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CLADISTIC RELATIONSHIPS AMONG PIMELIINE TENEBRIONIDAE (COLEOPTERA)

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Abstract.—The cladistic relationships among Tenebrionidae of the subfamily Pimeliinae (=Tentyriinae of authors) are analyzed based on 84 characters examined over 60 adult tribal or generic level taxa. Features of the mouthparts, coxal articulations, ovipositor and internal female reproductive tract are highly variable and important in determining cladistic topology. Nearly all the characters employed display extensive homoplasy, especially convergence, resulting in relatively low measures of consistency of the cladograms. Deletion of less consistent characters results in loss of cladistic detail, however, without significantly improving overall consistency, indicating that even the least consistent features are cladistically meaningful.

The female reproductive tract, which shows exceptional variation that is strongly correlated with cladistic position, is illustrated extensively. Primitively the female tract comprises a bursa copulatrix and accessory gland without a separate spermatheca, as in some Cnemeplatiini and Pimeliini. Most other Pimeliinae may be placed into one of five clades based on configuration of the female tract. In most members of the cnemeplatiine-stenosine clade a capsular or short tubular spermatheca and a short, saccate gland open into the vagina through a common duct. In the pimeliine clade one to several tubular spermathecae and a tubular gland open independently into the vagina or bursa copulatrix. In several taxa of this clade the spermatheca is poorly defined or absent. The asidine clade is characterized by multiple, long, slender spermathecal tubes which open as a fascicle into the base of the accessory gland duct or into the vagina near the duct. A bursa copulatrix is absent. In the eurymetopine clade multiple, slender, tubular spermathecae are attached serially to the base of the accessory gland duct. A bursa copulatrix is often retained. In the tentyriine clade the bursa is modified to form one to several thick, tapering annulate spermathecal chambers. The accessory gland opens into one of the chambers or into the vagina. A number of tribes or genera, including Zolodinini, Falsomycterini, Boromorphini, Lachnogyini, Anepsiini, Vacronini, Nyctoporini and Cryptoglossini do not fit into any of the major clades, because they either display mostly primitive features or discordant combinations of features from different clades.

The following taxonomic changes are indicated. *Alaudes* Horn is transferred to Cnemeplatiini; Araeoschizini and Typhlusechini are synonymized under Stenosini; Falsomycterini, containing *Falsomycterus* Pic and *Pteroctenus* Kirsch, merits recognition as a separate tribe of uncertain relationship; *Boromorphini* (*Boromorphus*) merits tribal status (probably near Caenocrypticini); Platyopini is synonymized under Pimeliini; Calognathini and Vansoniini should be placed in synonymy under Cryptochilini; Elenophorini should be retained to include *Elenophorus* Latreille, *Megelenophorus* Gebien and *Psammetichus* Latreille; Craniotini is synonymized under Asidini; Epitragini is restricted to its new world components; Old World genera previously placed in Epitragini belong in Tentyriini; Edrotini, Triorophini, Trientomini, Auchmobiini and Trimytini are synonymized under Eurymetopini; *Salax* Guérin, *Trilobocara* Solier, *Megalophrys* Waterhouse, *Eremoecus* Lacordaire and *Derosalax* Gebien are separated as the tribe Trilobocarini Lacordaire; *Orthonychius* Gebien is a junior synonym of *Trilobocara*. *Pseudothinobatis* Freude is transferred from Thinobatini to Epitragini. *Ascelosodis* Redtenbacher is transferred from Tentyriini to Eurymetopini, *Achanius* Erichson and *Ambigatus* Fairmaire are transferred from Evaniosomini to Eurymetopini. Three genera are removed from Pimeliinae: *Eschatoporis* Blaisdell is transferred from Cryptoglossini to Goniaderini; *Amnophorus* Guérin from Nyctoporini to Scotobiini; and *Phtora* (Germar) mistakenly included in Pimeliinae by Doyen and Lawrence (1979) to Phaleriini.

During the past two decades the higher classification of the family Tenebrionidae has been scrutinized by a number of workers (Watt, 1967, 1974; Doyen and Lawrence, 1979; Tschinkel and Doyen, 1980; Doyen and Tschinkel, 1982), resulting in major changes in the constitution of many tribes and in the arrangement of the tribes into subfamilies (Aalbu and Triplehorn, 1985; Doyen, 1984, 1985, 1989; Doyen et al. 1989; Endrödy-Younga, 1989). However, this work has centered almost exclusively on the tribes in which defensive glands are present or secondarily lost. This group of tribes includes the beetles formerly constituting the families Lagriidae, Alleculidae and Nilionidae, as well as perhaps 10,000 species in about 40 tribes of Tenebrionidae. These beetles generally inhabit relatively mesic environments, including temperate and subtropical grasslands and woodlands. They are especially speciose in tropical forest and savannah habitats. With occasional exceptions they are not particularly diverse in extremely arid habitats, but several tribes, such as Opatrini, Scaurini and Scotobiini, are abundant in subarid environments.

A second group of tribes, comprising the subfamily Pimeliinae (=Tentyriinae of Doyen and Lawrence, 1979; Doyen and Tschinkel, 1982), lacks defensive glands. In addition, all but a single genus of Pimeliinae have the aedeagus rotated 180° about the longitudinal axis, so that the median lobe is dorsal to the tegmen rather than ventral, and all except the tribe Pimeliini lack external membranes between the apical abdominal sternites, as discussed below in greater detail. Members of the Pimeliinae primarily occupy arid or subarid habitats, with many species able to survive even the exceptionally dry conditions of deserts such as the Namib, Atacama and Sahara, where they often form dominant faunal elements in terms of biomass and numbers of individuals (Crawford and Seely, 1987; Koch, 1961; Pierre, 1958).

It is still unsettled whether absence of defensive glands is a synapomorphy for Pimeliinae. If so, absence of glands would represent a secondary loss. Alternatively Pimeliinae could be the sister taxon to all other Tenebrionidae, in which case absence of glands would be primitive, since outgroup taxa lack glands. One bit of distributional evidence which suggests secondary gland loss is the almost complete absence of Pimeliinae from the Australian region. This absence could indicate that Pimeliinae are younger than most of the other major lineages, in which glands are present. A complicating difficulty is the fact that defensive glands have clearly arisen at least twice in Tenebrionidae (Tschinkel and Doyen, 1980). These problems have been addressed in earlier investigations (Watt, 1974; Doyen and Tschinkel, 1982), but need to be reevaluated in light of recent evidence, especially regarding the bauplan of Pimeliinae.

In Pimeliini and Platyopini the membranes between abdominal sternites five to seven are exposed, whereas in all other pimeliine tribes they are concealed. This variation has been interpreted as evidence that Pimeliinae might be polyphyletic (Doyen and Lawrence, 1979). Watt (1974, 1992) favored a monophyletic origin of Pimeliinae, and this view is supported by the present study, which indicates that the abdominal membranes are secondarily exposed in Pimeliini, as detailed below.

The name Tentyriinae is used in recent catalogs to refer to the beetles here termed Pimeliinae; the informal 'tentyrioid lineage' was used in the same sense (Doyen and Lawrence, 1979; Doyen and Tschinkel, 1982). Pimeliinae has clear priority (Watt, 1974, 1992) and was employed by Doyen et al. (1989).

In number of tribes and species, Pimeliinae comprise nearly half the Tenebrionidae

and the external body form of adults is extremely variable. Nevertheless, larval morphology and the adult characters mentioned above indicate that Pimeliinae comprise a single lineage. Consequently, in all previous analyses they have been represented by a few exemplars, with no attempts to depict relationships among the tribes. The intent of this paper is to survey the morphological variation among adult Pimeliinae and to make initial estimates of the cladistic structure of this subfamily.

LIMITS OF PIMELIINAE

The old pimeliine tribes Zopherini and Dacoderini were previously removed from Tenebrionidae (Watt, 1967, 1974; Doyen and Lawrence, 1972). A number of tribes or genera have been moved into Pimeliinae from other lineages of Tenebrionidae. These include Coniontini, Branchini, Physogasterini, Praocini (Doyen, 1972) Vacronini, Cnemeplatiini, Falsomycterini, *Psammetichus, Boromorphus* (Doyen and Lawrence, 1979) and *Zolodinus* (Doyen et al., 1989). The systematic importance of the last had been recognized by Watt (1974), who placed it, along with *Tanylypa,* in his subfamily Zolodininae. As discussed below, the affinities of *Zolodinus* and related genera are still somewhat uncertain. *Bius,* tentatively placed in Pimeliinae by Watt (1974) belongs in Tenebrionini (Doyen, 1989). Besides those mentioned above, only a few genera are improperly included in Pimeliinae in present catalogs. *Eschatoporis* Blaisdell is listed under Cryptoglossini in both catalogs by Gebien (1910, 1937), that by Leng (1920) and in the checklist by Papp (1961), despite the clear original placement in or near Scaurini (=Eulabini of Berry, 1973) by Blaisdell (1906: 76). There appears to be no published explanation of the transfer into Cryptoglossini, and, strangely, Blaisdell himself never commented on this catalog position which is so different from his original placement.

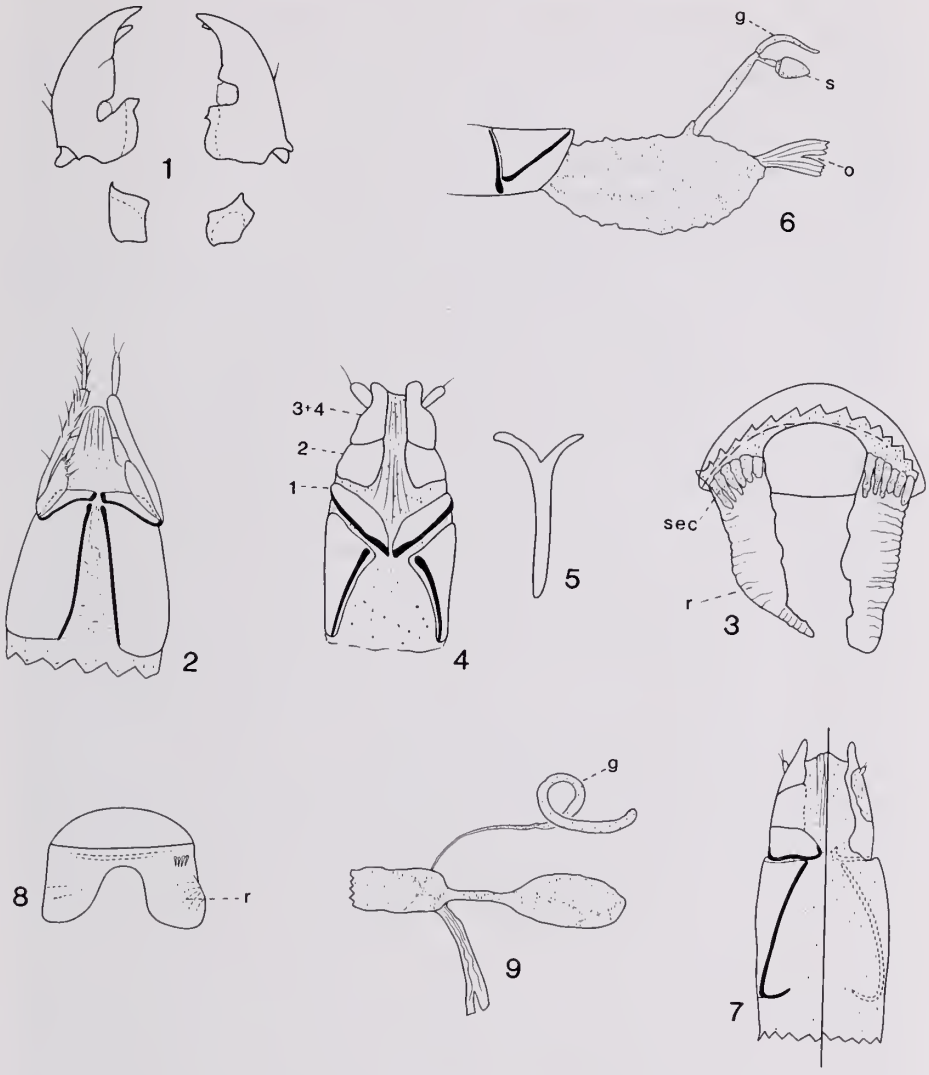
Examination of specimens in the California Academy of Sciences has revealed that Blaisdell was also incorrect in his assessment of this peculiar genus, which lacks eyes and has been found only in caves or in fissures in rocky, porous soil. The features he lists as shared with Eulabini (e.g., small mentum, antennae 11-jointed, abdomen with external membranes between apical segments, etc.) are without exception plesiomorphies distributed very widely among non-pimeliine Tenebrionidae. Probably the general similarity in body shape shared by *Eschatoporis* and some Eulabini influenced Blaisdell's placement, because none of his characters are diagnostic at the tribal level.

Because of the rarity of this beetle complete dissections have not been made, but it has been possible to examine the mouthparts, ovipositor and some internal features, which all indicate that *Eschatoporis* belongs in Lagriinae. The most important characters include: 1. Defensive glands absent (but abdominal sternites with external membranes); 2. Seventh abdominal sternite (fifth visible sternite) with distinct groove around posterior inner margin; medially the posterior margin is weakly but distinctly subangulate; 3. Elytra with 10 striae; 4. Labrum subquadrate; 5. Mandibles elongate, with long, highly asymmetrical molar lobes (Fig. 1); 6. Ovipositor with large, digitate gonostyli and elongate, subdigitate apical coxite lobe (Fig. 2). Among Lagriini defensive glands are absent in Goniaderini, some Lupropini, Laenini, Cossyphini and Belopini. Belopini and Cossyphini have the abdominal membranes internalized and

are specialized in other characters as well (Doyen and Tschinkel, 1982). Lupropini, Laenini and Goniaderini are closely related, with confusing distributions of characters (see discussion in Doyen et al., 1989). Nearly all the genera in these tribes lack the tentorial bridge, which is present in *Eschatoporis* and *Anaedus,* but presence of the bridge is plesiomorphic. The configuration of the ovipositor of *Eschatoporis* is distinctly lagrioid but not obviously very similar to those of *Anaedus* or other members of these tribes. The transverse basal coxite lobes with short longitudinal baculi and oblique second lobes are autapomorphous. The basal coxite lobes in *Adelium* are short and transverse, but the baculi are also transverse. In addition, *Adelium* has large defensive glands and differs in other features. *Eschatoporis* is here placed in Goniaderini, recognizing that future changes may be required when larvae and other internal features, especially the female reproductive tract can be examined.

Ammophorus Guérin, with about a dozen species in western South America, the Galapagos Islands and Hawaii, was originally placed in Nyctoporini (Lacordaire, 1859), along with *Eulabis* and *Epantius.* The last two were removed by subsequent workers, but *Ammophorus* remains in Nyctoporini in all current catalogs and checklists. Even superficial examination reveals that *Ammophorus* has external membranes between the apical abdominal sternites which removes it from Pimeliinae. The defensive glands are long, saccate and without common volume (Fig. 3). The reservoir walls bear circular wrinkles, but are not truly annulate. The secretions appear to drain through a line of basal ducts. The ovipositor (Figs. 4, 5) has short proctiger lobes and three distinct coxite lobes, with large, lateral gonostyli. The internal female tract (Fig. 6) consists of a saccate vagina bearing a single diverticulum which is apically branched. The tubular branch appears to be the spermathecal accessory gland and the capsular, ovoid structure the spermatheca. The aedeagus is unremarkable except that the median lobe is atrophied.

The configuration of the defensive reservoirs (Fig. 3) is similar to that of Opatrini (sensu lato), except that the reservoir bases are usually constricted in the latter, which also have a very different female tract, typically with a long, thin, tightly coiled spermatheca. *Ammophorus* is similar in body form to Eulabini, which also have short proctiger lobes on the ovipositor. However, in Eulabini the spermatheca again is long, slender and tightly coiled and the defensive reservoirs are very short and eversible, similar to those in *Neatus* and *Zophobas. Ammophorus* is also phenetically similar to Scotobiini, particularly to some species of *Scotobius. Scotobius* has a short proctiger lobe, but the apical part of the ovipositor is configured differently than in *Ammophorus.* In addition, *Scotobius* has short saccate glands which have the appearance of being eversible, and has a thick coiled spermatheca and long, slender gland. Despite these differences, Scotobiini and *Ammophorus* share a peculiar synapomorphy first noticed by Medvedev (1977) in *Scotobius*—namely, the presence on the truncate apex of the last antennomere of clusters on dome-shaped placoid sensoriae. These are readily visible under higher magnifications of a dissecting scope, and a few are also visible on the rims of the preterminal antennomeres. On the basis mainly of this character, *Ammophorus* is here referred to Scotobiini. It should be pointed out that large, placoid sensoriae also occur in Ulomini, which do not differ radically from Scotobiini in the other characters discussed above, but have very elongate defensive reservoirs with little common volume (Tschinkel, 1975a). In ad-



Figs. 1–9. Features of taxa removed from Pimeliinae. 1. *Eschatoporis nunenmacheri,* mandibles (dorsal) and molar lobes (medial); 2. Same, ovipositor, ventral; 3. *Ammophorus insularis* Boheman, abdominal defensive reservoirs, dorsal; 4. Same, ovipositor, ventral; 5. Same, spiculum ventrale; 6. Same, internal female reproductive tract; 7. *Phtora fossoria* Wollaston, ovipositor, ventral and dorsal; 8. Same, defensive reservoirs, dorsal; 9. *Phtora millingeni* Reitter, internal female tract. g = accessory gland; o = oviduct; r = reservoir; s = spermatheca; sec = secretory tissue of defensive gland; 1, 2, 3, & 4 = lobes of coxite.

dition, larvae of Ulomini mostly occur in old rotted wood, rather than soil, where scotobiine larvae are found (Cekalovic and Quezada, 1973). Larvae of the ulomine, *Eutochia,* inhabit soil (St. George, unpubl.; W. Steiner, pers. comm.), however, and have the ninth abdominal tergite configured much as in Opatrini (s.l.) rather than enlarged and paraboloid, as in Ulomini. These larval features, together with the unusual antennal sensoriae shared by Ulomini and Scotobiini, suggest that the possibility of a close relationship be examined more closely.

Phtora Germar (nec Mulsant)(=*Cataphronetis* Lucas; see Spilman, 1966) was transferred into Pimeliinae by Doyen and Lawrence (1979) on the basis of misidentified specimens. The apical abdominal sternites in *Phtora* are separated by distinct external membranes, defensive reservoirs are present and the aedeagus is in the normal (non-inverted) orientation, clearly excluding this genus from Pimeliinae.

Lacordaire placed *Phtora* (as *Cataphronetis*) in his Ulomides, which it resembles in general body form and in having the seventh abdominal tergite partially exposed and pygidiform. *Phtora* differs from all Ulomini in the form of the ovipositor, the defensive reservoirs and the structures of the internal female reproductive tract. The ovipositor is broad, with the coxites about ¼ times longer than the paraprocts (Fig. 7). Lobing of the coxite is somewhat obscure, but there appear to be four divisions, the apical being sclerotized and prong-shaped. The gonostyles, small but distinct, are markedly preterminal. The defensive glands are short-saccate without annular folding or thickening and with large common volume (Fig. 8). Each reservoir is bent slightly laterad toward its apex. The secretion collecting ducts are arranged in a basal line. The female reproductive tract (Fig. 9) consists of the vagina, constricted before the saccate bursa copulatrix, and a single diverticulum, non-glandular in its basal half, gradually enlarging to the glandular apical half.

In Ulomini the ovipositor generally is configured as in *Phtora,* with coxites and paraprocts of approximately equal length, but the gonostyles are terminal (*Eutochia*) or slightly preterminal (*Uleda, Uloma*). The defensive reservoirs are large and very elongate, with little common volume. The female tract includes both spermatheca and accessory gland, which open into the end of the vagina, without a bursa copulatrix.

The only taxon which is similar to *Phtora* in all the features cited above is Phaleriini (Tschinkel and Doyen, 1980: figs. 10, 27). The ovipositors of *Phaleria* species are generally configured as in *Phtora,* including markedly preterminal gonostyles. The internal tract of *Phaleria* has a large bursa set off from the vagina by a distinct constriction and has secretory cells only along the apical half of the gland diverticulum. Both the common oviduct and the accessory gland open into the vagina basad of the constriction, as in *Phtora.* The broad, flattened fore tibiae with spinose posterior surface; the slightly exposed, pygidiform seventh abdominal tergite; and the wing configuration (long membrane; small recurrent cell circumscribed by thick veins) are obvious external similarities between *Phtora* and Phaleriini. In addition, both have compound sensoriae on the inner and outer angles of the apical four or five antennomeres. Other basal members of the Diaperine lineage, such as *Corticeus* have the spermatheca differentiated as an enlarged saccate or capsular structure and have the apical lobes of the coxites digitate with gonostyles inserted terminally (Tschinkel and Doyen, 1980). Finally, *Phtora* is a soil inhabitant, where it is found beneath dry dung and stones (Lacordaire, 1859). Most records suggest oasis or littoral habitats; Phaleriini are restricted to seacoasts, mostly to sandy substrates.

Because of the preponderance of evidence *Phtora* is transferred into Phaleriini. I predict that larvae, when associated, will substantiate this placement.

MATERIALS AND METHODS

The analytical portion of this study is limited to adults. Larvae of at least 50 species of Pimeliinae have been associated with adults and described (Keleynikova, 1963, 1970, 1976; Marcuzzi and Rampazzo, 1960; Marcuzzi et al., 1980; Aalbu, 1985; Artigas and Brañas-Rivas, 1973; Brown, 1973; Costa et al., 1988; Doyen, 1974; Ghilarov, 1964; Schulze, 1962, 1964, 1974; Skopin, 1959, 1960; Watt, 1974). Nevertheless, most of these belong to a few tribes, principally Asidini, Coniontini, Tentyriini, Akidini, Pimeliini and Adesmiini. Several other tribes are known from a single larval association (e.g., Stenosini, Cnemeplatiini, Erodiini, Vacronini), while about half are undescribed as immatures (e.g., Falsomycterini, Araeoschizini, Typhlusechini, Ceratanisini, Cryptochilini, Lachnogyini, etc.). Where larvae are well enough known to influence classifications, the pertinent information is considered in the taxonomic discussions, but larval characters do not appear on the cladograms.

In order to examine internal features adults were softened in hot water, partially dissected, and then soaked overnight in cold 10% KOH. Mouthparts (and entire bodies of very small species) were preserved in glycerine on depression slides. Wings were dried in the expanded position on microslides and protected with coverslips. Internal female reproductive tracts were stained in chlorazol black and stored in glycerine on depression slides. Dissection methods were described in greater detail by Tschinkel and Doyen (1980).

Characters and character states were tallied for 148 genera, each represented by one or more species. These included all the tribes recognized by Gebien (1937, 1938–42) except Gnathosiini, Remipedillini and Leptodini, which were unavailable. For small tribes all or most of the genera were included. For large, diverse tribes a selection of genera, ranging from those appearing to have large numbers of plesiomorphic characters to those with many derived character states was examined. Critical characters, especially of the female reproductive tract, were sometimes examined without full dissections.

A conspectus of tribes and genera studied appears in Appendix I. Hierarchically the tribal level was used as the primary unit for cladistic analysis. This was necessary because the large number of genera would have enormously increased computation time. For each tribe the genera were scanned to determine the most primitive state present, which was used to construct a tribe by character matrix (Appendix III). In addition to the tribes listed in Appendix I, a number of genera were included as OTU's. These were either taxa which preliminary analysis showed not to fit well into existing tribes (e.g., *Salax, Trilobocara*) or whose position in current classifications is problematic (e.g., *Elenophorus, Megelenophorus, Boromorphus, Anchomma*, etc.). The tribe Asidini was represented by 4 OTU's, corresponding to the geographical regions of occurrence. The resulting matrix measured 84 characters by 60 OTU's (including Zolodinini)(Appendix III).

Cladistic computations were done with HENNIG86 by J. S. Farris. Cladograms were derived using three different outgroups, because the sister to Pimeliinae is uncertain. 1. *Zolodinus* as outgroup. Watt (1974: 19) proposed that *Zolodinus* is the

sister to Pimeliinae, based primarily on the lack of defensive glands and external abdominal membranes and the inverted aedeagus. Doyen and Tschinkel (1982) and Doyen et al. (1989) have pointed out some difficulties with accepting the sister status of *Zolodinus* and Pimeliinae, and these are explored below. 2. Belopini as outgroup. Adult Belopini share some features such as concealed abdominal membranes with Pimeliinae, even though characters of larvae clearly show that they are derived Lagriinae (Doyen, 1988). 3. Hypothetical outgroup. This character set consists of primitive states for every character.

The commands "mhennig*" and "bb*" were used to calculate trees, because the command "ie" did not terminate. The input sequence of the OTU's was repeatedly altered to avoid artifacts resulting from ordering (Griswold, 1993).

CHARACTERS AND CHARACTER STATES

Primitive members of several pimeliine lineages are winged (most Epitragini, Vacronini, some Cnemeplatiini, Eurymetopini, Tentyriini, Trilobocarini) but the great majority of these beetles are flightless, often with strongly altered body forms. Frequently the pterothoracic region is highly modified, with the metathorax reduced and the metendosternite fused with the mesocoxal cowlings and/or the mesotergum. The elytra are joined to one another and to the abdominal sternites by virtually immobile tongue and groove joints. These types of modifications and others such as fusion of the prothorax with the pterothorax, reduction of the abdomen or constriction of the pro-mesothoracic junction have produced highly distinctive body forms which characterize many genera and tribes of Pimeliinae. For example all Erodiini have subspherical bodies with the prothorax fused to the hind body, the head enlarged and the foretibiae flattened with serrate outer margins. This general body form represents a set of adaptations for life in unconsolidated sand and occurs in several other tribes of Pimeliinae (e.g., some Coniontini, Edrotini, Adesmiini) as well as several other subfamilies of Tenebrionidae. Other notable body forms include: 1. A strongly flattened, subcircular body with sharply explanate margins, as in many Eurychorini and some Zophosini. The flattened body appears in some cases to be an adaptation for allowing quick entry into the loose sand in which these beetles live and Koch (1955) referred to these beetles as sanddivers. 2. A moderately flattened body with reduced, narrow abdominal venter strongly interlocked with the metathorax. The elytra are expanded laterally far beyond the abdominal sternites and the metacoxae are strongly oblique. This body form is unique to the Zophosini, which are extremely active, diurnal beetles whose rapid and erratic escape behavior may be compared to that of Gyrinidae. Koch (1955) referred to them as sand-jumpers. 3. An elongate subcylindrical body with more or less strong constriction at the pro-mesothoracic joint. The lateral pronotal carinae are often obsolete or absent and the antennae are often moniliform. This general body form occurs in Elenophorini, Stenosini, Araeoschizini and some Tentyriini and Eurymetopini. Apocryphini is a comparable form in the group of Tenebrionidae with defensive glands. Larger beetles with this body form are apparently unspecialized ambulatory insects. Very small beetles with similar form are often described as ant-like and many Stenosini and Araeoschizini are myrmecophilous. The functional significance of the body configuration is unclear, however.

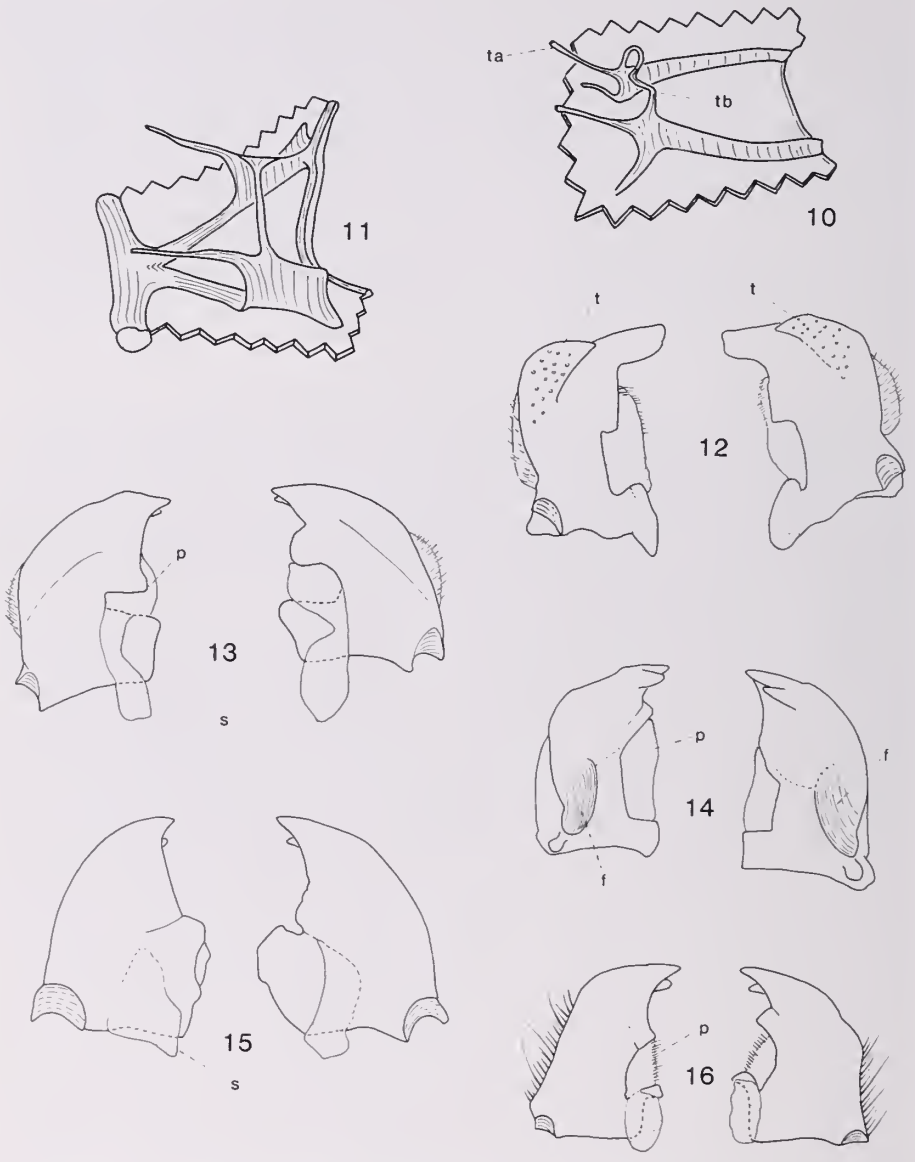
As implied above, similar body forms occur repeatedly in Pimeliinae, and such similarities appear to be exceedingly common when individual characters are considered. In some instances similarity is clearly the result of convergent adaptations for similar styles of life. In many other instances, however, it is unclear whether they represent synapomorphies or convergences. For example, *Elenophorus* (Mediterranean area) and *Megelenophorus* (southern South America) both with the waisted body form described above, share many other morphological characteristics, such as large body size, very long legs, inflated elytra with strong lateral costae, very long third antennal segment and clypeus with deep lateral emarginations. However, many of these features are also shared with *Psammetichus* (South America) and Akidini (Mediterranean-Asian). Since vicariance between the Mediterranean region and South America is not common, one might suspect that the similarity between *Elenophorus* and *Megelenophorus* is the result of convergence.

Similar problems attend the interpretation of numerous characters of Pimeliinae, such as the enlarged mentum, the dorsolateral teeth on the mandibles, closure of the mesocoxal cavities by the sterna rather than the epimeron, moniliform antennae, etc., and together with strong autapomorphism have stood as the major obstacle to defining relationships among the pimeliine tribes. Interpretation of homology and polarity of characters is discussed below, but in general all similarities were initially regarded as synapomorphies and distribution of derived states on the cladograms was considered as confirmation or rejection of homology.

Character states were coded as graded series whenever possible, with divergent states at opposite extremes of the scale. The resulting character state trees may be derived from Appendix II. A few characters, for which several divergent states were present, were treated as non-additive. Character polarity was established either by using Zolodinini or Belopini as outgroup, or by treating all non-Pimeliinae as the outgroup. For the latter case, used to create a hypothetical outgroup, character states occurring commonly among the non-pimeliine tribes were considered primitive.

Endocranial skeleton (Characters 0-8). The primitive configuration of the tentorium is similar to that of *Tenebrio* (Doyen, 1966: fig. 9; Doyen and Tschinkel, 1982: fig. 1), with a simple, transverse bridge connecting the laminar posterior arms. The bridge is absent in all Asidini and Craniotini, and absent or incomplete in members of several other pimeliine tribes, including Epitragini, Tentyriini and Eurychorini. The tentorial bridge is also lacking in some non-Pimeliinae, principally certain tribes of Lagriinae (Doyen and Tschinkel, 1982). A strongly arched bridge (Char. 5), characteristic of the subfamily Diaperinae, occurs among Pimeliinae only in the genus *Araeoschizus* (Doyen and Lawrence, 1979: Fig. 33). The bridge is modestly arched and bent anterad (Fig. 10) in scattered taxa in various genera, and in a few others is much thickened (Doyen and Lawrence, 1979: Fig. 32) (Char. 2). Neither of these states is synapomorphic at the tribal level, however, and neither appears in the cladograms.

Size (Char. 3) and position (Char. 4) of the tentorium vary in only a few taxa. The tentorium is relatively small in Cnemeplatiini and in Araeoschizini. In the latter the tentorium is located midway between the oral and occipital foramina, rather than close to the occipital, as in all other Tenebrionidae. This suggests that reduced size has evolved convergently in the two groups. In Zophosini the posterior arms of the tentorium continue anterad as low ridges meeting just behind the submentum (Char.



Figs. 10–16. Tentoria and mandibles. Tentoria of: 10. *Alaephus pallidus* LeConte; 11. *Zophosis testudinaria* Fabricius. Mandibles of: 12. *Himatismus* species (Thabazimbi, Transvaal), dorsal; 13. *Asida alaudi* Serville, dorsal; 14. *Aryennis* species (Santa Cruz, Bolivia), ventral; 15. *Zophosis testudinaria*, dorsal; 16. *Lepidocnemeplatia sericea* (Horn), dorsal. f = ventral fossa; p = prostheca; s = submola; t = dorsal tooth; tb = tentorial bridge.

6; Fig. 11). Similar ridges in the more derived genera of Adesmiini are not confluent and are regarded as representing convergence. The tentorium is open between the bridge and the gula (Char. 7) in all but a few Anepsiini.

An endocranial dorsomedial septum (Char. 8) occurs only in Edrotini and Cryptochilini, and does not appear as a synapomorphy in the cladograms. No functional significance can be assigned to any of these endocranial skeletal features.

Mandibular and labral configuration (Characters 9-14). A characteristic feature of the mandibles of many Pimeliinae is a tooth on the dorsolateral margin (Chars. 9, 10; Fig. 12). The tooth, which is usually at about the middle of the mandible, varies greatly in size and prominence among different genera and tribes. Typically the tooth is larger on the right than on the left mandible (teeth subequal in Fig. 12), sometimes occurring only on the right. Mandibular teeth are present in diverse Eurymetopini, Trimytini, Tentyriini and related tribes, where they are apparently a primitive feature, lost in some genera. They are uniformly absent in the asidine group of tribes (Fig. 13).

The dorsal mandibular teeth are often described as clasping the labrum, but actually they are adjacent to or sometimes slightly overlapping the labrum at rest, without gripping it. Large, overlapping teeth might serve a protective function by securing the labrum which closes the opening between the mandibles, but this would not seem a likely function when the teeth are very small. It is also unclear why the right tooth is often much larger than the left.

Apomorphic states of Characters 12 to 14 are restricted to single tribes or portions of tribes. Character 12 refers to a deep cavity near the ventral articulation of the mandibles of Evaniosomini (Fig. 14). A similar cavity occurs in *Cnemodinus*. Character 14, State 1 refers to the mandibular configuration of Zophosini (Fig. 15), where the retinaculum is subadjacent to or contiguous with the molar lobe and the prostheca is very narrow and transverse or absent between prostheca and mola. A similar configuration occurs in some Molurini. In a few genera such as *Trilobocara* the prostheca is entirely absent (Char. 13) but this is not a synapomorphy in any of the cladograms. In *Lepidocnemeplatia, Actizeta, Alaudes* and *Thorictosoma* the contact area of the molar lobe is reduced, in *Lepidocnemeplatia* and *Actizeta* to a punctiform or narrowly transverse prominence (Fig. 16)(Char. 14, State 3).

In lagriine tenebrionids the labrum is elongate, the primitive condition. Watt (1974) listed Pimeliinae as having the derived state (labrum much wider than long). However, in a number of Pimeliinae, including Epitragini, Thinobatini, Edrotini and Trimytini the labrum is subquadrate, or slightly longer than broad, which was coded as primitive in the following analyses. Nevertheless, in the cladograms the subquadrate labrum appears as a reversal in the tentyriine lineage. Thus, the primitive condition of this feature in Pimeliinae is not clear.

Form of maxilla, labium and labrum (Characters 15-28). Structure of the maxilla is relatively uniform throughout Tenebrionidae, the principal variation involving the form of the lacinia, which may be simply setose or may bear a coarse spine or uncus (Char. 15). The latter state was considered primitive by Doyen and Tschinkel (1982), as it is here. A bispined uncus is considered independently derived. However, it must be emphasized that variation in this character is confusing. Many tribes have the uncus either present or absent in different genera, and a distinct uncus is probably easily evolved by enlargement of one of the maxillary setae.

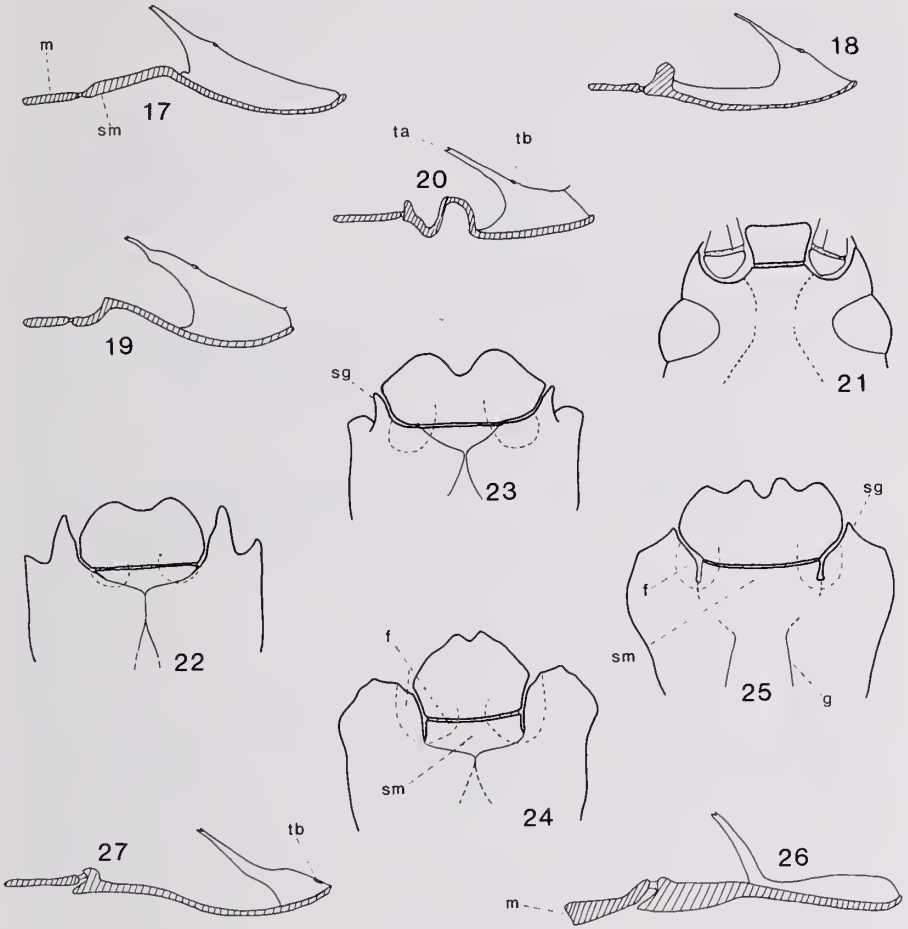
Characters 16 to 21 and 28 describe the articulatory region of the ventral mouthparts. Primitively in Pimeliinae, as in other Tenebrionidae, the maxillary articulations are exposed lateral to the labium (Fig. 21). In contrast, in many Pimeliinae the mentum is enlarged and subadjacent laterally to the large, forward projecting subgenal processes (Figs. 22–24), concealing at least the basal portion of the maxillae. The latter condition is obviously derived, and has been used in classification. Differences in details of structure, however, indicate that enclosure of the maxillae has occurred several times independently, and this is shown on the cladograms, as well. Moreover, in some tribes, such as Asidini, a range of conditions exists from primitive to derived.

In all Pimeliinae in which the maxillary bases are concealed, the posterior rim of the oral foramen becomes thickened and inflexed (Char. 28; Fig. 18), forming a marginal ridge to which the ventral mouthparts are articulated. The thickening may occur only behind the cardines, or may extend medially, forming a continuous ridge between the cardinal sockets. In many tribes, such as Eurymetopini and Tentyriini both conditions exist with intermediates. These tribes were coded with the primitive state. In most taxa the postoral region is flat or nearly so, but in a few, such as Triorophini, the oral rim is everted so that it appears elevated in relation to the ventral head capsule (Fig. 19). In *Edrotes* and a few others the submentum becomes invaginated as well (Fig. 20). These modifications appear to rigidify the head capsule, as well as provide a means for concealing the maxillary articulations.

Maxillary base concealment occurs by formation of large internal sockets for the cardines (Char. 16). The sockets may be located principally on the inner surface of the submentum, as in Epitragini and Adesmiini (Fig. 22), on the inner surface of the subgenal processes, as in the Zophosini and Eurychorini (Fig. 23), or in both, as in Eurymetopini, Tentyriini (Fig. 24), and several other tribes. In these forms the subgenal processes are closely contiguous with the submentum and at least the basal part of the mentum (Char. 20). In many Asidini the subgenal processes are subadjacent to the mentum, but in several Nearctic (*Asidopsis, Heterasida*) and Neotropical (*Cardigenius, Scotinus*) genera the subgenae and mentum are separated by an appreciable gap, and many intermediate conditions exist (see Brown, 1971; Figs. 14, 19, 25, 26). The proportion of the mentum which is in contact with the subgenae also varies, as do other structural details (see below), suggesting that enclosure of the ventral mouthparts has occurred several times independently. The joint between the submentum and gula (Char. 21) is almost always rigid, but is flexible in a few taxa such as Erodiini, Calognathini, and Praocini. A rigid joint is present in nearly all non-Pimeliinae, and it seems certain that the flexible condition is derived.

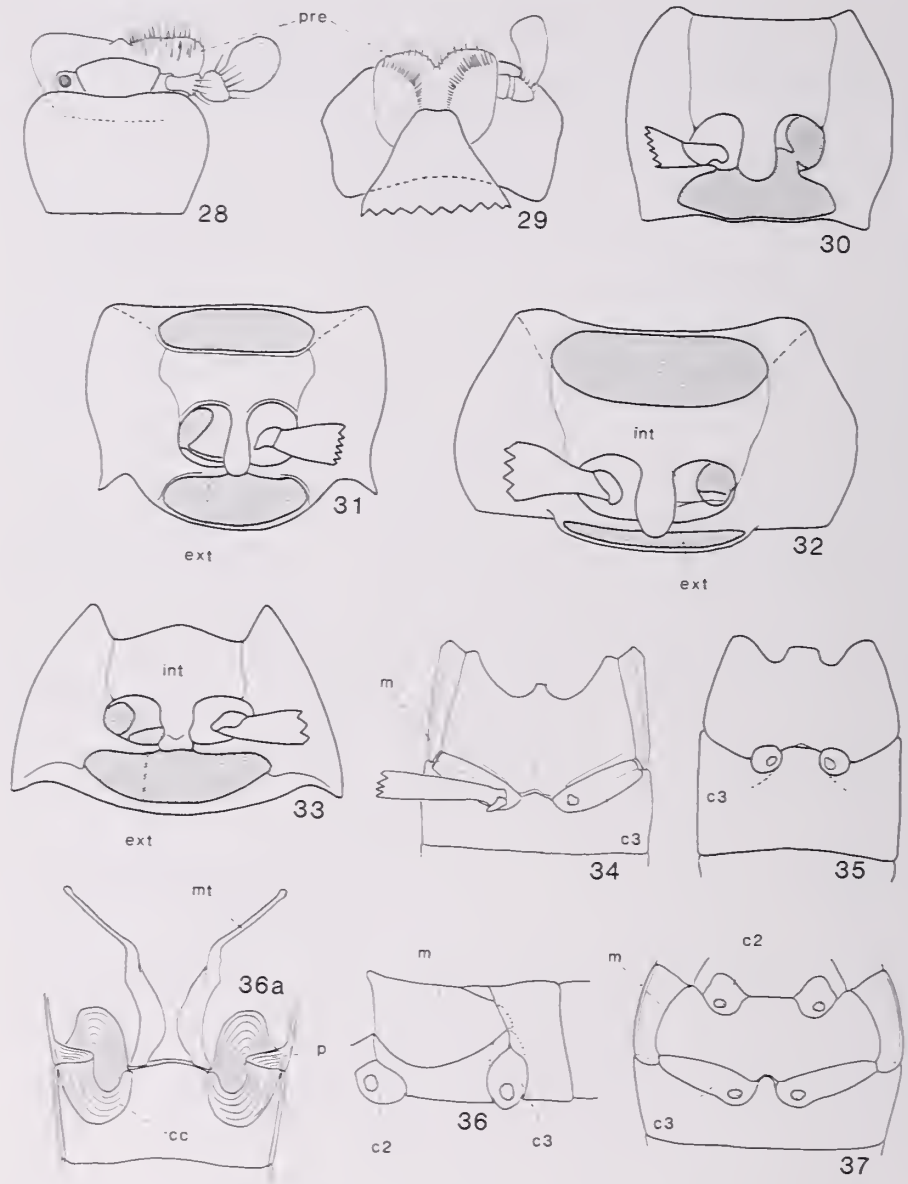
In most Pimeliinae the submentum remains as a distinct sclerite (Figs. 22–24), as in most other Tenebrionidae (Char. 18). In a few, such as *Edrotes*, the submentum is fused to the gula without trace of a suture (Fig. 25). In Akidini and in South African Asidini the submentum is greatly reduced and not visible externally. In most species the submentum is produced between the cardinal sockets as a pedicel (Char. 19) against which the mentum is hinged (Figs. 24, 25), and this is the condition in non-Pimeliinae. In a few taxa (e.g., Zophosini, Coniontini, some Eurychorini, etc.) the submentum is essentially flat between the sockets (Fig. 23). There is no obvious correlation between maxillary concealment and the development of the submentum, and the significance of the pedicellate and nonpedicellate states is not clear.

The shape of the mentum varies from subquadrate to transversely elongate, with



Figs. 17–27. Structural features of the oral region. Parasagittal sections (diagrammatic) of the postoral regions of: 17. *Zolodinus zealandicus* Blanchard; 18. *Zophosis (Gyrosis) orbicularis* Deyrolle; 19. *Chilometopon pallidum* Casey; 20. *Edrotes ventricosus* LeConte. Ventral aspects of postoral regions of: 21. *Eupsophulus castaneus* Horn; 22. *Adesmia chiyakensis* Kuntzen; 23. *Zophosis testudinaria*; 24. *Auchmobius sublaevis* LeConte; 25. *Edrotes ventricosus*. Parasagittal sections of: 26. *Eurychora barbata* Olivier; 27. *Vansonium bushmanicum* Koch. f = fossa for cardo; g = gular suture; m = mentum; sg = subgenal process; sm = submentum; ta = tentorial arm; tb = tentorial bridge (absent in *Eurychora*).

the anterior border either truncate to slightly emarginate or deeply concave or notched. These characters (25, 26) are easily polarized by comparison with non-Pimeliinae. The basal articulation of the mentum to the submentum is an external hinge (Figs. 17–20) in most taxa (as in non-Pimeliinae). In Eurychorini and Stenosini the base of the mentum is greatly thickened, with the hinge concealed beneath the submentum (Figs. 26, 27).



Figs. 28–37. Selected structural features. 28. Labium of *Zolodinus zealandicus*, ventral; 29. Labium of *Omopheres ardoini* Kulzer, dorsal; 30. Prothorax of *Zolodinus zealandicus*, coxal cavities internally open; 31. Same of *Lepidocnemeplatia sericea*, coxal cavities very narrowly open internally; 32. Same of *Pachychila intermedia* Haag, showing tentyriine style of internal closure; 33. Same of *Asida servillei* Solier showing asidine style of closure; 34. Metacoxal region (ventral) of *Eupsophulus castaneus*, showing metacoxal closure by attenuate metepimeron; 35. Same, *Alaudes singularis* Horn, closure by sternites; 36. Same (lateral), *Pachynotelus albonotatus* Haag, closure by sternites, metepimeron broadened; 36a. *Pachynotelus*, internal view of me-

The prementum is fully exposed and membranous or very lightly sclerotized (Chars. 22, 23) in a few Pimeliinae such as *Zolodinus* (Fig. 28). This condition is common to many non-Pimeliinae, and is undoubtedly the primitive state. In the derived state, present in most Pimeliinae, the prementum is largely retracted beneath the mentum (Fig. 29), and typically has a pair of basal sclerites. In a few taxa, such as Asidini, the entire prementum becomes strongly sclerotized. Primitively the prementum is subequal in width to the mentum, as in non-Pimeliinae, but in the great majority of pimeliines the mentum is much broader than the prementum.

The function of most of these ventral mouthpart modifications is probably defensive. Internalization of membranes and articulations has occurred repeatedly in Pimeliinae, and probably decreases vulnerability to suctorial feeders such as arachnoids, which are among the principal predators of arid land tenebrionids. I have observed solpugids unsuccessfully probing with the chelicerae around the highly modified mouthparts of *Edrotes*. In contrast they quickly penetrate the oral region of *Eusattus* of similar size, where the maxillae are exposed. The operculate closure of the oral opening may also be important in water conservation.

Procoxal cavity closure (Characters 30-32). Closure of procoxal cavities may be either external or internal (Figs. 30–33). External closure is derived through a ventral extension of the notum as the postcoxal bridge (Doyen and Tschinkel, 1982: Fig. 21). Internal closure is derived by a lateral fusion of the arms of the proendosternite with the postcoxal bridge. Originally species of *Zolodinini* (Fig. 30) were regarded as the only tenebrionids with externally open procoxal cavities (Watt, 1974), but Doyen and Lawrence (1979) pointed out that they are externally open (internally closed) in *Idisa*. In fact, the externally open condition also occurs in *Platyope* (Platyopini), *Ocnera* (Pimeliinae), *Cryptochile* and *Pachynotelus* (Cryptochilini). In the last two genera the prothorax and mesothorax are adnate, with the ventral articulatory membrane extremely thickened, tough and leathery. In *Pachynotelus* the intercoxal process is expanded laterally, partially closing the cavities. In both genera internal closure, which usually follows external closure, is complete. It seems obvious that the open condition here is secondary, resulting from the close association of the pro- and pterothoraces. In Pimeliini and Platyopini, the prothorax is relatively free, suggesting that open cavities could be the primitive condition. The cavities are internally closed, however, which suggests that the externally open state is again secondary. On the cladograms open cavities appear only as a reversal, even in Zolodinini.

Internal closure is more variable. In Erodiini, Stenosini, Cnemeplatiini, Eurychorini and some Asidini the cavities are narrowly open internally, apparently a primitive condition (Fig. 31). In the pimeliine and tentyriine lineages internal closure is effected by close apposition of the posterior edge of the procoxal cowling and the postcoxal bridge along their entire lengths (Fig. 32). In this type of closure (tentyriine closure) usually only a tiny aperture remains near the intercoxal process. The coxal

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tacoxal region; 37. *Vernayella ephialtes* Koch. ext = external procoxal closure; int = internal closure; c2 = mesocoxa; c3 = metacoxa; cc = coxal cowling; m = metepimeron; mt = metendosternite; p = process of metepimeron; pre = prementum.

cowling and postcoxal bridge are not fused, however, and may easily be separated by gentle pressure. In contrast in the asidine lineage (Fig. 33) the aperture near the intercoxal process is usually much larger and the contact between coxal cowling and postcoxal bridge much shorter, but the cowling and bridge are strongly, usually rigidly, fused. This configuration is termed asidine closure. Intuitively it would seem that these two styles of closure are independently derived from the open condition. In Fig. 209, however, the tentyriine type closure is derived from the asidine type; in Fig. 211 the asidine type is derived twice from the tentyriine type.

Thoracic fusion (Character 33). Compressed into this single character is extensive and complex variation. In the primitive state the prothorax is joined to the mesothorax by a flexible membrane, allowing the former to telescope over the constricted anterior margin of the latter. This condition allows torsion as well as dorsoventral and lateral flexibility, although these are relatively limited in many Pimeliinae. In some tribes, such as Pimeliini, Platyopini, and Cryptoglossini the pro- and mesothorax are very closely connected by a somewhat thickened membrane, but significant flexibility remains. In several others the thoracic segments are effectively fused by a variety of autapomorphic mechanisms which are described below. 1. Edrotine type fusion. The proendosternite and mesendosternite are fused as two solid rods between the procoxal and mesocoxal cowlings (Doyen, 1968: fig. 5). Probably this arrangement was evolved via fusion of opposed endosternal muscle discs. Fused pro- and mesendosternal muscle discs occur in *Epiphysa* and are clearly derived from the opposed discs joined by short, thick muscles in other genera of Adesmiini. In *Edrotes* the ventral part of the membrane connecting the pro- and mesosterna is thick and leathery. 2. Erodiine type fusion. In all genera of Erodiini the prothorax and mesothorax are very closely adjoined. The endosternites are contiguous but not fused. The ventral articulatory membrane is very short and ligamentous, affording almost no movement. The postcoxal bridges are absent, leaving the procoxal cavities (secondarily?) open. The elytra are mechanically interlocked with the posterior pronotal surface (Fiori, 1977), further rigidifying the prothoracic-mesothoracic joint. 3. Cryptochiline type fusion. The prothorax and mesothorax are solidly fused along their entire ventrolateral and ventral margins. Ventrolaterally the fusion is between the inwardly flanged edges of the hypomeron and the mesothoracic episternum. Ventrally the articulatory membrane has become strongly sclerotized so that the procoxal cowlings appear to be continuous with the mesosternum. The postcoxal bridges are abbreviated or absent. There is essentially no flexibility in this type of joint, which occurs in *Cryptochile, Pachynotelus, Horatoma, Calognathus* and *Vansonium*. 4. Nycteliine type fusion. As in Erodiini the thoraces are very tightly adjoined, with a very short articulatory membrane which is sclerotized, as in Cryptochilini. As in the latter, the procoxal cowlings appear to be continuous with the mesosternum. Unlike Cryptochilini the hypomera and mesepisterna are not fused. In most genera the postcoxal bridges are complete, so that the pro-mesothoracic joint appears normal externally. In *Nyctelia* and *Psectrascelis* the postcoxal bridge is extremely narrow and laminar, giving the external appearance of open procoxal cavities.

The most likely function of pro-mesothoracic fusion is probably defensive. Most of the taxa which display this modification are ambulatory surface dwellers; Erodiini and some Edrotini are sand swimmers, while *Pachynoteles* and *Calognathus* dig burrows in sand. This variation in substrate activity indicates that fusion does not

have a locomotary related function. Most of the taxa with the fused pro-mesothoracic joint also have very hard, tough cuticle, again suggesting a passively defensive function. Water conservation might also be important.

Mesocoxal closure (Character 34). This character has previously been considered at some length (Doyen and Tschinkel, 1982: 136; see also Doyen, 1987: figs. 4–6). In non-pimeliine lineages the mesocoxal cavities are almost always closed laterally by the mesepimeron which is certainly the primitive condition. Most non-pimeliines with closure effected by the sterna are of small body size, although no functional reason for this correlation is evident. In Pimeliinae closure is usually by the sterna (Figs. 36, 37) and there is no correlation with size. In the cladograms this character is changed to the derived state in the basal stem, then reversed in the asidine lineage (Stem 100) and in several individual OTU's, such as Ceratanisini and Anepsiini. Additional reversals (back to the derived state) occur in Nycteliini and Asidini, yielding a total of eight changes of state and a consistency index of 0.11. The retention index, however, is 0.66.

Configuration of mesendosternite (Characters 35–39). The primitive configuration entails a pair of arms that extend a short distance horizontally or in an oblique anterodorsal direction from the mesocoxal inflexions, then bend laterodorsad toward the mesopleural wing processes. The arm is usually expanded to accommodate muscle insertions near the point of the bend. This topology is closely matched in *Tenebrio* (Doyen and Tschinkel, 1982: fig. 23), and occurs in primitive Pimeliinae such as *Ceratanisus* and *Lixionica,* as well as many Asidini, and Coniontini. Modifications of the plesiomorphic structure involve (1) Elongation of the horizontal part of the arm, often to the vicinity of the mesothoracic foramen (Char. 38; see Doyen, 1972: fig. 14). (2) Enlargement of the apices of the horizontal arms (Char. 37), as an oblique or horizontal flange, or, in the most apomorphic condition as a large vertical muscle disc (Doyen, 1968: fig. 4). The large ventral muscles which retract the prothorax over the mesothoracic constriction insert on these discs. In a few taxa the apical muscle disc becomes fused with the mesosternal rim (Char. 35). (3) The dorsal part of each arm arises subterminally from the horizontal arm, often near its midpoint (Char. 39). The dorsal arms may also be much abbreviated or absent (Char. 36). Character 35 does not form synapomorphies above the tribal level. None of these characters has a very high consistency index, but the retention indices are mostly moderate.

Configuration of metendosternite (Characters 40–42). This structure exhibits extensive variation in form and proportion, most of which is very difficult to codify and polarize because of intermediacy and high levels of obvious homoplasy. Selected variation is illustrated by Doyen and Tschinkel (1982: figs. 25–31). Often metendosternal features are related to general body form. For example, width of the stalk is very strongly correlated to degree of separation of the hind coxae. Only a few, easily polarized characters were included here, including two fusions of the endosternite with the external body wall. Fusion with the mesocoxal inflexions occurs in a few diverse taxa, almost certainly as a homoplasy. Fusion also occurs with various parts of the dorsum (Char. 41). In Zophosini the large apical muscle disk is not actually fused to the membranous dorsum, but attached by a short, tendonous muscle. These various states appear to have arisen independently and were coded nonadditively. Relative arm length often is consistent within tribes, but forms few synapomorphies above the tribal level.

Metacoxal configuration (Characters 43-46). Primitively the metacoxae are elongate, oriented at nearly right angles to the longitudinal body axis, and almost contiguous medially, as in *Tenebrio, Zolodinus,* and most other winged species. Laterally the coxa abuts the metepimeron, which projects posteriorly as a rounded boss which fits into a socket in the laterotergite of the third abdominal segment (first visible segment)(Fig. 34). In many flightless Tenebrionidae, including Pimeliinae, the metacoxae are much less elongate, becoming almost round in tribes such as Adesmiini and Cryptochilini. This change in shape is usually accomplished by a great increase in the distance between the coxae, which in effect have become lateralized in position (Fig. 36a). In several other flightless taxa, however, such as Trientomini, Triorophini and Trimytini, the coxae have retained the primitive condition.

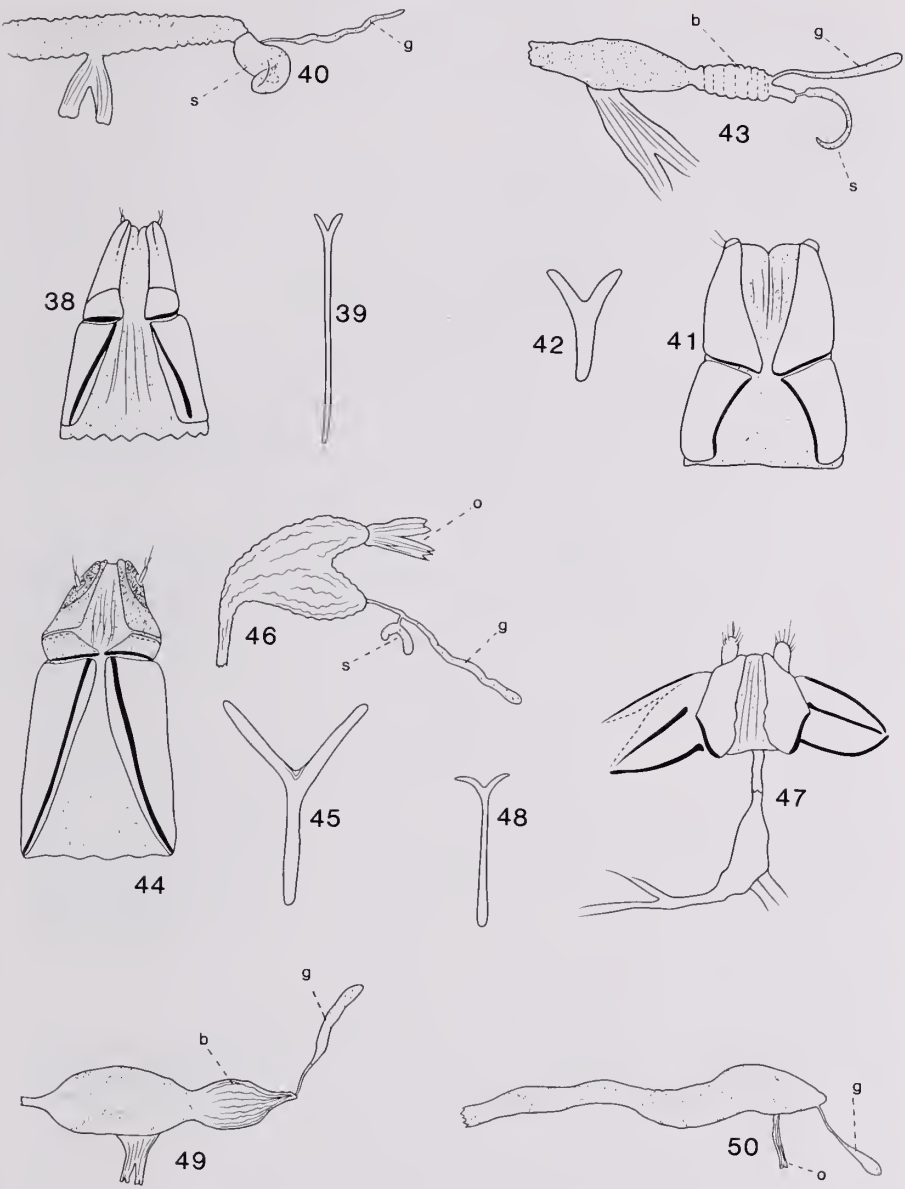
In a few specialized forms the metacoxal cavities are closed by the sterna of the metathorax and third (first visible) abdominal segment (Fig. 35). In these taxa the lateral part of the metacoxa is concealed by the sternites, and the coxal articulation is still with the metepimeron. The less specialized condition occurs in *Alaudes* and *Idisia,* where the metepimeron is not markedly modified (state 1; Fig. 35). In Cryptochilini the metepimeron is produced inward as a prominent boss on which the coxa articulates (state 3; Figs. 36, 36a). Cryptochilini and Cnemeplatiini differ in numerous other characters, and it is almost certain that these states have arisen independently.

In Caenocrypticini lateral coxal closure is between the metepimeron and abdominal sternite, but the metepimeron is broad, affording a much more rigid joint (Fig. 37).

Ovipositor configuration (Characters 47-64). The ovipositor is extremely variable in Tenebrionidae, ranging from a large, strongly sclerotized, blade-like organ (e.g., *Talanus, Hegemona, Saziches, Acropteron*) to an atrophied, membranous remnant (*Rhipidandrus,* Phrenapatini)(Tschinkel and Doyen. 1980). In the most primitive ovipositors the coxites are divided into four lobes, the apical being long and digitate and terminally bearing long, slender gonostyles. In more derived forms the apical lobe is incorporated into the ovipositor shaft, usually becoming shorter and more or less adnate to the preapical lobe. Fusions may occur, so that the number of lobes is two or three, and the reduced gonostyles usually attach laterally on the apical coxite lobe. Additional changes in the orientation of the basal coxite lobe or in the proportions of the coxites and paraprocts have resulted in dramatically apomorphic ovipositor configurations, as in the tribe Coelometopini, for example.

No Pimeliinae have the primitive type of ovipositor described above, and none show the major structural modifications of the type illustrated by Coelometopini or Talanini). Even so the range of variation is impressive, and, as in non-pimeliine lineages, the ovipositor appears generally to offer more information for classification at higher levels than do the male genitalia, which are more useful at the generic level and below.

The least derived pimeliine ovipositor appears to be that of *Boromorphus* (Fig. 72), where four short unsclerotized coxite lobes are present and the gonostyli are apical and moderately large. *Alaephus* (Fig. 148), *Ceratanisus* (Fig. 78) and Akidini (Figs. 83, 84) have relatively large gonostyli, but they are subapical and the coxite lobes are reduced to three with the apical one sclerotized. In most other groups of Pimeliinae gonostyli are lateral and greatly reduced, coxite lobing is more or less obliterated by fusion and sclerotization, and the apical lobe is often produced as a



Figs. 38–50. Female genitalia of Stenosini and Cnemeplatiini. 38–40. Ovipositor (ventral), spiculum and internal tract (lateral) of *Grammicus chilensis* Waterhouse; 41–43. Same, *Araeoschizus sulcicollis* LeConte; 44–46. Same, *Stenosis sardoa* Küster; 47, 48. Ovipositor and spiculum of *Typhlusechus ignotus* Doyen; 49. Internal tract of *Lepidocnemeplatia sericea*; 50. Same, *Alaudes singularis*. b = bursa copulatrix; g = spermathecal accessory gland; s = spermatheca.

sclerotized digging prong, sometimes of diagnostic shape. Pimeliini, Asidini and genera such as *Cnemodinus*, *Trilobocara* and *Salax* are good examples (Figs. 152, 154, 162). The usual variation in coxite: paraproct proportions is present, and several taxa have the ovipositor reduced, sometimes extremely so (e.g., *Typhlusechus* (Fig. 47), Cnemeplatiini, *Falsomycterus*).

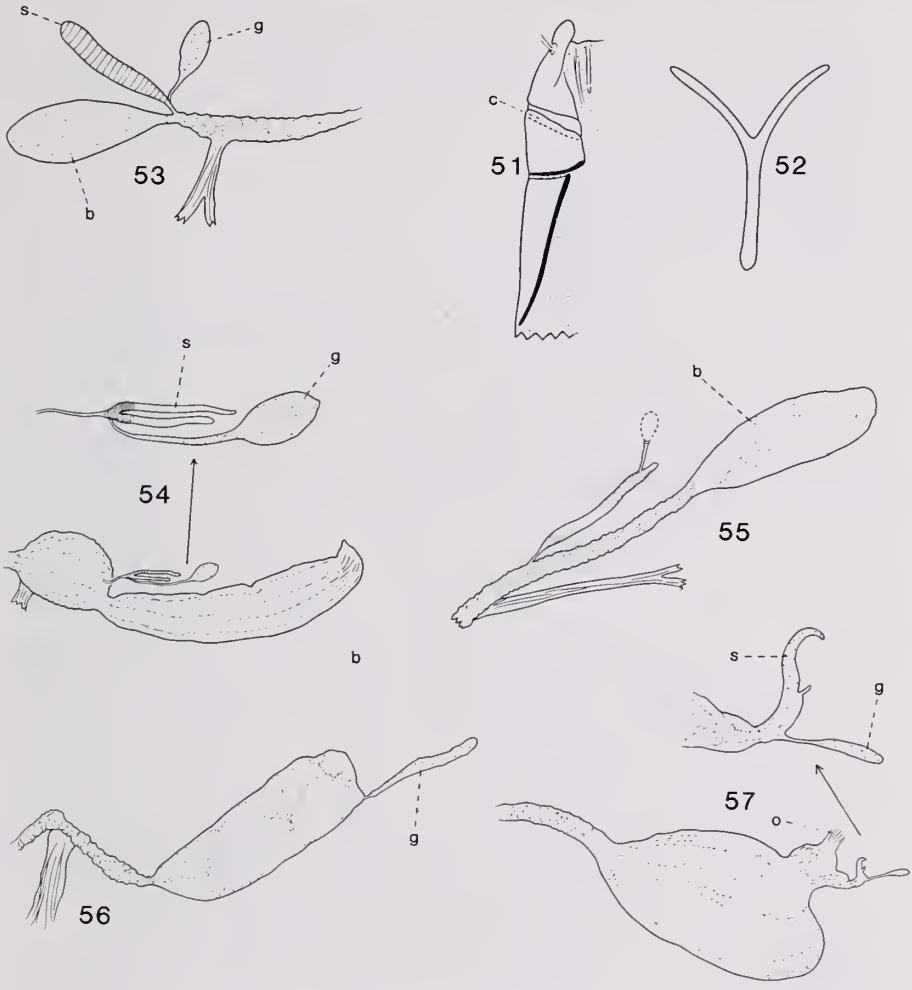
Since the female reproductive system has barely been investigated for Pimeliinae and because of the difficulty in adequately describing it, both the ovipositors and internal female tracts are extensively illustrated. These illustrations are ordered systematically, according to the arrangement in Appendix III. Variation in the salient features of pimeliine ovipositors is briefly characterized below.

Ovipositor size (Chars. 47, 60). Character 47 differentiates taxa in which the ovipositor is rudimentary. Coxites and proctigers are reduced, often unrecognizable, and the spiculum is rudimentary or absent, indicating that these ovipositors are not extruded and retracted. In other taxa the ovipositor ranges from very short but completely formed (e.g., *Araeoschizus*, Fig. 41) to very elongate (e.g., Asidini), as reflected by character 60. Derived states of both these characters are scattered on the cladogram, with low consistency but moderate retention indices.

Proportions of coxite, proctiger and spiculum (Chars. 48, 55, 59). In nearly all taxa the proctiger and its ventral baculus are about the same length (as in Figs. 38, 66, 87). In *Vernayella* (Caenocrypticini) and in a few genera of other tribes the baculus is much shorter than the dorsal part of the proctiger (Figs. 75, 84). Similarly, the spiculum, to which the ovipositor protractor and retractor muscles attach, is almost always subequal in length to the ovipositor shaft (not including the basal telescoping membrane). Relatively short but functional spicula occur primarily in taxa with long ovipositors, such as Asidini and Pimeliini (shortening occurs non-synapomorphously in taxa with rudimentary ovipositors, such as Cnemeplatiini). Conversely, long spicula occur mostly in taxa with short ovipositors (e.g., Edrotini, Fig. 186). Relative lengths of coxite and paraproct (Char. 59) vary by about a factor of three. Variation in ovipositor length is generally the result of change in paraproct length, so that taxa with long ovipositors (e.g., Asidini, Branchini; Figs. 137, 142) have long paraprocts, those with short ovipositors (Stenosini, Caenocrypticini, Anepsiini; Figs. 38, 41, 75, 114) have short paraprocts. Ovipositor proportions are extremely variable in non-Pimeliinae. Intermediate character states, which occur in the majority of taxa, were selected as hypothetically primitive.

Gonostyle size and position (Chars. 49, 50) are discussed above.

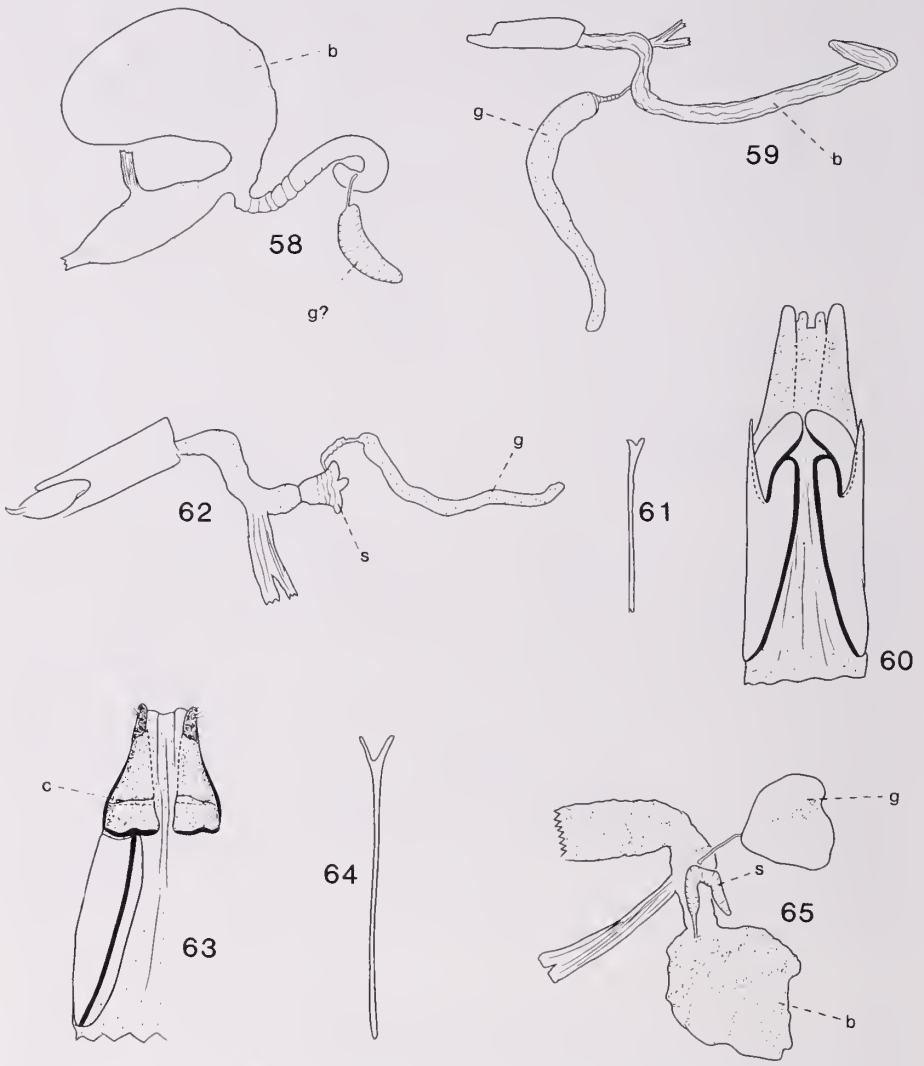
Coxite configuration (Chars. 51–54, 56, 64). In many non-pimeliine tenebrionids such as *Tenebrio* (Doyen, 1966: fig. 72), four distinct coxite lobes are apparent. In Pimeliinae four lobes seem to be present in *Boromorphus* and *Eupsophulus* (Figs. 72, 146) but the lobing is indistinct. Three evident lobes are present in a number of taxa such as *Lasostola*, *Nyctoporis* and *Megelenophorus* (Figs. 96, 120, 126), but in the great majority lobing is obscured by overall sclerotization of the coxites, especially apically. In most members of the large asidine and tentyriine-eurymetopine lineages the three apical lobes are largely consolidated with only faint divisions if any (Figs. 137, 144, 189, 193). The basal lobes, however, are almost always separated from the apical part of the coxite by a transverse pleat in the membrane which forms a shallow pocket opening posterad (Char. 53, Figs. 63, 78, 133, etc.) marking a point of dorsoventral flexibility in the ovipositor shaft. The function of this cleft is not known.



Figs. 51–57. Female genitalia of Eurychorini and Erodiini. 51–53. Ovipositor, spiculum and internal tract of *Adelostoma grande* Haag. 54. Internal tract of *Lepidochora eberlanzi* Gebien; 55. Same, *Eurychora barbata*; 56. Same, *Apentanodes globosus* Reiche; 57. Same, *Erodius carinatus* Solier. b = bursa copulatrix, c = cleft in coxite; g = accessory gland; s = spermatheca(e).

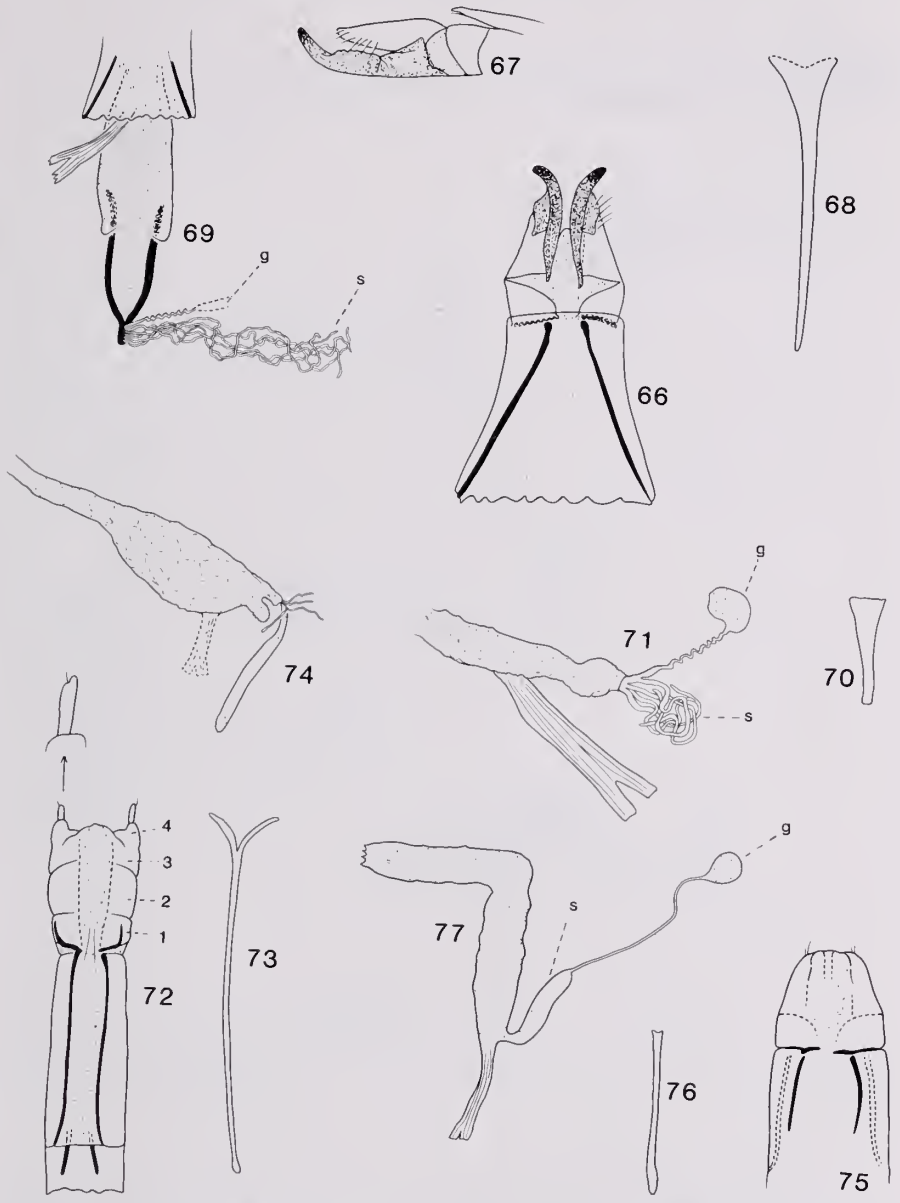
It could be important during insertion of the ovipositor into soil or in facilitating movement of the eggs, which are notably large in many Pimeliinae. On the cladograms this character has low consistency but high retention, characterizing most of the members of the combined pimeliine, asidine and tentyriine-eurymetopine lineages (stem 14). In stem 31 (Coniontini, Branchini, Asidini), in which the entire coxite becomes sclerotized, the transverse cleft is lost.

One of the most striking features of the pimeliine ovipositor is the elaboration of the fourth coxite lobes into strongly sclerotized digging structures (Chars. 54, 64).

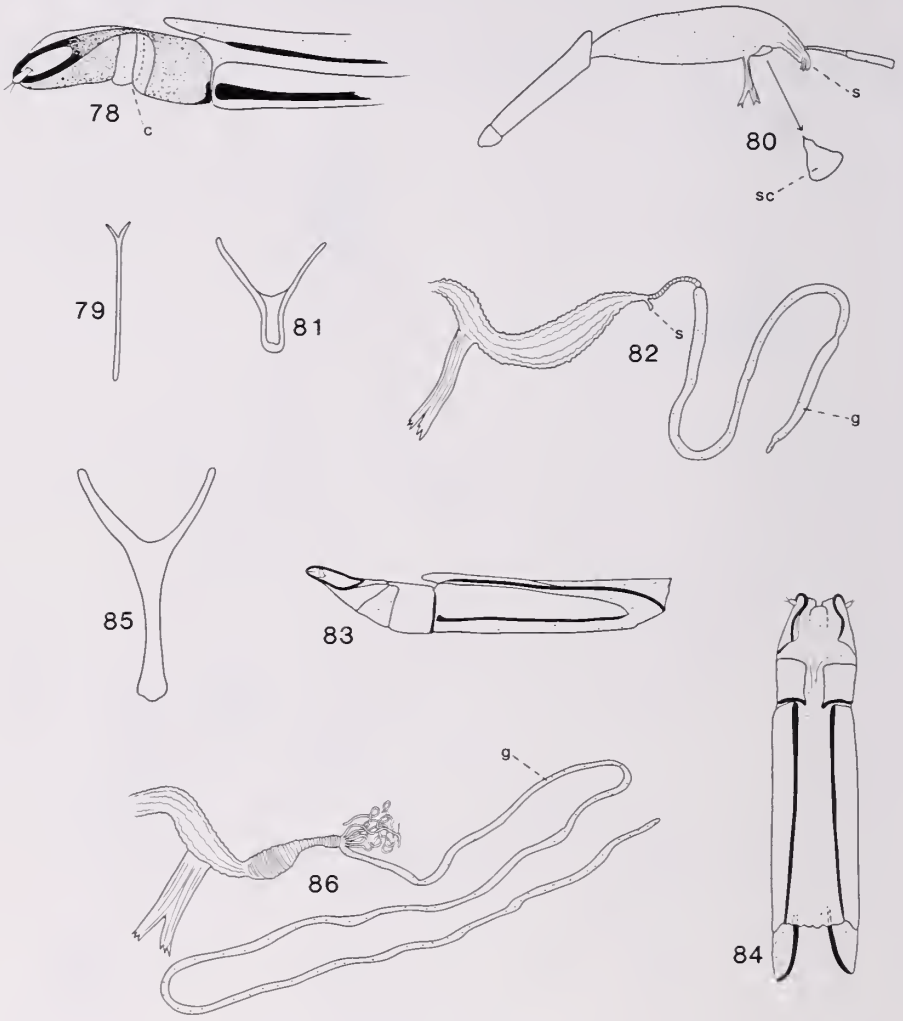


Figs. 58–65. Female genitalia of Zophosini. 58. Internal tract of *Zophosis (Gyrosis) orbicularis*; 59. Same, *Z. (Z.) testudinaria*; 60–62. Ovipositor, spiculum and internal tract of *Z. (Cerosis) herreroensis* Gebien; 63–65. Ovipositor, spiculum and internal tract of *Z. (Calosis) amabilis* Deyrolle. b = bursa copulatrix, c = cleft in coxite; g = accessory gland; s = spermatheca(e).

Commonly the coxites remain as evenly attenuate lobes when they become sclerotized, but distinctive configurations characterize tribes such as Akidini (Figs. 83, 84), Pimeliini (Figs. 96, 97) and Cryptochilini (Figs 87, 92). No obvious morphoclines connect these various forms, and the states of character 64 were considered non-additive.



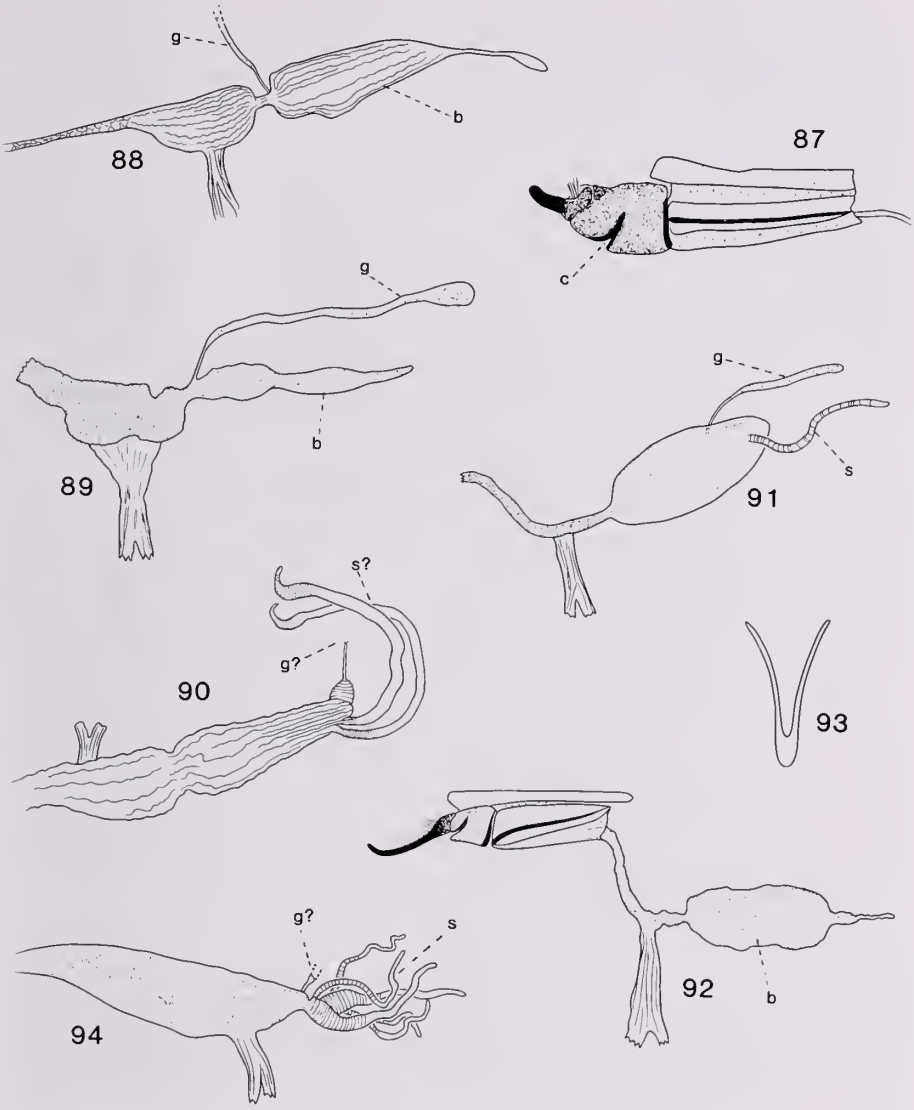
Figs. 66–77. Female genitalia of Boromorphini, Caenocrypticini and Falsomycterini. 66, 67. *Pteroctenus* species (Nova Teutonia, Brazil), ovipositor, ventral and coxite, lateral; 68, 69. Same, spiculum and internal tract; 70, 71. Spiculum and female tract of *Falsomycterus* sp. (Nova Tentonia, Sta. Catarina, Brazil); 72–74. Ovipositor, spiculum and internal tract of *Boromorphus tagenoides* Lucas; 75–77. Ovipositor, spiculum and internal tract of *Vernayella ephialtes*. g = accessory gland; s = spermatheca(e); sc = vaginal sclerite; 1, 2, 3 & 4 = coxite lobes.



Figs. 78–86. Female genitalia of Ceratanisini and Akidini. 78–80. Ovipositor, spiculum and internal tract of *Ceratanisus tristis* Faldeman; 81, 82. Spiculum and internal tract of *Morica planata* Fabricius; 83–86. Ovipositor (lateral and ventral), spiculum and internal tract of *Akis tingitana* Lucas. c = cleft in coxite; g = accessory gland; s = spermatheca(e); sc = vaginal sclerite.

The base of coxite lobe 1 is strengthened by a transverse baculus which pivots against the ventral paraproct baculus. The shape of this baculus is so variable that it was not possible to recognize meaningful character states. In Molurini, however, the baculus has a strongly oblique orientation, which was considered a derived feature (Char. 56, Fig. 104).

The paraprocts (Chars. 57, 58, 61) are of simple structure. Character states commonly present in non-Pimeliinae were used for polarizing.

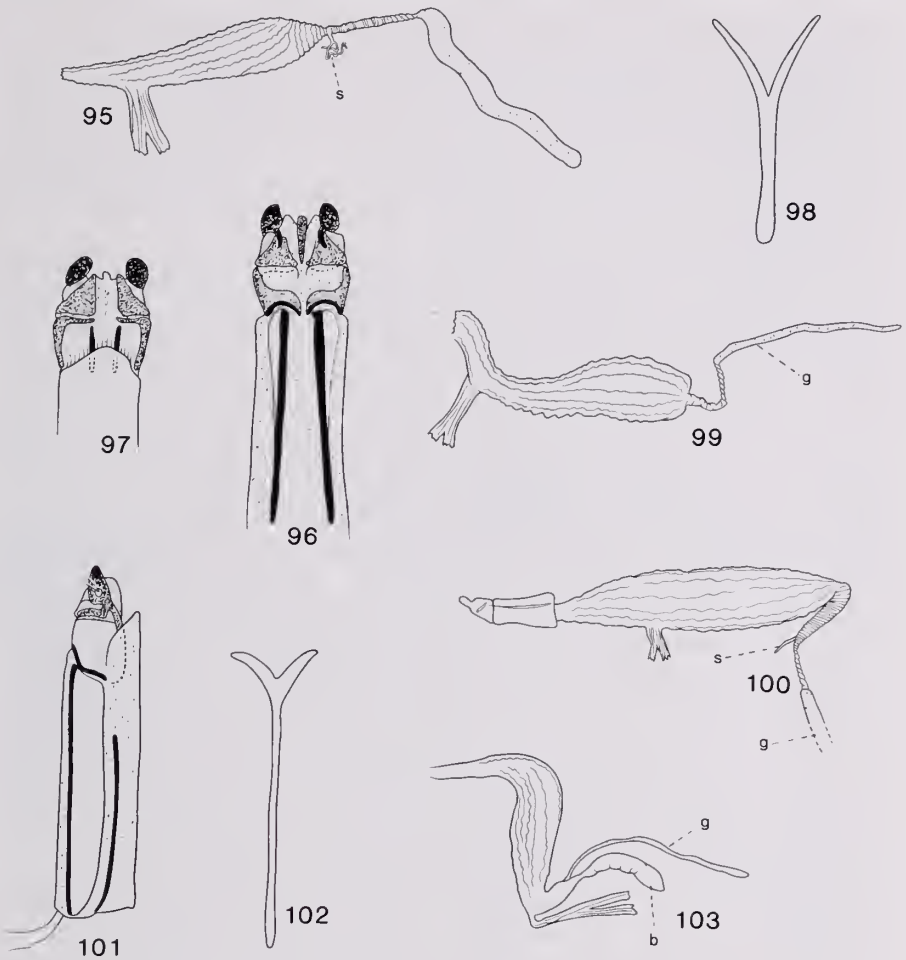


Figs. 87–94. Female genitalia of Cryptochilini and Calognathini 87–88. Ovipositor (lateral) and internal tract of *Cryptochile grossa* Erichson; 89–90. Internal tracts of *Cryptochile* species (Spektakalpas, Cape Province, South Africa) and *Horatoma parvula* Solier; 91. Internal tract of *Pachynotelus dimorphus* Koch; 92–93. Ovipositor and internal tract (lateral) and spiculum of *Pachynotelus albonotatus*; 94. Internal tract of *Calognathus chevrolati* Guérin. b = bursa copulatrix; c = cleft in coxite; g = accessory gland; s = spermatheca(e).

Spiculum configuration (Chars. 62, 63). The reflexed spicular arms of Molurini (Fig. 105) are certainly derived and almost autapomorphic (similar in a few Eurychorini and Vacronini). The primitive state of character 62, however, is problematic. States 2 (Figs. 45, 52, 118) and 3 (Figs. 39, 48, 121, 163), common outside Pimeliinae, occur in otherwise primitive taxa such as *Tenebrio* and *Zolodinus,* respectively. State 3 also occurs in Lagriinae, and is here treated as plesiomorphic. State 1, with the arms separate to the base (Fig. 93), could also be primitive, since the spiculum must have arisen from a structure that originally was paired. However, the paired condition is unknown outside Pimeliinae, and within Pimeliinae occurs only in Cryptochilini and Pimeliini, which are relatively apomorphic in most features. The functional significance of these different spicular forms is obscure.

Internal female reproductive tract (Characters 65–76). Tschinkel and Doyen (1980) considered the primitive form of the internal reproductive tract to be that of *Lagria.* In this configuration the vagina ends in a sac-like bursa copulatrix which bears dorsally (i.e., opposite the oviduct) a spermathecal gland, without a separate spermatheca. This arrangement occurs in several tribes of Lagriinae, in Phrenapatinae and in a few other non-Pimeliinae (see Tschinkel and Doyen, 1980; Appendix IV). In Pimeliinae comparable internal tracts occur in some Zophosini and Cryptochilini (Figs. 59, 88, 89), and tracts with apical gland and no spermatheca occur in Cnemeplatiini, Pimeliini, and *Thinobatis* (Figs. 49, 50, 99, 175). However, in all the tribes listed above, some genera have more derived configurations, with the Zophosini and Cryptochilini being particularly variable. In Erodiini and many Tentyriini and Adesmiini the primitive form is essentially retained, but the bursa copulatrix has become reduced in diameter and annulate (Figs. 57, 195, 198), forming a more or less definitive spermatheca. A vaguely similar, pouch-like spermatheca occurs at the base of the gland in *Evaniosomus, Melaphorus* and *Areyennis* (Figs. 160, 161). In many genera of Tentyriini and Adesmiini the spermatheca has become further differentiated by division into two or three chambers (Figs. 196, 197, 201) and in genera such as *Epitrichia* (Fig. 204) and *Derosphaerius* (Fig. 194) the gland empties into the spermatheca, rather than the vagina. Zophosini are exceptionally variable and not diagnostic at the tribal level. In *Z. (Zophosis) testudinata* (Fig. 59) the tract is as in *Lagria.* In *Z. (Zophosis) orbicularis* the gland empties into a narrow diverticulum of the bursa (Fig. 58), and in *Z. (Cerosis) hereroensis* the gland empties into a capsular spermatheca of peculiar shape (Fig. 62). This structural arrangement is similar to that of *Grammicus* (Fig. 40), but the latter could equally have arisen by specialization of the type of structure exemplified by Tentyriini. The arrangement in *Z. orbicularis* (Fig. 58) is suggestive of that in some Tentyriini, where a reduced, annulate bursa functions as spermatheca (e.g., Fig. 198). In Tentyriini, however, a large, saccate primary bursa is never retained. Finally, in *Z. (Calosis) amabilis,* two diverticula empty into the vagina by independent ducts, while a large bursa is retained (Fig. 65). Pimeliini (Figs. 95, 99, 100), and Cryptochilini (Figs. 88–94) are also variable in the degree of differentiation of the spermatheca, and the number of spermathecal tubes varies as well. I have dissected relatively few genera of these groups, and it may be expected that some of the inferences which follow will require reconsideration.

Most Pimeliinae have both a spermathecal gland and one or more spermathecae. In Stenosini (Figs. 40, 43, 46) and Eurychorini (Figs. 53–55) the spermatheca is a single locular capsule emptying into a common duct with the spermathecal gland.



Figs. 95–103. Female genitalia of Pimeliini and Sepidiini. 95. Internal tract of *Sternoplax zichyi* Csiki; 96, 97. Ovipositor, ventral and dorsal, of *Lasostola ashkabadensis* Bogdanovich and Kaszab; 98, 99. Spiculum and internal tract of same; 100. Internal tract of *Ocnera hispida* Latreille; 101–103. Ovipositor (lateral), spiculum and internal tract of *Sepidium perforatum* Allard. b = bursa copulatrix; g = accessory gland; s = spermatheca.

Caenocrypticini appear to have a similar system (Fig. 77), but additional species need to be examined. This arrangement could have been derived from the lagriine type via intermediates such as *Grammicus* (Fig. 40), which is basically similar to some Tentyriini, except that a definite constriction separates the spermatheca from the vagina.

Ceratanisini (Fig. 80) and some Pimeliini, Akidini and Cryptochilini have multiple spermathecae, as mentioned above. In these groups, as in Lagriinae, the spermathecal tube(s) are usually thick and do not join the vagina by a differentiated duct. The

exception is *Akis*, where the tubes arise laterally from the spermathecal gland duct (Fig. 86). This is basically similar to the arrangement in most Pimeliinae, where one to (usually) many spermathecal tubes empty into the common duct which also bears the spermathecal gland. The spermathecae may be arranged apically on a common duct, as in Asidini, Coniontini, etc. (Figs. 125, 128, 132, 134–145) or they may arise independently from the side of the gland duct, as in Eurymetopini and many others (Figs. 147, 150–152, 165, 172, 178–180). These major configurational differences are described by Characters 65, 67, 68 and 76.

The remaining reproductive tract characters describe more superficial differences, and are mostly self explanatory. The spermathecal duct (Char. 69) is undefined in *Akis* and *Asida* (Figs. 86, 143) but well developed in many other Asidini (Figs. 140, 142). The common duct receiving both the spermathecae and the gland (Char. 70) is usually unpigmented and flexible. In Epitragini it is brownish, thick walled, annulate and more or less rigid (Figs. 165, 168–171). This is an autapomorphy for Epitragini.

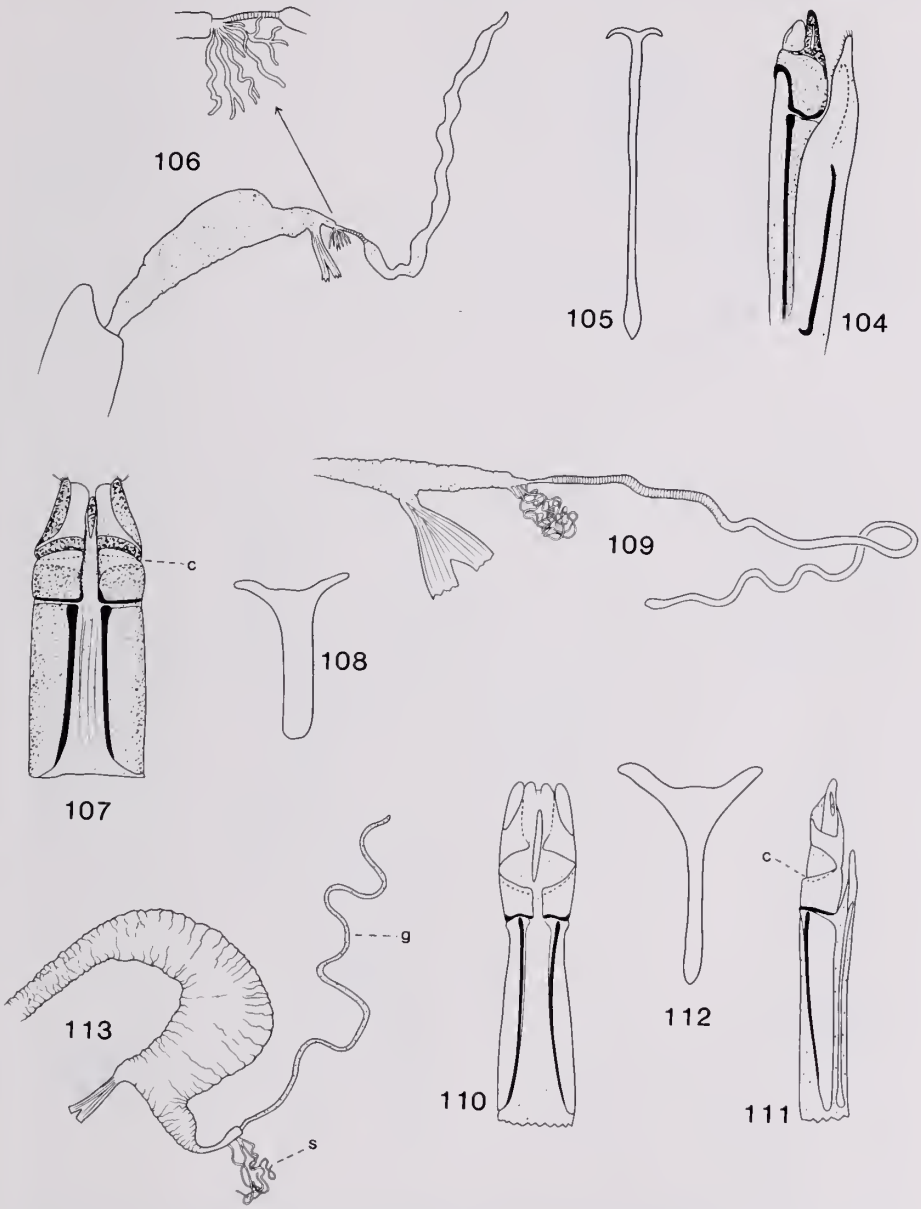
A secondary bursa copulatrix is seldom present in Pimeliinae. It may be recognized by the insertion of both oviduct and spermatheca/gland duct on the same side of the vagina, as in *Salax, Edrotes* (Figs. 164, 187) and a few other genera.

Abdominal venter and elytra (Characters 77, 79, 80). The internalization of the articulatory membranes between sternites five to seven has been discussed at length (Doyen, 1972; Watt, 1974; Fiori, 1977; Doyen and Tschinkel, 1982). It need be mentioned here only that among Pimeliinae the tribes Pimeliini and Platyopini are unique in having exposed membranes, possibly a secondarily evolved specialization.

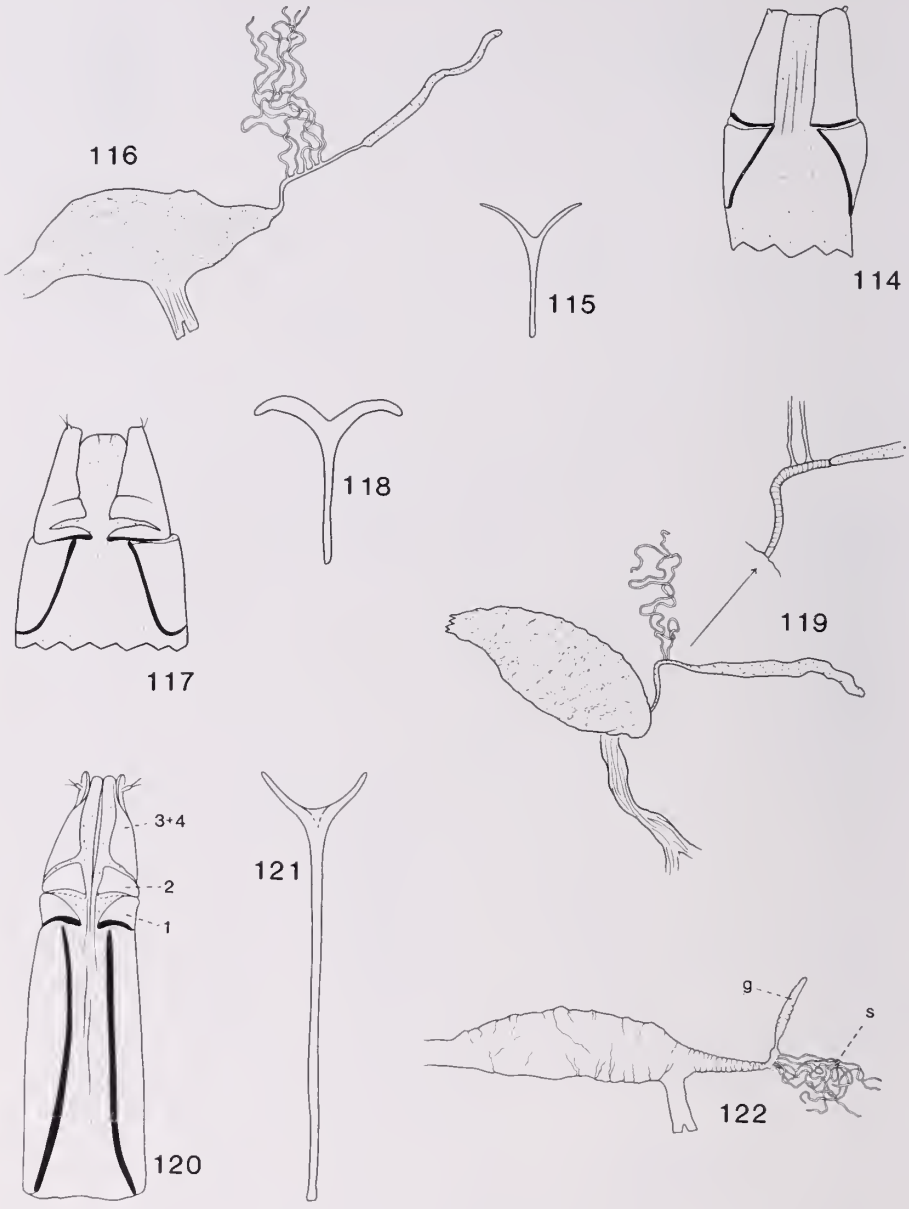
The joints between the elytra and the abdominal sternites were investigated in several pimeliine genera by Fiori (1977), who examined the joints between elytra and thoracic epimera and at the elytral midline, as well. The most generalized condition occurs in winged taxa, where an epipleural ridge on the elytron fits loosely into a groove on the sternum at rest. In nearly all other Pimeliinae the elytra and sternites are immovably coapted, as are the two elytra along the midline. Fiori (1977) recognized two different mechanisms of coaptation between elytra along the medial suture. One mechanism, involving a single dovetail, was observed in *Akis* and *Asida*. A different mechanism, involving double dovetails, was described in *Pimelia* and *Mesostena*. After comparing a much larger number of genera, I believe that elytral interlocking mechanisms cannot be simply divided into these two types. *Platyope*, for example, closely related to *Pimelia* has an interlocking structure which appears intermediate between the two types. *Pachychila*, close to *Mesostena*, has a single dovetail mechanism. *Heterasida*, a typical member of Asidini by other features, has a complex mechanism with two dovetails. In addition there is significant variation in details of the male and female parts of the structures.

Fiori recognized three categories of junction between elytra and abdominal sternites. Simple coaptation without interlocking was observed in winged and some wingless genera (Fig. 205); a single dovetail mechanism was observed in most wingless forms; and a double dovetail mechanism in *Blaps*. In my broader survey of Pimeliinae I recognized two types of single dovetail interlocking, differing in the degree of constriction of the male element (Figs. 206, 207), as well as a third, amplexiform type in Molurini in which the elytral epipleuron has a very broad overlap with the expanded laterotergite without any interlocking (Fig. 208).

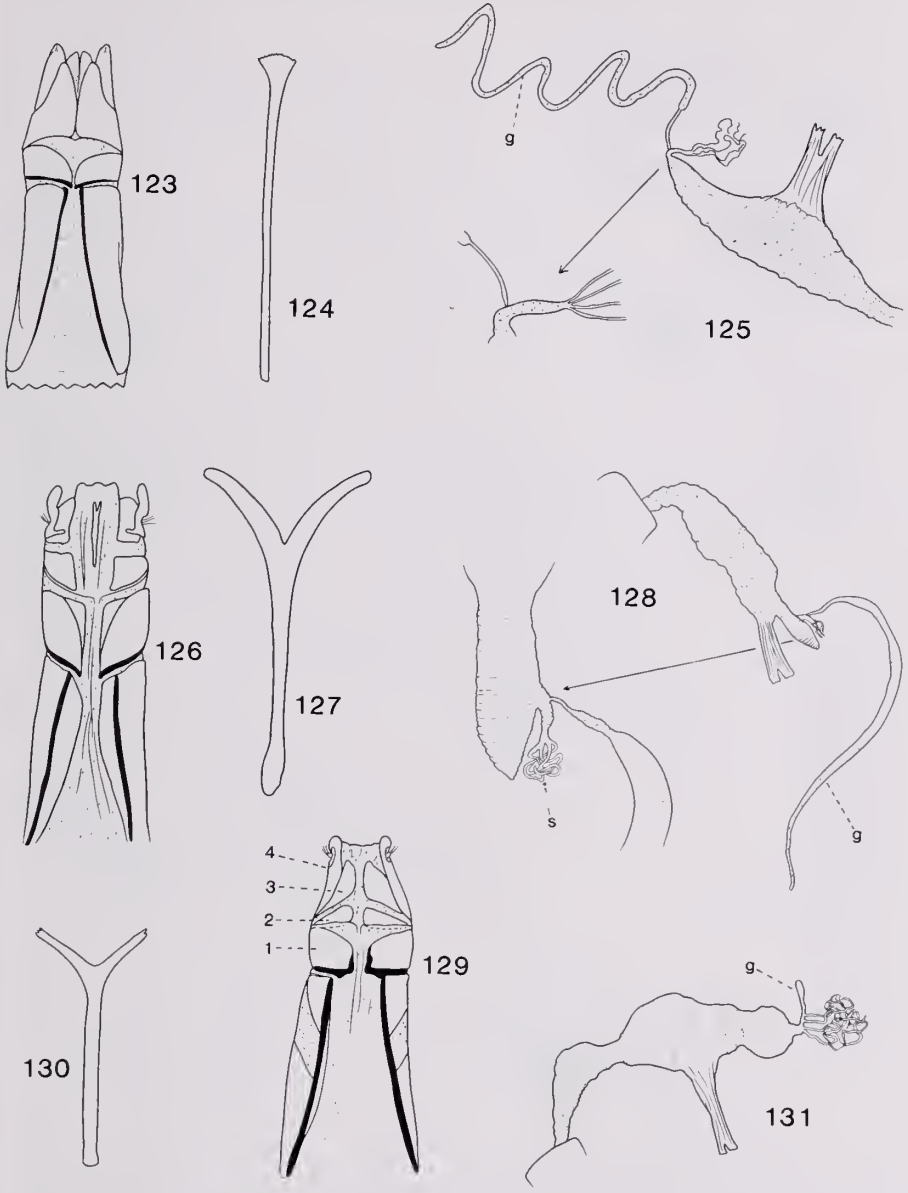
In general it seems obvious that elytral interlocking mechanisms have evolved



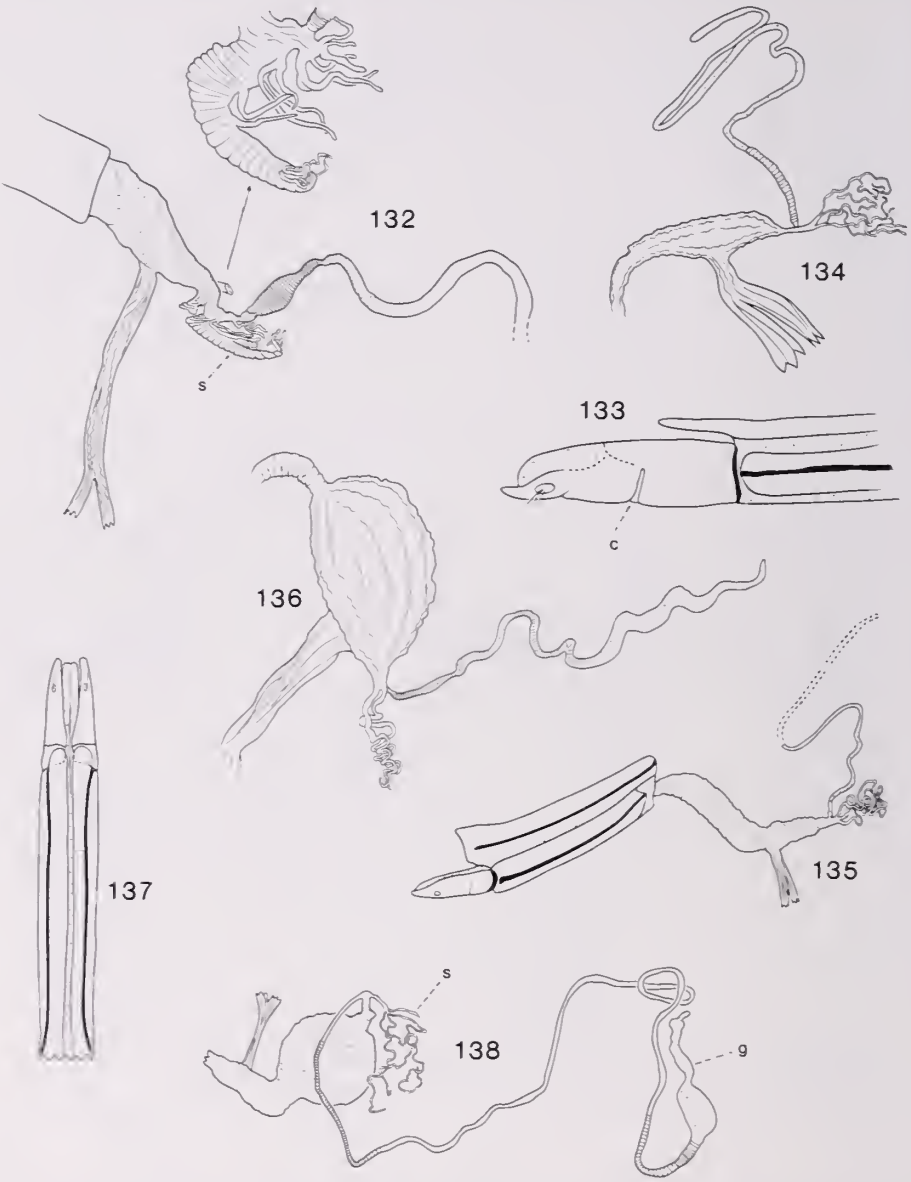
Figs. 104–113. Female genitalia of Molurini and Cryptoglossini. 104–106. Ovipositor (lateral), spiculum and internal tract of *Phrynocolus dentatus* Solier; 107–109. Ovipositor, spiculum and internal tract of *Cryptoglossa laevis* LeConte; 110–113. Ovipositor (ventral and lateral), spiculum and internal tract of *Centrioptera asperata* (Horn). c = cleft in coxite; g = accessory gland; s = spermathecae.



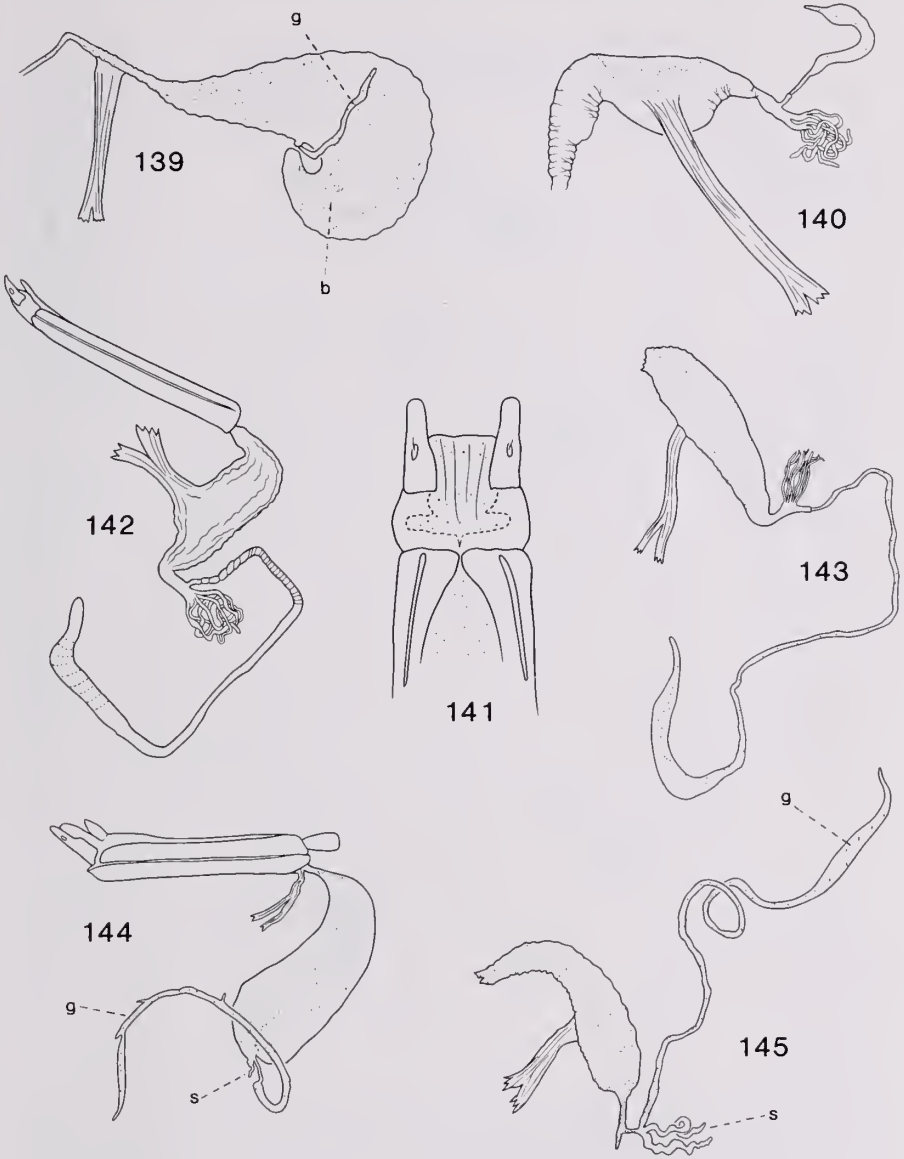
Figs. 114–122. Female genitalia of Anepsiini and Nyctoporini. 114–116. Ovipositor, spiculum and internal tract of *Anepsius delicatulus* LeConte. 117–119. Same structures, *Anchomma costatum* LeConte; 120–122. Same structures, *Nyctoporis carinata* LeConte. c = cleft in coxite; g = accessory gland; s = spermatheca; 1, 2, 3 & 4 = lobes of coxite.



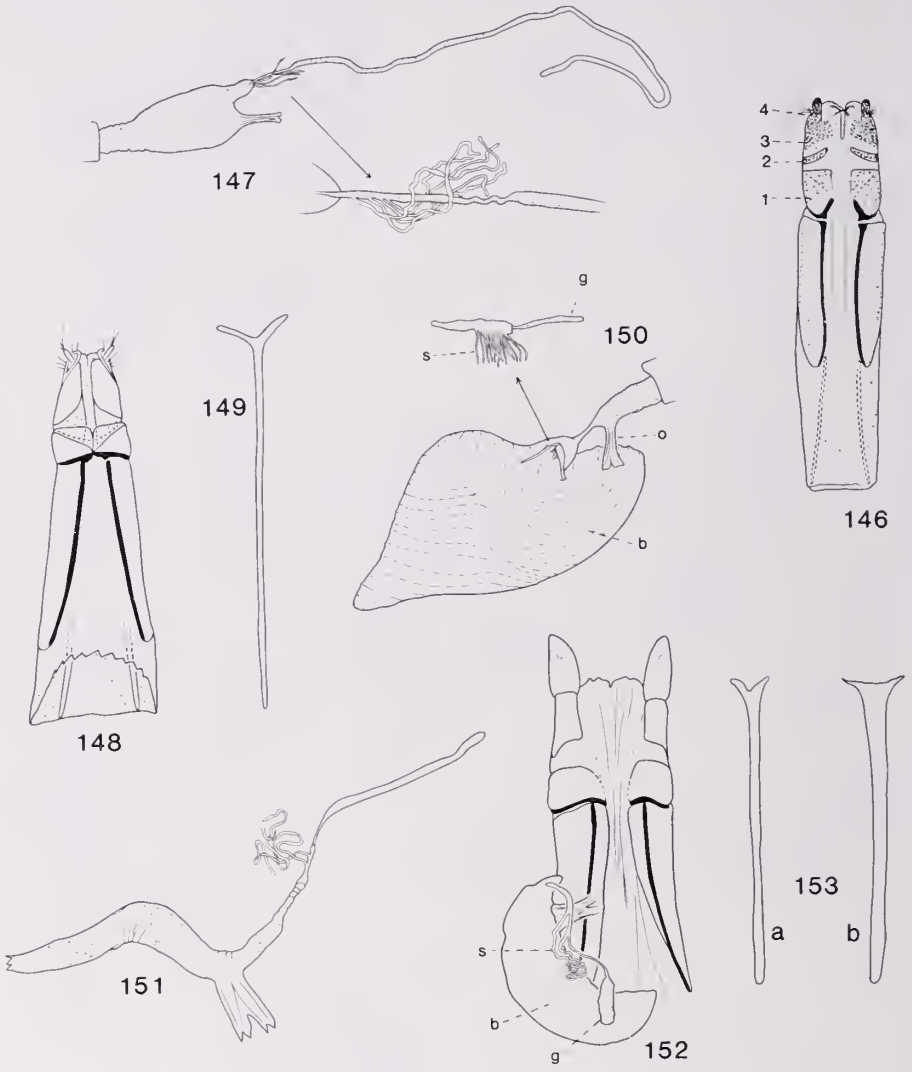
Figs. 123–131. Female genitalia of Elenophorini. 123–125. Ovipositor, spiculum and internal tract of *Elenophorus collaris* Linnaeus; 126–128. Same, *Megelenophorus americanus* Lacordaire; 129–131. Same, *Psammetichus pilipes* Guérin. g = accessory gland; s = spermatheca(e); 1, 2, 3 & 4 = lobes of coxite.



Figs. 132–138. Female genitalia of Nycteliini, Praocini, Physogasterini and Branchini. 132. Internal tract of *Gyriosomus paulseni* Fairmaire; 133, 134. Ovipositor (lateral) and internal tract of *Platestes depressus* Guérin; 135. Ovipositor and internal tract of *Physogaster penai* Kulzer; 136. Internal tract of *Branchus obscurus* Horn; 137, 138. Ovipositor (ventral) and internal tract of *Anectus sordidus* Champion. g = accessory gland; s = spermatheca(e).



Figs. 139–145. Female genitalia of Asidini. 139, 140. Internal tracts of *Scotinus* sp. (ex. San Francisco, Sta. Catarina, Brazil) and *Ucalegon pulchella* Champion; 141, 142. Ovipositor (ventral) and internal tract of *Craniotus pubescens* LeConte; 143. Internal tract of *Asida allaudi* Escalera; 144. Ovipositor (lateral) and internal tract of *Cardigenius laticollis* Solier; 145. Internal tract of *Pseudomachla* sp. (ex. Botswana, 35 km S Kang). g = accessory gland; s = spermatheca.



Figs. 146–153. Female genitalia of Vacronini and Cnemodini. 146, 147. Ovipositor and internal tract of *Eupsophulus castaneus*; 148–150. Ovipositor, spiculum and internal tract of *Alaephus pallidus*; 151. Internal tract of *Lixionica angustata* Blackburn; 152–153. Ovipositor plus female tract and spicula from 2 individuals of *Cnemodinus testaceus* Horn. b = bursa copulatrix; g = accessory gland; o = oviduct; s = spermatheca; 1, 2, 3 & 4 = lobes of coxite.

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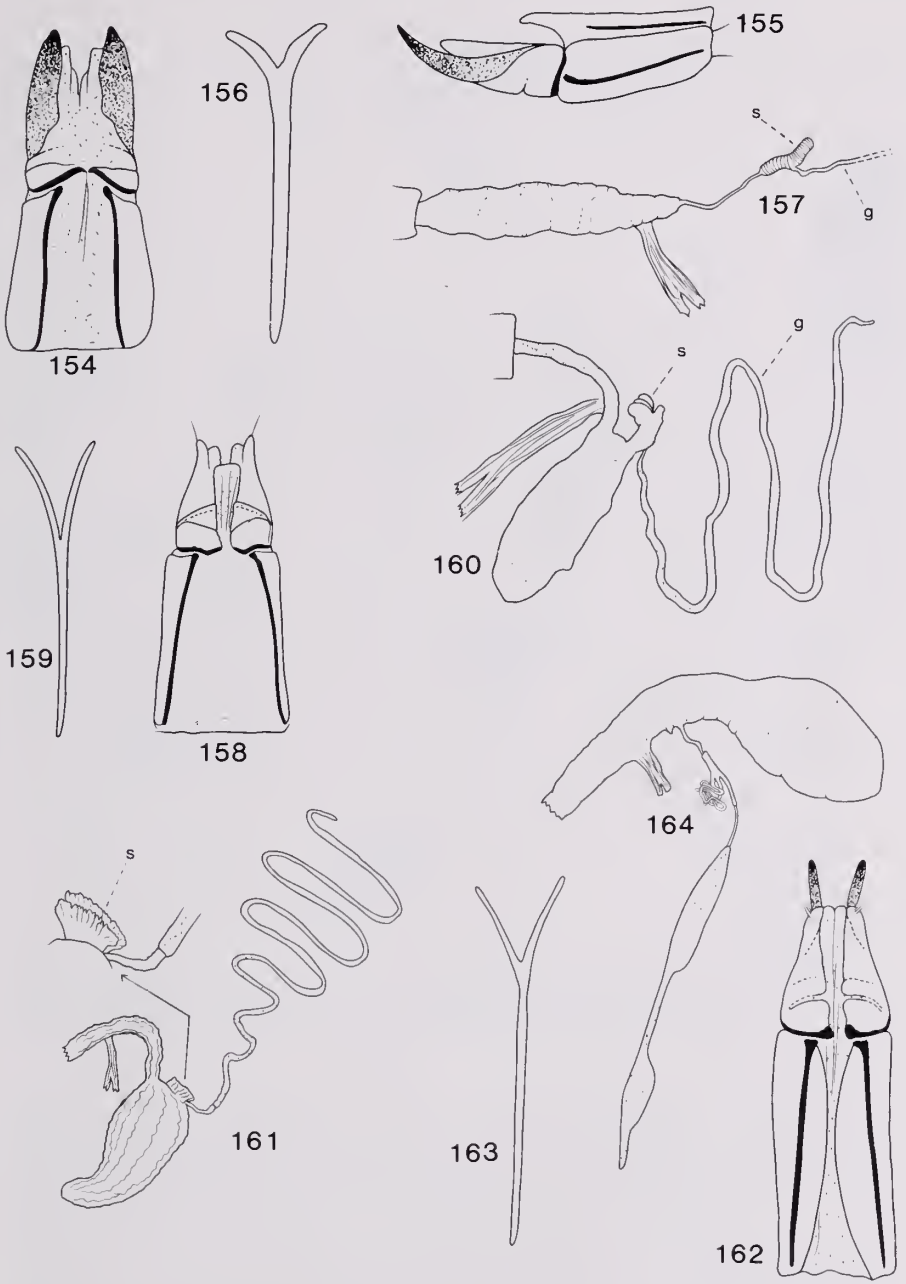
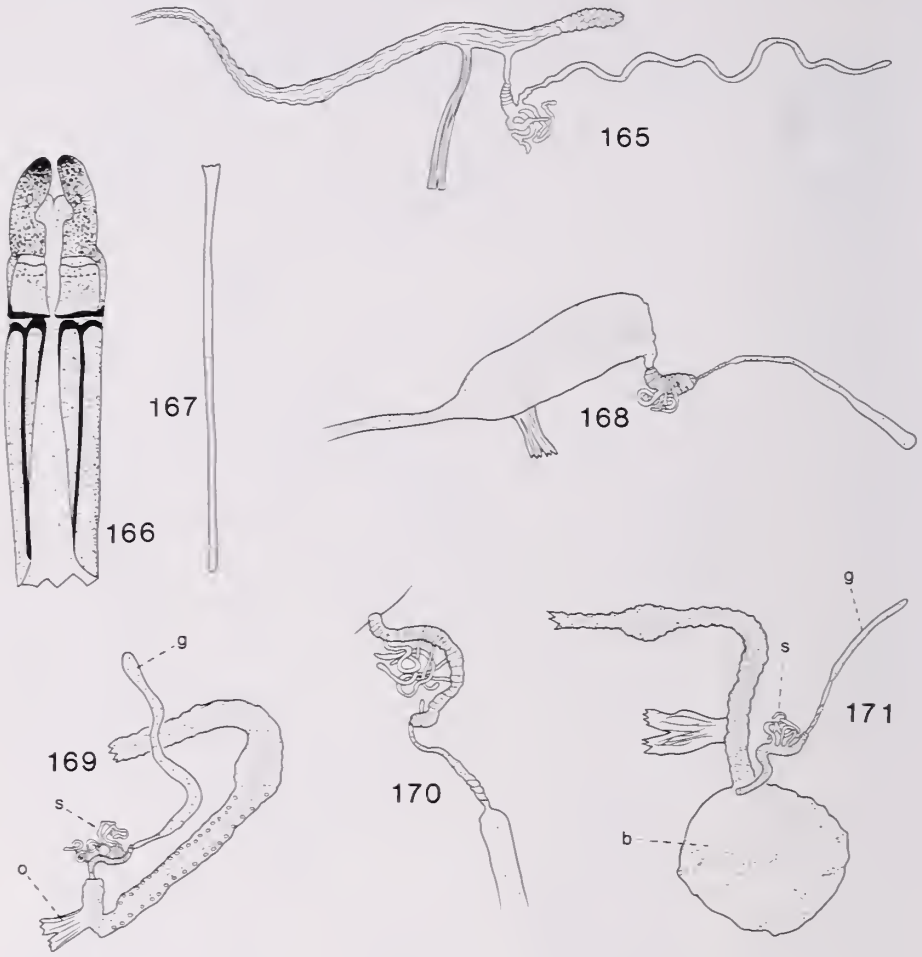
Figs. 154–164. Female genitalia of Trilobocarini and Evaniosomini. 154–157. Ovipositor (ventral and lateral), spiculum and internal tract of *Trilobocara ciliatum* Solier; 158–160. Ovi-

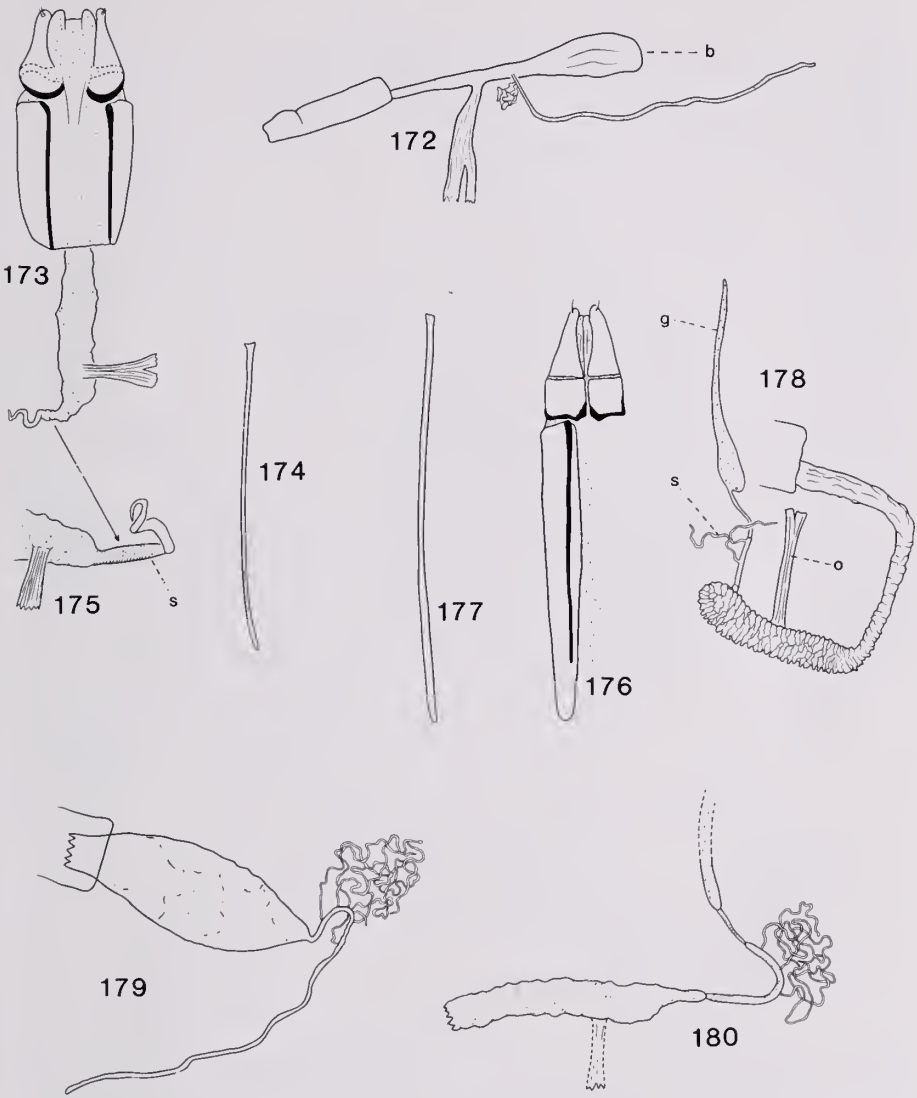


positor (ventral), spiculum and internal tract of *Melaphorus reichei* Guérin; 161. Internal tract of *Aryenis unicolor* Blanchard; 162–164. Ovipositor, spiculum and internal tract of *Salax lacordairei* Guérin. g = accessory gland; s = spermatheca.



Figs. 165–171. Female genitalia of Epitragini. 165. Internal tract of *Epitragus aurulentis* Kirsch; 166–168. Ovipositor, spiculum and internal tract of *Pseudothinobatis grandis* Kulzer; 169–171. Internal tracts of *Hypselops oblonga* Solier, *Nyctopetus rengoensis* Freude and *Lobometopon fusiforme* Casey. g = accessory gland; s = spermatheca.

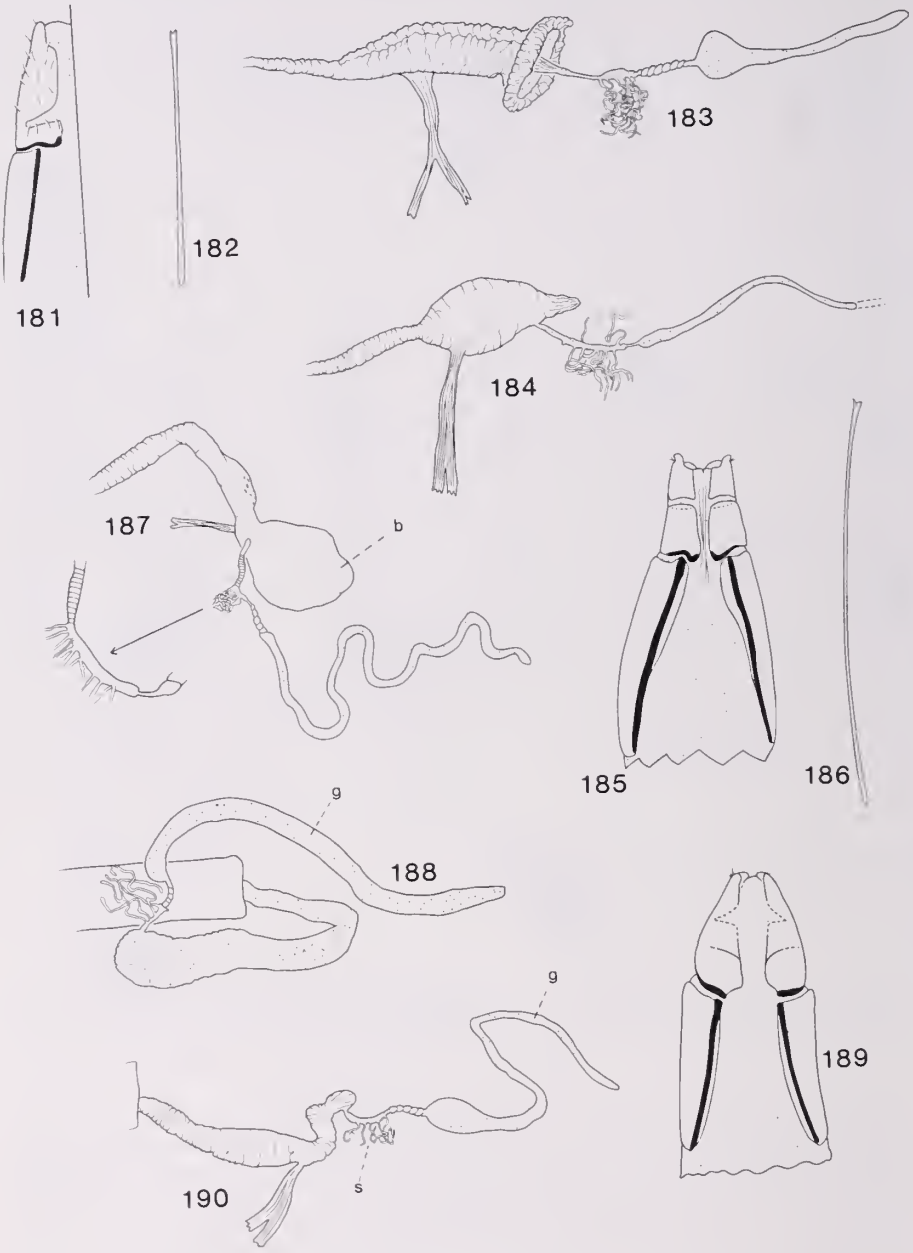
independently several times in Pimeliinae (and many times in non-Pimeliinae), and that interpretation of these characters is subject to great homoplasy. In this analysis I have considered only the elytral-sternal junction, feeling that at this time the variation in the elytra-elytra joint requires much more analysis to be useful as a taxonomic character. Although Fiori examined far too few genera to allow any meaningful taxonomic conclusions, his detailed study was seminal in pointing to a set of potentially valuable characters which has been almost completely neglected. Besides the mechanisms considered here, the elytra also interlock with the scutellum and the thoracic pleurites. Fiori also pointed out the unique interlock between the elytra and pronotum of *Erodius* (see Char. 33 above).



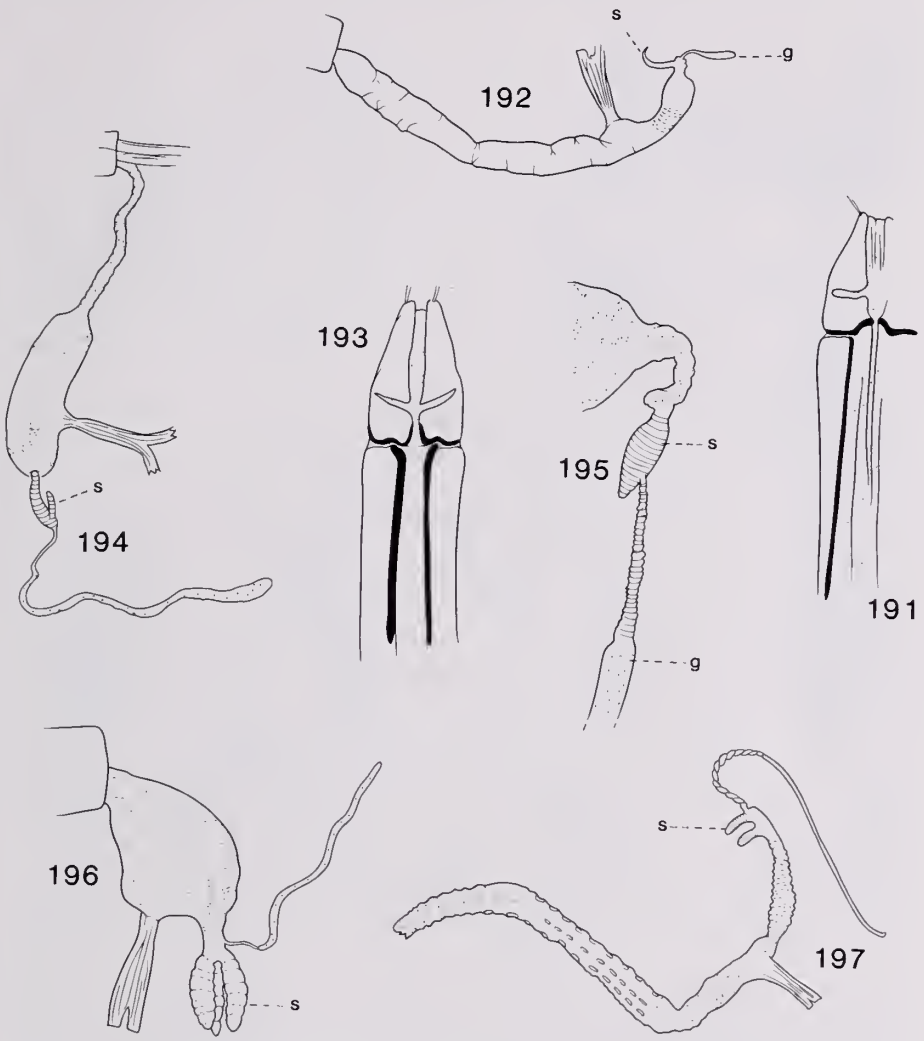
Figs. 172–180. Female genitalia of Thinobatini and Eurymetopini. 172. Internal tract of *Arthroconus fuscus* (Solier); 173–175. Ovipositor, spiculum and detail of female tract of *Thinobatis rufipes* Solier; 176–178. Ovipositor, spiculum and internal tract of *Trientoma puertoricensis*; 179. Internal tract of *Achanius* sp. (Natal, Brazil); 180. Internal tract of *Ambigatus* sp. (Natal, Brazil). b = bursa copulatrix; g = accessory gland ; s = spermatheca.

Enlarged abdominal laterotergites (Char. 80), especially on the basal sternites are mostly involved with amplexiform coupling with the elytra, but occur in a few taxa with other means of elytral-sternal interlocking.

Aedeagal orientation is of the inverted type (derived) in all Pimeliinae which have been examined except *Alaudes,* which has the 'normal' orientation found in all non-



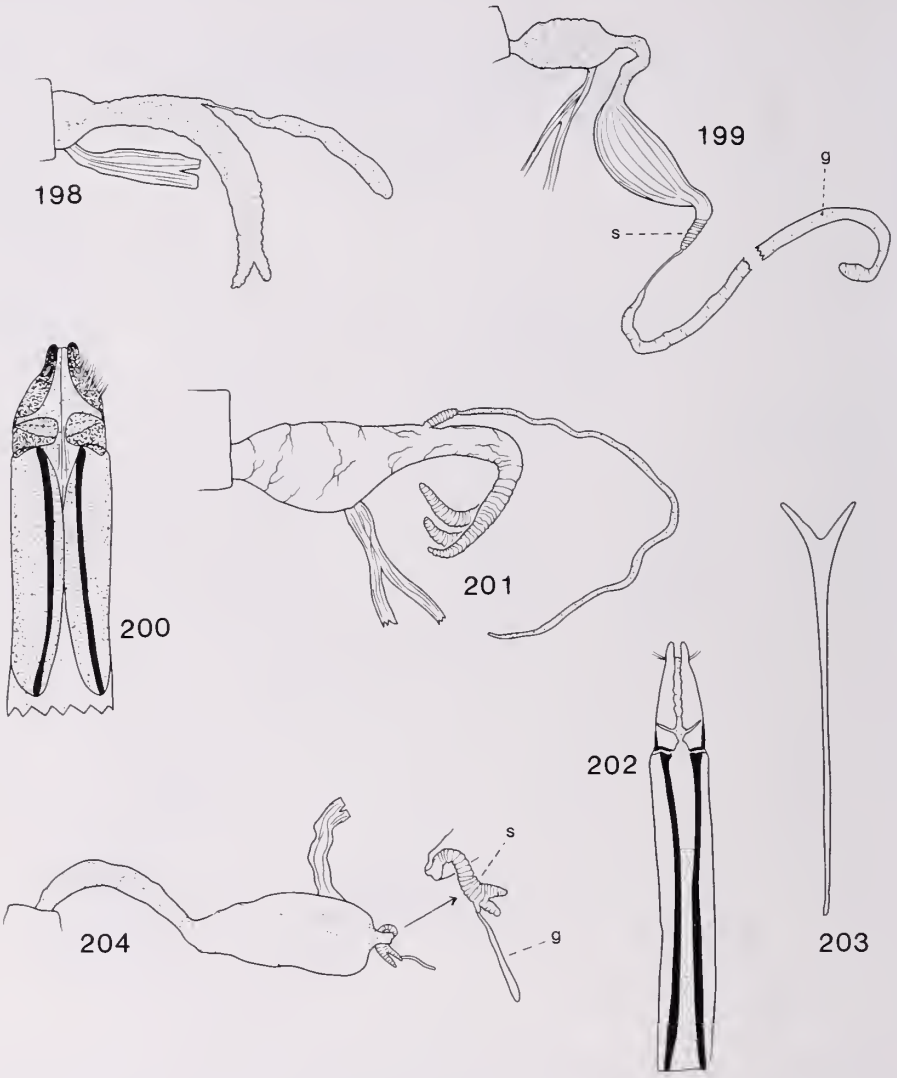
Figs. 181–190. Female genitalia of Eurymetopini. 181–183. Ovipositor (ventral), spiculum and internal tract of *Mencheres elongata* Champion; 184. Internal tract of *Cryptadius inflatus* LeConte; 185–187. Ovipositor, spiculum and internal tract of *Edrotes ventricosus* LeConte; 188. Internal tract of *Ascelosodis concinnus* Bates; 189–190. Ovipositor and internal tract of *Chilometopon pallidum* Casey. b = bursa copulatrix; g = accessory gland; s = spermatheca.



Figs. 191–197. Female genitalia of Tentyriini. 191, 192. Ovipositor (ventral) and internal tract of *Nerina furcilabris* (Fairmaire); 193, 194. Ovipositor and internal tract of *Derosphaerius anthracinus* Westwood; 195. Internal tract of *Tentyria moroccana* Solier; 196, 197. Internal tracts of *Mesostena angustata* Fabriceus and *Himatismus* sp. (Thabazimbi, Transvaal). g = accessory gland; s = spermatheca(e).

Pimeliinae except *Zolodinus*. In the cladograms the condition in *Alaudes* appears as a reversal.

Several tribes of Pimeliinae have distinctive antennal form (Chars. 82, 83), but the states of these characters are obviously subject to homoplastic interpretation because of their simple nature. This is also reflected in the large number of state

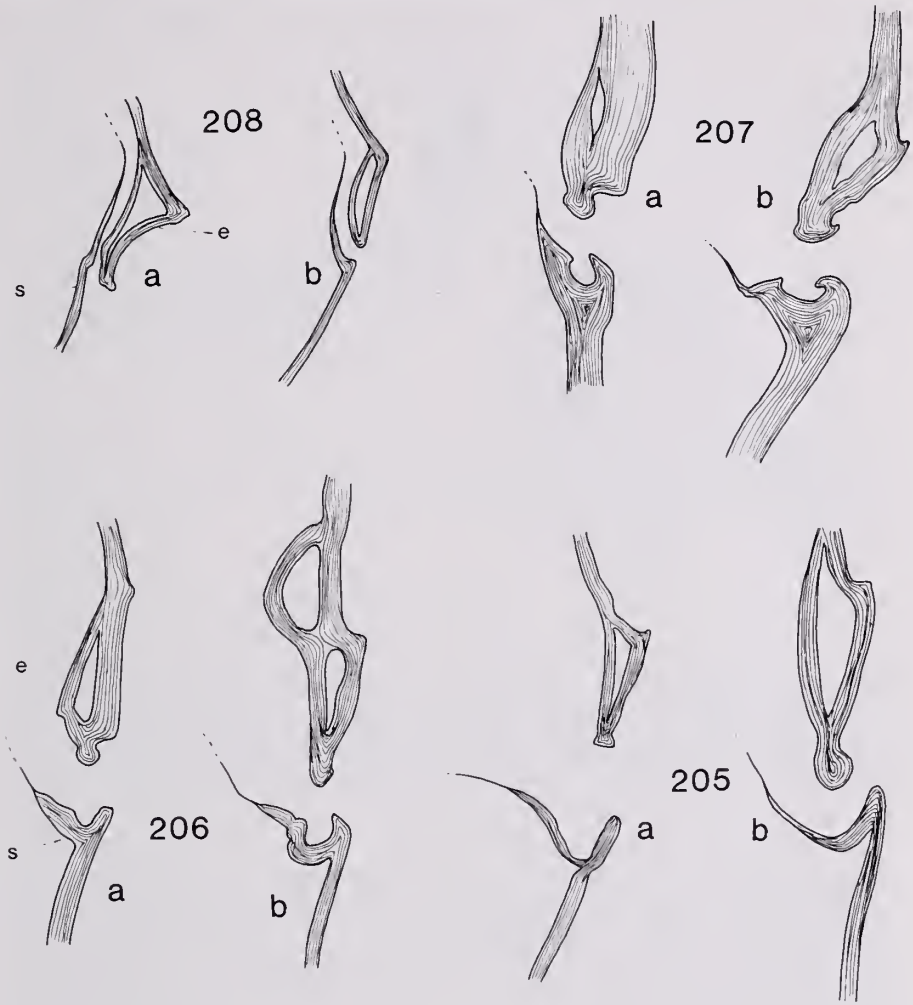


Figs. 198–204. Female genitalia of Adesmiini and Tentyriini. 198, 199. Internal tracts of *Onymacris plana* Peringuey and *Epiphysa flavicollis* Fabricius; 200, 201. Ovipositor (ventral) and internal tract of *Adesmia chiyakensis*; 202–204. Ovipositor, spiculum and internal tract of *Epitrichia tsendsureni* Kaszab. g = accessory gland; s = spermatheca(e).

changes (Char. 83). Antennal sensoriae, very useful in higher classification of non-Pimeliinae, are invariant in Pimeliinae, always consisting of sensillae basiconicae.

CLADOGRAMS

With a set of all primitive character states (HYPO) specified as out-group, ten equally parsimonious cladograms resulted (c.i. = 0.18; r.i. = 0.56; l = 743). With



Figs. 205–208. Cross sections of elytra and abdominal sternites, showing types of interlocking. 205. Type of joint typical of flighted forms; a. *Eupsophulus castaneus*; b. *Gyriosomus foveipunctatus* Fairmaire; 206. Open tongue and groove joint; a. *Edrotes ventricosus*; b. *Tentyria moroccana*; 207. Closed tongue and groove joint; a. *Heterasida bifurca* LeConte; b. *Pimelia* sp. 208. Amplexiform joint; a. *Brinkia debilis* Peringuey; b. *Phligra* sp. (Grahamstown, South Africa). e = epipleural ridge; s = sternite; the laminar structure of the cuticle is shown diagrammatically; the single line becoming dashed indicates the membranous tergum.

Belopini specified as out-group eight equally parsimonious cladograms resulted (same tree statistics). With *Zolodinus* specified as out-group four equally parsimonious trees were obtained (c.i. = 0.19; r.i. = 0.56; l = 734). The length of the last set of trees is reduced because the data set included one less taxon when *Zolodinus* was designated the out-group. If the hypothetical primitive OTU is left in the data set with *Zolodinus* as out-group, then the shortest tree length obtained is 743 and the c.i. is 0.18.

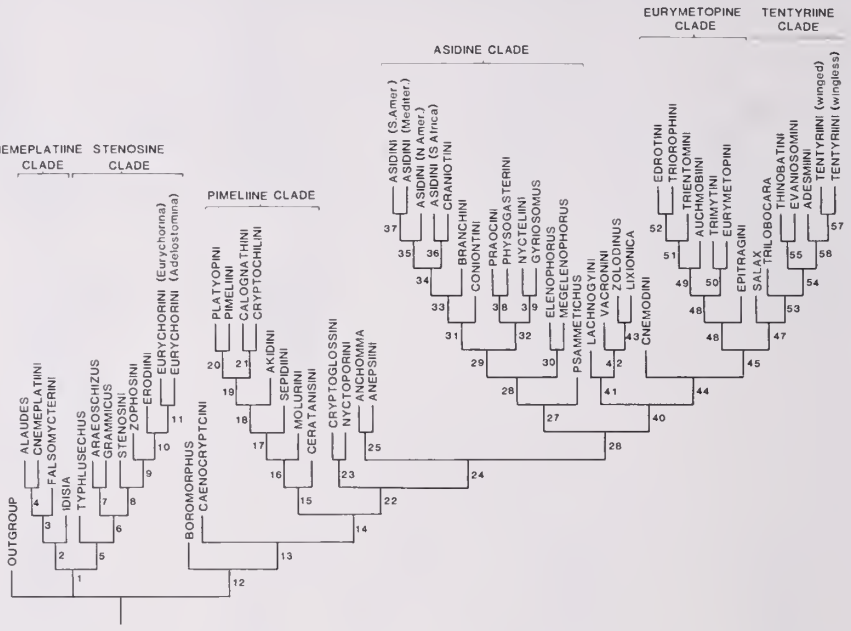


Fig. 209. Cladogram rooted by hypothetical out-group of all primitive character states. Taxa include genera of uncertain affinity as well as tribes. Numbers on stems refer to synapomorphies listed in Table 1. Characters and states are described in Appendix 2. States for each taxon are listed in Appendix 3. The number of steps, consistency index and retention index for each character are listed in Appendix 4. Total tree length = 743; c.i. = 0.18; r.i. = 0.56.

All the major clades show very high congruence over all the trees, but their positions relative to the base of the tree change, of course. One of the ten trees obtained with the hypothetical out-group is illustrated, along with consensus results (Figs. 209, 210). One of the four trees resulting from using *Zolodinus* as out-group is illustrated (Fig. 211). Only the consensus tree resulting from using Belopini as out-group is shown (Fig. 212; c.i. = 0.18; r.i. = 55; l = 761). Major aspects of cladogram topology are discussed below. Character changes, characterization of individual clades and relationship to classification are discussed later.

Six major clades are evident in all the cladograms, and the positions of nearly all taxa within these clades are constant. A few outlying taxa shift position unpredictably; most of these have previously been recognized as systematic problems.

With a hypothetical out-group specified, the cnemeplatiine and stenosine clades are basal. The combined cnemeplatiine-stenosine lineage is defined by only two synapomorphies, but taxa within each individual clade have five defining synapomorphies. The basal taxa of the stenosine clade change position in the various cladograms, and much of the structure of Fig. 209 disappears in the consensus cladogram (Fig. 210). If *Zolodinus* is specified as out-group the position of the cnemeplatiine-stenosine lineage changes (Fig. 211), but the included taxa are almost exactly the

Table 1. Character state changes for Figure 209, listed by stem number. Characters and states are described in Appendix 2.

1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
59:1 60:1	3:2 18:1 47:2 83:1	30:1 55:1	1:2 14:3 16:3 41:5	51:2 52:2 79:1 83:3	15:2 22:1 45:2 65:3	18:1 82:2	49:2 59:2	16:3 19:2 20:2 24:2 25:2 28:3 32:3 50:2 60:2	39:1 43:2 73:3 80:1 82:2 83:5	15:1 22:3 26:2 27:2 46:1 52:1 55:1 62:2 66:2 69:3 70:2	57:2 58:2 65:2	30:3 32:1 50:2 51:2	34:1 53:2	23:1 49:2 59:3 64:2 67:1	36:2 54:2

17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32
28:3 43:2 55:1 79:1	23:2 42:3 59:2 62:2	36:1 37:2 39:1 58:1	1:2 2:2 18:1 26:2 31:1 64:3 72:2	3:2 15:2 25:2 33:3 34:2 41:5 46:3 57:1 62:1 64:4 80:2 82:3	23:3 67:4 68:1 75:2	24:2 28:3 41:5	65:4 70:2 76:3	22:1	24:2 49:2 54:2	19:2 28:3 79:1	65:3 67:2 69:3 73:1	23:2 38:1 39:1 52:2 67:1	36:2 69:3 80:1	22:3 53:1 64:6	24:1 40:2

33	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48
59:4 60:3 61:3 83:1	0:2 25:2 57:1 58:1 80:1 82:2	18:1 55:1 69:1	34:2 42:1	65:2	21:2 23:1 64:6	57:1	30:1	23:1 59:3	24:1 50:1 78:1	15:2 30:2 67:3 69:3	16:4 20:2 22:1 25:2 34:2 78:1	9:2 11:2 29:1 32:3	52:2 62:4	9:3 10:3 67:3	49:1 54:1

49	50	51	52	53	54	55	56	57
42:3 78:3 79:3	39:1 58:1	9:3 10:3	17:2	52:2 65:3 67:2 68:3 75:1 76:2	64:1 65:2 70:1	10:2 49:1 54:1 76:1	66:2	48:1 74:3

same. The only exception is Falsomycterini, which on two of the trees with *Zolodinus* as out-group appears in a basal trichotomy with *Zolodinus* as sister to all other taxa (Fig. 211). In the other two cladograms with the same out-group Falsomycterini joins the cnemeplatiine clade distal to *Idisia*. In all four of these cladograms the cnemeplatiine-stenosine lineage occupies a derived position, coordinate with the pimeliine clade. With Belopini specified as out-group the cnemeplatiine-stenosine lineage is basal, but does not include Falsomycterini, which appears among a group of single taxa at the base of the combined eurymetopine-tentyriine-asidine clades (Fig. 212). In this cladogram *Idisia* appears at the base of the stenosine clade, rather than at the base of the cnemeplatiine clade, and the positions of several taxa show minor changes within the stenosine clade.

The pimeliine clade occupies a relatively plesiomorphic position with HYPO or Belopini as out-groups; in the cladogram with *Zolodinus* as out-group it holds a derived position coordinate with the stenosine clade. One tribe, Caenocrypticini, joins the pimeliine clade when the out-group is *Zolodinus* or Belopini; with HYPO as out-group Caenocrypticini occupies an isolated, plesiomorphic position near *Boromorphus*. In all cladograms the other taxa included in the pimeliine clade are identical and their relative positions show slight variation.

The asidine clade contains 14 taxa when HYPO is specified as the out-group (Fig. 209). If *Zolodinus* is the out-group the taxon pairs Cryptoglossini + Nyctoporini and Anepsiini + *Anchomma* join the asidine clade in a relatively basal position (Fig. 211). With HYPO as out-group both pairs branch separately just apical of the pi-

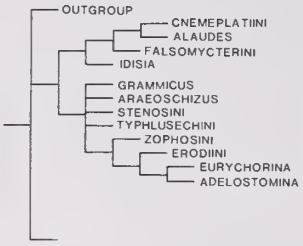


Fig. 210. Nelsen consensus for 10 trees obtained with hypothetical out-group. The only changes from Figure 209 are in the stenosine clade, shown here. Total tree length = 749; c.i. = 0.18; r.i. = 0.56.

meliine clade. With Belopini as out-group only Cryptoglossini + Nyctoporini joins the asidine clade (Fig. 212). The 14 core taxa that appear in the asidine clade in all cladograms always bear the same topological positions, and this clade is not modified in consensus trees.

The eurymetopine + tentyriine clades + Cnemodini form a stable unit which appears unchanged in all cladograms. The position of the combined clade varies, however, from relatively plesiomorphic with *Zolodinus* as out-group to derived with Belopini or HYPO as out-group. With HYPO as out-group Lachnogyiini, Vacronini and Zolodinini appear as outliers of the eurymetopine-tentyriine clade but with the other out-groups they have remote positions.

A few taxa have unstable relationships depending on the out-group. Lachnogyiini and Vacronini have already been mentioned above. In addition, *Boromorphus* always appears as a singleton while Falsomycterini shows major shifts of position among different cladograms. Finally the pairs Cryptoglossini + Nyctoporini and Anepsiini + *Anchomma* occupy rather divergent positions. The positions of most of these have previously been a matter of contention.

The consistency indices obtained here are low compared to many reported values. As shown empirically by Archie (1989a, b), however, and by Klassen et al. (1991) for random data sets the c.i. is inversely correlated with the number of taxa analyzed. Based on their scatterplots of data from the literature, a c.i. value of 0.18 is well above the expected average for data sets as large as those analyzed here. Higher values have been obtained for some large data sets, however (e.g., Loconte and Stevenson, 1991: 57 taxa, 107 characters, c.i. = 0.29).

The low consistency indices experienced with the large data sets reflect a high level of homoplasy, of course. In the present study, nearly all characters are homoplastic (Appendix 4). By recoding convergent conditions as separate states or as different characters homoplasy could be reduced and the c.i. increased considerably. For example, in Fig. 209 state 3 of character 28 (thickening of the rim of the oral foramen) occurs in stems 28 (asidine clade) and 17 (pimeliine clade). These clades are distinct and stable in all cladograms and are distinguished by numerous other characters. It is highly likely that the thickened foraminal rim is a convergence associated with armoring of the body in general and increased integrity of the mouthpart sclerites in particular. This likelihood is, perhaps, increased by differences in associated structures

such as the mentum and submentum. Nevertheless it remains impossible to distinguish more than a single character state based only on the features of the oral rim. Similar considerations attend many other characters, such as closure of the mesocoxal cavities, position of the gonostyles on the ovipositor coxites, shape of the transverse bridge of the tentorium, etc. However, when retained in the character data, homoplasy serves the function of flagging the features in which convergences might be expected. Conversely, recoding these characters would raise the consistency index without changing the cladogram or improving its reliability. For these reasons, the original character state coding was retained in all analyses.

Using HYPO as out-group the data were analyzed using the successive weighting option of Hennig86. The consistency index was greatly increased (to 0.43 after one cycle of weighting), but the number of trees found in subsequent cycles increased to over 1,600, overflowing the storage limits of the program. Thus, while homoplasy was reduced, decisiveness (sensu Goloboff, 1991) was lost.

Selected characters with low c.i. and r.i. were individually deleted in Hennig procedures using HYPO as out-group, resulting in marginal increases in c.i. and moderate changes in tree topology. If the seven characters (#'s 15, 22, 40, 42, 43, 45, 80) are inactivated the tree length decreases to 637, c.i. increases to 0.20, while the number of equal length trees increases to 124. In some of these trees several taxa from the stenosine clade shift onto the cnemeplatiine clade and the pimeliine clade loses Molurini, Sepidiini and Ceratanisini. The large asidine, tentyriine and eurymetopine clades are stable except for a few minor changes and *Zolodinus, Lixionica* and Vacronini remain at the base of the combined tentyriine-eurymetopine clade. I interpret these results to indicate that even the characters of low c.i. in this data set are important in determining cladogram topology and stability. Removing these characters lowers the decisiveness of the data by increasing the number of trees, while scarcely influencing consistency. This is not to imply that all the cladistic groupings in Figures 209–212 are unchangeable. Some clades, such as the stenosine are much more weakly supported than others, such as the asidine. Likewise, the positions of some taxa (such as Zolodinini) are relatively unstable. These taxa and the reasons for their problematic composition or position are discussed in more detail below.

TAXONOMIC INTERPRETATIONS

Position of Zolodinini. The sister taxon of Pimeliinae has been a matter of some disagreement. Based on its internally and externally open procoxal cavities, lack of defensive glands and inverted aedeagus, Watt (1974) placed Zolodinini as sister to Pimeliinae. The larva of *Zolodinus,* described by Watt, appears to be primitive compared to those of Pimeliinae, and Watt did not specify larval synapomorphies linking the two.

In their analysis of cladistic structure of the major tenebrionid lineages other than Pimeliinae, Doyen and Tschinkel (1982) suggested that Zolodinini might represent a specialized derivative of some other lineage. Most of the similarities shared with Pimeliinae are either primitive characteristics or convergences; the most convincing synapomorphy is the inverted aedeagus. A shortcoming of both studies was the abbreviated treatment accorded Pimeliinae. Watt mentioned details of only two other taxa, Nyctoporini, which he believed to represent a relatively primitive tribe, and Pimeliini, which he dismissed as a specialized derivative of the tentyriine clade. Both

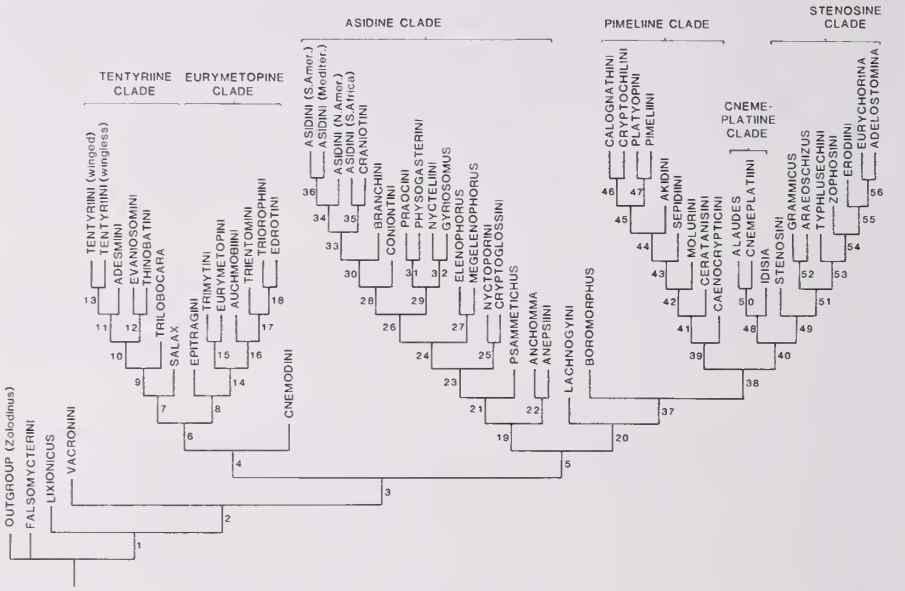


Fig. 211. Cladogram based on *Zolodinus* as out-group. Conventions as for Figure 209. Characters and states are listed in Table 2. Total length = 734; c.i. = 0.19; r.i. = 0.56.

these placements are refuted below. Doyen and Tschinkel examined only about a dozen relatively derived genera of Pimeliinae, representing few tribes in the large pimeliine, asidine, eurymetopine and tentyriine clades. Based on the present analysis, several of the character states they designated as primitive to the pimeliine clade were incorrect.

Comparison of Figures 209–212 reveals a basic difficulty in classifying Zolodinini as sister to Pimeliinae. If a hypothetical out-group of all primitive character states is designated (Fig. 209), then Zolodinini clusters at the base of the highly derived eurymetopine-tentyriine clade, a group which was also considered apomorphic by Watt (1974). Designating Belopinae as out-group likewise relegates Zolodinini to a relatively derived position. Only by designating Zolodinini as the out-group can it be forced into the sister group status. When this is done the cnemeplatiine clade, here considered primitive is moved to a highly derived position (Fig. 211). Examination of *Zolodinus* adults reveals a number of apomorphic features such as the sclerotized ovipositor with lateralized gonostyli and the structure of the internal female reproductive tract, which has numerous, extremely fine, apparently unbranched spermathecal tubes. These diverge individually from a common duct attached at the base of the spermathecal accessory gland (Tschinkel and Doyen, 1980: fig. 47), an arrangement which is vaguely similar to that of the asidine clade. In the asidine tribes, however, the spermathecal tubes are much thicker and many fewer, and usually branch from the common duct at a single point (Figs. 125, 128, 132–138, 140–143). Numerous, very fine spermathecal tubules occur in some Adeliini (e.g., *Adelodemus*), but that tribe differs in numerous other features and could not be close to Zolodinini.

Table 2. Character state changes for Figure 211. Characters and states are described in Appendix 2.

1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
57:2	15:1	24:2	16:4	16:1	9:2	9:3	52:2	42:3	65:2	42:2	10:2	18:1	49:1	39:1	42:3
58:2	67:4	50:2	20:2	18:2	11:2	10:3	62:4	52:2	70:1		51:1		54:1	58:1	78:3
67:3	69:1		22:1	78:3	18:2	67:3		65:3							
			23:3		25:2			67:2							
			34:2		29:1			68:3							
			46:2		30:3			76:2							
					32:3										

17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32
9:3	17:2	30:3	24:1	19:2	49:1	65:3	67:2	41:5	23:2	34:2	22:3	24:1	59:4	21:2	57:1
10:3		23:3	32:2	28:3	54:1		69:2	70:1	38:1	36:2	53:1	40:2	60:3	23:1	58:1
			34:2	79:1	58:1		73:1	76:2	39:1	69:3	64:6		61:3	59:3	76:2
			53:1		59:1				52:2	80:1	67:1		83:1	64:6	
			80:3												

33	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48
0:2	18:1	34:2	65:2	49:1	24:1	30:3	50:1	34:1	53:2	28:3	42:3	36:1	3:2	1:2	3:2
25:2	19:1			54:1	30:2	32:1	57:1	64:2		43:2	62:2	37:2	33:3	2:2	18:1
57:1	69:1			65:2	68:3	36:2	58:1	67:1		55:1		58:1	34:2	26:2	47:2
58:1				67:2	75:1		60:1			80:1			41:5	31:1	51:1
82:2				70:1	76:2								46:2	64:3	55:1
													80:2	77:1	59:1
													82:3		65:1

49	50	51	52	53	54	55	56
15:2	1:2	52:2	18:1	24:2	16:3	39:1	15:1
22:1	14:3	80:2	45:2	28:3	20:2	43:2	26:2
65:3	16:3	82:2	59:1		25:2	45:2	27:2
79:1	30:1				32:3	73:3	46:2
83:3	41:5				49:2	80:1	52:1
					50:2	83:5	55:1
					83:4		62:2
							69:3
							70:2

Zolodinus is similar in many adult features to Vacronini, near which it appears in the cladograms, but larval differences seem to preclude a close relationship. Larvae of *Zolodinus* are similar to generalized forms such as *Tenebrio,* while larvae of Vacronini are similar to those of Epitragini, Trimytini and related tribes, with greatly enlarged forelegs and mandibles bearing basolateral tufts of stout setae (Doyen and Lawrence, 1979). Larvae of the less specialized tribes of the cnemeplatiine and stenosine clades are known only from *Dichillus* and *Stenosus* (Keleynikova, 1976), and *Idisia* (Hayashi, 1966), which all have moderately enlarged forelegs and mandibles with only a few stout basolateral setae. The larva of *Vernayella* is similar (Endrödy-Younga and Doyen, in preparation) and larvae of this type may represent the primitive body plan for Pimeliinae. If tribes such as Cnemeplatiini and Stenosini represent primitive Pimeliinae, then it seems highly unlikely that Zolodinini is the sister group of Pimeliinae, based on the cladograms discussed above. The most likely alternative is that the apomorphies shared by *Zolodinus* and Pimeliinae (inverted aedeagus and lack of defensive glands) are convergent. A few other tribes have apparently lost the defensive glands (Phrenapatini, Goniaderini, Chaerodini), and in some Cyphaleini the reservoirs are extremely small. Inversion of the aedeagus is unknown among other non-Pimeliinae, but *Alaudes* (Cnemeplatiini) is unique among Pimeliinae in having the aedeagus in the normal position. Because of the complexity of these sometimes contradictory character distributions it seems best to reserve judgement on the position of Zolodinini until the relationships of the entire family can be reanalyzed.

Lixionica Blackburn (=*Exangeltus* Blackburn) clusters near *Zolodinus* in all cladograms, but its placement is problematic. Kaszab (1977) placed *Lixionica* in Ceratanisini, which it resembles in external characters. The internal female reproductive

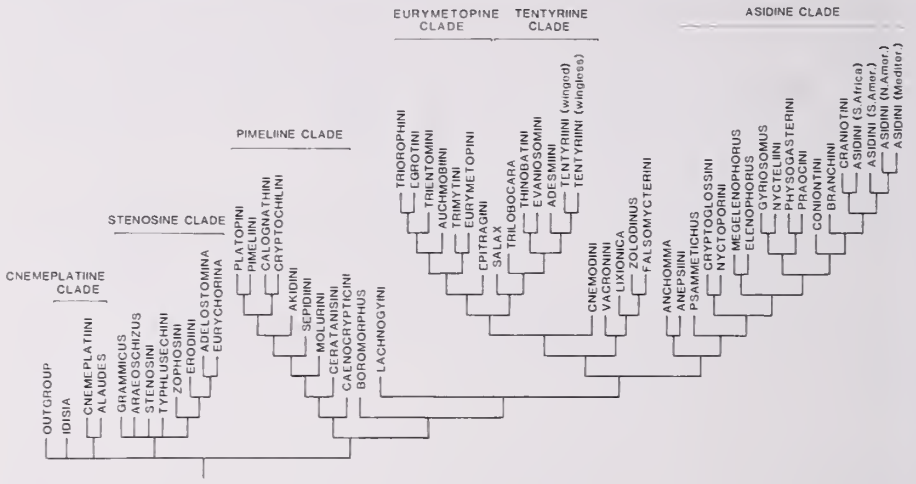


Fig. 212. Cladogram based on Belopini as out-group. Total length = 746; c.i. = 0.18; r.i. = 0.55. Character changes not shown.

tract, however, resembles the type found in the eurymetopine clade, with spermathecal tubules branching individually from the base of the accessory gland. The internal closure of the procoxal cavities (Character 30: 1) is also of the eurymetopine type. In Ceratanisini the internal female tract is autapomorphic (Fig. 80), but the ovipositor is similar to that of Akidini (Figs. 78, 83), with a distinct gonostyle set in a large membranous oval window in the sclerotized coxite; procoxal closure is of the asidine type (Char. 30: 3). The ovipositor of *Lixionica* is similar to that of *Nyctoporis* and *Alaephus,* with mostly generalized features. Based on the features cited above *Lixionica* is tentatively placed in Vacronini. Discovery of the larva, however, may dictate a different position.

Cnemeplatiine Clade. This lineage includes only a few genera, listed below. It is defined by five synapomorphies in Fig. 209. Reduced size of tentorium (3: 2) occurs convergently in Cryptochilini, but is otherwise unique to the cnemeplatiine clade. Consolidation of the submentum with the gula (18: 1) occurs also in *Araeoschizus* and *Grammicus* (stenosine clade) and in Pimeliini. Reduced ovipositor and spiculum (47: 2) do not appear elsewhere as a synapomorphy, but occur in *Araeoschizus* (stenosine clade). Clubbed antennae (83: 1) occur sporadically in many different Pimeliinae (see Appendix 3), but appear as a synapomorphy only in the cnemeplatiine (stem 2) and asidine (stem 33) clades. The clubbed antennae of the asidine tribes, much longer relative to body size, with a differently formed club with large sensory patches, are certainly convergent.

Idisia is differentiated from other members of the cnemeplatiine clade in having externally open procoxal cavities (31: 1) and very short spiculum (55: 1) in the female. Externally open procoxal cavities occur in Zolodinini, apparently as a primitive feature. Open cavities also occur in some Pimeliini, Platyopini and Cryptochilini, but probably as a secondary condition (see character analysis). The open condition

was coded as primitive in *Idisia,* but could well be secondary, since in all other Tenebrionidae external closure precedes internal closure.

Because of its numerous specialized features apparently related to myrmecophily, *Alaudes* was entered as a separate taxon in all analyses. It uniformly clusters with Cnemeplatiini, with which it shares six synapomorphies. One of these (14: 3) is unique; the others occur also in Pimeliini (1: 2; stem 20), Eurychorini, Erodiini and Zophosini (16: 3; stem 9) and Cryptochilini (41: 5; stem 21). All these other taxa differ in many important features, and it seems clear that *Alaudes* belongs in Cnemeplatiini.

With Zolodinini as out-group (Fig. 211) *Falsomycterus* drops out of the Cnemeplatiini clade, clustering at the base of the cladogram, coordinate with Zolodinini. The reduced cnemeplatiine clade (stem 48) is defined by seven synapomorphies. In this cladogram *Alaudes* and Cnemeplatiini share seven additional apomorphies. These synapomorphies are mostly the same as those on Fig. 209, in slightly different arrangement.

With Belopini as out-group both *Falsomycterus* and *Idisia* drop out of the cnemeplatiine clade (Fig. 212). *Falsomycterus* appears near *Zolodinus,* while *Idisia* is located at the base of the stenosine clade.

The cnemeplatiine genera are included under Opatrini in most catalogs, but Csiki proposed the tribe in 1953 and for some time specialists have recognized it as a member of Pimeliinae (Medvedev, 1968, 1973; Doyen and Lawrence, 1979; Doyen et al. 1989). Besides *Cnemeplatia* Costa and *Lepidocnemeplatia* Kaszab, Cnemeplatiini should contain *Thorictosoma* Lea (transferred from Opatrinae by Doyen et al., 1989), *Actizeta* Pascoe and *Philhammus* Fairmaire (transferred by Watt, 1992) and *Alaudes* Horn (hereby transferred). The first two genera are widely distributed, while *Thorictosoma* is endemic to Australia, *Actizeta* to New Zealand and *Alaudes* to western North America, all in seasonally or edaphically arid situations. *Philhammus* occurs in the Mediterranean region and in Armenia.

Watt (1992) detailed the morphological characteristics of several cnemeplatiine genera and described the larva of *Actizeta albata* Pascoe. He proposed that Cnemeplatiini are the sister taxon to all other Pimeliinae. Although he did not mention the stenosine clade, his results are clearly in accord with those presented here.

Idisia and *Falsomycterus* are phenetically quite different from Cnemeplatiini and should remain as separate tribes. Medvedev (1973) suggested that *Idisia* was close to Cnemeplatiini when he proposed Idisiini, citing similarities in male genitalia and mouthpart structure, without mentioning specific characters. Male genitalia are of rather simple structure as in most Pimeliinae. Mandibles do not have the molar lobe strongly reduced and modified in as *Lepidocnemeplatia* and *Alaudes* (less so in other Cnemeplatiini) and are generalized in the other features considered here. Moreover, *Idisia* does not always appear in the cnemeplatiine clade, depending on the out-group designated, and could justifiably be placed at the base of the stenosine clade.

Falsomycterini appears as a member of the cnemeplatiine clade only with HYPO as out-group. Doyen and Lawrence (1979) mentioned a peculiar secondary sexual feature (a mental gland) shared by male Anepsiini and Falsomycterini, but the present analysis does not support a close relationship. Among the more unusual falsomycterine features are the female tract which has multiple spermathecae (Figs. 69, 71) combined with a balloon-like gland. Enlarged, saccate glands occur in a few members

of the stenosine clade (Eurychorini, some Zophosini; Figs. 53–55, 71) and in *Vernayella* (Fig. 77), but these taxa differ in numerous other features. The mandibles of Falsomycterini are long and falciform. The apicale of the aedeagus bears a strong, slightly hooked tooth dorsally near the middle. The procoxal cavities are closed externally by a very broad postcoxal bridge and open internally. The multiple spermathecae are one of the characters causing *Falsomycterus* to cluster with *Zolodinus* in some analyses. The spermathecal tubes in *Pteroctenus* are long and slender (Fig. 69) as in *Zolodinus,* while those of *Falsomycterus* (Fig. 71) are much shorter and thicker. *Pteroctenus* and *Zolodinus* also differ greatly in ovipositor structure (Figs. 66, 67). In *Falsomycterus* the ovipositor is rudimentary. Thus, Falsomycterini cannot confidently be placed in any of the lineages discussed here, and must be accorded an isolated position in Pimeliinae.

Stenosine Clade. This lineage joins basally with the cnemeplatiine clade except when Belopini is designated as out-group. With a hypothetical out-group (Fig. 209) only two characters define the combined cnemeplatiine-stenosine clade, both involving ovipositor proportions. With *Zolodinus* as out-group, the combined lineage is defined by four synapomorphies (Fig. 211, stem 40), all characters of the ovipositor. In the classification of Gebien (1938–1942) and LeConte (Leng, 1920) the stenosine tribes were included in Asidinae, except for Erodiini and Zophosini, which belonged to Tentyriinae. The characters of the female reproductive tract strongly differentiate the stenosine group from Gebien's Asidinae, and all but Erodiini from Tentyriinae. In the Asidinae the female tract has multiple, fasciculate, tubular spermathecae attached either to the base of the spermathecal gland or to the bursa near the gland base (Figs. 140–143). In the stenosine groups the spermatheca is compact, either capsular or short-tubular and either single or, uncommonly, once branched (Figs. 40, 43, 46, 53–55). It shares a common duct with the spermathecal gland (Figs. 53–55) or appears as a differentiated part of the bursa to which the gland attaches (Fig. 40). *Anchomma,* originally associated with Colydiidae and later moved to Stenosini (Doyen and Lawrence, 1979), properly belongs in Anepsiini (see below).

The stenosine lineage has constant membership in all cladograms, with the exception of *Idisia,* which joins the cnemeplatiine clade in one arrangement with Belopini as out-group. The positions of the more basal taxa are variable, and in the consensus trees *Grammicus, Araeoschizus, Stenosini* and *Typhlusechini* all arise separately from the primary stenosine stem (Figs. 210, 212). Thus it would seem advisable to combine Araeoschizini and Typhlusechini under Stenosini, possibly as subtribes. The more specialized members of the lineage, however, are constant in position over all cladograms.

The basal stenosine stem is defined by four or five synapomorphies except in the consensus tree, where the synapomorphies from several dichotomies are compressed into the basal stem. None of the individual synapomorphies are unique, and changing the out-group changes the synapomorphies (only 79: 1 and 83: 3 are common to all analyses). The stenosine lineage is thus distinguished in part by lacking the more obvious synapomorphies involving mouthparts and the internal female genital tract which characterize the asidine, etc. clades.

The more derived members of the stenosine clade (Zophosini, Erodiini, Eurychorini) maintain the same position in all cladograms. Zophosini and Erodiini are structurally among the most specialized Tenebrionidae, but their specialized features

are very largely autapomorphic and do not influence the tree topology. However, each dichotomy is defined by numerous synapomorphies and several of these appear regardless of out-group. These synapomorphies represent many different organ systems and body regions. Overall this must be considered one of the best supported parts of the cladogram.

The members of Zophosini are strongly canalized for an active, heliotactic style of life, notably for extremely rapid running and the ability suddenly to change direction. This is facilitated by the reduction of the abdomen and the conformation of the entire thoracic-abdominal region into a rigidly joined attachment surface for the large coxal and trochanteral muscles which power the abrupt movements. Structural integrity of the thoracic-abdominal region is further increased by fusions of endoskeletal elements. Penrith (1986a), based on the high degree of similarity in external features, placed all Zophosini into the single genus, *Zophosis*. The internal female reproductive tract of Zophosini, however, shows remarkable variation (Figs. 58–65). While a condensed classification of Zophosini may prove desirable, a survey of the female tract over all subgenera of *Zophosis* (only four investigated here) is obviously needed.

The position of Eurychorini as the most derived member of the stenosine clade may seem surprising, since many eurychorine taxa, particularly of the Adelostomina, seem less specialized than Zophosini or Erodiini. Koch (1955: 24), however, recognized the highly derived nature of Eurychorini, and also suspected that they were related to Stenosini. One synapomorphy uniting Stenosini and Eurychorini is the form of the spiculum ventrale, which has the basal arms subequal to the stem (Fig. 52).

Erodiini fits least easily into the stenosine clade. The internal female reproductive tract of Erodiini includes a short, saccate accessory gland (Figs. 56–57). The bursa is differentiated as a small, attenuate appendage ("spermatheca") in *Erodius*, superficially similar to the more strongly differentiated spermathecae of Tentyriini and Adesmiini, especially genera such as *Nerina* (Fig. 192) and *Stenosida*. In the last two the accessory gland is also short and saccate, as in Erodiini, whereas in most Tentyriini the gland is long-tubular. In Erodiini, however, the ovipositor has specialized, spatulate apical coxite lobes (simple in Tentyriini, Figs. 191, 193) and the spiculum has long basal arms (as in Fig. 163; arms shorter in Tentyriini, Fig. 203). In Erodiini the maxillary bases are concealed entirely by the subgenal processes (Fig. 23) while in Tentyriini the maxillary socket is formed by both subgena and submentum (Fig. 24).

Larvae have been associated with Erodiini, Zophosini, Eurychorini and old world Stenosini (Keleynikova, 1962, 1976; Schulze, 1962, 1974) as well as Tentyriini (Keleynikova, 1959). Larvae of Erodiini have thick, moniliform bodies and strongly fossorial legs, apparently specializations for sand dwelling. The configuration of the ninth and tenth abdominal segments is similar to that of Eurychorini, but this may be convergent. Larvae of Zophosini also have moniliform bodies, but with very differently configured ninth abdominal tergites. Larvae of Stenosini are more generalized in gross body form, but show some highly apotypic features, such as a closed tracheal system. Details of mouthparts and legs need to be compared closely over larvae of all these tribes.

Pimeliine Clade. This lineage includes tribes which were placed in the Asidinae of Gebien, except for Pimeliini and Platyopini, which were included in Tenebrioninae

on the basis of the exposed membranes between the apical abdominal sternites. The balance of other characters, including those of larvae, clearly places these tribes in Pimeliinae (Watt, 1974; Doyen, 1972; Doyen and Lawrence, 1979). The tribes included here in the pimeliine clade are invariant, except for Caenocrypticini, which, on two of the cladograms, joins as sister to all the other pimeliine tribes. The order of tribes within the lineage is invariant except for Ceratanisini and Molurini, which exchange positions in one cladogram. The pimeliine clade appears as sister to the combined asidine + eurymetopine + tentyriine clades when the out-group is HYPO or Belopini (Figs. 209, 212). When the out-group is *Zolodinus,* the pimeliine clade moves to a highly derived position as sister to the combined cnemeplatiine + stenosine clades (Fig. 211). The pimeliine clade, alone among the major lineages, is restricted to the old world, where it is especially diversified in the Mediterranean region.

Most dichotomies of the pimeliine clade are defined by four or more synapomorphies. As usual these are seldom unique, mostly involving features that are subject to widespread convergence, such as consolidation of the mouthparts, lateralization of gonostyles, sclerotization of the apical coxite lobes, etc.

The most plesiomorphic tribes of the pimeliine group are Ceratanisini and Molurini. Members of the former are winged and generalized in most external characters. *Ceratanisus,* the only genus examined in detail, has an autapomorphic internal female tract (Fig. 80), with four short, smooth spermathecal tubes and a triangular sclerite in the bursal wall. One synapomorphy shared with Akidini is the form of the apical coxite lobe, which is peripherally sclerotized, leaving a large, central submembranous area into which is inserted the relatively large gonostyle (Figs. 78, 83).

The configuration of the internal female reproductive tract is highly variable in the pimeliine clade, even in some individual tribes. In Akidini, for example, there is a single (*Morica,* Fig. 82) or multiple fasciculate (*Akis,* Fig. 86) spermatheca(e). In Pimeliini the number of spermathecal tubes varies from none (*Lasostola, Pimelia;* Fig. 99) to one (*Ocnera*; Fig. 100) or two (*Sternoplax*; Fig. 95). Variation in Cryptochilini-Calognathini is even more extreme. In *Cryptochile* the bursa is constricted, without a distinct spermatheca (Fig. 88, 89); in *Pachynotelus dimorphus* Koch there is a single spermathecal tube, isolated from the accessory gland (Fig. 91), in *Horatoma parvula* Solier a pair of tubules (Fig. 90) and in *Calognathus* six tubules, two much larger than the others (Fig. 94). In all cases, however, other synapomorphies unite the members of these tribes. For example, all Calognathini and Cryptochilini have ovipositors with pronounced ventral cleft (Char. 53, state 2) and very large, sclerotized, upturned apical coxite lobes (64: 4) (Figs. 87, 92). Likewise, genera of Pimeliini-Platyopini share a distinctive ovipositor topology (64: 3; Figs. 96, 97) and several features of the mouthparts. An unusual character shared by Cryptochilini and some Pimeliini is the externally open procoxal cavities. As discussed earlier, the specialized thoracic form of Cryptochilini would suggest that this is a secondary feature. Thoracic form in Pimeliini is much more generalized, however, indicating a primitive character from which the Cryptochiline arrangement may have been derived.

Among the synapomorphies linking Akidini to the Pimeliini is the form of the spiculum ventrale, which has the basal arms subequal to the stem (Figs. 81, 85, 98). This configuration is unusual in Tenebrionidae (also in *Stenosus,* Cryptoglossini, Anepsiini). The spiculum form in Cryptochilini, with the stem absent (Fig. 93) appears

derived from the pimeliine type. In Sepidiini and Molurini the spiculum arms are relatively large, but are strongly reflexed, especially in the latter (Figs. 102, 105).

Members of Molurini display several notably primitive characters. The female reproductive tract of most of the genera examined has multiple spermathecae which attach to the bursal wall near the gland attachment, rather than onto the gland duct itself (Figs. 106, 109). This is essentially the same arrangement which occurs in Adeliini and Pycnocerini of the Lagriine lineage (Tschinkel and Doyen, 1980). The abdominal-sternal interlocking mechanism (79: 4) is distinct from all other Pimeliinae, as discussed previously, with the epipleural edge of the elytron overlapping the expanded sternite edge (Fig. 208), rather than dove-tailing into a groove. This mechanism must have been derived from a flighted form independently from the dove-tailing found in other tribes. It may be noted here than in *Phrynocolus dentatus* Solier interlocking is of the dove-tailed form, as in Sepidiini, which are similar to Molurini in many other characters. In this study *Sepidium* was the only representative of Sepidiini; comparison of additional genera may suggest merging of Molurini and Sepidiini, or transfer of some genera.

The present data suggest two-nomenclatural changes. Pimeliini and Platyopini share all essential features, differing in a few mouthpart characters (14, 15) the size of the accessory gland (73) and antennal form (83). Reitter (1893, 1915) distinguished his "unechte" (false) Pimeliiden (including Platyopini) from true Pimeliini by the cross-sectional shape of the 2 posterior pairs of tibiae: round or elliptical in the "false" Pimeliini; 3- or 4- angled in the "true" Pimeliini. Gebien (1938–1942) included eleven genera of the "false" Pimeliini in his Platyopini, without mentioning characters. A more broadly based comparison of pimeliine genera might show that the Platyopini comprise the primitive sister to other Pimeliini, but the present data (Appendix 3) suggest the opposite—that Platyopini are relatively derived. *Leucolaephus* Lucas has sometimes been placed in a separate tribe Leucolaephini. I have not made dissections, but based on external characters *Leucolaephus* should be included in Pimeliini.

An unusual feature of Pimeliini-Platyopini is the exposed membranes between the apical abdominal sternites (Char 77: 1). This has traditionally been considered a primitive feature, but in all the cladograms reversal to the internalized condition (77: 2) takes place in the basal stem. Subsequent reversal to the exposed condition then appears in the stem to Platyopini and Pimeliini. It therefore seems likely that the exposed membranes represent a specialized reversal, rather than a retained primitive feature.

Pimeliini are highly derived in numerous characters and in previous classifications have never been placed near the base of Pimeliinae. When Pimeliini was declared out-group in the present study (cladogram not illustrated) all the major lineages maintained their cohesiveness except the pimeliine clade. Most of the pimeliine tribes fell into three small basal lineages, while Molurini and Ceratanisini occupied isolated positions in the interior of the cladogram.

Endrödy-Younga (1989) placed Calognathini and Vansoniini as synonyms of Cryptochilini. The results presented here are in full accord with his changes. Endrödy felt that *Calognathus* was relatively derived, even though it lacks the stridulatory apparatus of all other Cryptochilini. It may be noted, however, that *Calognathus* is certainly primitive in regard to metacoxal structure (Chars. 43–45), in lacking a

middorsal endocranial carina (8) and in having the metendosternite free rather than fused with the mesocoxal inflections (40). Moreover, *Calognathus* females bear a striking superficial resemblance to *Storthocnemis* Karsh (Pimeliini). Only an exhaustive comparative study including pimeliine genera will reveal the details of cladistic structure of this group of highly specialized beetles.

Asidine Clade. Included here is most of the subfamily Asidinae (sensu Gebien, 1937, 1938–1942), with the addition of Physogasterini, Praocini, Branchini and Coniontini and less Zopherini (=Zopheridae) and those tribes placed here in the pimeliine clade. Even after removal of the pimeliine tribes, the asidine clade represents one of the great radiations of Tenebrionidae. This clade occurs exclusively in the New World, with the exception of Asidini and *Elenophorus*. The former has representatives in the Mediterranean region, in southern Africa and in Madagascar. Because of its widespread distribution, one would expect that Asidini would be relatively old and that it would occupy a relatively basal position within the clade. In all analyses, however, Asidini holds a highly derived position. Moreover, the stem (34: Fig. 209) basal to all the asidine taxa is defined by six synapomorphies, two of which (0: 2; 82: 2) are unique or nearly so in Pimeliinae.

Elenophorus, which occurs in the Mediterranean region, bears a striking resemblance to *Megelenophorus* from southern South America. The relationships of these genera were previously considered by Doyen and Lawrence (1979), who tentatively concluded that *Elenophorus* was derived from Akidini, while *Megelenophorus* was related to *Psammetichus* (also South American), based on features of the skeletal anatomy. In particular, both *Psammetichus* and *Megelenophorus* stridulate by rubbing the hind femora over the epipleuron. The additional characters examined here do not entirely support those conclusions. *Megelenophorus* and *Psammetichus* agree in the configuration of the spiculum gastrale (Figs. 127, 130), which has large basal arms, but differ in the form of the internal female tract (Figs. 128, 131). In *Megelenophorus* the tract has fasciculate spermathecae, typical of the asidine clade. In *Psammetichus* the spermathecal arrangement is serial, as in the eurymetopine clade, and the accessory gland is very short. *Psammetichus* always joins the asidine clade in a relatively basal position, and, with Pimeliini as out-group, joins Nyctoporini and Cryptoglossini in a small clade at the base of the tentyriine-eurymetopine lineage. Thus, its cladistic position must be considered problematic.

Elenophorus differs from both *Megelenophorus* and Akidini in the form of the ovipositor (Fig. 123) and especially in the shape of the spiculum (Fig. 124), which has a slight radial basal expansion without distinct arms. The three synapomorphies linking *Elenophorus* and *Megelenophorus* all show much homoplasy. Consequently, the relationship between these two must remain tentative, at least until additional Akidini (especially species of the phenetically similar *Cyphogenia*) can be compared.

Two small sub-clades, Anepsiini plus *Anchomma* and Cryptoglossini plus Nyctoporini, join the asidine clade when *Zolodinus* or Belopini is declared as out-group. When HYPO or Pimeliini is out-group both appear as isolated doublets at the base of the combined asidine + eurymetopine + tentyriine clades. Anepsiini have the spermathecae serially arranged on the accessory gland duct (Char. 67: 4; Figs. 116, 119) as in the eurymetopine clade, but lack the specialized eurymetopine mouthparts, and have a very different ovipositor configuration and spiculum shape (Figs. 115, 118). *Anchomma,* originally included in Colydiidae, then in Stenosini (Doyen and

Lawrence, 1979) always clusters with Anepsiini, with which it shares all important synapomorphies. These taxa are excluded from the stenosine clade, which they resemble in their unspecialized mouthparts and reduced ovipositor, by several characters, such as the internally closed forecoxal cavities, (Char. 30: 3), the primitively open mesocoxal cavities (Char. 34: 1) and the serial arrangement of spermathecae.

Cryptoglossini and Nyctoporini have the spermathecae serially arranged (67: 4) and located on the attenuate apex of the bursa rather than on the accessory gland duct (Figs. 109, 113, 122). They lack the specialized mouthpart enclosure of Eurymetopini, have very different ovipositors and spicula (Figs. 107–112; 120–121) and have the asidine type of procoxal closure (Char. 30: 3). As discussed above under "Limits of Pimeliinae," *Ammophorus* properly belongs in Scotobiini, leaving Nyctoporini monogeneric. Cryptoglossini is likewise a small, uniform group, restricted to North America and northern MesoAmerica. Despite their similarities, Nyctoporini and Cryptoglossini differ strongly in such features as gonostyle size (Char. 50), spiculum size and shape (55, 63; Figs. 108, 112, 121) and metendosternite form (41), and certainly warrant status as separate tribes.

Because of their confusing patterns of synapomorphies neither Cryptoglossini, Nyctoporini nor Anepsiini can be accommodated in the major clades and are best considered as relatively plesiomorphic derivatives as in Fig. 209.

The remaining members of the asidine clade occupy stable positions across all the cladograms. The South American tribes (Praocini, etc.) always bear a sister group relationship to the remainder of the lineage, which is North and MesoAmerican with the exception of Asidini. Branchini phenetically resemble some Praocini and Nycteliini as much as Asidini, but unquestionably are close to the latter (Stem 33 in Fig. 209 is supported by four synapomorphies; stem 31 by four). In particular, both Asidini and Branchini lack the tentorial bridge (0: 2). Doyen (1972) included Branchini in Coniontini. In retrospect it is apparent that the similarities to Coniontini are plesiomorphies. Branchini, which number only three genera and about a dozen species, could be merged with Asidini, but that tribe is well supported by at least four synapomorphies (Figs. 209, 211; stems 34 and 33, respectively). In addition all genera of Branchini share an apomorphy of the ovipositor (Char. 61: 3; Fig. 137) which is never present in Asidini. For these reasons Branchini is here recognized as a distinct tribe.

Craniotini (with the single genus *Craniotus*) is included in Tentyriinae (=tentyriine-eurymetopine clade) by Gebien (1937) and Leng (1920). Its very close relationship to Asidini is irrefutable, and Craniotini should be placed in synonymy as detailed by Aalbu and Doyen (in prep.). The sister status of *Craniotus* and South African Asidini is unexpected and difficult to explain. Craniotini and African Asidini share two synapomorphies, sternal closure of the mesocoxal cavities (34: 2) and shortening of the dorsal arm of the mesendosternite (42: 1). The former is an unusual character which usually occurs in tenebrionids of small body size; the latter is strongly homoplastic in the present data set. The sister group (North and South American plus Mediterranean Asidini) is supported by three synapomorphies, but all are relatively homoplastic. These characters need to be examined in a much broader representation of genera, which will probably show that *Craniotus* is derived from the North American Asidini.

The sub-clade of South American tribes (Praocini, etc., stem 32) is supported by

two synapomorphies (24: 1 and 40: 2). The former (mentum and prementum subequal in width) is a reversal; the latter (metendosternite arms fused with mesocoxal inflexions) also occurs in some Coniontini and Asidini. The relatively plesiomorphic nature of these tribes is particularly evident in *Gyriosomus*, in which the elytral-abdominal joint is of the open tongue and groove type found otherwise in flighted species (Char. 79: 2; Fig. 205). In contrast, the internal female tract of *Gyriosomus* is derived (Fig. 132) though clearly of the asidine type.

Eurymetopine and Tentyriine Clades. These two clades consistently cluster as sisters with Cnemodini as an outlier, regardless of out-group. The entire assemblage, including Cnemodini is defined by six or seven synapomorphies (Fig. 209, stem 44; Fig. 211, stem 4), and four to six additional synapomorphies define the Eurymetopini plus Tentyriini (less Cnemodini) depending on the out-group. The most important of these are the characters describing the enclosure of the maxillary bases (16: 4; 20: 2; 22: 1; 25: 2). Another character which differentiates this clade from the asidine group of tribes, the style of closure of the procoxal cavities (30: 1; Fig. 32), occurs earlier in the cladogram (stem 40 in Fig. 209). Another distinguishing feature, the presence of dorso-basal mandibular lobes which clasp the labrum (9: 2; 11: 2), is probably a primitive feature of this clade, but occurs sporadically and is of limited diagnostic value.

In contrast, fewer characters, principally features of the ovipositor and internal female reproductive tract, differentiate the eurymetopine and tentyriine clades. Most notably, the form of the internal tract is very different. In Eurymetopini and related tribes the spermathecae arise serially from the base of the accessory gland duct (Figs. 178–180; 183, 184). In the tentyriine group the apex of the bursa is attenuate and often divided into several lobes, (Figs. 195–197), but discrete spermathecae are absent. In the tentyriine group the spiculum ventrale has well developed basal arms (Fig. 203), whereas, in the eurymetopine group the arms are lacking altogether (Figs. 174, 177). The South American tribes Evaniosomini, Thinobatini and Trilobocarini, which do not fit easily into this dichotomy, are discussed at greater length below.

Both the eurymetopine and tentyriine groups are large and morphologically diverse, with much parallelism in specialized body forms. In both groups the more primitive species are winged and in catalogs are included in the same tribe, Epitragini. Other (flightless) genera are adapted for life on or in sand (e.g., *Edrotes, Cryptadius, Catomulus, Oxycara*), with globular bodies and modified forelegs. Another distinctive body form is waisted with long slender legs (e.g., *Triorophus, Tentyria*). Such similarities and parallel variation led Koch (1955) to suggest that the New World tribes should be combined under Tentyriini. The results presented here show definitively that the New and Old World lineages are separate, although several of the New World tribes do not merit separate recognition.

A less tractable problem relates to the validity of the relationship of the eurymetopine and tentyriine groups. Despite their high degree of similarity in various features discussed above and their adjacent position in the cladograms, the major differences in configuration of their internal female tracts do not suggest a close relationship. Moreover, no intermediate configurations exist, and it is difficult to envision how one configuration might have become changed into the other. Rather, the eurymetopine system seems obviously related to the arrangement in Cnemodini and Vacronini, while the tentyriine system is similar to the type present in some Stenosini

(e.g., *Grammicus*) or Zophosini (e.g., *Zophosis testudinatus*). If the female tract configurations were considered the defining character, then the similarities in mouthparts, coxal closure and larval body form would have to be attributed to convergence. Related to this problem is the phyletic position of Evaniosomini, Thinobatini and Trilobocarini (discussed below), which have unusual configurations of the female tract not easily derivable from either the eurymetopine or tentyriine group. The cladogram results are accepted as definitive for the present, but the eurymetopine-tentyriine relationship deserves additional study.

The most primitive tribe of the eurymetopine clade is Epitragini. Most Epitragini are winged; all are distinguished from the remaining eurymetopine tribes by the sclerotized and pigmented common duct to which the accessory gland and spermathecae attach (70: 3; Figs. 165, 168–171) and by the configuration of the metendosternite arms (41: 5). The remaining eurymetopine clade is defined by two or three synapomorphies, depending on out-group, but these are subject to high levels of homoplasy and not very convincing. The same is true of the remaining dichotomies defining the eurymetopine tribes (stems 49–52 in Fig. 209), where the synapomorphies involve either loss of wings and concommitant features or characters which are variable within tribes. In particular the use of epistomal configuration and presence or absence or dorso-basal mandibular cusps as tribal characters is unjustified. The epistomum is produced anterad as a prominent lobe in Evaniosomini, Trimytini, Triorophini and Trientomini, but is also developed in many Tentyriini and Eurymetopini. Many genera are intermediate in development of the epistomal lobe, and it may vary considerably in size among closely related species (e.g., *Chilometopon*: Doyen, 1982; *Telabis*: Casey, 1907: 318). The development of dorso-basal mandibular cusps is generally correlated with presence of the epistomal lobe, but many genera with undeveloped epistoma have large mandibular cusps. Of the eurymetopine tribes only Edrotini, which is monogeneric and strongly psammophilous, is easily defined. Triorophini, Auchmobiini, Trientomini, Trimytini and Eurymetopini show morphological intergradation, and tribal assignments of such genera as *Somias, Mencheres* and *Posides* appear to be more or less arbitrary. The above tribes should all be combined under Eurymetopini Casey. With this change Eurymetopini and Tentyriini will be approximately equivalent in range of morphological and ecological variation.

Cnemodini Casey, classified near Eurymetopini in catalogs, differs from typical eurymetopine tribes in ovipositor form (Fig. 152; coxites almost as long as paraprocts; apical coxite lobes explanate, upturned), and in configuration of the internal female tract (gland short, compact), and spiculum (Fig. 153; basal arms present). The ovipositor form is similar to that of *Salax* and *Trilobocara* (Figs. 154, 162) and the internal tract is similar to that of the former. *Salax* and *Trilobocara* also have spicula with well developed basal arms (Figs. 156, 163), longer than those of *Cnemodinus*. Various other features of *Cnemodinus* are autapomorphic. For example, the tentorial bridge is absent; the aedeagus and spiculum gastrale are extremely large in relation to body size extending at rest into the metathorax, where they are canted to the right. The median lobe has an unusual, vertically bifurcate apex and the external plates of the spiculum are large, sclerotized and melanized. The position of Cnemodini as an outlier to the combined eurymetopine plus tentyriine clades is due to the lack of dorsal mandibular cusps (Chars. 9: 2; 11: 2). As mentioned above the cusps are

sporadically present throughout both eurymetopine and tentyriine lineages, and were coded as primitively present for both. The absence of cusps in Cnemodini could well be secondary, and changing these two characters causes it to cluster just basal to *Salax*. The position of the latter is discussed at length below. *Salax* and *Cnemodinus* differ strongly in labral and mandibular structure, and Cnemodini should continue to be recognized as a distinct tribe for now.

Ambigatus Fairmaire and *Achanius* (treated as subgenera by Kulzer, 1950) are included in catalogs in Evaniosomini, which they phenetically resemble in having slender, elongate bodies. Most species agree closely with Eurymetopini in structure of the internal female reproductive tract (Figs. 179, 180) and spiculum. The former, especially, is strongly differentiated in Evaniosomini. *Ambigatus* and *Achanius* also lack the specialized mandibles of Evaniosomini (Fig. 14). Both taxa should be transferred to Eurymetopini.

The eurymetopine clade occurs almost exclusively in the New World, but in *Ascelosodis,* from the southern Himalayan region, both the internal female tract (Fig. 188) and the spiculum are of the eurymetopine type. In terms of other morphological features *Ascelosodis* agrees with the more generalized Eurymetopini. Probably all species of *Ascelosodis* will prove to be Eurymetopini, and it seems likely that some other eastern Asian genera of Tentyriini may also be Eurymetopini.

The tentyriine clade includes two major Old World tribes, Adesmiini and Tentyriini, which share all important features and are clearly sister taxa. Only one or two synapomophies shared by the two groups of Tentyriini are absent in Adesmiini, and both are subject to much homoplasy. The more derived genera of Adesmiini are differentiated from Tentyriini by several features. For example, the posterior tentorial arms extend as low ridges to the submentum (6: 2); the anterior margin of the mentum is deeply incised (26: 3); the metendosternite arms are fused with the mesocoxal inflexions (40: 2); the metacoxae are widely separated and much more broadly oval than in Tentyriini (45, 46). In primitive adesmiine genera (e.g., *Alogenius, Epiphysa*; Penrith, 1986b), however, these derived states are often absent. In other cases the derived state also occurs in some derived Tentyriini. Conversely, Adesmiini are primitive regarding enclosure of the maxillary bases (Char. 16), but *Cauricara* has the derived state which is typical of Tentyriini. Most notably, parallel patterns of variation occur in configuration of the internal female reproductive tracts of Adesmiini and Tentyriini (Figs. 196 and 201; 195 and 199). Adesmiini seem to form a single lineage, distinctive in their larger size and generally diurnal habits. Determination of whether tribal recognition of Adesmiini leaves Tentyriini paraphyletic, however, will require a more extensive analysis of tentyriine genera.

The remaining taxa which appear in the tentyriine clade all occur in southern or western South America. *Salax* and *Trilobocara* were treated separately because the aggregate of their characters clearly differentiated them from Trimytini, where they are classified in catalogs. *Achanius* and *Ambigatus,* included in Evaniosomini in catalogs properly belong in Eurymetopini, as discussed above.

Evaniosomini comprise a small group of genera characterized by having compact, locular spermathecae (Char. 65: 2, 68: 4; Figs. 160, 161) rather than the tubular type of Eurymetopini. Thinobatini have the apex of the bursa tapering, smooth and rigid (Fig. 175), similar at least superficially to Tentyriini, but lacking the accessory gland altogether. These structures resemble the spermathecae of Tentyriinae in being poorly

differentiated from the bursa, and received the same numerical code. This is the primary character responsible for their location in the tentyriine clade. However, the obvious differences in spermathecal structure suggest that the three arrangements have arisen independently. The synapomorphies linking Evaniosomini and Thinobatini are primitive (reversals on the cladograms), and these two are probably not very closely related. Besides the obvious spermathecal differences, in Evaniosomini the spiculum ventrale is deeply forked at the base (Fig. 159), whereas in *Thinobatis* it lacks basal branches (Fig. 167), as in the eurymetopine clade.

Salax Guérin and *Trilobocara* Solier both have specialized ovipositors with the apical coxite lobes sclerotized, explanate and upcurved (Figs. 154, 155, 162). The spicula are deeply forked at the base (Figs. 156, 163). In the structure of the female tract, however, they are divergent (Figs. 157, 164) and they also differ strongly in the shape of the mandibles and labra. Surprisingly both are fully winged, a condition belied by their stout bodies and relatively short metasterna. These genera fit only very uncomfortably in the tentyriine clade, nor could they be included easily in any existing tribes of the eurymetopine clade. Lacordaire (1859) proposed Trilobocarides for this group, and Trilobocarini should be resurrected to contain *Trilobocara, Salax, Megalophrys* Waterhouse, *Eremoecus* Lacordaire, and *Derosalax* Gebien. *Orthonychius* Gebien is almost certainly synonymous with *Trilobocara*. Evaniosomini should contain *Evaniosomus* Guérin, *Aryenis* Bates, *Evelina* Thomson, *Melaphorus* Guérin, and probably *Chorasmius* Bates, which I have not examined. *Melaphorus* appears under Triorophini in the Gebien (1937) catalog, but was placed in Evaniosomini by Peña (1966). Thinobatini should contain *Thinobatis* Eschscholtz and probably *Cordibates* Kulzer, which I have not dissected. *Pseudothinobatis* has the female tract, ovipositor and spiculum as in Epitragini, to which it is here transferred.

These South American genera and others such as *Psammetichus, Megelenophorus, Aspidolobus* and *Hypselops* display many primitive or aberrant features and need much further study. Association of immatures could be especially valuable for this group.

Miscellaneous Isolated Taxa (Vacronini, Lachnogyiini, Caenocrypticini, *Boromorphus*). These taxa either do not belong to the major lineages discussed above or occupy unstable positions.

Vacronini appears as an outlier to the combined eurymetopine and tentyriine clades where it clusters with *Zolodinus* and *Lixionica* and sometimes with *Falsomycterus*. Only when *Zolodinus* is declared as out-group does Vacronini assume a more basal position on the cladogram (Fig. 211). The relationships of the former genera were discussed at some length earlier, and only Vacronini is considered here.

The internal female reproductive tracts of *Alaephus* and *Eupsophulus* (Figs. 147, 150) are both of the eurymetopine configuration with serially arranged spermathecae. They differ from the eurymetopine tribes in both spiculum shape (Fig. 149) and ovipositor configuration (Figs. 146, 148), however, as well as in having completely exposed maxillary bases and internally open procoxal cavities. All Vacronini are fully winged. Vacronini is best considered an early derivative of the eurymetopine-tentyriine clade. *Lixionica* is tentatively included here, pending discovery of its larva.

The cladistic positions of *Lachnogya* and *Boromorphus* change drastically, depending on out-group. The female tract of *Lachnogya* has multiple, serially arranged spermathecae, as in Vacronini, but the specialized ovipositor is very different and

the procoxal cavities are internally closed (30: 1). The wings have a strong subcubital fleck and a jugal incision near the hind basal margin. *Boromorphus* has a primitive ovipositor with four distinct coxite lobes and large, apical gonostyli (Fig. 72). The internal tract has a fascicle of four or five short, thin spermathecal tubes attached to the bursa at the base of the gland (Fig. 74). The procoxal cavities are internally closed (30: 1). Both these taxa require tribal recognition, but their relationships cannot be more closely specified at present. I have examined only *Lachnogya squamosa* Menetries and *Boromorphus tagenoides* Lucas. Additional comparisons and especially association of larvae are needed.

Caenocrypticini (Koch, 1958) comprises a small group of genera in southern Africa and *Caenocrypticoides* Kaszab (1969) from the Andean region of South America. Only *Vernayella* represents the African group in this study; *Caenocrypticoides* was examined subsequently and is briefly discussed below. The internal female tract of *Vernayella* has a constricted bursa and small, subspherical accessory gland without separate spermatheca (Fig. 77). This arrangement is similar only to that of some Cnemeplatiini and Stenosini (e.g., *Lepidocnemeplatia, Grammicus*). The maxillary bases are exposed, the procoxal cavities are internally closed (30: 3) and the mesocoxal cavities closed by the sternites (34: 2). The ovipositor has the paraprocts and coxites subequal, with the minute gonstyli terminal (Fig. 75). The spiculum (Fig. 76) lacks basal arms. The most unusual feature of these small beetles is the closure of the metacoxal cavities; the metepimeron is exposed posteriorly as a very broad lobe, strongly interlocked with the adjacent abdominal sternite, so that the pterothorax and abdomen form an integral unit (Fig. 37). Analogous interlocking occurs in Cryptochilini and Cnemeplatiini, where the transversely shortened coxae allow the abdominal sternite to interlock with the metasternum.

Caenocrypticoides differs from *Vernayella* in internal tract configuration, having a single, coiled spermathecal duct attaching to the narrowed bursa near the gland base. The spiculum has short but distinct basal arms. The metacoxal closure is of the same form as in *Vernayella,* however, and this is their strongest synapomorphy.

Caenocrypticini display a confusing combination of primitive and specialized characters shared with various clades. The larva of *Vernayella* (Endrody-Younga and Doyen, in prep.) has mandibles with an ectal membranous patch, enlarged forelegs and a moderately large tenth sternite. Its most peculiar feature is the minute, apparently closed spiracles. A closed tracheal system was described in *Stenosus* and *Dichillus* by Keleinikova (1976). Because of the larval similarities Caenocrypticini is perhaps best considered as a derivative of the stenosine clade, but more genera clearly need to be examined. *Caenocrypticoides,* based primarily on the metasternal-abdominal interlocking mechanism. appears to be a valid member of this tribe, which is one of only a few pimeliine higher taxa showing vicariance between South America and Africa.

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APPENDIX I

Tribes and genera from which the data matrix used in cladistic analyses was derived. Placement of genera within tribes is according to the arrangement of Gebien (1938–1942); tribes and genera are arranged alphabetically.

Adesmiini: *Adesmia, Alogenius, Cauricara, Epiphysa, Metriopus, Onymacris, Physadesmia, Renatiella*
Akidini: *Akis, Morica*
Anepsiini: *Anepsius, Batulius, Batuliomorpha*
Araeoschizini: *Araeoschizus*
Asidini: *Asida, Asidina, Asidopsis, Cardigenius, Heterasida, Machla, Microschatia; Pseudomachla, Scotinus, Ucalegon*
Auchmobiini: *Auchmobius*
Belopini: *Adelonia, Belopus, Rhypasma*
Branchini: *Anectus, Branchus, Oxinthas*
Caenocrypticini: *Caenocrypticoides, Vernayella*
Calognathini: *Calognathus*
Ceratanisini: *Ceratanisus*
Cnemeplatiini: *Actizeta, Alaudes, Lepidocnemeplatia, Thorictosoma*
Cnemodini: *Cnemodinus*
Coniontini: *Coelus, Coniontis* (including *Coelotaxis, Coniontides*), *Conisattus, Eusattus*
Craniotini: *Craniotus*
Cryptochilini: *Cryptochile, Horatoma, Pachynoteles*
Cryptoglossini: *Centrioptera, Cryptoglossa*

Edrotini: *Edrotes*
Elenophorini: *Elenophorus, Megelenophorus, Psammetichus*
Epitragini: *Bothrotes, Cyrtomius, Epitragus, Hypselops, Lobometopon, Nyctopetus, Omopheres, Phegonius, Stictoderia*
Erodiini: *Apentanodes, Erodius, Spyrathus*
Eurychorini: *Adelostoma, Eurychora, Herpsis, Lepidochora, Stips*
Eurymetopini: *Ascelosodis, Arthroconus, Cryptadius, Emmenastus, Melanastus, Mencheres, Metaponium, Stictodera*
Evaniosomini: *Achanius, Ambigatus, Aryennis, Evaniosomus, Melaphorus*
Falsomycterini: *Falsomycterus, Pteroctenus*
Lachnogyiini: *Lachnogyia*
Molurini: *Brinckia, Moluris, Phligra, Phrynocolus, Somaticus, Uniungulum*
Nycteliini: *Entomochilus, Entomoderes, Epipedonota, Gyriosomus, Nyctelia*
Nyctoporini: *Nyctoporis*
Physogasterini: *Physogaster*
Pimeliini: *Lasostola, Ocnera, Pimelia, Sternoplax*
Platyopini: *Platyope*
Praocini: *Platestes, Praocis*
Sepidiini: *Sepidium*
Stenosini: *Ethas, Grammicus, Stenosus*
Tentyriini: *Anatolica, Ascelosodis, Asphaltesthes, Catomulus, Derosphaerius, Epitrichia, Hegeter, Himatismus, Mesostena, Microderopsis, Nerina, Oxycara, Pachychila, Rhytinotia, Scelosodis, Stenosida, Scythis, Tentyria*
Thinobatini: *Pseudothinobatis, Thinobatis*
Trientomini: *Trientoma*
Trimytini: *Chilometopon, Salax, Trilobocara, Trimytis*
Triorophini: *Stibia, Triorophus, Troglogenion*
Typhlusechini: *Typhlusechus*
Vacronini: *Alaephus, Eupsophulus*
Vansoniini: *Vansonium*
Zolodinini: *Zolodinus*
Zophosini: *Zophosis* (S.G. *Calosis, Cerosis, Prodactylus, Zophosis*)
Unplaced genera: *Boromorphus, Lixionica, Idisia*

APPENDIX II

Brief descriptions of characters and character states. Primitive states designated (p); derived states designated (d), (d_1), etc. Characters for which the derived states were not ordered are marked with asterisks.

0. Tentorium, bridge: 1. Present (p); 2. Absent or incomplete (d).
1. Tentorium, bridge position: 1. Anterad or in middle of tentorium (Fig. 10) (p); 2. Posterad near occipital foramen (Fig. 11) (d).
2. Tentorium, bridge structure: 1. Slender, subcylindrical in cross section (or absent) (p); 2. Stout, flattened in cross section (d).
3. Tentorium, size: 1. $\geq$½ length gula (p); 2. $\leq$⅓ length gula (d).
4. Tentorium, position: 1. In posterior half of gular region (p); 2. In middle of gular region (d).

5. Tentorium, configuration of bridge: 1. Looped or strongly arched (Figs. 2, 3, Doyen and Tschinkel, 1982) (d_1); 2. Straight or slightly arched (Fig. 11) (p); 3. Angulately bent anterad in middle, or with anteromedial process (Fig. 10) (d_2).
6. Tentorium, configuration: 1. Posterior arms remote from submentum (p); 2. Posterior arms extending as separate ridges to submentum (d_1); 3. Ridges confluent behind submentum (Fig. 11) (d_2).
7. Tentorium, posterior foramen: 1. Broadly open (Figs. 10, 11) (p); 2. Narrowed or closed (Fig. 2; Doyen, 1987) (d).
8. Endocranial septum: 1. Absent (p); 2. Present (d).
9. Right mandible, dorsolateral tooth: 1. Absent (Figs. 13–16) (p); 2. Present, small (d_1); 3. Present, large (Fig. 12) (d_2).
10. Left mandible, dorsolateral tooth: 1. Absent (p); 2. Present, small (d_1); 3. Present, large (Fig. 12) (d_2).
11. Mandibles, position of dorsal tooth: 1. On apical half of mandible (d_1); 2. Absent (p); 3. On basal half of mandible (d_2).
12. Mandible, ventral fossa: 1. Absent (p); 2. Present (Fig. 14) (d).
13. Mandible, prostheca: 1. Present (p); 2. Absent (Fig. 15) (d).
14.* Mandible, form: 1. Retinaculum and mola approximate; prostheca narrow, transverse (or absent) (Fig. 15) (d_1); 2. Retinaculum, mola and prostheca "normal" (Figs. 12–14) (p); 3. Mola reduced, attenuate (Fig. 16) (d_2).
15. Maxilla, lacinia: 1. Without uncus (d_1); 2. With single, simple uncus (p); 3. With bifid or double uncus (d_2).
16. Maxilla, articulation of cardo: 1. Concealed in socket in submentum (Fig. 22) (d_1); 2. Exposed laterad of submentum (Fig. 21) (p); 3. Concealed in socket overlain by subgena (Fig. 23) (d_2); 4. Overlain by both submentum and subgena (Figs. 24, 25) (d_3).
17. Postmental region, configuration: 1. Flat, even with subgenae (Figs. 17, 18) (p); 2. Elevated along oral foramen (d_1) (Fig. 19); 3. Elevated along foramen and invaginated behind (Fig. 20) (d_2).
18. Submentum, form: 1. Continuous with gula posteriorly (Figs. 21, 25) (d_1); 2. Distinct sclerite (Figs. 22–24) (p); 3. Reduced, transverse, internal (d_2).
19. Submentum, configuration of anterior edge: 1. Pedicellate, produced (Figs. 24, 25) (p); 2. Not produced (Figs. 22, 23) (d).
20. Subgenal processes: 1. Remote from submentum and mentum (Fig. 21) (p); 2. Contiguous with submentum and at least base of mentum (Figs. 22–25) (d).
21. Submental-gular articulation: 1. Submentum adnate to gula, immovable (p); 2. Submentum with slight flexibility against gula (d).
22. Prementum, structure: 1. Entirely membranous (d_1); 2. Membranous with basal sclerites (p); 3. Entirely sclerotized (d_2).
23. Prementum, position: 1. Entirely exposed anterad mentum; 2. Base concealed beneath mentum (Fig. 28) (d_1); 3. Nearly or entirely concealed beneath mentum (Fig. 29) (d_2).
24. Prementum, relative size. 1. Mentum and submentum subequal in width (Fig. 28) (p); 2. Mentum expanded, much broader than prementum (Fig. 29) (d).

25. Mentum, shape: 1. Subquadrate (Figs. 21, 24) (p); 2. Much broader than long (Figs. 23, 25) (d).
26.* Mentum, anterior margin: 1. Straight or slightly concave (Fig. 21) (p); 2. Strongly emarginate (Fig. 22) (d_1); 3. Narrowly notched (Figs. 24, 25) (d_2).
27.* Mentum, basal articulation: 1. Exposed (Figs. 17–20) (p); 2. Retracted partly beneath submentum, thickened, inflexed (Fig. 26) (d_1); 3. Concealed beneath expanded submentum (Fig. 27) (d_2).
28. Oral rim, thickening: 1. Not thickened (p); 2. Thickened behind cardo sockets (d_1); 3. Thickened behind cardo sockets and mentum (d_2).
29. Labrum, shape: 1. Subquadrate or slightly longer than wide (p); 2. Distinctly wider than long (d).
30. Procoxal cavity, internal closure: 1. Internally closed (tentyriine closure: see text and Fig. 32) (d_1); 2. Internally open (p) (Fig. 30, 31); 3. Internally closed (asidine closure, Fig. 33) (d_2).
31. Procoxal cavity, external closure. 1. Open (Fig. 30) (p); 2. Closed (Figs. 31–33) (d_1); 3. Secondarily open (d_2).
32. Procoxal cavity, internal foramen: 1. Undefined (e.g., cavities internally open; Fig. 30) (p); 2. Large, subovate (Fig. 33) (d_1); 3. Small or minute, sometimes long, very narrow (Fig. 32) (d_2).
33.* Pro-mesothoracic fusion: 1. Segments freely articulated (p); 2. Edrotine type fusion (see text) (d_1); 3. Cryptochiline type fusion (d_2); 4. Nycteliine type fusion (d_3); 5. Erodiine type fusion (d_4).
34. Mesocoxal cavity, closure: 1. By mesepimeron (Fig. 5; Doyen, 1987) (p); 2. By sternites (Figs. 36, 37) (d).
35. Mesendosternite, position: 1. Free in haemocoele (p); 2. Horizontal arm fused with anterior rim of mesosternum (d).
36. Mesendosternite, form of dorsal arm: 1. Long, slender, extending at least one third distance to elytral articulation (p); 2. Short or absent (d).
37. Mesendosternite, horizontal arm configuration: 1. Apex attenuate or horizontally flattened (p); 2. Apex expanded as vertical muscle disk (d).
38. Mesendosternite, form: 1. Horizontal portion of arm very short, often oblique (p); 2. Horizontal portion of arm at least half length of dorsal arm, often much longer (d).
39. Mesendosternite, position of dorsal arm: 1. Arising from apex of horizontal arm (or absent) (p); 2. Arising preapically on horizontal arm (d).
40. Metendosternite, form: 1. Arms free in haeomocoel (p); 2. Arms fused with mesocoxal inflections (d).
41.* Metendosternite, configuration of arms: 1. Arms free, apically attenuate (p); 2. Apically fused to mesopleuron at wing process (d_1); 3. Apically fused with mesotergum (d_2); 4. With large apical muscle disk, held against tergum by very short muscle (d_3); 5. With apical muscle disk but not approximate to tergum (d_4).
42. Metendosternite arm length: 1. Short, ending about at mesocoxal inflections (d_1); 2. Extending beyond mesocoxal inflections about half distance to tergum (p); 3. Long, reaching tergum or nearly so (d_2).
43. Metacoxal separation: 1. Coxae approximate (p); 2. Coxae separated by at least one coxal length (d).

44. Metacoxa, orientation: 1. Transverse or slightly oblique (p); 2. Oriented at about 45° from longitudinal body axis (d).
45. Metacoxa, proportions: 1. Length (distance between articulations) at least twice width (p); 2. Length less than 1.5 times width (Fig. 35) (d).
46. Metacoxa, lateral enclosure: 1. By metasternum and abdominal sternite 3 (Fig. 35) (d_1); 2. By metepisternum (Figs. 34, 37) (p); 3. By sternites and metepisternum (Figs. 36, 36a) (d_2).
47. Ovipositor, form: 1. With coxites, proctiger, paraproct and spiculum (Figs. 38, 41, 44) (p); 2. Rudimentary, proctiger, paraproct and sometimes coxites atrophied or lacking; spiculum usually absent (d).
48. Proctiger, length of ventral baculus: 1. Subequal to proctiger (Fig. 44) (p); 2. Much shorter than proctiger (Fig. 166) (d).
49. Gonostyle, position: 1. Terminal or subterminal (Figs. 38, 72) (p); 2. Markedly lateral or preterminal (Figs. 44, 51) (d).
50. Gonostyle, size: 1. Moderate or small, but distinct, digitate or pedunculate with apical seta(e) (Figs. 44, 72) (p); 2. Rudimentary or absent (Figs. 101, 107, 123) (d).
51. Coxite, lobes 3 and 4: 1. With separate sclerites (Figs. 129, 146) (p); 2. Fused (Figs. 51, 84) (d).
52. Coxite, lobe 2: 1. Separate from lobes 3 and 4 (Figs. 107, 120) (p); 2. Fused with 3 and 4 (Figs. 133, 137) (d).
53. Invagination between coxite lobes 1 and 2: 1. Absent (Figs. 60, 72) (p); 2. Present (figs. 44, 63, 129) (d).
54. Apical coxite lobe, texture: 1. Membranous (p); 2. Sclerotized (d).
55. Spiculum, length (as ratio to ovipositor length): 1. Short, $r < 0.8$ (d_1); 2. Moderate, $0.8 \leq r \leq 1.2$ (p); 3. Long, $r > 1.2$ (d_2).
56. Coxite, baculus basal lobe: 1. Transverse (Figs. 38, 44) (p); 2. Oblique (Fig. 104) (d).
57. Paraproct, extent of apicodorsal lobe: 1. Ending approximately at coxite base (p); 2. Extending ¼ to ½ length of coxite (Fig. 78) (d_1); 3. Extending about ¾ length of coxite (Fig. 104) (d_2).
58. Paraproct, position of dorsal baculus: 1. Even with ventral baculus (Figs. 101, 104) (p); 2. Extending proximad much beyond ventral baculus (Figs. 73, 84, 146) (d).
59. Paraproct length (as ratio to coxite length): 1. Proctiger short, $r < 1.2$ (d); 2. Moderate, $1.2 \leq r \leq 2.0$ (p); 3. Long, $2.0 < r \leq 3.0$ (d_2); 4. Very long, $r > 3.0$ (d_3).
60. Ovipositor length (as ratio to head length): 1. Short, $r < 1.0$ (d_1); 2. Moderate, $1.0 \leq r \leq 2.1$ (p); 3. Long, $r > 2.1$ (d_2).
61. Paraproct, extent of ventral lobe: 1. Adjacent to coxite (Fig. 133) (p); 2. Barely overlapping coxite (Fig. 144) (d_1); 3. Strongly overlapping coxite (Fig. 137) (d_2).
62. Spiculum (♀), form: 1. Paired, divergent arms only (Figs. 81, 93) (d_2); 2. Forked, with stem and arms subequal in length (Fig. 45) (d_1); 3. Forked, stem much longer than arms (Figs. 39, 48) (p); 4. Stem without arms (Figs. 167, 174) (d_3).
63. Spiculum (♀), form: 1. Arms inclined at about 45° to stem (or absent) (Figs. 45, 127) (p); 2. Arms reflexed (Figs. 105, 118) (d).

64.* Coxite, form of apical lobe: 1. Evenly attenuate, straight (Figs. 107, 137) (p); 2. Akidine type (Figs. 83, 84) (d_1); 3. Pimeliine type (Figs. 96, 97) (d_2); 4. Strongly upcurved (Figs. 67, 92, 155) (d_3); 5. Downcurved (Fig. 78) (d_4); 6. Weakly upcurved, flat (Fig. 142) (d_5).

65.* Spermatheca, form: 1. Saccate, unmodified bursa, without separate spermatheca (Figs. 49, 50) (p); 2. Differentiated spermathecal lobe(s) or tube(s) without separate connecting duct to bursa (Figs. 80, 198, 199) (d_1); 3. Spermathecal tube(s) apical on common duct (Figs. 128, 134) (d_2); 4. Spermathecal tube(s) lateral on common duct (Figs. 116, 150) (d_3).

66. Spermatheca, annulation: 1. Nonannulate (Figs. 106, 116) (p); 2. Annulate (Figs. 94, 201) (d).

67. Spermatheca, arrangement of tubes: 1. Multiple, fasciculate tubes (Figs. 86, 135) (d_1); 2. Single or few fasciculate tubes (or undifferentiated) (Figs. 80, 95) (p); 3. Few serial tubes (Figs. 119, 171) (d_2); 4. Multiple, serial tubes (Figs. 122, 179, 184) (d_3).

68. Spermathecal tubes, form: 1. Long, thin, tubular (Figs. 109, 179) (d_2); 2. Both thick and slender tubes present (Fig. 94) (d_1); 3. Short, thick (or undefined) (Figs. 43, 74, 89) (p); 4. Locular or capsular (Figs. 40, 46, 62) (d_3).

69. Spermatheca, form of common duct: 1. Undefined (Figs. 69, 71) (p); 2. Short, thick (Figs. 135, 142) (d_1); 3. Longer, slender (Figs. 125, 134) (d_2).

70. Spermatheca—accessory gland common duct, form: 1. Undefined (p); 2. Smooth, flexible, unpigmented (Figs. 140, 183) (d_1); 3. Rigid, pigmented, annulate (Figs. 165, 170) (d_2).

71. Spermathecal tube structure: 1. Tubes unbranched; 2. At least some tubes branched (d).

72. Accessory gland duct, form: 1. Straight (or undifferentiated) (Figs. 125, 128) (p); 2. Spiral (Figs. 183, 190) (d).

73. Accessory gland, size: 1. At least twice length of bursa or vagina (Fig. 86) (d_1); 2. Subequal to bursa, elongate, tubular (Figs. 49, 62) (p); 3. Shorter than bursa, often saccate (Figs. 50, 54) (d_2); 4. Absent (Fig. 92) (d_3).

74. Secondary bursa copulatrix: 1. Absent (p); 2. Present (Figs. 150, 164, 165) (d_1).

75. Spermathecal tubes, configuration: 1. Straight or slightly curved (or absent) (p); 2. Coiled or convoluted (d).

76. Accessory gland, position: 1. Lateral on bursa or vagina, remote from spermatheca (or absent) (Figs. 89, 198, 201) (p); 2. Apical near spermatheca(e) or at its base (Figs. 74, 80, 86) (d_1); 3. On spermathecal duct (Figs. 116, 134) (d_2).

77. Abdominal sternites 5 to 7, articulatory membranes: 1. Membranes exposed, external (p); 2. Membranes concealed (d).

78. Flying wings: 1. Present, functional (p); 2. Reduced, brachypterus (d_1); 3. Absent (d_2).

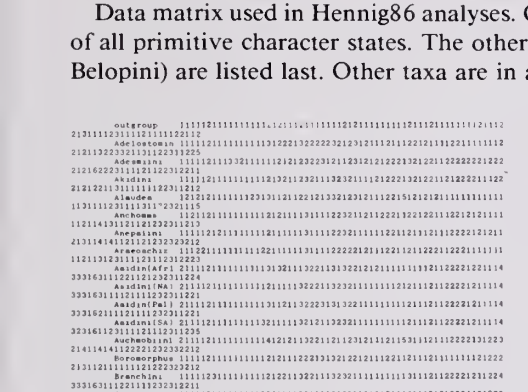
79.* Elytral-abdominal joint: 1. Enclosed tongue and groove (Fig. 207) (d_1); 2. Open trough (winged forms (Fig. 205)) (p); 3. Open tongue and groove (Fig. 206) (d_2); 4. Amplexiform coupling (Fig. 208) (d_3).

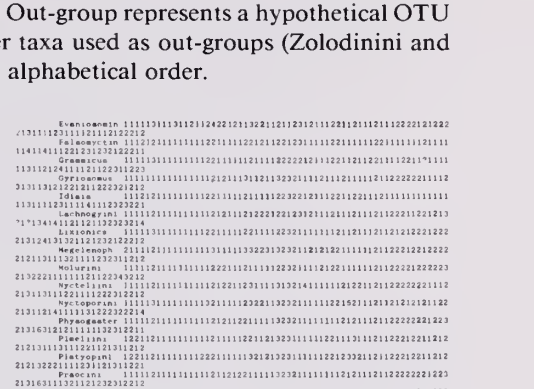
80. Abdominal laterotergites: 1. Extremely small (d_1); 2. Moderate (p); 3. Very large, at least on some segments (d_2).

81. Aedeagus, orientation: 1. Medial lobe ventral to tegmen (p); 2. Median lobe dorsal to tegmen ("inverted") (d).
82. Antennal segment number: 1. Eleven (p); 2. Ten plus reduced eleventh segment (d_1); 3. Ten (d_2).
83. Antennal form: 1. Serrate-clubbed (d_1); 2. Filiform or serrate (p); 3. Serrate-moniliform (d_2); 4. Moniliform (d_3); 5. Moniliform-clubbed (d_4).

APPENDIX III

Data matrix used in Hennig86 analyses. Out-group represents a hypothetical OTU of all primitive character states. The other taxa used as out-groups (Zolodinini and Belopini) are listed last. Other taxa are in alphabetical order.





APPENDIX IV

Number of changes of state, consistency indices and retention indices for 84 characters used in Hennig86 analyses. A. Hypothetical out-group; B. Out-group = Zolodinini; C. Out-group = Belopini (Nelsen consensus tree).

tree 3 length 743 ci 18 ri 56

character/steps/ci/ri

	0	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18
	9	5	3	3	1	9	6	2	2	8	7	5	2	2	3	19	14	7	19
A	11	20	33	33	100	22	33	50	50	25	28	20	50	50	66	10	21	28	10
	33	33	33	66	100	0	0	0	0	71	58	63	0	0	50	22	68	16	32
	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37
	11	2	3	12	17	11	9	11	4	10	7	16	5	12	5	9	1	10	7
	0	50	33	16	11	9	11	18	50	20	14	12	40	16	80	11	100	10	14
	28	94	33	67	59	56	69	18	33	71	64	72	25	79	50	65	100	18	33
	38	39	40	41	42	43	44	45	46	47	48	49	50	51	52	53	54	55	56
	4	12	10	9	20	12	2	11	4	2	1	9	7	4	11	6	8	14	4
	25	8	10	44	10	8	50	9	50	50	100	11	14	25	9	16	12	14	25
	76	59	25	37	30	21	0	28	50	75	100	65	57	57	60	76	72	42	0
	57	58	59	60	61	62	63	64	65	66	67	68	69	70	71	72	73	74	75
	12	12	14	10	2	12	1	13	19	4	22	18	11	9	3	6	16	2	7
	16	8	21	20	100	25	100	38	15	25	13	16	18	22	33	16	18	50	14
	61	59	63	57	100	57	100	57	65	50	56	69	59	74	0	16	35	0	78
	76	77	78	79	80	81	82	83											
	15	2	16	12	20	2	10	35											
	13	50	12	25	10	50	20	11											
	63	50	50	65	33	0	52	26											

APPENDIX IV Continued.

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tree 0 length 734 ci 19 ri 56
character/steps/ci/ri
   0   1   2   3   4   5   6   7   8   9  10  11  12  13  14  15  16  17  18
   9   5   3   4   1   9   6   2   2   8   7   5   2   2   3  18  14   7  19
B 11  20  33  25 100  22  33  50  50  25  28  20  50  50  66  11  21  28  10
  33  33  33  50 100   0   0   0   0  71  68  63   0   0  50  27  68  16  32

  19  20  21  22  23  24  25  26  27  28  29  30  31  32  33  34  35  36  37
  10   3   3  13  17   9  10  11   4   7   6  17   4  14   4   8   1  10   7
  10  33  33  15  11  11  10  18  50  28  16  11  50  14 100  12 100  10  14
  40  89  33  64  57  63  64  18  33  81  68  70  33  75 100  69 100  18  33

  38  39  40  41  42  43  44  45  46  47  48  49  50  51  52  53  54  55  56
   3  11  10   9  20  11   2  12   8   3   1  12   8   5  10   8  11  13   4
  33   9  10  44  10   9  50   8  12  33 100   8  12  20  10  12   9  15  25
  83  61  25  37  30  23   0  21  66  50 100  50  46  33  62  66  58  47   0

  57  58  59  60  61  62  63  64  65  66  67  68  69  70  71  72  73  74  75
  12  12  17  11   2  12   1  13  16   4  21  14  11   9   3   6  17   2   5
  16   8  17  18 100  25 100  38  18  25  14  21  18  22  33  16  17  50  20
  60  59  53  52 100  57 100  57  70  50  59  76  59  73   0  16  30   0  85

  76  77  78  79  80  81  82  83
  14   1  10  12  18   1   9  36
  14 100  20  25  11 100  22  11
  65 100  69  64  40 100  58  23

tree 0 length 761 ci 18 ri 55
character/steps/ci/ri
   0   1   2   3   4   5   6   7   8   9  10  11  12  13  14  15  16  17  18
   9   5   3   5   1   9   6   2   2   8   7   5   2   2   3  19  15   7  21
C 11  20  33  20 100  22  33  50  50  25  28  20  50  50  66  10  20  28   9
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  63 100  64  65  37   0  52  23
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THE MORPHOLOGY, NATURAL HISTORY, AND BEHAVIOR OF THE EARLY STAGES OF *MORPHO CYPRIS* (NYMPHALIDAE: MORPHINAE)—140 YEARS AFTER FORMAL RECOGNITION OF THE BUTTERFLY

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Abstract.—The morphology, natural history and behavior of *Morpho cypris* immature stages are described for the first time. The location and use of two secretory glands, one that was previously undescribed, are noted and discussed with respect to glands found in other groups of Lepidoptera. A comparison of *Morpho cypris* early stage development, behavior, defenses, and host plant use within the context of the genus *Morpho*, and the subfamily Morphinae is provided.

A survey to elect a butterfly that exemplifies the neotropics would very likely result in most ballots being cast for the genus *Morpho*—one of the most conspicuous of all butterflies. Historically these butterflies have captured the imagination of visitors to the neotropics; testimonies to this are found in accounts of the early naturalists (e.g., Bates, 1864; Belt, 1874). Today frequent references to *Morpho* are found in travel brochures and natural history articles, and they are often centerpieces for the popular butterfly houses. No one can fail to be impressed by the sight of *Morpho* butterflies because, alive or dead, they delight the imagination, and give pause for thought.

A literature inspired mainly by collectors and insect dealers treats *Morpho* butterflies as art objects. In this system the collectors want their cabinets filled with as many named specimens as possible, and it is to the advantage of dealers to offer a variety of units for sale. The collectors/dealers interested in *Morpho* found that many of the species are wide ranging and variable, and thus fertile ground for the naming of forms, aberrations, and even individual specimens. For example, the magnum opus written by the enthusiastic dealer and collector Eugene Le Moult recognizes over 70 species, and hundreds of forms of *Morpho*—at least 77 forms of which he described himself (Le Moult and Real, 1962). Perhaps the proliferation of names was good for business, but to the serious student of butterflies it was excessive. In his overview of the neotropical fauna, D'Abrera soberly recognizes 27 species of *Morpho*, and points out that Le Moult and Real's work is more of a commercial catalogue than a serious taxonomic revision (D'Abrera, 1984).

Although there is a substantial anecdotal literature, relatively little work has been published on the early stages or life cycles of *Morpho*. The work of A. Young and his colleagues has furthered our understanding of the Central American species (see Young, 1982 and included citations), while Otero (1966) has summarized natural history information on some of the South American species. Two broader systematic works that provide information relevant to *Morpho* early stages include a summary

of host plant associations (Ackery, 1988) and morphological details of caterpillars in the Morphinae (DeVries et al., 1985). However, despite their historical popularity and obvious presence in lowland tropical habitats, the early stages of most *Morpho* species remain unknown.

Morpho cypris Westwood, 1851, ranges from Nicaragua to Colombia and Venezuela occurring in rain forest habitats from sea level to about 700 m elevation. The males of *M. cypris* possess a brilliant blue structural coloration on the dorsal surface, whereas the female may either be yellowish on the dorsal surface, or have a blue coloration similar to the males. Both sexes typically utilize thermal upwellings along rivers and streams to 'float' high in the forest canopy, and thus largely elude observation or capture. The coloration and elusive habits of *M. cypris* have made it one of the most sought after butterflies in the world. Nevertheless, our understanding of the early stages of this spectacular species is confined to a few illustrations and notes (DeVries, 1987). The goals of this paper are to provide a more detailed account of early stage morphology and behavior of *M. cypris,* as well as briefly to compare our findings to other studies of *Morpho* immatures. After more than 140 years since its original description we hope that the rudimentary biology of *M. cypris* will assist students of natural history and conservation biology: 140 years into the future, there may be nothing left of these organisms and their habitats to understand.

MATERIALS AND METHODS

Observations were made on *Morpho cypris* by DeVries from 1 July to 12 November 1984 at the Sirena station, Parque Nacional Corcovado, Costa Rica located on the Pacific coast. The surrounding forest types at Sirena include: lowland primary rain forest, degraded primary forest, flood plain forest, mangrove forest, second-growth forest that has regenerated after being clear-cut, and maintained pasture. Early instars were kept in small plastic containers with tight fitting lids, and as the caterpillars matured, they were kept in plastic bags that were cleaned twice daily. All observations and rearings were done in the field at ambient temperatures. Adults, immatures, and behaviors were photographed by DeVries, and these photos were later used for drawings by Martinez. Terminology of immature morphology and chaetotaxy follows Peterson (1962) and Stehr (1987). Representative early stage material was preserved in alcohol, and these specimens, along with cast skins and adult vouchers are deposited in the collection of DeVries, and in The Natural History Museum, London. Voucher material of the host plant was deposited in the herbarium of the Museo Nacional de Costa Rica.

RESULTS

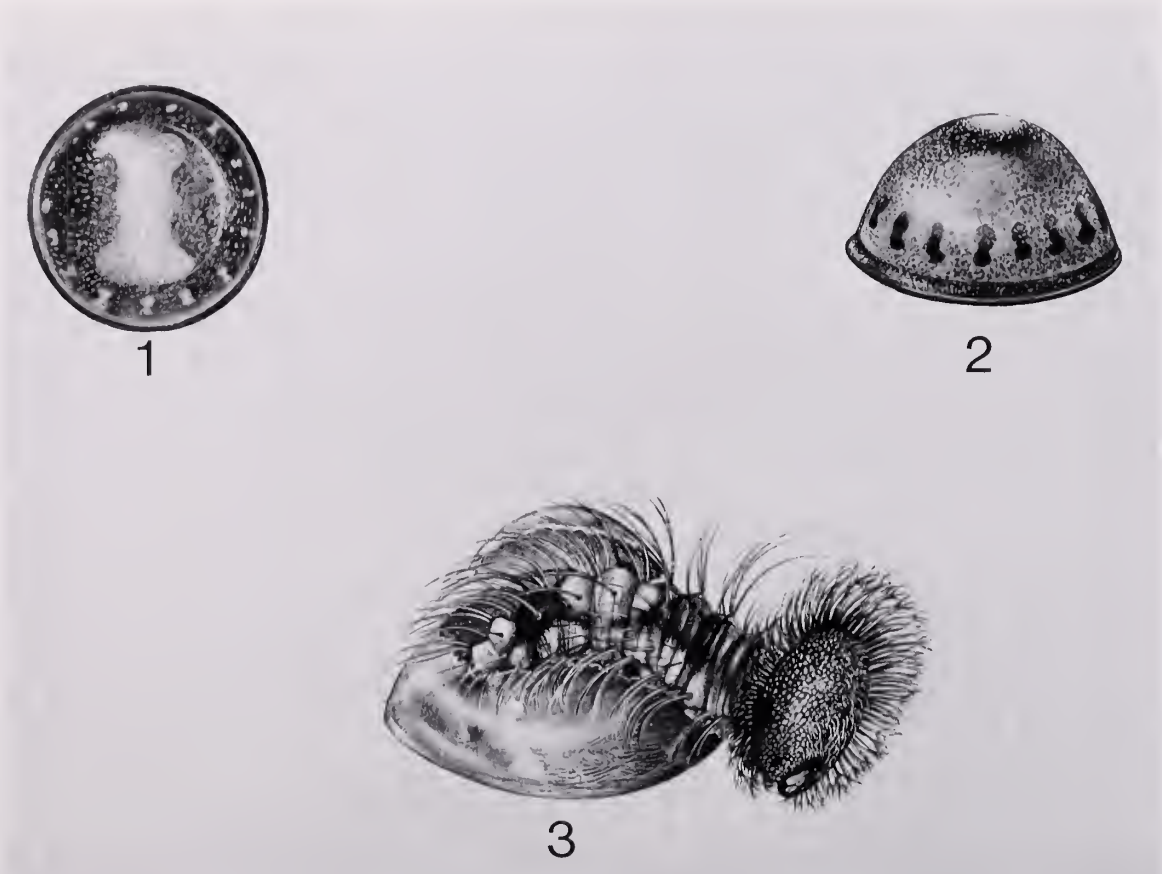
Oviposition behavior: Between 09:55 and 10:05 hours on 1 July 1984 PJD observed a female *M. cypris* (yellow form) oviposit at least 14 eggs on the leaves of a large, isolated *Inga marginata* (Fabaceae) tree that was growing in a pasture used to maintain horses. The tree was located about 25 m from the forest edge, and had a full, rounded canopy that presumably was the result of having grown in the open for at least five years. Within a few seconds after landing on the foliage, the female deposited a single egg on the dorsal surface of a leaflet, then immediately took flight, circled

the tree, landed, and repeated oviposition. There were generally 10–20 second intervals between egg depositions, and oviposition sites ranged from leaves located on the inside of the tree crown within 1.5 m of the ground to leaves 15 m above the ground on the outside of the crown. All ovipositions took place in direct, bright sunshine. The female flew about and landed on the foliage in a haphazard fashion, exhibiting none of the inspection behavior prior to oviposition seen in other butterflies, such as *Parides* or *Heliconius* (see DeVries 1987). Presumably, the rapid, haphazard oviposition behavior in *M. cypris* reflects two related traits: 1) flight speed and agility are affected by an abdomen heavily loaded with eggs, and 2) *Morpho* butterflies are palatable to vertebrate predators (Chai, 1990). When PJD later climbed the tree he was able to find only 2 of the 14 oviposition sites, despite over an hour of careful searching. The eggs are extremely cryptic, and appear similar to small galls that occurred on many of the *I. marginata* leaves.

At 10:05 the fresh, undamaged female (wing length = 80.5 mm) was captured and confined with cuttings of the host plant in a 4 × 4 m screened cage. Between 2–4 July she was induced to oviposit under artificial conditions. After being fed on fruit juices, she was held by the fore wings, allowed to flutter the hind wings, and then placed on an *I. marginata* leaf. Upon contact she typically 'tasted the leaf' by rapidly and audibly drumming on the leaf surface with the forelegs. After drumming she brought her abdomen in contact with the leaf surface, pressed the characteristic Morphinae papillae anales (see DeVries et al., 1985) tightly to the leaf surface, opened them, and usually deposited a single egg (although treated in this manner she occasionally laid 5–7 eggs sequentially). This process was repeated intermittently until the female became fatigued and refused to oviposit.

The total egg output during induced oviposition was 36 eggs on 2 July, 18 eggs on 3 July, and 5 on 4 July, yielding a total of 59 eggs, 57 of which were fertile. The female died from injuries sustained from *Solenopsis* sp. (Myrmecinae) ants that attacked her during the evening of 4 July. She weighed 1.7 grams the morning of 5 July, and an autopsy revealed 9 almost completely developed eggs plus whitish-yellow lipids in her abdomen. Had she lived, presumably this female would have continued to produce more eggs.

Egg: (Figs. 1–3)—Hemispherical, smooth, with no visible sculpturing, but with a rounded rim where base contacts leaf surface. When laid the entire egg is pale translucent yellow-green, and without markings. Within 24 hours the egg appears to contain a milky, bone shape (presumably the embryonic larva) suspended in the center (when viewed dorsally), and in lateral view there is a broken, milky row of short, irregular, vertically oriented peanut-shapes that encircle the egg slightly above the base. Within 38 hours the egg becomes semi-translucent and golden-green, the peanut-shapes turn crimson, and the dome bears a crimson circle surrounding a whitish micropyle. Nine days after being laid the chorion becomes transparent, and the red head of the larva can be seen easily at the dome of the egg (including the mandibles and stemmata), surrounded by the red and white patches of the body that is coiled around the lateral edges of the egg. Close inspection at this phase reveals that the egg contains a fluid, and a well defined air pocket between the base of the head and the body. Between 10 and 11 days after being laid the caterpillar cuts through the chorion, extrudes the mandibles, cuts the dome away in a circular fashion, then exits the egg (Fig. 3). Upon exiting the egg, first instars typically ate all of the



Figs. 1–3. Egg and hatching first instar caterpillar of *Morpho cypris*. 1. Dorsal view of egg. 2. Lateral view of egg. 3. First instar emerging from the egg.

chorion excepting the opercular dome and the base, performed a grooming behavior (see below), and did not feed for 24 hours.

First instar: (Fig. 4) *Head*—deep maroon; frons convex without setae, but bearing many pits and surface granulations; area above the frontoclypeus with a tuft of short, maroon setae that project forward; outside perimeter of head capsule with a prominent, dense corona of long, maroon setae that almost encircle head, excepting near mandibular area where setae are shorter; coronal setae curved forward and forked distally into 3–4 finer filaments; head much wider than body. *Body*—pale cream-yellow with three conspicuous, reddish-maroon rectangular patterns on dorsum, each with six filamentous arms (three per side) which extend dorsally, then downward along lateral portion of body; first maroon pattern extends from T-1 to A-1, second from A-4 to A-5 (leaving a yellow spot that will become one of two ovals in later instars), and last maroon pattern extends from A-7 to A-8; all subdorsal and lateral setae bear spurs along shafts and arise from pinaculae; abdominal setae blonde and curved to posterior; setae on T-1 and T-2 maroon-red, curve to anterior, and flow into corona of head setae; anal plate terminates in a distinct cream-yellow bifid tail.

Caterpillars fed at the leaf edges, producing deep, irregular-edged sinuses. Typically a caterpillar began at an undamaged portion of a leaf each time it began a feeding bout. The caterpillars fed intermittently during 24 hour periods, and rested on the host plant leaves. Premolt duration from first to second instar = 24 hours. Total first instar duration 17.7 days (N = 20, SE = 0.424).

Second instar: (Fig. 5) *Head*—deep maroon, wider than body; frons with a sparse covering of setae interspersed with surface pits and granulations; ecdysial lines and mandibular area with short, downy white setae; maroon coronal setae denser, more robust, and interspersed with stiff, darker maroon (almost black) setae along perimeter of head; all coronal setae are distally plumose and curved forward. *Body*—bright, chrome yellow with the three dorsal, rectangular patterns very dark maroon (almost black); pattern on T-1 to A-1 has narrowed considerably, with its posterior arms fusing with anterior arms of pattern on A-4 to A-5 to embrace a yellow oval; center of maroon pattern on A-5 bears two dense tufts of crimson subdorsal setae that curve to posterior, and these tufts persist in all subsequent instars; posterior arms of dorsal rectangular pattern on A-4 to A-5 almost join anterior arms of pattern on A-7 to A-8, and begin to define a yellow oval; all setae are denser and more obviously spurred on shafts; lateral setae now within tufts of long and short setae; subdorsal setae on T-1 and T-2 obviously spurred, flow into coronal setae, and now pale maroon to blonde; bifid tail on A-10 red with short translucent setae.

Feeding behavior was similar to that described for first instars. Caterpillars fed intermittently during 24 hour periods, and rested on the host plant leaves. Premolt duration from second to third instar = 24–36 hours. Total second instar duration 16.9 days (N = 13, SE = 0.265).

Third instar: (Fig. 6) *Head*—similar to second instar, wider than body but slightly more proportionate and more evenly covered with maroon and black setae; setae along the ecdysial lines now gray, and include wider lines of gray setae on either side of ecdysial lines. *Body*—yellow with a tinge of green; arms of dark maroon patterns are prominent and fused, defining the two dorsal ovals; red bifid tail on A-10 slightly more prominent.

Feeding behavior now included removing most of one side of an *Inga marginata*

leaflet, leaving a few irregular lobes near the mid-vein. Caterpillars fed intermittently throughout 24 hour periods, and rested on the host plant leaves. Premolt duration from third to fourth instar = 36 to 48 hours. Total third instar duration 19.3 days (N = 9, SE = 0.33).

Fourth instar: (Fig. 7) *Head*—similar to third instar, but slightly wider than body, with setae covering the entire head; setae longest along perimeter of head, shorter on frons, and shortest near mandibles; gray setae along ecdysial lines, and on either side wider, more diffuse, and generally more conspicuous, especially on frons. *Body*—overall color now distinctly yellow-green (especially dorsal ovals); dark maroon patterns inset with fine filigree cream and pale maroon patterns; A-1 with two tufts of short, erect subdorsal setae that define the location of grooming gland (see below); subdorsal setal tufts on A-5 are now bicolored, composed of longer white anterior setae, and shorter red posterior setae; posterior edge of maroon pattern on A-5 now contains a small, roundly triangular, yellow-green spot (that will persist in subsequent instar) which weakly joins posterior oval; A-8 now with two small, subdorsal tufts of setae that curve to posterior and colored as in tufts on A-5; bifid tail on A-10 now deep maroon with reddish setae.

Feeding behavior was similar to that described for third instars, except the caterpillar can now devour an entire leaflet. Feeding typically occurred at dawn and dusk, but caterpillars occasionally fed during the day. This instar remained on the host plant leaves when not feeding. Premolt duration from fourth to fifth instar = 36 to 48 hours. Total fourth instar duration 35.7 days (N = 7; SE = 0.286).

Fifth instar, first color phase: (Fig. 8) *Head*—slightly wider than body; dominant coronal setae gray interspersed with reddish-brown, all setae of uniform length; setae along ecdysial lines and frons white, shorter and denser than coronal setae. *Body*—overall a deep banana yellow, without green overcast as in previous instars; dorsal patterns dark red-brown, completely framing two ovals, and extensively marbled with cream-colored filigree; center of each oval bearing a barely discernible filigree of two elongate, jagged rectangles separated by dorsal line; in addition to subdorsal tufts on A-1 and A-5, now A-2 with subdorsal tufts straddling the anterior section of anterior oval, A-4 with pair of subdorsal tufts that straddle posterior section of anterior oval, A-7 with pair of subdorsal tufts that straddle posterior section of posterior oval, and A-8 with a pair of subdorsal tufts; these four pairs of newly developed subdorsal tufts are short, maroon-red in center with some white on anterior portion, and curved to posterior; longest subdorsal setae are denser, obviously spurred, and curve to posterior; lateral setae are blonde to white, obviously spurred, and completely obscure legs; subdorsal setae on T-1 and T-2 flowing into corona now maroon and gray; bifid tail on A-10 deep maroon with maroon setae.

After molting to the fifth instar the caterpillar began to steadily lose its deep yellow color, and became more and more cryptic. Between days six and eight of this instar the caterpillar completed its extraordinary change in appearance.

Fifth instar, second color phase: (Fig. 9) *Head*—same width as body; dominant coronal setae grayer than previously; head capsule itself faded to red-brown, showing only a blush of maroon. *Body*—overall coloration gives the impression of yellowed and grizzled antique ivory covered with an overlay of the fine scrimshaw, including both dorsal ovals which are filled with a complex pattern of black elongate rectangles and tiny brown dots. Excepting bifid tail on A-10 (which remains red), all bright

yellow, red, and maroon body coloration has been lost. Even more remarkable is that, excepting the maroon subdorsal tufts on A-1, the other five pairs of subdorsal tufts have mostly faded to white, retaining only central maroon setae. The overall appearance of the caterpillar now suggests a dry twig of gray wood.

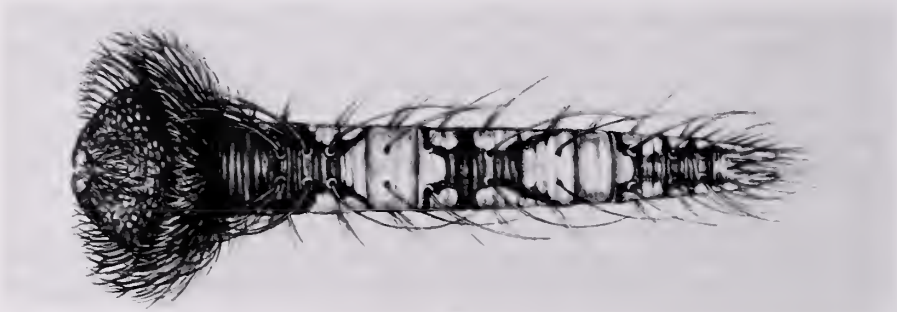
In both color phases the fifth instar caterpillars exhibited feeding behavior similar to the fourth instars. However, fifth instars fed nocturnally, only between dawn and dusk, and rested off the host plant. Premolt duration from fifth star to pupa = 3 to 4 days. Total fifth instar duration 30.3 days (N = 3, SE = 0.66).

Secretory glands: The caterpillars of *M. cypris* possess at least two secretory glands, both likely to serve a defensive function. The cervical gland, which occurs on caterpillars of Hesperiidae, Pieridae, Nymphalidae, and Notodontidae (Bourgone, 1951; Peterson, 1962; Miller, 1991), secretes a volatile chemical when a caterpillar is molested. The other gland, which has apparently never been described previously, secretes a liquid that is groomed into the subdorsal tufts of setae. Studies describing the morphology of these glands are currently in progress, and will be reported elsewhere (DeVries and Shinn, in prep.).

The cervical gland: When a third and later instar was prodded or molested, the caterpillar raised the head such that the mandibles projected forward, and extruded a red, bluntly cylindrical cervical gland from a slit located anterior to the first set of legs. The gland usually remained extruded for about five seconds before being retracted. While extruded it emitted an odor, reminiscent of rotten tomatoes, that lingered for a few seconds after the gland had been retracted. Larger caterpillars produced a stronger odor than did the smaller ones. It has not been determined whether first and second instars possess this gland. Unlike those described for some notodontid caterpillars (Forbes, 1948; Kearby, 1975), the cervical gland of *M. cypris* did not produce a spray or cause a noticeable irritation when the extruded gland was brought into contact with the skin.

The grooming gland: Within an hour after molting all instars vibrated their heads up and down rapidly and shallowly, and produced a drop of clear liquid from a dorsal pore located between the subdorsal tufts on A-1, which we term the 'grooming gland'. The drop of liquid was held suspended at the distal portion of these tufts for a few moments (Fig. 10), then the head arched toward the posterior, and the drop was combed into the subdorsal setae on T-1 and T-2. Then with a slow, rotating motion of the head, the drop was combed into all abdominal subdorsal tufts and the setae on the caudal tails. This action was first performed on one side of the body, then after a moment, repeated on the other side, leaving the setal tufts gleaming with the liquid. After about two minutes exposure to sunlight the liquid evaporated from the subdorsal tufts, and they lost their gleaming appearance. Depending on the individual caterpillar, post-molting combing behavior was repeated from three to five times during the span of 30 minutes. The secretion of liquid from the grooming gland and combing behavior was rarely observed the day after molting. However, it may be a common nocturnal behavior that went undetected during this study.

Caterpillar behaviors: Several incidental behaviors are worth noting. First, caterpillars in all instars were observed to eat the dense mat of resting-silk that had been spun prior to molting, and then subsequently eat their cast skin. This behavior took place two to four hours after completing a molt, and always preceded eating leaf tissue. Second, when tickled with a splinter of wood, all instars would violently bring



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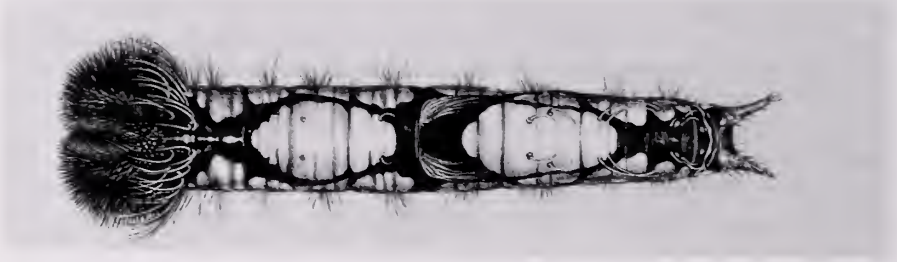

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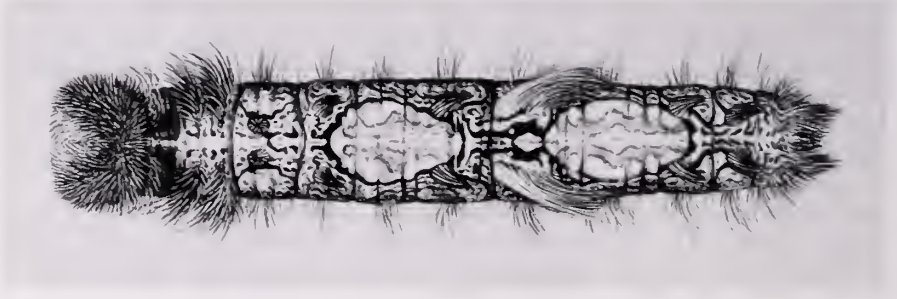

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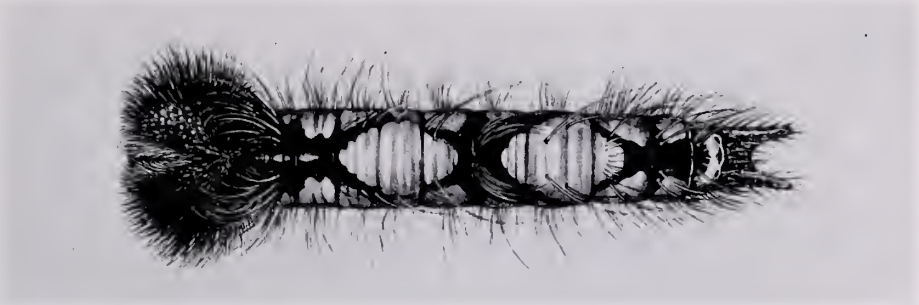
Figs. 4–9. The five caterpillar instars of *Morpho cypris* in dorsal view. 4. First instar. 5. Second instar. 6. Third instar. 7. Fourth instar. 8. Fifth instar (first color phase). 9. Fifth instar



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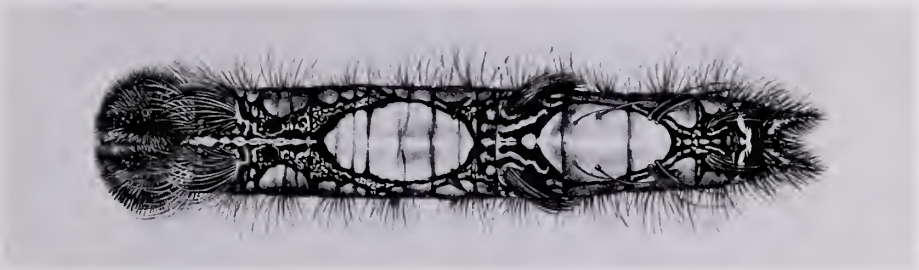

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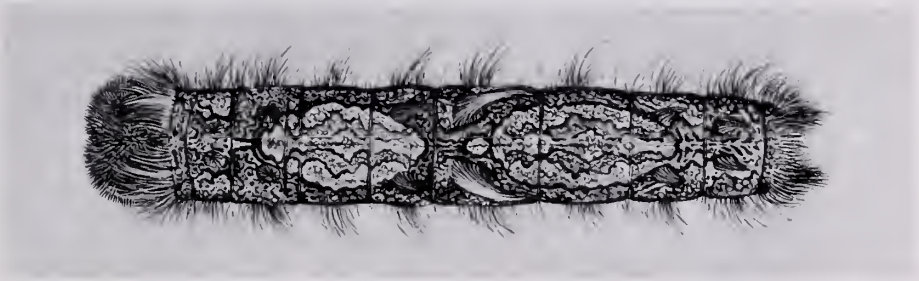

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(second color phase). Note the changes in developmental allometry of the head, subdorsal setae, color pattern, and caudal tails.

their head toward the area of contact, bring the head against the wood, and briskly flicked the head laterally. This action caused the stiff head setae to be used like an 'armed comb' to rebuff the wood away from the body. After being molested in this fashion, various portions of the epidermis slowly twitched, much like a horse trying to rid itself of bothersome flies. At this point the caterpillars were very sensitive to air currents, and the entire body flinched when they were gently blown upon. Finally, when prodded with a finger, third and later instar caterpillars occasionally beat a rapid and audible tattoo on the substrate with their heads. The extrusion of the cervical gland often accompanied the latter two behaviors.

Pupa: (Fig. 11)—Ovoid, with a noticeably globose abdomen widest at A-5, and tapering dramatically toward head; head terminating in a short bifid projection; entire body pale green with a faint whitish bloom, except for yellow spiracles, and a single white ovoid spot covering spiracle on A-5; overall surface smooth except for two minute, brown, rod-like nipples on segment A-10; cremaster brown, granulate, and curved slightly ventrally. When molested the pupa articulated laterally from segments A-5 and A-6, and made an audible "snick" sound each time it moved from side to side. Duration of pupal stage 24 to 25 days (N = 2).

Discussion

In this study 59 viable eggs were recovered from a single, yellow form *M. cypris* through natural and induced oviposition. Of these eggs, all produced first instar caterpillars that were subsequently reared in captivity under field conditions. Three of these first instar caterpillars developed to pupation, but only two of these pupae produced adults. One male, and one yellow form female eclosed (Figs. 12–13); one male pupa died. Based on the two adults that eclosed, the total time duration of egg to adult was 144 days, several weeks longer than the egg to adult times estimated for three other species of *Morpho* (Young and Muyshondt, 1972; Young, 1982). Comparison of our data with that presented for *M. polyphemus* (Young and Muyshondt, 1972) indicates that although duration of the egg stage was the same (11 ± 0.5 days), tenure of all other instars, including the pupal stage, was longer for *M. cypris*.

The vast majority of caterpillars in this study died. One fifth instar died from an undetermined tachinid fly maggot that emerged from the caterpillar (but failed to pupariate). In this instance, a minute tachinid egg laid on the host plant leaf was probably introduced into the rearing container, and fed on by a caterpillar. The death of all other caterpillars typically had its onset immediately prior to or following each molt, at which time a caterpillar would stop moving, void very wet frass, die, and putrefy within 24 hours. Although the exact cause of death is unknown, these symptoms strongly suggest infection from a lethal virus.

The 95% caterpillar mortality observed in this study was similar to the 92% mortality found in *M. polyphemus* when reared under laboratory conditions (Young and Muyshondt, 1972). As noted in that study, laboratory mortality rates probably have little relationship to those occurring under natural conditions. Thus, even though *M. cypris* adults are extremely rare at the Sirena station—less than one sighting per year (P. J. DeVries, P. Chai, independent pers. obs.)—the mortality observed in *M. cypris* is likely an artifact of being kept in captivity. Why such a large fraction of caterpillars

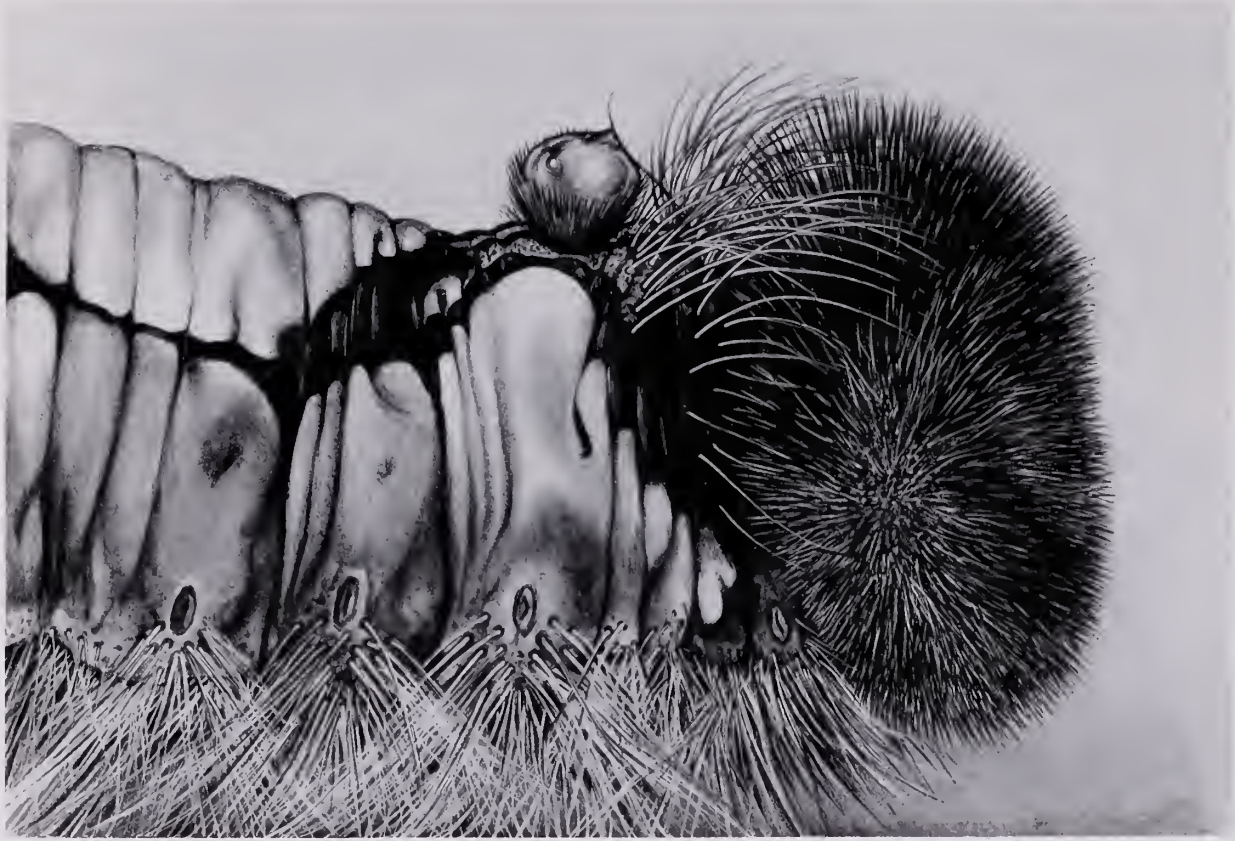

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Fig. 10. Lateral view of newly molted fourth instar *Morpho cypris* showing the clear drop of fluid secreted from the grooming gland, and suspended between the dorsal tufts.

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Fig. 11. Lateral view of *Morpho cypris* pupa.

died before pupation remains unknown: every attempt was made to ensure that each caterpillar always had access to fresh host plant leaves, and all instars were reared in regularly cleaned individual containers. Such high mortality is in contrast to hundreds of other butterfly species reared by PJD previously, and we feel that if this study had been done under appropriate conditions, whatever those may be, *M. cypris* caterpillar survivorship should have been much higher.

All post–third instar *M. cypris* caterpillars possess a cervical gland that extrudes when a caterpillar is molested. This gland was apparently first noted in caterpillars of *Morpho polyphemus* (Young and Muyshondt, 1972), and has been found subsequently in caterpillars of *Morpho peleides, granadensis, amathonte,* and *theseus* (DeVries, 1987, and unpublished observations). These observations suggest that the cervical gland is a trait shared by all members of the genus *Morpho,* and is at least analogous to cervical glands reported from other groups of Lepidoptera (Bourgone, 1951; Peterson, 1962; Miller, 1991). Within the Nymphalidae the nature of the cervical gland, the conditions when it is extruded, and the odor it emits strongly suggest that it serves as a defense to repel predators. However, we know nothing about the chemistry of this gland for any nymphalid, and have no evidence to indicate what type of predators the gland might repel.

Here we described the dorsal grooming gland found on segment A-1 in all instars of *M. cypris,* and the grooming behavioral response following secretion of a drop of liquid (Fig. 10). The liquid anointed onto the subdorsal tufts may have some defensive function, perhaps serving to repel ants or parasitoids in some way, but we have no observations to support this notion. Six species of *Morpho* caterpillars (*cypris, peleides, granadensis, amathonte, theseus, deidamia*) are known to have a dorsal groom-

Figs. 12–13. Female *Morpho cypris* that emerged from a pupa resulting from this study (Forewing length = 70.0 mm). 12. dorsal view. 13. ventral view.

ing gland and to show grooming behavior (DeVries, 1987, and unpublished), which suggests that these glands too are widespread within the genus *Morpho*. However, additional *Morpho* species and other genera (e.g., *Antirrhea, Caerois*) should be examined to determine how widely these traits occur within the Morphinae. Our observations suggest that caterpillars in other groups of Lepidoptera that possess setal tufts (e.g., Amathusiinae, Arctiidae, Apatelodidae, Noctuidae, Lymantriidae) should be examined for the presence of similar grooming glands.

Fourth and fifth instar *M. cypris* caterpillars may possess two potential defenses that are directed at vertebrate predators. First, when prodded with a splinter of wood the caterpillars contract their bodies such that the dorsal tufts of setae expand and expose the concealed red-maroon setae. Although none of these setae caused discomfort when brought into contact with the inner arm (DeVries, pers. obs.), the behavior is similar to some tropical lymantriid and megalopygid moth caterpillars that possess urticating, often colored spines buried in setal tufts that are exposed when the caterpillars are molested (DeVries, pers. obs.). Secondly, when molested the *M. cypris* caterpillars bring their heads violently into contact with the stimulus. Some of the head setae are stiff enough to enter the soft skin between the fingers if pushed hard enough, much like a tiny plant spine (DeVries, pers. obs.). However, when embedded into the skin and thrummed with another finger the spines do not produce a chemical burning sensation. The behavior of exposing the red-maroon setae, and the possession of stiff head setae, suggest that *M. cypris* caterpillars may mimic caterpillar species whose urticating spines and warning coloration deter vertebrate predators, like monkeys (DeVries, pers. obs.).

The host plant of *M. cypris* reported here (*Inga marginata*) is a widespread, medium-sized tree that occurs in lowland to montane rain forest habitats ranging from Costa Rica to Brazil—a distribution overlapping that of *M. cypris*. However, several observations suggest that *M. cypris* caterpillars may feed on other plant species as well. During June 1989 at about 14:00 hr DeVries observed a *M. cypris* female ovipositing high in the canopy of several large *Inga* trees growing inside the forest at Rara Avis (El Plastico, Heredia Province, 750 m, Atlantic slope of Costa Rica). In this case, the tree was definitely not *I. marginata* (I. Chacon, pers. comm.). A summary by Ackery (1988) indicates that host plants of 11 *Morpho* species include various genera of the Fabaceae. The report of Brazilian *M. rhetenor* (Cramer, 1777) feeding on *Macrolobium* (Fabaceae) by Ackery (1988) is important in the context of a potential sister species relationship between *M. cypris* and *M. rhetenor* (Le Moult and Real, 1962; DeVries et al., 1985). The trend for *Morpho* to use Fabaceae broadly, and the relationship of *cypris* and *rhetenor* suggest that both species may use *Inga* and *Macrolobium* as hosts, and that their diet will eventually include more members of the Fabaceae than is currently known. With respect to conservation biology this may be good news, because remnant patches of forest are likely to sustain a variety of suitable host plant species for these butterflies. On the other hand, all of our observations on *M. cypris* in Costa Rica and Panama suggest that adult territorial and courtship interactions occur only in or adjacent to sizable tracts of intact forest. Thus, in the face of increasing tropical deforestation, population levels of *M. cypris* may become critically low even in the presence of abundant larval host plants.

Butterflies live, interact, and die within dynamic biological systems, and as such they cannot be protected or conserved as objects or things (Sibatani, 1992). More

than 140 years after *M. cypris* received its formal scientific name, our understanding of its early stage biology is confined to the information presented here—a sobering commentary on one of the most spectacular of all butterflies, and on our knowledge of tropical systems in general. Current devastation of these tropical systems is widespread. It is our hope that this paper will encourage further study of the biology and conservation of *M. cypris* butterflies and its tropical forest habitats. If such studies are not undertaken and published, then this and other papers will serve as an elegy.

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A NEW GENUS AND SPECIES OF COLEOPTEROID OZOPHORINE FROM MEXICO (HEMIPTERA: LYGAEIDAE)

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Abstract.—A new genus and species, *Brailovskyocoris curculionoides,* is described from the mountains of Oaxaca, Mexico. It is placed in the lygaeid tribe Ozophorini of the subfamily Rhyparochrominae. Comments are made on the extreme coleoptery shown and habitats and examples of such conditions discussed. Figures are included of the entire insect and details of the abdomen and genital capsule.

Through the kindness of Dr. Roy Danielsson of Lund University I have been able to examine a series of remarkable coleopteroid lygaeids from the mountains of Oaxaca, Mexico.

Slater (1985) described as *Icaracoris montanus* a completely flightless coleopteroid lygaeid taken at 12,000 ft in the mountains of Colombia. I placed the genus in the tribe Ozophorini with some hestiation because of the loss of several diagnostic features due to modifications (presumably) in the development of the coleopteroid body form.

DIAGNOSIS

The species described below shows as great a degree of coleoptery as does *Icaracoris,* but retains a complete trichobothrial component (Fig. 2) together with many modifications also seen in *Icaracoris.* This strengthens the placement of both genera in the tribe Ozophorini.

While, as noted by Slater (1985), it is true that the Ozophorini is defined (in the absence of nymphs) chiefly by the loss of the abdominal inner laterotergites, there are several features that indicate placement of these taxa in that tribe. The presence of all ventral spiracles precludes all Neotropical tribes but the Antillocorini, Lethaeini and Plinthisini. The latter have an intersegmental membrane in the abdomen. The Antillocorini have inner laterotergites. The Lethaeini have linear abdominal trichobothria and a reduced posterior abdominal scent gland.

Most rhyparochromine taxa that possess a Y-suture in the nymph also have the anterior scent gland scar in the adult much larger than the scars between terga 4–5 and 5–6. This is true of *Icaracoris,* but it is of little value in determining the position of the present genus as the scent gland scars (and presumably the nymphal scent glands) are very reduced, due to the extreme desclerotization of the abdominal tergum. In addition to the lack of inner laterotergites, the ventral position of the spiracles, the trichobothria in the plesiomorphic position and the spines on the forefemur set upon distinct tubercles all support the placement of the genus in the Ozophorini. This combination of characters is a common situation in the Ozophorini, but is not, to my knowledge, present in other tribes of Neotropical Lygaeidae with ventral spiracles.

Since Ozophorini are abundant, diverse and apparently of very long occurrence in the Neotropics it is not surprising that highly modified montane taxa occur. Indeed a number of other genera of Ozophorini possess a flightless morph, although the body modifications are less extreme than in *Icaracoris* and the genus described below. For example, species of *Balboa* Distant, *Ozophora* Uhler, *Bergidea* Breddin, *Micrymenus* Bergroth and *Allotrophora* Slater & Brailovsky all contain species that have modified forewings (sometimes coleopteroid) and are flightless.

Brailovskyocoris, new genus

Type species: *Brailovskyocoris curculionoides,* new species.

Body short, elliptical, strongly convex. Head markedly declivent; eyes sessile; vertex tumidly convex. No ocelli. Bucculae strongly produced downward at anterior end. Pronotum not separated into anterior and posterior lobes; calli large, swollen particularly mesally to form a median trough between them; lateral pronotal margins sharply carinate. Prothorax less thickened dorso-ventrally than mesothorax, metathorax and abdomen. Scutellum lacking a median carina; basal half depressed, distal half elevated evenly to apex. Hemelytron consisting of a strongly convex, coarsely punctatae beetle-like structure. Each hemelytron meeting evenly at midline for most of length. Clavus and corium completely fused, but claval suture presumably represented by an elevated pale calloused stripe. No membrane present. Hemelytra extending posteriorly to 7th abdominal tergum. Hind wings absent. Metathoracic scent gland auricle curving slightly and evenly caudad. Evaporative area small, truncate at outer margin, extending dorso-laterad only over inner half of metapleuron, present on posterior rim of mesopleuron. Forefemora with 2 large spines arising from tubercles ventrally on distal ⅓. Abdominal terga 2 through 5 largely desclerotized sclerotization on terga 3, 4 and 5 reduced to transversely quadrate or elliptical mesal plates (Fig. 3). Dorsal abdominal scent gland scars present between terga 3–4, 4–5 and 5–6, but minute (Fig. 3). No inner laterotergites present. All spiracles ventral and located below sternal shelf (Fig. 2). Trichobothria with a pair of posterior trichobothria located one above the other and posterior to spiracle on sterna 5, 6 and 7 (Fig. 2). Male genital capsule with a rounded posterior projection (Figs. 4, 5).

Despite a similar forewing modification *Brailovskyocoris* and *Icaracoris* are not closely related. The latter has mutic forefemora, a much larger anterior abdominal scent gland scar between terga 3–4 than between terga 4–5 and 5–6; a deeply concave posterior pronotal margin, a short almost circular metathoracic scent gland auricle, long conspicuous hairs on the dorsal body surface, a tylus that attains or exceeds the end of the first antennal segment, an evenly convex pronotum with lateral margins produced and "flange-like."

There is no obvious ozophorine that appears to be the sister group of this highly modified species.

As noted by Slater (1985) such extreme coleoptery is usually accompanied by loss of, or extreme reduction of, the hind wing and often by a partially desclerotized abdominal tergum. Such lygaeids appear to occur primarily, if not exclusively, in two habitats. First, at high elevations in mountains (*Icaracoris*; *Brailovskyocoris*, undescribed species of Antillocorini—Neotropics; *Microlugenocoris* Scudder; *Scoloposthethus coleoptratus* Slater; undescribed species of Lethaeini—Ethiopian. Second, in

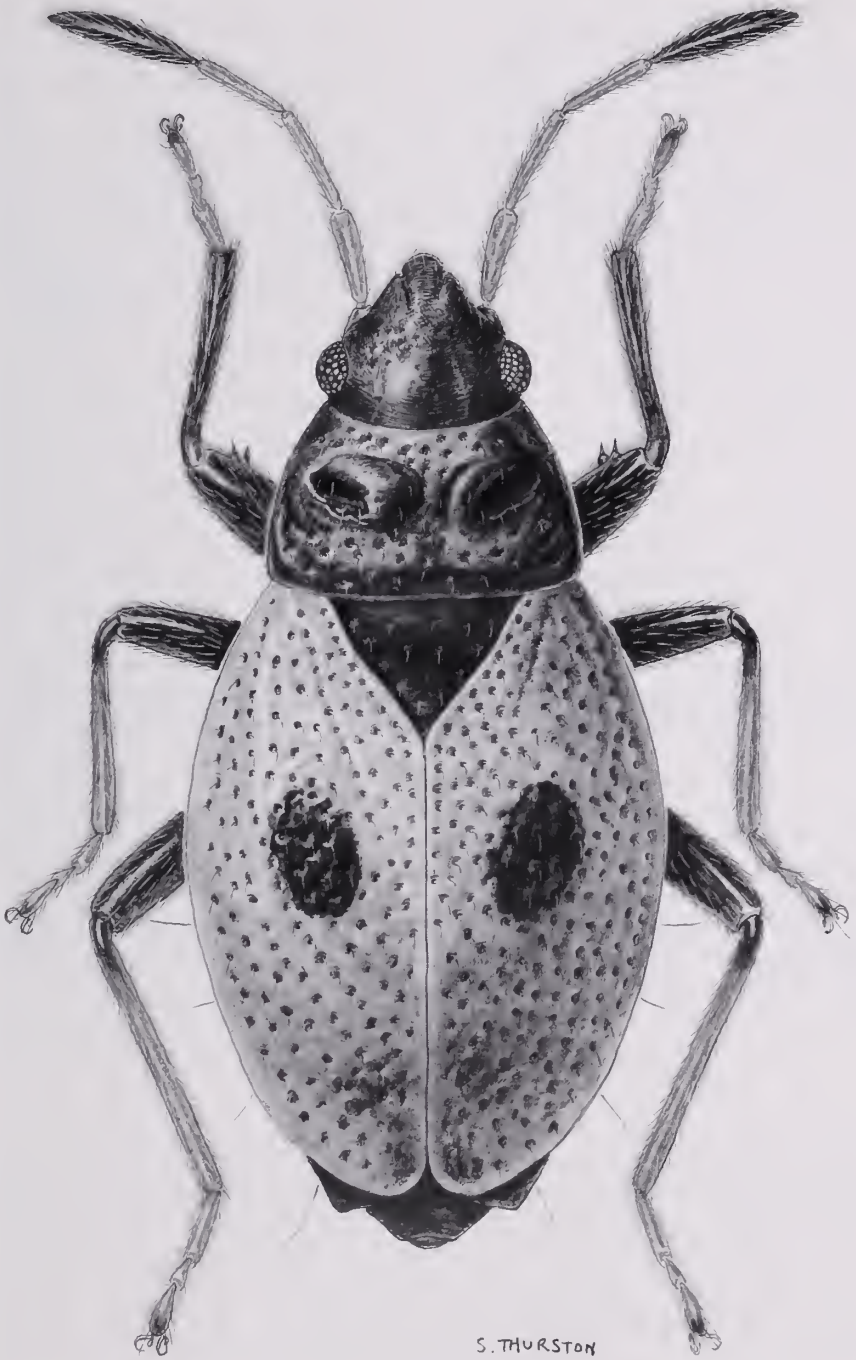
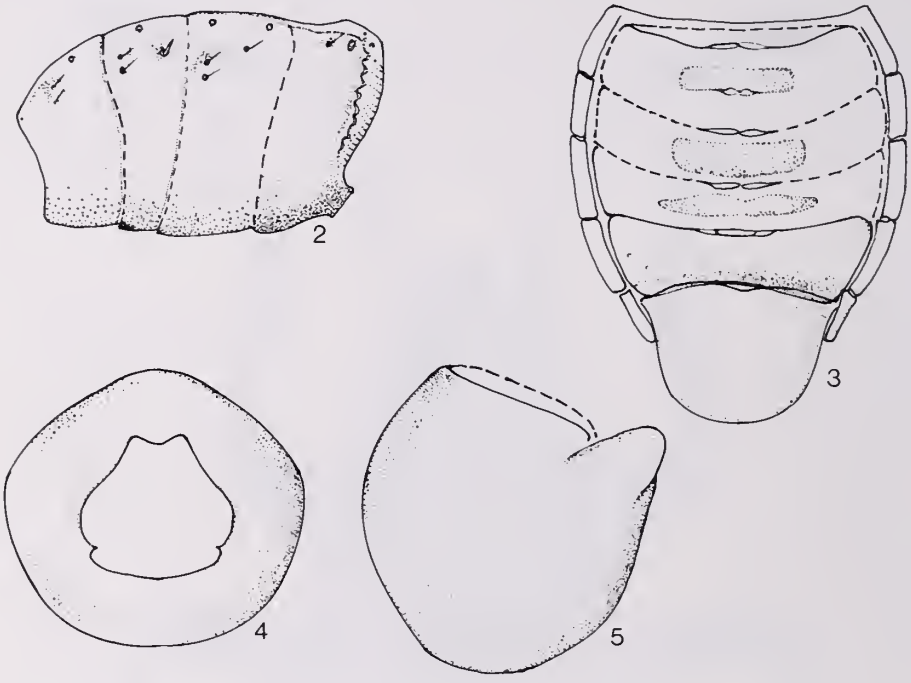


Fig. 1. *Brailovskyocoris curculionoides,* new species, dorsal view.



Figs. 2–5. *Brailovskyocoris curculionoides* new species. *2.* Abdomen, lateral view. *3.* Abdomen, dorsal view. *4.* Genital capsule, dorsal view. *5.* Genital capsule, lateral view.

xeric habitats of long time ecological stability (*Coleocoris* Gross; *Carabocoris* Gross—Australia; *Saxicoris* Slater, *Psammium* Breddin—south western Africa; *Sympeplus* Bergroth—India). (However, in other families of Hemiptera coleoptery occurs under very different conditions).

This remarkable genus is named for my good friend and colleague Dr. Harry Brailovsky of the University of Mexico in recognition of his major contributions to our knowledge of Mexican and Neotropical Hemiptera.

Brailovskyocoris curculionoides, new species
(Fig. 1)

Head, pronotal calli, scutellum, a large spot near middle of each hemelytron, a smaller spot on either side of midline near apex of each hemelytron, all femora, fore and middle tibiae, proximal and distal ends of hind tibiae, fourth antennal segments, labium and entire pleural and sternal surfaces black to dark chocolate brown. Remainder of dorsal surface a strongly contrasting mottled yellowish to reddish brown with irregular calloused white maculae on hemelytra adjacent to scutellum, posterior to and slightly mesad of black hemelytral patches and as an elevated stripe outlining fused claval suture. Tarsi and shaft of hind tibiae and antennal segments 1, 2 and 3 yellow. Entire body surface deeply and coarsely punctate. Surface subshining, no

pruinosity present. Appearing glabrous, but with minute hairs arising from many punctures.

Eyes small, set slightly away from antero-lateral margins of pronotum. Tylus attaining middle of first antennal segment. Length head 0.60, width 0.66, interocular space 0.40. Inner portion of pronotal calli and dark spots on hemelytra swollen to give a "lumpy" appearance to convex body surface. Anterior pronotal collar poorly differentiated, lacking a deep impressed posterior line; lateral pronotal margins evenly rounded, posterior margin straight. Length pronotum 0.50, width 0.92. Length scutellum 0.42, width 0.52. Hemelytral surface most strongly convex at middle, sloping downward both anteriorly and posteriorly; lateral margins carinate, evenly and broadly rounded, strongly tapered to posterior end. Length wing pad 1.68. Length "claval commissure" 1.26. Labium extending between metacoxae. Approximate length labial segments I 0.36, II 0.36, III 0.24, IV 0.20. Antennae terete, fourth segment broadly fusiform. Length antennal segments I 0.30, II 0.38, III 0.32, IV 0.42. Total body length 2.64.

Holotype: Male. MEXICO: *Oaxaca*: 57 km. S. Valle Nacional. 2600 m. 13.XI.1989. (R. Baranowski). In Lund University Museum.

Paratypes: MEXICO: *Oaxaca*: 2 males, 2 females. 58 km. S. Valle Nacional. 2,700 m. 10.XI.1989. (R. Baranowski). 1 female same except 7. IX.1986. 1 female. 61 km. S. Valle Nacional. 2,900 m. 10. XI.1989. (R. Baranowski). In Lund University and J. A. Slater collections.

These remarkable beetle-like lygaeids are apparently adapted for living at high altitudes. As can be seen above the type series was taken at 3 separate localities (and in two different years) at 9,000 ft or above. The beetle resemblance is enhanced by the convexity and "bumpiness" of the fore wings and the reduction in depth of the prothorax.

It seems unlikely that given the extreme modifications in both sexes that a macropterous morph exists.

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I wish to express my deepest thanks to Dr. Roy Danielsson (Lund University) for the loan of material and to Dr. R. Baranowski of the same institution for the collection of many rare ground living Lygaeidae.

My appreciation is extended to Mr. Steven Thurston (formerly U. of Connecticut) for the execution of the dorsal view drawing and to Ms. Mary Jane Sping (U. of Connecticut) for providing the other illustrations.

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A NEW SPECIES OF *THRASSIS* FROM BAJA CALIFORNIA, MEXICO (SIPHONAPTERA: CERATOPHYLLIDAE: OROPSYLLINAE)

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Abstract.—A new species of the ceratophyllid genus *Thrassis* Jordan, 1933, from Baja California is described. Its phylogenetic affinities in the subfamily Oropsyllinae are briefly discussed and its host preference for antelope ground squirrels of the genus *Ammospermophilus* is noted.

The history of the ceratophylline taxon here referred to as the Oropsyllinae may be traced to the work of Ioff (1936) in which the author erected the "sub-class" Oropsyllini. In it he placed the genera *Oropsylla* Wagner and Ioff, 1926, *Opisocrostis* Jordan, 1933, *Diamanus* Jordan, 1933, and *Thrassis* Jordan, 1933. Stark (1970) referred these genera to the Oropsyllinae Ioff, 1936, on the basis of their morphological similarities and their differences from other ceratophyllid genera. He went on to suggest that members of these genera are more generalized and are thus lower on the evolutionary scale in both morphological development and host preferences.

Today this subfamily contains the genera *Thrassis* and *Oropsylla,* and 45 species-group named taxa, 43 of which occur in the Nearctic Region. One of these is shared with the eastern Palaearctic Region as far west as Dagestan in the Caucasus Mountains west of the Caspian Sea. With few exceptions, fleas belonging to this subfamily parasitize sciuromorph rodents and some are known to play a major role in the maintenance of sylvatic plague in ground squirrel and prairie dog populations in western North America, and ground squirrels and marmots in Central Asia. For the present, these genera are viewed as being the most primitive in the family, with members of the subgenus (*Oropsylla*) being nearest the ancestral condition, parasitizing as they do the more primitive sciurids, the marmots or woodchucks, and ground squirrels of the genera *Spermophilus* and *Ammospermophilus.* Nowak (1991) placed these rodents between the chipmunks and the tree squirrels.

Smit (1983) demoted the previously recognized genera *Diamanus* Jordan, 1933, *Opisocrostis* Jordan, 1933, and *Thrassis* Jordan, 1933, to subgenera of *Oropsylla* Wagner and Ioff, 1926. He also erected the subgenus *Hubbardipsylla* for two species originally assigned to *Opisocrostis.* Although these taxa are obviously closely related, not all students of the order were in accord with this action, and Lewis (1990) restored *Thrassis* to full generic status, although not supporting the subgenera erected by Stark (1970).

Since its revision by Stark (1970), the genus *Thrassis* has remained static, with no additional taxa described or existing names synonymized. However, Stark (*in litt.*) recently suggested that *Thrassis spenceri alpinus* Stark, 1957 "is probably not a valid taxon, and may have been described from an aberrant specimen." I have examined the holotype male (USNM No. 104579) of this subspecies and, while it may be inseparable from the nominate taxon, it is not aberrant in any way that I can detect.

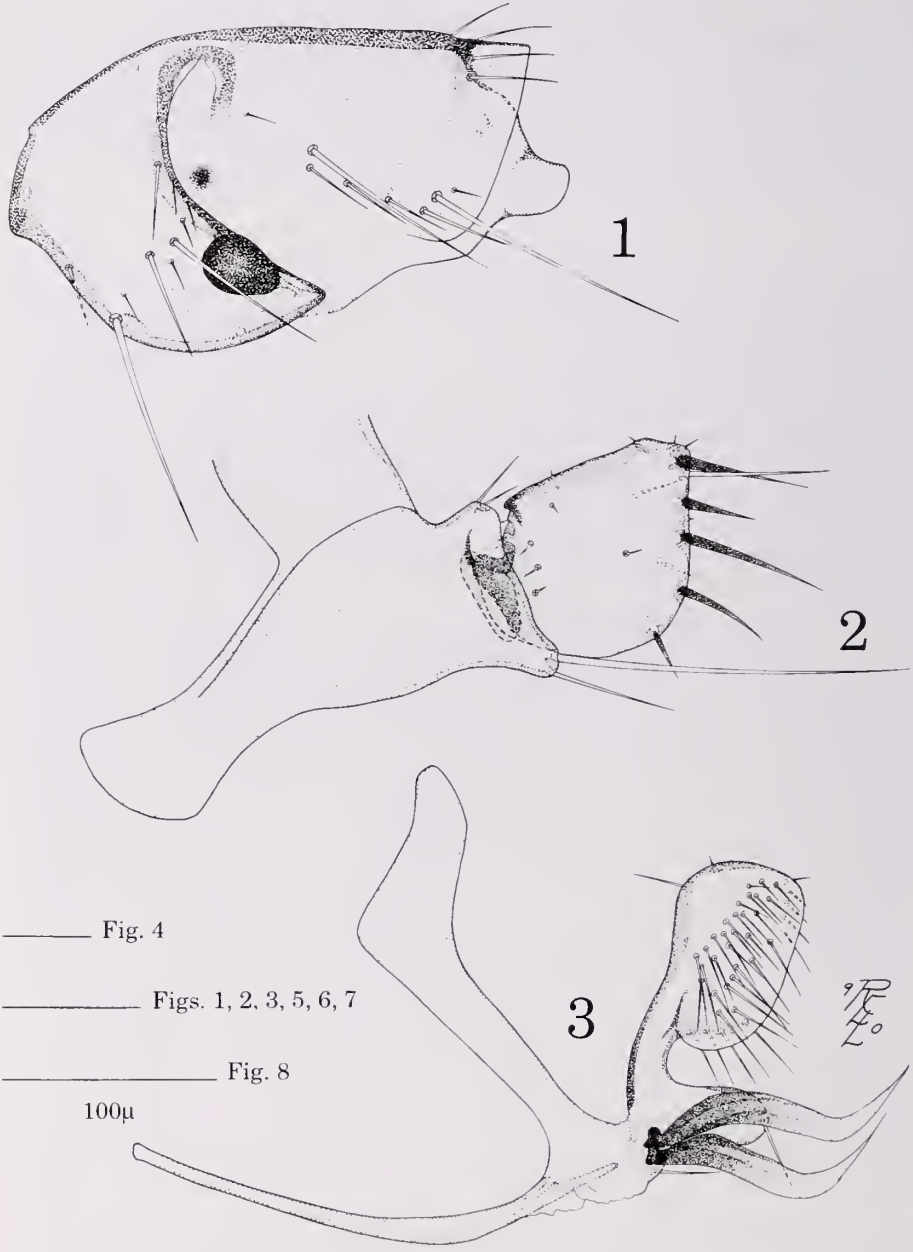
Under the circumstances the name must stand until additional collections become available.

Because of its association with plague transmission, the genus *Thrassis* has been studied more closely than many related genera. It therefore came as a surprise when an undescribed species appeared in collections of mammalian ectoparasites from northern Baja California. Following is the description of the new form.

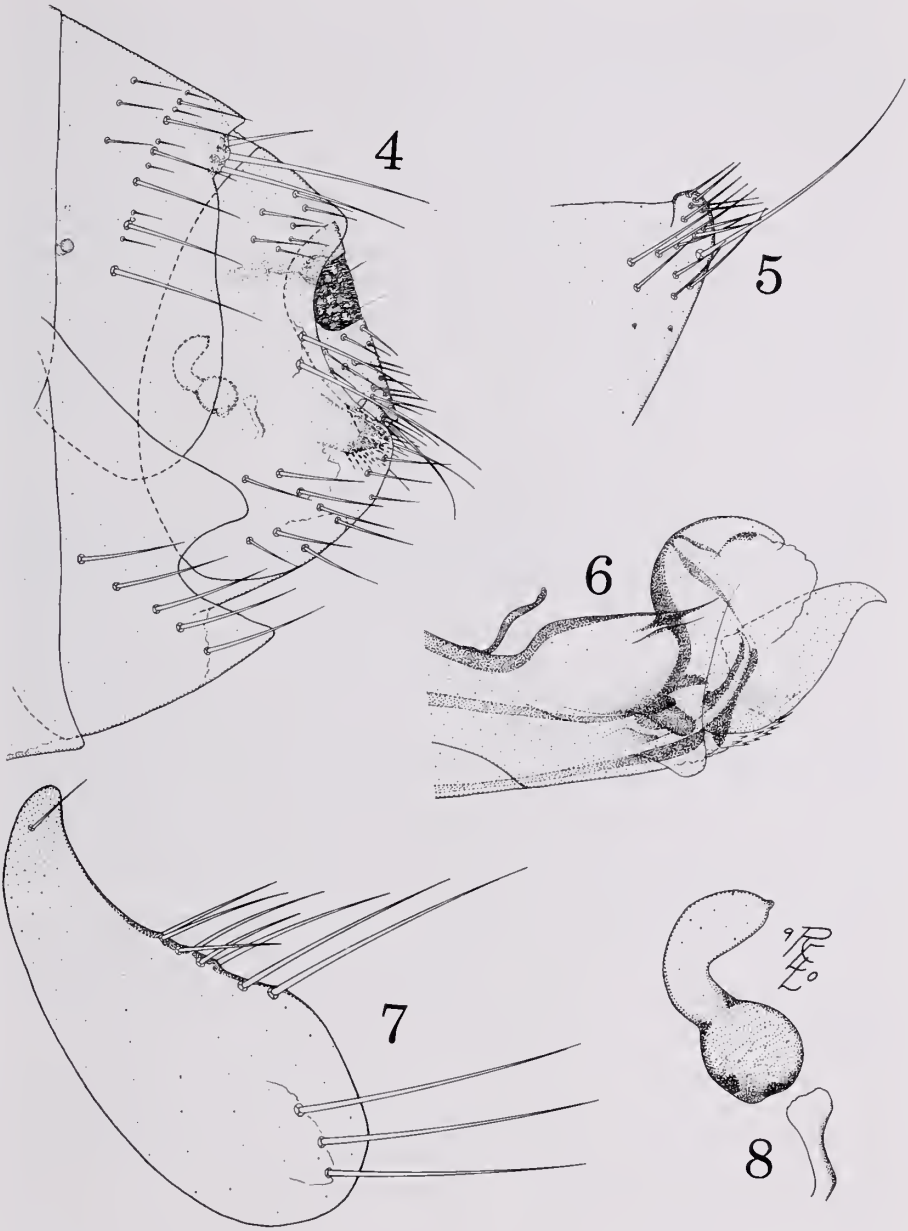
Thrassis peninsularis, new species
Figs. 1–8

Diagnosis: While this species is not particularly close to any other member of the genus, there are some superficial similarities with *T. augustsoni* Hubbard, 1949, in the modified abdominal segments of both sexes. Males differ in the shape and configuration of the fixed and movable processes of the clasper; the degree of development of both tergum and sternum VIII; the form and chaetotaxy of sternum IX; the form of the aedeagus and the presence of five spiniform bristles on the movable process, a character unique in the genus. Females are similar but the subventral sinus and lobe on the caudal margin of sternum VII are better developed in *T. peninsularis* and the bulga of the spermatheca is somewhat more globose and its hilla more inflated apically.

Description: **Head.** (Fig. 1). Eye, frontal tubercle and trabecula centralis well developed in both sexes. Ocular row usually of 3 long bristles in both sexes. Frontal row of 1 long bristle near antennal fossa and another on genal margin in males; genal bristle present, but fossal bristle absent in females. Pedicel of male antenna with 3–4 long bristles extending to apical claval segment but not beyond it. Pedicel of female antenna with 10–12 long bristles, most of which extend beyond the apex of the clavus. Postantennal chaetotaxy consisting of 2 long bristles arising along the dorsal margin of the antennal fossa, as well as a few finer bristles, and a dorsal occipital row of 3 setae per side in both sexes. Labial palpi extending well beyond apex of trochanter. **Thorax.** Pronotal comb with 17–18 spines in both sexes, occasionally one fewer in males, one more in females. Pronotal setal row of 6 setae per side in both sexes. Mesonotum with 5 long setae in main row per side and 5 pseudosetae per side under the mesonotal collar in both sexes. Mesepisternum with 3-4 long setae, mesepimeron with 4 long setae arranged in two vertical rows. Metanotum with 5-6 long setae per side in main row preceded by 3 shorter bristles. Caudal margin of metanotum with 2 apical spinelets per side in both sexes. Lateral metanotal area with 2–3 long bristles, metepisternum with 1 and metepimeron with 5, arranged in 3 vertical rows of 2, 2 and 1. **Legs.** Forecoxa with 15–18 long setae arranged in oblique rows on outer surface. Forefemur with 10–12 fine setae on outer surface remote from dorsal margin and a row of 3–4 on inner surface. Caudal margin of foretibia with 5 subapical notches bearing the following heavy bristles from base to apex: 1, 2, 2, 2, 2. Apex with 3 heavy bristles. Foretarsal segment II slightly longer than segments I or III, segment IV about as wide as long. Foretarsal segment V with 5 pairs of lateral plantar setae, the third pair shifted slightly onto the plantar surface. Midcoxa with an irregular row of fine submarginal setae along anterior margin on inner surface. Outer surface of midfemur bare, its inner surface with a row of 4–5 setae remote from ventral margin. Caudal margin of midtibia with 5 notches bearing pairs of stout setae.



Figs. 1–3. *Thrassis peninsularis* n. sp. 1. Head of holotype ♂. 2. Clasper of paratype ♂ (dissection). 3. Sternum IX of paratype ♂ (dissection).



Figs. 4–8. *Thrassis peninsularis* n. sp. 4. Terminal abdominal segments of allotype ♀. 5. Apex of sternite VIII of holotype ♂. 6. Apex of aedeagus of paratype ♂ (dissection). 7. Tergum VIII of holotype ♂. 8. Spermatheca and sclerotized duct of bursa copulatrix of allotype ♀.

Unpaired stout setae not arising from distinct marginal notches between notches II and III and IV and V. Apex with 3 stout setae dorsally and 3 more ventrally. Midtarsal segments I and II slightly subequal, segment III somewhat shorter, segment IV only slightly longer than wide. Segment V with 5 pairs of lateral plantar setae, pair number 3 shifted slightly onto the plantar surface. (Numbers here were taken from paratype males as the mesothoracic legs are damaged in the holotype male.) Outer surface of hindcoxa with a few scattered setae along anterior margin on outer surface and with a well developed submarginal row along anterior margin on inner surface. Hindfemur with 2–3 submarginal setae ventrally on outer surface and a well developed row of 6–8 setae ventrally on inner surface. Hindtibia with 5 preapical notches on caudal margin bearing paired stout setae with unpaired stout setae arising on the margin between notches II and III and IV and V. Three stout bristles both dorsally and ventrally on apex. Hindtarsal segment I about twice as long as II which is about twice as long as III. Segment IV is approximately 1.5 times as long as wide. Segment V bears 5 pairs of lateral plantar bristles with the third pair shifted slightly onto the plantar surface. **Unmodified abdominal segments.** Setae per side in main row on tergites I–VII; 5, 7, 7, 7, 7, 7, 6 in both sexes. Marginal spinelets per side on tergites I–IV; 1-2, 1-2, 1-0, 1-0. Setae per side in main row of sternites II–VII; 1, 1-2, 2-3, 2-3, 2-3, 2 in males, 1, 2-3, 3-4, 3-4, 2-4, 5-6 in females. One antepygidial bristle per side in males, 3 in females. **Modified abdominal segments: Male.** (Figs. 2, 3, 5–7). Neither tergum VIII (Fig. 7) nor sternum VIII (Fig. 5) are as large as in other members of the genus. Movable process of the clasper as shown in Figure 2. Ventral apodeme of manubrium expanded apically. Dorsal lobe and acetabular projection well developed, the latter usually bearing 2 setae of unequal length and substance. Movable process quadrate, its caudal margin bearing 5 spiniform bristles, a character unique in the genus. Distal arms of sternum IX strongly divided into proximal and distal lobes. Distal lobes bearing a number of fine bristles on both surfaces. Proximal lobes with a pair of expanded, feather-like setae arising on outer surface. Similar setae are known in other members of the genus but in none are they so hypertrophied. Apex of aedeagus as shown in Figure 6. Modified abdominal segments of the **female** as shown in Figures 4 and 8.

Etymology: The name alludes to the peninsular nature of the collection localities.

Holotype: ♂, allotype ♀, México, Baja California, 9 km NW Rancho Santa Inez, 29.46N 115.09W, from *Ammospermophilus leucurus canfieldae,* 15 I 1984, E. Yensen. Deposited in the United States National Museum of Natural History, USNM No. 104870.

Paratypes: Same data as holotype, 6 ♂♂, 13 ♀♀; same data but 19 I 1984, 5 ♀♀; same data but 11 I 1984, H. Thomas, 1 ♂, 3 ♀♀, 18 I 1984, 5 ♂, 7 ♀♀. México, Baja California, 11.2 km S. Catavina, from *Ammospermophillus leucurus,* 19 V 1988, Hafner, 15 ♂♂, 9 ♀♀. Paratypes have been deposited in the USNM and the British Museum (Natural History). Most of the Hafner collection has been returned to the University of Manitoba.

Comment: At first glance it appeared that this new species actually belonged to an undescribed genus closely related to *Thrassis* but distinct from it. As is the case with the remainder of the family, the supraspecific oropsylline taxa are extremely similar and difficult to separate. Further comparison with other species in the genus *Thrassis* revealed that although the males of the new species were strikingly distinct with

respect to genitalic characters, there were no precise differences in characters used to separate the supraspecific taxa in the subfamily. Exclusively genitalic characters are not employed to separate genera in this order, although there is evidence that aedeagal morphology is useful in some families. This organ is only now being scrutinized in the family Ceratophyllidae and its value in taxonomic discrimination has yet to be determined.

The host *Ammospermophilus leucurus* has a rather broad range from western Colorado, northwestern New Mexico and northern Arizona, north to southwestern Idaho and southeastern Oregon, south to the tip of Baja California. Throughout much of its range it is parasitized by *Thrassis bacchi gladiolus* (Jordan, 1925). The nominate subspecies of *A. leucurus* extends only slightly into northern Baja California as does the southern distribution of *T. b. gladiolus.* The nominate subspecies of host is first replaced by *A. l. peninsulae,* and further south by *A. l. canfieldae,* the type host of this flea.

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NEW SPECIES OF *OCHROTRICHIA* (*OCHROTRICHIA*) FROM THE SOUTHWESTERN UNITED STATES AND NORTHERN MÉXICO (TRICHOPTERA: HYDROPTILIDAE)

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Abstract.—Four new species of *Ochrotrichia*, subgenus *Ochrotrichia*, are described and figured: *Ochrotrichia guadalupensis* (Texas), *O. contrerasi* (Tamaulipas), *O. cieneguilla* (Nuevo León), and *O. yepachica* (Chihuahua). The new species are compared to other closely related congeners.

The genus *Ochrotrichia* is presently divided into two subgenera, *Ochrotrichia* Mosely and *Metrichia* Ross, both of which are limited to the New World. The subgenus *Ochrotrichia* is widely distributed throughout North America, south to northern South America and throughout the islands of the Antilles (Bueno and Santiago, 1992). Marshall (1979) listed 69 species in her review of the Hydroptilidae, but an additional 25 species have been described in the intervening years, primarily from the Neotropical region. The nominate subgenus appears to be especially diverse in the western United States and northern Mexico where 24 species have been recorded. From this region, we describe four additional new species.

Morphological terminology follows that of Marshall (1979). Length is measured from the top of the head to the tip of the forewing, and is given as a range with more than one specimen. Type material is deposited in the National Museum of Natural History, Smithsonian Institution (NMNH), Illinois Natural History Survey (INHS), Universidad Nacional Autónoma de México, (UNAM), University of North Texas (UNT), and in the collections of the authors (SCH, SRM).

Ochrotrichia guadalupensis Harris and Moulton, new species
Fig. 1

Diagnosis: In the shape of the inferior appendages and configuration of the tenth tergum, this species is similar to several species found in the southwestern United States, notably *O. argentea* Flint and Blickle, *O. rothi* Denning and Blickle, and *O. alexanderi* Denning and Blickle. It differs from these species in the banded configuration of processes at the base of the tenth tergum.

Description: Male: Length 3.2–3.6 mm. 27 antennal segments. Brown in alcohol. Abdominal segment VII with short ventromesal process. Segment VIII rectangular in lateral view, rounded posteriorly in dorsal aspect. Segment IX narrowing posteriorly in lateral view, posteroventral margin incised; truncate in ventral view; dorsum deeply incised. Tenth tergum with pair of thin, oblique processes basally, narrowing distally to rounded apex; in lateral view attenuate distally, downturned at apex, lateral

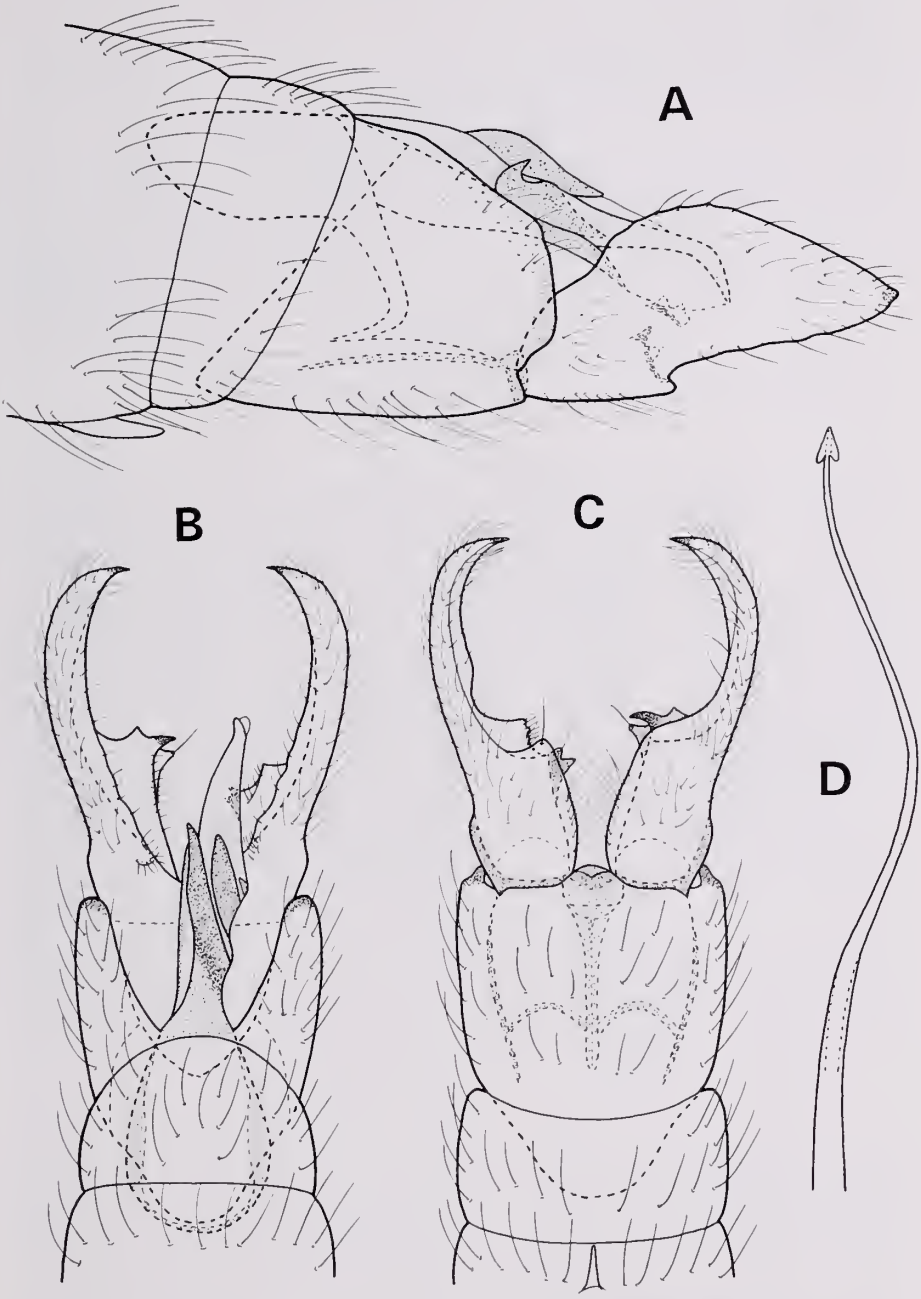

Fig. 1. *Ochrotrichia guadalupensis* n. sp. Male genitalia. A. Lateral view; B. Dorsal view; C. Ventral view; D. Phallus, dorsal view.

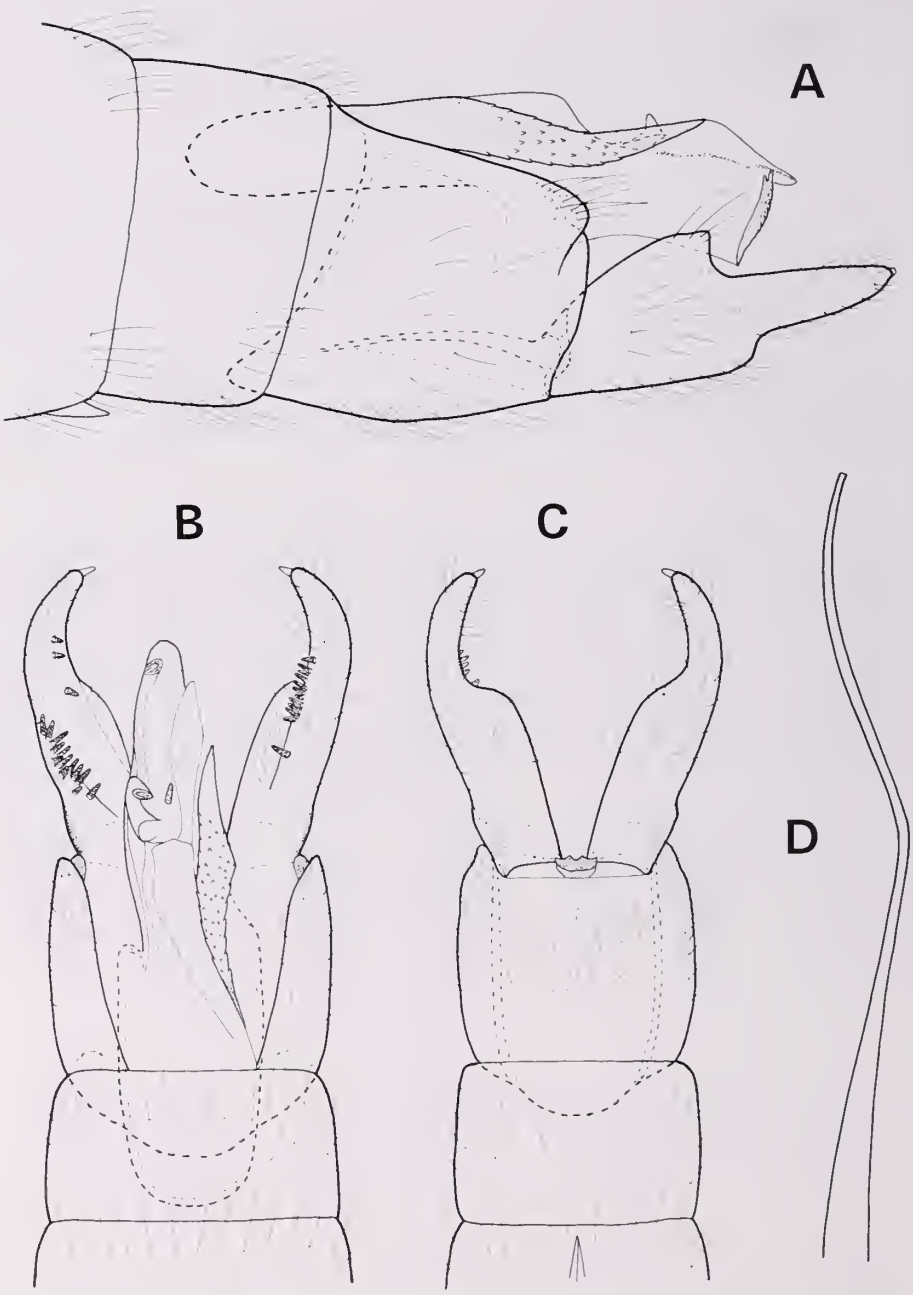

Fig. 2. *Ochrotrichia contrerasi*, n. sp. Male genitalia. A. Lateral view; B. Dorsal view; C. Ventral view; D. Phallus, dorsal view.

process upturned to acute apex at midlength. Inferior appendages in lateral view with small projection on ventrobasal margin, rounded on dorsal margin, attenuate distally; each with acute projections on mesal margins in ventral and dorsal views. Phallus thin and sinuate, triangular apically.

Type material: Holotype; male. United States: Texas, Culberson County, Smith Spring, 2.4 km N Park headquarters, Guadalupe Mountains National Park, 20 May 1991, R. Hood (NMNH). Paratypes: Same data as holotype, 1 ♂ (NMNH); Culberson County, McKittrick Canyon above Pratt cabin, Guadalupe Mountains National Park, 23 May 1991, R. Hood, 3 ♂ (NMNH, INHS, UNT); McKittrick Canyon Creek, Guadalupe Mountains National Park, 14 January 1987, Baumann, Sargent, Kondratieff, 2 ♂ (SCH, SRM).

Etymology: Named for the Guadalupe Mountains of Texas.

Ochrotrichia contrerasi Harris, new species
Fig. 2

Diagnosis: On the basis of the tenth tergum, this species is probably most similar to that of *O. tenanga* (Mosely) and other members of the *lometa* group. The inferior appendages which are incised on both the dorsal and ventral margins, and the elongate lateral process from the tenth tergum are distinctive for *O. contrerasi.*

Description: Male: Length 2.7–2.9 mm. 26 antennal segments. Brown in alcohol. Abdominal segment VII with short ventromesal process. Segment VIII annular. Segment IX rectangular in lateral view; truncate in ventral view; dorsum deeply incised. Tenth tergum with elongate lateral process from inner margin, tapering distally and bearing numerous minute spines, narrow sclerotized band on outer margin with short curved process at midlength, short peg mesally; in lateral view truncate distally with narrow sclerotized band, lateral process attenuate and curving upward, small dorsal process at midlength. Inferior appendages incised near midlength on dorsal and ventral margins; in lateral view, bearing small lobe apically; in ventral view wide basally, narrowing distally and curving inward; in dorsal view, left appendage with row of pegs on mesal ridge, right appendage with numerous pegs basolaterally. Phallus thin and sinuate, truncate apically.

Type material: Holotype; male. México: Tamaulipas, Municipio de Gómez Farias, Río Frio at La Poza Azul, 6 km S. Gómez Farias, 7 August 1988, A. Contreras and A. Moreno (NMNH). Paratypes: Same as holotype, 3 ♂ (NMNH, INHS, UNAM).

Etymology: Named for Atilano Contreras-Ramos who collected the type series.

Ochrotrichia cieneguilla Harris, new species
Fig. 3

Diagnosis: The structure of the inferior appendages places this species in the group containing *O. moselyi* Flint, *O. pectinifera* Flint and *O. arranca* (Mosely). The new species is distinguished by the attenuate dorsal lobe of the inferior appendage which is rounded in the other species of the group.

Description: Male: Length 3.2–3.3 mm. 28 antennal segments. Brown in alcohol. Abdominal segment VII with short ventromesal process. Segment VIII annular. Segment IX rectangular in lateral view, incised dorsally and ventrally on posterior margin; dorsum with posteromesal incision; in ventral view truncate posteriorly,

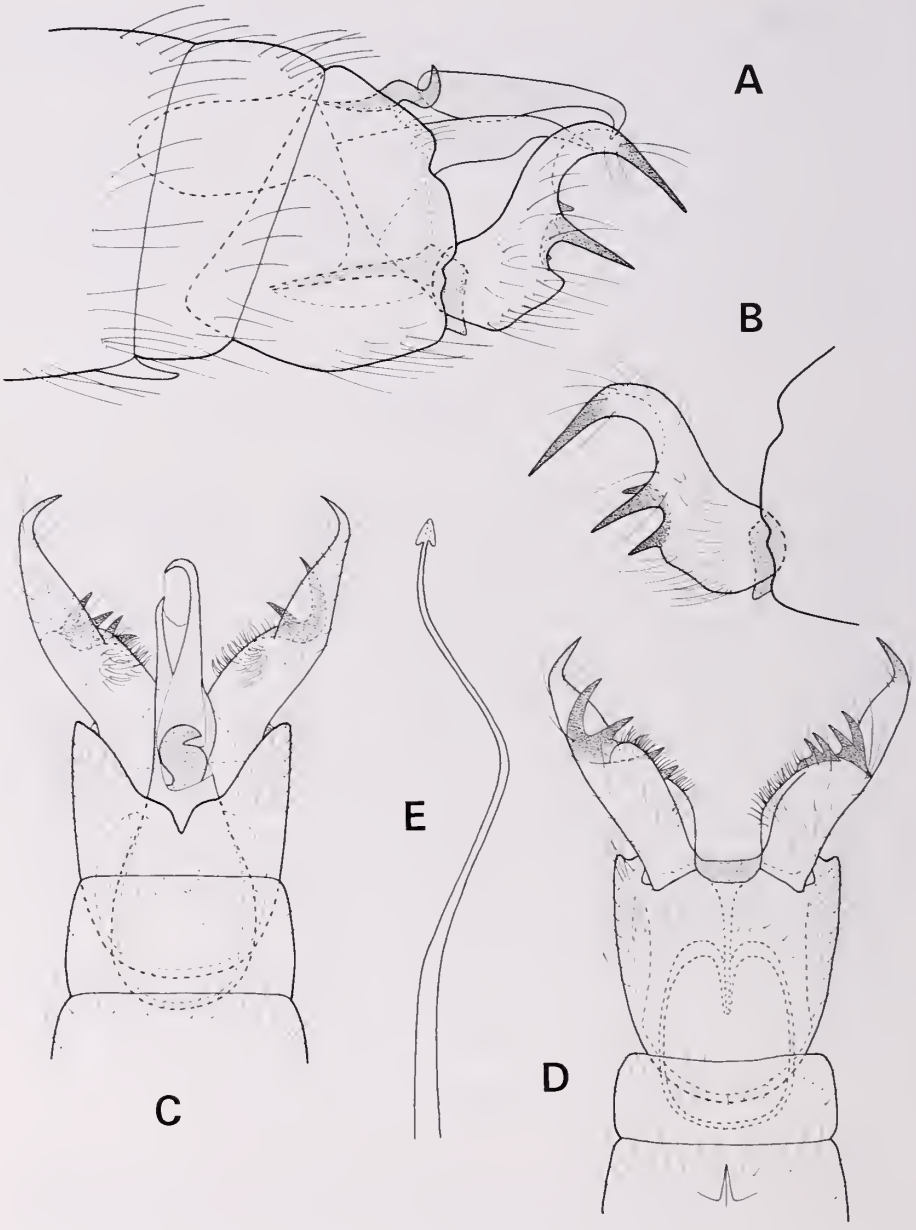

Fig. 3. *Ochrotrichia cieneguilla,* n. sp. Male genitalia. A. Lateral view; B. Right inferior appendage, lateral view; C. Dorsal view; D. Ventral view; E. Phallus, dorsal view.

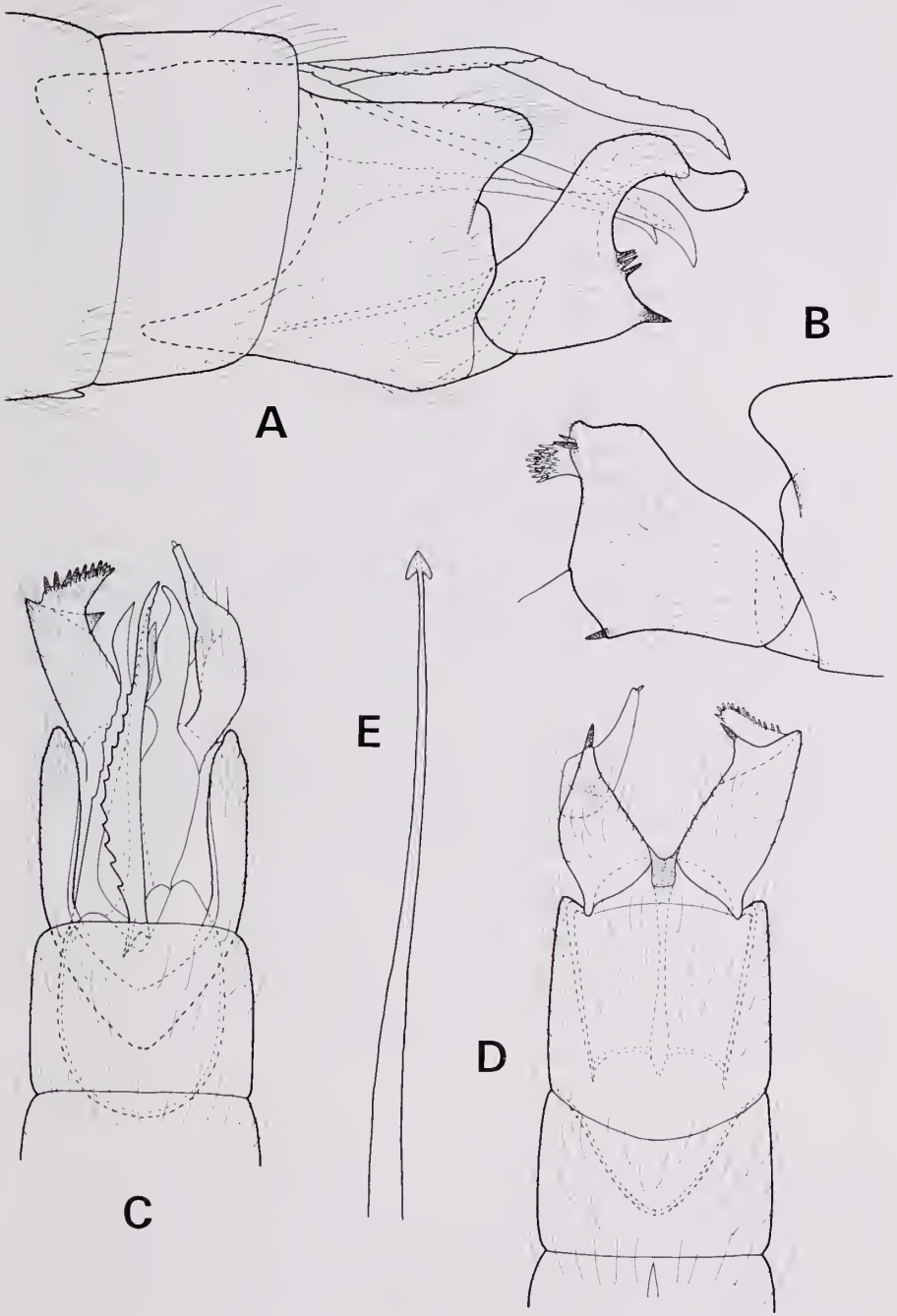

Fig. 4. *Ochrotrichia yepachica,* n. sp. Male genitalia. A. Lateral view; B. Right inferior appendage, lateral view; C. Dorsal view; D. Ventral view; E. Phallus, dorsal view.

lateral margins rounded. Tenth tergum posteriorly divided into two narrow, elongate processes, basally with mesal, hook-like sclerite. Inferior appendages in lateral view narrowing dorsally to elongate sclerotized spine, left appendage with one of the mesal spines elongate, right appendage with two of the mesal spines elongate; in ventral view, right appendage with outer pair of mesal spines longer than inner pair, left appendage with all four spines similar in length. Phallus thin and sinuate, triangular apically.

Type material: Holotype; male. México: Nuevo León, Municipio de Santiago, Cola de Caballo, downstream falls, 3 km SW Cieneguilla, 19 May 1989, S. Harris and A. Contreras (NMNH). Paratypes: Same as holotype, 1 ♂ (NMNH), Rio Blanco, near Aramberri, 10 November 1985, R. Barbra, 1 ♂ (UNAM).

Etymology: Named for the town of Cieneguilla, which is located near Cola de Caballo.

Ochrotrichia yepachica Harris, new species

Fig. 4

Diagnosis: With respect to the inferior appendages, this species is remotely similar to *O. pectinifera* Flint. However, the structure of the tenth tergum with the elongate, serrate mesal process clearly distinguishes *O. yepachica.*

Description: Male: Length 3.1 mm. 24 antennal segments. Brown in alcohol. Abdominal segment VII with short ventromesal process. Segment VIII annular. Segment IX rectangular in lateral view, dorsomesal incision posteriorly; square in ventral view; dorsum deeply incised. Tenth tergum with two elongate mesal processes, serrate dorsal process wide near base, attenuate distally, ventral process thin and tapering distally, right lateral process thin, serrate at midlength, left lateral process wide basally, tapering posteriorly to thin rounded apex; in lateral view dorsal process elongate and narrow, serrate on upper margin, thin, attenuate lateral process projecting ventrad, pair of thin ventral processes which curve downward apically. Inferior appendages asymmetrical; left appendage in lateral view with elongate dorsal lobe bearing stout seta apically, ventral margin produced into heavy spine, series of short spines on posteromesal margin, right appendage triangular in shape, posterodorsally with spinose lobe on inner margin, pair of short spines on outer margin, heavy spine on posteroventral margin; in ventral view, right inferior appendage wide basally, narrowing distally, basal lobe ending in heavy spine, left appendage with dorsal spinose lobe, basally with heavy spine on inner margin. Phallus thin, triangular apically.

Type material: Holotype; male. México: Chihuahua, Río Concheno at Hwy. 16, 12 km SW Yepachic, 25 May 1991, S. Harris and A. Contreras (NMNH).

Etymology: Named for the town of Yepachic which is located near the type locality.

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A NEW SPECIES OF *ACRONEURIA* FROM VIRGINIA (PLECOPTERA: PERLIDAE)

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Abstract.—A new species, *Acroneuria kosztarabi* is described from Tazewell County, Virginia. The new species is distinguished from related species in the male by the penial armature, and in the female by the completely punctate egg and subgenital plate shape.

The Nearctic species of *Acroneuria* Pictet were revised by Stark and Gaufin (1976). Since that work, two additional new species have been described, one from Kentucky (Kondratieff and Kirchner, 1988) and one from Arkansas and Missouri (Poulton and Stewart, 1991). Also Stark and Brown (1991) provided a new name, *A. frisoni* for the species previously regarded as *A. evoluta* Klapalek (sensu Frison, 1942; Stark and Gaufin, 1976). They considered *A. mela* Frison as a synonym of the true *A. evoluta.*

A new species of *Acroneuria* was collected using an ultraviolet light trap along Station Spring Creek in Burkes Garden, Tazewell County, Virginia. Burkes Garden is a rather high (939 m), narrow, "canoe-shaped" anticlinal valley, with the highest point at Beartown Mountain (1,430 m) on the southwestern rim (Hoffman, 1969). This unique region has previously yielded a new stonefly—*Isoperla major* (Nelson and Kondratieff, 1983). The descriptive terminology follows Stark and Gaufin (1976) and Stark and Brown (1991).

Acroneuria kosztarabi Kondratieff and Kirchner, new species
Figs. 1–6

Male: Macropterous. Length of forewings 22 mm; length of body 20 mm. General color pale yellow brown. Head pattern as Fig. 3, prothoracic rugosities not conspicuously darkened (Fig. 3). Wings hyaline, veins light brown. Tergum 9 spinule patch separated and sparse (Fig. 1), tergum 10 spinule patches separated mesally (Fig. 1). Paraprocts slender, finger-like, tips acute (Fig. 1). Aedeagus, dorsally with apical patch of red-brown thick spines expanded, narrowed and connecting basal band (Fig. 4); ventrally apical patch of red brown thick spines cordate and medially interrupted posteriorly (Fig. 5). In lateral view, aedeagus with apical lobe bulbous and elongate tip; basoventral lobe truncate. Basal lobe of aedeagus with short fine hairs.

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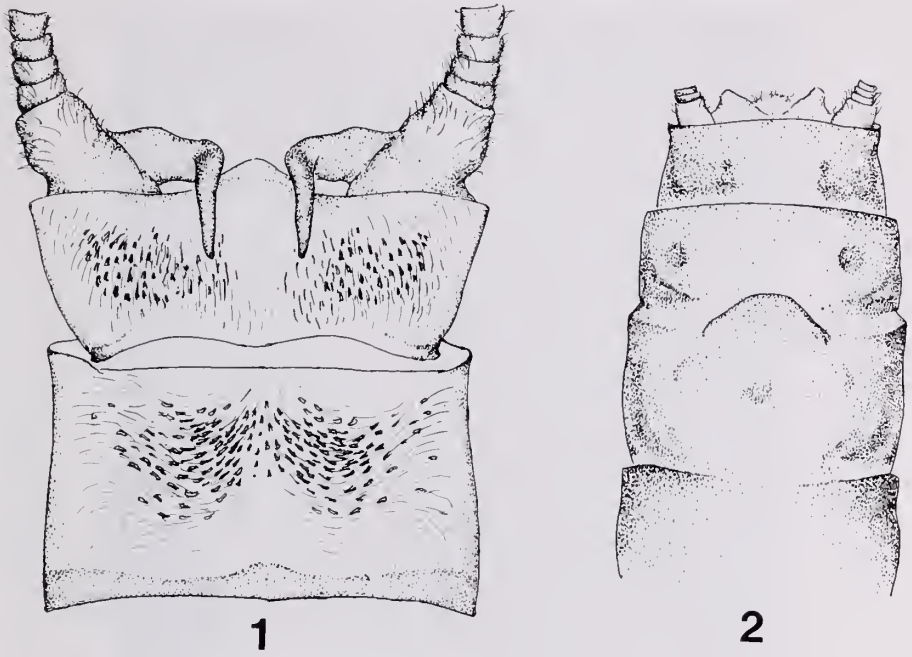
[3] The views of the author do not purport to reflect the position of the Department of the Army or the Department of Defense.



Figs. 1–2. *Acroneuria kosztarabi.* 1. Male terminalia, dorsal view, 2. Female terminalia, ventral view.

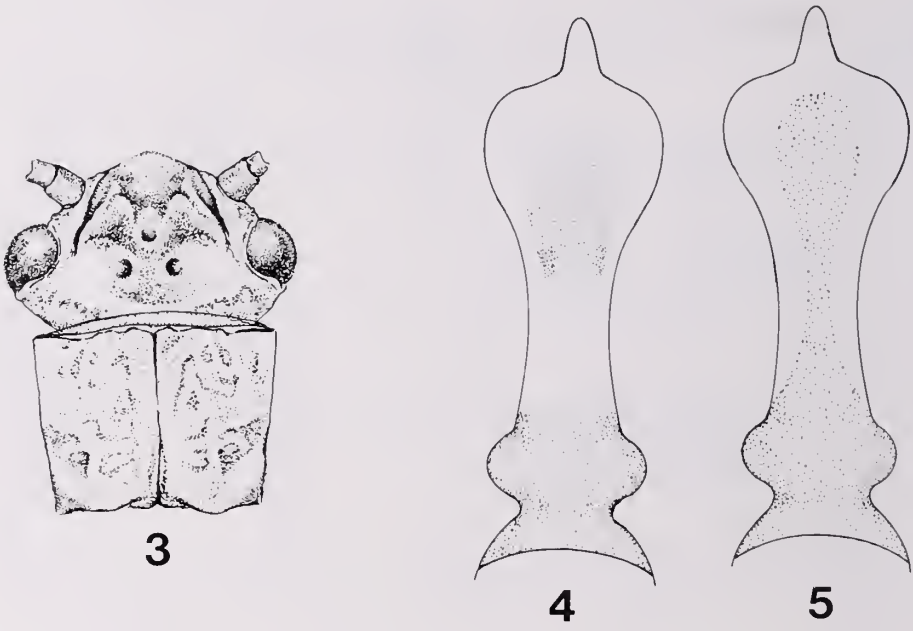
Female: Macropterous. Length of forewing 28–29 mm; length of body 25-27 mm. Color similar to male. Subgenital plate produced over a third or more of sternum 9, anterior outline variable (Fig. 2). Ova pear shaped, cross section circular. Collar buttonlike. Chorion entirely punctate (Fig. 6).

Types: HOLOTYPE male and allotype female, Virginia: Tazewell County, Burkes Garden, UV, 2330 hr, 17 August 1987, V. M. Dalton; Paratypes, Burkes Garden, Flatwoods, 5 July 1987, V. M. Dalton, 1 female; same but (site 1) UV 2200 pm, 6 July 1987, 1 female, same but (site 2) 6 July 1987, 1 female.

The holotype, allotype and a paratype female will be deposited in the National Museum of Natural History. The other paratypes will be deposited in the C. P. Gillette Arthropod Biodiversity Museum, Colorado State University and the Virginia Natural History Museum.

Etymology: The species is named in honor of Dr. Michael Kosztarab, Professor Emeritus, Virginia Polytechnic Institute and State University, for his many contributions to the study of Virginia insects.

Diagnosis: The male of *A. kosztarabi* can be distinguished from similar species with slender finger-like paraprocts (*A. evoluta, A. frisoni, A. filicis* Frison, *A. hitchcocki* Kondratieff and Kirchner, *A. internata* (Walker), *A. ozarkensis* Poulton and Stewart, *A. perplexa* Frison and *A. petersi* Stark and Gaufin) by the penial armature. It is most similar to *A. filicis,* but the basal band completely encircles the aedeagus, and in ventral view it is expanded apically (Figs. 4, 5). The completely punctate egg chorion



Figs. 3–5. *Acroneuria kosztarabi.* 3. Adult head and pronotum, 4. Aedeagus, dorsal, 5. Aedeagus, ventral.

of *A. kosztarabi* (Fig. 6) is similar to *A. flinti* Stark and Gaufin, known from a single female from Fairfax County, Virginia and *A. ozarkensis,* recently described from Arkansas and Missouri. The shape of the subgenital plate of *A. kosztarabi* (Fig. 2) will distinguish it from these two species (apical margin triangularly notched in *A. flinti*; oval shaped and evenly rounded in *A. ozarkensis*). The subgenital plate of the female is similar to *A. filicis,* but the chorion of the latter species is only punctate in the apical third (see Stark and Gaufin, fig. 57).

Stark and Gaufin (1976) divided *Acroneuria* into seven groups based primarily on penial armature and egg characteristics. Based only on penial armature, *A. kosztarabi* could be included in the *perplexa* group, however, using egg characteristics, this species fits the *flinti* group. Poulton and Stewart (1991) suggested that *A. ozarkensis* may also be a member of the *flinti* group based on the egg and dark color (body color of the holotype of *A. flinti* is yellow brown). The pattern of the penial armature of *A. ozarkensis* is similar to *A. perplexa.*

Remarks: With the description of *A. kosztarabi,* eight species of *Acroneuria* have been recorded from Virginia (Kondratieff and Kirchner, 1987). Virginia records of *A. evoluta* should now be considered to be *A. frisoni.* Station Spring Creek, the type locality, is rich in Perlidae, supporting large populations of *Acroneuria carolinensis* (Banks), *Paragnetina media* (Walker) and *Agnetina capitata* (Pictet).

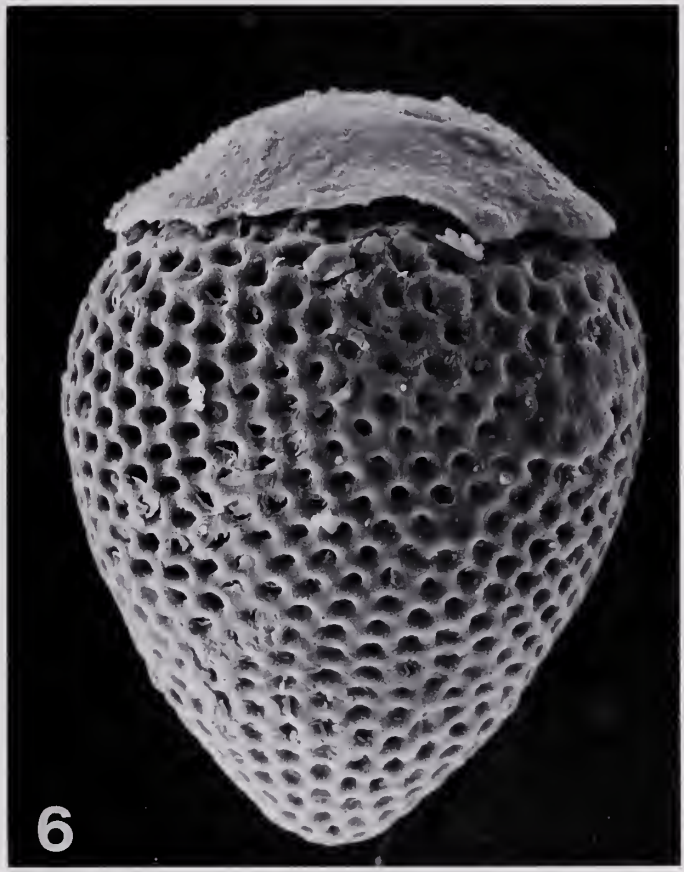


Fig. 6. *Acroneuria kosztarabi*. Ovum, 1.94 × 10^2.

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SYNONYMY OF *PENTACANTHOIDES* METCALF WITH *SINOPHORA* MELICHAR (HOMOPTERA: APHROPHORIDAE), WITH A DISCUSSION ON THE TRIBAL PLACEMENT OF THE GENUS

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Abstract.—The monotypic genus *Pentacanthoides* Metcalf, 1952, is synonymized with the genus *Sinophora* Melichar, 1902. A diagnosis is given for the genus. One new combination, *S. brunnea* (Lallemand), is established. Evidence is given to support the placement of *Sinophora* in the tribe Aphrophorini.

Lallemand (1922) erected the genus *Pentacantha* for a single new species, *P. brunnea,* on the basis of a single female specimen collected by H. Fruhstorfer in Darjeeling, India. The species is still known only from the unique female holotype. In 1952, Metcalf proposed the replacement name *Pentacanthoides* for *Pentacantha* Lallemand, 1922, nec *Pentacantha* Stål, 1871, Öfv. Svenska Vet.-Akad. Förh. 28: 400, and established the new combination *Pentacanthoides brunnea* (Lallemand). Since then, neither the genus nor the species has been mentioned in the literature, except in the catalogue of world Aphrophoridae of Metcalf (1962).

I have recently examined Lallemand's holotype. A direct comparison of the female holotype of *P. brunnea* (Lallemand) with material of *Sinophora* species, clearly revealed the synonymy of the two genera.

GENUS *SINOPHORA* MELICHAR

Sinophora Melichar, 1902:113. Type-species: *S. maculosa* Melichar, 1902, by original designation.

Pentacantha Lallemand, 1922:64. Type-species: *P. brunnea* Lallemand, 1922, by original designation and monotypy.

Pentacanthoides Metcalf, 1952:228; 1962:73. Nom. nov. pro *Pentacantha* Lallemand [1922] [nec *Pentacantha* Stål 1871]. **NEW SYNONYMY.**

Remarks. Sinophora species can be recognized most easily by their hind tibiae which are armed with 3–6 lateral spurs and the structures of the male genitalia, especially the very small subgenital plates, the very large styles and the very complex aedeagus. Although *Sinophora* is readily distinguishable from all other spittlebug genera, the differentiation of the species is considerably more difficult. As in most spittlebugs it is dependent upon the characters of the male genitalia.

Metcalf (1952) placed *Pentacanthoides,* for the first time, in the tribe Ptyelini; later in 1962 he treated the genus as a member of the tribe Philaenini. Examination of specimens clearly assignable to the genus indicates closer affinities to the Aphro-

phorini. I am here moving the *Sinophora* from the Philaenini to the Aphrophorini on the basis of the following characters: (1) crown is short and broad, with a distinct median carina; (2) tylus is very short and broad, about twice as broad as median length; (3) ocelli are nearer to each other than to the eyes; (4) antennal segment three is visible; (5) antennal ledges are thin, foliaceous; (6) face moderately inflated with prominent punctures and a median carina; (7) rostrum long, extending beyond bases of hind legs; (8) pronotum with a median carina, the anterior margin usually distinctly and angularly produced, the anterior lateral margins relatively long; (9) forewings with prominent punctures; and (10) the structures of the male genitalia, especially the very small subgenital plates, the very large styles and the very complex aedeagus.

Sinophora brunnea (Lallemand), NEW COMBINATION

Pentacantha brunnea Lallemand, 1922:65. Holotype ♀, INDIA 'Darjeeling' (BMNH) [examined].

Pentacanthoides brunneus (Lallemand); Metcalf, 1952:228; 1962:74.

Type material. The holotype female is housed in the Natural History Museum, London. It bears the labels: "India, Darjeeling, Juni, Fruhstorfer leg.; LALLEMAND Coll., Brit. Mus. 1955-832; Pentacantha brunnea Lallemand, V. Lallemand determ. 1914." The specimen is in excellent condition.

Remarks. Originally described in *Pentacantha, brunnea* clearly belongs to *Sinophora* on the basis of its general appearance. This species is still known only from the unique female holotype. It will be necessary to associate a male with this species and study the genitalia to establish the correct status.

ACKNOWLEDGMENTS

I wish to thank Mr. Michael D. Webb of the Department of Entomology of the Natural History Museum, London, UK, for the loan of the holotype of *P. brunnea*, and Dr. Christopher H. Dietrich and Mr. Robert L. Blinn of the Department of Entomology, North Carolina State University, Raleigh, North Carolina, USA, for the loan of specimens of *Sinophora*. I would also like to thank Dr. K.G.A. Hamilton, Biosystematics Research Centre, Ottawa, for reviewing the manuscript.

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ON THE IDENTITY OF *CUBANIELLA TROTTERI* RUSSO (HYMENOPTERA: TANAOSTIGMATIDAE)

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Abstract.—The genus *Cubaniella* Russo is synonymized with *Tanaostigmodes* Ashmead, and the placement of *C. trotteri* within *Tanaostigmodes* is discussed.

Resumen.—El género *Cubaniella* Russo es sinonimizad con *Tanaostigmodes* Ashmead, y se reconoce a *C. trotteri* dentro de éste último.

The New World Tanaostigmatidae were recently revised by LaSalle (1987), however he left both the genus *Cubaniella* and the species *C. trotteri* unplaced because he was unable to locate type material, or any other material assignable to this species. Since that time, Dr. G. Viggiani has located the holotype of *C. trotteri,* and kindly loaned it to us for study. Examination of this type reveals that *Cubaniella* is a junior synonym of *Tanaostigmodes* Ashmead, and that *C. trotteri* is a valid species which does not fit into any of the species groups defined by LaSalle (1987).

GENUS *TANAOSTIGMODES* ASHMEAD

Tanaostigmodes Ashmead, 1896:9,18–19. Type species *Tanaostigmodes howardii* Ashmead (original designation).
Cubaniella Russo, 1930:133–134. Type species *Cubaniella trotteri* Russo (original designation). **NEW SYNONYMY**.
Further synonyms of *Tanaostigmodes* are given by LaSalle (1987:13).

Cubaniella would key to *Tanaostigmodes* in the key to tanaostigmatid genera given by LaSalle (1987), and agrees completely with the description. It has remained unplaced solely because specimens have not been available for study previously.

Tanaostigmodes trotteri (Russo)

Tanaostigmodes trotteri (Russo). **NEW COMBINATION.**
Cubaniella trotteri Russo, 1930:134–139. Holotype ♀, Cuba, Havana, galls on *Belaira mucronata* [Portici, examined].

Diagnosis. *T. trotteri* is the only *Tanaostigmodes* with the stigmal vein swollen at junction of the marginal vein (Fig. 1), and this character should serve to distinguish it from any other New World species. Other important characters are: entire dorsum of mesosoma with coriaceous (engraved) sculpture; basal cell of fore wing without any setae on dorsal surface (some setae present on ventral surface); scape without

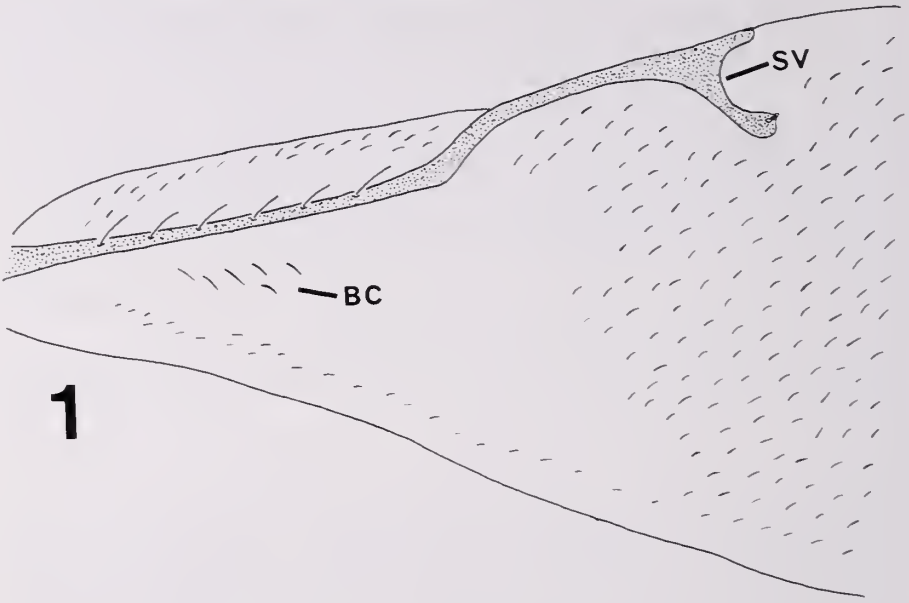

Fig. 1. *Tanaostigmodes trotteri* (Russo), ♀, base of fore wing. bc = basal cell (note that these setae are on the ventral surface of the wing; sv = stigmal vein).

ventral expansion, more than 3 times longer than wide; body without metallic coloration; scrobal impression not carinate; frons without transverse furrow.

Type material. Russo (1930) did not state how many specimens he had when he described *C. trotteri,* however he did state: "Tipo.—Coll. R. Labor. Entom. Portici." His use of the singular indicates that he did consider a unique specimen as the holotype, and we consider the specimen sent to us by Dr. Viggiani to be this holotype. It was the only specimen that Dr. Viggiani could locate in the collection in Portici, and it bears a label stating, "Cubaniella Trotteri Russo; Habana (Cuba)." We have added a holotype label to this specimen.

The holotype is glued to the point with the face down, so that the lower scrobes and area between the toruli are hidden. The antennae are broken (one antenna is missing the flagellum past F4, the other the flagellum past F2). It appears, however, that there should be at least some funicular segments that are quadrate and not distinctly longer than wide (see also illustrations in Russo, 1930).

Discussion. *T. trotteri* does not fit into any of the species groups defined by LaSalle (1987). It would key correctly as far as couplet 16 in his key to species of *Tanaostigmodes.* This couplet gives the options:

16. Scutellum coriaceous. Speculum separated from posterior margin of wing by more setae (on ventral surface) than a single line representing subcubital vein. Face and frons with scattered, minute punctures. 17

16′. Scutellum reticulate, imbricate, or with otherwise raised sculpture. Speculum usually open to posterior margin of wing, or at most separated by a single line of setae representing subcubital vein; only rarely separated from posterior margin of wing by

Table 1. **Caribbean Tanaostigmatidae.** Distributional information taken from LaSalle (1987). An asterisk (*) indicates that a species is known only from one locality. Abbreviations as follows: B, Barbados; BI, Bahama Islands; C, Cuba; CA, Central America; CI, Cayman Islands; D, Dominica; DR, Dominican Republic; F, Florida; G, Grenada; H, Haiti; J, Jamaica; M, Mexico; PR, Puerto Rico; SA, South America; T, Trinidad; VI, Virgin Islands.

Species	Distribution	
	Caribbean	Other
Tanaoneura ashmeadi Howard	*G	
Tanaoneura flavilineata LaSalle	*T	
Tanaoneura portoricensis (Crawford)	PR, VI	CA, SA
Tanaostigma bennetti LaSalle	*T	
Tanaostigma chapadae (Ashmead)	T	SA
Tanaostigma coursetiae Howard	DR, PR	CA, M
Tanaostigma slossonae (Crawford)	BI, C	F
Tanaostigmodes anellarius LaSalle	BI	M
Tanaostigmodes dominicensis LaSalle	*D	
Tanaostigmodes haematoxyli (Dozier)	C, CI, D, H, J	M
Tanaostigmodes mayri Ashmead	*G	
Tanaostigmodes tenuisulcus LaSalle	*BI	
Tanaostigmodes tetartus Crawford	B	SA
Tanaostigmodes trotteri (Russo)	*C	

more setae than a single line. Face and frons usually without, rarely with, scattered minute punctures. 18

T. trotteri possesses a coriaceous (lightly engraved) scutellum, however the speculum is separated from the posterior margin of the wing by only a single line of setae, and the face and frons do not have any punctures. It can be separated from the two species of *Tanaostigmodes* which would key at couplet 16 as having the scutellum coriaceous (*T. kiefferi* (Mayr), *T. insculptus* LaSalle) by two additional characters.

In *T. trotteri* the stigmal vein is distinctly swollen basally where it joins marginal vein (Fig. 1). This character is unique among all species of *Tanaostigmodes.*

In *T. trotteri* the basal cell has no setae on the dorsal surface of wing (Fig. 1) (although there are 5–6 setae on the ventral surface). There are over 30 setae in the basal cell of *kiefferi* and *insculptus.*

Biology. *C. trotteri* has been reared from a gall on *Belaira mucronata* (Fabaceae: Faboidea) (Russo, 1930).

Caribbean Tanaostigmatidae: The 14 species of Tanaostigmatidae presently known from the Caribbean are listed in Table 1, along with their distribution within the Caribbean and outside of the region. Three species are known from Cuba, with *T. trotteri* being known only from Cuba.

Seven of the 14 species are known only from a single locality, however it is highly unlikely that tanaostigmatids actually display such a high percentage of endemism. This pattern is more likely to be due to inadequate collections and our poor knowledge of the Caribbean fauna than to most of these species actually being endemic to a single island.

It is certain that further collecting in the area will show that there are several more tanaostigmatid species present, and that the range of most species is greater than currently known. However, due to the fragility of island ecosystems, many species are probably already eliminated through much of their original range, so that we will never know the true extent of their former distributions.

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We would like to thank Dr. G. Viggiani for kindly locating and loaning us the holotype of *C. trotteri.*

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DISCONTINUOUS DISTRIBUTION AND SYSTEMATIC RELATIONSHIPS OF THE GENUS *OROTHRIPS* (THYSANOPTERA: AEOLOTHRIPIDAE) AND RELATED TAXA IN MEDITERRANEAN CLIMATES

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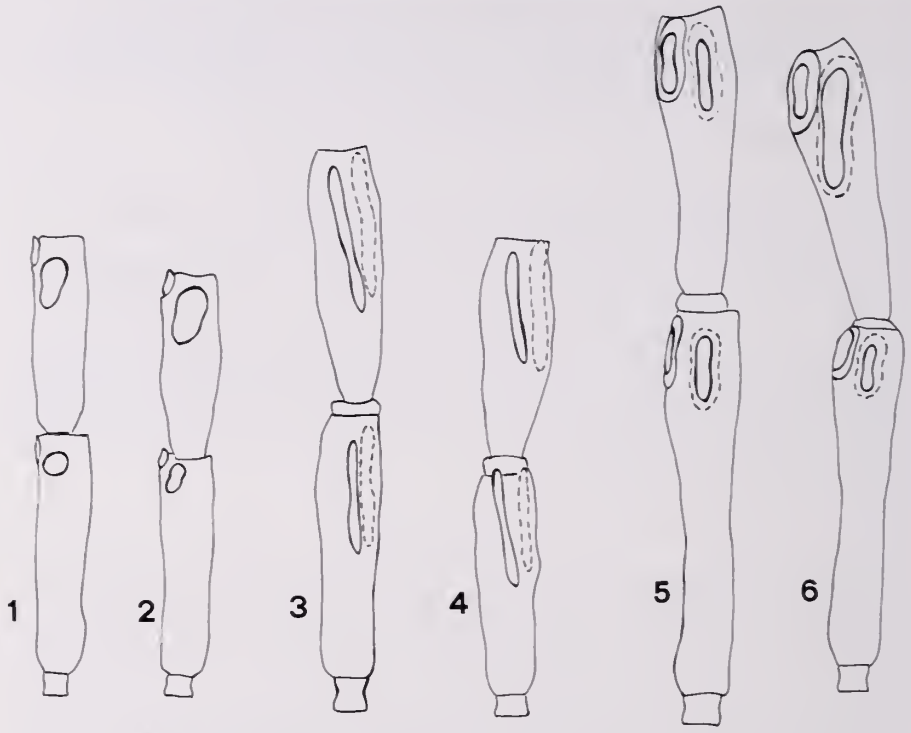
Abstract.—A key is provided to the three species of *Orothrips,* and two new synonyms are recognized. Two of these species are from western U.S.A. but the third is from southern Europe. This discontinuous distribution, also similar distribution patterns amongst other taxa in the basal clades of the Thysanoptera which involve the five areas of the world with a Mediterranean climate, is discussed. The systematic significance of the duplicated antennal sensoria found in *Orothrips* species is briefly discussed.

The genus *Orothrips* has been used for a group of large, flower infesting, banded-winged thrips which have two sensoria on each of antennal segments III and IV. Four species have been described from California and Oregon, and one species from India. In recent independent studies the authors concluded that the monobasic Mediterranean genus *Ekplectothrips* cannot be distinguished from *Orothrips.* Mound (1991) synonymized *Ecplectothrips* with *Orothrips* without further comment about the included species. Marullo (in press) compared the antennae and other morphological features of *Orothrips kelloggii* Moulton, *O. yosemitii* Moulton and *Ekplectothrips priesneri* Titschack, and concluded that they were congeneric. The purpose of this paper, therefore, is to re-examine the six nominal species, and to consider the systematic relationships of *Orothrips* and the geographic distribution of the included species. The members of this genus and those of several related genera appear to be associated largely with one or more of the five major areas in the world with a "Mediterranean" climate and vegetation.

OROTHRIPS MOULTON

Orothrips Moulton, 1907:45. Type-species *O. kelloggii* Moulton, by monotypy.
Ekplectothrips Titschack, 1958:4. Type-species *E. priesneri* Titschack, by monotypy. Synonymized by Mound, 1991:649.
Ecplectothrips Titschack, 1960:3. Invalid emendation.

Members of this genus are large dark-bodied Aeolothripinae, and share the following characters: Antennae 9-segmented, III and IV each with two sensoria. Head with no long setae; maxillary palps usually with more than three divisions. Pronotum with posteroangular setae no more than 1.5 times as long as discal setae; fore tarsus with a recurved claw and apposed seta. Mesopreepisternum not distinct; metanotal median setae near posterior margin. Forewing broad with transverse dark bands. Abdominal sternites with 4 pairs of marginal setae, but no discal setae.



Figs. 1–6. Antennal segments III and IV of *Orothrips* species. Female and male: 1–2, *O. yosemitii*; 3–4, *O. kelloggii*; 5–6, *O. priesneri*.

KEY TO SPECIES OF *OROTHRIPS*

1. Sensoria on antennal segment III strongly emergent, each produced into a broadly based sense cone (Figs. 1, 2) ..... *yosemitii*
– Sensoria on antennal segment III scarcely emergent, not produced into sense cones ... 2
2. Antennal segment III almost parallel sided, with sensoria slender, 4 to 10 times as long as wide (Figs. 3, 4) ..... *kelloggii*
– Antennal segment III club-shaped, distal third distinctly broader than basal two-thirds, sensoria broad, scarcely 1.5 times as long as wide (Figs. 5, 6) ..... *priesneri*

Orothrips kelloggii Moulton

Orothrips kelloggii Moulton, 1907:45.
Orothrips keeni Moulton, 1927:183. **NEW SYNONYMY**.

This species was described from nine males and six females collected in California, and it is now known from British Columbia, Oregon and Arizona (Bailey, 1957). It is found particularly in the flowers of *Arbutus*, *Arctostaphylus* and *Ceanothus*, and is sometimes taken with *O. yosemitii*. Bailey (1949) gives notes on its life history.

Moulton described *keeni* from a single small female from Oregon, which he distinguished by the "less deeply coloured" wing bands, and the sensory areas on the antennae being "distinctly shorter." Examination of more than 30 females of *kelloggii* from California and Oregon has indicated that an allometric relationship exists between the length of antennal segment III and the length of its longest sensory area. These two measurements are given here in microns for four females: the largest available female 135/55; the two smallest available females 93/36 and 90/16; the holotype female of *keeni* 84/20. The wing colour of the *keeni* holotype falls within the range of variation shown by material of *kelloggii*. Since *keeni* cannot be distinguished from *kelloggii* on any other characters it is here placed in synonymy. Males of *kelloggii* are smaller than females, but there are no significant differences in the antennal sensoria (Figs. 3, 4).

Orothrips yosemitii Moulton

Orothrips kelloggii yosemitii Moulton, 1911:34.
Orothrips yosemitei (sic) Moulton; Moulton, 1927:183.
Orothrips raoi Moulton, 1927:184. **NEW SYNONYMY**.
Orothrips variabilis Moulton, 1927:184.

This species was described from an unspecified number of syntypes collected in California. It is widespread and abundant in California, particularly on *Ceanothus* blossoms in spring, and is known from British Columbia, Washington, Oregon and Wyoming. Bailey (1949) recognized that *variabilis* represented the same species. Moreover, he was unable to find any characters to distinguish the holotype female of *raoi* from *yosemitii* satisfactorily. This specimen was apparently sent to Moulton from India with a sample of *Thrips florum,* according to his collections record card in the California Academy of Sciences. However, the species has never been collected again in India (Bhatti, 1991), and because the holotype cannot be distinguished from *yosemitii* females, it seems likely that it entered the Indian sample after this arrived in California. Moulton gave no characters to distinguish the species; he stated "Very similar to *yosemitei* and yet I cannot assign it to that species." Under these circumstances the species is here placed in synonymy. Males of *yosemitii* are slightly smaller than females, but have the sensoria on segment IV distinctly larger than those of females (Figs. 1, 2).

Orothrips priesneri (Titschack), **New Combination**

Ekplectothrips priesneri Titschack, 1958:5–10.

Although described originally from a single female collected in Spain, this species is widespread in the Mediterranean region from Spain to Turkey, and is common in southern Italy between March and May. Adults of both sexes have been taken in the flowers of a wide range of plants, particularly *Crataegus* and other Rosaceae. However, the larvae have not been collected and the true host-plant remains unknown. Females vary considerably in size, but the lengths of antennal segment III and its sensoria do not seem to have an allometric relationship, unlike *kelloggii*. The sensoria on segment IV of males are considerably larger than those of females (Figs. 5, 6).

SYSTEMATIC RELATIONSHIPS

The species of *Orothrips,* unlike almost all other Aeolothripidae, have two sensoria on both the third and the fourth antennal segments. This condition is otherwise found in this family only in the six species of *Dactuliothrips* and the single species of *Cycadothrips.* The remaining 240 or so species in the other 23 genera of Aeolothripidae all have only a single sensorium on each of these two antennal segments.

The phylogenetic significance of this apparent duplication of the antennal sensoria is difficult to assess, whether it is an apomorphy uniting the three genera or a symplesiomorphy derived from a common ancestor. The first seems inherently unlikely due to the very considerable differences between the three genera; *Dactuliothrips* species have long setae on the head and pronotum as in typical Melanthripinae; *Cycadothrips* has males unlike any other member of the family, and *Orothrips* species are otherwise similar to typical Aeolothripinae. The possibility that the sensoria represent a plesiomorphic condition must therefore be considered further.

The plesiomorphic structure of the sensoria on the third and fourth antennal segments of Terebrantia is presumably the circumpolar condition retained by the Merothripidae, the family which retains the largest number of plesiomorphies (Mound, Heming and Palmer, 1980). This condition is also found in the Heterothripidae, and the Melanthripinae of the Aeolothripidae, these groups also being amongst the least advanced Terebrantia. Some Aeolothripid species have the sensoria partially encircling the apex of each segment before extending basally (e.g., *Desmothrips*), although in *Aeolothrips* species the sensoria are usually shorter and linear. A further possible condition, with a circumpolar area extending basally as a pair of linear sensoria, is found in *Aulacothrips* and *Lenkothrips* of the Heterothripidae (see figs. in Mound *et al.,* 1980) and *Euceratothrips* of the Aeolothripidae. This may indicate the way in which twin sensoria evolved on antennal segments three and four, but the condition has been expressed rarely. It is not evidence that the three genera discussed here are closely related, although each may represent a basal branch within its own lineage. This is not the place for a phylogenetic analysis of aeolothripid genera. However, it seems possible that genera such as *Desmothrips* and *Stomatothrips,* which are currently placed in the Orothripini because they have subdivided maxillary palps (Priesner, 1949), are actually more closely related to *Aeolothrips* in the Aeolothripinae than they are to *Orothrips.*

GEOGRAPHIC RELATIONSHIPS

Most species of the insect order Thysanoptera live in the humid tropical and subtropical parts of the world, and the most plesiomorphic family, the Merothripidae, is restricted to such areas, as is the Uzelothripidae. The largest family, the Phlaeothripidae, is mainly tropical, although one genus, *Haplothrips,* has evolved many species in the flowers of various Asteraceae in temperate regions. The other large family, the Thripidae, is probably also mainly tropical, but is well represented in temperate regions with several genera restricted to such areas. The largest genus, *Thrips,* was considered to be primarily northern temperate until recently, but is now recognized to have many species in the Old World tropics although none in the Neotropics (Palmer, 1992). The other four families, all of which represent clades basal to the

Thripidae and Phlaeothripidae (Mound *et al.*, 1980), are relatively small, with restricted distributions.

The Heterothripidae includes about 50 species widespread in north and south America. In contrast, the Aeolothripidae includes more than 200 mostly holarctic species, with two genera predominating, *Aeolothrips* in the holarctic and *Melanthrips* in the paleartic. In this family, *Orothrips* now includes three species: two from western North America and one from the Mediterranean. This disjunct distribution is interesting because it is also found at generic level in the family Adiheterothripidae. This small family includes just two genera: *Oligothrips,* with a single species from California and Oregon, and *Holarthrothrips,* with several closely related species from the Mediterranean across to India, possibly associated with date palms. Furthermore, in the Aeolothripidae-Melanthripinae, the genus *Ankothrips* has 11 species, distributed as follows: seven between New Mexico and Washington State, two Mediterranean, two central Europe, and one from South Africa. Similarly, *Cranothrips,* which is scarcely separable from *Ankothrips,* has one species in South Africa and seven in Australia. Moreover, the genus *Dorythrips,* also a Melanthripine, has one species from Chile and two from Western Australia. Finally, the seventh recognized family, the Fauriellidae, includes three genera, two from South Africa and one from Spain, Turkey and Germany.

In contrast to the pantropical distributions of the two largest and most advanced families, the smaller families in the more basal clades, Fauriellidae, Adiheterothripidae and Aeolothripidae, have more restricted distributions. The taxa discussed here appear to be involved with the five areas of the world that have a "Mediterranean" climate of winter rainfall and hot summers; California, Chile, southern Australia, South Africa, and the Mediterranean. However, the floras of these five areas are not closely related to each other, and it is not possible to decide whether the thrips distributions are determined by ecological factors or represent some form of relict distribution.

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DESCRIPTIONS OF NYMPHS OF THE PLANTHOPPER *HARMALIA ANACHARSIS* FENNAH, A SPECIES NEW TO THE UNITED STATES (HOMOPTERA: DELPHACIDAE)

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Abstract.—Adult male and female genitalia and first through fifth instar nymphs of the delphacid planthopper *Harmalia anacharsis* Fennah, collected from Amazon swordplant (*Echinodorus paniculatus* Micheli, Alismataceae) in southern Florida, are described and illustrated, and a key to instars is provided. Features useful in separating nymphal instars include differences in body size and proportions; spination of metatibiae, metatibial spurs, and metatarsomeres; and number of metatarsomeres.

The delphacid planthopper *Harmalia anacharsis* Fennah was first described from New Caledonia in the South Pacific (Fennah 1969). Since its initial description it has been found in Indonesia, the Philippine Islands, Sri Lanka and Vietnam (Wilson and Claridge, 1991). This delphacid has often been collected in rice fields but is not considered a pest, and may feed on some other host plant or plants (Claridge and Wilson, 1981; Holdom *et al.,* 1989). The adult brachypterous male of *H. anacharsis* was described, and the head and genitalia illustrated by Fennah (1969). Adults and nymphs of this delphacid were collected (by JHT) on Amazon swordplant (*Echinodorus paniculatus* Micheli, Alismataceae) in southern Florida. Adult males can be separated from other delphacids by the morphology of the external genitalia. At present, too little is known about delphacid nymphal morphology to allow comparisons among taxa. The present paper includes the first report of this species in the New World and detailed descriptions and illustrations of adult male and female genitalia, and first through fifth instar nymphs and a key for the separation of nymphal instars.

DESCRIPTION

Specimens used for description are housed in the Central Missouri State University insect collection and have the following collecting data: UNITED STATES: FLORIDA: Broward County, Fort Lauderdale, 11 April 1989, ex. Amazon swordplant (5 males, 10 females, 56 first instars, 27 second instars, 2 third instars, 4 fourth instars, 5 fifth instars).

The fifth instar is described in detail but only major differences are described for fourth through first instars. Arrangement and number of pits is provided for the fifth and fourth instars; this information is not given for earlier instars because the pits are extremely difficult to discern (those that could be observed relatively easily are

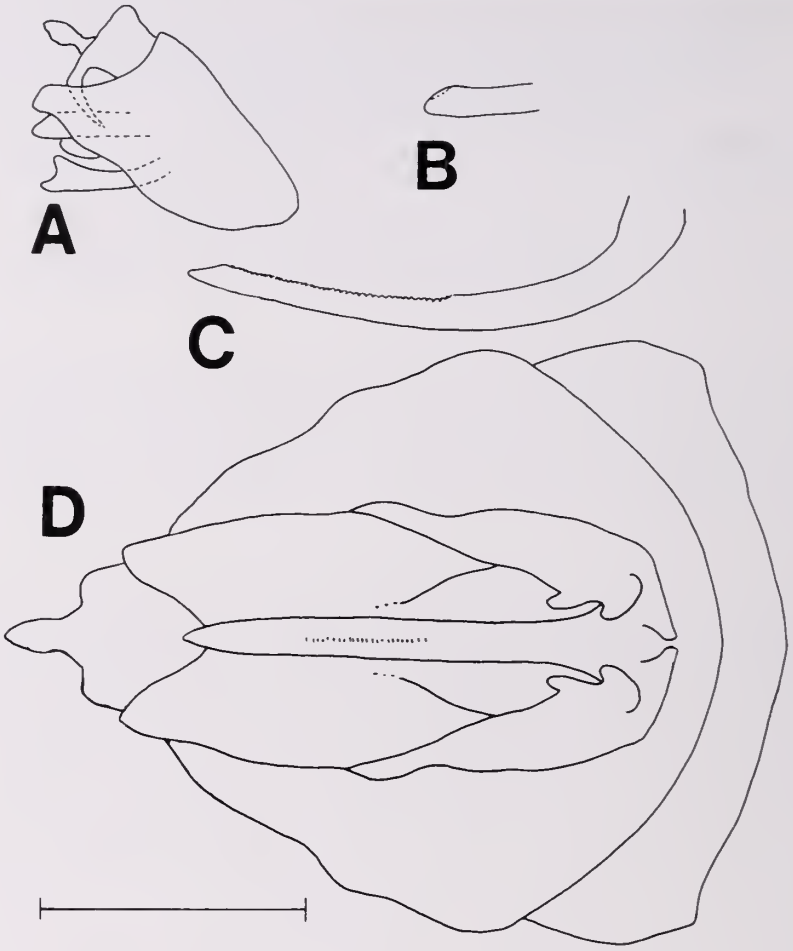

Fig. 1. *H. anacharsis* adult genitalia. A. Lateral view of male genitalia. B. Lateral view of aedeagus. C. Lateral view of ovipositor (median gonapophyses of segment 9). D. Ventral view of female genitalia. Bar = 0.5 mm.

illustrated). Measurements are given as mean ± SD. Length was measured from apex of vertex to apex of abdomen, width across the widest part of the body, and thoracic length along the midline from the anterior margin of the pronotum to the posterior margin of the metanotum.

Adults (Fig. 1A–D): Adults of *H. anacharsis* from Florida were found to be identical in all respects to specimens from Indonesia and the Philippine Islands with the following data: INDONESIA: WEST JAVA: Cikampek, January 1986, ex. rice, coll. D. Holdon (7 males) (S. W. Wilson Insect Collection); PHILIPPINE ISLANDS: LUZON ISLAND: GBTN Lightrap, February 1976 (1 male) (British Museum (Nat-

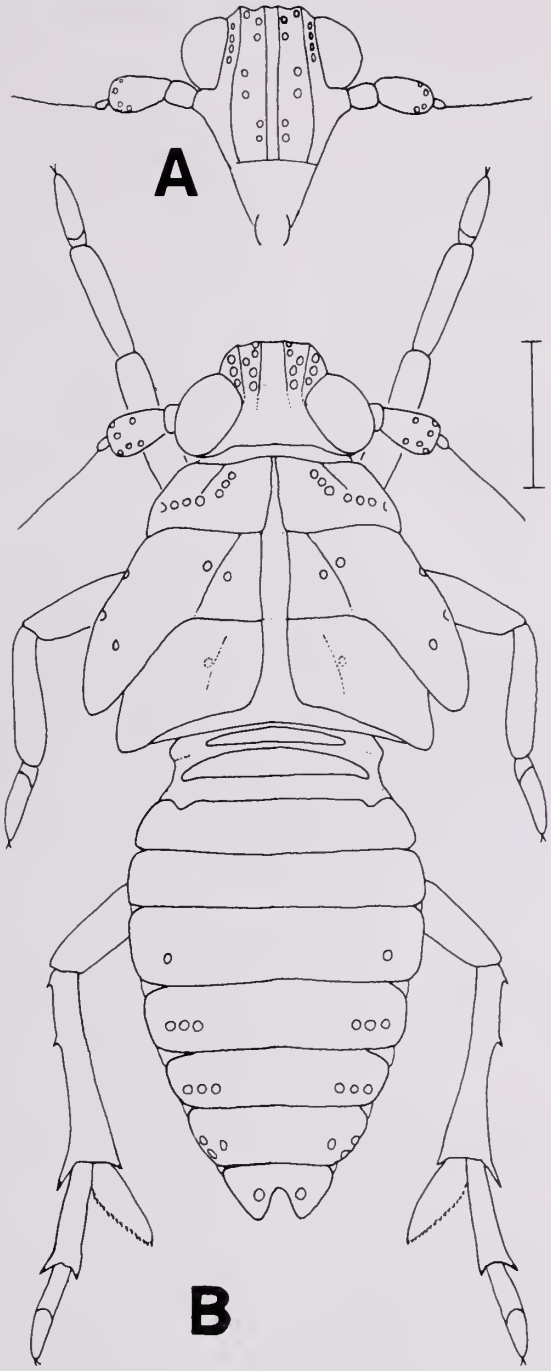

Fig. 2. *H. anacharsis* fifth instar nymph. A. Frontal view of head. B. Habitus, dorsal view. Bar = 0.5 mm.

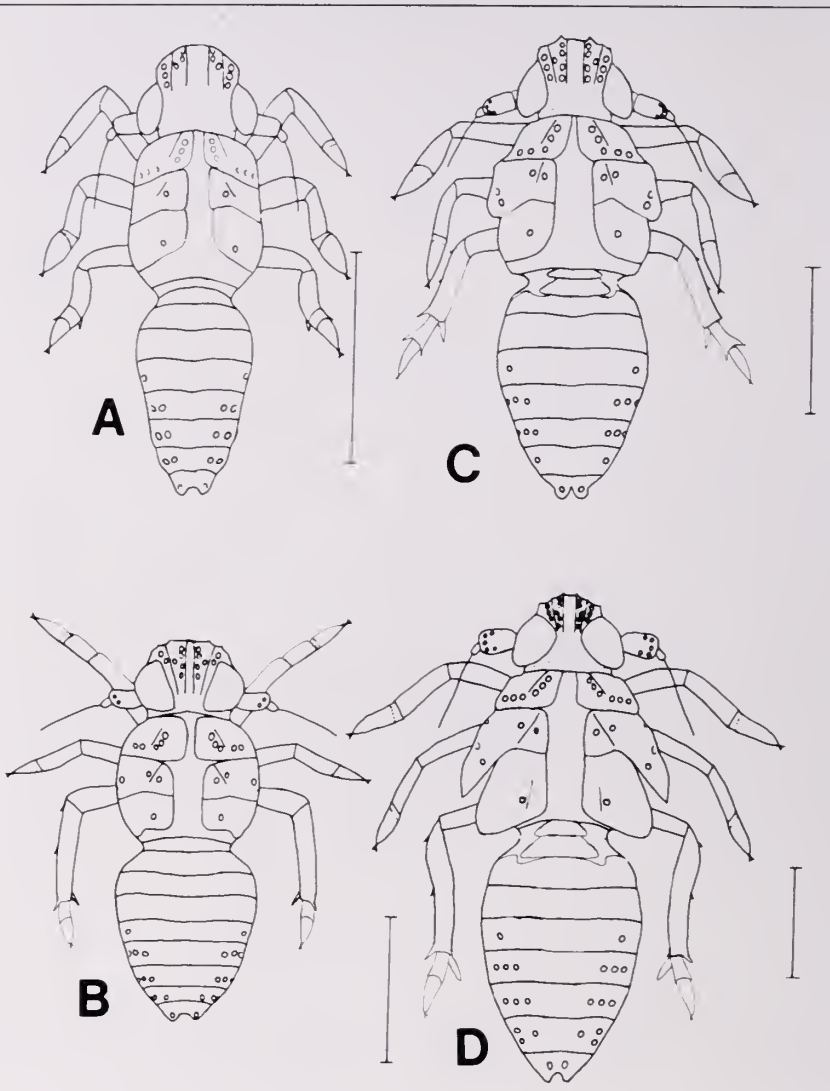

Fig. 3. *H. anacharsis* first through fourth instar nymphs. A. First instar. B. Second instar. C. Third instar. D. Fourth instar. Bars = 0.5 mm.

ural History)). Male genitalia were illustrated by Fennah (1969) and Wilson and Claridge (1991).

Male genitalia (Fig. 1A, B): Pygofer, in lateral view, subtriangular; in caudal view, diaphragm armature subtriangular. Anal tube with a pair of elongate ventrally directed spines originating on dorsocaudal aspect of the tube. Styles broadest across basal third (Wilson and Claridge, 1991, fig 3.109); with short, thumb-like projection bearing an elongate seta on median aspect near base; flaring slightly near apex, with

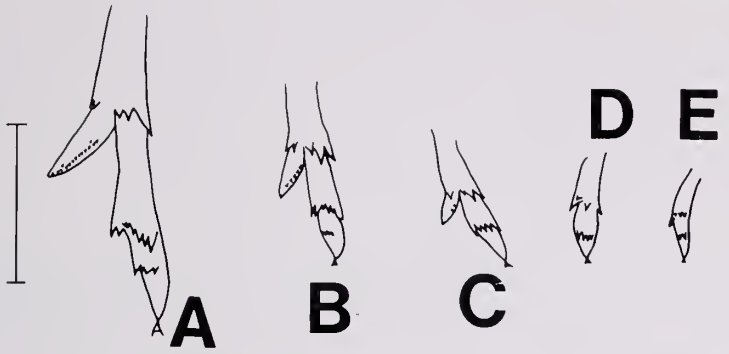

Fig. 4. *H. anacharsis* apices of metathoracic legs, plantar surface. A. Fifth instar. B. Fourth instar. C. Third instar. D. Second instar. E. First instar. Bar = 0.5 mm.

elongate thumb-like projection on median aspect. Aedeagus subcylindrical, with no ornamentation; gonopore subapical, dorsal.

Female genitalia (Fig. 1C, D): Terminology used in the description of the female genitalia follows Asche (1985) and Heady and Wilson (1990). Tergite nine oriented anteroventrally (see Asche 1985), elongate, longitudinally concave in ventral midline. Anal tube subcylindrical. Valvifers of segment eight each covering approximately one-third of tergite nine anterolaterally; with two lobe-like processes in anterior one-fourth on medial aspect. Lateral gonapophyses of segment nine elongate, broadly rounded posteriorly. In lateral view, median gonapophyses of segment nine saber-shaped, with approximately thirty-five shallow teeth on dorsal margin in distal one-half and four to five teeth present on posterior-most portion of ventral margin (not all teeth apparent in ventral view). Gonapophyses of segment eight slender, subacute apically.

Fifth instar (Figs. 2A, B; 4A): Length 3.3 ± 0.12; thoracic length 0.9 ± 0.10; thoracic width 1.2 ± 0.09; N = 5.

Form elongate, subcylindrical slightly flattened dorsoventrally. Widest across mesothoracic wing pads. Body whitish, infused with light brown (when preserved in alcohol); antennal segments and apices of tarsi darker brown.

Vertex subquadrate; length ca. 3× width at base; anterior one-half with two pairs of longitudinal carinae which extend onto frons. Frons with outwardly convex outer carinae forming lateral margins; paralleled by straight inner carinae; nine pits (seven visible in frontal view) between each inner and outer carina; four pits between each outer carina and eye. Clypeus narrows distally; basal postclypeus subconical, distal anteclypeus cylindrical. Beak extends to base of metatrochantors, three segmented; segment one obscured by anteclypeus; segment three slightly longer than segment two, apex black. Antennae three segmented; scape short, cylindrical; pedicel subcylindrical, 2× length of scape, with 10 sensoria; flagellum bulbous at base, one-fourth length of pedicel.

Thorax divided by a mid-dorsal line into three pairs of plates. Pronotal plates subrectangular; each plate with anterior margin slightly concave, posterolaterally directed carina and a row of seven pits paralleling the carina (lateralmost pits barely

visible in dorsal view). Mesonotum median length slightly longer than that of pronotum; wingpads extend from two-thirds the distance to apices of metanotal wingpads to the apices of the wingpads; each plate with a posterolaterally directed carina, one pit on either side of each carina, and three pits on lateral aspect of wingpad. Metanotum median length subequal to that of pronotum; wingpads extend to second tergite; weak carinae extend posterolaterally from near anterior margin; one weak pit lateral to carina. Pro- and mesocoxae elongate and directed posteromedially. Metacoxae fused to sternum. Metatibia with two spines on lateral aspect of shaft; transverse apical row of five black-tipped spines on plantar surface; moveable spur subtriangular, flattened, with one apical tooth and eleven to fifteen marginal teeth. Pro- and mesotarsi with two tarsomeres; tarsomere one wedge-shaped; tarsomere two subconical, with two apical claws and a membranous pulvillus. Metatarsi with three tarsomeres; tarsomere one with apical transverse row of seven black-tipped spines; tarsomere two with apical transverse row of four black tipped spines, ca. 0.5× length of tarsomere one; tarsomere three subequal in length to tarsomere two, with two apical claws and a membranous pulvillus.

Abdomen nine segmented; widest across fourth and fifth segments. Tergite one small, partially obscured by juncture of thorax and abdomen. Tergite two subtriangular; not extending to lateralmost aspect of segment. Tergites five through eight each with the following number of pits on either side: tergite five with one pit, six through eight each with three pits. Segment nine surrounding anus; three pits on each side; females with pair of processes extending posteriorly from juncture of tergites eight and nine; males lacking processes.

Fourth instar (Fig. 3D, 4B): Length 2.4 ± 0.08; thoracic length 0.8 ± 0.06; thoracic width 0.9 ± 0.05; N = 4.

Antennal pedicel with six sensoria; basal portion of antennal flagellum one-third length of pedicel.

Mesonotal wingpads shorter, covering up to one-half of metanotal wingpad laterally. Metatibial spur smaller, with one apical tooth and five to seven marginal teeth. Metatarsi with two tarsomeres; metatarsomere one with apical transverse row of six black-tipped spines; metatarsomere two with three black-tipped spines in middle of tarsomere.

Third instar (Figs. 3C, 4C): Length 1.6 ± 0.01; thoracic length 0.6 ± 0.04; thoracic width 0.6 ± 0.03; N = 2.

Antennal pedicel with four sensoria; length of base of antennal flagellum 0.5× that of pedicel.

Mesonotal wingpads shorter, barely extending onto metanotal wingpads. Metatibial spur smaller, with one apical tooth and one to two marginal teeth. Metatarsomere one with apical transverse row of five black-tipped spines.

Second instar (Figs. 3B, 4D): Length 1.3 ± 0.03; thoracic length 0.5 ± 0.03; thoracic width 0.4 ± 0.02 N = 10.

Antennal pedicel with two sensoria.

Mesonotal length subequal to that of pronotum; wingpads undeveloped. Metatibia with apical row of three spines; spur with one apical tooth and no marginal teeth, ca. 3× longer than longest metatibial spine. Metatarsomere one with four apical black-tipped spines.

First instar (Figs. 3A, 4E): Length 1.0 ± 0.04; thoracic length 0.4 ± 0.02; thoracic width 0.3 ± 0.02 N = 10.

Antennal pedicel lacking sensoria.

Metatibia lacking lateral spines on shaft; spur smaller, ca. 1.5× longer than longest metatibial spine.

Abdominal tergites six through eight each with two lateral pits on either side.

KEY TO *H. ANACHARSIS* NYMPHAL INSTARS

1. Metatibial spur with five or more marginal teeth (Figs. 4A, B); mesonotal wingpads extending to half length of metanotal wingpads (Figs. 2B, 3D) 2
   Metatibial spur with fewer than five marginal teeth (Figs. 4C–E); mesonotal wingpads not extending beyond half length of metanotal wingpads (Figs. 3A–C) 3
2. Metatarsi with three tarsomeres; metatibial spur with more than ten marginal teeth (Fig. 4A) ..... 5th instar
   Metatarsi with two tarsomeres; metatibial spur with fewer than eight marginal teeth (Figs. 4B–E) ..... 4th instar
3. Metatibia with transverse row of five apical spines; spur with one to two marginal teeth (Fig. 4C) ..... 3rd instar
   Metatibia with transverse row of three apical spines; spur lacking marginal teeth (Figs. 4D, E) 4
4. Metatibia with two lateral spines on shaft; spur more than 2× length of longest apical spine (Fig. 4D) ..... 2nd instar
   Metatibia without lateral spines on shaft; spur less than 2× length of longest apical spine (Fig. 4E) ..... 1st instar

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NOTES AND COMMENTS

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QUEENLESS REPRODUCTION IN A PRIMITIVE PONERINE ANT *AMBLYOPONE BELLII* (HYMENOPTERA: FORMICIDAE) IN SOUTHERN INDIA

Colonies of most ant species consist of two morphologically distinct female castes; queens and workers. In the subfamily Ponerine, however, a few species lack morphologically distinct queens in their colonies, and select workers become inseminated and lay eggs instead. Currently, social organization of such queenless ponerine ants has been well studied in various localities; however, queenless species are only known in nine genera of three tribes: Ectatommini, Platytireni and Ponerini (Peeters, 1991). Recently, Ito (1991) found queenless reproduction in *Amblyopone* sp. (*reclinata* group) as the first record of queenlessness in the primitive ant tribe Amblyoponini. In this short paper the author presents the social structure of Indian *Amblyopone bellii* Forel as the second example of queenless reproduction in Amblyoponini.

A colony of *Amblyopone bellii* was collected in Mudigere, southern India. The colony nested under a stone at the edge of the forest and consisted of 40 workers, several larvae and eggs without a morphologically distinct queen. The colony was kept in the laboratory for two months. Then all but two workers, which died soon after sampling, were dissected to check spermathecae and ovarian development. All workers had a spermatheca and a pair of four ovarioles. Of 38 workers dissected, only one mated worker (=gamergate) was observed. The gamergate had dense accumulations of yellow bodies in the basal part of the ovarioles. She did not have well developed oocytes nor chorionated eggs in her ovaries, however, many eggs had already been laid in the laboratory. Many uninseminated workers had slightly developing but immature oocytes. Only one virgin worker had a well developed oocyte, however, yellow bodies in her ovaries were tiny. These results suggest that the gamergate performed as the functional queen and the virgin workers rarely laid eggs. Even though only one colony was examined here, the strong assumption of queenlessness in *A. bellii* may be reasonable, due to the fact that the appearance of both winged queen and mated workers in the same species is uncommon and has been shown in only *Rhytidoponera* spp. (Ward, 1983).

Most species of *Amblyopone* so far studied have winged queens in their colonies which monopolize reproduction (Brown, 1960; Gotwald and Levieux, 1972; Traniello, 1982; Masuko, 1986). Queenless reproduction shown in *Amblyopone* sp. (Ito, 1991) and *A. bellii* seems an exceptional phenomenon in this primitive genus. However, since the two queenless species are undoubtedly closely related and form the *A. reclinata* group with some other species (Brown, 1960), it is likely that this reproductive system is a general characteristic of the *A. reclinata* group.—*Fuminori Ito, Biological Laboratory, Faculty of Education, Kagawa University, Takamatsu 760, Japan.*

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BOOK REVIEWS

J. New York Entomol. Soc. 101(4):576–580, 1993

Systematics, Ecology, and the Biodiversity Crisis.—N. Eldredge (ed.). 1992. Colombia University Press. $40.

It is not an elaborate advertising campaign, hoax, or political ploy. Awareness of the biodiversity crisis is compulsory for everyone on earth. The recent emergence of conservation biology as a profession in many countries (complete with university degrees) attests to the importance of being aware. Newly born out of desperate necessity, conservation biology draws upon numerous schools of thought, and has as many definitions, methods, and solutions as there are people involved in it.

Some popular ideas from the politico-economic cognoscenti remind me of a quip that I read in the British humor magazine *Punch* sometime in the late 1980's. If memory serves, the setting was a meeting where an administrative spokesman delivered a talk on policy regarding nature, and a paraphrase goes something like: "Nature is divided into three genera—animals, the weather, and plants. Animals contains three species: game, stock and vermin, and they can only be told apart when dead. If exterminated, it's vermin: if bagged, it's game, and if insured, it's stock." The question "What about butterflies?" was answered, "Vermin. There are no game insects." Such satire is not entirely without a basis in reality because we live in a world where money talks. Hence it is not surprising that proponents of the business school of conservation of biodiversity have perhaps the loudest public voice. However, can we literally buy our way out of the biodiversity crisis? Economics plays an important role in conservation, but in order to develop solutions to the biodiversity crisis the voices of organismal biologists need also to be heard. It is therefore heartening to see a volume composed of voices almost entirely from systematists and ecologists. The introduction indicates that this book covers three topics: 1) the different approaches ecologists and systematists have to biodiversity, 2) the recent interest in all biological fields in conservation biology, and 3) how the role of systematics can be enhanced with respect to the biodiversity crisis.

Chapter 1 concerns the separation of ecology and systematics. After a maze of jargon and definitions, Eldredge informs us that systematics deals with genealogy, and ecology deals with the economics of how organisms interact. The text that follows continues to point out that systematics and ecology are different, and that populations bridge economics and genealogy in nature. The chapter closes with, "We need now to see what factors of niche utilization at the population level produce characteristic genealogical patterns and which ecological patterns. There should be many interesting connections made in the coming years as we follow up these lines of thought" (p. 13). Did I miss something? Is this the obfuscation of an election year? If there was a main point to this chapter (besides the difference between ecology and systematics) it evaded me, as did the reason why this essay was included in a book about the biodiversity crisis. Eldredge may well ask, where does the twain of ecology and systematics meet? Certainly not in this chapter.

Chapter 2 addresses the tropical megafauna bias in conservation biology. Here

Platnick reiterates his intriguing idea that southern temperate zones may have a greater number of endemics than do the tropics, and crisply points out that biodiversity is synonymous with arthropods, not vertebrates. If areas of endemism are important considerations in conservation biology, then arthropod systematists are in the unique position to define areas for conservation efforts. Drawing on his own expertise he tells us that the biodiversity crisis is occurring just as strongly in the southern temperate zones as in the tropics, but the study of spiders doesn't tell us any more than butterflies or nematodes because the answers are the same—we don't know enough about arthropods to say how many there are or just what their ranges are—there simply are too few arthropod systematists. Nobody has a clue as to just how bad (or potentially good) things are—all we do know is that the world is composed mainly of arthropod species, many which are being extirpated without a trace. Can threatened species keep their toeholds, make a comeback after the long history they have had of human disturbance, or provide clues for their survival? Time may tell, but perhaps only if we take off the vertebrate colored glasses and start looking seriously at arthropods.

With the perspective of someone who has spent a lot of time in museums and in the field amongst live organisms, Chapter 3 examines the role of systematics and ecology in museums in understanding biodiversity. Tattersall's message is that we must **DO** something rather than talk about it. He suggests a "consultation of nature, rather than of navels" (p. 27) is required to understand biodiversity, and uses his work on Malagasay primates as an elegant example to show how systematics and ecology both provide important questions, answers, understanding, and future directions. I like this man. He sees clearly that the problem gives us little time to sit around and discuss definitional fluff—an advocate of deeds not words who is squarely on the side of nature and knowledge. Tattersall's closing comments provide reasons why symbiotic associations between ecologists and systematists have important roles to play in conservation biology at large, and in museums. We are left with the sobering thought that without active collaboration between the two disciplines that champion natural history, the biodiversity crisis may leave us with only history museums—mute testimonies to what was diversity.

Based on his previous work, Chapter 4 by Stevens advocates what he calls Rappaport's Rule as a subtly different hypothesis (from the 12 or so extant ones) of why there are so many species in the tropics. We are told that the reason the tropics contain so many species is that they are composed of significant proportions of the "living dead"—individuals that disperse into a particular habitat, become established at very low abundance, but cannot ever reproduce due to lack of other individuals to do it with. In other words, communities are organized differently in temperate and tropical latitudes, and the living dead are constantly going extinct in many tropical habitats. Stevens feels that these rare species will be the first to go extinct in threatened habitats, and thus not good choices for conservation efforts. The message for conservation biology seems twofold. First, focus conservation efforts on species common enough to reproduce, and preserve large tracts of habitats. Secondly, universities and museums should promote eco-tourism to help save tropical habitats. My experience suggests that, like cattle, tourists seriously degrade tropical habitats physically, and artificially bloat local economy by creating commercial demand for nature artifacts, land, and trinkets. Call me a pessimist, but I remain unconvinced that buying our

way out is the end-all answer—it may spread it around, but it seems a weak solution to the problem.

Cracraft's ambitious chapter 5 focuses on speciation and patterns of biospheric evolution, historical patterns of diversity, thermodynamics and transduction of energy, and the richness of extant tropical communities in terms of biomass. His detailed synthetic observations and analyses suggest that historically biomass is not at equilibrium, but typically increases when weather patterns allow warm, humid conditions to prevail. The implication is that should warm climates spread, the present global biomass of organisms would increase through tropical expansion (roll on global warming, roll on?). This chapter is a nice scientific synthesis, but unless one can take solace in the potential for increased biomass through time, it seems out of place in a volume directed at the biodiversity crisis.

In chapter 6, Sepkoski shows with fossil evidence that historically, marine biodiversity has demonstrated a continued increase, and uses these data to address present day concerns. During the earth's history of increasing biodiversity there have been differential expansions of particular groups at unequal rates, followed by extinctions of many phylogenetic lineages also at varying rates. Extinction events have been followed by recovery events that suggest a quasi or semi-quasi equilibrium states for global diversity. These events of increased phylogenetic diversity were likely to have been a function of local ecological processes as evolution requires pools of genomic material to stock communities that may diverge; phylogenetic diversity reflects local ecosystems. Sepkoski's historical message to the present world is clear: continued human disturbance will continue to alter the course of evolution, but if the disturbance is stopped, the world's biota may recover. However, recovery time will likely be measured in thousands or millions of years.

In chapter 7, Novacek points out how systematists are considered by the majority of the world as "a bunch of drawer pullers" (p. 102). We are reminded, however, of the connections systematics has to physiology, ecology, evolution, and that systematics provides a basis for much of the rest of the biological sciences. Although still a nascent field, systematists have described the 1.4 million species known to occur on earth, and estimates suggest there remain approximately 80 million yet to describe. The message of this chapter is that the skills of the systematists may have much to offer toward our understanding biodiversity. Are these surprising conclusions?

Stiassny in chapter 8 demonstrates what practicing systematists can do in the face of the biodiversity crisis. Using the fish family Cichlidae she illustrates how, in a triage situation, phylogenetic methods provide valuable insight into the evolution of the entire group, and a means of choosing which taxa to preserve. Her study indicates why in the African Cichlidae, a group bursting with endemic species, it may be more important to put conservation efforts into saving a phylogenetically basal taxon rather than other more derived ones. Stiassney in fact shows very nicely the vital role that museum-based systematics plays in the biodiversity crisis.

Chapter 9 finds Barrowclough showing the contributions museums and systematists make to biodiversity and conservation biology. He begins by pointing out the great disparity between how diverse a group actually is and how many taxonomists work on it, and then points out the fact that even though the ranks of taxonomists are thinning, proportionally few systematists are working on insects. The fact that institutions of higher learning passively observe the loss of systematists without striving

to rectify the situation is alarming, but in the face of a global biodiversity crisis it is damning. Speaking directly to the subject of what museums and systematists can do his suggestions include: start popularizing systematics, educating about its importance and what it can do in deciding where reserves should be placed and what taxa should be saved. This essay provides potential solutions to the biodiversity crisis that can be acted upon now, not tomorrow. But will institutions listen?

Chapter 10 by Winston begins with a brief but chilling list documenting how badly the marine environment has been degraded by human effluence. Her point is that although earth is a marine planet, humans treat it as a rubbish pit. Continuing a sadly common theme she reflects that we do not know much at all about the biodiversity of the oceans, that there are few working marine systematists, fewer positions available, and little funding to help understand marine environments. In the face of these discouraging practicalities Winston strongly recommends that museums and systematists increase public awareness, lean on the political machinery, and encourage advocacy for the environment. All practicing biologists, and anyone with common sense should recognize that her recommendations will help. However, will they?

Historical destruction and reconstruction on a local scale are treated in chapter 11. Taboada presents a case history of how 40 years of socio-economic factors severely affected the natural habitats of Cuba, and how socio-economic factors may help preserve and rebuild them. Pointing to a time when, "in 1959 there were more lawyers than biologists, veterinarians, chemists, physicists, and engineers of every kind, all taken together" (p. 172), Taboada indicates that after a long, rocky road there are now systematists and other scientists involved and concerned with understanding the biodiversity crisis in Cuba. This is good news. However, it should remind us that, as usual, conservation efforts come after a long history of human habitat destruction. Thus, our understanding of Cuba's very special flora and fauna must now be relegated to paleontology, a few organisms that escaped the holocaust, those that invaded after the holocaust, and the ecology of reconstructive gardening.

The first sentence of chapter 12 by Flesness reads, "There is not a solution to the catastrophe we are witnessing" (p. 178). This acknowledges what we all know—that this is serious, and everyone needs to help provide a variety of solutions. Flesness acknowledges that he does not have THE answers, but after enthusiastically telling us that zoos and botanical gardens are educational institutions of great importance, he provides three ideas of how systematists could help the administrators: study focal taxa, freely and actively disseminate knowledge about organisms, and make museum labels that include some computerized ecological information on it. Interesting suggestions, should some funding source magically appear to finance them, but do I detect a certain administrative naivete about the environment natural historians work in? Why preach to the converted? Naturalists and systematists, like artists, typically do what they do from an inner drive, not because it is lucrative or generously funded. It seems to me a more immediate and practical suggestion would be to use the talents of both systematists and institutions by calling for strong, innovative public programs that teach systematics and natural history along with simple demonstrations as to why people need to curb their runaway reproductive habits. After all, the lack of basic natural history education and reproductive common sense are central to the biodiversity crisis—aren't they?

Vanzolini's chapter 13 provides a history of the role systematics and museums

have played in our understanding and documentation of biodiversity. Fundamentally the reason we are aware of the biodiversity crisis is because of faunistic and floristic works traditionally done by systematists. His messages for the future are good: integrate ecological and evolutionary interactions into the systematist's tools (as they historically have been), repeatedly sample areas with the idea of monitoring change (both ecological and evolutionary), utilize the morphoclimatic domain system of habitat classification (versus the Holdridge system), and land preservation efforts should include areas surrounding the focal core area. The reminder that systematics and ecology should be viewed as a mutualistic interaction, and that institutions themselves must form symbioses among themselves has never been more timely. With over 40 years as a practicing museum systematist in an area of the world that contains a staggering number of species, I think Vanzolini does not have a political agenda, but the calm, good sense that years of experience provide.

The diverse collection of essays assembled here ranges over themes, opinions, and interpretations both old and new. Most acknowledge the seriousness of the biodiversity crisis, and the paucity of funding available for organismal biology at any level. Potential solutions to the crisis offered here span a normal distribution. Laurels to the doers and advocates of being involved with habitats and organisms, hope for eventual enlightenment to the talkers. To me the value of this volume is the public announcement that: 1) systematists from the Americas are sufficiently concerned to attempt providing solutions from their area of expertise, 2) institutions of higher education provide little encouragement to students interested in a career in systematic biology, even though it is central to understanding nature, and 3) institutions and naturalists of all persuasions need strongly to promote natural history as an educational imperative. In response to the question from the *Punch* article 'What about butterflies?', the answer is—they are representatives of the most diverse group of organisms in the world, the arthropods, and potentially the most useful group for generating solutions to the biodiversity crisis.

This book can provide professionals a new perspective about what some systematists and ecologists think about conservation biology and the biodiversity crisis. I liked this book, and without detracting from its value I suggest there are at least two alternatives to buying it. First, a donation to a favorite museum, a specialist journal, or practicing naturalist will certainly be utilized for understanding nature. Second, a favorite field guide given to a child—along with a few words about why knowing about natural history, museums, and the interplay of systematics and ecology is important—seems an elegant alternative. Ultimately the fate of biodiversity falls to what the inheritors of this scarred planet think and do. As donors we owe it to the young to pass on knowledge and inspiration about natural history that was gleaned from our mistakes, and those of our ancestors. Such things can be taught, but it is unlikely that they can be bought.—*P. J. DeVries, Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts 02138.*

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Life in Amber.—G. O. Poinar, Jr. 1992. Stanford University Press. $55.

> . . . for I do not allow that there is any river, to which the barbarians give the name of Eridanus, emptying itself into the northern sea, whence (as the tale goes) amber is procured . . . I have never been able to get an assurance from an eye-witness that there is any sea on the further side of Europe. Nevertheless tin and amber do certainly come to us from the ends of the earth.
>
> Herodotus, *The History*, III, 115.

One of the few and probably the most promising areas where systematic entomology interfaces with the fossil record is amber studies. To a systematic entomologist, the fossil record of terrestrial arthropods consists of two fundamental types of deposits: compression deposits formed by the settling out of various fine-grained, water-lain sediments, and amber, the lithified result of wood resins produced by gymnosperm and angiosperm trees. Unlike amber, compression deposits form the stratigraphic context that provides our understanding of the major patterns of terrestrial arthropod evolution during the past 400 million years of deep geologic time. These include the diversification of various paleopterous and orthopteroid insect clades of the Paleozoic Entomofauna during the Paleozoic Era, and the appearance and frenzied radiation of hemimetabolous and holometabolous clades of the Modern Entomofauna during the late Paleozoic Era and the first half of the Mesozoic Era. Amber, by contrast, divulges the relatively recent patterns of the Modern Entomofauna during the past 140 million years, corresponding to the flowering of angiosperms during the Cretaceous Period of the Mesozoic and their continued diversification during all of the Cenozoic Era. It is intriguing to note that, unlike virtually any other major terrestrial clade (e.g., vertebrates or vascular plants), the Modern Entomofauna largely would be recognizable to an entomology student time-travelling back to a Cretaceous forest and keying insects to the family level. In this latter context, G. O. Poinar's book, *Life in Amber,* provides a welcome summary of current research and a comprehensive taxonomic compendium of amber inclusions (principally insects and arachnids) for all major amber deposits that have come to us, as Herodotus put it, from the ends of the earth.

In his preface, Poinar states that the goal of *Life in Amber* is a synthesis ". . . to include plant and animal remains as well as information on the sources of fossiliferous amber deposits in the world, their location, their history, and, especially, their geological ages" (pp. vii–viii). This far-ranging goal is admirably realized for most discriminating readers in the 288 pages of written text. The first chapter is a fifteen page précis devoted to a cultural appreciation of amber in mythology, the classical world and more recent European history, followed by a practicum on differentiating recent resins (known as copal) from more ancient ambers, and it concludes by a succinct discussion of diagenetic processes involved in the formation of amber. In the second chapter, we are presented with more focused discussions, largely from the author's personal experience, of Cenozoic ambers from Chiapas, Mexico and the Dominican Republic, as well as a more extensive exposition on Baltic amber. More abbreviated sections are devoted to other Cenozoic amber deposits, principally because of their inaccessibility and less productive yields of inclusions—namely Chinese (Fu Shun), Romanian, Burmese and Sicilian ambers. The last section on Cretaceous ambers

provides information on Canadian, Alaskan, Mideastern (principally Lebanese), Siberian, Atlantic Coastal Plain (especially New Jersey), and other lesser known amber deposits. Chapter 3 consists of a list of museums that are amber repositories, and a brief note of what constitutes value in amber. (It is no surprise that, unfortunately, what is of scientific value for the biologist also can command outrageous prices in Manhattan jewelry stores!) By far the overwhelming bulk of the text (177 pages, or 60 percent) is devoted to a systematic compendium, generally at the family level, of all major taxa that have been described or are known from amber. The taxonomic spectrum ranges from bacteria to mammals, although, fortunately for entomologists, 82 percent of the chapter is devoted to terrestrial arthropods, mostly insects and arachnids. Although this chapter adequately provides basic data for the specialist and nonspecialist interested in a synoptic overview of occurrences of taxonomic groups in amber, cognoscenti may be misled by some omissions and errors (more on this later). Chapter 5 comprises 10 pages of what is known of symbiotic relationships among amber taxa, addressing evidence for commensalism, mutualism, and parasitism and disease. For me, this was the most fascinating section of the book, and it reflects the research of Poinar and his collaborators. The types of interorganismic interactions in amber that are rarely obtainable in compression deposits include mite and pseudoscorpion phoresy on insects, ectoparasitism of an apid bee by a meloid tringulin larva, and nematode endoparasitism of flies. The concluding chapter presents topical and timely digressions of the principal implications of amber for evolutionary biology, other than the sheer documentation of alpha diversity through time.

Given the price of many technical books in the life sciences, a 350 page book with eight color plates for $55.00 seems reasonable. The organization of the book is logical and the format is pleasing. The 144 black-and-white photographs reproduced on text pages, some of which have been reproduced elsewhere, range from the stunning to the unidentifiable; the average quality is quite high, given the translucent nature of amber. Squeakers include the listrophorid fur mite of p. 227, which resembles an ink-splatter spot, and the photo of the Brodzinskys on p. 46, which is somewhat less than flattering. (The Brodzinskys, incidentally, have assisted entomologists immeasurably in obtaining access to important amber specimens.) The 37 color photographs of the plates are superb and reveal considerable detail, although some could have been enlarged and still be accommodated within the page margins. Although the figures with graphics are stylistically uneven, they adequately document what is referred to in the text.

My principle qualm with the book are isolated, misleading statements in Chapter 4 that fall into three categories. They are: (1) erroneous accounts stating that the earliest known occurrences of many insect families occur in amber, when in fact reliably identified representatives of these families occur in older compression deposits; (2) outdated usage of higher-level designations of taxonomic rank; and (3) general proofreading and typographical errors. With regard to the earliest occurrences of insect families that predate amber deposits, examples include the earliest known gryllotalpid occuring during the Aptian Stage of the early Cretaceous of Brazil (Martins-Neto et al., 1991), rather than in Cenozoic Mexican amber (p. 102), the earliest identified bibionid is not from upper Cretaceous Canadian amber (p. 165) but from the mid-Cretaceous of Botswana (Rayner, 1987), and the earliest known flea is a

specimen from the early Cretaceous Aptian Stage of Australia (Jell and Duncan, 1986), and not from Baltic amber (p. 189). There are other examples. Lastly, the earliest known feather is not from lower Cretaceous Lebanese amber (p. 239), but can be found individually and on the wings of *Archaeopteryx,* from the upper Jurassic Solnhofen limestone (Meyer, 1861; Feduccia, 1980), the protestations of Hoyle and Wickramasinghe notwithstanding. Much of the inaccuracy regarding earliest insect occurrences arises from a flurry of systematic activity within the last decade from seven, well-worked, mostly lower Cretaceous compression deposits from Australia, Botswana, Brazil, China, Mongolia and Russia, whose results are published in journals and edited volumes that are relatively inaccessible (Grimaldi and Maisey, 1990). Unfortunately, Carpenter's new compendium (1992) has a literature cutoff date of 1983, and virtually all of these discoveries are not documented in his compendium.

As to the inappropriate use of higher level taxa, it would have been useful to standardize taxonomic terminology by following the scheme of a universally used reference, such as the second edition of *The Insects of Australia* (1991). Examples include the anachronistic use of the term, Orthoptera (p. 99), to include at least six, currently recognized orthopteroid orders; and use of Thysanura to include Archaeognatha plus Zygentoma (p. 96), which contravenes recent progress in delineating fundamental distinctions between these two clades. General errors of fact include the claim that ". . . there have been two great coal-forming periods, the first lasting from the Carboniferous to the Permian, some 120 million years in duration, and the second in the Tertiary Period, . . ." (p. 14), when, in fact, coal deposits of the Cretaceous are as volumetrically impressive as those of the Carboniferous (Averett, 1975; Cross and Phillips, 1990). The Mengeidae are extinct strepsipterans and are not extant (p. 155). The Axiidae are not primitive Paleozoic homopterans but modern ditrysian lepidopterans without a fossil record; and the nematoceran fly subfamily L*i*moniinae (p. 246) is misspelled L*e*moniinae, suggesting that another group of ditrysian lepidopterans possess a fossil record they do not have. Lastly, the thysanopteran families Ceratothripidae and Pygothripidae (p. 61) are apparently not recognized as such by modern systematists (Heming, 1993).

I recommend this book for all entomologists—even those with just a passing interest in fossil insects. When compared to other book-length, biological summaries of amber deposits, Poinar's book fills a major vacuum for three reasons. First, unlike previous summaries, Poinar's book focuses on all major amber deposits, and not just Baltic amber, thus providing a spatiotemporal perspective for important amber depoists. Second, of the nine or so previous volumes on amber, almost all are in German, and only Larsson's (1978) and Poinar's volume are accessible to most English-speaking readers. Last and more importantly, unlike his predecessors, Poinar poignantly explores in his last chapter those current research areas where the study of amber is headed, including studies that go beyond the description and enumeration of taxa. These include calculation of extinction rates for insect species and genera, of which recent studies support the observation that insect taxa have exceptionally long geochronologic ranges when compared to other organisms; intriguing distributional patterns that paleobiogeographically unite amber taxa with their descendants that presently occur on separate continents or in isolated corners of the world; reconstruction of plaeoenvironments and the ecologies of ancient organisms; and, most intriguing of all, the possibility of extracting DNA as a tool for conducting phylogenetic analyses

of extinct taxa, their modern descendants, and related lineages (see also Cano et al., 1992; DeSalle et al., 1992).

As exciting as these research programs are, I am still left with one unsolved mystery that was unaddressed in *Life in Amber*. Why are there no pre-Cretaceous ambers of biological importance? Although recently there has been identification of apparently araucariaceous Triassic amber (Litwin and Ash, 1991), it lacks biological inclusions and is highly fractured. Notably, the major amber-producing conifers of the families Araucariaceae, Taxodiaceae and Pinaceae all are traceable back to the Triassic Period of the early Mesozoic (Taylor and Taylor, 1992), and good araucariaceous and taxodiaceous woods with resin canals are found in sedimentary rocks from the subsequent Jurassic Period. Whether pre-Cretaceous conifers produced resin in significant volumes to be geologically widespread and noticed remains unexplored, although Litwin and Ash's report gives us cause to be optimistic for the possibility of amber-entombed, Triassic and Jurassic insects!—*Conrad C. Labandeira, Smithsonian Institution, National Museum of Natural History, Department of Paleobiology, MRC: 121, Washington, D.C. 20560.*

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Reproductive Behavior of Insects. Individuals and Populations.—W. J. Bailey and J. Ridsdill-Smith (eds.). 1991. Chapman and Hall. 339 pp. $95.

It may surprise many people that students of insect behavior have few books in their discipline with which to line their shelves. I know of three that purport to cover the broad spectrum of insect behavior, and frankly, they come up somewhat short. Considering the tremendous amount of work that has been done in this field, why does this void exist? The great diversity of behavior across this taxon obviously makes it a daunting task and the scarcity of college courses offered for this speciality translates to limited sales for the effort. Thus, the literature consists largely of edited volumes with narrower foci, often the outcome of a conference symposium. *Reproductive Behaviour of Insects* falls into this category. Its eleven chapters are the work of thirteen authors, some but not all of whom were part of a symposium of the Australian Entomological Society. The obvious question to be asked is "How far does this contribution go towards helping to fill the void?" The quick answer, unfortunately, is "not far."

Reproductive behavior can be viewed as a subset of behavior, but its boundaries are difficult to define. Arguably, few behaviors could be divorced from a direct or indirect role in the ultimate context of fitness—reproductive success. So, when the editors define reproductive behavior in chapter 1 as "the finding of mates, choice of mates, selection of oviposition sites, and the factors affecting the fitness of larvae," one would be hardpressed to eliminate any of these factors. However, it seems likely that this is a convenient definition based on the contents of the contributed chapters, given that other behaviors influencing reproductive fitness are omitted (e.g., adult feeding and predator avoidance). But I won't complain too much about the selective inclusion because the leaf-feeding larvae chapter is one of the better ones.

Most accounts of insect reproductive behavior limit themselves to the more narrow focus of mating and oviposition. The literature on the behavioral ecology of insect mating systems has two volumes that stand out: *Sexual Selection and Reproductive Competition in Insects,* edited by Blum and Blum; and the highly acclaimed *The Evolution of Insect Mating Systems* by Thornhill and Alcock. *Reproductive Behaviour in Insects* falls well short of either with respect to new contributions towards evolutionary explanations of mating behavior (although Alcock and Gwynne's chapter does a very good job of summarizing the evolutionary approach to studying and understanding insect mating behavior). Therefore, it is fortunate that the majority

(seven) of the chapters in this volume deal with oviposition behavior and that five of these are specifically related to host location and/or host selection.

It is not easy to provide a coherent, and yet brief, overview of this eclectic assemblage of chapters. The first two chapters are efforts to inform the uninitiated that individual variation is important to consider for a full (evolutionary) understanding of reproductive behavior in any species. In the remaining chapters, only two deal directly with mating behavior (Chapter 3: sensory cues, primarily acoustic, and Chapter 10: aspects of mating in dung insects as they relate to competition for the dung resource). Chapters 4 through 8 review host location and oviposition by insects on animals in general, on plants in general, by tephritids specifically, by Heliothinae specifically, and by aphids specifically. Chapter 9 describes oviposition and brood defense in social wasps and Chapter 11 discusses the empirical and theoretical studies on the relationship between larval feeding behavior and overall fitness in leaf feeders. Inevitably, the amount of research that has been done on these subjects is revealed in the thoroughness of coverage for each chapter. Only a couple of the chapters consistently provide suggestions for empirical studies that would be worthy of pursuit in the future.

The subtitle "Individuals and Populations" reflects a stated objective of this volume which is to help bridge the gap between the population biology view of reproductive behavior and the focus on individual variation and its effect on reproductive success. Tied to this is another stated goal of introducing "selectionist thinking to a wider audience of entomologists," meaning those in the applied area whose backgrounds have not provided an evolutionary perspective to their research. Are these goals accomplished? Some chapters, those by Alcock and Gwynne, Jones, and Reavey and Lawton in particular, champion these aims with clear presentations. However, many other chapters not only do little to help enlighten readers, but are actually guilty of much population and species level generalization regarding behavior. Also the book suffers from the same problems found with most symposia volumes, a lack of connectivity across the chapters and highly variable quality of writing between contributors. The lack of continuity means that this is not the best source for "learning" the importance of a selectionist perspective in applied problems. Some chapters are exceptionally lucid, but others have sections that must be read multiple times to grasp the point. And in some cases the end result is a message that would be outright misleading to a reader naive in the realm of evolutionary ecology. In particular, chapters by Wellings and Ridsdill-Smith contain several claims that one or another behavior has an impact on individual fitness, but fail to explain how. I should point out that Ward's chapter provides very clear explanations of "adaptive" arguments.

Although the editing with respect to readability is weak for some chapters, I found few outright typographical, spelling, or grammatical errors with the exception of one chapter (ironically, it is coeditor Bailey's chapter). The print and figures are excellent and the binding seems to be high quality.

Since applied entomologists were a declared target audience of this book, I was curious as to whether it was hitting this mark. I conducted a small, highly nonstatistically-sound survey of applied entomologists with respect to two questions: Have you heard of this book? If so have you read or purchased it? Of the 26 applied entomologists from four institutions, five individuals had heard of the book, and of

those, two had purchased it. Interestingly, four out of six evolutionary biologists (working with insects) that I asked were aware of the book.

Unfortunately, I cannot in good conscience recommend the purchase of this book to all those interested in insect reproductive behavior. I would suggest looking through a copy if possible to determine whether or not more than one chapter is pertinent to your work and provides you with new perspectives. Let that perusal be your guide to a purchase decision. At US$95 it is hardly a take-a-chance bargain.—*Gary Dodson, Biology Department, Ball State University, Muncie, Indiana 47306.*

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A Field Guide to Eastern Butterflies.—P. A. Opler and V. Malikul. 1992. The Peterson Field Guide Series. Houghton Mifflin Company, Boston, New York, London. xiii +396 pp., 48 color plates. $16.95.

As would be expected of a new "Peterson Field Guide," particularly this one as successor to A. B. Klots' classic "Guide" of the 1950's (Klots, 1951), this new book must fill the role of "be all and end all" concerning butterflies in the eastern United States. To its great credit, it generally succeeds.

A reviewer is, of course, asked to assess "pluses and minuses." Regarding these, I have had a chance not only to gather my own impressions over the last months, but also to listen to numerous other lepidopterists who have used the new field guide since it appeared.

Opler and Malikul's text closely follows Opler's previous work with Krizek on eastern butterflies (Opler and Krizek, 1984), which won considerable popular and professional acclaim. Taking off westward from the Opler and Krizek text, however, the new "Peterson Guide" includes treatments for many additional species whose distributions either overlap, or abut, the authors' arbitrary "eastern" border (the 100th geographic meridian). Most of the book's comparatively few problems result from inconsistencies or omissions in this latter effort. The book also appears to be the first popular guide to use the new standardized "common names" for North American butterflies (Miller, 1991).

Overall book format follows the standard for Peterson Guides, departing mostly from Klots' by the addition of (1) distribution maps and (2) thirteen color plates showing butterflies in nature. The latter, so-called "natural pose" photos have been the rage in recent years, but are of questionable value for diagnostic purposes. Fortunately (and in contrast to some other recent field guides), Opler and Malikul do not rely exclusively on these field-photos for butterfly identification. Rather, Malikul has skillfully executed thirty-five color plates in the "diagnostic" painting style employed by other Peterson Guides—concise renderings with pointer arrows noting outstanding features. These illustrations are excellent and, in contrast to Klots', not simply limited to the "higher" butterflies. Full color plates are also included for the dingier-looking skipper butterflies, and these add greatly to the usefulness of the

book. The only negative comment I have heard from some workers concerning the color plates is that a few appear to exaggerate the angle of the forewing apex.

One valid complaint about the format concerns the distributions maps, some of which are figured with state/province boundaries and some without: 392 *with* (including some smaller regional maps), 57 *without* (these being of North America and all within the "higher" butterflies sections). I have published considerably on butterflies of the central United States and must admit that, even armed with good distributional knowledge, it is hard to discern the actual ranges of butterflies for which no state boundaries are shown (some examples, Baird's Swallowtail, p. 50; Anise Swallowtail, p. 51; Large Marble, p. 70; Mustard White, p. 66; etc.). This matter is not without import; workers in the central United States will be interested in range extensions, new records, and so on. However, wherever there is a map with no state boundaries shown, but a long, straight or meandering, shading crossing the middle United States, it is very difficult to discern what local areas are included.

Generic usages in the book mostly follow the binominal combinations employed earlier by Opler and Krizek. Where different, Opler and Malikul have done a commendable job in tailoring generic nomenclature to recent systematic literature (many field guides opt for old usages more familiar to collectors). In instances where there is controversy among specialists about the status of certain genera or species, the authors appear to have made their choices with some consultation of the literature. Thus, with taxa like Joan's Swallowtail (p. 49 [vindicated more recently by DNA sequencing results, Lepidopterist News 1992]), the authors are in a position to appear correct in hindsight when questions go beyond those of simple allopatry (as in the ongoing controversy concerning widely disjunct members of *Boloria*). Opler and Malikul are also to be complimented on their treatment of numerous groups in the Lycaenidae as separate genera. This is also generally consistent with recent literature and is a first among the several more recently published popular guides. Previously, numerous binominal combinations (in genera like *Strymon* Hübner, *Electrostrymon* Clench, *Ministrymon* Clench, etc.) have been confused either by uncertain affinities or tendencies to cluster based on the North American fauna alone. It is likely, however, that some generic usages in the book will soon be obsolete (I am aware, in particular, of *Hemiargus* and *Incisalia* in the Lycaenidae) with the publication of new taxonomic assessments extending beyond the Nearctic.

Opler and Malikul's field guide also has left certain species out. Omissions appear in some cases to be either inadvertant or arbitrary. For instance, the Colorado White (*Pieris sisymbrii* W. Edwards), a butterfly distributed much like many of the other western species treated in the text (e.g., occurring across the western Dakotas and into central Nebraska) is not included by the authors although the Large Marble, a butterfly much harder to find on the western Great Plains, appears in the pierid treatment. This could be an oversight; published records for the above species occur mostly in regional literature concerning Nebraska not cited in the authors' References section. In other cases, omissions appear to result from taxonomic choices. For example, Opler and Malikul treat [rightly it appears, given the systematic literature] the Canadian Tiger Swallowtail and Tiger Swallowtail as separate species with an intervening hybrid zone. However, in a classically similar situation in the hairstreak butterflies, the "western" and "eastern" Olive Hairstreaks, the eastern and western segregates are considered the same species but only the eastern entity's distribution

is illustrated. If indeed these are the same species, the distribution map should show all of western to central Nebraska, South Dakota and North Dakota where the "western" Olive Hairstreak is well known. Some of these inconsistencies may have resulted from the authors not being able to revise distribution maps after final work on their text. It is traditional in the preparation of popular guides that "marginal" taxa are treated last and in a hurry.

In summary, there are many good things one can say about this book—it is well-prepared; it is cheap; it is quite complete; you can put it in your pocket; you won't miss many taxa if you don't go too far west. The authors can be proud of their efforts on this work—most lepidopterists will be very happy to have it.—*Kurt Johnson, Department of Entomology, American Museum of Natural History, Central Park West at 79th St., New York, New York 10024.*

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Contents Volume 101, 1993, Numbers 1-4

Number 1

Number 2

Number 3

Number 4

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CONTENTS