinal and transverse sections, is a cylinder with a posteriorly-directed ridge spiralling down along its surface. This therefore resembles a solid-cored corkscrew. Observations of living sperm indicate that the profile of the sperm head does follow the nuclear cork-screw, and that this shape may serve some fluid dynamic function, perhaps inducing the observed rotatory motion. The spiral ridge may therefore have significance for the fertilisation process.

Spirally formed sperm are known in two other groups of Hymenoptera, an un-

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Figs. 6–11. Features of of *Leptopilina heterotoma* sperm: 6, large mitochondrial derivative (open arrow) overlaps the nucleus (N) which abuts the axoneme at the level of the basal body (B) (scale bar = 100 μm); 7, transverse section showing overlap of large mitochondrial derivative and nucleus (N), with a electron dense
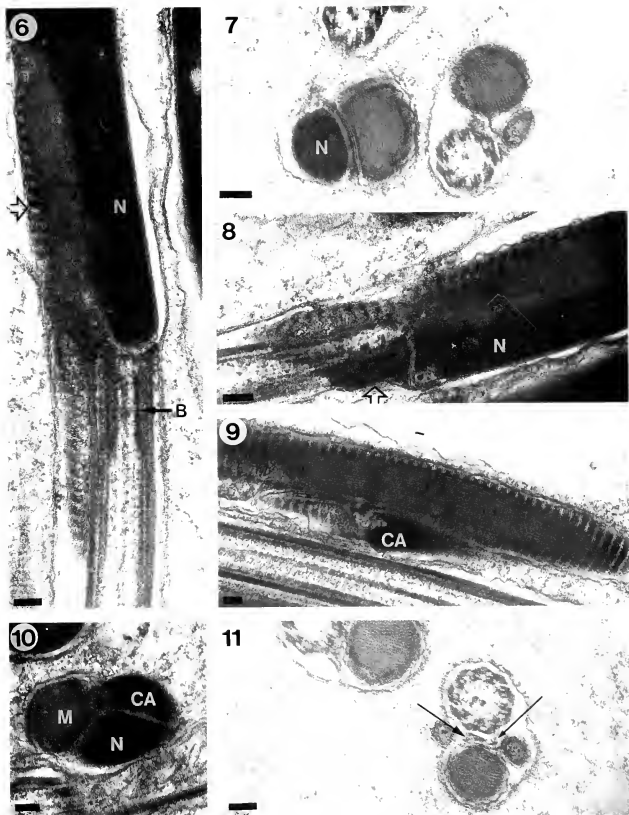
area separating the two (scale bar = 100 μm); 8, centriolar adjunct (open arrow) abutting nucleus (N) anteriorly (scale bar = 100 μm); 9, posterior portion of the centriolar adjunct (CA) abuts the smaller mitochondrial derivative (scale bar = 100 μm); 10, showing close proximity of the nucleus (N) mitochondrial derivative (M) and centriolar adjunct (CA) which means that in oblique sections it is possible to have all three in the same plane (scale bar = 100 μm); 11, tail piece showing that the larger mitochondrial derivative has an associated large deltoid body (large arrow), whereas the smaller mitochondrial derivative has a correspondingly smaller deltoid body (small arrow) (scale bar = 100 μm).

identified member of the Diapriidae which belongs to the Proctotrupoidea *sensu lato* (Quicke *et al.* 1992) and some but not all chalcidoids (Lee and Wilkes 1965; Hogge and King 1975; Quicke 1997). However, the sperm of the only other cynipoid studied to date, *Figites* sp. (Cynipoidea: Figitidae), shows no sign of spiralling (Quicke *et al.* 1992). In all the other hymenopterans with spiral sperm structure, the spiralling includes the axoneme and mitochondrial derivatives as well as the nucleus, and there is no protuberance from the nucleus itself which has a normal circular profile in cross section. The spiralling in wasps other than *Leptopilina* can be better likened to that of an open corkscrew. This phylogenetic distribution of spiralling suggests that this feature is quite homoplastic, but until a robust phylogeny for the Chalcidoidea is available, and more taxa have been investigated spermatologically, it is not possible to say how many times the open corkscrew type spiralling has evolved or been lost. The solid corkscrew form of nucleus with a protruding ridge or keel has not been observed in any other insect, but a quite similar arrangement is found in all Chilopoda, and in the Onychophora and some oligochaetes (Jamieson 1987). In these, the keel is not so well developed as in *Leptopilina* and in some the nucleus itself additionally forms a more or less open corkscrew.

Most of the spermatozoa observed in the sections through the vas deferens were mature, but a few still had a membrane-bound layer of granular cytoplasm surrounding them (Fig. 3) probably indicating that these were still at a late stage of spermiogenesis, implying that not all sperm are mature in the seminal vesicle and vas deferens at least of recently eclosed imaginal wasps.

ACKNOWLEDGMENTS

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Cladistics of the *Aleiodes* Lineage of the Subfamily Rogadinae (Hymenoptera: Braconidae)

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Abstract.—A cladistic analysis was made for 208 *Aleiodes* species. Seventy three characters were examined. Host association data from literature and museum specimens were mapped onto the cladogram. The genus consists of 18 species-groups within three sections: basal, intermediate, and derived. Basal and intermediate species tend to be generalist feeders while derived species tend to attack noctuids. The monophyly of seven subgenera was discussed, which were subsumed under *Aleiodes*.

The purpose of this research was to provide a cladistic analysis of world species of *Aleiodes* Wesmael 1838, which could be used to interpret patterns of host-use by these wasps. Particular attention was given to defining species-groups by way of cladistic analysis based on morphological characters. Host association data was mapped onto the cladogram to determine any associations between parasitoid phylogeny and host-utilization. Such associations might indicate coevolutionary patterns within host-parasitoid relationships that developed over evolutionary time.

Efforts have also elucidated intergeneric relationships within subfamily Rogadinae, as well as interspecific relationships within the genera *Aleiodes* (Achterberg 1991, 1993b; Shaw 1983, Shaw 1993, Shaw 1994, Shaw *et al.* 1997, Whitfield 1992). For many years there has been confusion about the definitions of the genera *Aleiodes* and *Rogas* Nees von Esenbeck. This problem has been clarified by Achterberg (1982, 1991), Achterberg and Penteado-Dias (1995), Shaw (1993) and Shenefelt (1969).

Morphological synapomorphies which define the subfamily: Rogadinae are: 1) propodeum either without distinct area superomedia, or if present, small; 2) dorsal carinae of metasomal tergite I converging posteriad; 3) metasomal tergites II and III well sclerotized and with extensive, distinct surface sculpturing (Shaw 1995).

The following features define *Aleiodes* as monophyletic: 1) basal portion of tarsal claw rounded with a pectin of spines (Shaw 1995); 2) tergite II carinate and anteromedial area with a polished triangular region that continues posteriad as a median carina (Shaw 1995); 3) median carina of propodeum never forking in anterior half of the segment and never diverging posteromedially into an areola (Shaw 1995); 4) fore wing RS+MB vein long (Shaw 1995); 5) emergence hole from host mummy even and circular (Shaw 1995); 6) ovipositor sheath widened and flattened (Achterberg 1991).

Most Rogadini appear to be solitary parasitoids, but two gregarious species are known (*A. stigmator* (Say), *A. pallescens* Hellen). As far as known, most *Rogas* species attack Limacodidae, Lycaenidae, Riodinidae, and Zygaenidae (Shaw, 1995). *Aleiodes* species utilize a wide variety of

hosts (Shenefelt 1975; Shaw and Huddleston 1991, Shaw 1995).

Aleiodes usually glue their host mummies to a substrate by way of a hole chewed in the ventral area of the host prothorax. Emerging *Aleiodes* adults cut an emergence hole at the posterior end of the mummified caterpillar (Shaw 1995).

Aleiodes is a useful group of parasitoids for comparative studies for three reasons: 1) the physiological character of host mummification preserves the host for taxonomic study; 2) the genus is relatively species-rich, and thus offers a large sample of species with which to carry out a phylogenetic analysis; 3) in general, *Aleiodes* species tend to have narrow host ranges (Shaw 1994), yet across the genus, a wide variety of lepidopteran groups are attacked.

METHODS AND MATERIALS

Characters and character states.—Two hundred eight *Aleiodes* species were analyzed. A list of 62 evolutionary transformation series (Hennig 1966, Mickevich 1982, Mickevich and Weller 1990, and Wiley 1981) including 73 characters (numbered 0–72) and component character states, was derived from *Aleiodes* specimens examined (see Character Summary). Terms used to describe sclerite sculpturing features follow those of Harris (1979), while those used for sclerites and appendages follow Huber and Sharkey (1993). Wing venation terminology follows Shaw *et al.* (1997).

The characters used fell under two general categories: qualitative and morphometric. Qualitative categories included 1) sculpturing on specific sclerites, 2) shape of specific sclerites, 3) presence or absence of setation on specific body parts, 4) presence or absence of tarsal claw features, 5) presence or absence of specific wing veins, and 6) coloration. Morphometric categories included 1) number of flagellomeres, and 2) morphometric ratios of sizes of parts, or distances between parts.

Species included in the study.—Descriptions of each character are included below (Character Summary). Appendix I lists the *Aleiodes* species analyzed, including host information. The following species of *Rogas*, the putative sister-group of *Aleiodes* (Whitfield 1992) were used for outgroup comparison to best estimate polarization of transformation series for each character: *R. discoideus* (Cresson), *R. fusciceps* (Cresson), and *R. bucculatricis* (Ashmead). Four unnamed morphospecies of *Clinocentrus* Haliday were also used, as well as the following *Stiropius* (Whitfield) species: *S. bucculatricis* (Ashmead) and *S. californicus* Whitfield.

Character polarization.—*Aleiodes* character states which most closely resembled those of *Rogas*, *Stiropius*, and/or *Clinocentrus* (Whitfield, 1992) were hypothesized to resemble most closely the ancestral state (Hennig, 1981). For those characters for which there was significant, consistent departure in the *Rogas* state in comparison to the *Aleiodes* state(s), the latter two genera were examined to determine whether the *Aleiodes* or *Rogas* condition should be considered ancestral. If a given character state for *Rogas* species departed from that of *Stiropius* species, *Clinocentrus* species, and *Aleiodes* species, it was hypothesized to be derived. The state the latter three genera expressed in common was then hypothesized to be the ancestral state. If a given state expressed by *Stiropius* species departed from one that *Aleiodes* and *Clinocentrus* held in common, but not *Rogas*, and the *Rogas* state differed from the *Stiropius* state, the state that *Aleiodes* and *Clinocentrus* shared was hypothesized to be ancestral to *Aleiodes*, and the other two were hypothesized to be independently derived autapomorphies with respect to the four genera taken together. For cases in which a *Rogas* state was hypothesized to be derived, *Stiropius* was hypothesized to be more closely related to the ancestor of *Rogas* + *Aleiodes* than *Clinocentrus* (Whitfield 1992).

Ordering transformation series.—The ordering of character states with respect to one another was determined by polarization based on the hypothetical ancestor, as described above, and parsimony, as follows: For those transformation series with more than one state, once the ancestral state was hypothesized, various combinations of states for a given transformation series were tested with the Hennig86 phylogenetic analysis program (Farris 1988) as described in the next section. The ordering of character states for the character in question on the most parsimonious Nelson consensus tree among those derived from respective Hennig86 runs was hypothesized to represent the best estimation of phylogeny for that transformation series. All characters in this study consist of ordered character states. The Nelson consensus provides a strict consensus tree from equally parsimonious trees derived from a Hennig86 run. Exceptions to assigning '0' to the ancestral state were the following classes of hypotheses: 1) bipolar linear evolutionary transformation series, in which character states evolved in two directions from the ancestor, diagrammed thus:

$$a \leftarrow b \rightarrow c$$

and reticulate transformation series (Mickevich 1982, Mickevich and Weller 1990), in which either *i)* character states were hypothesized to have evolved from more than two directions from the ancestor, and/or *ii)* the ancestral character state for a given *Aleiodes* lineage or closely related lineages was an *Aleiodes* character state other than the ancestral *Aleiodes* character state for that entire transformation series.

We adopted the method of TSA for treating complex multi-state characters such as vertex sculpturing (Shaw *et al.* 1997), tarsal claw form, clypeal carina shape, propodeum sculpturing (Shaw *et al.* 1997), mesopleuron sculpturing, metasomal tergite sculpturing, and hind wing RS vein shape (Achterberg 1993a). This

method has been described by Lipscomb 1992, Mickevich and Lipscomb 1991, and Mickevich and Weller 1990, and is commonly used (Lipscomb 1992, Mitter and Silverfine 1988, and Schuh 1991). It has been critiqued by Lipscomb (1992).

Alternate arrangements of character states of transformation series, in which more than one arrangement was possible, and it was not obvious from morphology alone how these character states were most logically ordered, were tested using Hennig86 program 1.5 (Farris, 1988) on a Dell Omniplex 466 system, to find the most parsimonious scheme for each respective reticulate transformation series. The most parsimonious scheme was then incorporated into the matrix.

The matrix and execution of the phylogenetic analysis.—An integer matrix (Table 1) based on integers representing coding for the states of the characters (see Character Summary), arrayed with the hypothetical ancestor and *Aleiodes* species in rows and characters in columns was analyzed by computerized algorithms (Farris 1970), using the Hennig86 program Version 1.5 (Farris 1988) on a Dell Omniplex 466 system. The results were expressed as Nelson consensuses of multiple equally parsimonious, minimum length Wagner trees, obtained by using the mhennig* option with extended branch swapping (bb*) with and without successive approximations to character weighting (xs w; cc;) until stable solutions were reached (Farris 1988), in tandem with the CLADOS program (Nixon 1991). The CLADOS program was useful for 1) obtaining definitions of nodes based on transformation series changes for characters at each given node, 2) carrying out manual branch swapping to further minimize Nelson consensus tree lengths, and 3) illustration. The trees obtained were the most parsimonious explanations of the distribution of the observed data set that could be found, barring use of the Hennig86 ie* option (Farris 1988), which was found impractical (see below). After
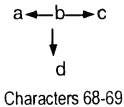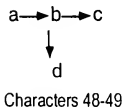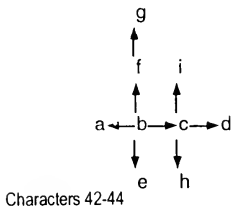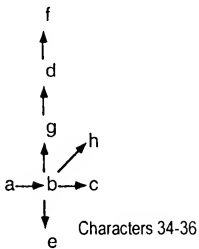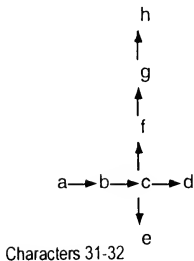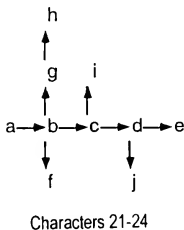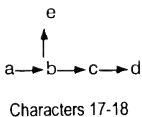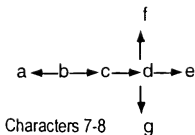
Fig. 1. Diagrams of reticulate transformation series.

Table 1. Matrix of *Aleiodes* species and character states. See Appendix for complete species names and text for explanation of characters.

```
          0          1          2          3          4          5          6          7
ANCESTOR  00000001100000000000001000100000100100000001100000000100000010000001000000
ABDOMINA  02110203110100001300021000110113210001002100000212100010100002210000
ACICULAT  01110103110000000100001100012101000000121002002101002002101000
AESTUOSU  02111203110100021300121000100021212100010021001121023000001000211001000
AGILIS    11111203110000002130013100110001211100010021000121212300000100110000100
ALBITIBI  01110113110000001100021001100011110000001100000101101010001000210100000
ALBOANNU  01111203010100000300021000117011311011100210211220001010002101010000
ALUTACEU  01111203110000000300012001110001111001010110000021010000000001101000000
ALIGARHE  01110012110000000100010011000111010000001101000101100000100002210000000
ALTERNAT  01110103110000001000100011000121110000001210010021001000002210000000
ANGUSTAT  01110103110000001000100011000121100010021001007010000000100210101000
ANNULATU  010101021100007000300011001110001101000001210000000021010000000100710100000
ANTENNAT  01111203110000101300002100011110001111031100002110100000100210101000
APICALIS  02110203110100001300012100011101132100010021000021210001000221000000
ARCTICUS  01110103110000000100011000111000000313003002101101000200021001000
ARIZONIE  01311203110100030002100010011111210010031000010000220001002211000000
ARMATUS   01110112110000000100011000110011110000010210000201000000001002100000
ARNOLDI   01111203110100000130012100011701131111000010210002022000000010101000
ARSENJEV  01111203101001010030002100010011111011110311000020001000010001070100000
ATRICEPS  02110203110100001300020001110113210001002110000021122000001000221000
ATRICORN  01111203101003010030012110011401110001002110002021121200000100210101000
AUTOGRAP  01110112110000000100010001111100000001110000011010000011002101000000
BAKERI    11101121100000002000110011100011110000001100007101100000100210010000
BICOLOR   0111010310000001000100011100012100000001310010021011010001000210010000
BOREALIS  01110112110000001000110011000111100000011000011101000011000210100000
BRETHESI  02110203110100001300021000110113210001002110000021131000001000221000
BREVIPEN  01110103110017000301013001100010000011110000200000000000100101010000
BREVIRAD  01110312100000000300010011100121100000001210000021001700001000710100000
BUOCULUS  01110121100001001000011000111111000000110000010012010000100121010000
BURRUS    01110203110100010013001011001131100000100210002122200000001000201010
CAMERONI  02110203010100100300012000100111121000000310000021100002000022101000
CANTHARI  01101121100000001000100011001111100000011017000011007710100000
CARINATU  0111120311010001000130011001131110010021001021211200001000221010000
CARINIVE  02112203110100013001300111001311110001002120000021122010001000221000
CAUCASIC  01112131100000013001210001101131100010002110000210010000010002771000000
CAZIERI   0211120311100100300021000100011321000002110000211100000200021100000
CHLOROTI  01111301000010010021001100701112100000031100000211100000100110100000
CIRCUMSC  01101121100000001000100011000111100000011000011010000011000210100000
COMPRESS  02210012110000010001000110001111000001101001010100000100022010010
CONFORMI  01112031101000013001300111001311100010021001021122000000100210101000
CONVEXUS  02110203110100013000210001110121210001002110000121210100000221100001
COXALIS   02110311010000000100001100012100000013100100210110100001000210100000
COXATOR   02110103110100000100010011000121100000012100100210100000100002210000
CRASSIPE  01010113117000001000110011110001111100000010710100000010007710100000
CRUENTIS  02111203101000013001310001100131120001002120001021122000001000221101100
CURTISPI  01101031100000001000120011000111100000001100002101001000000710100000
DENDROLI  01110112110000001001000110001111100000011100001010100100000210100000
DESERTUS  01112031100000213001210010012111000010021000171?123000000100121000100
DISPAR    01110203110100003010130011001111110010111100000021000000000100101010000
DISSECTO  02112031101000130001210001000131100010021001122001001100002101100
DIVERSIC  011101031107000030001200111000121010010101100100211000000101010100000
DIVERSUS  0111203101000013001210001070121110001002120002202110010000221101100
DUCTOR    02110203110100030002100011001321100010021000021121000101000221010000
EARINOS   01111213110000100300121001001132100000031100000200022010000
ECUADOR   01111203101000030014100111001311001100210000021020000010021010100
EURINUS   01111203101000001300131001100113110000102100010211220001010021010100
EXCAVATU  01110103110100000301013001100011121000011121030020000000000110110100000
FAHRINGE  01110203110100002130012100100012121000100221001200210123000010002100
FEMORATU  11110102110000000300011001110001110000001100001011000001002100010000
FERRUGIL  02110203110000013001300111001141110001002110002120000100021001000
FLAVIDUS  0111121301170010030002100020001321000003110000211100000100021110000
FLAVISTI  0211020321010001300121000000001101300010021100002113211000100002210101100
```

Table 1.   Continued.

```
                0         1         2         3         4         5         6         7
FLAVITAR  01110203110100000300021000110011121100010021000006211120000100001000000
FORTIPES  0111121311070000030012100011011133110000003110000021011000010000310100000
FORTIS    0111120311010000130013100111001131110001002110001021122000001002210100000
FUSCIPEN  0111021311000000010002100110001111000001110000070210000010003701000005
GASTERAT  0211120311010000130013100111001131110001002110001021122000010100021110100
GASTRITO  0111011211000100010001100011000111110000011100000101100000100111010000
GEOMETRA  0211121301000010030001210000100111112100000031100000210110000020000221100
GLABER    01212031101001213001210011000121112000100021000011210230000020001000100
GOSSYPII  01110112110000000100010001100011111000000111000001101101000010000210100000
GRANDIS   02111203110100000300110000111011211000010021100000211101000100002210000
GRANULAT  0111010311001000010001100111000110110000012100200110100000011100210100000
GRAPHICU  0111110311000010110021000010001110000101110000102100000010002101000000
GRASSATO  01110203110000013001310011001131110000100211000002112100000107021010100
GRESSITT  01110010110000000100111000110001111100000111000000110120000010002210000
HARRIMAN  0111020311010000130012100110011311100010021000021121000010000210101000
HELLENIC  0111011311000000010001000110012110000012170200021010000000000710100000
HIRTUS    01110203110100001300121001110011311110001002110001211210001010000210101000
INCERTOI  01110103110000000100010001100012110000000021002007101100000100021010000
INCERTUS  01110103111700000301012001110011100011021001000210100021110000100021000000
INDESCRE  0211011311000010001000110001111100000111000001101100000100021100000
JAKOWLEW  01110103111000000100010001100021100010001003100211100001110000210000
JAROSLAW  0211120311010000130012100017001311100010021000002102100010000221101000
KRULIKOW  01110203101010002130013100110001131200010021200010211030001000010101100
KUZTLIZK  11110112110000000100011001110001121100000012100000110100000110002101000000
LAPHYGMA  01110112110000000100010001100011110000000110000011011000000100121010000
LONGICOR  711101031117000003010120011100011101010010001110000100002107201000000
LONGIPEN  0111010311101000030101300111000120100000101210000200000000100110100000
LUCIDUS   021102032101000011300121000000011011400010021000002013212100010002212011000
LYMANTRI  02110112110000100100010001000111121000000111000011010001000221100000
MALACOSO  011101121100000001000110001111110000000111000011011000000100110100000
MANDIBUL  021112031101000213001210011000121111000100210000202112300000100022110100
MEDIANUS  022102031101000003000210011100111110000007102100000100010000221101000
MELANOPT  02110203210100011300121000000011014000100210000202123210000100022012010000
MEXICANU  0211020311010001130012100000000110130001002110002021132000001000221101100
MICROCUL  01112031101000003000310011177031012000110211000022101010001000221101100
MINIATUS  01211203110100001300131011110031121200000021200020212123000001000210001100
MODESTUS  0111010311000000010012100110000111200000021200010210220000001000210100000
MOLDAVIC  0101010311000000010000110011210000000131002002101200000100710100000
MOLESTUS  02110203110100001300021001110132110001002112100001211200000100022110000
MORIO     02110203110000013001210011100131111000010021100000212101000100002211000000
NARANGAE  01110102110017000100010000100011110000021002001100000000100110100000
NEGATIVU  02110103110000000100010011000112111000010121000002111000000100002211000
NEOTROPI  7111011311170000010001000110001111100000011100002101100000107071010000
NIGRIBAS  11110112110001002000010011000111110000007110000001000022010100000
NIGRICOR  01110112100000000100010000111100000011100000110100000110021010000
NIGRISTE  01110102110000000200011001110001101000000311000001010000031002101000000
NOCTURNU  01120012110000100100110010000111110000000112000071011000000100121010000
NOLOPHAN  011101121100000001000100011111100000011100000110100000100110110000
NOTOZOPH  02111213010000100300021000100113121000000311000002101000000200022110000
NUNBERGI  0111010311000000010001100110011210000010131001002101010001000021010000
PALLESCE  0111011211000100010001000110001111100000011100001101100000100110100000
PALLIDAT  0211012111000000010001000110000111100000011100000110100000100221110000
PALLIDIS  011112031101000130003100110001011311110010021100010211120000000021010000
PALMATUS  02110012111000000100010001000111110000000111010001010000100022010010
PARASITI  02110203110100001300021001110113121000010021000021210000001000221100000
PEDALIS   01111213011100010030002100020071133121000003110000211100000100022110000
PELLUCEN  011101021100000001000100011111110000011100000110100000100210100000
PERCURVE  11110112110000000100010001100011110000000110000011011000010071010000
PERINETE  01110103110000030001200111001101000000011000002100000000000010100000
PERISCEL  011102031101000013001210001000131120000001120001012012210001001210100000
PERPLEXU  01110112110000000100010001100011110000001110000011011000000100210100000
PICTUS    0111011211000000010001000110001111110000011100000110100000100210100000
PLATYPTE  01110112110000000100010001100111110000000011100000110110000100210100000
```

Table 1.   Continued.

	0	1	2	3	4	5	6	7
PLEURILI	0111010311010000030101000111000121010000001210000021001000000000110100000
POLITICE	0211120311010001130012100000000110113001002110002021122000000100022110100
PRAETOR	0111110311000010111012100011000111110000101110000001021000000100021010000
PROCERUS	0111010311101000010?01100011001121110000000111001007101100000100210100000
PULCHRIP	0211120311010010030012100100013111000000021100002101001000000200022110000
PUNCTIPE	0111010311000?000100011001110001111100000021100000210100000010001011000000
QUADRUM	0211120311110001300121001100121111000100210?01021122000000010?0221101000
QUEBECEN	0211120301010010010012100011312101100031100000210110000002000221100000
RILEYI	0211120311010000010012100011101131110000021100000211110000010000221100000
ROGEZENS	0110103111000000301012011110000110100100011100000201100000100?10100000
ROSSI	0211121301000010030012100010011111210000003110000021011000002000221100000
ROSSICUS	010100121100000001000110001110001111000000111000002111010000010002110100000
RUFICEPS	0111121311010000130012101001001211100010021100000221122000000100022101000
RUFICORN	0111203110100001300131001110011311100010021000000211220001001000210101000
RUFIPES	011112031101000013000210011100113111000100211000010212200000100211101000
RUGOSICO	0111010311001000030101300111001110011000011111100002000000000001100110100000
RUGULOSU	02111203110100001300121001110013111100010022000021121010100010002221100100
SANCTIHY	011101031200000001000100011100012110000010131001002101100100100210100000
SANCTIVE	1111000211100000010010011100111110000001000100000000000000002101000000
SATANAS	0111010311000000010001000111001121110000001210010070101101100100021010000
SCHIRJAE	0110203110?000013000210011100131110010021100000211210000001000210101000
SCRIPTUS	11101012110000000100011001111011110100001110000021010000001000?0101000000
SCRUTATO	011101121100000000010010011000111110000001110000011011000011000210100000
SERIATUS	11101012110000000300011001110011110000011100001101000000001000210101000
SHESTAKO	02111203010100001300021001100013121200011021200000211221100100002221100100
SIBIRICU	021102031101000013000210011100113111000100211000002121200000010000222110000
SIGNATUS	01110103110000000010001000110001210010000011001002101100110100022110000
SIMILIS	011101121100000000100011001100011110000011100000110110000011000210100000
SIMILLIM	0111011211000001000010010000111110000011110000011010000001001210100000
STIGMATO	0211011211000100010001000110001111100000110000011010100000010011111110000
SUDATORI	0111010311000000010011000111110000011100000210100000100010000?10100000
TATIANAE	01110203111010000030101300111000121100101113170300200000010001100101000000
TESTACEU	011100121100001000100010001100111110000000111000011011010000100121010000
TERMINAL	0111020311010000130012100110011311100010021000002121000010100020101000
TETRASPH	01101031010000000010000011000121100000000131004002101100000100021010000
TEXANUS	0111110411000010111002100010001001011100001011100000021010000010002101000
TRANSVER	011020311110000030001200111000121010000000011000002111000000100?70100000
TRISTIS	02101031100000001000100011000121110000001210010070101101000100021011000
TURKESTA	0211120311071000001300131001110011311100010021122000010100021010100
UFEI	011112031111000013001210011100121110001002110101071122000101000210101010
UNGULARI	02110103110100000000021001100012110000000210000021010000001000210101000
UNIPUNCT	011102031101000001300121001100113111000100210000002112200001010002101000
VAUGHANI	0211020301010010030012100010001312100000031100000210110000002000221100000
VENUSTUL	011102031107000113001210001100121112000100212000000212200000100210101100
WADAI	0111203010100002130002100211100012111200010021200010211220000001000210101100
XANTHOPS	0111071211000010001000110001100111011210000000110000010110100000100190101000
NEW SP.1	0111011211101000010001300111000110000002100200010100000000010210100000
NEW SP.2	0111010312000000010001000011100121210000001310010010110101010100021010000
NEW SP.3	011101121100000010001000110011111100000011100002011000010100010011101000000
NEW SP.4	011112031101000013001310011001131110001002110010211220000001002211010000
NEW SP.5	0111010311010000010001000111111100000021100001021022000000100021010000
NEW SP.6	011120311010001300131001100113111000010021000102102200000100022110100
NEW SP.7	0111011211010000010001000110001111100000011100000210100000010002101000000
NEW SP.8	0111103110000101110011000110011111100000111000000211000000010021010000
NEW SP.9	01110112110100000100010001100111111000000111000011100001010000000210100000
NEW SP10	011101031100000000010001100012111000000012100100210110000010000210100000
NEW SP11	0111010311000000010001000111001211100000031001002101010010002101000000
NEW SP12	0111011211101001000010011001000011110000021001001101000000010002101000000
NEW SP13	0211010311000000010001000111001211000000131001002101010100010002101000000
NEW SP14	0111010311000000100010011001110001110000010131003002101101000100021010000
NEW SP15	0111001211000100010001000110001111100000121000010110000001011210100000
NEW SP16	02210010110000000100011000110011111100000010100001011000010001111110000
NEW SP17	0111010311000000010001000110001111000001310030021010100010002101000000

Table 1. Continued.

```
        0         1         2         3         4         5         6         7
NEW SP18 02110112110000100100001100010000111110000001110000011011000000200022110000
NEW SP19 01110012110000000100011000100011111100000011100000110110000001011210100000
NEW SP20 01111203110100001300131001110011311100010021000102112200000010002101010000
NEW SP21 01110203110000213001210010001211110001002100010211210230000010002100100100
NEW SP22 01111203110100021300121001000013111100010021000102113300000010002210100100
NEW SP23 02111203110100001300121001100012111100010021000102112300000010002210011000
NEW SP24 01110112110000000100011000111010000000011010011011000000100002201000
NEW SP25 01110203110100001300121001100011311100010021000102112100010001000210101000
NEW SP26 02110103120000000100010001110001211100010121001002101100000010002211000000
NEW SP27 01110103110010000100100011000121110000000131001002101100000010002101000000
NEW SP28 01110103110100000300141001110001311100110021000002111200000010002101000100
NEW SP29 01111104110000001110021000010001011100000210210000010002101000000
NEW SP30 01110112110000000100110001110100000001110000011010000000100002101000000
NEW SP31 01111203110100001300121001110011311100010021000102112200000010002101010000
NEW SP32 01110112110000000100010001110001111000001110000101101100000010012101010000
NEW SP33 11110112110000000200011001110001110100000011100000?1010010000010002101000000
NEW SP34 01110103110000000100010001110001211000000121001002111100000010002221100000
NEW SP35 01110012110000000100010001100011111000000110000011011000000101121010000
NEW SP36 01010103110000000100010001110001211000000121000002101100000010002101000000
NEW SP37 02110103110000100100011001110011111100000011100000?1011000000010002221100000
NEW SP38 01110112101000100100010001100111111100000011100001101100000011000210100000
```

the analysis exceeded 128 taxa, a comprehensive matrix (Table 1) was maintained from which 'sample matrices' were drawn for analysis of newly analyzed species within the context of a representative sampling of species analyzed to date.

'Species-group' definition refinement.—It was found that "species-groups" consistently clustered on cladograms derived from Nelson consensuses throughout the course of the study (see Results). Refinement of these species-group definitions was aided by use of sample matrices. For a given species-group, all species previously found to be in the group were included in a sample matrix as described above, as well as most or all species in contiguous species-groups. Manual branch swapping was applied to the Nelson consensus tree after running the matrix on Hennig86 (m*; bb*; xs w; cc) in order to further refine the definition of the species-group by further reducing the length of the tree.

After definitions of all characters, character states, transformation series, and species-groups had been finalized, a final matrix with an approximately equal percentage of species from each species-

group (about 61.5%) was analyzed using the mhennig*; option of the Hennig86 program, in order to find the most parsimonious tree (Farris 1988). This percentage was found to meet the requirement of obtaining the tree with 128 taxa, with taxa most evenly distributed across it with respect to species-groups.

Host association analysis.—After a cladogram had been generated as described above, host associations were mapped onto the cladogram. Based on available literature (Shenefelt 1975, Achterberg 1985, Marsh 1979, Shaw 1983, 1994; Shaw 1995, Shaw et al. 1997), and museum specimens with host information attached were examined (Rocky Mountain Systematic Entomology Museum, Laramie, WY and Canadian National Collection, Ottawa, ON), host associations were assigned.

CHARACTER SUMMARY

Following is a list describing characters and evolutionary transformation series of those characters in this analysis, along with explanations of how polarities were hypothesized for each transformation series. The number assigned to each character identifies it on the matrix and on the

cladogram illustrated by CLADOS. The numbers in brackets indicate character states within the transformation series for a given character, and also appear underneath the numbers assigned to the respective characters in the matrix, and on the CLADOS-generated cladograms for each species-group. Squares on cladogram branches below designated character numbers represent character state transformations which help define the node or species following the squares. If the square is darkened, the square represents an increase in character state number; if white, a reversal is indicated. Unless otherwise stated, the [0] state was that hypothesized to be ancestral based on *Clinocentrus*, *Rogas* and *Stiropius* specimens examined.

1. *Head Characters*

4. *Shape of 15th flagellomere from base, females*: [0] width/length less than 0.83; [1] compact: width/length greater than 0.83. State [1] was found only in some *Aleiodes* species. Thus, state [0] was hypothesized to be ancestral.

6. *Occipital carina*: [0] strong, complete medially; [1] weak or effaced medially. State [1] was found in most *Stiropius* and no *Clinocentrus* or *Rogas* examined, and was hypothesized to be ancestral. This hypothesis was tested by comparing relative parsimony with respect to character polarization. The same matrix was run on Hennig86 as described above for two runs except that polarization was switched for each. Since the alternate polarity was most parsimonious (strong, complete occipital carina ancestral), this alternate hypothesis was accepted; the *Rogas/Clinocentrus* condition was hypothesized to be ancestral.

13. *Flagellum, female*: [0] > 33 flagellomeres; [1] ≤ 33 flagellomeres. All *Stiropius* species examined expressed state [1], and no *Clinocentrus* or *Rogas* species did. The more parsimonious character polarization was found by running each of the two possibilities on Hennig86. Based on par-

simony, the reduced number of flagellomeres was hypothesized to be derived where it occurred in *Aleiodes*.

14. *Ocellar diameter/distance between lateral ocellus and compound eye*: [0] < 2.5; [1] ≥ 2.5 (Shaw *et al.* 1997, Figs. 1–5). State [1] was observed in all *Rogas* species examined, and no *Stiropius*. A comparison of parsimony in which the polarity of this character was switched between two otherwise identical matrices showed that the polarization used here was most parsimonious. Thus, state [0] was hypothesized to be the ancestral state.

15. *Ratio of clypeo-antennal space to width of oral space*: [0] greater than 0.82; [1] 0.69–0.82; [2] less than 0.69. Since states [1] and [2] were not found in non-*Aleiodes* species examined, state [0] was hypothesized to be ancestral.

20. *Occipital carina at hypostomal carina*: [0] complete or nearly so; [1] incomplete, effaced well before reaching hypostomal carina. Determining polarity was problematic, since of four *Rogas* species examined, two expressed state [0], and two expressed [1]. The *Clinocentrus* species examined (four unnamed morphospecies) consistently exhibited state [0]. Two *Stiropius* species examined consistently possessed state [1]. Both codings were tried for the ancestor, with no change in the consistency index (c.i.). The above polarization represents the most parsimonious solution. Thus, state [0] was hypothesized to be the ancestral state.

27. *Ratio of malar space to mandibular basal width*: [0] less than 1; [1] greater than or equal to 1. State [0] was found in all *Rogas* and *Clinocentrus* species examined. State [1] was observed in all *Stiropius* examined. A comparison of parsimony between alternate polarizations revealed that the polarization presented here is the simplest explanation.

31. *Vertex sculpturing (path a–d)*: [0] coarsely granulate; [1] smooth, granulate, or faintly rugulose (Shaw *et al.* 1997, Fig. 6); [2] smooth with shallow, dense punc-

tation; [3] shiny, coarsely and densely punctate.

32. *Vertex sculpturing (path e–h)*: [0] nitid; [1] one of conditions in #31; [2] with strong laterally running ridges, or rugose; [3] with fine laterally running ridges (generalized advanced condition; Shaw *et al.* 1997, Fig. 5); [4] finely rugulose. The reticulate character described by the above 2 paths is hypothesized as follows: a = 31[0]; b = 31[1]; c = 31[2]; d = 31[3]; e = 32[0]; f = 32[2]; g = 32[3]; h = 32[04].

	a	b	c	d	e	f	g	h	path
n	0	1	2	3	1	1	1	1	a–d (#31)
n + 1	1	1	1	1	0	2	3	4	e–h (#32)

The above phylogenetic hypothesis is illustrated in Fig. 1d. *Stiropius* species observed all expressed state (a), and *Rogas* species all expressed state (e). A comparison of parsimony between alternate polarizations revealed that the polarization presented here is the simplest explanation.

33. *Medial carina extending down frons*: [0] absent; [1] present, extending less than 0.55 of distance from line between bases of scapes to clypeus; [2] present, extending 0.55 or more of distance from line between bases of scapes to clypeus. States [1] and [2] were observed in no non-*Aleiodes* species examined. Thus, state [0] was hypothesized to be the ancestral state.

38. *Lightness of midsection of antennae*: [0] not lighter than both basal and apical sections; [1] lighter than both basal and apical sections (Shaw *et al.* 1997, Fig. 23). State [1] was not found in non-*Aleiodes* species examined. Thus, state [0] was hypothesized to be the ancestral state.

48. *Clypeal carina (path a–c)*: [0] absent; [1] present, shelflike; [2] shelflike.

49. *Clypeal carina (path b–d)*: [0] clypeus either not elongate, or with a carina; [1] elongate clypeus without carina. The reticulate character described by the above 2 paths is hypothesized as follows: a = 49[0]; b = 49[1]; c = 49[2]; d = 50[1]

	a	b	c	d	path
n	0	1	2	1	a–c (#48)
n + 1	0	0	0	1	b–d (#49)

The above phylogenetic hypothesis is illustrated in Fig. 1g. States [1] and [2] were observed in no non-*Aleiodes* examined. Thus, state [0] was hypothesized to be the ancestral state.

51. *Length of first flagellomere*: [0] ≥ scape length; [1] < scape length. State [1] was not observed in non-*Aleiodes* species examined. Thus, state [0] was hypothesized to be the ancestral state.

54. *Clypeus height divided by width*: [0] > 0.65; [1] ≤ 0.65 ≥ 0.42; [2] < .42 > .30; [3] ≤ 0.30. Height was defined as distance between clypeo-labral suture and dorsal edge of clypeus. Width was defined as distance between inner edges of tentorial pits. All *Stiropius* and *Rogas* examined expressed state [0]. *Clinocentrus* expressed state [1]; However, given that *Stiropius* and *Rogas* are phylogenetically closer to *Aleiodes* than *Clinocentrus* (Whitfield 1992), the elongated clypeal condition in *Clinocentrus* was hypothesized to be independently derived with respect to the *Aleiodes* condition, and state [0] was hypothesized to be ancestral.

55. *Third maxillary palpomere*: [0] not swollen; [1] swollen. State [1] was not observed in non-*Aleiodes* species examined. Thus, state [0] was hypothesized to be the ancestral state.

69. *Clypeus shape*: [0] not abruptly edged, not flat ventrad (ancestor); [1] abruptly edged, flat ventrad. State [1] was not observed in non-*Aleiodes* species examined. Thus, state [0] was hypothesized to be the ancestral state.

70. *Wide, flat flange on lower side of mandible*: [0] not strongly present; [1] strongly present. State [1] was not observed in non-*Aleiodes* species examined. Thus, state [0] was hypothesized to be the ancestral state.

II. *Mesosomal Characters*

3. *Median carina of propodeum*: [0] short and forking before halfway point of propodeum (Achterberg 1991, Fig. 121); [1] not forking before halfway point of propodeum. *Rogas* and *Clinocentrus* species examined expressed the [0] state. *Stiropius* and *Aleiodes* independently expressed different states which were not [0]. Thus, state [1] was hypothesized to be the ancestral state for *Aleiodes*.

7. *Sculpture of propodeum antero-laterally (path a–e)*: [0] finely, smoothly granulate; [1] coarsely granulate, or areolate; [2] rugulocostate over granulate surface, not shiny; [3] rugose over granulate surface or no underlying granulation; [4] smooth-punctate.

8. *Sculpture of propodeum antero-laterally (path f–g)*: [0] granulate with faint rugulosity or granulate (Shaw *et al.* 1997, Figs. 7–10); [1] one of states in #7; [2] nitid. The above two paths constitute a reticulate transformation series, which is hypothesized as follows: a = 7[0]; b = 7[1]; c = 7[2]; d = 7[3]; e = 7[4]; f = 8[0]; g = 8[2]

	a	b	c	d	e	f	g	path
n	0	1	2	3	4	3	3	a-e (#7)
n + 1	1	1	1	1	1	1	2	0	f-g (#8)

The above phylogenetic hypothesis is illustrated in Fig. 1a. The states represented by (b) were not found in *Aleiodes*. The propodeums of *Clinocentrus* and *Rogas* were areolate; that of *Stiropius* was coarsely granulate. Thus, one of the states represented by (b) was hypothesized to be the ancestral state.

12. *Pronotum angle*: [0] not shelflike (Achterberg 1991, Figs. 283, 294, 380); [1] shelflike (Achterberg and Penteado-Dias 1995, Figs. 6, 11, 16, 21, 26) State [1] was not observed in any non-*Aleiodes* species examined. Thus, state [0] was hypothesized to be the ancestral state.

16. *Large setal pits on scutellum*: [0] absent; [1] present. Since state [1] was not found in any non-*Aleiodes* species examined, state [0] was hypothesized to be ancestral.

19. *Prescutellar carina*: [0] without an anterior invagination; [1] with an anterior invagination. State [1] was observed in no non-*Aleiodes* species. Thus, state [0] was hypothesized to be the ancestral state.

21. *Mesopleuron central disc sculpturing (path a–e)*: [0] shiny coarse granulation; [1] granulate; [2] smooth-punctate; [3] heavily punctate.

22. *Mesopleuron central disc sculpturing (path f–h)*: [0] coarsely rugulose; [1] granulate, or other states in #21; [2] costate from granulate or partly costate, partly granulate; [3] partly smooth, partly rugulose.

23. *Mesopleuron central disc sculpturing (c–i)*: [0] not nitid; [1] nitid.

24. *Mesopleuron central disc sculpturing (d–j)*: [0] not costate from punctate; [1] costate from punctate. The reticulate character described by the above 4 paths is hypothesized as follows: a = 21[0]; b = 21[1]; c = 21[2]; d = 21[2]; e = 21[4]; f = 22[0]; g = 22[2]; h = 22[3]; i = 23[0]; j = 24[1].

	a	b	c	d	e	f	g	h	i	j	path
n	0	1	2	3	4	1	1	1	2	3	a-e (#21)
n + 1	1	1	1	1	1	0	2	3	1	1	f-h (#22)
n + 2	1	1	1	1	1	1	1	1	0	1	c-i (#23)
n + 3	0	0	0	0	0	0	0	0	0	1	d-j (#24)

The above phylogenetic hypothesis is illustrated in Fig. 1c. In this case, a reticulate transformation series was considered the best way to interpret the data because of the high degree of variability. No *Aleiodes* species was coded with (a). *Clinocentrus* and *Rogas* species examined expressed the nitid condition, and *Stiropius* expressed shiny, coarse granulation. Given the plasticity of mesopleural sculpturing within genus *Aleiodes*, as can be seen by the above complex reticulation of character states, the *Aleiodes* nitid condition was hypothesized to have evolved inde-

pendently from the *Rogas* nitid condition. The shiny coarse (a) condition was hypothesized to have been the ancestral condition for *Aleiodes*.

25. *Sternaulus*: [0] not sculptured; [1] rugose or rugulose. *Stiropius* expressed state [0]. *Rogas* expressed a uniquely foveate condition not found anywhere else, and *Clinocentrus* expressed rugation less regular than the *Rogas* condition, but more so than the condition observed in *Aleiodes*. Since only *Aleiodes* species expressed the [0] condition in common with *Stiropius*, the [0] condition was hypothesized to be ancestral.

39. *Mesopleural pit posteriad to central disc of mesopleuron*: [0] absent; [1] present. State [1] was not found in non-*Aleiodes* species examined. Thus, state [0] was hypothesized to be the ancestral state.

40. *Protuberances or a raised ridge immediately anteriad to propodeal apex*: [0] absent; [1] present. State [1] was not found in non-*Aleiodes* species examined. Thus, state [0] was hypothesized to be the ancestral state.

41. *Pronotal anterior flange*: [0] < 0.28 of pronotal length; [1] ≥ 0.28 of pronotal length. State [1] was not found in non-*Aleiodes* species examined. Thus, state [0] was hypothesized to be the ancestral state.

50. *Postero-dorsal surface of scutum*: [0] mostly nitid, sometimes weakly rugulose; [1] weakly rugulose, not shiny; [2] at least some strong costae; costae smooth; [3] smooth, not nitid. State [0] was observed in *Clinocentrus*, *Rogas*, and *Stiropius* species examined, but in no *Aleiodes*, and was hypothesized to be the ancestral condition.

52. *Notauli at mid-dorsal surface of scutum*: [0] without carinae or foveae or finely foveate, non-carinate; [1] coarsely foveate, and/or usually carinate posteriad; [2] smooth, not nitid. States [1] and [2] were not found in any *Rogas* or *Stiropius* examined. However, the coarsely foveate condition was ubiquitous in *Clinocentrus*. Given the above, it was hypothesized that state [0] was ancestral, and that the *Cli-*

nocentrus condition was derived in parallel with the state's appearance in *Aleiodes*.

53. *Scutal sculpturing excluding postero-dorsal surface and notauli*: [0] rugulose sculpturing over a nitid surface; [1] granulate; [2] punctate; [3] nitid or smooth, not nitid. States [1], [2], and [3] were not expressed by non-*Aleiodes* species examined. *Stiropius* expressed the coarsely granulate condition, *Rogas* expressed rugulose sculpturing over a nitid surface, and *Clinocentrus* expressed a nitid-punctate scutal surface. Since *Rogas* is considered the sister group of Aleiodes (Whitfield 1992), state [0] was hypothesized to be ancestral.

61. *Propodeum dorsal profile*: [0] rounded; [1] flattened. State [1] was not observed in non-*Aleiodes* species examined. State [0] was hypothesized to be ancestral.

63. *Ratio of pronotal medial length to head length*: [0] ≥ 0.30; [1] < 0.30. Head length was defined as distance from the occipital carina at the vertex to the line between posterior edges of antennal sutures. State [1] was observed in *Stiropius* and some *Aleiodes*, but not in *Rogas* or *Clinocentrus*. Given the very small ocelli of *Stiropius*, such that the ocellocular distance/ocellar diameter ratio was consistently much greater than one, the vertex broad in comparison with the three other genera, and the antennal flagellomeres over twice as long as wide in contrast with the three other genera, it was hypothesized that the *Stiropius* condition was independently derived. Thus, it was hypothesized that state [0] was the ancestral condition.

III. *Metasomal Characters*

2. *Median carina of tergite II*: [0] undifferentiated from other coarse carinae (Achterberg 1991, Fig. 124); [1] differentiated from other carinae (Achterberg 1991, Fig. 377); [2] undifferentiated from other fine carinae. State [0] is the *Stiropius/Rogas* condition. *Clinocentrus* shared [1] with some *Aleiodes*. Since *Clinocentrus* is considered most distantly related to *Aleiodes* of the three outgroup genera (Whitfield

1992), it was hypothesized that state [1] was independently derived in *Clinocentrus* and *Aleiodes*.

5. *Median triangle of tergite II*: [0] absent; [1] small and without well developed anterior carinae (Achterberg 1991, Fig. 290); [2] large and associated with anterior carinae which run laterally nearly to margins of tergite (Achterberg 1991, Fig. 300). The presence of a median triangle differentiates most *Aleiodes* with respect to *Rogas* and *Stiropius*. Thus, state [0] was hypothesized to be the ancestral state.

10. *Length of metasomal tergite I, female*: [0] tergite apical width/tergite length greater than or equal to 0.87 (not elongate); [1] tergite apical width/tergite length less than 0.87 (elongate). An elongate first metasomal tergite was not present in *Stiropius*, and only occasionally present in *Clinocentrus* and *Rogas*. Thus, its occasional presence in *Aleiodes, Clinocentrus, and Rogas* was hypothesized to be independently derived.

28. *Setal mat on metasomal tergites 4–6 of males*: [0] absent; [1] present (Shaw *et al.* 1998, Fig. 1). State [1] was expressed by no non-*Aleiodes* species examined. Thus, state [0] was hypothesized to be the ancestral state.

29. *Medial pits on tergites 4–7, males*: [0] absent; [1] present (Shaw *et al.* 1997, Figs. 13, 15, 17) State [1] was expressed by no non-*Aleiodes* species examined. Thus, state [0] was hypothesized to be the ancestral state.

34. *Sculpturing of metasomal tergite I (path a–c)*: [0] weakly or strongly costate, costae relatively widely spaced, often over weak granulation; [1] rugulocostate or rugocostate; or costate, costae narrowly spaced, no underlying sculpturing; [2] finely rugulose to finely rugulocostate (Shaw *et al.* 1997, Figs. 11, 12).

35. *Sculpturing of metasomal tergite I (path e–f)*: [0] rugose or rugulose; [1] one of conditions of #34; [2] smoothly rugose; [3] strongly costate, costae narrowly spaced, no underlying sculpturing; [4]

weakly costate, costae narrowly spaced, no underlying sculpturing, or nitid.

36. *Sculpturing of metasomal tergite I (path b–h)*: [0] not smoothly, finely granulate; [1] smoothly, finely granulate. The reticulate character described by the above two paths is hypothesized as follows: a = 34[0]; b = 34[1]; c = 34[2]; d = 35[3]; e = 35[0]; f = 35[4]; g = 35[2]; h = 36[1].

	a	b	c	d	e	f	g	h	path
n	0	1	2	1	1	1	1	1	a-c (#34)
n + 1	1	1	1	3	0	4	2	1	e-f (#35)
n + 2	0	0	0	0	0	0	0	1	b-h (#36)

The above phylogenetic hypothesis is illustrated in Fig. 1e. State (a) was observed in all *Clinocentrus* and *Rogas* examined, and in some *Aleiodes* species. The coarsely granulate *Stiropius* condition was hypothesized to be a derived synapomorphy for that group, and (a) was hypothesized to be ancestral.

42. *Metasomal tergite III sculpturing (path a–d)*: [0] completely, finely smooth-aciculate; [1] weakly to strongly rugulocostate or weakly costate over granulate background; costae not smooth, tergite not shiny; [2] smooth-aciculate or smoothly rugulose anteriad, nitid or smooth-punctate posteriad, or entirely nitid or smooth punctate; [3] shallowly rugulose or rugulopunctate anteriad, finely punctate posteriad or completely finely punctate.

43. *Metasomal tergite III sculpturing (path e–g)*: [0] smooth, faintly granulate, shiny; [1] one of states of #42; [2] entirely carinate; [3] strongly rugose.

44. *Metasomal tergite III sculpturing (path h–i)*: [0] completely smooth, shiny, no trace of granulation; [1] one of conditions of #42; [2] densely punctate or rugulopunctate anteriad; shiny posteriad, or entirely densely punctate. The reticulate character described by the above 3 paths is hypothesized as follows: a = 42[0]; b = 42[1]; c = 42[2] d = 42[3]; e = 43[0] f = 43[2]; g = 43[3]; h = 44[0]; i = 44[2].

	a	b	c	d	e	f	g	h	i	path
n	0	1	2	3	1	1	1	2	2	a-d (#42)
n + 1	1	1	1	1	0	2	3	1	1	e-g (#43)
n + 2	1	1	1	1	1	1	1	0	2	h-i (#44)

The ancestral state is (b). The above phylogenetic hypothesis is illustrated in Fig. 1f. Since state (a) was ubiquitous in all *Rogas* species examined and in many *Aleiodes*, it was hypothesized to be ancestral.

45. *Excavated medial areas on metasomal tergites II and III*: [0] absent; [1] present (Achterberg 1985, Fig. 12). State [1] was not found in non-*Aleiodes* species examined. Thus, state [0] was hypothesized to be the ancestral state.

46. *Apex of abdomen, females*: [0] not compressed; [1] compressed. State [1] was not found in non-*Aleiodes* species examined. Thus, state [0] was hypothesized to be the ancestral state.

47. *Fourth metasomal tergite (MT IV)*: [0] MT IV unsculptured; [1] MT IV slightly sculptured; [2] MT IV mostly sculptured, not heavily rugulose; [3] MT IV heavily rugulose, but not a complete carapace over apicad tergites; [4] MT IV a heavily rugulose, complete carapace over apicad tergites. States [1] through [4] were found in no non-*Aleiodes* species examined. Thus, state [0] was hypothesized to be the ancestral state.

56. *Metasomal dorsum color*: [0] not entirely black; [1] entirely black. State [1] was observed in some unicolored *Stiropius* and *Clinocentrus* species, and in some *Aleiodes* species. Since all *Rogas* species observed were uniformly yellow, and many *Aleiodes* expressing state [1] had heads and/or mesosoma that were not black, it was hypothesized that the *Stiropius* and *Clinocentrus* conditions were independently derived from the condition in *Aleiodes*, and that state [0] was ancestral.

57. *Metapleural pit*: [0] not slightly larger than propodeal spiracle, deep and round;

[1] slightly larger than propodeal spiracle, deep and round. State [1] was not observed in non-*Aleiodes* species examined. Thus, state [0] was hypothesized to be the ancestral state.

58. *Head/mesosoma/apical metasomal coloration (metasomal tergite III and posteriad; females)*: [0] not all black with bicolored metasoma; [1] all black with bicolored metasoma. State [1] was not observed in non-*Aleiodes* species examined. Thus, state [0] was hypothesized to be the ancestral state.

59. *Metasomal tergite II coloration*: [0] not consistently black laterally, yellow medially; [1] consistently black laterally, yellow medially. State [1] was not observed in non-*Aleiodes* species examined. Thus, state [0] was hypothesized to be the ancestral state.

62. *Ovipositor length*: [0] less than ½ length of metafemur; [1] greater than or equal to ½ length of metafemur. All *Stiropius* species examined had short ovipositors, and most *Rogas* species and all *Clinocentrus* species examined had long ovipositors. Since most *Aleiodes* species examined had short ovipositors, short ovipositor length was hypothesized to be the ancestral condition.

71. *Lateral edges of metasomal tergite I*: [0] not parallel; [1] parallel. State [1] was not observed in non-*Aleiodes* species examined. Thus, state [0] was hypothesized to be the ancestral state.

72. *Metasomal tergite III*: [0] not carapace-like; [1] carapace-like, extending over apicad tergites. State [1] was not observed in non-*Aleiodes* species examined. Thus, state [0] was hypothesized to be the ancestral state.

IV. *Wing Characters*

9. *Second submarginal cell*: [0] long, narrow, vein 2RS/vein 2-M less than 0.4; 2RS parallel or nearly so with r-m; [1] trapezoidal or rectangular, defining veins often arched, 2RS/2-M greater than 0.45 and less than 0.71; [2] quadrate; 2RS parallel or nearly so with r-m, and 2RS/2-M greater

than 0.71. Since the second submarginal cells of *Clinocentrus*, *Rogas*, and *Stiropius* species examined all expressed state [1], and since the ordering described above is most logical, it was hypothesized that this is a bipolar character

17. *RS vein of hind wing (path a–d)*: [0] marginal cell widest basally, RS vein not recurved apically (Achterberg 1991, Fig. 54); [1] marginal cell narrowest in middle; RS vein moderately to slightly recurved apically, never nearly touching wing margin (Achterberg 1991, Fig. 278); [2] RS vein parallel with costal wing margin in basal ½–⅔, abruptly angling posteriad apically; [3] marginal cell not narrowest in middle; RS vein not recurved or angling; straight or nearly (Achterberg 1991, Fig. 291).

18. *RS vein of hind wing (path b–e)*: [0] not extremely narrow in middle; vein not nearly touching wing margin; [1] extremely narrow in middle, vein nearly touching wing margin (Achterberg 1993a, plate 31). The reticulate character described by the above two paths is hypothesized as follows: a = 17[0]; b = 17[1]; c = 17[2]; d = 17[3]; e = 18[1].

	a	b	c	d	e	path
n	0	1	2	3		1	a-d (#17)
n + 1	0	0	0	0	1	b-e (#18)

State (a) was observed in *Clinocentrus*, *Rogas*, and *Stiropius* species examined, but not in any *Aleiodes*. Thus, it was hypothesized to be the ancestral state. State (b) was hypothesized to be the most basal state for this character within *Aleiodes*, since it represents only one modification from the ancestral state: the recurvation of the apical section of the RS vein. States (c) and (d) were hypothesized to represent a progressive straightening of the RS vein from the original curved condition. State (e) was hypothesized to represent a bifurcation in the evolution of this character, such that the (b) condition evolved in some Aleiodes lineages into the straightened (c) and (d) conditions, and on the other hand into the extremely recurved (e) condition in another. The above phylogenetic hypothesis is illustrated in Fig. 1b.

26. *Wing coloration*: [0] fumate; [1] hyaline; [2] patterned. State [1] was universal for all *Clinocentrus*, *Rogas*, and *Stiropius* species examined, and most *Aleiodes* species. States [0] and [2] were not observed in any non-*Aleiodes* species examined. Given the ubiquity of state [1], were non-hyaline wings to occur in non-*Aleiodes* species, they would almost certainly represent a parallel derived condition. Thus, state [1] was hypothesized to be the ancestral state.

30. *Hindwing vein 1A*: [0] not extending past vein cu-a; [1] extending past vein cu-a. State [1] was found in no non-*Aleiodes* species examined. Thus, state [0] was hypothesized to be the ancestral state.

60. *Fore wing width divided by length*: [0] less than 0.29 (long, narrow); [1] 0.29–0.34; [2] greater than or equal to 0.35 (broad). States [0] and [2] were not observed in non-*Aleiodes* species examined. State [1] was hypothesized to be ancestral; thus, the character was hypothesized to be bipolar.

V. Leg Characters

0. *Inner apex of hind tibia*: [0] with setae normal and unmodified; [1] with setae flattened coming to a point apically, forming an apical fringe (Achterberg 1991, Fig. 122). State [1] is the norm for *Rogas*, but does not occur in any *Stiropius* or *Clinocentrus* species so far as known (Shaw 1993). It was considered to be derived in *Rogas* and in any *Aleiodes* in which it occurred. Thus, state [0] was hypothesized to be the ancestral state.

1. *Tarsal claw*: [0] either no tarsal teeth or if present, preapical lobe present (Achterberg 1991, Figs. 123, 322); [1] no preapical lobe, with basal tarsal teeth only; [2] no preapical lobe, tarsal teeth extending almost to apical tooth, or tarsi completely pectinate (Fig. 2c; Shaw *et al.* 1997, Figs. 20–22). Since the presence of tarsal teeth with no preapical lobe is an autapomor-
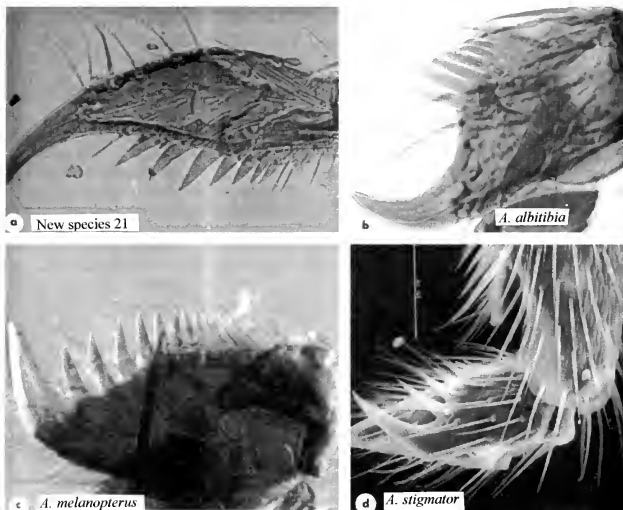
Fig. 2.   Tarsal claws. a, "new species 21;" b, *A. albitibia*; c, *A. melanopterus*; d, *A. stigmator*.

phy for genus *Aleiodes* distinguishing it from *Clinocentrus*, *Rogas*, and *Stiropius*, state [0] in part defines the hypothetical ancestor. Thus, state [0] was hypothesized to be the ancestral state for these four genera, and state [1] was hypothesized to be the ancestral state for *Aleiodes*.

11. *Tarsal segment 4, female*: [0] elongate: length ≥ 1.6 times apical width; [1] compact: length < 1.6 times width. State [1] was not observed in non-*Aleiodes* species examined. Thus, state [0] was hypothesized to be the ancestral state.

37. *Lightness of hind tarsus*: [0] not considerably lighter than tibia; [1] considerably lighter than tibia (Shaw et al. 1997, Fig. 24). State [1] was not found in non-*Aleiodes* species examined. Thus, state [0] was hypothesized to be the ancestral state.

64. *Number of tarsal claw teeth*: [0] none;

[1] 5 or less; [2] more than 5. State [0] was shared by some *Rogas*, all *Clinocentrus* and *Stiropius*, so far as known, and was hypothesized to be the ancestral state.

65. *Shape of apical tarsal tooth*: [0] not present; [1] incompletely toothed; [2] completely toothed (Fig. 2c; Shaw et al. 1997, Figs. 19–22). The incomplete form was reminiscent of a thickened seta, with a hair-like, flexible apex. State [0] was hypothesized to be ancestral, for reasons stated for character 64.

66. *Setae between apical tarsal tooth and claw*: [0] present (Fig. 2a, b); [1] absent (Fig. 2c, d). Several *Aleiodes* species which expressed incompletely toothed apical tarsal teeth, also expressed basal tarsal teeth only. In addition, they expressed a gradation of thickened, prominent setae which became progressively thinner with

increasing apical position apicad of the apical tooth. Thus, it was hypothesized that state [1] represented the completion of a transformation of apical setae into teeth, and thus that state [0] was ancestral.

67. *Shape of apical tarsal claw (path a–c)*: [0] nearly without a hook (Fig. 2a); [1] not abruptly hooked (Fig. 2b); [2] abruptly hooked with straight shank which angles at nearly 90 degrees (Fig. 2c).

68. *Shape of apical tarsal claw (path b–d)*: [0] one of above states; [1] abruptly hooked with straight shank which angles at less than 90 degrees (Fig. 2d). The reticulate character described by the above two paths is hypothesized as follows: a = 67[0]; b = 67[1]; c = 67[2]; d = 68[1].

	a	b	c	d	path
n	0	1	2	1	a-c (#67)
n + 1	0	0	0	1	b-d (#68)

State (b) was universal in all non-*Aleiodes* species examined, and most *Aleiodes* species. Thus, it was hypothesized to be the ancestral state. The above phylogenetic hypothesis is illustrated in Fig. 1h.

RESULTS

Throughout the development of this analysis, species-groups emerged and defined themselves by consistently clustering on the most parsimonious consensus tree. Once all species had been analyzed, 18 well-defined species-groups had emerged. Figs. 6 to 8 show the major species-groups within genus *Aleiodes*. Fig. 5 shows the overall phylogenetic pattern of the genus, with species-groups represented by exemplar species.

Initially assigning equal weight to all characters resulted in one most parsimonious tree using the mhennig* option. This tree had a length of 475 steps, a consistency index (c.i.) of .25, and a retention index (r.i.) of .78. Extended branch swapping (bb* option) resulted in 755 equally parsimonious trees all with lengths of 475 steps.

The final solution for successive iterations to character weighting applied to the trees before the Nelson consensus was run resulted in 755 most parsimonious trees, each with length of 624 steps, a c.i. of .56, and an r.i. of .91. The modified Nelson consensus tree of the final solution for the overall unweighted analysis, after manual branch swapping, is shown in Fig. 5. The Nelson consensus tree length of the unweighted tree loaded into CLADOS was reduced by 140 steps by manual branch swapping.

The genus can be divided into three major sections: basal, intermediate, and derived species. Basal species are defined as those in which 1) the occipital carina is usually weak or effaced medially, 2) hindwing RS vein is recurved, 3) hind-wing vein 1A usually does not extend past vein cu-a, 4) propodeal sculpturing is coarsely granular, or rugulocostate over a granulate surface, 5) mesopleuron is granulate, 6) mesopleural pit posteriad to mesopleuron central disk is absent, and 7) median triangle of tergite II is small or absent and without well developed anterior carinae. In the overall cladogram (Fig. 3), groups 1–6 are basal groups.

Intermediate species are defined as those with above characteristics except 1) the occipital carina is complete medially, 2) propodeal sculpturing is rugose, 3) the hind-wing RS vein may be straight, and 4) mesopleuron may be rugulose (groups 7–9).

Derived species are defined as those with the characteristics for intermediate species except 1) mesopleuron sculpturing is smooth punctate or smooth, 2) the hind-wing RS vein is almost always straight, 3) third metasomal tergite is either smooth-aciculate or smoothly rugulose or rugulocostate anteriad and either smooth-shiny or smoothly rugulose posteriad, or entirely smooth or entirely punctate 4) hind-wing vein 1A extends past vein cu-a, and 5) the antero-medial triangle of metasomal tergite II is large and associated with an-

terior carinae which run laterally. There is an increasing tendency with derived position on the cladogram for the mesopleural pit posteriad to mesopleuron central disk to be present (groups 10–18).

Species-group definitions

Some species in unresolved clusters, or which did not clearly fall within any cluster, were not placed within any species-group. These species either were in the basal section, or fell at the base of a well-defined species-group. Such species were *A. armatus*, *A. arnoldi*, *A. cariniventris*, *A. ferrugileti*, *A. jaroslawensis*, *A. medianus*, *A. modestus*, *A. pellucens*, *A. quadrum*, *A. rossicus*, *A. ruficeps*, *A. sibiricus*, *A. ungularis*, and new species 7 and 9.

Species included below which will be published later by Shaw *et al.* are designated as new species (number). This text does not constitute a publication of any new species.

1. The *gressitti* species-group (Fig. 4a) consists of *A. gressitti* (Muesebeck) and new species 16. This is the basal-most group in the genus, and is defined by propodeum and metasomal tergite I finely, smooth-shiny granulate.

2. The *compressor* species-group (Fig. 4a) consists of known species *A. aligarhensis* (Quadri), *A. compressor* (Herrich-Schaffer), *A. palmatus* (Walley), and new species 24. The group is monophyletic, and defined by the following synapomorphies: 1) apex of female abdomen compressed, and 2) apical tarsal tooth complete.

3. The *gastritor* species-group (Fig. 4b) is a large monophyletic basal group defined by pronotal medial length ≤ .30% of head length. It consists of *A. buoculus* Marsh, *A. cantharius* (Lyle), *A. dendrolimi* (Matsumura), *A. gastritor* (Thunberg), *A. laphygmae* (Viereck), *A. malacosomatos* (Mason), *A. nocturnus* Telenga, *A. nolophanae* (Ashmead), *A. pallescens* Hellen, *A. perplexus* (Gahan), *A. platypterygis* (Ashmead), *A. similli-*mus (Ashmead), *A. stigmator* (Say), *A. testaceus* (Telenga), *A. xanthus* (Marshall), and new species 3, 15, 32, and 35.

4. The *circumscriptus* species-group (Fig. 6c) is a basal, monophyletic group defined by metasomal tergite II consistently yellow medially and black laterally. Species within the group are: *A. autographae* (Viereck), *A. borealis* Thomson, *A. circumscriptus* (Nees von Esenbeck), *A. nigricornis* Wesmael, *A. pictus* (Herrich-Schaffer), *A. similis* (Curtis), *A. scrutator* (Say), and new species 38.

5. The *pallidator* species-group (Fig. 4d), also basal and monophyletic, is defined by eye diameter greater than 2.5× ocellocular space, and tarsal claws pectinate. The species in this group are *A. indiscretus* (Reardon), *A. lymantriae* (Watanabe), *A. martini* Marsh and Shaw, *A. pallidator* (Thunberg) and new species 37.

6. The *seriatus* species-group (Marsh *et al.* 1998; Fig. 4e) is basal and monophyletic and is defined by hind tibial apex with flattened setae forming a fringe. The group consists of *A. bakeri* (Brues), *A. femoratus* Cresson, *A. kuslitzkyi* Tobias, *A. nigribasis* (Enderlein), *A. nigristemmaticum* (Enderlein), *A. sanctivincentensis* (Shenefelt), *A. percurrens* (Lyle), *A. scriptus* (Enderlein), *A. seriatus* (Herrich-Schaffer), and new species 30 and 33.

7. The *procerus* species-group (Fig. 5a), which is monophyletic, consists of *A. angustatus* (Papp), *A. crassipes* Telenga, *A. granulatus* (De Gant), *A. narangae* (Rohwer), and *A. procerus* Wesmael, and new species 1. It is closely related to the *A. dispar* species-group. The group shares the following synapomorphies: 1) metasomal tergite 4 slightly sculptured, and 2) metasomal tergite 1 elongate. All except *A. crassipes* and *A. angustatus* share a long, shelflike pronotum.

Host Legend

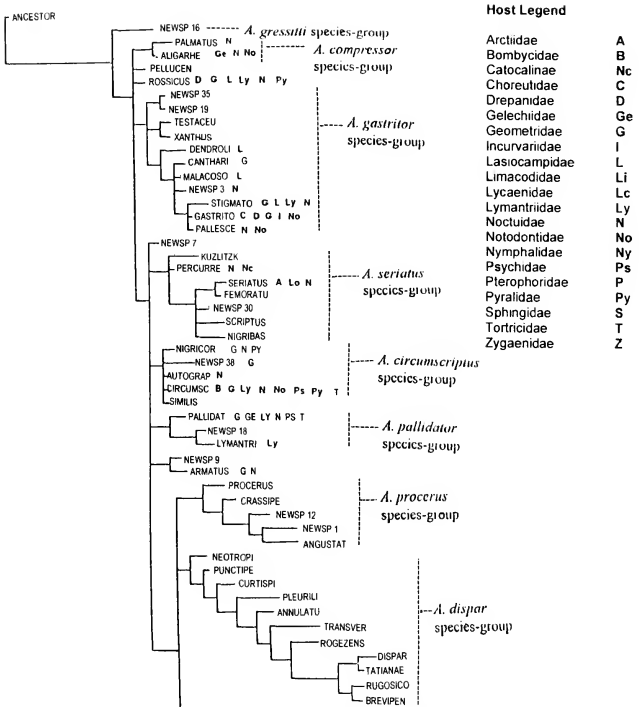|	
Arctiidae	A
Bombycidae	B
Catocalinae	Nc
Choreutidae	C
Drepanidae	D
Gelechiidae	Ge
Geometridae	G
Incurvariidae	I
Lasiocampidae	L
Limacodidae	Li
Lycaenidae	Lc
Lymantriidae	Ly
Noctuidae	N
Notodontidae	No
Nymphalidae	Ny
Psychidae	Ps
Pterophoridae	P
Pyralidae	Py
Sphingidae	S
Tortricidae	T
Zygaenidae	Z

Fig. 3. Cladogram showing overall phylogenetic pattern of *Aleiodes*. Species-groups are represented by exemplar species. Hosts and respective codes are listed in legend. Host associations for *Aleiodes* species are represented by codes next to species.

8. The *coxalis* species-group (Fig. 5b) is an intermediate monophyletic group defined by: 1) rugulose to rugose mesopleuron, and 2) vertex with widely separated laterally running ridges. The following species fall in this group: *A. aciculatus* Cresson, *A. alter-*nator (Nees von Esenbeck), *A. arcticus* Thomson, *A. bicolor* (Spinola), *A. coxalis* (Spinola), *A. coxator* Telenga, *A. hellenicus* Papp, *A. incertoides* Telenga, *A. incertus* Kokoujev, *A. jakolewi* Kokoujev, *A. moldavicus* Tobias, *A. negativus* Tobias, *A. nunbergi* Noskiewicz,
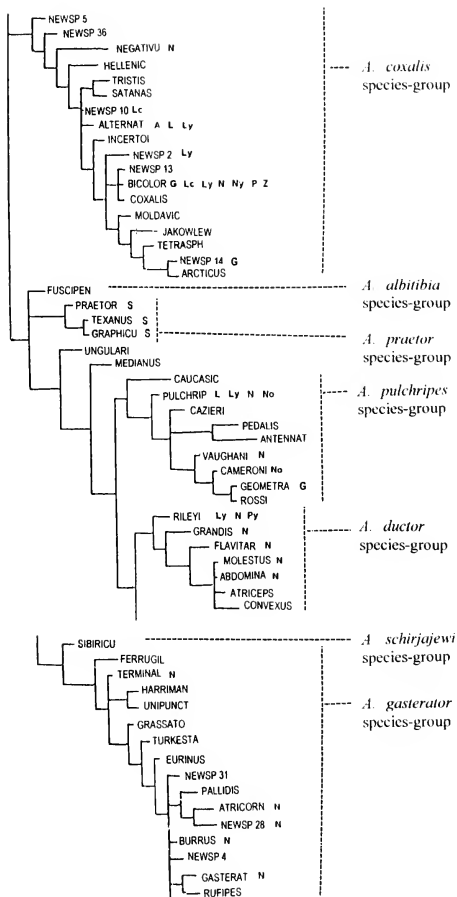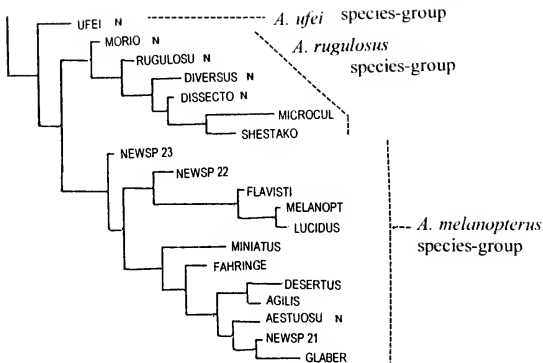
Fig. 3. Continued.

Fig. 3. Continued.

A. *sanctihyacinthi* (Provancher), A. *satanus* Telenga, A. *signatus* (Nees von Esenbeck), subgenus *Tetrasphaeropyx* Ashmead; A. *tristis* Wesmael, and new species 2, 5, 10, 11, 13, 14, 17, 26, 27, 34, and 36.

9. The ***dispar*** species-group (Fig. 5c), a monophyletic group, consists of A. *aleutaceus* Granger, A. *annulatus* Granger, A. *brevipendulatus* Achterberg, A. *breviradialis* Granger, A. *curtispina* Granger, A. *dispar* (Curtis), A. *diversicornis* Granger, A. *excavatus* (Telenga), A. *longicornis* Granger, A. *longipendulatus* Achterberg, A. *neotropicalis* (Shenefelt), A. *perinetensis* Shenefelt, A. *plurilineatus* (Cameron), A. *punctipes* Thomson, A. *rogezensis* Granger, A. *rugosicostalis* Achterberg, A. *tatianae* (Telenga), and A. *transversestriatus* Granger. It is defined by the narrow forewing, which has a length/widest width ratio ≤ 0.29.

10. The ***albitibia*** species-group (Shaw et al. 1998b; Fig. 6b), consisting of A. *albitibia* (Herrich-Schaffer) and A. *fuscipennis* (Szepligeti), is defined by nitid

mesopleuron. This character state also occurs in A. *pulchripes* Wesmael, which falls well outside of this group.

11. The ***praetor*** species-group (Shaw et al. 1998b; Fig. 6b) is monophyletic and consists of A. *graphicus* (Cresson), A. *praetor* (Reinhard), A. *texanus* Cresson, and new species 8 and 29. The group is defined by: 1) the strongly recurved hindwing radiellen vein which nearly touches the costal margin; 2) lateral ocellar diameter greater than 2.5 times ocellocular distance; and 3) short 15th flagellomere.

12. The ***apicalis*** species-group (Shaw et al. 1998a; Fig 6a) is a derived monophyletic group.

13. The ***pulchripes*** species-group (Shaw et al. 1997; Fig. 6c) is a derived monophyletic group.

14. The ***gasterator*** species-group (Fig. 7a) is paraphyletic, and it is the basal species-group within the derived species-group cluster of the derived section. This species-group cluster is defined by clypeus abruptly edged, flat ventrad (69[1]), and is composed of the A.

Fig. 4.   Species-groups within the basal section of *Aleiodes*. Numbers over boxes represent character numbers; those underneath represent character states of taxa distal of the boxes.
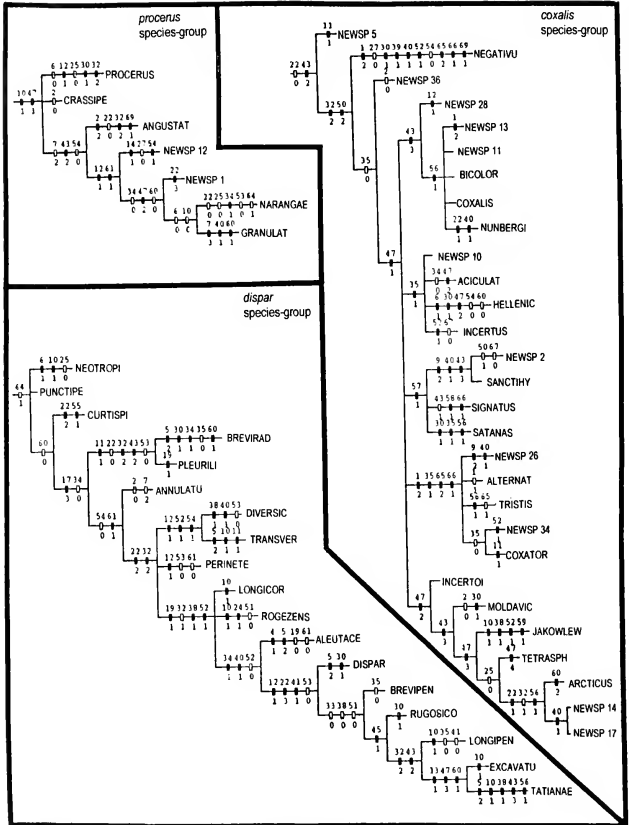
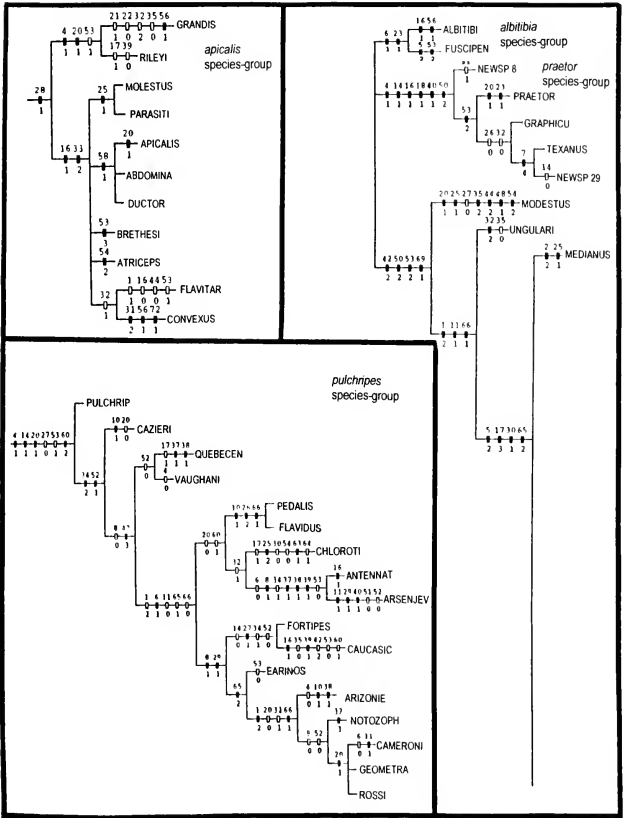Fig. 5.   Species-groups within the intermediate section of *Aleiodes*.

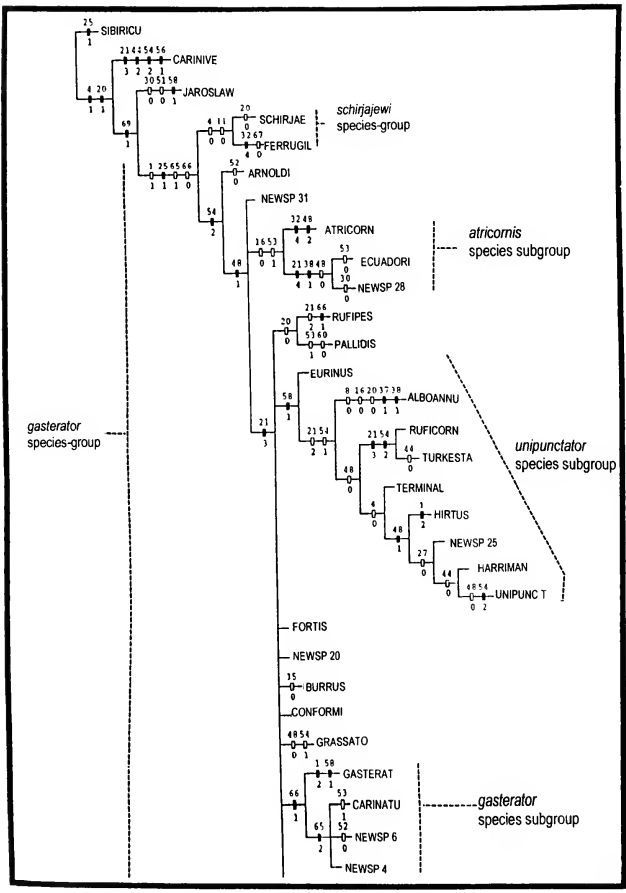Fig. 6.   Species-groups at and near the base of the derived section.

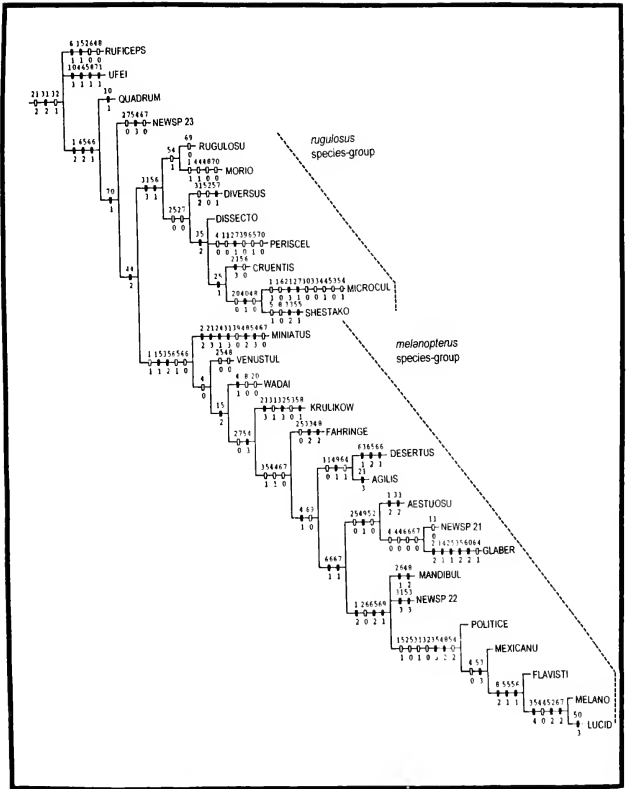Fig. 7. The base of the apical species-group cluster of the derived section.

Fig. 8.   The apex of the apical species-group cluster.

gasterator (Jurine), *A. rugulosus* (Nees von Esenbeck), *and A. melanopterus* (Erichson) species-subgroups.

The *A. gasterator* species-group is composed of *A. arnoldi* Tobias and new species 31 basally, and three species subgroups: the *A. atricornis* (Cresson), *A. gasterator* (Jurine), and *A. unipunctator* (Thunberg) species-subgroups. The group does not easily cluster based on any good synapomorphy. The retention of tarsal claw teeth basal only in the *A. gasterator* species-group distinguishes it from species-groups apicad to it. Although three species clusters exist within the *A. gasterator* species-group, they were considered subgroups, since they 1) clustered based on characters which reversed within the species-group or subgroup (*A. atricornis* species-subgroup); 2) were based on a color character, which are notoriously plastic across the genus (*A. unipunctator* species-subgroup), or 3) resulted in a paraphyletic group, such as the *A. unipunctator* species-subgroup, in which *A. eurinus* shares character states which define both the *A. unipunctator* and *A. gasterator* species-groups.

15. The *ufei* species-group (Fig. 8) is composed of one species, so far as known: *A. ufei* (Walley). The bicolored body is similar to the *A. unipunctator* species-subgroup, but the species differs in that the sides of the first metasomal tergite are parallel, and the female abdominal apex is compressed. Although this group is monospecific so far as known, it was given species-group status based on the unique metasomal features described above.

16. The *rugulosus* species-group (Fig. 8a) is monophyletic and is defined by the uniquely shiny, coarsely and densely rugulopunctate vertex sculpturing and all black body. It consists of *A. cruentus* (Nees von Esenbeck), *A. dissector* (Nees von Esenbeck), *A. diversus* (Szepligeti), *A. microculatus* Watanabe, *A. morio* (Reinhard), *A. periscelis* (Rein-

hard), *A. rugulosus* (Nees von Esenbeck), and *A. shestakovi* (Shenefelt).

17. The *melanopterus* species-group (Fig. 8b) is monophyletic and is defined by the clypeo-antennal space/width of oral space ratio ≤ 0.69, scutal sculpturing excluding postero-medial dorsal surface smooth or finely punctate, and clypeus height/width less than 0.42. Members of the group are *A. aestuosus* (Reinhard), *A. agilis* (Telenga), *A. desertus* (Telenga), *A. fahringeri* (Telenga), *A. flavistigma* Shaw, *A. glaber* (Telenga), *A. krulikowskii* Kokoujev, *A. lucidus* (Szepligeti), *A. melanopterus* (Erichson), *A. mexicanus* Cresson, *A. mandibularis* (Cresson), *A. miniatus* (Herrich-Schaffer), *A. politiceps* (Gahan), *A. ruficeps* (Telenga), *A. venustulus* (Kokoujev), *A. wadai* (Watanabe), and new species 21, 22, and 23.

17a. The *melanopterus* species-subgroup (Shaw 1993, Fig 8b), a monophyletic subset of the above, consists of *A. flavistigma* Shaw, *A. lucidus* (Szepligeti), *A. mandibularis* (Cresson), *A. melanopterus* (Erichson), *A. mexicanus* Cresson, *A. politiceps* (Gahan) and new species 23. The subgroup is defined by pectinate tarsal claws (Fig. 2c) and strongly protruding clypeal carina.

DISCUSSION OF HOST ASSOCIATION

The following data and that in Appendix I were drawn from Shenefelt (1975), Shaw (1983, 1994), and S. R. Shaw and P. M. Marsh (unpublished data). Of 208 *Aleiodes* species analyzed, host records were available for 40.4% of *Aleiodes* species. Host records were available for 65.4% of basal species, 27.3% of intermediate species, and 39.4% of derived species (Appendix I).

Basal species for which host associations were known either attacked host species from more than one family, or attacked hosts other than non-catocaline Noctuidae, Notodontidae, or Sphingidae. Exceptions were *A. gossypii, A. laphygmae, A. noc-*

turnus, and *A. nolophanae.* Two basal species in the *A. gastritor* species group (*A. pallescens* and *A. stigmator*) are gregarious.

Within intermediate species, the *A. coxalis* species-group showed a tendency to attack setose hosts within Arctiidae, Lasiocampidae, and Lymantriidae. *Aleiodes coxalis* species-group species comprise 50.0% of *Aleiodes* species known to attack arctiids and lymantriids. Of the 15 intermediate species with host records, 40% attack exclusively non-catocaline noctuids so far as known.

Within the derived section apicad of the *A. pulchripes* and *A. apicalis* species groups, only trifine Noctuidae are attacked so far as known. The *A. praetor* species-group attacks only sphingids. The *A. albitibia* species-group attacks only notodontids. Within the *A. pulchripes* species-group, geometrids, noctuids, and notodontids are attacked, so far as known.

Of the seven of 11 *A. apicalis* species-group species with known hosts, four attack plusiine noctuids (*A. brethesi, A. apicalis, A. molestus,* and *A. parasiticus*). One is associated with an unidentified noctuid mummy (*A. abdominalis*), and three attack non-noctuids.

Of all derived *Aleiodes* with host records, 69.7% attack trifine noctuids. Of the above except the *A. albitibia* and *A. praetor* species groups, 84.6% attack trifine noctuids.

Basal and intermediate species tend to have broad host ranges, and derived species tend to specialize on Noctuidae, Notodontidae, or Sphingidae. The only monophyletic groups which specialize on Notodontidae and Sphingidae lie at the base of the apical section. In the basal section, the *A. pallidator* species-group tends to specialize on Lymantriidae. The only *Aleiodes* species with host records for Catocalinae are in the *A. seriatus* species-group in the basal section. Among intermediate species, the *A. coxalis* species-group tends to specialize on setose hosts, especially arctiids and lymantriids.

According to the classification scheme of Nielsen and Common (1991), Noctuidae is the most derived lepidopteran family. The lepidopteran families Notodontidae, Lymantriidae, and Arctiidae are placed in superfamily Noctuoidea with Noctuidae. Notodontidae is the most basal noctuoid family (Nielsen and Common, 1991). Superfamily Sphingoidea, consisting of one family (Sphingidae), is immediately basal to Noctuoidea (Nielsen and Common, 1991).

Based on order of placement in a list of 19 subfamilies of Noctuidae, subfamily Catocalinae is placed within the four basal-most subfamilies (Nielsen and Common, 1991). Catocaline noctuids are utilized only by one *Aleiodes* species-group in the basal section, so far as known.

Family Arctiidae is placed just basad to the noctuid subfamilies referred to in the study (Nielsen and Common 1991). The only basal *Aleiodes* species known to attack arctiids are within the *A. seriatus* species-group.

Mitchell *et al.* have recently investigated the phylogeny of superfamily Noctuoidea by using characters derived from the nuclear gene EF-1α, which encodes elongation factor-1α protein (Mitchell *et al.* 1997). Based on their most parsimonious tree derived from all sites of EF-1α, the authors concluded that 1) Notodontidae comprises a monophyletic group at the base of Noctuoidea; 2) "quadrifine" Noctuidae comprise a paraphyletic group which consists of a monophyletic subgroup (Eutellinae, Nolinae, Sarrothripinae), and the basal-most subfamilies (Catocalinae, Herminiinae) of a more derived monophyletic group. Arctiidae and Lymantriidae are sister-groups at the apex of this latter monophyletic group; 3) the "trifine" noctuids, which comprise the remainder of Noctuidae, form a monophyletic group at the apex of the cladogram (Mitchell *et al.* 1997).

The findings of Mitchell *et al.* corroborate Nielsen and Common with respect to

Noctuoidea, except that Mitchell *et al.* find that Noctuidae is a paraphyletic group, with the quadrifine noctuids (including Catocalinae) more closely related to Arctiidae and Lymantriidae than to trifine noctuids (Mitchell *et al.* 1997). The latter finding is corroborated by Weller *et al.* (1994).

Since older koinobiont parasitoid species are thought to have broader host ranges while newer species are thought to have narrower ranges (Shaw 1994), and since this study provides evidence that basal and intermediate *Aleiodes* species have broader host ranges while derived species have narrower host ranges, the overall pattern of phylogenetic inferences made from morphological data in this study is corroborated by host association data in light of the above.

This study suggests that genus *Aleiodes* overall has co-evolved with its Lepidopteran hosts. Basal host families appear more likely to be attacked by basal *Aleiodes* species while the most derived host family, trifine Noctuidae, is more likely to be attacked by derived *Aleiodes* species. Non-derived groups with well defined synapomorphies such as the basal *A. seriatus* and *A. pallidator* species groups, and the intermediate *A. coxalis* species-group, appear to have co-evolved with noctuoid groups basal to trifine Noctuidae such as catocalines, lymantriids and arctiids. The exclusive associations of *Aleiodes* species within the derived section with specific host groups, such as that of the *A. praetor* species-group with sphingids, of the *A. albitibia* species-group with notodontids, and of *Aleiodes* species apicad of the *A. apicalis* and *A. pulchripes* species-groups with Noctuidae add weight to this co-evolutionary hypothesis.

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Appendix I. List of *Aleiodes* species examined.

Aleiodes species	Host family(ies)
abdominalis Cresson 1869	Noctuidae
aciculatus Cresson 1869	Noctuidae
aestuosus (Reinhard) 1863	Noctuidae (Noctuinae, Ophiderinae)
agilis (Telenga) 1941	unknown
albitibia (Herrich-Schäffer) 1838	Notodontidae
alboannulatus Belokobylskyj	unknown
alutaceus Granger 1949	unknown
aligharensi (Quadri) 1933	Gelechiidae, Noctuidae, Notodontidae
alternator (Nees von Esenbeck) 1934	Arctiidae, Lasiocampidae, Lymantriidae
angustatus (Papp) 1969	unknown
annulatus Granger 1949	unknown
antennatus Belokobylskyj 1996	unknown
apicalis (Brulle) 1832	Arctiidae, Geometridae, Lasiocampidae, Noctuidae (Hadeninae, Plusiinae)
arcticus Thomson 1891	unknown
arizoniensis Marsh and Shaw 1997	unknown
armatus Wesmael 1838	Geometridae, Noctuidae
arnoldii Tobias 1976	unknown
atriceps Cresson 1869	unknown
atricornis (Cresson) 1872	Noctuidae (Hadeninae)
autographae (Viereck) 1910	Noctuidae
bakeri (Brues) 1912	unknown
bicolor (Spinola) 1808	Geometridae, Lycaenidae, Lymantriidae, Noctuidae, Nymphalidae, Pterophoridae, Zygaenidae
borealis Thomson 1891	unknown
brethesi (Shenefelt) 1909	Noctuidae (Plusiinae)
brevipendulatus Achterberg and Penteado-Dias, 1995	unknown
breviradialis Granger 1949	unknown
buoculus Marsh 1989	unknown
burrus Cresson 1869	Noctuidae (Acronictinae, Noctuinae)
cameronii (Dalla Torre) 1898	Notodontidae
cantherius (Lyle) 1919	Geometridae
carinatus (Ashmead) 1888	unknown
cariniventris (Enderlein) 1912	unknown
caucasicus Tobias 1976	unknown
cazieri Marsh and Shaw 1997	unknown
chloroticus Shestakov 1940	unknown
circumscriptus (Nees von Esenbeck) 1834	Bombycidae, Geometridae, Lymantriidae, Noctuidae, Notodontidae, Psychidae, Pyralidae, Tortricidae
compressor (Herrich-Schäffer) 1838	Gelechiidae, Geometridae, Limacodidae, Noctuidae, Notodontidae
conformis (Muesebeck) 1960	unknown
convexus Achterberg 1991	unknown
coxalis (Spinola) 1808	Hesperiidae, Satyridae
coxator Telenga 1941	unknown
crassipes Thomson 1891	unknown
cruentis (Nees von Esenbeck) 1834	Noctuidae (Hadeninae), Lymantriidae
curtispina Granger 1949	unknown
dendrolimi (Matsumura) 1925	Lasiocampidae
desertus (Telenga) 1941	unknown
dispar (Curtis) 1834	Noctuidae, Nymphalidae
dissector (Nees von Esenbeck) 1834	Noctuidae (Acronictinae, Hadeninae)
diversicornis Granger 1949	unknown
diversus (Szepligeti) 1903	Noctuidae (Acronictinae, Hadeninae)

Appendix I. Continued.

Aleiodes species	Host family(ies)
earinus Marsh and Shaw 1997	unknown
ecuadorensis (Brues) 1926	unknown
eurinus (Telenga) 1941	unknown
excavatus (Telenga) 1941	unknown
fahringeri (Telenga) 1941	unknown
femoratus Cresson 1869	unknown
ferrugilei (Shenefelt) 1975	unknown
flavidus (Cresson) 1865	unknown
flavistigma Shaw 1993	Unknown
flavitarsus Marsh & Shaw 1998	Noctuidae
fortipes (Reinhard) 1863	unknown
fortis (Muesebeck) 1960	unknown
fuscipennis (Szepligeti) 1904	unknown
gasterator (Jurine) 1807	Noctuidae (Plusiinae)
gastritor (Thunberg) 1822	Choreutidae, Drepanidae, Geometridae, Incurvariidae, Notodontidae
geometrae (Ashmead) 1888	Geometridae
glaber (Telenga) 1941	unknown
gossypii (Muesebeck) 1960	Noctuidae
grandis Giraud 1857	Noctuidae (Acronictinae)
granulatus (De Gant) 1930	Noctuidae
graphicus Cresson 1872	Sphingidae
grassator (Thunberg) 1822	unknown
gressitti (Muesebeck) 1964	unknown
harrimani (Ashmead) 1902	unknown
hellenicus Papp 1985	unknown
hirtus (Thomson) 1891	unknown
incertoides Telenga 1941	unknown
incertus Kokoujev 1898	unknown
indiscretus (Reardon)	Lymantriidae
jakolewi Kokoujev 1898	unknown
krulikowskii Kokoujev 1898	unknown
kuslitzki Tobias 1976	unknown
laphygmae (Viereck) 1912	Noctuidae
longicornis Granger 1949	unknown
longipendulatus Achterberg and Penteado-Dias 1995	unknown
lucidus (Szepligeti) 1906	unknown
lymantriae (Watanabe) 1937	Lymantriidae
malacosomatos (Mason) 1979	Lasiocampidae
mandibularis (Cresson) 1872	unknown
medianus (Thomson) 1896	unknown
melanopterus (Erichson) 1848	unknown
mexicanus Cresson 1869	unknown
microculatus (Watanabe) 1937	unknown
minutus (Herrich-Schatter) 1838	unknown
modestus (Reinhard) 1863	Geometridae, Lasiocampidae
moldavicus Tobias 1986	unknown
molestus (Cresson) 1872	Noctuidae (Plusiinae, Noctuinae)
morio (Reinhard) 1863	Noctuidae
narangae (Rohwer) 1934	unknown
negativus Tobias 1960	Noctuidae
neotropicalis (Shenefelt) 1975	unknown
nigribasis (Enderlein) 1918	unknown
nigricornis Wesmael 1838	Noctuidae, Pyralidae, Geometridae

Appendix I. Continued.

Aleodes species	Host family(ies)
nigristemmaticum (Enderlein) 1918	Noctuidae (Catocalinae)
nocturnus Tobias 1960	Noctudae
nolophanae (Ashmead) 1888	Noctuidae
notozophus Marsh and Shaw 1997	unknown
nunbergi Noskiewicz 1956	Geometridae
pallescens Hellen 1927	Noctuidae, Notodontidae (gregarious)
pallidator (Thunberg) 1822	Gelechiidae, Geometridae, Lymantriidae, Noctuidae, Psychidae, Tortricidae
pallidistigmus (Telenga) 1941	unknown
palmatus (Walley) 1941	Noctuidae
parasiticus Norton 1869	Noctuidae
pedalis Cresson 1869	unknown
pellucens (Telenga) 1941	unknown
percurrens (Lyle) 1921	Noctuidae (Catocalinae, Acronictinae)
peruetensis (Shenefelt) 1975	unknown
periscelis (Reinhard) 1863	unknown
perplexus (Gahan) 1917	Geometridae, Noctuidae
pictus (Herrich-Schaffer) 1838	unknown
platypterygis (Ashmead) 1888	Drepanidae
plurilineatus (Cameron) 1911	unknown
politiceps (Gahan) 1917	Noctuidae (Hadeninae, Noctuinae)
praetor (Reinhard) 1863	Sphingidae
procerus Wesmael 1838	unknown
pulchripes Wesmael 1838	Lasiocampidae, Lymantriidae, Noctuidae (Acronictinae), Notodontidae
punctipes Thomson 1891	unknown
quadrum Tobias 1976	unknown
quebecensis (Provancher) 1880	Noctuidae (Acronictinae)
rileyi Cresson 1869	Lymantriidae, Noctuidae (Acronictinae, Hadeninae), Pyralidae
rogezensis Granger 1949	unknown
rossi Marsh and Shaw 1997	unknown
rossicus Kokoujev 1898	Drepanidae, Geometridae, Lasiocampidae, Lymantriidae, Noctuidae, Pyralidae
ruficeps (Telenga) 1941	unknown
ruficornis (Herrich-Schaffer) 1838	Lasiocampidae, Lymantriidae, Noctuidae (Hadeninae, Noctuinae, Plusiinae)
rufipes (Thomson) 1891	unknown
rugosicostalis Achterberg and Penteado-Dias, 1995	unknown
rugulosus (Nees von Esenbeck) 1811	Noctuidae (Acronictinae)
sanctihyacinthi (Provancher) 1880	Arctiidae
sanctivincentensis (Shenefelt), 1975	unknown
satanas Telenga 1941	unknown
schirjajewi (Kokoujev) 1899	unknown
scriptus (Enderlein) 1918	unknown
scrutator (Say) 1836	Choreutidae, Incurvariidae, Notodontidae
serratus (Herrich-Schaffer) 1838	Arctiidae, Lyonitiidae, Noctuidae
shestakovi (Shenefelt) 1975	unknown
sibiricus (Kokoujev) 1903	unknown
signatus (Nees von Esenbeck) 1911	unknown
similis (Curtis) 1834	unknown
simillimus (Ashmead) 1889	Geometridae
stigmator (Say) 1824	Geometridae, Lasiocampidae, Lymantriidae, Noctuidae (gregarious)

Appendix 1. Continued.

Aleiodes species	Host family(ies)
sudatorius Papp 1985	unknown
tatianae (Telenga) 1941	unknown
testaceus (Telenga) 1941	unknown
terminalis (Cresson) 1869	Noctuidae (Acronictinae, Hadeninae, Noctuinae)
Tetrasphaeropyx Ashmead 1888 spp.	Geometridae
texanus (Cresson) 1869	Sphingidae
transversestriatus Granger 1949	unknown
tristis Wesmael 1838	unknown
turkestanicus (Telenga) 1941	unknown
ufei (Walley) 1941	Noctuidae (Noctuinae)
ungularis Thomson 1891	unknown
unicolor Wesmael 1838	unknown
unipunctator (Thunberg) 1822	Noctuidae (Acronictinae, Hadeninae)
vaughani (Muesebeck) 1960	Noctuidae (Acronictinae)
venustulus (Kokoujev) 1905	unknown
wadai (Watanabe) 1937	unknown
xanthus (Marshall) 1892	unknown
new species 1	unknown
new species 2	Lymantriidae
new species 3	Noctuidae
new species 4	unknown
new species 5	unknown
new species 6	unknown
new species 7	unknown
new species 8	Sphingidae
new species 9	unknown
new species 10	Lycaenidae
new species 11	unknown
new species 12	unknown
new species 13	unknown
new species 14	Notodontidae
new species 15	unknown
new species 16	unknown
new species 27	unknown
new species 18	unknown
new species 19	unknown
new species 20	unknown
new species 21	unknown
new species 22	unknown
new species 23	unknown
new species 24	unknown
new species 25	Noctuidae (Cuculliinae)
new species 26	Arctiidae
new species 27	unknown
new species 28	Noctuidae (Hypeninae)
new species 29	Sphingidae
new species 30	unknown
new species 31	unknown
new species 32	Lycaenidae
new species 33	unknown
new species 34	unknown
new species 35	unknown
new species 36	unknown
new species 37	Lymantriidae
new species 38	Geometridae

Does the Mating System of *Trissolcus basalis* (Wollaston) (Hymenoptera: Scelionidae) Allow Outbreeding?

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Abstract.—The quasi-gregarious egg parasitoid *Trissolcus basalis* (Wollaston) is generally considered to be an entirely inbreeding species because it is a sib-mating species that has female-biased sex ratios. Whether the species also outbreeds has not been previously investigated although several aspects of its mating behaviour suggest this might be possible. This question was investigated indirectly in two ways by quantifying: (1) the inseminative capacity of *T. basalis* males in relation to the rate of female emergence, and (2) the effects of age and mating status on sexual receptivity of *T. basalis*. *Trissolcus basalis* females emerged over a period of several days, concentrating their emergence in the morning hours. Males were able to inseminate many females (> 50) in rapid succession, apparently without sperm depletion. However, approximately 20% of females did not produce female offspring, probably because they did not mate. Although the mated females produced proportionately more male offspring with time, this outcome is not readily explained by sperm depletion of their mating partners and remains an unresolved issue. Male sexual receptivity appears to be unaffected by age and would be expected to be unaffected by mating status because males typically are polygynous. Although a previously successful mating encounter did not preclude females from mating again, female sexual receptivity decreased significantly after mating. Female sexual receptivity also decreased significantly with age. These results suggest that both *T. basalis* males and females have the ability to mate away from the natal site and that outbreeding is possible in this species. Whether males and females can locate one another away from their own natal site therefore warrants further investigation.

Arrhenotokous parthenogenesis is the usual means of reproduction in Hymenoptera. Female-biased sex ratios and sib-mating are characteristic of many arrhenotokous species, especially those whose males develop in the vicinity of their female siblings and emerge before them (protandry). This occurs most frequently in gregarious parasitoids, which deposit many eggs per host, and quasi-gregarious ones (van den Assem et al. 1980), which lay one egg per host into hosts that are invariably aggregated. Hamilton's (1967) local mate competition (LMC) theory is generally seen as the best explanation of female-biased sex ratios (e.g. Waage and Lane 1984; Waage and Ng 1984; Hardy et al. 1993; Godfray 1994; but see Walter and Clarke 1992; Ode et al. 1997). Because female Hymenoptera can control the fertilisation of each egg they deposit, LMC theory predicts that single foundress broods of gregarious and quasi-gregarious species will contain only enough male offspring to mate all of their sisters in the immediate vicinity (Hardy et al. 1998).

Several recent studies have shown that strict local mating does not occur in some species with female-biased sex ratios and which therefore should be inbreeding species (e.g. Myint and Walter 1990; Nadel and Luck 1992; Molbo and Parker 1996; Hardy et al. 1999). The term partial local mate competition has been often used for

such cases. Another species whose mating behaviour appears not to be strictly local is *Trissolcus basalis* (Wollaston) (Hymenoptera: Scelionidae), a quasi-gregarious egg parasitoid of the green vegetable bug, *Nezara viridula* (L.) (Hemiptera: Pentatomidae). *Trissolcus basalis* is regarded as an inbreeding species that manifests local mate competition (LMC) (Hamilton 1967) because it has female-biased sex ratios and sib-mating (Noble 1937; Anon. 1939; Smith 1945; Wilson 1961; Thomas 1972). However, several aspects of its mating system are inconsistent with LMC and indicate that a proportion of each brood may outbreed if they are to transmit genes beyond the next generation. Field observations indicate that nearly 20% of newly-emerged females depart the egg mass unmated, approximately 25% of mated females were mated more than once and often by multiple males, virgin and mated females remained nearby the egg mass for up to several hours after emergence, and males dispersed from the natal site (A. D. Loch and G. H. Walter unpublished data). Given that both males and females leave the natal site in the field, it is certainly possible that unrelated males and females meet and mate away from their natal site.

The female mating pattern in *T. basalis* may be a consequence of the males mating many females in quick succession, and becoming sperm depleted. Females mated by sperm depleted males may receive insufficient sperm to produce the usual proportion of daughters in a brood. They may therefore mate again, with outbreeding being more likely in such circumstances. The inseminative capacity of *T. basalis* males was therefore investigated in relation to the rate and sequence of female emergence from the host patch. The experiment was designed to emulate typical rates of sibling emergence and mating in the field, rather than the unnaturally high rates used in some studies (e.g. Nadel and Luck 1985). Specifically, the number (and proportion) of females emerging from a single egg mass and inseminated by one male was quantified. The consequence of female emergence position for the amount of sperm received from the male was quantified by recording the number and sex ratio of progeny from every tenth female to emerge. Whether *T. basalis* males become sperm depleted at mating rates typical in the field could thus be determined.

The potential for outbreeding in *T. basalis* was also evaluated by determining whether males and females are sexually receptive after mating and/or leaving the natal site. We therefore investigated the effects of age and mating status (virgin or mated) on *T. basalis* sexual receptivity in the laboratory, by exposing different aged virgin and once-mated females to newly-emerged virgin males. For completeness, the effect of age on male sexual receptivity was also studied by mating different aged virgin males with newly-emerged virgin females.

MATERIALS AND METHODS

Laboratory cultures.—Green vegetable bugs were reared at 28 ± 1°C, 65 ± 10% R.H., 16L:8D in mesh cages (0.45 m sides) on a diet of green bean pods (*Phaseolus vulgaris* L.), shelled peanuts (*Arachis hypogea* L.) and water. Cultures were augmented regularly with field-collected bugs. Green vegetable bug egg masses were collected daily from cages and were used to maintain cultures of green vegetable bug or *T. basalis* (see below).

Laboratory cultures of *T. basalis* were established from parasitoids that emerged from green vegetable bug egg masses collected from mungbean, *Vigna radiata* (L.) Wilezek, and soybean, *Glycine max* (L.) Merr., during March–April 1997 and January–April 1998 at Pittsworth (27° 43'S, 151° 38'E), Bongeen (27° 34'S, 151° 27'E) and Cecil Plains (27° 32'S, 151° 12'E) in south-eastern Queensland, Australia. All *T. basalis* individuals that emerged from a single egg mass were held together in a

ventilated vial streaked with honey. Cultures of *T. basalis* were kept at 15 ± 1°C, 65 ± 10% R.H. and 16L:8D. The identification of *T. basalis* was confirmed by Dr Norman Johnson (Ohio State University). Voucher specimens from the *T. basalis* culture are deposited in The University of Queensland Insect Collection.

In all experiments, virgin wasps of the F_1– F_5 generation were used. Wasp virginity was ensured by holding single wasp pupae in ventilated vials with honey, after breaking the host egg mass into individual eggs soon after parasitoid pupation. For each experimental replicate, wasps were derived from different field-collected egg masses to ensure siblings were not included as replicates.

Inseminative capacity.—To determine male inseminative capacity, all of the *T. basalis* females that emerged from each of 10 parasitised green vegetable bug egg masses were tested for insemination (see below). These original egg masses contained 85 ± 5 eggs, the mean size for green vegetable bug egg masses in southeastern Queensland. Each egg mass had been parasitised by a single, once-mated female *T. basalis* over two days in a 50 × 25 mm ventilated vial. Self-superparasitism is unlikely to arise under such conditions because females use a chemical marker to mark parasitised eggs (Wilson 1961; Ganesalingam 1966; Field et al. 1998). After 9–10 days, when the first males began to emerge, vials containing the parasitised egg masses were monitored frequently (every 5–10 minutes) during the 10 hours of artificial laboratory light each day. Before females began to emerge, all males were removed except for the dominant male occupying the egg mass. The dominant male was lightly marked on the thorax with fluorescent dust to distinguish him from males that emerged subsequently. These latter males were removed immediately they appeared.

At each monitoring period any females

that had emerged were removed and each was placed alone in a ventilated vial and provided with honey. Females were typically found at the top of the vial. All females, except those used to assess fecundity (see below), were provided 5–10 fresh green vegetable bug eggs to establish whether they produced female offspring, a certain indication that males had been inseminated (Wilson 1961). Females were allowed 24 hours to parasitise eggs before being removed.

Lifetime fecundity was assessed for the first emerging female and for every tenth female that emerged from each egg mass. Each was provided with a frozen (−70°C) green vegetable bug egg mass each day for the first 12 days. The frozen eggs were < 1 month old and still viable for *T. basalis* (Powell and Shepard 1982, Kelly 1987). Earlier trials (n = 6) indicated that daily fecundity decreased rapidly and females were unlikely to produce offspring after 12 days. Large egg masses (85 ± 5 eggs each) were supplied on each of the first two days, half masses (40 ± 5 eggs) for each of the next four days, and small masses (20 ± 5 eggs) for each of the last six days, so that females had an excess of hosts at all times (see Results). Parasitised egg masses were placed singly in ventilated vials and incubated until all offspring had emerged. Eggs that were obviously parasitised, but from which parasitoids failed to emerge, were dissected and the parasitoid removed for sexing. Counts of the numbers of male and female offspring produced per female per day were then made.

Adult size.—Adults were measured to assess whether their size was affected by emergence sequence and whether fecundity was influenced by size. Two measurements were taken from all males and females to emerge from each egg mass: head width and right hind tibial length. Head width was measured as the distance between the outermost points of the eyes.

Measurements were made under a dissecting microscope, accurate to 0.01 mm.

Sexual receptivity.—Two experiments were conducted to investigate the effect of adult age and mating status (virgin or mated) on sexual receptivity. The first examined whether age affected the male's readiness to mate. A single virgin male aged 1, 5, 10, 15 or 20 days old was introduced into one end of a 50×12 mm ventilated vial containing a virgin female less than 24 hours old at the other end. The male and female were observed until mating occurred or for 20 minutes, as virgin males and females would usually mate within 10 minutes with an average pre-mating time of *ca* 3 minutes.

The number of contacts between the male and female before mating was recorded, as were the pre-mating and mating times. In addition, pre-mating and mating behaviours were observed for any differences between treatments. Once mating had taken place, the male was removed and the female provided with *ca* 10 green vegetable bug eggs. The eggs were removed one day later and incubated at $28 \pm 1°C$ until offspring emerged. Because *T. basalis* is arrhenotokous (Wilson 1961), a female was regarded as successfully inseminated if any female offspring were produced.

The other experiment examined whether female age and mating status affected her readiness to mate. Virgin females were assigned to two groups. Those in one group were not mated, whereas the others were mated within 24 hours of emergence by a virgin male. All females were held, until needed, in a ventilated vial streaked with honey. Subgroups of females (virgin or once-mated) were exposed to virgin males less than 24 hours old, at ages 1, 5, 10, 15 or 20 days, one pair per 50×12 mm ventilated vial. Procedures and conditions were the same as for the first experiment. For both experiments 15 replicates of each treatment were conducted, all at $25 \pm 2°C$ and $65 \pm 10\%$ R.H.

Statistical analysis.—Logistic analyses were conducted to test whether emergence position influences the probability of a female being inseminated. A logistic regression was conducted for each of the 10 experimental replicates, in which the binary response variable, whether a female was inseminated (assigned 1) or uninseminated (assigned 0), was regressed against her position in the emergence sequence.

The fecundity of females in different emergence positions and their offspring's sex ratio were analysed by 1-way ANOVA after $\log(x + 0.5)$ and $\arcsin(\sqrt{p})$ transformations, respectively. The significance of any differences was assessed by Fisher's protected least significant difference test. Linear regression was employed to assess the relationship between fecundity and female head width or hind tibial length.

The effect of age of males, virgin females and mated females on the number of pre-mating contacts, pre-mating time and mating time was tested by 1-way ANOVA after data were $\log(x + 0.5)$ trans-

Table 1. Summary statistics from logistic analyses testing whether emergence position influences the probability of a female being inseminated. A logistic regression was conducted for each of the 10 experimental replicates, in which the binary response variable, whether a female was inseminated (assigned 1) or uninseminated (assigned 0), was regressed against her position in the emergence sequence. Relationship refers to whether females later in the emergence sequence tended to be uninseminated (negative) or inseminated (positive).

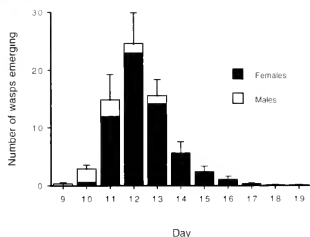| Replicate	No females	χ	p-value	Relationship
1	78	0.58	0.45	negative
2	40	1.52	0.22	positive
3	30	0.56	0.45	negative
4	73	0.30	0.58	positive
5	59	5.74	0.02	negative
6	55	0.80	0.37	positive
7	60	11.41	<0.01	negative
8	57	0.15	0.70	negative
9	61	2.78	0.10	positive
10	78	2.56	0.11	positive

Fig. 1. Pattern in which *Trissolcus basalis* siblings emerged from parasitised green vegetable bug egg masses. Number of males and females that emerged each day from each of 10 egg masses (parasitised on day 0) in the laboratory at 28 ± 1°C, 65 ± 10% R.H. and 16L:8D. Error bars represent standard errors for the mean number of siblings (males and females) that emerged each day.

Table 2. Overall number of offspring and offspring sex ratio (mean ± s.e.) produced by *Trissolcus basalis* females in different positions in the entire emergence sequence. Fecundity and sex ratio values derive only from those females that had been inseminated (as indicated by their production of daughters). See Fig. 2 and Table 1 for details.

Emergence position	No. mated	No. not mated	Fecundity[1]	Sex ratio (α male)[1]
1	8	2	139 ± 13	0.23 ± 0.03
10	8	1	125 ± 17	0.26 ± 0.04
20	9	1	129 ± 16	0.29 ± 0.05
30	9	1	116 ± 11	0.36 ± 0.06
40	8	0	100 ± 12	0.30 ± 0.08
50	7	1	153 ± 23	0.30 ± 0.04
60	5	1	95 ± 15	0.22 ± 0.08
70	1	2	116	0.72

[1] Column means for fecundity ($F_{7, 48} = 1.12$, $p = 0.37$) and sex ratio ($F_{7, 48} = 1.61$, $p = 0.16$) were not significantly different.

formed. G-tests were employed to test the effect of age of males, virgin females and mated females on the number of females mated within 20 minutes. G-tests were also employed to test if the number of females inseminated was related to age of males and virgin females. The effect of mated female age on the probability of being inseminated was not analysed statistically because mated females were presumed to have been successfully inseminated at their first mating.

The effects of female age and mating status (virgin or once-mated) on the number of pre-mating contacts, pre-mating time and mating time were tested by two-way ANOVA after data were log($x + 0.5$) transformed. A log-linear analysis was employed to test the effects of female age and mating status on the number of females mated within 20 minutes.

RESULTS

Emergence patterns.—Most wasps (> 95%) emerged under lighted conditions, with the majority emerging during the first 3–4 hours of morning light. A mean ± s.e. of 67.9 ± 4.6 wasps emerged from each of the 10 original egg masses, comprising 59.1 ± 5.0 females and 8.8 ± 2.3 males. Males began emerging on day nine with emergence peaking on days 10 and 11 (Fig. 1). Few males, if any, emerged from egg masses later than day 14. Females emerged on days 10–19 with emergence peaking on days 11–13. The largest number of females that emerged from any one egg mass in one day was 57 females on day 12.

Inseminative capacity and fecundity.—The dominant males that were left alone on egg masses to mate their sisters inseminated a mean ± s.e. of 48.3 ± 3.9 females, with 68 females being the maximum number inseminated by one male. The proportion (mean ± s.e.) of emerging females that was inseminated by the dominant males was 0.82 ± 0.02 across egg masses. Of the 10 replicates conducted, five showed a positive relationship between the probability of a female being inseminated and her emergence position and five showed a negative relationship (Table 1). Two of the negative relationships were significant at < 5% and two of the positive relationships were significant at < 11% (Table 1).

Table 3. Number and sex ratio (mean ± s.e.) of offspring produced by females that emerged as adults during a single day, but in different positions in the emergence sequence. Only females that emerged on the first day of female offspring emergence were included in the analysis because at this stage males would presumably have had a full sperm supply, and short term rates of sperm depletion could be assessed most accurately. Fecundity and sex ratio values are calculated only from mated females in each position.

Emergence position	No. mated	No not mated	Fecundity	Sex ratio (α male)
1	8	2	139 ± 13	0.23 ± 0.03
10	6	0	112 ± 19	0.27 ± 0.04
20	3	1	150 ± 4	0.27 ± 0.05
30	2	0	108 ± 4	0.46 ± 0.17
40	2	0	99 ± 45	0.21 ± 0.00
50	1	0	257	0.35

Column means for fecundity ($F_{5,16} = 2.31$, $p = 0.09$) and sex ratio ($F_{5,16} = 1.47$, $p = 0.25$) were not significantly different.

Fecundity was highly variable, and ranged from 42 to 257 (mean ± s.e. = 121 ± 5, n = 65) offspring per female. Progeny production peaked during the first 24 hours after emergence with about 40–50 offspring on average, and then decreased rapidly with time (Fig. 2). The number of offspring produced per day was always less than the number of hosts provided. The sex ratio (proportion male) of offspring increased with time such that females produced few or no female off-

spring after 10 days, although by then few offspring were being produced (Fig. 2). Fecundity and brood sex ratio were not significantly affected by the position of parent females in the overall emergence sequence (Table 2), nor by the position of females in the emergence sequence on the first day of female emergence (Table 3).

Adult size.—Head widths and hind tibial lengths for male and female *T. basalis* showed little variation within and across replicates. Females were significantly larger than males: mean ± s.e. head widths were 0.61 ± 0.001 mm and 0.58 ± 0.002 mm for females and males respectively ($F_{1,622} = 410.3$, $p < 0.0001$), and their respective hind tibial lengths were 0.41 ± 0.001 mm and 0.39 ± 0.001 mm ($F_{1,622} = 52.3$, $p < 0.0001$). No trend between emergence position and head width or hind tibial length was apparent except that the last 1–5 wasps to emerge from an egg mass tended to have head widths and hind tibial lengths up to 0.05 mm smaller than previously emerged wasps.

Fecundity increased significantly with increases in female head width and hind tibial length (Fig. 3). However, regressions of fecundity against each of the two size measurements fitted poorly ($r^2 \leq 0.10$).

Sexual receptivity—The age of males had no significant effect on the number of pre-mating contacts, mating time or the num-

Table 4. Effect of virgin male age on their propensity to mate within 20 minutes of exposure to a virgin female (expressed as number of females mated). Also given is the number of females inseminated, number of pre-mating contacts, pre-mating time and mating time (last three values are mean ± s.e.). The number of males used to calculate each mean and s.e. is the number of males mated in 20 minutes (first row) from the 15 replicates.

	Male age (days)				
	1	5	10	15	20
No. mated	15a	15a	15a	15a	15a
No. inseminated	12a	12a	15a	12a	12a
No. contacts	2.6 ± 0.3a	1.9 ± 0.3a	1.8 ± 0.3a	2.7 ± 0.4a	2.2 ± 0.2a
Pre-mating time (s)	173 ± 37a	92 ± 17b	88 ± 21b	181 ± 33a	176 ± 24a
Mating time (s)	12.0 ± 1.3a	10.8 ± 1.0a	12.6 ± 0.6a	12.4 ± 0.8a	14.5 ± 2.1a

Row means followed by the same letter are not significantly different (G-test for first 2 rows, 1-way ANOVA for last 3 rows, P > 0.05).

Table 5. Effect of virgin female age on their propensity to mate within 20 minutes of exposure to a virgin male (expressed as number of females mated). Also given is the number of mated females that was successfully inseminated, number of pre-mating contacts, pre-mating time and mating time (last three values are mean ± s.e.). The number of females used to calculate each mean and s.e. is the number of females that mated within 20 minutes (first row) from the 15 replicates.

	Virgin female age (days)				
	1	5	10	15	20
No. mated	15a	15a	14ab	11b	10b
No. inseminated	12a	11a	10a	8ab	3b
No. contacts	2.6 ± 0.3a	5.3 ± 0.8b	8.6 ± 1.9b	5.0 ± 1.1b	5.8 ± 0.8b
Pre-mating time (s)	173 ± 37a	303 ± 43b	419 ± 113b	275 ± 93ab	370 ± 73b
Mating time (s)	12.0 ± 1.3a	11.5 ± 0.7a	8.1 ± 0.8b	10.9 ± 0.7a	9.3 ± 1.5ab

Row means followed by the same letter are not significantly different (G-test for first 2 rows, 1-way ANOVA for last 3 rows, P > 0.05).

ber of females mated or inseminated (Table 4). Pre-mating time was affected by male age with males aged 5 and 10 days old having a significantly shorter pre-mating time than males aged 1, 15 and 20 days old. No differences in male pre-mating or mating behaviour were observed between males of different ages.

In contrast, virgin female pre-mating and mating behaviours were affected by their age (Table 5). Females aged 5–20 days old tended to resist the males' mating attempts by moving away from them, aggressively chasing males away and/or refusing to allow males to copulate after mounting. The numbers of pre-mating contacts and pre-mating times were greater for females aged 5–20 days than for 1 day old females (Table 5). Females aged 1, 5 and 15 days old mated for significantly

longer than 10 day old females. The number of females mated within 20 minutes and the number successfully inseminated decreased significantly with female age (Table 5).

The age of mated females also affected their pre-mating and mating behaviours, with mated females aged 5–20 days generally resisting mating attempts in the way described above for virgin females of different age. The mating propensity of mated 5–20 day old females was significantly less than that of one day old mated females (Table 6). The numbers of pre-mating contacts and pre-mating times increased significantly with female age, but mating time was not significantly affected by their age (Table 6).

Two-way ANOVA examining the effects of female age and sexual status (vir-

Table 6. Effect of age of previously-mated females on their propensity to mate within 20 minutes of exposure to a virgin male (expressed as number of females mated). Also given is the number of pre-mating contacts, pre-mating time and mating time (values are mean ± s.e.). The number of females used to calculate each mean and s.e. is the number of females that mated within 20 minutes (first row) from the 15 replicates.

	Age of previously-mated female (days)				
	1	5	10	15	20
No. mated	15a	6b	8b	9b	6b
No. contacts	4.7 ± 1.0a	9.7 ± 2.9b	7.0 ± 1.0ab	8.1 ± 1.1b	9.3 ± 3.4b
Pre-mating time (s)	235 ± 48a	549 ± 143b	373 ± 74ab	514 ± 97b	547 ± 205ab
Mating time (s)	8.6 ± 0.7a	8.4 ± 1.1a	6.1 ± 1.1a	7.4 ± 1.5a	9.7 ± 2.2a

Row means followed by the same letter are not significantly different (G-test for first row, 1-way ANOVA for last 3 rows, P > 0.05).

Table 7. Summary of results from 2-way ANOVA (log $(x + 0.5)$ transformed) testing whether the individual and interactional effects of the factors, female age and mating status (virgin or once-mated), affected the number of pre-mating contacts, pre-mating time and mating time.

Factor	No. contacts	Pre-mating time	Mating time
Age	$F_{4,99} = 7.06$, $P < 0.0001$	$F_{4,99} = 4.50$, $P = 0.002$	$F_{4,99} = 3.31$, $p = 0.01$
Mating status	$F_{1,99} = 8.37$, $P = 0.005$	$F_{1,99} = 8.65$, $P = 0.004$	$F_{1,99} = 10.01$, $P = 0.002$
Age × mating status	$F_{4,99} = 0.89$, $P = 0.47$	$F_{4,99} = 0.83$, $P = 0.51$	$F_{4,99} = 0.96$, $P = 0.44$

gin or once-mated) on mating propensity indicated that the interaction between female age and mating status was not significant for all three measures of mating propensity (Table 7). As single factors, female age and mating status significantly affected the number of pre-mating contacts, pre-mating time and mating time (Table 7).

A log-linear analysis on the effect of female age on the propensity of virgin and mated females to mate within 20 minutes revealed that the model could be described best by two interactions: female mating status and the number of females mated, and female age and the number of females mated (Maximum likelihood $\chi^2 = 8.38$, $df = 8$, $p = 0.40$). The propensity of females to mate within 20 minutes was significantly greater for virgin females and younger females.

DISCUSSION

The results from this study suggest that strict local mating does not occur in *T. basalis* and that outbreeding away from the natal site may commonly occur. Results that are inconsistent with LMC theory include: (1) males do not achieve the maximum rate of insemination expected despite showing no apparent signs of sperm depletion, (2) males remain sexually receptive probably throughout their lifetime (Table 4), and (3) females can be mated multiple times, despite becoming decreasingly sexually receptive after mating and with age (Tables 6, 7). We discuss the implications that these results have on the mating system of *T. basalis* and ask whether this species is likely to outbreed.

Emergence of *T. basalis* females is concentrated during the early morning hours over several days (Wilson 1961; Fig. 1). In the field a dominant male usually guards the parasitised egg mass from which females are emerging. These females are his sisters unless the egg mass has been superparasitised. In the laboratory, the single male left on the mass successfully mated many females in succession, with sometimes up to 50 or more females emerging over several hours (Table 3). Females in all positions in the emergence sequence apparently received similar quantities of sperm because their offspring sex ratios were not affected by emergence position (Table 2; Fig. 2), even if those females all emerged and were mated on the same day by a single male (Table 3).

Although the above results suggest that a single *T. basalis* male can fully inseminate each of his female siblings from the same egg mass, two observations indicate that the dominant male does not achieve the maximum rate of insemination that is possible. First, only *ca* 80% of females were inseminated by dominant males (Table 1, see also Wilson 1961). Wilson (1961) proposed that temporary sperm depletion in the dominant male may be the cause. But even when large numbers of females emerged in a day, the offspring sex ratio produced by inseminated females did not vary with their position in the mating sequence (Table 3). In addition, uninseminated females appeared throughout the emergence sequence (Tables 1–3). Field observations have shown that a similar percentage of emerging females is not

mated by the dominant male guarding the egg mass (A.D. Loch and G.H. Walter unpublished data). Also, ca 18% of matings between virgin males and females in the laboratory do not lead to successful insemination (A.D. Loch and G.H. Walter unpublished data). In our experiments, we did not observe females to confirm they mated or to ascertain why they may not have mated. However, the high rate of uninseminated females is likely to be partly the consequence of simultaneous female emergences, during which males become occupied with some emerging females, while others remain unmated to the top of the vial, a behaviour that has parallels in the field (A.D. Loch and G.H. Walter unpublished data).

The second observation suggesting that maximum insemination rates are not achieved by the dominant male, is that even those females that were inseminated produced proportionately more male offspring with age (Fig. 2). This trend has also been reported in other studies of *T. basalis* fecundity (Powell and Shepard 1982; Corrêa-Ferreira and Zamataro 1989; Awan et al. 1990) and in work on the confamilial *Telenomus busseolae* (Gahan) (Chabi Olaye et al. 1997). Females apparently do not receive sufficient sperm to fertilise all their eggs. However, temporary sperm depletion in males or insufficient sperm transfer by males are unlikely explanations. First, this trend was uniform for females in all emergence positions (Fig. 2), indicating that sperm depletion in the male was not the cause. Second, females held with males throughout their lifetime, and therefore assumed to be mated multiple times, also produce proportionately more male offspring with time (Powell

and Shepard 1982; Awan et al. 1990), suggesting that this trend occurs irrespective of the number of times a female is mated. The reason for this trend is not clear, but a decrease in sperm viability over time is possible, or it could have a behavioural or physiological basis.

Results from this study suggest that *T. basalis* males do not become sperm depleted at rates of mating that are typical for this species in nature. In this study, green vegetable bug egg masses of 85 ± 5 eggs were used, and represent the largest known host masses for *T. basalis*, in terms of the number of eggs. The test males were, therefore, exposed to a high number and frequency of matings. In any case, dominant males in control of egg masses in the field are unlikely to become sperm depleted because changeovers in male dominance occur frequently (A.D. Loch and G.H. Walter unpublished data), and female emergence continues over several days (Fig. 1).

Sexual receptivity of *T. basalis* males appears unaffected by age (Table 4) and mating status, thus enabling males to mate probably throughout their lifetime. The only aspect of male sexual receptivity that was affected by age was pre-mating time, which was significantly shorter for 5–10 day old males than for 1, 15 and 20 day old males. They may be more receptive at 5–10 days because they emerge up to several days before females (Anon. 1939; Noble 1937; Smith 1945; Wilson 1961; Thomas 1972) and would therefore not normally need to mate immediately upon emergence.

In contrast, female sexual receptivity decreased rapidly after mating and with age (Tables 5–7). Such decreases are con-

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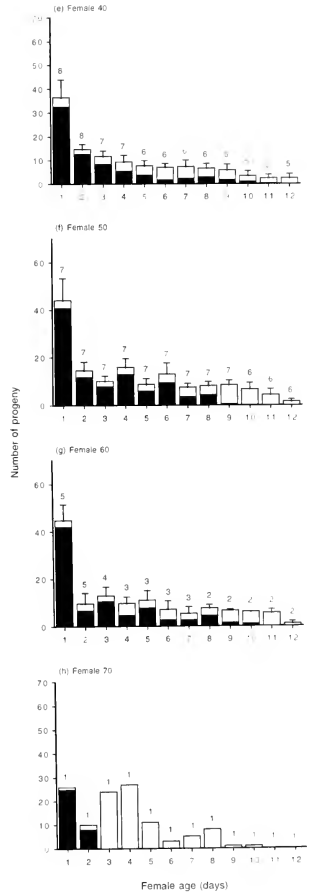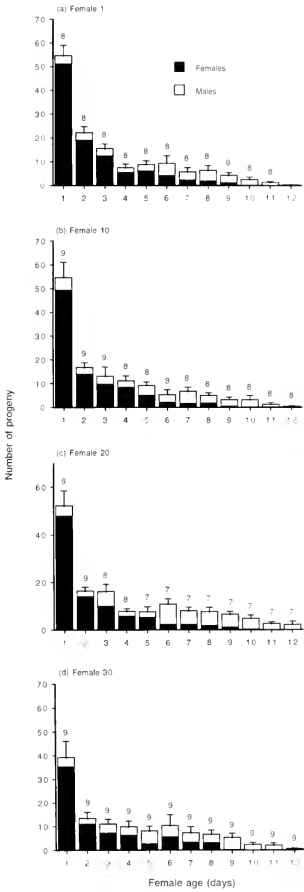
sistent with LMC theory because mating is assumed to occur only at the natal site among siblings (Hamilton 1967). However, females can be mated multiple times, which is inconsistent with LMC theory. This inconsistency coupled with others such as male dispersal from the natal site (A. D. Loch and G. H. Walter unpublished data), and males remaining sexually receptive probably throughout their lifetime (Table 4) suggest that *T. basalis* of both sexes may mate away from the natal site and therefore outbreed.

Trissolcus basalis may outbreed if males and females can locate and/or attract each other once they have left the natal site. Males may be able to locate unrelated, newly-emerged (and thus sexually receptive) females directly, or they could do so indirectly by locating hosts parasitised by *T. basalis* and then competing with emerging males for mating access to females. Similarly, newly-emerged females may be able to locate males directly, or indirectly by searching for parasitised hosts with males in occupation. Currently, no evidence is available on whether males or females can locate potential mating partners away from the natal site. LMC models assuming strict local mating (Hamilton 1967) suggest that *T. basalis* males and females will not be able to locate each other in the field. However, in other hymenopterous species with female-biased sex ratios, such as *Spalangia cameroni* (Perkins) (Myint and Walter 1990) and *Pachycrepoideus vindemiae* (Rondani) (Nadel and Luck 1992), males are able to locate hosts and thus potential mating partners, a feature likely to be found in other species (Hardy 1994).

Males may not only be able to outbreed with newly-emerged virgin females but also with newly-emerged mated females because a previous mating encounter did not preclude females from mating again (Table 6). This result is not likely to be an artefact of laboratory conditions or procedures because females have been ob-
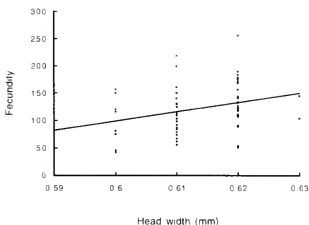

Fig. 3. Fecundity of *Trissolcus basalis* females in relation to head width (y = 1711x − 928, r² = 0.10, n = 65, p = 0.01). The trend for fecundity versus hind tibial length (y = 1294x − 407, r² = 0.07, n = 65, p = 0.04) is not shown because it was similar to the displayed trend. Both trends were determined irrespective of female position in the emergence sequence (see Table 2).

served to be mated multiple times and by multiple males in the field (A. D. Loch and G. H. Walter unpublished data). Whether *T. basalis* females are truly polyandrous has yet to be established, for matings after the first successful mating may not lead to successful insemination. For instance, mating plugs may be used by males to ensure additional matings do not result in insemination.

This study also made a number of findings pertaining to the fecundity of *T. basalis*. The mean fecundity recorded in this study is higher than fecundities recorded by Noble (1937), Ganesalingam (1966) and Thomas (1972), but similar to values recorded by Powell and Shepard (1982) and Corrêa-Ferreira and Moscardi (1994), and lower than fecundities recorded by Corrêa-Ferreira and Zamataro (1989) and Awan et al. (1990) for the same species. These differences are likely to be the result of differences in laboratory procedures and conditions, although differences in adult female size may have contributed because fecundity is greater for larger females (Fig. 3). The trend whereby fecundity peaked on the first day after female emergence and decreased rapidly over

time, differs somewhat from the results of Ganesalingam (1966) and Powell and Shepard (1982), who showed that fecundity peaked on day 2. These differences are less readily attributable to different laboratory procedures and conditions, and their significance is unclear. The claim by Field et al. (1998) that *T. basalis* is a synovigenic species was supported by our results because females laid eggs for 10–12 days with progressively fewer eggs each day (Fig. 2) despite sufficient hosts being available during the first few days for them to have deposited their lifetime complement of eggs then.

In conclusion, although uninseminated females leaving the egg mass may well be mated by the other males (also likely to be their siblings) that wait around the egg mass, the possibility that these females could mate unrelated males near or away from the natal site may not be low. Although we have no direct evidence of *T. basalis* outbreeding in nature, the results from this study and other related studies (A.D. Loch and G.H. Walter unpublished data), suggest that it may be more frequent than anticipated by LMC theory. In addition, outbreeding is likely to occur when > 1 female oviposits in an egg mass. Further research investigating the mating system of *T. basalis* is required before the question of the species' outbreeding can be resolved. Specific issues that need to be addressed include the questions of whether *T. basalis* haa a means of mate-attraction, and whether *T. basalis* females are truly polyandrous.

ACKNOWLEDGMENTS

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The Nearctic Species of *Protarchus* Foerster (Hymenoptera: Ichneumonidae: Ctenopelmatinae)

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Abstract.—The Nearctic species of the Holarctic genus *Protarchus* Foerster (Ichneumonidae, Ctenopelmatinae, Mesoleiini) are reviewed. A key to the Nearctic species is provided. Seven species are recognized. *P. testatorius* (Thunberg) and *P. sorbi* (Ratzeburg) are Holarctic, **P. bolbogaster Leblanc, n. sp.** and *P. mellipes* (Provancher) are transcontinental Nearctic, *P. magnus* (Davis) and *P. pallidicornis* (Walley) are eastern Nearctic, and **P. atrofacies Leblanc, n. sp.** is found in Alaska. The name *P. longipes* (Cushman) is synonymized with *P. sorbi*, **new synonymy.**

The Holarctic genus *Protarchus* Foerster belongs to the ichneumonid subfamily Ctenopelmatinae (Scolobatinae sensu Townes 1970) and tribe Mesoleiini. The tribe is the most speciose and taxonomically difficult in the subfamily. Only a few genera have been studied in detail (Kaur 1989, Leblanc 1989, Viitasaari 1979). The Palearctic species of *Protarchus* were revised by Viitasaari (1979), who recognized four species and discussed the biology of the species that parasitize sawflies of the genus *Trichiosoma* (Cimbicidae) in bogs, based on extensive collecting and rearing. The Nearctic *Protarchus* were studied by Walley (1938), who recognized four species based on specimens in the Canadian National Collection.

Ichneumonids of the genus *Protarchus* are large sized, the nervellus in the hind wing is intercepted above its middle, the areolet is present, the clypeus is small and the medial dorsal carinae on the first metasomal tergite extend beyond the spiracles. Both Nearctic and Palearctic species parasitize *Trichiosoma* spp.

Study of the Nearctic and Palearctic specimens shows that the Nearctic *P. longipes* (Cushman) and the Palearctic *P. sorbi* (Ratzeburg) represent a single Holarctic species. In addition, *P. testatorius* (Thunberg) is Holarctic but had not been reported for the Nearctic region by previous authors. The discovery of Holarctic distribution patterns and of two undescribed Nearctic species encouraged me to revise the Nearctic species of *Protarchus*.

MATERIALS, METHODS AND TERMINOLOGY

Material studied.—A total of 87 Nearctic specimens were examined from 5 collections as follows (collections acronyms are from Arnett and Samuelson (1986)): AEIC: American Entomological Institute, Gainesville, Florida, D.B. Wahl, 31 specimens; ANSP: Academy of Natural Sciences, Philadelphia, Pennsylvania, D. Azuma, 2 specimens; CNCI: Canadian National Collection of Insects, Ottawa, Ontario, J.R. Barron, 43 specimens; LLIC: Luc Leblanc private collection, Montréal, Canada, 1 specimen; USNM: National Museum of Natural History, Washington, D.C., B. Danforth, 10 specimens.

Morphological terms.—The morphological terms used in the descriptions are from Gauld (1984) except that mesosoma is used instead of thorax, and metasoma is used instead of gaster. Terms used to

characterize microsculpture are from Allen and Ball (1980). In characterizing metasomal punctures and sculpture, only the second tergum was utilized as sculpture is best defined on that segment.

Color descriptions.—Areas used to describe color patterns are as follows. Antennae are divided into dorsal and ventral surfaces and legs are divided into anterior, posterior, dorsal and ventral surfaces if imagined as stretched out horizontally at right angles from the body. Areas in bilaterally symmetrical parts (face, clypeus, epicnemium, dorsal and ventral surfaces of mesosoma and metasomal terga) are identified as median/lateral and basal/apical for face, clypeus and epicnemium, or median/apical and anterior/posterior for other parts. Areas in asymmetrical parts are identified as anterior/posterior and upper/lower.

Measurements.—A total of 37 females and 20 males were measured with an ocular micrometer. Length of the forewing was measured from the junction of costal vein with humeral plate to the most distant tip between the ends of veins Rs and M. Height of face is the distance between a line connecting the lower margins of antennal sockets and a line connecting the tentorial pits. Width of face is the distance between the inner margins of the compound eyes at the level of the middle of face height. Length of the first metasomal tergum was measured in lateral view from the base to the tip of its dorsal surface. Width of the first metasomal tergum was measured in dorsal view at its widest part near the apex. The length of the hind femur was measured on the anterior surface from the base to the apex. The width of the hind femur was measured at its mid length. The widths of the hind tibia and hind tarsomere 1 were measured at their widest part in lateral view.

Genus *PROTARCHUS* Foerster

Protarchus Foerster 1869:201. Type species: *Tryphon rufus* Gravenhorst (= *testatorius* Thun-

berg). Designated by Woldstedt 1877:460. Lectotype not examined.

Zacalles Foerster 1869:204. Type species: *Zacalles magnus* Davis. Designated by Davis 1898:283. Synonymized by Cushman 1924:8. Holotype examined.

Protarchoides Cushman 1922:25. Type species: *Protarchoides longipes* Cushman. Original designation. Synonymized by Townes 1945:505. Holotype examined.

Diagnostic characters.—Large (forewing 9.8 to 18.3 mm long). Clypeus (Fig. 3) small, transversly convex near base (near middle in *P. sorbi*), apically almost flat, and with apical margin truncate. Mandible short and broad, its upper tooth a little wider and longer than lower tooth (Fig. 4) or much wider than lower tooth (Fig. 5). Forewing with areolet usually present, large (Fig. 28) or very small (Fig. 29). Vestige of vein 1/Rs+M (= ramulus) often present (Fig. 29) (always absent in other genera of Mesoleiini). Vein cu-a separated from vein Rs+M by 0.2 to 0.5 of its length. Hind wing with vein 1/Cu longer than vein cu-a ("nervellus intercepted above middle"). Tibial spurs of middle and hind legs unequal, the longest spur about 0.3 to 0.4 as long as first tarsomere. First tergum moderately stout, with median dorsal carinae well defined and strong (Figs. 17,19), or reduced to a median furrow (Fig. 21) but always extending beyond spiracle. Terga 2 to 4 in some species each with two large sublateral swellings where punctures are sparser (Fig. 23). Hairs on female hypopygium directed backward.

Biology and biogeography.—Hosts of *Protarchus* are almost invariably larvae of *Trichiosoma* (Hymenoptera: Cimbicidae). Published host records for the Palearctic region are: *T. nanae* Vikberg & Viitasaari, parasitized by *P. testatorius* in Finland (Viitasaari 1979, Vikberg & Viitasaari 1991); *T. ?lucorum* L., parasitized by *P. testatorius* and *P. sorbi* in Finland (Viitasaari 1976, 1979). Records of *Palaeocimbex femorata*, parasitized by *P. testatorius* (Townes et al. 1965) and *Cimbex* parasitized by *P. heros*

(Holmgren 1876) would require confir-
mation. Label data included with Nearctic
specimens indicate that *Trichiosoma trian-
gulum* is attacked by *P. testatorius*, *P. sorbi*
and *P. mellipes*. Bogs are the usual habitat
of *Protarchus* spp. (Viitasaari 1979). *P. tes-
tatorius*, *P. sorbi* and *P. bolbogaster* release
a strong odor when picked up, as indicat-
ed by label data. The species *P. sorbi* and
P. testatorius are present in the boreal zone
of North America (Figs. 31–32) as well as
across the Palearctic region. The new spe-
cies *P. atrofascies*, from Alaska, may also
be Holarctic. The remaining three species,
on the other hand, are apparently restrict-
ed to north-eastern North America.


KEY TO NEARCTIC SPECIES OF *PROTARCHUS*

1. Hind tibiae entirely light colored, brown or yellowish brown; ocelli enlarged and hind
   ocelli separated by about their diameter (Fig. 1) 2
 – Hind tibiae apically to entirely dark, reddish black to black; ocelli smaller and hind ocelli
   separated by more than their diameter (Fig. 2) 4
2. Epomia clearly defined and prominent (Fig. 12); metasoma black or brownish black beyond
   tergum 2; size forewing 12.3–16.0 mm long 3
 – Epomia indistinct; metasoma generally mostly brown, but in some specimens black beyond
   tergum 2; forewing 16.5–18.3 mm long . . . . *magnus* **(Davis)**
3. Face black, or sometimes black with a yellowish brown median spot; mesosoma entirely
   black except light tegula; metasoma entirely black . . . . *mellipes* **(Provancher)**
 – Face brown or yellowish brown; mesosoma brownish black with extensive yellowish or-
   ange and brown markings; metasoma brownish black with tergum 1 and part of tergum
   2 brown . . . . *pallidicornis* **(Walley)**
4. Metasomal terga black, with extensive orange on terga 2 to 4; areolet usually present and
   very small (Fig. 29) . . . . *testatorius* **(Thunberg)**
 – Metasomal terga entirely black; areolet large (Fig. 28) or absent 5
5. Metasomal terga 2 to 4 each with two large sublateral swellings (Fig. 22); upper mandibular
   tooth much wider than lower tooth (Fig. 5); hind tibia entirely black . . . .
   . . . . *bolbogaster* **Leblanc, n. sp.**
 – Metasomal terga 2 to 4 without sublateral swellings (Fig. 23); upper mandibular tooth
   subequal to lower tooth (Fig. 4); hind tibia basally yellow to orange and apically black . . . 6
6. Notaulus weak and reduced to shallow impressions (Figs. 6,7); hind tibia of male black in
   apical 0.6; face of male yellow . . . . *sorbi* **(Ratzeburg)**
 – Notaulus anteriorly strong and sharply defined (as Figs. 8,9); hind tibia of male black in
   apical 0.5; face of male black except faint brown median spot (female unknown) . . . .
   . . . . *atrofacies* **Leblanc, n. sp.**

Protarchus atrofacies Leblanc,
new species
(Fig. 32)

Diagnostic combination.—Face 1.2 × as
wide as high (wider in other species), are-
olet absent, face of male black except
faint light spot (female unknown), meso-
soma and metasoma predominantly black.

Description.—**Structure**: Antenna with
>20 flagellomeres (broken). Ocelli en-
larged and sitting on a swelling, hind ocel-

li separated by about their diameter. An-
tennal sockets in lateral view forming a
moderately strong angle with vertical axis
of compound eye. Frons not strongly de-
pressed. Face 1.2 × as wide as high. Me-
dian swelling of face moderate. Upper
mandibular tooth subequal in size and
shape to lower tooth. Notaulus strong and
sharply defined only at anterior end of
mesoscutum. Epomia weak. Mesopleuron
separated by 0.5–2.0 of their diameter and
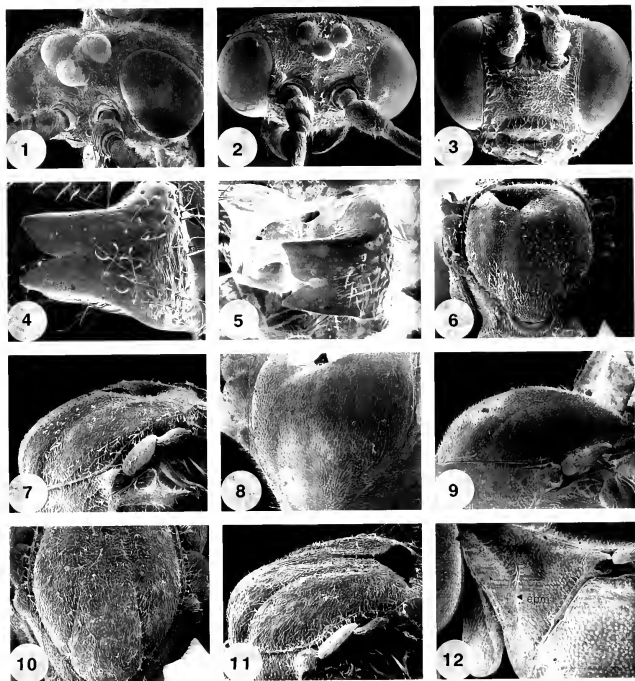
Figs. 1–12.   1–2, head in dorsal view: 1, *P. magnus*; 2, *P. testatorius*. 3, face of *P. sorbi*. 4–5, mandibular teeth: 4, *P. testatorius*; 5, *P. bolbogaster*. 6–11, mesoscutum and notauli, dorsal and lateral: 6–7, *P. sorbi*; 8–9, *P. magnus*; 10–11, *P. testatorius*. 12, pronotum of *P. mellipes*, with epomia (EPM).

microsculpture with meshes well outlined and sculpticells convex; well defined on posterior 0.3 of mesopleuron below speculum and gradually fading towards other parts of mesepisternum. Carinae of propodeum strongly defined. Forewing 12.3 mm long, areolet absent. Hind femur 3.7 mm long and 6.2 × as long as wide. Hind tarsomere 1 weakly compressed laterally and 0.55 × as wide as hind tibia near apex. First metasomal tergum 2.1 × as long as wide, with median dorsal carinae reduced to a median furrow; in lateral view weakly and regularly curved at midlength. Sublateral swellings on terga absent. Metasomal tergum 2 with punctures almost coalescent with outlines almost polygonal when close, and microsculpture
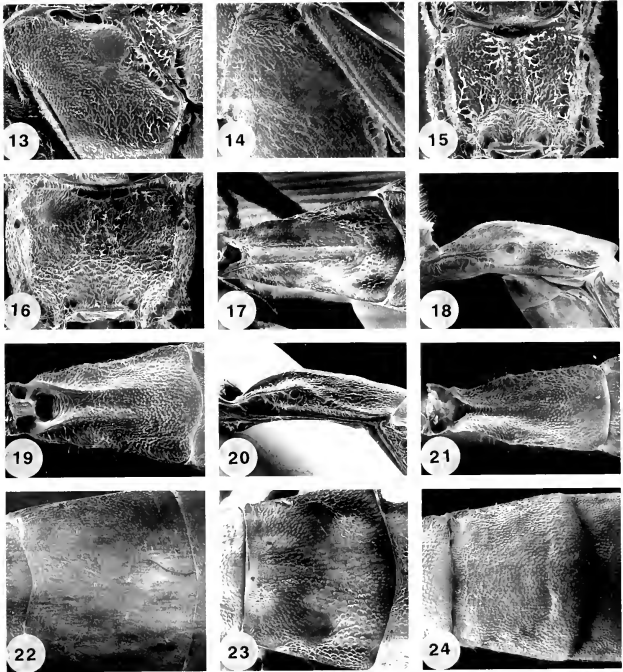
Figs. 13–24. 13–14, mesopleuron: 13, *P. sorbi*; 14, *P. bolbogaster*. 15–16, propodeum: 15, *P. sorbi*; 16, *P. testatorius*. 17–21, metasomal tergum 1, dorsal and lateral: 17–18, *P. bolbogaster*. 19–20, *P. sorbi*. 21, *P. testatorius*. 22–24. metasomal tergum 2, dorsal: 22, *P. magnus*; 23, *P. bolbogaster*; 24, *P. sorbi*.

well defined with sculpticells convex along posterior and lateral borders of tergum, at most suggested at centre of tergum and almost entirely faded anteriorly. **Coloration**: Antenna with scape, pedicel and flagellum black except traces of yellowish brown on flagellomeres 9 to 13. Head black except faint brown median spot on face below tubercle, brown clyp-

eus and brown anterior surfaces and apical third of lateral surfaces of mandibles. Mesosoma black. Wings with light yellow infuscation. Legs with all coxae and trochanters black. Femur, tibia and tarsus of all legs orange except apical half of hind tibia and whole hind tarsus black. Metasoma black.

Etymology.—From the Latin *ater* (black)

and *facies* (face), referring to the dark colored face.

Distribution.—Known only from the type locality (Fig. 32).

Specimen examined.—Holotype male: "Unalakleet, Alaska 8.viii.1961 R. Madge". Condition of type: missing left antenna beyond flagellomere 17 and right antenna beyond flagellomere 20. [CNCI].

Protarchus bolbogaster Leblanc, new species
(Figs. 5,14,17,18,23,30)

Diagnostic combination.—Upper mandibular tooth much wider than lower tooth (Fig. 5) (subequal in other species), sublateral swellings on metasomal tergites 2 to 4 (Fig. 22) (absent in other species), mesosoma and metasoma predominantly black.

Description.—**Structure**: Antenna with 48–53 flagellomeres. Ocelli of moderate size and not sitting on a swelling, hind ocelli separated by more than their diameter. Antennal sockets in lateral view forming a moderately strong angle with vertical axis of compound eye. Frons not strongly depressed. Face 1.7–1.8 (female) and 1.5–1.7 (male) × as wide as high. Median swelling of face moderate. Upper mandibular tooth much wider than lower tooth (Fig. 5). Notaulus strong and sharply defined to middle of mesoscutum. Epomia indistinct. Mesopleuron (Fig. 14) with punctures separated by 0.5–2.0 of their diameter and microsculpture with meshes lightly impressed and sculpticells slightly convex, but more convex anterior to speculum. Carinae of propodeum strongly defined. Forewing 13.6–15.2 (female) and 13.9–14.8 (male) mm long, areolet present and large. Hind femur 4.2–4.6 mm long and 5.2–6.2 × as long as wide. Hind tarsomere 1 weakly compressed laterally and 0.50 × as wide as hind tibia near apex. First metasomal tergum 1.8–2.1 × as long as wide, with median dorsal carinae well defined and strong (Fig. 17); in lateral view decurved with a strong angle before

midlength (Fig. 18). Terga 2 to 4 each with two large sublateral swellings with sparser punctures (Fig. 23). Metasomal tergum 2 (Fig. 23) with punctures almost coalescent with outlines polygonal, but sparser and faded on sublateral swellings, and microsculpture well defined along posterior and lateral borders, but with meshes much smaller and flat along anterior border. Dorsal notch on ovipositor with anterior margin without a strong angle, gradually sloping. **Coloration:** *Female.*—Antenna with scape and pedicel reddish black, and flagellum with flagellomeres dorsally reddish brown and ventrally brownish orange gradually turning reddish brown near apex. Head black except anterior surfaces and apical half of lateral surfaces of mandibles brown. Mesosoma black except tegulae yellowish brown. Wings with yellow infuscation. Legs orange except hind tibia and tarsus reddish black to black. Metasoma black. *Male.*—Antenna with scape and pedicel brown, and flagellum with flagellomeres dorsally reddish brown and ventrally brown. Head black except usually brown median longitudinal spot on face below tubercle, brown to reddish black clypeus and brown anterior surfaces and apical half of lateral surfaces of mandibles. Mesosoma black except tegulae yellowish brown. Wings with yellow infuscation. Legs orange except hind tibia and tarsus reddish black to black. Metasoma black.

Etymology.—From the Greek *bolbos* (swelling) and *gaster* (belly), referring to the characteristic sublateral swellings on metasomal terga 2 to 4.

Distribution.—Transcontinental in cold temperate and boreal regions (Fig. 30).

Specimens examined.—3 females and 6 males. Holotype *male*, "Estes Pk. Colo.[rado] 7500 ft 7 mi. E. 8-18-48 Evans"; "*Protarchus* Det. W.R.M. Mason '48". Condition of type: intact. [CNCI]. *Paratypes:* CANADA. BRITISH COLUMBIA: Jesmond, 14.ix.1938, J.K. Jacob (1F,CNCI); Racing River, 2400',

24.viii.1973, H.&M. Townes (1F,AEIC). ONTARIO: Orrville, 21.vii.1958, L.L. Pechuman (1M,AEIC). QUEBEC: Lac Rolland, R.I.F. 41, specimen no. 12150-B (1M,CNCI). YUKON TERRITORY: 14 mi.E.Dawson, 1300', 30.vi.1962, R.E. Leech (1F,CNCI) (used for SEM). UNITED STATES. MAINE: Dryden, 30.viii.1959 (1M,AEIC); Roque Bluff, 10.viii.1907, J.A. Cushman, "*Protarchoides mandibularis*" Allotype # 25975, USNM (1M,USNM). MICHIGAN: Huron Mts, 25.viii.1959, H. Townes, "strong *Pimpla* odor" (1M,AEIC).

Remarks.—This species is closely related to the Palearctic *P. heros* (Holmgren), both species sharing as synapomorphies the unique mandible shape and the large sublateral swellings on terga 2 to 4. *P. bolbogaster* differs from *P. heros* by its predominantly orange legs. Cushman's original allotype of *P. mandibularis* belongs to *P. bolbogaster*.

Protarchus magnus (Davis)
(Figs. 1,8,9,22,26,30)

Zaccales magnus Davis 1898 (1897):283.

Diagnostic combination.—Whole body predominantly light colored (brown), hind tibiae entirely light colored, ocelli enlarged and hind ocelli separated by about their diameter, dorsal notch on ovipositor with anterior margin with strong angle, abruptly sloping (Fig. 26).

Description.—**Structure**: Antenna with 47–48 flagellomeres. Ocelli enlarged and sitting on a swelling, hind ocelli separated by about their diameter (Fig. 1). Antennal sockets in lateral view forming a moderately strong angle with vertical axis of compound eye. Frons not strongly depressed (Fig. 1). Face 1.5–1.7 × as wide as high. Median swelling of face very weak. Upper mandibular tooth subequal in size and shape to lower tooth. Notaulus strong and sharply defined only at anterior end of mesoscutum (Fig. 8,9). Epomia weak. Mesopleuron with punctures separated by 0.5–2.0 of their diameter and microsculp-

ture with sculpticells very convex, making surface mat; meshes well outlined on posterior half below speculum, but gradually fading anteriorly. Carinae of propodeum strongly defined. Forewing 16.5–18.3 mm long, areolet present and large. Hind femur 4.6–5.2 mm long and 6.8–8.0 × as long as wide. Hind tarsomere 1 weakly compressed laterally and 0.50–0.55 × as wide as hind tibia near apex. First metasomal tergum 2.1–2.6 × as long as wide, with median dorsal carinae reduced to a median furrow; in lateral view weakly and regularly curved at midlength. Sublateral swellings on terga absent. Metasomal tergum 2 (Fig. 22) with punctures round and not coalescent, and microsculpture uniform over all tergum, with sculpticells convex. Dorsal notch on ovipositor with anterior margin with a strong angle, abruptly sloping (Fig. 26). **Coloration:** *Female.*—Body uniformly brown except the following. Yellowish brown parts are antennae, clypeus, mandibles, hind corner lobe of pronotum, tegula, subalar prominence, mesepimeron and legs beyond coxae. Black parts are base of first antennal flagellomere and narrow bands at apices of metasomal terga 3 to 8. Wings with yellow infuscation. Color variation: Some females have extensive black markings: frons, vertex and genae, propleuron, all pronotum except upper and posterior margins and hind corner lobe, dorsal surface of forecoxa, anteromedian band on mesoscutum to half of mesoscutum length and two bands on mesoscutum lateral to notauli, upper fourth of epicnemium, upper fourth to third of mesopleuron except anterior and posterior margins, subtegular ridge, speculum, mesosternum except anterolateral corners, large central spot on metasomal tergum 2 and whole metasoma beyond tergum 2.

Distribution.—Northeastern United States and Southeastern Canada (Fig. 30).

Specimens examined.—10 females. *Holotype female,* 4 labels, "N!N"; "HoloTYPE 4340"; "*Zaccales magnus* Davis"; "Collec-
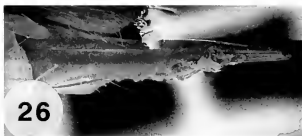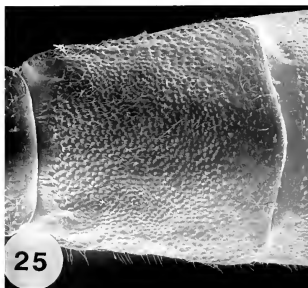
Figs. 25–27. 25, *P. testatorius*, metasomal tergum 2, dorsal. 26–27, ovipositor: 26, *P. magnus*; 27, *P. sorbi*.

tion of THE ACADEMY OF NATURAL SCIENCES of Philadelphia. ANSP". Condition of type: missing left flagellum beyond flagellomere 11, right antenna, left fore wing; right fore and hind wings pinned below specimen. [ANSP]. *Other specimens*: CANADA. QUEBEC: Joliette Co., Ste-Béatrix, 24.VIII.1978 (1F,LLIC) (used for SEM). UNITED STATES. MICHIGAN: Midland, vii.1950 (1F,AEIC). NEW YORK: Allegany St.Pk., 30.vii.1938 (1F,USNM), 31.vii.1938 (1F,USNM), A.R. Shaddle; Essex Co., Keene Valley, 17.ix.1917, H. Nortman (1F,ANSP); Six Miles Creek, Ithaca, 17.vii.1947, J.G. Franclemont (3F,AEIC). PENNSYLVANIA: Glenside, "10.12.1929", G.G. Sleesman (1F,USNM).

Protarchus mellipes (Provancher)
(Figs. 12,31)

Coelocentrus mellipes Provancher 1886:113.
Protarchoides mellipes: Walley 1938:231.
Protarchoides pallipes Cushman 1927:15. Synonymy by Walley 1938:231.

Diagnostic combination.—Epomia clearly defined and prominent (Fig. 12), ocelli enlarged and hind ocelli separated by about their diameter, face entirely black, or at most with yellowish brown median spot,

mesosoma and metasoma almost entirely black, hind tibiae entirely light colored.

Description.—**Structure**: Antennal flagellum with 43–46 (female) and 41–43 (male) flagellomeres. Ocelli enlarged and sitting on a swelling, hind ocelli separated by about their diameter. Antennal sockets in lateral view forming a moderately strong angle with vertical axis of compound eye. Frons not strongly depressed. Face 1.5–1.7 × as wide as high. Median swelling of face moderate. Upper mandibular tooth subequal in size and shape to lower tooth. Notaulus strong and sharply defined only at anterior end of mesoscutum. Epomia clearly defined and prominent (Fig. 12). Mesopleuron with punctures separated by 0.5–2.0 of their diameter and microsculpture with sculpticells convex, making surface slightly mat; meshes well outlined on posterior half below speculum, but gradually fading anteriorly. Carinae of propodeum well defined and strong. Forewing 13.8–16.0 (female) and 12.3–13.2 (male) mm long. Areolet present and large. Hind femur 3.9–4.9 mm long and 6.0–7.0 × as long as wide. Hind tarsomere 1 weakly compressed laterally and 0.50–0.55 × as wide as hind tibia near apex. First metasomal tergum 2.3 × as long as

wide with median dorsal carinae reduced to a median furrow and; in lateral view weakly and regularly curved at mid-length. Sublateral swellings on terga absent. Metasomal tergum 2 with punctures round and not coalescent, and microsculpture uniform over all tergum with sculpticells convex. Dorsal notch on ovipositor with anterior margin without a strong angle, gradually sloping. **Coloration**: *Female*.—Antenna with scape and pedicel black or black with ventral surfaces yellowish orange, and flagellum with basal section yellowish orange, except basal half of first flagellomere and dorsal surfaces of first few flagellomeres generally black, and apical section black to brown. Head black except clypeus reddish brown to yellowish brown, lower margin of face along clypeus sometimes yellowish brown and mandibles black to yellowish brown. Mesosoma black except yellowish brown to reddish black tegula. Wings with yellow infuscation. Legs yellowish brown except fore, middle and hind coxae and usually fore, middle and hind trochanters 1 black, usually a narrow brownish orange longitudinal line on black dorsal surface of hind coxa and brownish orange fore and middle tarsomeres 5. Metasoma black. *Male*.—Antenna with scape and pedicel black, and flagellum with basal section yellowish orange, except dorsal surfaces of first few flagellomeres black and with apical section dark brown. Head black except clypeus yellowish brown and, in one specimen, faint traces of yellowish brown on face. Mesosoma black except tegula yellowish brown. Wings with yellow infuscation. Legs yellowish brown except fore, middle and hind coxae and trochanters 1 reddish black. Metasoma black.

Distribution.—Transcontinental in boreal region (Fig. 31).

Specimens examined.—5 females and 2 males. *Type material*: Lectotype of *Coelocentrus mellipes* Provancher, designated by Barron 1975:508; male, 6 labels: "Holotype

male *Coleocentrus mellipes* Provancher No. 4235"; "*Coleocentrus* n. spec!"; "G 484"; "This must be the type of *Coleocentrus mellipes* Prov. which g.[ahan] & R.[ohwer] could not locate. It was evidently returned to geddes by Prov. & the label [# 2] in red ink is in Geddes hand (note by G.S. Walley april/20/37)"; "Lectotype *Coleocentrus mellipes* Provancher *Comeau* '40"; "LECTOTYPE *Coleocentrus mellipes* Provancher G 484 Barron '71". Specimen from Rocky Mountains according to Walley, 1938. Condition of type: missing right fore and middle legs beyond coxae, left middle leg beyond tibia and both hind tarsi but tarsomeres 1–2 of one hind leg glued on first label. [CNCI]. Holotype of *Protarchoides pallipes* Cushman. Female. 3 labels: "Edmonton, Alberta 23.viii.1916 G. Salt"; "Type No. 40444 U.S.N.M."; *Protarchoides pallipes* Type. Cush.". Condition of type: missing entire left antenna and right hind tarsus; left hind tarsus broken and reglued between tarsomeres 2 and 3. [USNM]. *Other specimens*. CANADA. ALBERTA: 15 mi.E.Morley, 14.viii.1962, K.C. Herrmann (1F,CNCI) (used for SEM); Edmonton, 23.VIII.1926, G. Salt, paratype # 40444, USNM (1F,USNM). BRITISH COLUMBIA: Houston, 17.vi.1959, Forest Insect Survey specimen no. 58-1792-0119, ex. *Trichiosoma triangulum* (1M,CNCI); Robson, 13.ix.1949, H.R. Foxlee (1F,CNCI). ONTARIO: Smoky Falls, near Kapuskasing, 9.viii.1937, R.V. Whelan (1F,CNCI).

Remarks.—The specimen used by Provancher, collected by G. Geddes in the Rocky Mountains (Provancher 1886), could not be located by Rohwer in his 1915 visit to the Provancher collection (Gahan and Rohwer 1917, Cushman and Rohwer 1920). Walley (1938) discovered a specimen in the Geddes collection, donated to CNCI, labelled "*Coleocentrus* n sp" and agreeing with Provancher's description. He accepted this specimen as the one originally used by Provancher. Barron (1975) designated the specimen as lectotype.
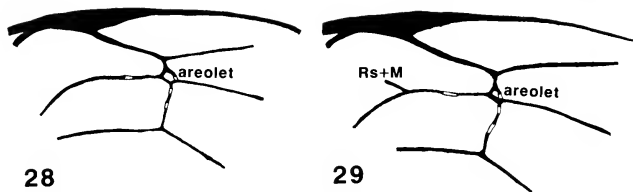
Figs. 28–29. Forewing, showing areolet: 28, *P. sorbi*; 29, *P. testatorius*.

Protarchus pallidicornis (Walley)
(Fig. 30)

Protarchoides pallidicornis Walley, 1938:231.

Diagnostic combination.—Epomia clearly defined and prominent (Fig. 12), ocelli enlarged and hind ocelli separated by about their diameter, face entirely brown or yellowish brown, mesosoma and metasoma predominantly brownish black with extensive yellowish orange and brown markings, hind tibiae entirely light colored.

Description.—**Structure**: Antenna with 45 (female) flagellomeres. Ocelli enlarged and sitting on a swelling, hind ocelli separated by about their diameter. Antennal sockets in lateral view forming a moderately strong angle with vertical axis of compound eye. Frons not strongly depressed. Face 1.5 × as wide as high. Median swelling of face moderate. Upper mandibular tooth subequal in size and shape to lower tooth. Notaulus strong and sharply defined only at anterior end of mesoscutum. Epomia clearly defined and prominent. Mesopleuron with punctures separated by 0.5–2.0 of their diameter apart and microsculpture with sculpticells convex, making surface slightly mat and meshes well outlined on posterior half below speculum, but gradually fading anteriorly. Carinae of propodeum strongly defined. Forewing 14.5 (female) and 12.8 (male) mm long, areolet present and large. Hind femur 4.3 (female) and 4.7 (male)

mm long and 6.9 (female) and 7.8 (male) × as long as wide. Hind tarsomere 1 weakly compressed laterally and 0.50 × as wide as hind tibia near apex. First metasomal tergum 2.4 × as long as wide, with median dorsal carinae reduced to a median furrow; in lateral view weakly and regularly curved at midlength. Sublateral swellings on terga absent. Metasomal tergum 2 with punctures round and not coalescent, and microsculpture uniform over all tergum with sculpticells convex. Dorsal notch on ovipositor with anterior margin without a strong angle, gradually sloping. **Coloration**: *Female.*—Antenna brownish orange except dorsal half of scape brownish black. Head brown except frons, area around ocelli and vertex behind ocelli brownish black. Mesosoma brownish black except the following. Yellowish orange parts are hind corner lobe of pronotum, tegula, subalar prominence, anterior margin of mesopleuron, mesepimeron and upper division of metapleuron. Brown parts are sublateral longitudinal bands on mesoscutum along notauli from anterior margin to three quarters of scutum length and lateral bands along mesoscutum margin from wing tegula to end of mesoscutum, lower half of epicnemium, anterolateral corner of mesosternum, lower margin of mesopleuron, speculum, scutellum including axillae, postscutellum, upper anterior corner of metapleuron, anterior half of area lateralis of pronotum and along median furrow of propodeum. Wings
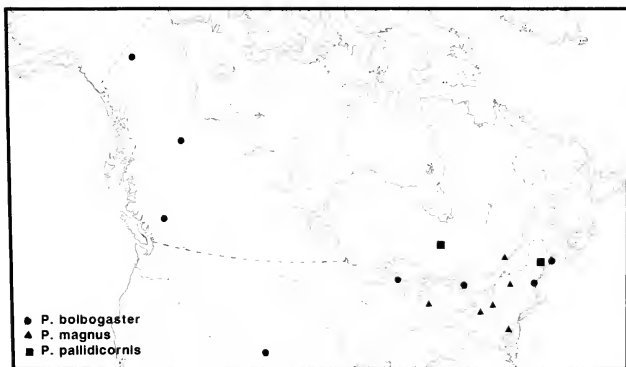
Fig. 30. Distribution of *P. bolbogaster* (circles), *P. magnus* (triangles) and *P. pallidicornis* (squares).

with yellow infuscation. Legs yellowish brown except faint traces of brownish black on dorsal surface of forecoxa and apical half of dorsal surfaces of mid and hind coxae. Metasoma brownish black except first tergum brown and faint traces of brown on second tergum. *Male.*—Antenna with scape and pedicel dorsally brownish black and ventrally yellowish brown, and flagellomere 1 yellowish brown (rest of antennae missing). Head brownish black except face, clypeus, malar space and mandibles yellowish brown. Mesosoma brownish black except the following. Yellowish orange parts are hind corner lobe of pronotum, tegula, subalar prominence and mesepimeron. Brown parts are two sublateral longitudinal bands on mesoscutum along notauli from anterior margin to three quarters of scutum length and two lateral bands along margins of scutum from base of sublateral band to three quarters of scutum length, lower two thirds of epicnemium, anterolateral corner of mesosternum, lower margin of mesopleuron, speculum, scutellum including axillae, postscutellum and entire propodeum ex-

cept faint brownish black on metapleuron. Wings with yellow infuscation. Legs yellowish brown. Metasoma brownish black except first tergum and basal half of second tergum brown and faint brown traces on anterolateral corners of third tergum.

Distribution.—Ontario, Maine (Fig. 30).

Specimens examined.—1 female and 1 male. *Holotype,* examined, female, 2 labels: "Holotype female *Protarchoides pallidicornis* Walley No. 4410"; "Smokey Falls, Ont[ario] (near Kapuskasing) Aug 4, 1937 R.V. Whelan". Condition of type: missing hind tarsomeres 4–5. [CNCI]. *Other specimen.* UNITED STATES. MAINE: Glenburn, 5.vii.1928, Gypsy moth Lab., 10088 NIG, ex. Tenthredinid (!) (1M,USNM).

Remarks.—This species is closely related to *P. mellipes.* The prominent epomia (Fig. 12) is a synapomorphy.

Protarchus sorbi (Ratzeburg)
(Figs. 3,6,7,13,15,19,20,24,27,28,31)

Tryphon sorbi Ratzeburg 1844:126. Holotype lost.
Psilosarge (!) *longipes* Ashmead, in Slosson 1902: 321 (*nomen nudum*).

Protarchoides longipes Cushman 1922:26. *Protarchus longipes*: Townes, 1945:505. NEW SYNONYM.

Protarchoides mandibularis Cushman 1924:9. Designated synonym with *P. longipes* by Townes 1945:505. NEW SYNONYM.

Diagnostic combination.—Hind tarsomere 1 strongly compressed laterally and 0.55–0.70 as wide as hind tibia near apex, metasomal tergum 1 decurved with a strong angle (Fig. 20), face of male yellow, mesosoma and metasoma predominantly black.

Description.—**Structure:** Antenna with 36–45 flagellomeres. Ocelli of moderate size and not sitting on a swelling, hind ocelli separated by more than their diameter. Antennal sockets in lateral view forming a moderately strong angle with vertical axis of compound eye. Frons not strongly depressed. Face (Fig. 3) 1.6–1.9 × as wide as high. Median swelling of face almost absent. Upper mandibular tooth subequal in size and shape to lower tooth. Notaulus weak and reduced to shallow impressions (Figs. 6,7). Epomia indistinct or very weak. Mesopleuron (Fig. 13) with punctures separated by less than 0.1 of their diameter and microsculpture variable in different specimens from absent over all mesopleuron to almost absent with meshes absent to lightly convex below speculum to irregularly striated through fusion of sculpticells on posterior 0.5 of mesopleuron below speculum. Carinae of propodeum strongly defined (Fig. 15). Forewing 9.9–13.9 (female) and 9.8–12.5 (male) mm long, areolet present and large (Fig. 28). Hind femur 2.8–3.9 mm long and 5.2–6.5 × as long as wide. Hind tarsomere 1 strongly compressed laterally and 0.55–0.70 × as wide as hind tibia near apex. First metasomal tergum 1.4–1.9 × as long as wide, with median dorsal carinae well defined and strong (Fig. 19) or reduced to a median furrow; in lateral view decurved with a strong angle before midlength (Fig. 20). Sublateral swellings on terga absent. Metasomal tergum 2 (Fig. 24)

with punctures very dense, polygonal, crater-like but not coalescent, and microsculpture with sculpticells convex along posterior border of tergum, otherwise completely faded on the rest of tergum. Dorsal notch on ovipositor with anterior margin without a strong angle, gradually sloping (Fig. 27). **Coloration:** *Female.*—Antenna with scape and pedicel black, and flagellum with flagellomeres dorsally brownish black and ventrally brownish orange and gradually turning brownish black near apex, or sometimes entire flagellum brownish black. Head black except anterior surface of mandible to entire mandible yellowish orange, and clypeus brownish orange to reddish black or black. Mesosoma black except hind corner lobe of pronotum and tegula reddish brown. Wings hyaline. Legs orange except sometimes traces of reddish black anteriorly at base of each coxae, and apical two thirds to nine tenth of hind tibia and whole hind tarsus reddish black or black. Metasoma black. *Male.*—Antenna with scape and pedicel reddish black except usually yellow ventral surface of scape and sometimes yellow ventral surface of pedicel, and flagellum with flagellomeres dorsally brownish black and ventrally brownish black to brownish orange. Head black except orbits between compound eyes and antennal sockets yellow, and face, clypeus and mandibles yellow. Mesosoma black except tegula yellow. Wings hyaline. Legs orange except apical six tenths of hind tibia and whole hind tarsus reddish black or black and sometimes yellow fore and middle coxae, fore, middle and hind trochanters, foretibia, foretarsus and basal half of middle tibia. Metasoma black.

Distribution.—Palearctic (Sweden, Finland, Russia) and transcontinental in North America (Fig. 31).

Specimens examined.—17 females and 14 males. Type material. *Holotype* of *Protarchoides longipes* Cushman. Female. 5 labels: "MT.WASH'[ingto]N."; "39"; "Type No.
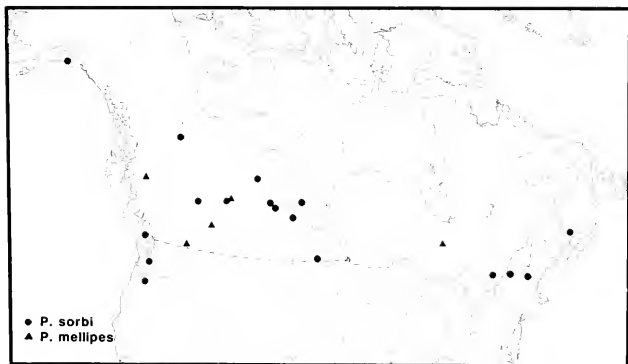
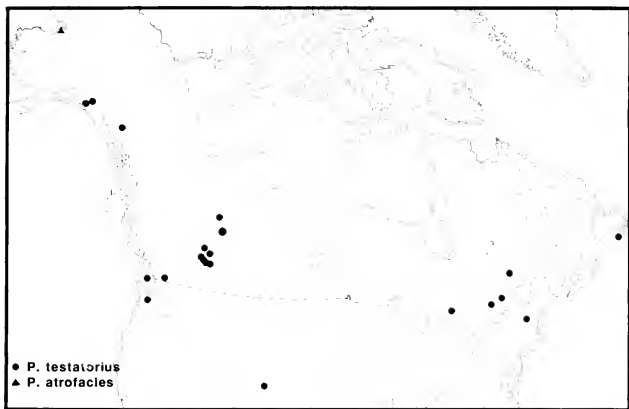Fig. 31. Distribution of *P. sorbi* (circles) and *P. mellipes* (triangles).

Fig. 32. Distribution of *P. testatorius* (circles) and *P. atrofacies* (triangles).

25030 U.S.N.M."; "*Psilosage longipes* _ Type Ashm[ead]"; "*Protarchoides longipes* Type. Cush.". [New Hampshire, A.T. Slosson, 1902]. Condition of type: missing left hind tarsus; both antennae broken and glued on first label. [USNM]. *Holotype* of *Protarchoides mandibularis* Cushman. Female. 4 labels: "Wellington B.C. 28.VII.[19]04"; "1260"; "Type No 25975 U.S.N.M."; "Protarchoides mandibularis Type. Cush.". Condition of type: missing: left antenna beyond flagellomere 7, right antenna beyond flagellomere 37, right foreleg tarsus beyond tarsomere 1 and right hind leg tarsus beyond tarsomere 1; right antenna section containing flagellomeres 4 to 37 and right hind leg beyond coxa broken and glued on locality label. [USNM]. *Other specimens*: CANADA. ALBERTA: Edmonton, 28.vii.1926, E.H. Strickland (1M,AEIC); Entranse, emerged 21.iii.1950, Forest Insect Survey specimen no. A113313, ex. *Trichiosoma* sp. (1M,CNCI). BRITISH COLUMBIA: Summit Lake, Mile 392, Alaska Hwy, 4600', 16.vii.1959 (1F,CNCI), 4700', 15.vii.1959 (1F,CNCI), 5000', 6.vii.1959 (1M,CNCI); Stone Mtn Nat. Pk., "3800', 12.vii.1973 13.vii.1973 18.vii.1973, 20.vii.1973 (7M,AEIC). MANITOBA: Christopher Lake, emerged 4.iii.1963, Forest Insect Survey specimen no. 1914(02), ex. *Trichiosoma triangulum* (1F,CNCI); Turtle Mtn., 21.vii.1953, Brooks-Kelton (1F,CNCI); Wanless, 29.vi.1961, H.E. Milliron (1F,CNCI). PRINCE EDWARD ISLAND: Alberton, 15.vii.1940, G.S. Walley (1F,CNCI). QUEBEC: Hemmingford, 1.vii.1928, G.H. Hammond (1F,CNCI); Aylmer, 20.v.1920, G.H. Hammond, ex. *Trichiosoma* sp. (1M,CNCI). SASKATCHEWAN. Buffalo Narrows, emerged 4.iii.1964, Forest Insect Survey specimen no. 63W-2241(03), ex. *Trichiosoma triangularis* (!) (1F,CNCI); Candle Lake, emerged 10.ii.1951, Forest Insect Survey specimen no. W50-42786, ex. *Trichiosoma triangulum* (1M,CNCI); Parr Hill, emerged 17.ii.1961, Forest Insect Survey specimen no. W61-2392(04), ex. *Trichiosoma triangulum*

(1F,CNCI); Waskesiu, 21.vi.1938, J.G. Rempel (1F,AEIC). UNKNOWN PROVINCE: Crimson Lake, emerged before 12.vii.1961, Forest Insect Survey specimen no. 60A1409-03, ex. *Trichiosoma* sp. (1F,CNCI) (used for SEM). UNITED STATES. ALASKA: Seaward, <300', 25.vii.1951, W.J. Brown (1F,CNCI). OREGON: Mt. Hood, 3500', 19.vii.1978, 24.vii.1978, H.&M. Townes (2F,AEIC). WASHINGTON: Mt. Rainier, 4200', 15.vii.1940, H.&M. Townes, "odor like *Pimpla*" (1M,AEIC). UNKNOWN LOCALITY. Reared specimen labelled "99 88281" (1M,CNCI).

Protarchus testatorius (Thunberg)
(Figs. 2,4,10,11,16,21,25,29,32)

Ichneumon testatorius Thunberg 1822:276. Lectotype (designated by Roman, 1912) not examined.

Tryphon rufus Gravenhorst 1829:200. Holotype lost.

Mesoleius (Protarchus) melanurus Thomson 1895: 2020. Leptotype designation and synonymy by Viitasaari 1979:34. Lectotype not examined.

Diagnostic combination.—Areolet very small or sometimes absent (Fig. 29), metasoma black with extensive orange markings on tergites 2 to 4.

Description.—**Structure:** Antenna with 40–44 flagellomeres. Ocelli of moderate size and not sitting on a swelling, hind ocelli separated by more than their diameter (Fig. 2). Antennal sockets in lateral view forming a very strong angle with vertical axis of compound eye. Frons strongly depressed (Fig. 2). Face 1.3–1.4 × as wide as high. Median swelling of face moderate. Upper mandibular tooth subequal in size and shape to lower tooth (Fig. 4). Notauli strong and sharply defined to middle of mesoscutum length (Figs. 10,11). Epomia indistinct. Mesopleuron with punctures separated by 0.5–2.0 of their diameter and microsculpture generally absent, at most expressed as slightly convex sculpticells below speculum. Ca-

rinae of propodeum weakly defined to almost absent (Fig. 16). Forewing 11.2–13.3 mm long. Areolet in forewing very small (Fig. 29) or sometimes absent. Hind femur 3.6–4.4 mm long and 6.0–6.8 × as long as wide. Hind tarsomere 1 weakly compressed laterally and 0.45–0.50 × as wide as hind tibia near apex. First metasomal tergum 1.8–2.2 × as long as wide, with median dorsal carinae reduced to a median furrow (Fig. 21); in lateral view weakly and regularly curved at midlength. Sublateral swellings on terga absent. Metasomal tergum 2 (Fig. 25) with punctures very dense, slightly polygonal but not coalescent, but density decreasing towards posterior margin, and with microsculpture well defined on apical 0.3, flat in middle 0.3 and completely faded basally. Dorsal notch on ovipositor with anterior margin without a strong angle, gradually sloping. **Coloration**: *Female.*—Antenna with scape and pedicel reddish black, and flagellum brownish orange except basal portion of flagellomere 1 reddish black and dorsal surfaces of first few flagellomeres reddish black gradually turning brownish orange to yellowish orange near apex. Head black except the following. Yellow parts are orbits between eyes and antennal sockets, clypeus, mandibles and face except narrow median reddish black line below tubercle. Brownish orange parts are genal orbits from posterior ocelli down to two thirds to a quarter of eye height. Mesosoma black except the following. Yellow parts are tegula, scutellum, postscutellum and often four small spots on anterior margin of mesoscutum on the sides of notauli. Wings with light yellow infuscation. Legs with coxae black except anteromedian line on or whole anterior surface of forecoxa yellow and anteroapical spot on middle coxa yellow. Trochanters 1 black except anterior surface of foretrochanter 1 and apex of dorsal surface of middle trochanter 1 yellow. Fore and middle legs beyond trochanters 1 yellowish orange except ventral basal

quarter to half of middle femur reddish black. Hind trochanter 2 yellowish orange. Hind femur black except yellowish orange at base and apex. Hind tibia with basal 0.6 yellowish orange and apical 0.4 reddish black. Hind tarsi yellowish orange to brownish orange. Metasoma black with the following brownish orange: apical 0.25 of tergum 1, apical 0.33 to 0.5 of tergum 2 to entire tergum 2 except lateral black markings on basal 0.5, entire tergum 3 except sometimes a large median black spot, basal 0.15 of tergum 4 with a small subapical spot to entire tergum 4 except apical 0.1. *Color variations*: Two females have brownish orange markings on propodeum anterior to postpectal carina and lateral to median furrow and extending laterally below lateral carinae. These markings are present in most Palearctic specimens of *P. testatorius*.

Distribution.—Palearctic (Sweden, Finland, Germany, Russia) and transcontinental in North America (Fig. 32).

Remarks.—The lectotypes from Europe have not been examined because a good series of Palearctic material (AEIC, USNM) was studied and found to be conspecific with the Nearctic material.

Specimens examined.—28 females. ALBERTA: Banff, 18.viii.1946, E.H. Strickland (1F,AEIC); Banff, Black's Camp Ground, emerged 28.vi.1958, Forest Insect Survey specimen no. 58A108-03, ex. *Trichiosoma* sp. on alder (1F,CNCI); Cameron Lake, 9.vii.1949, C.P. Alexander (1F,AEIC); Canyon Creek, emerged 9.iii.1953, Forest Insect Survey specimen no. A2182A, ex. *Trichiosoma* sp. (1F,CNCI); Eisenhower Junction, Banff National Park, 9.viii.1962, K.C. Hermann (1F,CNCI); Fawcett, emerged 9.vii.1956, Forest Insect Survey specimen no. 55A1438-12, ex. *Trichiosoma* sp. (1F,CNCI); Kanamaskis, emerged 23.ii.1949, Forest Insect Survey specimen no. A-455-K, ex. *Trichiosoma* sp. (1F,CNCI); Lake Louise, 5600', 26.vii.1938, G.S. Walley (1F,CNCI); Nordegg, 21.vii.1926, E.H. Strickland (1F,CNCI); 18 mi.W. Strachan,

emerged 24.iii.1959, Forest Insect Survey specimen no. 58A1821-02, ex. *Trichiosoma* sp. (1F,CNCI). BRITISH COLUMBIA: Hope Mts, 20.viii.1931, A.N. Gartrell (1F,CNCI) (used for SEM); Saanich, emerged 23.v.1958, Forest Insect Survey specimen no. 58-3-01-A, ex. *Trichiosoma triangulum* (1F,CNCI). ONTARIO: Sudbury, 1891 (1F,CNCI). QUEBEC: Lac St-Jean, 20.viii.1939, P.L. Mercier (1F,AEIC); Kazabazua, 28.viii.1928, G.H. Fisk (1F,CNCI); Ste-Agathe des Monts, 7.viii.1937, G.S. Walley (1F,CNCI). YUKON TERRITORY: Whitehorse, 7.viii.1948, W.R. Mason (1F,CNCI). UNKNOWN PROVINCE: Hot Springs Road, 2.viii.1902, N.B. Sanson (1F,CNCI). FRANCE. Miquelon Island, 15.viii.1990, D. Abraham, collected in bog (1F,CNCI). UNITED STATES. ALASKA: Thompson Pass, 14.viii.1973, H.&M. Townes (1F,AEIC); Tsaina River, 17.viii.1973, 18.viii.1973, H.&M. Townes (2F,AEIC). COLORADO: Gould, 5.viii.1974, 6.viii.1974, H.&M. Townes (3F,AEIC). NEW HAMPSHIRE: Franconia (1F,USNM). WASHINGTON: Mt. Rainier, 22.vii.1940, H.&M. Townes, "strong *Pimpla* odor" (2F,AEIC).

ACKNOWLEDGMENTS

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BOOK REVIEW

Geologische und biologische Entomoökologie der rezenten Seidenbiene Colletes. *Volume I.* Detlef Mader. Logabook, Köln, 1999. xliii+807. Price: Germany DM 98.00 or 50.00 Euro (hardcover). ISBN 3-87361-263-1.

In our concept-driven time dominated by molecular biology, few authors dare to publish lengthy accounts on pure natural history, summarizing raw facts of organismal life or the idiosynchrasies of a particular species. I happen to enjoy pulling those books off library shelves and immersing myself in organismal trivia. I frequently find a library note slipped into those books saying that they have not been circulating for a decade and that, unless soon used, they will be permanently impounded in compact storage. So I regularly check out these books from the library, often to return them immediately. I like to think that this fools the librarians, such that they will grant these books another decade of accessible existence on a prime shelf. And I imagine that some future scientist will stumble, like me, over these books and keep alive some natural history minutia that otherwise may be buried forever.

Detlef Mader's book on the Geological and Biological Entomo-Ecology of Colletes Bees is one of those natural history accounts. It is thick in detail, particularly the nesting idiosynchrasies of the species *Colletes daviesanus*. It is a specialist's book, therefore, and its audience may be rather limited. But it has enourmous depth in natural history, inspired by a Humboldtian appetite for careful and complete documentation. Leafing through pages and pages of flower records, or the geological details of the substrate used by *C. daviesanus* for nest construction, I came to admire Mader for taking the time to summarize his decades of work on the nesting

habits of this species. Few of us ever make the time to do that for the species that are close to our heart.

Bees in the basal bee genus *Colletes* are best known for their unique nest architecture. The typical colletid bee is solitary, constructs an underground nest (some species use twigs or rotting wood), and lines the nest tunnel with a cellophanelike tapestry derived from glandular secretions. A series of cells are constructed inside this tunnel, separated by partitions of additional tapestry. The tapestry linings are tranlucent, giving the appearance that these bees keep their brood in a series of plastic bags. Hence also the vernacular name of the plastic-bag bee.

Most colletids prefer to nest in level ground, but *C. daviesanus*, the most common species in central Europe, is an exception. It prefers to nest in vertical embankments or cliffs, and there only in substrate of particular kinds, such as loose sandstone. Much of Maders' book is devoted to documenting these substrate preferences for populations in central Germany, with comparative references to other populations throughout Europe. This treatment has a rather geological flavor, and I admit that the geological aspects of this work were rather lost on me, as I assume they will be lost on anyone unfamiliar with the geology and stratigraphy of central Europe. Other parts of Mader's book are more accessible, summarizing for example the literature on flowers visited by *Colletes*, or profiling the communities of other soil-dwelling species that secondarily use tunnels of abandoned *C. daviesanus* nests.

Mader's book actually comes in two volumes, only the first of which is published at this point. The second volume is scheduled for publication next year, but a

table of contents is already available. While both volumes are organized around aspects of the nesting biology of *C. davieanus* and other *Colletes* species, the first volume seems to focus more on biological aspects (e.g., presenting information on *Colletes* parasites, flower visitation, etc.), while the second volume seems more specialized and appears to concentrate more on geological aspects.

Who would benefit from these volumes? Clearly the readership is rather limited, yet it certainly should not be missing from libraries specializing on hymenopteran literature or general natural history. But apart from *Colletes* afficionados interested in knowing everything about *Colletes*, including the geological trivia of nest substrate choice of a single species in central Europe, I do not think that these volumes will find much use among bee biologists. This is not a reflection of the quality of the work, but more a reflection of the currently perceived value of natural history accounts. So I imagine that the true value of these volumes will not be apparent until *C. daviesanus*, though abundant at this point, may become extinct some time in the future. The same is certainly true for many other species for which time did not permit a comprehensive study of all life-history aspects, as for example the nesting habits of the passenger pigeon.

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INSTRUCTIONS FOR AUTHORS

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All papers will be reviewed by at least two referees. The referees will be chosen by the appropriate subject editor. However, it would be helpful if authors would submit the names of two persons who are competent to review the manuscript.

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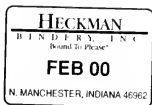
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