

# MORPHOLOGY, PHYLOGENY AND CLASSIFICATION OF ADULT ENDOMYCHIDAE (COLEOPTERA: CUCUJOIDEA)

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**Abstract.**— The cucujoid family Endomychidae is characterized. Detailed morphology of 36 exemplar genera representing 12 recently recognized subfamilies is presented. Cladistic analysis was accomplished based on 50 taxa (47 genera from Endomychidae and Coccinellidae – the ingroup, and 3 genera from Helotidae, Brachypteridae and Proto cucujidae – the outgroups) coded for 40 adult, morphological characters. Based on the analysis, a phylogeny of the family is hypothesized. Results of the analysis suggest that the Endomychidae form a monophyletic taxon, which may be divided into 12 subfamilies: Danascelinae (**subfam. nov.**), Xenomycetinae, Endomychinae, Anamorphinae, Merophysiinae, Lycoperdininae, Stenotarsinae, Epipocinae, Eupsilobiinae, Pleganophorinae, Mycetacinae and Leiestinae. Short diagnoses for the family and subfamilies, as well as a key to the subfamilies are provided. The following two new, subfamily synonyms are proposed: Anamorphinae Strohecker, 1953 (=Acritosomatinae Pakaluk and Ślipiński, 1995) and Merophysiinae Seidlitz, 1872 (=Holoparamecinae Seidlitz, 1888). *Adamiä gen. nov.* (type species: *A. mexicana sp. nov.*) and *Erotendomychus lawrencei sp. nov.*, are described. Type species are designated for the following genera: *Niteta* Weise, 1890 (*N. quatuordecimpunctata* Weise, 1890), *Oediarthrus* Gerstaecker, 1858 (*O. natalensis* Gerstaecker, 1858) and *Stenotarsoides* Csiki, 1900 (*S. quadrimaculatus* Csiki, 1900). History of classification and known facts concerning the biology of the family are provided.



**Key words.**— Coleoptera, Cucujoidea, Endomychidae, genera, morphology, phylogeny, classification.

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## INTRODUCTION

### 1. History of classification

The first described genus of this family was *Endomychus*, established by Panzer (1795) for the Linnaean species *Chrysomela coccinea*, described in 1758. A few additional genera were proposed by various authors during the early nineteenth century, but most of the endomychid species described in that period were referred to such genera as *Galleruca*, *Erotylus*, *Chrysomela* and *Tritoma*. The family Endomychidae was proposed by Leach in 1815, for *Endomychus coccineus* (Linnaeus), *Eumorphus kirbyanus* Latreille and *Lycoperdina bovistae* (Fabricius).

The first general survey of the family was accomplished by Gerstaecker. His monograph of the Endomychidae (1858) had been the basis for study by subsequent workers, for many years. Very few additional works of broad scope have appeared since then. Most important of these include early catalogues of Endomychidae by Gorham (1873a) and Csiki (1910), Arrow's fauna of British India (1925), and Strohecker's (1953) generic review and world catalogue, the largest work on the Endomychidae of the 20th century.

### 2. Systematic position

**2.1. The cerylonid-group of the Cucujoidea.** In his "Natural classification of the families of Coleoptera" Crowson (1955) placed Endomychidae within the superfamily Cucujoidea. He (Crowson 1955, 1960) proposed the cerylonid-group to include the most derived families of this superfamily as follows: Endomychidae (including Alexiidae=Sphaerosomatidae), Coccinellidae, Corylophidae, Cerylonidae, Discolomatidae, Merophysiidae and Latridiidae. More recently, Pal and Lawrence (1986) formally transferred Bothrideridae, as an independent taxon, from Colydiidae (Tenebrionoidea) to Cucujoidea, next to Cerylonidae, as one more family of the cerylonid-group.

The members of this group are generally characterized by the following characters: adult with tarsi 4-4-4 or 3-3-3 in both sexes; wings without a closed radial cell and with reduced number of anal veins (if more than one anal vein, the first runs into a medial fleck); aedeagus resting on one side when retracted, tegmen strongly reduced, median lobe strongly curved, without median struts; larvae with tarsungulus unisetose, spiracles almost always annular, and sensory appendage of second antennal segment usually as long as the third segment (Ślipiński and Pakaluk 1992).

There are a number of exceptions to these supposedly diagnostic characters. Some Bothrideridae have a closed radial cell; some Bothrideridae and some Coccinellidae have more than one anal vein and the first does not run into the medial fleck; there are a number of taxa with several anal veins but without a medial fleck; Coccinellidae have the tegmen well-developed; and an

aedeagus resting on the side when retracted, which is characteristic for cerylonid-group, also occurs in several other cucujoid taxa (e.g. Sphindidae, Protocucujidae, Boganidae, Erotylidae and Languriidae).

Although long established as a group and generally considered monophyletic (although without clear relationships to any other group of Cucujoidea), the above exceptions to diagnostic characters and the lack of rigorous family definitions, which are based exclusively on apomorphic characters, show that the relationships of members within the cerylonid-group remain uncertain. Ślipiński and Pakaluk (1992) drew attention to many problems in classification of the cerylonid group and emphasized that for a better understanding of relationships a critical reappraisal of the taxa and a phylogenetic study was desperately needed.

The aims of the current study, apart from reviewing the classification and biology of the Endomychidae, was to make a detailed morphological study of representative genera followed by cladistic analysis. The aim of the analysis being the resolution of three problems: the relationships between Endomychidae and Coccinellidae; the limits of Endomychidae as a monophyletic taxon; and the limits and relationships of endomychid suprageneric taxa, the last in order to provide a more soundly based subfamily or tribal classification.

**2.2. The Endomychidae and their relatives - relations with the family Coccinellidae.** The relationship between Endomychidae and Coccinellidae has always been a source of interest for taxonomists. Because of the peculiar appearance of the tarsi (pseudotrimerous), both these taxa were often combined in a taxon called Trimeria, which had been placed at the end of the coleopterous system. This unique character, common for almost all Coccinellidae (except Lithophilinae) and higher Endomychidae, is evidently an advanced condition, but it is perhaps not a synapomorphy derived from a common ancestor of both families. Members of the endomychid subfamily Eupsilobiinae, at least partially combine characters historically considered unique for Endomychidae and Coccinellidae - e.g., a characteristic median lobe and the loss of a fronto-clypeal suture (Pakaluk and Ślipiński 1990, Ślipiński and Pakaluk 1992). The other characters common for both families, including 5 pairs of functional abdominal spiracles and middle coxal cavities open outwardly (both characters seem to be important in the classification of superfamily Cucujoidea), are also present in some other families of the cerylonid-group. Although Endomychidae are generally considered closely related to Coccinellidae, Ślipiński and Pakaluk (1992) indicated that Endomychidae are probably polyphyletic, and Coccinellidae have basal clades with uncertain relationships, some of which may include certain endomychids. Moreover, some of the diagnostic characters for these two families are probably plesiomorphic and cannot be used to define monophyletic taxa in the sense of cladistic taxonomy. All of these factors suggest, that the limits

and relationships between Endomychidae and Coccinellidae, as well as the limits and relationships of endomychid subfamilies, are unclear and should be reconsidered in a broader context using phylogenetic methods.

Feeding habits of both families seem to be very interesting in the context of mutual relations between these taxa. While most endomychids are fungivorous in both adult and larval stages, and are usually found on or within rotten wood, decaying vegetable matter or fungi, a few species are collected on leaves of living plants, e.g. *Saula japonica* Gorham, which is predacious (Sasaji 1978b). On the other hand Coccinellidae, which are usually thought of as beneficial predators of plant pests (aphids, scale insects, chrysomelid larvae), include typical leaf-feeders, members of the subfamily Epilachninae (e.g. *Epilachna* and *Subcoccinella*), and members of the Psylloborini, a tribe of the subfamily Coccinellinae have acquired the habit of feeding on fungal hyphae and spores (Drea and Gordon 1990).

Although the larvae of Endomychidae are highly variable in form, sculpture and vestiture, such that they may be confused with a number of other cucujoids, typical endomychid larvae tend to resemble those of coccinellids in having their body broadly ovate to fusiform, without urogomphi [small urogomphi occur on some endomychid larvae, e.g. *Mycetaea subterranea* (Fabricius)]. However, they differ from coccinellid larvae by having a well-developed mola, and by lacking such characters as the fusion of cardo and stipes, enlarged tibia bearing group of clavate setae, small tarsungulus with broad base and transverse row of 6 protuberances on most abdominal segments (Lawrence 1991).

### 3. Larvae of the Endomychidae – their diversity and similarities

The cucujoids, other than the coccinellids, with which certain endomychid larvae may be confused, include representatives of seven families. The general appearance of larvae of *M. subterranea* (Mycetaeinae) resembles that of *Sphaerosoma* (Alexiidae), genera within Monotomidae (Rhizophaginae) and Languriidae. *Mycetaea* larvae differ from those of *Sphaerosoma* by lack of raised, spiracular tubes or paired tubercles on abdominal tergite 8; and from Rhizophaginae and Languriidae in having an obtuse mala and annular spiracles. The disc-like larva of *Agaricophilus* may be confused with those of the cerylonid *Murmidius ovalis* (Beck) and some corylophid larvae. *Agaricophilus* larvae differ from those of *Murmidius* in having a much shorter basal antennal segment and lacking a median endocarina and barbed setae; from the corylophid larva, *Agaricophilus* differs in having abdominal segment 1 and 8 without paired gland openings. Larvae of the endomychids Leiestinae and Merophysinae resemble those of Biphylidae and Cryptophagidae that lack urogomphi. An obtuse mala and a mandible without pros-

theca distinguish Leiestinae and Merophysinae from members of these two families.

Too few larvae within each subfamily of Endomychidae are known and described to be fundamentally instrumental in improving the higher-level classification. Fortunately this situation has been improving recently with each additional description of a new larva, and with any comparative studies. Such comparative studies of the larval stages of Epipocinae (McHugh and Pakaluk 1997), in which six genera were treated, have resulted in interesting conclusions. Epipocinae may be divided into three informal groups, based on larval morphology. The first group only includes the genus *Periptyctus*, whose larvae differ greatly from all known epipocines and have characters unique for the family. These characters include: concealment of the head from above by prothorax; frontal arms V-shaped, distant at base; mandibles endognathous; fusion of the labrum to the head capsule; fusion of the cardo and stipes; and fusion of the base of the maxillolabial complex to the head capsule. Although unique for Endomychidae, some of these characters do occur in the larval stages of Corylophidae and Cerylonidae. Studies of the adult morphology indicate, that the genus *Periptyctus* is related to corylophid beetles, and probably should be transferred to the family Corylophidae (Ślipiński and Tomaszewska, in preparation). The second group formed by *Epipocus*, *Anidrytus* and *Ephebus* is comparatively distinct and can be separated from the third group (*Stenotarsus* and *Saula*) by having lateral lobe-like projections on the abdominal and thoracic terga and pleura. *Stenotarsus* and *Saula*, have abdominal and thoracic terga and pleura without similar lobes.

Among Anamorphinae (=Mychotheninae), larval stages for *Mychothenus*, *Anagaricophilus* and *Bystus* are known and described. Pakaluk (1986) listed the following characters that separate anamorphinae larvae from those of the remaining endomychids: body without tergal plates and with simple setae only; reduced, transverse mandible without incisor lobe, and mola with tubercles arranged in distinct rows; maxillary mala falciform and head without frontal sutures or stemmata. Leschen and Carlton (1993) indicated that a character which may be important for uniting the Anamorphinae is the posterior row of three setae on the labrum. This is an unusual feature, because setae are usually symmetrical between body halves.

Known larvae of Lycoperdininae may be grouped into a few, more or less distinct morphological groups. Larva of *Mycetina cruciata* (Schaller), described recently (Burakowski 1997), seems to be most similar to *Aphorista vittata* (Fabricius) with their short thoracic and abdominal lateral tergal lobes; vestiture of specialized fan-shaped setae, tergal plates with weak protuberances and tergum 9 emarginate. Among the other Lycoperdininae, *Amphix* as well as *Lycoperdina* form monogeneric groups, while *Eumorphus* seems to be most similar to *Ancylopus*.

#### 4. The recent classification

Endomychidae is a relatively large and diverse family with about 1300 species, described in approximately 120 genera (Lawrence 1982). According to the most recent classification of subfamilies, published by Pakaluk, Ślipiński and Lawrence (1994) and Lawrence and Newton (1995), Endomychidae consisted of 11 subfamilies. The following subfamilies: Leiestinae, Endomychinae, Epipocinae (=Stenotarsinae), Lycoperdinae (=Eumorphinae), Mycetaeinae, Pleganophorinae (=Trochoideinae) and Xenomycetinae, have traditionally been classified in the Endomychidae. Holoparamecinae and Merophysinae were sometimes treated as a distinct family Merophysidae (Crowson 1955, 1981), although Lawrence (1982), Lawrence and Newton (1995), Pakaluk, Ślipiński and Lawrence (1994), Ślipiński (1990), and Ślipiński and Pakaluk (1992) have included them into an expanded Endomychidae. Eupsilobiinae were moved from Cerylonidae by Sen Gupta and Crowson (1973). Crowson (1981) suggested a close relationship of Eupsilobiinae with Coccinellidae, while Sasaji (1986, 1987) placed them in the Endomychidae. Sasaji (1978a) established the subfamily Anamorphinae (=Mychotheninae) for a few genera of former Mycetaeinae and later (Sasaji 1990) elevated the taxon to family status. The later status has not been generally accepted. Pakaluk and Ślipiński (1995) established Acritosomatinae for the new genus *Acritosoma*, from Mexico and Peru, and since this addition the family Endomychidae has consisted of 12 subfamilies. At least some of them have been based solely upon a combination of characters or overall appearance and are probably polyphyletic.

#### 5. Biology

**5.1. Feeding habits and habitats.** Endomychidae are mostly mycophagous, feeding on a wide variety of fungal types. Their most frequent habitats are rotten wood and fungus-infested bark. The larvae may occur under bark, in rotting wood or more often, on wood or bark surfaces. Most mycophagous endomychids feed on fungal spores or hyphae. Gut material of *Endomychus biguttatus* Say, studied by Leschen and Carlton (1988), consisted of thick walled hyphae and spores. *Endomychus* spp. appear to have obligate relationships with lignicolous Basidiomycetes. Both *E. coccineus* (Linnaeus) and *E. biguttatus* Say are known to breed in the fruiting bodies of *Hirneola mesenterica* (Auriculariaceae), while *Schizophyllum commune* (Schizophyllaceae) is the only other known basidiomycete host for *E. biguttatus* (Leschen and Carlton 1988, after Lawrence, pers. comm.). Other North American Endomychidae with obligate host relationships to Basidiomycetes, include *Mycetina perpulchra* (Newman), *Lycoperdina* spp., *Xenomycetes laversi* Hatch and *Aphorista vittata* (Fabricius).

*Xenomycetes laversi* appears to be restricted to *Paxillus atrotomentosus* (Basidiomycetina: Agari-

cales). The larvae and most specimens of adults have been collected from sporocarps or mycelia of this fungus, found associated with rotted wood. Both larvae and adults were observed grazing upon the basidia and mycelia (Johnson 1986). Species of *Lycoperdina* have internally feeding larvae, which occur in puffballs of the genus *Lycoperdon* (Lawrence 1991). Although generally *Lycoperdina* exhibit a strong preference for puffballs, specimens of *L. ferruginea* LeConte have also been collected from forest litter or debris (Pakaluk 1984). For mycophagous Coleoptera the larvae generally have a more restricted diet, and it is possible, that the adults tolerate a greater diversity of fungal hosts. The internally feeding larvae have mouthparts highly adapted for sporophagy, and Lawrence (1977) has referred to the mandibular morphology of puffball beetles as a "spore mill", which is powerful enough to crush any spores before they are swallowed. The enlarged mola is provided with numerous tubercles, and the top of the mandible is reduced and truncate.

Similar adaptation for sporophagy occurs in species of Anamorphinae. Pakaluk (1986) and Leschen and Carlton (1993) indicated that members of this subfamily may be obligate spore feeders. Guts of most examined adults and larvae were filled with spores. The adult mandibles of *Bystus*, *Clemmus* and other genera have a bifid apical incisor lobe, a brushy protheca and a well-developed mola, while the larvae of *Mychothenus* (Sasaji 1978a) and *Anagoricophilus* (Pakaluk 1986) have the incisor lobe reduced or completely absent. Sometimes the specific food sources appear to be difficult to determine, e.g. *Aphorista morosa* LeConte was found in association with a yellow plasmodium of a slime mould (Myxomycetes), while a Neotropical species of *Amphix*, was found feeding on spore capsules of an ascomycete fungus.

Various endomychids live in leaf litter and feed on moulds and other fungi on decaying plant products. Among the mould feeders, species of *Holoparamecus* and *Mycetaea* are pests of stored products, occurring in granaries and warehouses and causing minor damage.

*Saula japonica* Gorham has been reported to have coccinellid-like habits, with both adults and larvae preying on scale insects (Sasaji 1978b). The larvae of *Trycherus* seems to feed on lichens (Strohecker 1953).

Some endomychids occur in special habitats. Species of *Pleganophorus*, *Trochoideus*, *Merophysia* and *Coluocera* seem to be myrmecophiles or termitophiles, but little is known of their food habits.

**5.2. Behaviour.** Some very interesting correlations between fungal ecology and larval behaviour of mycophagous Coleoptera were discussed by Leschen (1994). He hypothesized that many larval behavioural patterns have evolved for defence. These behavioural patterns are probably influenced by the ephemeral nature of the fungus and whether the beetles feed at the fungus surfaces or internally. The antipredator adaptations include egg protection, aposematism and larval gregariousness, pupal location, parental care etc. Some

of these patterns seem to occur also in the family Endomychidae.

Physical egg protection appears to be most common in Coleoptera that feed upon tough and persistent fungi. Within Endomychidae egg protection was reported for *Endomychus biguttatus*. Females of this species deposit eggs on persistent and tough, small lignicolous sporocarps of *Schizophyllum commune*. Leschen (1994) reported that in the laboratory, females of *E. biguttatus* cover individual eggs with hyphae taken from the tops of *Schizophyllum* sporocarps or even filter papers.

Reports of larvae that pupate within the sporocarps concern taxa that feed on tough and persistent fungi. Larvae feeding on lignicolous fungi, e.g. *Amphix* spp., may pupate in clusters, although the significance of this is uncertain. Interesting protective behaviour was reported for the larvae of *Bystus*, which cloak themselves with debris collected from the fungal substrates upon which they feed. This probably acts as camouflage making them invisible to potential predators.

Duration of the larval development probably depends (among others) on structural features of fungi, e.g. the development of *E. biguttatus* larvae, which feed on tough and persistent fungi, requires about 16 days (Leschen and Carlton 1988), while some Staphylinidae (Aleocharinae, Oxyporinae), that feed upon relatively ephemeral fungi, require 3–11 days.

Unfortunately, neither parental care nor aposematism have been explored within the Endomychidae.

## MATERIAL, METHODS AND TERMINOLOGY

This study is based on the examination of types and material from the following institutions:

- ANIC – Australian National Insect Collection, Division of Entomology, CSIRO, Canberra, Australia;
- BMNH – The Natural History Museum, London, England;
- BPBM – Bernice P. Bishop, Museum, Honolulu, USA;
- CASC – California Academy of Sciences, San Francisco, USA;
- FMNH – Field Museum of Natural History, Chicago, Illinois, USA;
- MAIC – Michael A. Ivie, private collection, USA;
- MCZ – Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts, USA;
- MHNG – Muséum d'Histoire Naturelle, Genève, Switzerland;
- MIIZ – Museum i Instytut Zoologii PAN, Warszawa, Poland;
- MNHN – Muséum National d'Histoire Naturelle, Paris, France;
- TMB – Természettudományi Múzeum, Budapest, Hungary;
- NHMB – Naturhistorisches Museum, Basel, Switzerland;
- NMB – Naturhistorisches Museum für Naturkunde der Humboldt Universität, Berlin, Germany.

For detailed examination of characters that might be used for cladistic analysis, at least one male and one female of one or more species of the studied genus, were

completely cleared, disarticulated and placed in glycerine on slides for further study. The structural illustrations were made from these preparations using a camera lucida attached to an Olympus dissecting microscope or to a Zeiss Amplital microscope (smaller structures). Measurements of the following were made using a filar micrometer: body length, from apical margin of clypeus to apex of elytra; width, across both elytra (maximum); pronotal length, from the middle of anterior margin to margin of basal foramen; pronotal width, across widest part; elytral length, along suture including scutellum.

Terminology used for adult morphology follows Lawrence and Britton (1991, 1994) and that of wing venation terminology, Kukalová-Peck and Lawrence (1993).

## FAMILY ENDOMYCHIDAE

### 1. Adult characteristics

Body broadly oval to elongate and narrow, strongly convex to weakly flattened (Figs 813–836); 1–14 mm long; dorsal surface shiny, smooth and glabrous or often pubescent. Vestiture either of short and fine hairs, or in species of *Mycetaea*, *Agaricophilus*, *Symbiotes*, *Mychothenus* and *Stenotarsus* of long and suberect setae (Figs 829–832). Colour black, brown, red or yellow, often with contrasting markings on the elytra and/or pronotum.

Head (Figs 1–73) of prognathous type; sometimes deeply retracted into prothorax; in *Micropsephodes* tucked up under prothorax, not visible from above. Cranium weakly to distinctly transverse, slightly narrowing from eyes towards labrum. No distinct demarcation between vertex and frons, or between vertex and occiput; also occiput has no distinct limits; occipital suture invisible; vertex and occiput occupy broad area between eyes and postoccipital suture. In Lycoperdininae (*Lycoperdina*, *Beccariola* etc.) occiput with cephalic stridulatory area (occipital file) (Figs 50, 52). Gular sutures short or moderately long, widely separated, weakly convergent anteriorly or subparallel; sometimes indistinct (*Epipocus*) or absent (*Acritosoma*). Eyes placed on sides of head, variable; large or moderately large and prominent in most endomychids, to small and weakly prominent in *Holoparamecus*, *Merophysia* and *Pleganophorus* (Figs 1, 3, 66) or poorly-developed, reduced to 6 ocelli in *Displotera* (Fig. 5). Antennal grooves short (with apex not expanding to posterior edge of eye) in Eupsilobiinae (Figs 20, 22, 24), long in Merophysinae (Figs 4, 6), absent in other Endomychidae. Antennal sockets either visible from above or in Merophysinae, Leiestinae and *Acritosoma* (Figs 1, 3, 5, 7, 9, 11, 13, 15, 17, 72) concealed by projections of frons. Frontoclypeal ridge present (exceptionally absent in the eupsilobiine, *Chileolobius*), sharply defined, usually straight or weakly arcuate but in *Merophysia* it is strongly curved, semilunar (Fig. 3), and in *Displotera* obtusely angled (Fig. 5). Clypeus transverse, usually flat, and almost always weakly convergent

anteriorly. Antenna (Figs 74, 110) usually 11-segmented, with a distinct but loose 3-segmented club; sometimes 8–10-segmented, with 1, 2 or 3-segmented club; exceptionally antenna 4 or 5-segmented (only Pleganophorinae, Figs 106–108), and in females of some species of *Trochoideus* 7-segmented. Mouthparts of normal chewing-type with mandibular mola well-developed. Labrum (Figs 111–146) free, partially exposed, transverse, sclerotized, punctured and setose; tormae elongate with mesal arms usually recurved posteriorly but *Holoparamecus*, *Perrisina*, Endomychinae (except for *Endomychus*), Eupsilobiinae, Pleganophorinae, *Mycetaea* and *Agaricophilus* have them recurved anteriorly, and rarely they are straight. Mandibles (Figs 147–206) articulated dorsolaterally by articulatory fossa which fits under dorsal mandibular process, and ventrolaterally by articulatory condyle, which is received in ventral mandibular fossa; usually short and broad, convex dorsally and weakly concave ventrally, with mola large, strongly sclerotized, most often transversely ridged; prosthema large, membranous, setose, rarely with additional elongate, sclerotized projections on the top (*Merophysia* and *Displotera*) (Figs 148–151). Mandibular muscles inserted on elongate, flattened apodemes; adductor apodeme broad and irregularly oval, abductor apodeme as long as adductor apodeme but much more slender. Maxilla (Figs 207–242) articulated in maxillary fossa; cardo articulated distally with triangular basistipes; basistipes joined by membranes to palpifer and mediostipes. Maxillary palp 4-segmented; with palpomere 1 smallest and terminal palpomere usually at least as long as 2 and 3 combined, variable in shape. Galea well-developed, distinctly broader than lacinia, densely setose apically; with long, stout apical setae in Merophysiinae, *Micropsephodes* and *Acritosoma* (Figs 208, 209, 237, 242). Lacinia slender, often with apical and mesal spines. Labium (Figs 243–278) with 3-segmented palp; with terminal palpomere variable in shape; palpomere 2 transverse or subcylindrical, sometimes oval and inflated (*Holoparamecus*, *Merophysia* and *Displotera*) (Figs 243–245). Mentum transverse, often with produced anterior angles; usually flat, with large medial triangular area in Eupsilobiinae (Figs 252–254) and Merophysiinae (Figs 243, 245) but with small, triangular, setose convexity in *Mycetaea* and *Agaricophilus* (Figs 269, 270). Prementum most often transverse with apically expanded and/or laterally lobed membranous ligula, however Endomychinae (Figs 256–259) have whole prementum evenly sclerotized with ligula indistinct (weakly marked, submembranous ligula occurs in *Endomychus* – Fig. 255). Tentorium with anterior arms usually fused medially, separate in most species of Anamorphinae and *Acritosoma* (Figs 59, 61, 63, 73) always widely divergent anteriorly; corpotentorium distinct, without median process, absent in *Holoparamecus*, Merophysiinae and *Saula* (Figs 2, 4, 6, 43).

Prothorax (Figs 279–351) joined flexibly to head by cervical membrane and to mesothorax by similar membrane. Pronotum transverse, rarely subquadrate, widest

at base or near the middle of its length; often bordered laterally, in some species of Epipocinae, Anamorphinae and Mycetaeinae with broad, lateral, raised margins (Figs 317, 321, 323, 331, 333, 335, 337); lateral edges smooth or rarely crenulate or denticulate; basal and lateral sulci usually sharply defined, rarely absent, in *Holoparamecus* base of pronotum with characteristic tubercles (Fig. 279), in *Merophysia* and *Displotera* with a pair of small, round cavities (Figs 281, 283), in *Danascelis* with two pairs of deep, oval cavities provided with pits (Fig. 325). Pronotal disc almost flat or weakly convex. Ventrally, pronotum is joined to prosternum by tergosternal sutures which usually run obliquely from sides of anterior prothoracic foramen to anterolateral margins of procoxal cavities. Prosternum weakly convex, in *Merophysia* and *Displotera* (Figs 282, 284) sides of its anterior part with a pair of cavities where antennae rest in repose. Prosternal process variable, most often 0.5–1.0 × as broad as coxal diameter, extends at least to posterior margins of front coxae; in some species of Leiestinae, Lycoperdininae and Pleganophorinae hardly separates front coxae (Figs 286, 290, 296, 328, 345, 347), while in *Meilichius*, *Bolbomorphus* and *Eucteanus* it is broader than coxal diameter (Figs 308, 310, 312). Procoxae usually circular in outline, with cavities externally open behind and internally closed, trochantin concealed; rarely procoxae transverse with partially exposed trochantin (*Micropsephodes*) (Figs 340, 341); *Acritosoma* is the only exception in having procoxal cavities externally closed (Fig. 351).

Meso- and metathorax (Figs 389–437). Mesonotum (Figs 352–387) has only scutellum exposed dorsally between closed elytra; usually weakly sclerotized with scutellum of variable shape, moderately large, rarely longer than wide. Ventrolateral part of mesothorax occupied by mesopleuron, which consists of episternum (anterior part) and epimeron (posterior part). Mesepisternum contacts mesosternum by its inner edge; sometimes mesepisternum fused with mesosternum, with more or less visible trace of suture (*Merophysia*, *Displotera*, *Mycetaea*, *Pleganophorus* and *Trochoideus*) (Figs 390, 391, 422, 433, 434). Mesepimeron contacts metasternum posteriorly and usually closes mesocoxal cavity laterally; in Anamorphinae, Merophysiinae, Holoparamecinae, Pleganophorinae and *Acritosoma*, where middle coxal cavities are closed outwardly by sterna, mesopleuron is obviously separated from coxal cavity. Mesocoxa almost always circular in outline, its cavity outwardly open or closed by sterna (broadly – in Anamorphinae and *Acritosoma* – Figs 426, 427, 429, 431, 437, narrowly in Merophysiinae, Holoparamecinae and Pleganophorinae – Figs 389, 390, 391, 433, 434), then trochantin concealed; taxa with mesocoxal cavities open outwardly, usually have trochantin exposed, although Leiestinae, *Mycetaea* and *Agaricophilus* have trochantin concealed (Figs 392–397, 422, 424). Mesosternum variable, from almost smooth to strongly carinate, sometimes with oval pits in its antero-lateral part; intercoxal

process usually almost flat and smooth, in Leiestinae boat-shaped (Figs 392–397), in *Eidoreus* covered by anterior metasternal process (Fig. 399), in *Danascelis* with median ridge (Fig. 418), in *Micropsephodes* prominent anteriorly (Fig. 431) and in *Xenomycetes* and some Lycoperdininae strongly carinate (Figs 435, 419); always distinctly separates coxae. Meso-metasternal junction often of straight-line type, without internal knobs, but in some Lycoperdininae, Pleganophorinae, Epipocinae and *Xenomycetes* small internal knobs are present. Elytra (Figs 438–507) completely covering abdomen; punctures usually irregular, rarely arranged with regular rows of dark punctures (in some species of *Stenotarsus*, *Mycetaea*, *Danascelis*); in some instances rows of punctures visible only on cleared specimens; epipleura most often incomplete apically. Metasternum simple, large, transverse, weakly convex, sometimes with pits near anterior margin; median line often present, short; femoral lines occur in Eupsilobiinae (Figs 398–400). Metapleuron divided into larger, elongate episternum anteriorly, and smaller epimeron posteriorly. Anterior part of metepisternum sometimes provided with a small pit; this part of episternum forms on its inner side, metapleural wing process. Dorsally to episternum, in membrane, there is dorsal epimeral sclerite, connected posteriorly to anterior postnotal process. Metacoxae widely separated and transverse, except for Holoparamecinae and Merophysinae, where they are oval (Figs 389–391). Metendosternite (Figs 508–540) usually with very short stalk and widely separated anterior arms and tendons.

Wings sometimes absent or strongly reduced. If present and well-developed (Figs 541–561) anal lobe occurs in Endomychinae, Epipocinae, Lycoperdininae and *Trochoideus*; one anal vein, except for *Bolbomorphus* and *Eucteanus* (Fig. 551) where there are two; closed radial cell reduced; medial bridge almost always distinct; medial fleck sometimes large of irregular shape, without distinct limits, rarely distinctly divided (e.g. in *Beccariola*) (Fig. 557); radial part of wing well-developed with subcosta anterior (ScA), subcosta posterior (ScP) and long, strong sclerotized radius anterior (RA); radial bar is formed by fused radius anterior and subcosta posterior. Wings of Anamorphinae and *Holoparamecus* have deep incision behind medial fleck (Figs 541, 558–560).

Legs (Figs 562–618) relatively long. Trochanters usually oblique, sometimes heteromeroid, rarely elongate (*Holoparamecus*, *Merophysia*) (Figs 562, 563). Femur usually at least twice as wide as tibia, covered with moderately dense pubescence; tibia and tarsus more densely pubescent than femur; tibia rarely with apical spurs, sometimes with short spines surrounding apex; male tibiae sometimes bear characters of sexual dimorphism. Tarsal formula most often 4-4-4 in both sexes, in *Holoparamecus*, *Merophysia*, *Displotera* and some Anamorphinae 3-3-3 (Figs 562–565, 605, 607, 608); 4-segmented tarsi may be simple (Leiestinae, Eupsilobiinae, Mycetaeinae, some Anamorphinae and *Acritosoma*) or pseudotrimerous (Figs 582, 584, 585, 587–595, 598–601,

613) with tarsomeres 1 and 2 flattened and ventrally lobed, tarsomere 3 very short, usually almost hidden in tarsomere 2 (Endomychinae, Lycoperdininae, Epipocinae and *Xenomycetes*). Claws simple or modified in *Anamorphinae*. Empodium usually very small, bisetose, in some Anamorphinae unisetose, while *Acritosoma* has empodium reduced without setae.

Abdomen (Figs 619–626, 628, 630–657) with five or six freely articulated ventrites; ventrite 1 (sternite 3) at least as long as two following combined, rarely with femoral lines; ventrites 2–5 with internal, anterolateral apodemes. Five pairs of functional spiracles on abdominal segments 1–5, situated dorsally on pleurites. Apical ventrite sometimes modified (especially in males), emarginate or truncate. Male genital capsule (Figs 658–716) formed by segment 9 (sternite and tergite 9), usually weakly sclerotized, with paired apophyses usually fused apically.

Aedeagus almost always resting on its side when retracted; consists of median lobe (penis) and tegmen; usually moderately sclerotized, except for Lycoperdininae and some Epipocinae, where they are strongly sclerotized. Median lobe usually long and curved, without additional struts; in Eupsilobiinae coiled with T-shaped capsule at base (Figs 739, 740, 742), in Lycoperdininae and some Epipocinae stout and most often ramificate apically (Figs 748, 749, 755); usually with membranous gonopore at apex. Tegmen often reduced (rarely absent, e.g. Merophysinae, *Saula*, *Erotendomychus*) with very short tegminal plate, short, fused parameres and membranous tegminal strut, in Eupsilobiinae tegmen bears long, articulated strut (Figs 739, 741, 742); in some Anamorphinae tegmen has ventral, ring-like structure (Fig. 770); well-developed, articulated parameres occur rarely (e.g. *Phymaphora*, *Mycetaea*, *Trochoideus*) (Figs 736–738, 762, 763, 777, 778).

Female genitalia without spiculum gastrale. Ovipositor (Figs 779–812) usually simple, reduced to two separated coxities, which are fused in Lycoperdininae (Figs 802, 803); styli present or absent; if present, usually terminal. Spermatheca of variable size, membranous; sperm duct attached to spermatheca, except for most Endomychinae and *Stenotarsus* (Figs 792–795, 800), where it is attached to broad connection between spermatheca and accessory gland; accessory gland usually small and membranous, in most Endomychinae large and sclerotized (Figs 792–795). Sperm duct usually short; sclerotized infundibulum-like structure occurs in most Eupsilobiinae (Figs 788–790).

## 2. Morphology of investigated genera

### *Holoparamecus* Curtis, 1833

(Figs 1, 2, 76, 111, 147, 207, 244, 279, 280, 352, 388, 389, 438, 439, 508, 541, 562, 619, 779)

*Holoparamecus* Curtis, 1833: 186. Type species, by monotypy: *Holoparamecus depressus* Curtis, 1833.

**Description.** Length 1.2 mm. Body elongate, weakly convex; shiny, smooth, covered with sparse and short pale setae. Colour light brown.

Head (Figs 1, 2) deeply retracted in prothorax, as long as wide; sparsely and moderately densely punctured. Gular sutures subparallel, widely separated. Eyes small, oval, coarsely faceted. Antennal sockets concealed by sides of frons; antennal grooves absent. Antenna (Fig. 76) reaches to about half of pronotum length, 9 to 11-segmented with 2-segmented, loose, scarcely flattened club. Fronto-clypeal ridge weakly arcuate. Clypeus transverse, flat, convergent anteriorly. Labrum (Fig. 111) subquadrate, with submembranous apex; punctured, covered by sparse, long setae; truncate apically; tormae with mesal arms recurved anteriorly; labral rods absent. Mandible (Fig. 147) with two apical teeth, and with blunt, small teeth on incisor edge; prosthema fringed; submola small, membranous. Maxilla (Fig. 207) with palpomeres 1 and 3 very short; palpomere 2 large, broad; terminal palpomere as long as 2 and 3 palpomeres combined, narrow, tapering, rounded at apex; galea moderately broad, twice as broad as lacinia, with long, apical setae; lacinia elongate, with apical and mesal spines. Labium (Fig. 244) with palpomere 1 smallest; palpomere 2 largest, oval, inflated; terminal palpomere subquadrate, truncate at apex. Mentum transverse, with produced anterior angles; finely punctured, covered with long and sparse setae. Prementum transverse, sclerotized, with apically expanded, membranous ligula. Tentorium (Fig. 2) with anterior arms fused medially, and widely divergent anteriorly; corporentorium absent.

Prothorax. Pronotum (Fig. 279) almost as long as wide, widest at anterior  $\frac{1}{5}$ ; pronotal surface coarsely and sparsely punctured; lateral edges smooth, arcuately widening at anterior  $\frac{3}{4}$ , and almost parallel at basal  $\frac{1}{4}$ ; pronotal sides of basal  $\frac{1}{3}$  with raised, straight and parallel carinae; base of pronotum with a pair of characteristic transverse, elliptical tubercles; area around tubercles depressed; anterior margin nearly straight with rounded angles; posterior angles almost right-angled. Pronotal disc weakly convex. Prosternal process (Fig. 280) narrow, flat; extends posteriorly beyond front coxae. Procoxa circular in outline; its cavity externally open behind, internally closed; trochantin concealed.

Meso- and metathorax. Mesonotum (Fig. 352) sclerotized; scutellum small, strongly transverse, with widely rounded apex. Mesosternum (Fig. 389) smooth, almost flat; intercoxal process elongate, rather broadly separates mesocoxae (slightly narrower than coxal diameter) not extending beyond them. Mesosternum fused with mesoepisternum (trace of suture visible). Mesocoxa circular in outline, its cavity narrowly closed outwardly by sterna; trochantin concealed. Meso-metasternal junction of straight-line type, without internal knobs. Elytron (Figs 438, 439) elongate, convex, irregularly, finely punctured; epipleuron narrow, incomplete at apex. Sutural stria broad basally, converging towards elytral apex,

incomplete apically. Metasternum (Fig. 389) weakly transverse, twice as long as mesosternum, weakly convex; median line short. Metacoxae oval, widely separated. Metapleuron as in Fig. 388. Metendosternite (Fig. 508) with very short stalk and moderately widely separated anterior tendons. Hind wing (Fig. 541) reduced (almost as long as elytron but narrower); anal, medial and radial fields elongate and narrow; apical field shortened.

Legs. Trochanter elongate (Fig. 562). Femur widest near middle of its length, more than twice as wide as tibia, sparsely setose; tibia and tarsus covered with long, dense setae; tibia narrow, gradually widening towards tarsus, with two short apical spurs. Tarsal formula 3-3-3 in both sexes; tarsomere 1 longer than 2; tarsomere 3 longer than remaining tarsomeres combined. Claws simple. Empodium very small.

Abdomen (Fig. 619) with five freely articulated ventrites; ventrite 1 slightly longer than three following ventrites together; ventrites 2-4 almost equal in length.

Aedeagus resting on its side when retracted. Median lobe stout, with basal  $\frac{2}{3}$  strongly curved. Tegmen very short and thin; parameres short, but distinct; tegminal strut absent (Sasaji 1991).

Female genitalia (Fig. 779). Ovipositor weakly sclerotized, with separated coxities; styli vestigial or well-developed, placed apically. Spermatheca small, elongate-oval, membranous; sperm duct moderately long, slender; accessory gland membranous, small, elongate with finger-like projections.

**Species examined.** Two unnamed species from Greece and Burma.

**Distribution.** Widely distributed in all main zoogeographical regions.

### *Merophysia* Lucas, 1852

(Figs 3, 4, 74, 112, 148, 149, 208, 243, 281, 282, 353, 390, 440, 441, 509, 563, 564, 620, 658, 717, 780, 813)

*Merophysia* Lucas, 1852: XXVIII. Type species, by monotypy: *Merophysia formicaria* Lucas, 1852.

**Description.** Length about 1.6 mm. Body (Fig. 813) short-oval, convex; shiny, smooth, finely punctured and pubescent. Colour yellowish-brown to reddish-brown.

Head (Figs 3, 4) transverse. Gular sutures moderately long, subparallel, widely separated. Eye small, moderately coarsely faceted, weakly prominent. Antennal sockets concealed by projections of frons; antennal grooves long. Antenna (Fig. 74) short, about as long as head; 8-segmented with 1-segmented, large, triangular club. Fronto-clypeal ridge strongly curved; clypeus transverse, flat, divergent anteriorly, truncate at apex. Labrum (Fig. 112) with membranous apex; punctured, covered by sparse, short setae; tormae with mesal arms recurved posteriorly; labral rods absent. Mandible (Figs 148, 149) with two apical teeth, and with blunt, small teeth on incisor edge; prosthema fringed with sclerotized, elongate projections on its apex; submola small, membranous. Maxilla (Fig. 208) with

palpomere 2 distinctly wider and longer than 3; terminal palpomere as long as remaining palpomeres combined, narrow, subcylindrical, rounded at apex. Galea moderately broad, almost twice as broad as lacinia, with long apical spines and subapical setae. Lacinia elongate, sparsely setose, with apical and mesal spines. Labium (Fig. 243) with palpomere 1 smallest; palpomere 2 largest, oval and inflated; terminal palpomere subquadrate, truncate at apex. Mentum transverse, with large, triangular area medially; finely punctured, covered with short and sparse setae. Prementum short, transverse, sclerotized, with membranous ligula lobed at sides. Tentorium (Fig. 4) with anterior arms fused medially, and widely divergent anteriorly; corpotentorium absent.

Prothorax. Pronotum (Fig. 281) transverse, widest near middle of its length; pronotal surface coarsely and sparsely punctured; anterior and lateral margins very finely bordered; base of pronotum with a pair of small, dark, round cavities; anterior margin weakly emarginate with weakly produced, blunt angles; posterior angles almost right-angled. Pronotal disc convex. Prosternal process (Fig. 282) moderately broadly separates front coxae, extends posteriorly beyond them, flat, parallel-sided with rounded apex. Anterior margin of prosternum with a pair of cavities, where antennae rest in repose. Procoxa circular in outline its cavity externally open behind, internally closed; trochantin concealed.

Meso- and metathorax. Mesonotum (Fig. 353) weakly sclerotized; scutellum very small, strongly transverse, with broadly rounded apex. Mesosternum (Fig. 390) short and transverse, smooth, almost flat; intercoxal process broadly separates mesocoxae (slightly narrower than coxal diameter) not extending beyond them. Mesosternum fused with mesoepisternum (trace of suture visible). Mesocoxa circular in outline, its cavity narrowly closed outwardly by sterna; trochantin concealed. Meso-metasternal junction of straight-line type. Elytron (Figs 440, 441) elongate-oval, convex, irregularly, finely punctured; epipleuron broad at base, narrowing towards apex, incomplete apically. Metasternum (Fig. 390) transverse, weakly convex; median line very short; femoral lines absent. Metacoxae oval, widely separated. Metendosternite (Fig. 509) with very short stalk and widely separated anterior arms and tendons. Hind wing absent.

Legs (Fig. 563). Trochanter elongate. Femur slightly swollen in middle, tibia hardly widening towards tarsus, with two short apical spurs; tibia and tarsus densely setose. Tarsal formula (Fig. 564) 3-3-3 in both sexes; tarsomere 1 longer than 2; tarsomere 3 longest. Claws simple. Empodium small, bisetose.

Abdomen (Fig. 620) with five freely articulated ventrites; ventrite 1 almost as long as three following together, without femoral lines; ventrites 2-4 subequal in length. Male abdominal segment 9 as in Fig. 658.

Aedeagus (Fig. 717). Median lobe short and rather stout, resting on its side when retracted, sclerotized, weakly curved, with moderately large, submembranous gonopore at its base. Tegmen absent.

Female genitalia (Fig. 780). Ovipositor weakly sclerotized; coxities elongate, separated, with sinuate apical edges; styli absent. Spermatheca small, bean-shaped, membranous; sperm duct long, slender; accessory gland very small, elongate with finger-like projections at apex, membranous.

*Species examined.* An unnamed species from Rhodes.

*Distribution.* Warmer parts of the Old World, excluding Australia and Madagascar.

### *Displotera* Reitter, 1887

(Figs 5, 6, 75, 113, 150, 151, 209, 245, 283, 284, 354, 391, 442, 443, 510, 565, 621, 659, 718, 781, 814)

*Displotera* Reitter, 1887: 9. Type species, by monotypy: *Displotera simoni* Reitter, 1887.

*Lioclemmus* Jeannel, 1934: 172. Type species, by original designation: *Lioclemmus petiti* Jeannel, 1934.

*Description.* Length 1.5–1.6 mm. Body (Fig. 814) short-oval, convex; shiny, smooth, finely punctured and pubescent. Colour yellowish-brown to reddish-brown.

Head (Figs 5, 6) transverse with front margin evenly rounded. Gular sutures short, subparallel, widely separated. Eye poorly-developed, consists of 6 ocelli. Antennal sockets concealed by projections of frons; antennal grooves long. Antenna (Fig. 75) short, about as long as head; 8-segmented with 1-segmented, large, triangular club. Fronto-clypeal ridge obtusely angled. Clypeus transverse, flat, divergent anteriorly. Labrum (Fig. 113) weakly transverse with submembranous truncate apex; punctured, covered with sparse, long setae; tormaes with mesal arms recurved posteriorly. Mandible (Figs 150, 151) with two apical teeth, and with blunt, small teeth on incisor edge; prostheca fringed with sclerotized, elongate projections on its apex; submola small, membranous. Maxilla (Fig. 209) with palpomere 1 shortest, 2 and 3 subequal; terminal palpomere as long as remaining palpomeres combined, narrow, tapering, rounded at apex. Galea moderately broad, almost twice as broad as lacinia, with long, apical spines. Lacinia elongate, sparsely setose, with apical and mesal spines. Labium (Fig. 245) with palpomere 1 smallest; palpomere 2 largest – weakly oval, inflated; terminal palpomere subquadrate, truncate at apex. Mentum transverse, with large, triangular area medially; finely punctured, covered with short and sparse setae. Prementum transverse, sclerotized, with ligula membranous, expanded apically. Tentorium (Fig. 6) with anterior arms fused medially, and widely divergent anteriorly; corpotentorium absent.

Prothorax. Pronotum (Fig. 283) strongly transverse, widest at base; pronotal surface coarsely and sparsely punctured; anterior and lateral margins finely bordered; base of pronotum with a pair of small, dark, round cavities; anterior margin emarginate with strongly produced, blunt angles; posterior angles obtuse. Pronotal disc convex. Prosternal process (Fig. 284) flat, broadly separates front

coxae; extends posteriorly beyond them. Anterior margin of prosternum with a pair of cavities, where antennae rest in repose. Procoxa circular in outline; its cavity externally open behind, internally closed; trochantin concealed.

Meso- and metathorax. Mesonotum (Fig. 354) sclerotized; scutellum small, transversely triangular, with rounded apex. Mesosternum (Fig. 391) short and transverse, smooth, almost flat; intercoxal process broadly separates mesocoxae (broader than coxal diameter), not extending beyond them. Mesosternum fused with mesepisternum (trace of suture indistinct). Mesocoxa circular in outline, its cavity narrowly closed outwardly by sterna; trochantin concealed. Meso-metasternal junction of straight-line type. Elytron (Figs 442, 443) weakly elongate, convex, irregularly, finely punctured; epipleuron broad at base, narrowing towards apex, incomplete apically. Metasternum (Fig. 391) transverse, weakly convex; median line absent; femoral lines distinct, incomplete. Metacoxae oval, widely separated. Metendosternite (Fig. 510) with very short stalk and widely separated anterior arms and tendons. Hind wing absent.

Legs (Fig. 565). Trochanter stout (long and broad). Femur slightly swollen in middle, tibia very gradually widening towards its apical third, with two short apical spurs; tibia and tarsus densely setose. Tarsal formula 3-3-3 in both sexes; tarsomere 1 longer than 2; tarsomere 3 longest. Claws simple. Empodium small, bisetose.

Abdomen (Fig. 621) with five freely articulated ventrites; ventrite 1 longer than three following ventrites together; femoral lines well-developed; ventrites 2-4 subequal in length. In male, ventrite 5 weakly emarginate medially, as in Fig. 621. Male abdominal segment 9 as in Fig. 659.

Aedeagus (Fig. 718). Median lobe short and lightly sclerotized, resting on its side when retracted, weakly curved, with large, membranous gonopore at its base. Tegmen absent.

Female genitalia (Fig. 781). Ovipositor weakly sclerotized, with elongate coxities; styli long, placed apically. Spermatheca small, irregularly oval, membranous; sperm duct slender; accessory gland membranous, very small, elongate with finger-like projections.

*Species examined.* *D. beloni* (Wasmann).

*Distribution.* India, Sri Lanka, Burma, Madeira Is., S. America.

#### *Leiestes* Dejean, 1836

(Figs 7, 8, 77, 114, 152, 153, 210, 246, 285, 286, 355, 392, 444, 445, 511, 542, 566, 567, 622, 660, 661, 719, 720, 721, 782)

*Leiestes* Dejean, 1836: 464. Type species, by monotypy: *Cryptophagus seminiger* Gyllenhal, 1808.

*Description.* Length 3.0-3.6 mm; body elongate (about 2.3 × as long as wide), with dorsal surface shiny and smooth.

Head (Figs 7, 8) transverse, finely and rather sparsely punctured. Eyes large, prominent, moderately coarse-

ly faceted. Antennal insertions not visible from above nor from below. Antenna (Fig. 77) reaches almost to pronotal base, with scape stout, slightly longer than pedicel; antennomere 3 slightly shorter than antennomere 2; antennomeres 4-8 subequal in length, about as long as wide; antennomeres 9-11 form elongate, narrow, loose and scarcely flattened club. Fronto-clypeal ridge distinct, almost straight. Clypeus transverse, flat, truncate apically. Labrum (Fig. 114) with narrow membranous apex and rounded anterior margin; labral rods absent; mesal arms of tormae asymmetrical, recurved posteriorly. Mandible (Figs 152, 153) short and stout; bifid at apex, incisor edge smooth; protheca with short setae; mola with transverse ridges. Maxilla (Fig. 210) with palpomere 1 and 3 very short; palpomere 2 twice as long as 1 or 3; terminal palpomere almost as long as palpomeres 2 and 3 together, tapering, weakly rounded apically. Galea narrow, elongate with apical setae; lacinia slender with a few apical spines. Labium (Fig. 246) with palpomere 1 smallest, palpomeres 2 and 3 subequal in size, weakly elongate; terminal palpomere feebly rounded at apex. Mentum transverse, punctured; prementum almost as long as wide, with laterally expanded, membranous ligula. Tentorium (Fig. 8) with anterior arms fused medially and widely divergent anteriorly; corpotentorium curved.

Prothorax (Fig. 285) 0.63-0.65 × as long as wide; widest near middle of its length; lateral edges of pronotum evenly and moderately arcuate; anterior angles blunt, posterior angles almost straight; disc evenly convex; lateral sulci in form of triangular, concave impressions limited from outside by elongate ridges, basal sulcus hardly visible. Prosternal process (Fig. 286) very narrow and short; procoxae contiguous, circular in outline; procoxal cavity externally open, internally closed, with small rounded slit in its antero-lateral outer edge; trochantin concealed.

Meso- and metathorax. Mesosternum (Fig. 392) bicarinate with intercoxal process boat-shaped; with two rounded, pubescent pits on sides of antero-lateral edges of mesosternal process; mesocoxal cavities narrowly separated (mesosternal process about 0.50 × as broad as coxal diameter), open outwardly; mesocoxa circular in outline; trochantin concealed. Meso-metasternal junction with internal knob. Elytron (Fig. 444, 445) elongate, moderately convex; irregularly punctured (with more or less regular rows of punctures visible on cleared specimens); sutural stria fine, entire, weakly divergent from apex to elytral base; epipleuron narrow, incomplete. Scutellum (Fig. 355) moderately large, strongly transverse (about 2.30 × wider than long), rounded apically. Metasternum (Fig. 392) transverse, nearly twice as broad as long, more than 2 × as long as mesosternum, slightly narrower anteriorly; with two pairs of pubescent, postcoxal pits; median line extending to beyond middle. Metendosternite (Fig. 511) with anterior arms widely, and anterior tendons very narrowly separated. Hind wing (Fig. 542) without anal lobe; venation reduced.

Anal anterior (AA) vestigial; media posterior (MP 1+2) moderately long, fused with short, reduced radius posterior (RP). Medial bridge distinct; medial fleck undivided; radial cell reduced.

Legs (Fig. 566) moderately long with tarsal formula 4-4-4 in both sexes; tarsomere 2 weakly lobed ventrally, tarsomere 3 small but distinct; claws simple, empodium bisetose. Femur subclavate, sparsely pubescent; tibia and tarsus more densely pubescent than femur; apex of tibia (except of outer edge) surrounded by short spines; tibial spurs absent. Mesotibia of male with deep insertion in its apical third, limited from above and from below by small tooth (Fig. 567).

Abdomen (Fig. 622) with five freely articulated ventrites; ventrite 1 as long as three following together; ventrite 2 slightly longer than 3; ventrites 3 and 4 subequal. In male of type species, tergite 5 with two, characteristic, bean-shaped, weakly sclerotized structures (each of this structures bears one of fifth pair of spiracles). Male abdominal segment 9 as in Figs 660, 661.

Aedeagus resting on the side when retracted; median lobe (Fig. 719) curved, moderately long, rather slender, weakly sclerotized with membranous, elongate gonopore at apex. Tegmen (Figs 720, 721) lightly sclerotized; tegminal plate long, slightly shorter than median lobe; with fused parameres; tegminal strut moderately long.

Female genitalia (Fig. 782). Ovipositor weakly sclerotized, with two elongate coxities; styli small, terminal. Spermatheca small, membranous, oval; accessory gland very small, membranous. Apex of tergite 10 (proctiger) acute.

*Species examined.* *L. seminiger* (Gyllenhal).

*Distribution.* Europe, Asia: Japan, Iran.

#### *Panamomus* Gorham, 1873

(Figs 9, 10, 78, 115, 154, 155, 211, 247, 287, 288, 357, 393, 446, 447, 512, 568, 623, 662, 663, 722, 723, 724, 783, 815)

*Panamomus* Gorham, 1873b: 207. Type species, by monotypy: *Panamomus lewisi* Gorham, 1873.

*Description.* Length 2.3–2.6 mm. Body (Fig. 815) elongate (2.10–2.17 × as long as wide), convex; shiny, smooth, covered with fine, pale pubescens; dark ferruginous, with legs and antennae dark yellow; pronotum and elytra unicoloured, or with darker, contrasting markings. Head (Figs 9, 10) transverse, evenly convex with surface covered with distinct or fine, irregular microsculpture between coarse and sparse punctures. Eyes moderately large, prominent, coarsely faceted. Antennal insertions not visible from above nor from below. Antenna (Fig. 78) 11-segmented, with scape stout, slightly longer than pedicel; antennomere 3 very slightly shorter than antennomere 2; antennomere 5 slightly longer than 4 or 6; antennomeres 6–8 subequal, almost as long as wide; antennomeres 9–11 form elongate, narrow, loose and scarcely flattened club. Fronto-clypeal ridge distinct, weakly arcuate. Clypeus transverse, flat, truncate apical-

ly. Labrum (Fig. 115) with narrow membranous apex and rounded anterior margin; labral rods absent; mesal arms of tormae asymmetrical, recurved posteriorly. Mandible (Figs 154, 155) short and stout; bifid at apex, incisor edge smooth; prostheca shortly setose; mola with transverse ridges. Maxilla (Fig. 211) with palpomere 1 and 3 very short; palpomere 2 twice as long as 1 and 3; terminal palpomere slightly longer than palpomeres 2 and 3 combined, tapering, weakly rounded apically. Galea narrow, elongate with apical setae; lacinia slender with a few apical spines. Labium (Fig. 247) with palpomere 1 smallest; terminal palpomere 2 × as long as palpomere 2, cylindrical, weakly rounded at apex. Mentum transverse with fine microsculpture; prementum almost as long as wide, with laterally expanded, membranous ligula. Tentorium (Fig. 10) with anterior arms fused medially and widely divergent anteriorly; corpotentorium weakly curved.

Prothorax (Fig. 287) 0.78–0.80 × as long as wide; widest near middle of its length; pronotal surface with, distinct or fine irregular microsculpture between coarse and sparse punctures; lateral edges evenly and moderately arcuate, narrowly bordered and scarcely sinuate; anterior angles weakly acute, posterior angles almost straight; lateral sulci in form of triangular; concave impressions limited from outside by elongate ridges, basal sulcus hardly visible. Prosternal process (Fig. 288) narrow, but distinctly separate front coxae, extends to their posterior margins; procoxa circular in outline; its cavity externally open, internally closed, with small rounded slit in its antero-lateral outer edge; trochantin concealed.

Meso- and metathorax. Mesosternum (Fig. 393) bicarinate with intercoxal process boat-shaped; with two rounded, pubescent pits on sides of antero-lateral edges of mesosternal process; mesocoxal cavities moderately narrowly separated (mesosternal process about 0.70 × as broad as coxal diameter) open outwardly; mesocoxa circular in outline; trochantin concealed. Elytron (Figs 446, 447) elongate, moderately convex; covered with regular rows of micropunctures; sutural stria fine, entire, weakly divergent from apex to elytral base; epipleuron narrow, incomplete. Scutellum (Fig. 357) moderately large, strongly transverse (2.50–2.80 × wider than long), rounded apically. Metasternum (Fig. 393) short and transverse, more than twice as broad as long, and as long as mesosternum with two pairs of pubescent, postcoxal pits. Metendosternite (Fig. 512) with very short stalk, anterior arms and anterior tendons widely separated. Hind wing absent.

Legs (Fig. 568) moderately long with tarsal formula 4-4-4 in both sexes; tarsomere 2 weakly lobed ventrally, tarsomere 3 small but distinct; claws simple, empodium bisetose. Femur subclavate, sparsely pubescent; tibia and tarsus more densely pubescent than femur; apex of tibia (except of outer edge) surrounded by short spines; tibial spurs absent. Legs similar in both sexes.

Abdomen (Fig. 623) with six freely articulated ventrites; ventrite 1 longer than four following combined, and longer than metasternum; ventrite 6 partly exposed. Male abdominal segment 9 as in Figs 662, 663.

Aedeagus resting on the side when retracted; median lobe (Fig. 722) curved, short, moderately stout, sclerotized with internal sclerites. Tegmen (Figs 723, 724) lightly sclerotized; tegminal plate large, longer than median lobe, with fused parameres; tegminal strut short.

Female genitalia (Fig. 783). Ovipositor weakly sclerotized, with two elongate coxities; styli small, terminal. Spermatheca small, oval, membranous with internal sclerite; accessory gland very small, oval, membranous.

**Species examined.** *P. lewisi* Gorham, *P. brevicornis* Gorham.

**Distribution.** Asia: Japan.

### *Rhanidea* Strohecker, 1953

(Figs 11, 12, 79, 116, 158, 159, 212, 248, 287, 288, 356, 394, 448, 449, 513, 543, 569, 624, 725, 726, 727, 785, 816)

*Rhanis* LeConte, 1854: 360 (nec *Rhanis* Koch, 1846). Type species, by monotypy: *Lycoperdina unicolor* Ziegler, 1844.

*Rhanidea* Strohecker, 1953: 35. Replacement name for *Rhanis* LeConte, 1854.

**Description.** Length 2.5–2.9 mm. Body (Fig. 816) elongate (2.4–2.5 × as long as wide), moderately convex; smooth, shiny, covered with very fine, sparse pubescence. Prevailing body colour rufous to ferruginous; elytra with black contrasting markings.

Head (Figs 11, 12) finely and rather sparsely punctured. Eyes large, strongly prominent, moderately coarsely faceted. Antennal insertions not visible from above nor from below. Antenna (Fig. 79) 11-segmented, slender, with scape stout, antennomeres 2, 3 and 5 elongate, antennomeres 4, 6, 7 and 8 subequal in size, slightly longer than wide; antennomeres 9–11 form elongate, narrow, loose and scarcely flattened club. Fronto-clypeal ridge weakly arcuate. Clypeus transverse, flat, truncate apically. Labrum (Fig. 116) with narrow membranous apex and rounded anterior margin; labral rods absent; mesal arms of tormae recurved posteriorly. Mandible (Figs 158, 159) short and stout; with two prominent, moderately large apical teeth and a few very small teeth on incisor edge; prostheca with short setae; mola with transverse ridges. Maxilla (Fig. 212) with palpomere 1 and 3 very short; palpomere 2 twice as long as 1 and 3; terminal palpomere almost as long as palpomeres 2 and 3 combined, tapering, weakly rounded apically. Galea narrow, elongate with apical setae; lacinia slender with a few apical spines. Labium (Fig. 248) with palpomeres 2 and 3 subequal in size; terminal palpomere subquadrate, weakly truncate at apex. Mentum transverse; prementum almost as long as wide, with ligula expanded laterally, membranous. Tentorium (Fig. 12) with anterior arms fused medially, and widely divergent anteriorly; corpotentorium weakly curved.

Prothorax (Fig. 289) 0.79–0.81 × as long as wide; lateral edges evenly and moderately arcuate from anterior margin towards its middle, thence weakly convergent, becoming parallel before posterior, weakly acute angles;

anterior angles rounded; disc with two longitudinal, sub-parallel grooves extending from basal margin to about middle of disc; lateral sulci in form of triangular, concave impressions limited from outside by elongate ridges, basal sulcus hardly visible. Prosternal process (Fig. 290) very narrow and short; procoxae contiguous. Procoxal cavity externally open, internally closed, with small rounded slit in its antero-lateral outer edge; procoxa circular in outline; trochantin concealed.

Meso- and metathorax. Mesosternum (Fig. 394) bicarinate with intercoxal process boat-shaped; with two rounded, pubescent pits on sides of antero-lateral edges of mesosternal process; Mesocoxal cavities narrowly separated (mesosternal process about 0.35 × as broad as coxal diameter) open outwardly; mesocoxa circular in outline; trochantin concealed. Elytron (Figs 448, 449) elongate, moderately convex; irregularly punctured (with more or less regular rows of punctures visible on cleared specimens); sutural stria fine, entire, weakly divergent from apex to elytral base; epipleuron narrow, incomplete. Scutellum (Fig. 356) moderately large, weakly transverse (1.50–1.60 × wider than long), rounded apically. Metasternum (Fig. 394) 1.5 × as long as mesosternum, nearly twice as broad as long; with two pairs of pubescent, postcoxal pits. Metendosternite (Fig. 513) with anterior arms widely, and anterior tendons very narrowly separated. Hind wing (Fig. 543) without anal lobe; venation reduced. Anal anterior (AA) vestigial; media posterior (MP 1+2) moderately long, fused with short, reduced radius posterior (RP). Medial bridge distinct; medial fleck undivided; radial cell reduced.

Legs (Fig. 569) with tarsal formula 4-4-4 in both sexes; tarsomere 2 weakly lobed ventrally, tarsomere 3 small but distinct; claws simple, empodium bisetose. Femur subclavate, sparsely pubescent; tibia and tarsus more densely pubescent than femur; apex of tibia (except of outer edge) surrounded by short spines; tibial spurs absent. In male, inner edge of anterior tibia with small tooth near middle of tibial length.

Abdomen with six freely articulated ventrites; ventrite 1 longer than two following together, ventrites 2–4 subequal in length; in male, ventrite 5 deeply, broadly, arcuately emarginate at apex, exposing emarginate ventrite 6 (Fig. 624); in female, ventrite 5 truncate at apex, little of ventrite 6 exposed.

Aedeagus resting on the side when retracted; median lobe (Fig. 725) moderately long, sclerotized, rather stout, with weakly sclerotized gonopore at apex. Tegmen (Figs 726, 727) lightly sclerotized; tegminal plate long, slightly shorter than median lobe, with fused parameres; tegminal strut short.

Female genitalia (Fig. 785). Ovipositor weakly sclerotized, with two elongate coxities; styli small, terminal. Spermatheca small, bean-shaped, membranous; accessory gland very small, elongate-oval, membranous.

**Species examined.** *R. unicolor* (Ziegler), monotypic genus.

**Distribution.** North America: USA, Canada.

*Phymaphora* Newman, 1838

(Figs 15, 16, 80, 117, 156, 157, 213, 249, 291, 292, 358, 395, 450, 451, 514, 544, 570, 625, 626, 627, 664, 734, 735, 736, 737, 738, 784, 817)

*Phymaphora* Newman, 1838: 389. Type species, by monotypy: *Phymaphora pulchella* Newman, 1838.

**Description.** Length 3.5–4.5 mm. Body (Fig. 817) about 2.5 × as long as wide, moderately convex; smooth, shiny, covered with fine, sparse pubescence; prevailing colour rufous to ferruginous; pronotum and elytra with black contrasting markings.

Head (Figs 15, 16) finely and sparsely punctured. Eyes large, strongly prominent, moderately coarsely faceted. Fronto-clypeal ridge weakly arcuate. Antennal insertions not visible from above nor from below. Antenna 11-segmented, dissimilar in both sexes. In male (see Fig. 817), scape stout, antennomere 2 slightly shorter; antennomeres 3–7 subequal in size, short, transverse; antennomere 8 also transverse, about 3 × as wide as 7, fitting in concave area beneath club; antennomeres 9–11 form greatly dilated and flattened club, which is as long as remaining antennomeres together, or longer. In female, antenna as in Fig. 80. Labrum (Fig. 117) with narrow membranous apex and rounded anterior margin; labral rods absent; mesal arms of tormae asymmetrical, recurved posteriorly. Mandible (Figs 156, 157) with two prominent, moderately large apical teeth and a few very small teeth on incisor edge; protheca with short setae; mola with transverse ridges. Maxilla (Fig. 213) with palpomere 1 and 3 very short; palpomere 2 twice as long as 1 or 3; terminal palpomere almost as long as palpomeres 2 and 3 together, tapering, rounded apically. Galea narrow, elongate with apical setae; lacinia slender with a few apical spines. Labium (Fig. 249) with palpomeres 2 and 3 subequal in size; terminal palpomere subquadrate, truncate at apex. Mentum transverse; prementum almost as long as wide, with ligula expanded laterally, membranous. Tentorium (Fig. 15) with anterior arms fused medially, and widely divergent anteriorly; corpotentorium lyriform.

Prothorax (Fig. 291) 0.77–0.79 × as long as wide. Pronotum finely and sparsely punctured; microsculpture very fine; lateral edges of pronotum evenly and moderately arcuate in apical half, thence straight and weakly convergent towards posterior, weakly acute angles; anterior margin sinuate, anterior angles obtuse; lateral margins very narrow in apical half, gradually broadening towards basal angles; lateral sulci in form of triangular, concave impressions limited from outside by elongate ridges; basal sulcus distinct. Prosternal process (Fig. 292) narrow, but distinctly separates front coxae; extends beyond their posterior margin. Procoxal cavity externally open, internally closed, with small rounded slit in its antero-lateral outer edge; procoxa circular in outline; trochantin concealed.

Meso- and metathorax. Mesosternum (Fig. 395) bicarinate with intercoxal process boat-shaped; with two rounded, pubescent pits on sides of antero-lateral edges

of mesosternal process; mesocoxal cavities moderately narrowly separated (mesosternal process about 0.50 × as broad as coxal diameter) open outwardly; mesocoxa circular in outline; trochantin concealed. Elytron (Figs 450, 451) elongate, moderately convex; irregularly punctured (with fine regular punctures visible on cleared specimens); sutural stria fine, entire, weakly divergent from apex to elytral base. Scutellum (Fig. 358) moderately large, weakly transverse (about 1.58 × wider than long), rounded apically. Metasternum (Fig. 395) 2.0 × as long as mesosternum, about 1.52 × as broad as long; with two pairs of pubescent, postcoxal pits. Metendosternite (Fig. 514) with anterior arms widely separated; anterior tendons long, narrowly separated. Hind wing (Fig. 544) without anal lobe; venation reduced. Anal and cubital veins absent. Media posterior (MP 1+2) moderately long, fused with short, reduced radius posterior (RP). Medial bridge present; medial fleck undivided; radial cell reduced.

Legs (Fig. 570) with tarsal formula 4-4-4 in both sexes; tarsomere 2 weakly lobed ventrally, tarsomere 3 small but distinct; claws simple, empodium bisetose. Femur subclavate; apex of tibia (except of outer edge) surrounded by short spines; tibial spurs absent. In male, legs slightly longer than in female; anterior tibia with small thickening or armed with small tooth on inner edge near apex; middle tibia with small tooth on inner edge near apex; posterior tibia with small angulation at apical third.

Abdomen (Figs 625, 626) with five freely articulated ventrites; ventrite 1 longer than two following together, ventrites 3 and 4 subequal in length, ventrite 2 slightly longer than 3 or 4; ventrite 5 as long as 3 and 4 together. Sternite 8, apex of which sometimes visible, in male consists of two parts connecting by membrane, truncate apically (Fig. 627). Male abdominal segment 9 as in Fig. 664.

Aedeagus placed with dorso-ventral position inside abdomen; median lobe (Figs 734, 735) moderately long, sclerotized, stout, with weakly sclerotized gonopore at apex. Tegmen (Figs 736, 737, 738) well-developed, large (as long as median lobe), with articulated parameres; tegmental strut moderately long.

Female genitalia (Fig. 784). Ovipositor weakly sclerotized, with two elongate coxities; styli small, terminal. Spermatheca bean-shaped, membranous; accessory gland very small, oval, membranous.

**Species examined.** *P. pulchella* Newman, *P. californica* Horn.

**Distribution.** North America: USA, Canada.

*Stethorhanis* Blaisdell, 1931

(Figs 13, 14, 81, 118, 160, 161, 214, 250, 293, 294, 359, 396, 452, 453, 515, 571, 572, 573, 574, 628, 629, 665, 666, 728, 729, 730, 787)

*Stethorhanis* Blaisdell, 1931: 380. Type species, by original designation: *Stethorhanis vandykei* Blaisdell, 1931.

**Description.** Length 2.37–2.60 mm. Body 2.26–2.48 × as long as wide, moderately convex; smooth, shiny, cov-

ered with fine, sparse pubescence; colour light brown to dark brown, with legs and antennae lighter; pronotum and elytra with more or less distinct, dark contrasting markings.

Head (Figs 13, 14) surface covered with fine, irregular microsculpture between moderately coarse and sparse punctures. Eyes large, prominent, moderately coarsely faceted. Fronto-clypeal ridge weakly arcuate. Antennal insertions concealed. Antenna 11-segmented (Fig. 81) with scape stout, slightly longer than pedicel, which is slightly longer than antennomere 3; antennomeres 3 and 4 subequal in size, elongate; antennomere 5 slightly longer than 4 or 6; antennomeres 6–8 subequal, almost as long as wide; antennomeres 9–11 form elongate, narrow, loose and scarcely flattened club. Labrum (Fig. 118) with narrow membranous apex and rounded anterior margin; labral rods absent; mesal arms of tormae asymmetrical, recurved posteriorly. Mandible (Figs 160, 161) short and stout with distinctly denticulate outer edge; bifid apically and with a few very small teeth on incisor edge; prostheca shortly setose; mola with transverse ridges. Maxilla (Fig. 214) with palpomere 1 and 3 very short; palpomere 2 twice as long as 1 or 3; terminal palpomere almost as long as palpomeres 2 and 3 together, tapering, weakly rounded apically. Galea narrow, elongate with apical setae; lacinia slender with a few apical spines. Labium (Fig. 250) with palpomeres 2 and 3 subequal in size; terminal palpomere tapering, rounded at apex. Mentum transverse; prementum almost as long as wide, with ligula expanded laterally, membranous. Tentorium (Fig. 14) with anterior arms fused medially, and widely divergent anteriorly; corpotentorium lyriform.

Prothorax (Fig. 293)  $0.71\text{--}0.75 \times$  as long as wide; pronotal surface with fine, irregular microsculpture between moderately coarse and sparse puncturation; lateral edges evenly and moderately arcuate from anterior margin towards its middle, thence weakly convergent, becoming parallel before posterior, almost right angles; anterior angles obtuse; lateral sulci in form of triangular, concave impressions limited from outside by elongate ridges, basal sulcus rather distinct. Prosternal process (Fig. 294) distinctly separates front coxae, extends beyond their posterior margin. Procoxal cavity externally open, internally closed, with small rounded slit in its antero-lateral outer edge; procoxa circular in outline; trochantin concealed.

Meso- and metathorax. Mesosternum (Fig. 396) bicarinate with intercoxal process boat-shaped; with two rounded, pubescent pits on sides of antero-lateral edges of mesosternal process; with mesocoxal cavities narrowly separated (mesosternal process  $0.41\text{--}0.45 \times$  as broad as coxal diameter) open outwardly; mesocoxa circular in outline; trochantin concealed. Elytron (Figs 452, 453) elongate, moderately convex; irregularly punctured (with more or less regular rows of punctures visible on cleared specimens); sutural stria fine, entire, weakly divergent from apex to elytral base. Scutellum (Fig. 359) moderately large, transverse (about  $2 \times$  wider than long), rounded apically.

Metasternum (Fig. 396)  $1.70 \times$  as long as mesosternum,  $1.70 \times$  as broad as long; with two pairs of pubescent, postcoxal pits. Metendosternite (Fig. 515) with anterior arms widely, and anterior tendons narrowly separated. Hind wing reduced, comparatively long but very narrow.

Legs (Fig. 571) with tarsal formula 4-4-4 in both sexes; tarsomere 2 weakly lobed ventrally, tarsomere 3 small but distinct; claws simple, empodium bisetose. Femur subclavate, sparsely pubescent; tibia and tarsus more densely pubescent than femur; apex of tibia (except of outer edge) surrounded by short spines; tibial spurs absent. All tibiae show sexual differences. In male, protibia (Fig. 574) weakly or distinctly arcuato-angulate, with small dentiform projection at inner apical angle; mesotibia (Fig. 572) with very small spine on inner edge, at apical third; metatibia (Fig. 573) weakly or distinctly dilated in apical half, with more or less distinct angulation at beginning of dilated part.

Abdomen (Fig. 628) with five freely articulated ventrites; ventrite 1 longer than two following together; ventrite 2 slightly longer than 3; ventrites 3–5 subequal in length. Sternite 8, apex of which sometimes visible, in male as in Fig. 629, in female widely rounded. Male abdominal segment 9 as in Figs 665, 666.

Aedeagus resting on the side when retracted, short and stout; median lobe (Fig. 728) curved, moderately sclerotized, with weakly sclerotized gonopore at apex. Tegmen (Figs 729, 730) lightly sclerotized; tegminal plate large, almost as long as median lobe; with fixed, short parameres; tegminal strut moderately long.

Female genitalia (Fig. 787). Ovipositor weakly sclerotized, with two elongate coxities; styli small, terminal apically. Spermatheca elongate-oval, membranous; accessory gland very small, elongate, membranous; sperm duct with short, sclerotized infundibulum.

*Species examined.* *S. vandykei* Blaisdell, *S. borealis* Blaisdell.

*Distribution.* North America: USA (California), Canada (British Columbia).

#### *Panaleies* Tomaszewska, 2000

(Figs 17, 18, 82, 119, 162, 163, 215, 251, 295, 296, 360, 397, 454, 455, 516, 545, 575, 630, 667, 668, 731, 732, 733, 786)

*Panaleies* Tomaszewska, 2000: 80. Type species, by original designation: *Panamomus decoratus* Gorham, 1887: 649.

*Description.* Length about 3.0 mm. Body elongate-oval ( $2.18\text{--}2.22 \times$  as long as wide), moderately convex; glabrous, shiny; yellowish-brown, with antennae darker, under surface brown; head, pronotum and elytra with brownish-black, contrasting markings.

Head (Figs 17, 18) surface covered with comparatively dense and fine punctures between distinct, sparse and coarse puncturation. Eyes large, prominent, coarsely faceted. Antennal insertions concealed. Antenna 11-segmented (Fig. 82) with scape stout, pedicel slightly shorter than scape and longer than antennomere 3;

antennomere 4 scarcely shorter than 3 or 5; antennomere 5 longer than antennomeres 4 or 6; antennomeres 6–8 subequal, almost as long as wide; antennomeres 9–11 form elongate, narrow, loose and scarcely flattened club; antennomeres 9 and 10 equal in size and shape. Frontoclypeal ridge almost straight. Clypeus transverse, flat, with sides weakly convergent from base towards middle of its length, thence subparallel, truncate apically. Labrum (Fig. 119) with narrow membranous apex and rounded anterior margin; coarsely and sparsely punctured; mesal arms of tormae asymmetrical, recurved posteriorly. Mandible (Figs 162, 163) short and stout with two, moderately large apical teeth and a few very small, blunt teeth on incisor edge; prostheca shortly setose; mola with transverse ridges. Maxilla (Fig. 215) with palpomere 1 and 3 very short; palpomere 2 twice as long as 1 or 3; terminal palpomere as long as remaining together, cylindrical, rounded apically. Galea narrow, elongate with apical setae; lacinia slender with a few apical spines. Labium (Fig. 251) with terminal palpomere scarcely longer than palpomere 2, cylindrical, rounded at apex. Mentum transverse; prementum almost as long as wide, with ligula expanded laterally, membranous. Tentorium (Figs 17, 18) with anterior arms fused medially, and widely divergent anteriorly; with short additional projections on anterior arms; corpotentorium curved.

Prothorax (Fig. 295) 0.65–0.68 × as long as wide; pronotal surface with fine, rather dense puncturation between coarse and sparse punctures; lateral edges of pronotum moderately arcuate, distinctly and comparatively widely bordered, sinuate; anterior angles weakly acute, posterior angles acute; lateral sulci in form of triangular, concave impressions limited from outside by elongate ridges basal sulcus rather distinct. Prosternal process (Fig. 296) very narrow, hardly separate front coxae; not extending to their posterior margin. Procoxal cavity externally open, internally closed, with small rounded slit in its antero-lateral outer edge; procoxa circular in outline; trochantin concealed.

Meso- and metathorax. Mesosternum (Fig. 397) bicarinate with intercoxal process boat-shaped; with two rounded, pubescent pits on sides of antero-lateral edges of mesosternal process; mesocoxal cavities narrowly separated (mesosternal process about 0.40 × as broad as coxal diameter) open outwardly; mesocoxa circular in outline; trochantin concealed. Elytron (Figs 454, 455) elongate, moderately convex; irregularly punctured (covered with regular rows of dark punctures visible on cleared specimens); sutural stria fine, entire, weakly divergent from apex to elytral base. Scutellum (Fig. 360) moderately large, transverse (about 1.80 × wider than long), rounded apically. Metasternum (Fig. 397) about twice as broad as long, 1.45 × as long as mesosternum; with two pairs of pubescent, postcoxal pits. Metendosternite (Fig. 516) with comparatively short stalk, anterior arms widely, and anterior tendons rather narrowly separated. Hind wing (Fig. 545) without anal lobe. Anal and cubital veins absent. Media posterior (MP 1+2) moderately long, radius poste-

rior (RP) indistinct. Medial bridge present; medial fleck undivided; radial cell reduced.

Legs (Fig. 575) similar in both sexes; moderately long. Tarsal formula 4-4-4, with tarsomere 2 weakly lobed ventrally; tarsomere 3 small but distinct; claws simple, empodium bisetose. Femur subclavate, sparsely pubescent; tibia and tarsus more densely pubescent than femur; apex of tibia (except of outer edge) surrounded by short spines; tibial spurs absent.

Abdomen (Fig. 630) with six freely articulated ventrites; ventrite 1 longer than two following together; ventrites 2–5 subequal in length. In male, ventrite 6 emarginate apically. Male abdominal segment 9 as in Figs 667, 668.

Aedeagus resting on its side when retracted; median lobe (Fig. 731) curved, rather long and stout, sclerotized with internal sclerites. Tegmen (Figs 732, 733) lightly sclerotized; tegminal plate moderately large, a half as long as median lobe; with fused parameres; tegminal strut comparatively long.

Female genitalia (Fig. 786). Ovipositor weakly sclerotized, with two elongate coxities; styli small, terminal. Spermatheca elongate-oval, membranous; accessory gland very small, elongate, membranous.

*Species examined.* *P. decoratus* (Gorham), monotypic genus.

*Distribution.* Asia: Japan.

#### *Microxenus* Wollaston, 1861

(Figs 19, 20, 83, 120, 164, 165, 216, 252, 297, 298, 361, 398, 456, 457, 517, 576, 577, 631, 669, 670, 739, 788, 818)

*Microxenus* Wollaston, 1861: 139. Type species, by monotypy: *Microxenus laticollis* Wollaston, 1861.

*Description.* Length 1.3–1.5 mm. Body (Fig. 818) long-oval, gradually narrowing from about half of the body length towards elytral apex; moderately convex; brown, shiny, smooth, covered with sparse and short pubescence.

Head (Figs 19, 20) transverse; rather coarsely punctured. Gular sutures short, convergent anteriorly, widely separated. Eyes moderately large, weakly oval, prominent, coarsely faceted. Antennal groove short, weakly impressed, with apex not expanding to posterior edge of eye; antennal sockets visible from above. Antenna reaches to about a half of length of prothorax, 10-segmented (Fig. 83) with 2-segmented club. Frontoclypeal ridge weakly arcuate. Clypeus transverse, flat, very weakly convergent anteriorly, truncate at apex. Labrum (Fig. 120) covered with short setae and with long setae at sides of apex; middle part of apex membranous, truncate; tormae with mesal arms recurved anteriorly; labral rods divergent anteriorly. Mandible (Figs 164, 165) with strongly, arcuately curved outer edge; bifid at apex, with one small tooth on incisor edge; mola moderately large, transversely ridged; prostheca fringed; submola very small, membranous. Maxilla (Fig. 216) with palpomeres 1 and 3 very short; palpomere 2 about twice as long as 1

or 3; terminal palpomere longer than remaining palpomeres combined, tapering, rounded at apex. Galea blunt, moderately wide with long, apical setae; twice as wide as lacinia. Lacinia long, narrow, with a few apical spines, and setae on inner edge. Labium (Fig. 252) with palpomere 1 smallest; terminal palpomere as long as 1 and 2 combined, stout, oval, weakly truncate at apex. Mentum trapezoidal, with raised, triangular area medially; finely punctured, covered sparsely with short setae. Prementum weakly transverse, sclerotized with ligula membranous, lobed at sides. Tentorium (Fig. 20) with anterior arms fused medially, and widely divergent anteriorly; corpotentorium curved.

Prothorax. Pronotum (Fig. 297) transverse, widest at base; pronotal surface coarsely and sparsely punctured; lateral edge bordered for basal  $\frac{2}{3}$ ; basal sulcus rather distinct, lateral sulci hardly visible; anterior angles, blunt; posterior angles almost right-angled. Pronotal disc convex. Prosternal process (Fig. 298) broad, flat, expanded apically, with apex weakly emarginate; extends posteriorly beyond front coxae. Procoxa circular in outline, its cavity externally open, internally closed; trochantin concealed.

Meso- and metathorax. Mesonotum (Fig. 361) sclerotized; scutellum very small, strongly transverse, with weakly emarginate apex. Mesosternum (Fig. 398) smooth, flat; intercoxal process broadly separates mesocoxae (broader than coxal diameter), not extends beyond them. Mesocoxa circular in outline, its cavity outwardly open; trochantin exposed. Meso-metasternal junction of straight-line type. Elytron (Figs 456, 457) elongate, tapering, abruptly convex, with lateral margin almost invisible from above; punctations irregular; epipleuron incomplete apically. Metasternum (Fig. 398) strongly transverse, as long as mesosternum, weakly convex; median line absent; femoral lines complete; postcoxal pits absent. Metacoxae transverse, widely separated. Metendosternite (Fig. 517) with very short stalk and widely separated anterior arms and anterior tendons. Hind wing absent.

Legs. Trochanterofemoral attachment oblique (Fig. 576). Femur swollen; tibia gradually widening towards tarsus, surrounded by stout spines. Tarsal formula 4-4-4 in both sexes; tarsomere 2 and 3 weakly lobed ventrally; tarsomere 4 as long as remaining tarsomeres combined (Fig. 577). Claws simple. Empodium small, bisetose.

Abdomen (Fig. 631) with six freely articulated ventrites; ventrite 1 slightly longer than two following together, with v-shaped, complete femoral lines; ventrites 2-4 subequal in length; in male, ventrite 6 deeply emarginate. Male abdominal segment 9 lightly sclerotized (Figs 669, 670).

Aedeagus (Fig. 739) resting on its side when retracted. Median lobe sclerotized, very long, thin, coiled, with T-shaped capsule at base. Tegmen short, subcylindrical, with tegminal strut long and articulated; parameres fused.

Female genitalia (Fig. 788). Ovipositor weakly sclerotized, with separated, elongate coxities; styli small, ter-

minial. Spermatheca small, membranous, elongate with round apex; accessory gland very small, elongate, membranous; sperm duct rather long, slender; connection between bursa copulatrix and sperm duct characteristically broad and flat (infundibulum-like structure).

*Species examined.* *M. laticollis* Wollaston, monotypic genus.

*Distribution.* South Africa.

### *Eidoreus* Sharp, 1885

(Figs 21, 22, 84, 121, 166, 167, 217, 253, 299, 300, 362, 399, 458, 459, 518, 546, 578, 579, 632, 671, 672, 740, 741, 789, 819)

*Eidoreus* Sharp, 1885: 146. Type species, by monotypy: *Eidoreus minutus* Sharp, 1885.

*Eupsilobius* Casey, 1895: 454. Type species, by monotypy: *Eupsilobius politus* Casey, 1895.

*Pseudalexia* Kolbe, 1910: 34. Type species, by monotypy: *Pseudalexia sechellarum*, Kolbe, 1910.

*Eupsilobius* Sasaji, 1986: 230 (error).

*Description.* Length about 1.2 mm. Body (Fig. 819) oval, moderately convex; brown, shiny, smooth, covered with very sparse and short pubescence.

Head (Figs 21, 22) transverse; rather coarsely punctured. Gular sutures short, subparallel, widely separated. Eyes prominent, coarsely faceted. Antennal groove short, distinctly impressed, apex not expanding to posterior edge of eye; antennal sockets visible from above. Antenna almost as long as head width, 10-segmented (Fig. 84) with 2-segmented compact, large club. Frontoclypeal ridge weakly arcuate. Clypeus transverse, flat, weakly convergent anteriorly, truncate at apex. Labrum (Fig. 121) coarsely punctured, covered with short setae and with long setae at sides of apex; middle part of apex membranous, truncate; tormae with mesal arms recurved anteriorly; labral rods short, subparallel. Mandible (Figs 166, 167) with strongly arcuately curved outer edge; bifid at apex, with two blunt, small teeth on incisor edge; mola transversely ridged; prosthema fringed; submola very small, membranous. Maxilla (Fig. 217) with palpomeres 1 and 3 very short; palpomere 2 about twice as long as 1 or 3; terminal palpomere longer than remaining palpomeres combined, tapering, rounded at apex. Galea blunt, moderately broad with long, apical setae; about twice as wide as lacinia. Lacinia long, narrow, with a few apical spines, and setae on inner edge. Labium (Fig. 253) with palpomere 1 smallest; terminal palpomere as long as 1 and 2 combined, stout, oval, weakly truncate at apex. Mentum trapezoidal, with raised, triangular area medially; finely punctured, covered sparsely with short setae. Prementum as long as wide, sclerotized with ligula membranous, lobed at sides. Tentorium (Fig. 22) with anterior arms fused medially, widely divergent anteriorly, and connected by arcuate corpotentorium.

Prothorax. Pronotum (Fig. 299) strongly transverse, widest at base; pronotal surface finely punctured; lateral edges hardly bordered; basal edge overhanging elytral

base; sulci absent; anterior angles, blunt, very slightly produced. Pronotal disc evenly convex. Prosternum (Fig. 300) T-shaped, with anterior edge emarginate medially, and arcuately produced anteriorly at each half; prosternal process moderately broad, flat, parallel-sided, dilated apically; extends to posterior margin of front coxae. Procoxa circular in outline, with cavity externally open, internally closed; trochantin concealed.

Meso- and metathorax. Mesonotum (Fig. 362) sclerotized; scutellum small, cordiform, with rounded apex. Mesosternum (Fig. 399) almost invisible externally, except for short lateral parts; mesocoxae widely separated, circular in outline, their cavities outwardly open; trochantin exposed. Elytron (Figs 458, 459) elongate-oval, with lateral margin almost invisible from above; punctured irregularly; epipleuron incomplete. Metasternum (Fig. 399) transverse, weakly convex; median line absent; femoral lines complete, arcuate; postcoxal pits absent. Metasternal process arcuately produced anteriorly touching prosternal process (covering mesosternum). Metacoxae transverse, widely separated. Metendosternite (Fig. 518) with extremely short (virtually absent) stalk and widely separated anterior arms and anterior tendons. Hind wing (Fig. 546) without anal lobe. Anal and cubital veins absent; media posterior (MP 1+2) rather long, sclerotized, connected with vestigial radius posterior (RP). Medial bridge present; medial fleck undivided; radial cell reduced.

Legs. Trochanterofemoral attachment oblique (Fig. 578). Femur strongly swollen with wide and long cavity to receive tibia; tibia widest near middle of its length, with two distinct spurs at apex. Tarsal formula 4-4-4 in both sexes; tarsomere 2 and 3 weakly lobed ventrally; tarsomere 4 almost as long as remaining tarsomeres combined (Fig. 579). Claws simple. Empodium small, bisetose.

Abdomen (Fig. 632) with six freely articulated ventrites; ventrite 1 as long as three following together, with incomplete femoral lines, and additional, arcuate, lateral, slender lines at sides; ventrites 2-4 subequal in length. In male (see Fig. 632), ventrite 5 weakly emarginate medially. Male abdominal segment 9 weakly sclerotized (Figs 671, 672).

Aedeagus resting on its side when retracted. Median lobe (Fig. 740) sclerotized, very long, thin, coiled, with characteristic T-shaped capsule at base. Tegmen (Fig. 741) cylindrical, with tegminal strut long, articulated; parameres fused.

Female genitalia (Fig. 789). Ovipositor weakly sclerotized, with separated, elongate coxities; styli distinct, terminal. Spermatheca small, membranous; accessory gland very small, elongate, membranous; sperm duct long, slender; connection between bursa copulatrix and sperm duct characteristic – stiff, broad and inflated (infundibulum-like structure).

*Species examined.* *E. minutus* Sharp.

*Distribution.* Known mainly from widely scattered islands: Cuba, the Virgin Islands, Guadeloupe, the

Galapagos, the Mascarene Islands, Seychelles, Sri Lanka, Fiji, French Polynesia, the Solomon Islands, Hawaii.

#### *Adamia* gen. nov.

(Figs 23, 24, 85, 122, 168, 169, 218, 254, 301, 302, 363, 400, 460, 461, 519, 547, 580, 581, 633, 673, 674, 742, 790, 820)

*Type species.* *Adamia mexicana* sp. nov., gender feminine.

*Etymology.* Dedicated to my tutor Adam Ślipiński, who brought this interesting beetle to my attention.

*Diagnosis* (the following diagnosis and description is based on the only known species). The mouthparts and male and female genitalia are closely similar to those of *Microxenus* and *Eidoreus*. *Adamia* is easily separated from both of these genera by the following characters: pronotum widest near middle of its length, with distinct, deep lateral and basal sulci; prosternum with longitudinal, median ridge and prosternal process rounded apically. Moreover, the presence of hind wings and evenly oval elytra, distinguish *Adamia* from *Microxenus* and the shape of tentorium, absence of tibial spurs, and metasternal process not covering mesosternum, distinguish it from *Eidoreus*.

*Description.* Body (Fig. 820) elongate-oval, moderately convex; shiny, smooth, covered with sparse and short pubescence.

Head (Figs 23, 24) transverse. Gular sutures short, convergent anteriorly, widely separated. Eyes moderately large, weakly oval, prominent, coarsely faceted. Antennal groove short, weakly impressed, with apex not extending to posterior edge of eye; antennal sockets visible from above. Antenna reaches to about a half of prothorax length, 10-segmented (Fig. 85) with 2-segmented club. Fronto-clypeal ridge weakly arcuate. Clypeus transverse, flat, very weakly convergent anteriorly, truncate at apex. Labrum (Fig. 122) coarsely punctured, covered with moderately long setae; middle part of apex membranous, truncate; tormae with mesal arms recurved anteriorly; labral rods subparallel. Mandible (Figs 168, 169) with strongly, arcuately curved outer edge; bifid at apex, with one small tooth on incisor edge; mola moderately large, transversely ridged; prostheca fringed; submola very small, membranous. Maxilla (Fig. 218) with palpomeres 1 and 3 very short; palpomere 2 about twice as long as 1 or 3; terminal palpomere longer than remaining palpomeres combined, tapering, rounded at apex. Galea blunt, moderately wide with long, apical setae; twice as wide as lacinia. Lacinia long, narrow, with a few apical and mesal spines, and setae on inner edge. Labium (Fig. 254) with palpomere 1 smallest; terminal palpomere as long as 1 and 2 combined, stout, oval, weakly truncate at apex. Mentum trapezoidal, with raised, triangular area medially; coarsely punctured. Prementum weakly transverse, sclerotized with ligula membranous, lobed at sides. Tentorium (Fig. 24) with anterior arms fused medially, and widely divergent anteriorly; corpotentorium lyriform.

Prothorax. Pronotum (Fig. 301) transverse; lateral margin narrowly bordered; posterior edge with medial lobe; basal and short lateral sulci distinct; anterior angles, obtuse; posterior angles almost right-angled. Pronotal disc convex. Prosternal process (Fig. 302) moderately broad, with raised, longitudinal, median line, parallel-sided, bordered, rounded apically; extends posteriorly beyond front coxae. Procoxa circular in outline, with long, narrow, internal extension (Fig. 580); its cavity externally open, internally closed; trochantin concealed.

Meso- and metathorax. Mesonotum (Fig. 363) sclerotized; scutellum very small, transverse, with weakly rounded apex. Mesosternum (Fig. 400) smooth, almost flat; intercoxal process widely separates mesocoxae (as wide as coxal diameter), not extends beyond them. Mesocoxa circular in outline, its cavity outwardly open; trochantin exposed. Meso-metasternal junction of straight-line type. Elytron (Figs 460, 461) elongate, convex; epipleuron narrow, incomplete. Metasternum (Fig. 400) strongly transverse, weakly convex; median line absent; femoral lines complete; postcoxal pits absent. Metacoxae transverse, widely separated. Metendosternite (Fig. 519) with very short stalk and widely separated anterior arms and anterior tendons. Hind wing (Fig. 547) without anal lobe; with single, reduced anal vein; medial fleck present, undivided.

Legs. Trochanterofemoral attachment subheteromeroïd (Fig. 580). Femur swollen; tibia gradually widening towards tarsus; surrounded by stout spines. Tarsal formula 4-4-4 in both sexes; tarsomere 2 and 3 weakly lobed ventrally; tarsomere 4 as long as remaining combined (Fig. 581). Claws simple. Empodium small, bisetose.

Abdomen (Fig. 633) with six ventrites; ventrite 1 as long as two following together, with v-shaped femoral lines, weakly interrupted near ventrite 2; ventrites 2-5 subequal in length; ventrite 6 partially exposed, flexible; in male emarginate medially. Male abdominal segment 9 lightly sclerotized (Figs 673, 674).

Aedeagus (Fig. 742) resting on its side when retracted. Median lobe sclerotized, very long, thin, coiled, with T-shaped capsule. Tegmen short, cylindrical, with tegminal strut long, articulated; parameres fused.

Female genitalia (Fig. 790). Ovipositor weakly sclerotized, with separated, elongate coxites; styli elongate, terminal. Spermatheca small, membranous, of characteristic shape; accessory gland very small, elongate, membranous; sperm duct long, slender; connection between bursa copulatrix and sperm duct broad and flat, gutter-shaped (infundibulum-like structure).

**Species examined.** *Adamia mexicana* sp. nov., monotypic genus.

**Distribution.** Known only from Mexico.

*Adamia mexicana* sp. nov.

**Etymology.** The name *mexicana* is based upon the country where this species has been collected.

**Description** (see also the detailed generic description which is based on this species). Length 1.25-1.40 mm; body about  $1.80 \times$  longer than wide; pronotum about  $0.52 \times$  as long as wide; elytra  $1.12 \times$  wider than pronotum, and  $2.57 \times$  longer than pronotum.

Colour brown. Vestiture consists of sparse and short hairs. Head covered with fine, irregular microsculpture between moderately coarse and sparse puncturation. Pronotum widest near middle of its length; moderately coarsely punctured; edges smooth. Elytra widest in about basal third, with weakly sinuate outer edge; irregularly punctured. Aedeagus as in Fig. 742. Female genitalia as in Fig. 790.

**Types.** Holotype: Mexico: "Tezonapa, Veracruz, Mex. 8.VIII.41/ Col. & pres. By Henry S. Dybas" (FMNH). Paratypes. ♂: "MEX.: S.L. Potosi Palitla. 5 mi, N. of Tamazunchale. 22.XII.1948/ H.B. Leech Collector" (MIZ, completely dissected on slide). ♀: "MEX. S.L.P. Quinta Chila, Tamazunchale, 20.XII.1948/ H.B. Leech Collector" (FMNH, dissected on slide).

#### *Endomychus* Panzer, 1795

(Figs 25, 26, 27, 86, 123, 170, 219, 255, 303, 304, 364, 401, 402, 403, 462, 463, 520, 548, 549, 582, 634, 675, 676, 743, 791, 821)

*Endomychus* Panzer, 1795: 175. Type species, by subsequent designation of Latreille 1810: 432: *Chrysomela coccinea* Linnaeus, 1758.

*Cyanauges* Gorham: in Gorham and Lewis, 1874: 54 (nec *Cyanauges* Philippi, 1865). Type species, by original designation: *Cyanauges gorhami* Lewis: in Gorham and Lewis, 1874. *Caenomychus* Lewis, 1893: 153. Replacement name for *Cyanauges* Gorham, 1874.

**Description.** Length 3.40-6.56 mm. Body (Fig. 821) elongate to ovate, convex to highly convex, glabrous, shiny; finely to distinctly, densely and confusedly punctured; rarely with fine pubescence. Colour yellow, orange-brown, brownish-black or black; often with black or yellow spots or stripes on elytra.

Head (Figs 25, 26, 27) weakly transverse, slightly narrowing from eyes towards labrum. Gular sutures short; widely separated, weakly convergent anteriorly. Eyes moderately large, prominent, coarsely faceted. Antennal grooves absent; antennal sockets well visible from above. Antenna almost as long as a half of body length, 11-segmented with, 3-segmented club (Fig. 86); scape slightly longer than pedicel, antennomere 3, longer than 2 or 4, 4-7 subequal in length; antennomere 8 slightly shorter than 7 and distinctly shorter than 9; antennomeres 9-11 form narrow, loose and weakly flattened club; terminal antennomere obliquely rounded. Frontoclypeal ridge almost straight. Clypeus transverse, flat, slightly narrower at apex than at base, truncate apically. Labrum (Fig. 123) weakly transverse rounded apically; tormae elongate, labral rods sclerotized, parallel, perpendicular to mesal arms of tormae, which are straight or somewhat recurved posteriorly. Mandible (Fig. 170)

broad, weakly convex dorsally, with two prominent apical teeth and one small subapical tooth; prostheca covered with short setae; submola distinct, membranous. Maxilla (Fig. 219) with palpomere 1 smallest; palpomeres 2 and 3 distinctly widened toward their apices; palpomere 2 twice as long as 3; shape of terminal maxillary palpomere characteristic for species – from elongate, cylindrical, narrowed and rounded at apex, to subcylindrical, truncate at apex, or axe-shaped, strongly enlarged apically. Galea more than twice as broad as lacinia, elongate, slightly enlarged and densely setose apically. Lacinia slender, with brush of long setae at apex. Digitus small, blunt, hardly visible. Labium (Fig. 255) with palpomere 2 more than twice the length of 1; palpomere 3 longest and widest – elongate, widest in the middle of its length, narrowing towards apex, weakly rounded. Mentum transverse, almost rectangular, sparsely punctured with a few setae at anterior angles. Prementum longer than wide, weakly narrower at base than at apex, sclerotized, punctured, with brush of short setae at anterior margin, and with several long setae, especially in central part of prementum; ligula not lobed at sides, submembranous. Tentorium (Figs 26, 27) with anterior arms fused medially, and widely divergent anteriorly; corpotentorium straight, without median process.

Prothorax. Pronotum (Fig. 303) transverse, 0.43–0.61 × as long as wide; most often widest at base; weakly to distinctly bordered laterally; basal sulcus distinct or hardly visible, lateral sulci short, deep. Anterior and posterior angles distinct; posterior angles acutely produced, anterior angles acute or finely to distinctly rounded. Pronotal disc almost flat or weakly convex. Prosternal process (Fig. 304) moderately broad (0.6–0.9 × as broad as coxal diameter), distinctly separates front coxae and extends posteriorly beyond them. Procoxa circular in outline, its cavity externally open, internally closed; trochantin concealed.

Meso- and metathorax. Mesonotum (Fig. 364) weakly sclerotized with scutellum moderately large, cordiform, punctured. Mesosternum (Fig. 401) with a pair of pits near anterior margin, separated by nearly the width of intercoxal process, which is almost square to slightly transverse, flat, 0.9–1.2 × as wide as coxal diameter. Mesocoxa circular in outline, its cavity outwardly open; trochantin exposed. Meso-metasternal junction of straight-line type, without internal knobs. Elytron weakly elongate (Figs 462, 463) with punctures distinct and irregular; epipleuron incomplete apically. Metapleuron as in Fig. 403. Metasternum (Fig. 402) simple, large, transverse, nearly twice as broad as long, almost flat, slightly narrower anteriorly; with two pairs of postcoxal pits. Metacoxae transverse, widely separated; femoral lines absent. Metendosternite (Fig. 520) with very short stalk and widely separated anterior arms and tendons.

Wing (Figs 548, 549) venation nearly complete. Anal anterior (AA) fused with cubital anterior (CuA) extends towards the back of medial field as single vein (AA+CuA); media posterior (MP 1+2) moderately long,

sclerotized, fused with partially reduced radius posterior (RP). Medial bridge distinct; MP-CuA cross vein reduced; medial fleck rather large, of irregular shape, without distinct limits, seems to be divided; anal vein single; closed radial cell reduced.

Legs (Fig. 582). Trochanterofemoral attachment oblique. Femur twice as wide as tibia; tibia without apical spurs. Tarsal formula 4-4-4 in both sexes; tarsomeres 1 and 2 flattened and ventrally lobed; tarsomere 3 very small, 3 × shorter than 2 and four or more times shorter than tarsomere 4 (tarsi pseudotrimerous). Claws simple. Empodium very small, bisetose.

Abdomen (Fig. 634) with six freely articulated ventrites; ventrite 1 almost as long as metasternum, and longer than two following together; ventrites 2–4 subequal in length, 5 slightly longer than 2, 3, or 4. Male abdominal segment 9 as in Figs. 675, 676.

Aedeagus (Fig. 743) moderately long, curved, resting on its side when retracted. Tegmen reduced; tegminal plate small, more than three times shorter than median lobe; with short, fused parameres; tegminal strut present. Median lobe sclerotized, with membranous gonopore at apex; from inside gonopore there extends slender but distinct sclerite of variable length.

Female genitalia (Fig. 791). Ovipositor moderately sclerotized, simple, reduced to two coxities, which are triangular or elongate; styli small, terminal. Spermatheca moderately large, membranous; accessory gland weakly sclerotized. Ejaculatory duct short; sclerotized infundibulum absent.

**Species examined.** *E. coccineus* (Linnaeus), *E. thoracicus* Charpenter, *E. gorhami* (Lewis), *E. flavus* Strohecker, *E. humeralis* (Pic).

**Distribution.** Europe, North America and Asia: Palaearctic area and northern Orient (Indo-China, Taiwan).

### *Cyclotoma* Mulsant, 1851

(Figs 28, 29, 87, 124, 171, 220, 256, 305, 306, 365, 404, 405, 406, 466, 467, 521, 550, 583, 635, 677, 678, 744, 792, 822)

*Cyclotoma* Mulsant, 1851: 71. Type species, by monotypy:

*Cyclotoma testudinaria* Mulsant, 1851.

*Panomoea* Gerstaecker, 1857: 241. Type species, by monotypy:

*Panomoea coccinellina* Gerstaecker, 1857.

*Niteta* Weise, 1890: 21. Type species, by present designation:

*Niteta quatuordecimpunctata* Weise, 1890.

**Description.** Length 5.0–7.0 mm. Body (Fig. 822) circular in outline, strongly convex, almost hemispherical; surface smooth and shiny; finely to distinctly, confusedly punctured. Colour red or yellowish-red, most often with black spots on the elytra and pronotum.

Head (Figs 28, 29) deeply retracted in prothorax, weakly transverse, narrowing from eyes towards labrum. Gular sutures short, moderately widely separated, somewhat convergent anteriorly. Eyes oval in outline, prominent, coarsely faceted. Antennal grooves absent; anten-

nal sockets visible from above. Antenna short, 11-segmented (Fig. 87), or 10-segmented (in one species); with, 3-segmented club; scape more than twice longer than pedicel, antennomere 3 slightly longer than broad; antennomeres 3 and 4 subequal in length; antennomeres 5–8 (or 5–7) very short, subequal; antennomeres 9–11 or 8–10 form narrow and rather loose club, which is almost as long as remaining antennomeres together. Fronto-clypeal ridge straight. Clypeus strongly transverse, flat. Labrum (Fig. 124) truncate at apex; tormae elongate, with mesal arms recurved anteriorly; labral rods absent. Mandible (Fig. 171) broad, with two prominent apical teeth; mola strongly sclerotized; prosthema moderately large, covered with short setae; submola distinct, setose, membranous. Maxilla (Fig. 220) with palpomeres 2 and 3 distinctly widening towards their apices, especially that of 2; terminal palpomere elongate, subcylindrical, truncate at apex. Galea weakly elongate, enlarged and densely setose apically. Lacinia with digitus visible; densely setose on inner edge. Labium (Fig. 256) with palpomere 1 smallest, palpomere 2 and 3 subequal in length; terminal palpomere elongate, tapering, rounded at apex. Mentum transverse, almost rectangular. Prementum longer than wide, rectangular, sclerotized, punctured, covered with comparatively long setae; limits of ligula invisible. Tentorium (Fig. 29) of *Endomychus* – type.

Prothorax. Pronotum (Fig. 305) strongly transverse, widest near base; lateral and anterior margins finely and very narrowly bordered; sulci absent; anterior angles produced, rounded; posterior angles widely rounded. Pronotal disc flat or weakly convex. Prosternal process (Fig. 306) broadly separates front coxae and extends posteriorly beyond them. Procoxa circular in outline, its cavity externally open, internally closed; trochantin concealed.

Meso- and metathorax. Mesonotum (Fig. 365) with scutellum moderately large, cordiform, acute apically. Mesosternum (Fig. 404) with intercoxal process transverse or almost square, somewhat concave in its basal part; broadly separates mesocoxae, not extends beyond them. Mesocoxa circular in outline, its cavity outwardly open; trochantin fully exposed. Meso-metasternal junction of straight-line type, without internal knobs. Elytron (Figs 466, 467) oval, strongly convex, moderately densely and irregularly punctured; epipleuron broad, complete. Metapleuron as in Fig. 406. Metasternum (Figs 404, 405) transverse, almost flat, without postcoxal pits, with long median line. Metacoxae transverse, widely separated; femoral lines absent. Metendosternite (Fig. 521) with comparatively short stalk and widely separated anterior arms and anterior tendons. Hind wing (Fig. 550) with venation nearly complete. Anal anterior (AA) slender, fused with cubital anterior (CuA) extends towards the back of medial field as single vein (AA+CuA); media posterior (MP 1+2) moderately long, sclerotized, connected with partially reduced radius posterior (RP). Mp-CuA cross vein incomplete near MP; medial bridge present; medial fleck

rather large, of irregular shape, without distinct limits, seems to be divided; closed radial cell reduced.

Legs (Fig. 584). Trochanterofemoral attachment oblique. Femur comparatively stout, of almost equal breadth throughout, twice as wide as tibia; tibia distinctly widened toward its apex, without apical spurs. Tarsal formula 4-4-4 in both sexes; tarsomeres 1 and 2 flattened and ventrally lobed; tarsomere 3 very small, about 3 × shorter than 2, and four or more times shorter than tarsomere 4 (tarsi pseudotrimerous). Claws simple. Empodium small, bisetose.

Abdomen (Fig. 635) with five freely articulated ventrites; sixth ventrite partially visible; ventrite 1 as long as two following together; ventrite 2 slightly longer than 3, 4 or 5; ventrites 3–5 subequal in length. Male abdominal segment 9 as in Figs 677, 678.

Aedeagus (Fig. 744) long, thin, weakly curved, resting on its side when retracted. Tegmen reduced; tegminal plate very small, with fused parameres; tegminal strut membranous. Median lobe sclerotized, curled along 1/3 of its basal length; with small, membranous gonopore at apex.

Female genitalia (Fig. 792). Ovipositor sclerotized, reduced to two coxities; styli hardly visible, terminal. Spermatheca large, oval, membranous; sperm duct long, slender, attached to long and broad connection between spermatheca and accessory gland; accessory gland moderately large, long-oval, sclerotized, with internal sclerites.

**Species examined.** *C. cingalensis* (Gorham), *C. quinquepunctata* Arrow (externally) and one unnamed species from Java.

**Distribution.** Southeastern Asia: India, Sri Lanka, Indo-China, Taiwan, Philippines, Borneo, Sumatra, Java.

#### *Meilichius* Gerstaecker, 1857

(Figs 30, 31, 88, 125, 172, 221, 257, 307, 308, 366, 407, 408, 409, 464, 465, 584, 636, 679, 680, 745, 793)

*Meilichius* Gerstaecker, 1857: 240. Type species, by monotypy: *Meilichius nigricollis* Gerstaecker, 1857.

*Milichius* Gemminger and Harold, 1874: 3737. (Unnecessary replacement name for *Meilichius* Gerstaecker).

*Thelgetrum* Gorham, 1875: 314. Type species, by monotypy: *Thelgetrum ampliatum* Gorham, 1875.

*Gibbiger* Csiki, 1900a: 375 (subgenus). Type species, by monotypy: *Milichius fasciatus* Heller, 1898.

**Description.** Length 3.7–4.2 mm. Body short-oval in outline, strongly convex; surface smooth and shiny; confusedly, densely and rather coarsely punctured. Colour red-brown, brown to almost black, sometimes with contrasting markings on the elytra.

Head (Figs 30, 31) weakly transverse, narrowing from eyes towards labrum. Gular sutures very short, weakly convergent anteriorly. Eyes moderately large, oval in outline, prominent, coarsely faceted. Antennal grooves absent; antennal sockets visible from above. Antenna almost as long as a half of body length, 11-segmented (Fig. 88) with, 3-segmented, narrow, rather com-

compact and scarcely flattened club; remaining antennomeres may be weakly elongate or quadrate; apical antennomere elongate, rounded. Fronto-clypeal ridge straight. Clypeus transverse, flat, narrower at apex than at base. Labrum (Fig. 125) weakly transverse; tormae elongate, with mesal arms recurved weakly anteriorly; labral rods absent. Mandible (Fig. 172) narrow, elongate, convex dorsally; with deeply concave incisor edge; mola moderately large; prostheca covered with long setae; submola densely setose, membranous. Maxilla (Fig. 221) with palpomeres 2 and 4 subequal in length; palpomeres 2 and 3 widened toward their apices, 2 more so than 3; terminal palpomere tapering, truncate apically. Galea elongate, weakly enlarged and densely setose at apex, recurved apically toward lacinia. Lacinia elongate, densely setose; digitus absent. Labium (Fig. 257) with palpomere 2 longest and widest; terminal palpomere elongate, cylindrical, weakly rounded apically. Mentum weakly transverse, rectangular. Prementum elongate, widest near middle of its length, truncate apically, covered with few moderately long setae (especially at apex), sclerotized, punctured, limits of ligula indistinct. Tentorium (Fig. 31) of *Endomychus*-type.

Prothorax. Pronotum (Fig. 307) transverse, widest at its base; distinctly bordered laterally; basal sulcus distinct or hardly visible, lateral sulci short; anterior angles produced, more or less blunt, posterior angles right-angled or weakly produced, acute. Pronotal disc weakly convex. Prosternal process (Fig. 308) broadly separates front coxae and extends posteriorly beyond them. Procoxa circular in outline, its cavity externally open, internally closed; trochantin concealed.

Meso- and metathorax. Mesonotum (Fig. 366) with scutellum moderately large, cordiform, acute apically. Mesosternum (Figs 407, 408) with intercoxal process transverse, broadly separates mesocoxae, not extends beyond them. Mesocoxa circular in outline, its cavity outwardly open; trochantin fully exposed. Meso-metasternal junction of straight-line type. Elytron (Figs 464, 465) elongate, convex or highly convex, distinctly and irregularly punctured; epipleuron narrow or moderately broad, incomplete apically. Metasternum (Fig. 408) transverse with moderately long median line, almost flat, with two postcoxal pits at anterior edge. Metacoxae transverse, widely separated; femoral lines absent. Metapleuron as in Fig. 409. Metendosternite (Fig. 408) with short stalk and widely separated anterior arms and tendons.

Wing venation as in *Cyclotoma*, except of medial fleck which is small, oval, with more or less distinct limits, rather undivided, because (AA+CuA)+CuA2 as a single, very slender vein, seems to fade a short distance before medial fleck; closed radial cell reduced.

Legs (Fig. 585). Trochanterofemoral attachment oblique. Femur widest in middle of its length, twice as wide as tibia; tibia weakly widening towards tarsus, without apical spurs. Tarsal formula 4-4-4 in both sexes; tarsomeres 1 and 2 flattened and ventrally lobed; tarsomere 3 three times shorter than 2 and four or more

times shorter than tarsomere 4 (tarsi pseudotrimerous). Claws simple. Empodium very small, bisetose.

Abdomen (Fig. 636) with five freely articulated ventrites; sixth ventrite partially visible; ventrite 1 slightly shorter than metasternum, longer than two following ventrites together; ventrite 2 slightly longer than 3 or 4; ventrite 5 slightly longer than 2, 3 or 4. Male abdominal segment 9 as in Figs 679, 680.

Aedeagus (Fig. 745) long, thin, weakly curved, resting on its side when retracted. Tegmen reduced; tegminal plate very small, with fused parameres; tegminal strut membranous. Median lobe sclerotized, curled along  $\frac{1}{3}$  of its basal length; with elongate, membranous gonopore at apex.

Female genitalia (Fig. 793). Ovipositor sclerotized, with two, elongate coxities; styli distinct, subterminal. Spermatheca large, round, membranous; sperm duct rather short, slender, attached to long and broad connection between spermatheca and accessory gland; accessory gland large, bean-shaped, sclerotized.

*Species examined.* *M. impressicollis* Strohecker and one, unnamed species from Philippines.

*Distribution.* Southeastern Asia: South India, Laos, Philippines, Borneo, Sumatra, Java, Celebes and Nias Island.

#### *Bolbomorphus* Gorham, 1887

(Figs 32, 33, 89, 126, 173, 222, 258, 309, 310, 367, 410, 468, 469, 522, 551, 586, 587, 637, 681, 682, 746, 794)

*Bolbomorphus* Gorham, 1887: 647. Type species, by monotypy: *Bolbomorphus gibbosus* Gorham, 1887.

*Description.* Length 7.0–9.0 mm. Body long-oval in outline, strongly convex; smooth and shiny; very densely and rather coarsely, confusedly punctured. Colour brown to black, with yellow contrasting markings on the elytra.

Head (Figs 32, 33) almost as long as wide, narrowing from eyes towards labrum. Gular sutures short, moderately widely separated, convergent anteriorly. Eyes large, oval in outline, prominent, moderately coarsely faceted. Antennal grooves absent; antennal sockets obvious visible from above. Antenna slightly shorter than a half of body length, 11-segmented (Fig. 89) with, 3-segmented, rather compact club, which may be comparatively narrow and weakly flattened or very broad and flattened; scape about  $1.5 \times$  as long as pedicel; antennomere 3 elongate; antennomeres 4–8 gradually shorter. Fronto-clypeal ridge straight. Clypeus transverse, flat, weakly narrower at apex than at base. Labrum (Fig. 126) punctured, covered densely with short setae, and with brushes of moderately long setae at sides of anterior margin; apical edge truncate medially; tormae elongate, with mesal arms recurved anteriorly; labral rods short, divergent anteriorly. Mandible (Fig. 173) broad, stout, strongly convex dorsally, weakly concave ventrally; with two prominent apical teeth; mola heavily sclerotized; prostheca oval, covered densely with short setae; sub-

mola distinct, elongate, setose, membranous. Maxilla (Fig. 222) with palpomere 2 and 3 distinctly widening towards their apices; terminal palpomere elongate, cylindrical, rounded at apex. Galea weakly elongate, enlarged and moderately densely setose apically, weakly recurved apically toward lacinia. Lacinia comparatively large, elongate (as long as galea), distinctly narrowing towards its apex, covered with long, moderately dense setae on its inner edge; digitus obvious. Labium (Fig. 258) with palpomere 2 weakly enlarged toward its apex; terminal palpomere elongate, cylindrical, weakly rounded apically. Mentum transverse, almost rectangular, punctured, covered with several long setae. Prementum elongate, evenly sclerotized, punctured, covered with moderately long setae; with few, long setae in its apical part; limits of ligula indistinct. Tentorium (Fig. 33) of *Endomychus*-type.

Prothorax. Pronotum (Fig. 309) transverse, widest at base; distinctly bordered laterally; basal sulcus indistinct (or absent), lateral sulci short; anterior angles produced and acute; posterior angles weakly produced. Pronotal disc flat or scarcely convex, sometimes weakly uneven. Prosternal process (Fig. 310) broadly separates front coxae and extends posteriorly beyond them. Procoxa (Fig. 586) circular in outline, its cavity externally open, internally closed; trochantin concealed.

Meso- and metathorax. Mesonotum (Fig. 367) with scutellum moderately large, transverse, weakly acute apically. Mesosternum (Fig. 410) with intercoxal process transverse (hardly broader than prosternal process); broadly separates mesocoxae, not extends beyond them, but riches near their posterior margins. Mesocoxa circular in outline, its cavity outwardly open; trochantin fully exposed. Meso-metasternal junction of straight-line type. Elytron (Figs 468, 469) elongate, highly convex, very densely and irregularly punctured; epipleuron moderately broad, complete. Humeral plates prominent. Metasternum (Fig. 410) transverse, flat; without postcoxal pits; with long median line. Metacoxae transverse, widely separated; femoral lines absent. Metendosternite (Fig. 522) with short stalk and widely separated anterior arms and tendons. Hind wing (Fig. 551) with two anal veins. Anal anterior (AA) fused with cubital anterior (CuA) extends as single vein (AA+CuA) towards the back of medial field, where it is connected with vestigial CuA 2; anal posterior (AP) slender, hardly visible, runs across anal field; media posterior (MP 1+2) moderately long, sclerotized, connected with partially reduced radius posterior (RP). Mp-CuA cross vein incomplete near MP; medial bridge present; medial fleck small, oval, with more or less distinct limits, (AA+CuA)+CuA2 as a single, slender vein seems to fade a short distance before medial fleck; radial cell reduced.

Legs (Figs 586, 587). Trochanterofemoral attachment oblique. Femur of almost equal breadth throughout, less than twice as wide as tibia, covered with very short setae; tibia and tarsus more densely setose than femur; tibia weakly widening towards tarsus, without apical

spurs. Tarsal formula 4-4-4 in both sexes; tarsomeres 1 and 2 flattened and ventrally lobed; tarsomere 3, 3 times shorter than 2 and five or more times shorter than tarsomere 4 (tarsi pseudotrimerous). Claws simple. Empodium small, bisetose.

Abdomen (Fig. 637) with six freely articulated ventrites; ventrite 1 longer than two following together; ventrites 2–5 subequal in length. Male abdominal segment 9 as in Figs 681, 682.

Aedeagus (Fig. 746) long, thin, strongly sclerotized, weakly curved, resting on its side when retracted. Tegmen reduced; tegminal plate very small, with short, fused parameres; tegminal strut present. Median lobe with curled  $\frac{1}{3}$  of its basal part; with elongate, membranous gonopore at apex.

Female genitalia (Fig. 794). Ovipositor sclerotized, with elongate coxities; styli small, subterminal. Spermatheca large, oval, membranous; accessory gland long-oval, sclerotized; sperm duct short, rather slender, attached to broad, membranous connection between spermatheca and accessory gland.

*Species examined.* *B. sexpunctatus* Arrow.

*Distribution.* Eastern Asia: China (incl. Taiwan), Japan.

#### *Eucteanus* Gerstaecker, 1857

(Figs 34, 35, 90, 127, 174, 223, 259, 311, 312, 368, 411, 470, 471, 523, 583, 588, 638, 683, 684, 747, 795, 823)

*Eucteanus* Gerstaecker, 1857: 240. Type species, by monotypy:

*Eucteanus coelestinus* Gerstaecker, 1857.

*Homalosternus* Guérin, 1857: 581. Type species, by monotypy:

*Eumorphus hardwickii* Hope, 1831.

*Description.* Length 8.0–14.0 mm. Body (Fig. 823) long-oval in outline, strongly convex; smooth and most often shiny; very densely but rather finely, confusedly punctured. Colour black or bluish-black with two large, yellow spots on each elytron.

Head (Figs 34, 35) as long as wide, weakly narrowing from eyes towards labrum. Gular sutures moderately long, widely separated, convergent anteriorly. Eyes oval in outline, prominent, moderately coarsely faceted. Antennal grooves absent; antennal sockets obvious from above. Antenna slightly shorter than a half of body length, 11-segmented (Fig. 90) with, 3-segmented, broad or very broad, compact and flattened club; scape, at least twice as long as pedicel; antennomere 3 elongate; antennomeres 4–8 gradually shorter. Fronto-clypeal ridge weakly arcuate. Clypeus transverse, flat, narrower at apex than at base. Labrum (Fig. 127) covered with short setae; with anterior edge rounded; tormae with mesal arms recurved anteriorly; labral rods short, divergent anteriorly. Mandible (Fig. 174) weakly convex dorsally; with two prominent apical teeth; mola large; prosthema covered densely with short setae; submola setose, membranous. Maxilla (Fig. 223) with palpomere 2 longest and distinctly widening towards its apex; terminal palpomere elongate, cylindrical, rounded at apex. Galea weakly

elongate, enlarged and moderately densely setose apically, slightly recurved apically toward lacinia. Lacinia elongate, distinctly narrowing towards its apex, covered with long, moderately dense setae; digitus well visible. Labium (Fig. 259) with palpomere 2 weakly enlarged toward its apex; terminal palpomere elongate, cylindrical, rounded apically. Mentum transverse, widest in middle of its length, punctured, covered with several long setae. Prementum elongate, slightly narrower at base than at apex, sclerotized, punctured, covered with few moderately long setae (mainly in its apical part); limits of ligula indistinct. Tentorium (Fig. 35) of *Endomychus*-type.

Prothorax. Pronotum (Fig. 311) transverse, widest at its base or near the middle of its length, weakly bordered laterally; basal sulcus indistinct or hardly visible, lateral sulci very short; anterior angles acutely produced; posterior angles weakly produced, blunt. Pronotal disc sometimes uneven (reflexed). Prosternal process (Fig. 312) broadly separates front coxae and extends posteriorly beyond them, rounded apically. Procoxa (Fig. 583) circular in outline, its cavity externally open, internally closed; trochantin concealed.

Meso- and metathorax. Mesonotum (Fig. 368) with scutellum moderately large, transverse, widely rounded apically. Mesosternum (Fig. 411) almost flat, with intercoxal process slightly longer than broad, hardly broader than prosternal process; widely separates mesocoxae; not extending beyond them, but reaches near their posterior margins. Mesocoxa circular in outline, its cavity outwardly open; trochantin fully exposed. Mesometasternal junction of straight-line type. Elytron (Figs 470, 471) elongate, highly convex, very densely and irregularly punctured; epipleuron moderately broad, complete. Humeral plates prominent. Metasternum (Fig. 411) transverse, flat, with long median line, without postcoxal pits. Metacoxae weakly transverse, widely separated; femoral lines absent. Metendosternite (Fig. 523) with short stalk and widely separated anterior arms and tendons. Hind wing as in *Bolbomorphus*.

Legs (Figs 583, 588). Trochanterofemoral attachment oblique. Femur of almost equal breadth throughout, less than twice of the width of tibia, hardly setose; tibia and tarsus more densely setose than femur; tibia weakly widening towards tarsus, without apical spurs. Tarsal formula 4-4-4 in both sexes; tarsomeres 1 and 2 flattened and ventrally lobed; tarsomere 3, 3 × shorter than 2 and five or more times shorter than tarsomere 4 (tarsi pseudotrimerous). Claws simple. Empodium small, bisetose.

Abdomen with six freely articulated ventrites; ventrite 1 as long as two following together; ventrites 2–5 subequal. Male abdominal segment 9 as in Figs 683, 684. In some species, ventral abdominal surface of male, longitudinally concave, with sharp carina on each side of the concavity (Fig. 638).

Aedeagus (Fig. 747) long, thin, strongly sclerotized, weakly curved, resting on its side when retracted. Tegmen reduced; tegminal plate very small, with fused parameres; tegminal strut present. Median lobe curled

along  $\frac{1}{3}$  of its basal length; with elongate, membranous gonopore at apex

Female genitalia (Fig. 795). Ovipositor sclerotized, with elongate coxities; styli small, subterminal. Spermatheca very large, oval, membranous; sperm duct moderately long, slender, attached to connection between spermatheca and accessory gland; accessory gland long-oval, sclerotized.

*Species examined.* *E. coelestinus* Gerstaecker and one unnamed species from India.

*Distribution.* Asia: Northern India, Burma, Nepal, Tibet.

### *Epipocus* Germar, 1843

(Figs 36, 37, 91, 128, 175, 224, 260, 313, 314, 369, 412, 474, 475, 524, 552, 598, 639, 685, 686, 748, 796, 824)

*Epipocus* Germar, 1843: 86. Type species, by subsequent designation of Strohecker 1953: 66: *Endomychus tibialis* Chevrolat, 1834.

*Description.* Length 8.3–9.2 mm. Body (Fig. 824) long-oval, subparallel, moderately convex; shiny, covered with comparatively dense, short pubescence; confusedly punctured. Colour brown to black; elytra often with contrasting markings.

Head (Figs 36, 37) almost as long as wide, coarsely punctured. Gular sutures indistinct. Eyes large, oval, prominent, moderately coarsely faceted. Antennal grooves absent; antennal sockets visible from above. Antenna about a half of body length, 11-segmented (Fig. 91), with 3-segmented, narrow, loose, scarcely flattened club; antennomere 3 characteristically elongate, antennomeres 9 and 10 triangularly produced internally. Fronto-clypeal ridge straight. Clypeus transverse, flat, weakly widened at its base. Labrum (Fig. 128) strongly transverse, coarsely punctured; covered with moderately dense, short setae; with apical edge densely setose, membranous, emarginate medially; tormae elongate, with mesal arms recurved posteriorly; labral rods absent. Mandible (Fig. 175) with one apical tooth, and one subapical tooth; mola large, strongly sclerotized; prosthema elongate, covered with short setae; submola small, setose, membranous. Maxilla (Fig. 224) with terminal palpomere subcylindrical, weakly rounded at apex. Galea large, sclerotized at base, membranous and obliquely enlarged apically, covered densely with short setae at apex; 2 to 3 times as wide as lacinia. Lacinia sclerotized, of equal breadth throughout, obliquely truncate apically; a half as long as galea, densely setose at apex, and on inner edge; digitus absent. Labium (Fig. 260) with palpi distinctly separated at base; terminal palpomere weakly oval. Mentum transverse, covered densely with short setae; with long setae at its sides. Prementum strongly transverse, sclerotized; ligula submembranous, finely punctured, setose, lobed at sides. Tentorium (Fig. 37) of *Endomychus*-type.

Prothorax. Pronotum (Fig. 313) strongly transverse, widest at base, finely bordered laterally, sometimes with uneven lateral areas (broadly reflexed); basal sulcus hardly visible or absent, lateral sulci short; anterior

angles produced, blunt; posterior angles acute. Pronotal disc weakly convex. Prosternal process (Fig. 314) finely bordered, narrow between front coxae, extends posteriorly beyond them with narrowly rounded apex. Procoxa circular in outline, its cavity externally open, internally closed; trochantin concealed.

Meso- and metathorax. Mesonotum (Fig. 369) with scutellum comparatively large, transverse, weakly acute at its apex, coarsely punctured. Mesosternum (Fig. 412) flat, with a pair of pits at sides, near anterior margin; intercoxal process weakly elongate; moderately broadly separates mesocoxae, not extends beyond them. Mesocoxa circular in outline, its cavity outwardly open; trochantin exposed. Meso-metasternal junction of straight-line type, without internal knobs. Elytron (Figs 474, 475) elongate, convex, truncate at apex (especially in males); finely and irregularly punctured; epipleuron narrow, incomplete apically.

Metasternum (Fig. 412) transverse, weakly narrowing towards its anterior margin; with comparatively long median line; with two pairs of postcoxal pits. Metacoxae transverse, widely separated. Metapleuron with one pit at anterior part of metepisternum. Metendosternite (Fig. 524) with moderately long stalk and widely separated anterior arms and tendons. Hind wing (Fig. 552) with anal anterior (AA) fused with cubital anterior (CuA) and extends as single vein (AA+CuA) towards the back of medial field, where it is connected with cubital anterior 2 (CuA 2); media posterior (MP 1+2) long, sclerotized, connected with partially reduced radius posterior (RP). Mp-CuA cross vein reduced; medial bridge present; medial fleck undivided; radial cell reduced.

Legs (Fig. 598). Trochanterofemoral attachment subheteromeroid. Femur widest near middle of its length, about twice as wide as tibia; tibia weakly widening towards tarsus, without apical spurs; front tibia of male widened distally (in  $\frac{1}{3}$  length from its apex). Tarsal formula 4-4-4 in both sexes; tarsomeres 1 and 2 flattened and ventrally lobed; tarsomere 3 about six times shorter than tarsomere 4 (tarsi pseudotrimerous). Claws simple. Empodium distinct, bisetose.

Abdomen (Fig. 639) with six freely articulated ventrites; ventrite 1 as long as three following together; ventrites 2-4 subequal in length; ventrite 5 as long as two proceeding together; ventrite 6 of male deeply emarginate medially, exposing sternite 9. Male abdominal segment 9 strongly sclerotized (Figs 685, 686), with asymmetrical lateral edges of sternite.

Aedeagus (Fig. 748) stout, comparatively long, strongly sclerotized, straight, ramificate apically. Tegmen very short, ring-shaped, heavily sclerotized, with parameres fused; placed at base of median lobe; tegmental strut reduced. Median lobe, with submembranous gonopore near apex.

Female genitalia (Fig. 796). Ovipositor sclerotized, with separated, elongate coxities; styli absent. Spermatheca small, oval, hardly sclerotized; sperm duct short, slender; accessory gland very small, elongate, membranous.

**Species examined.** *E. tibialis* (Chevrolat), *E. mutilatus* Gerstaecker.

**Distribution.** Known mainly from Mexico, extending southward to Colombia and northward to northern states of USA.

#### *Epopterus* Chevrolat, 1844

(Figs 38, 39, 92, 129, 176, 177, 225, 261, 315, 316, 370, 413, 476, 477, 525, 589, 590, 591, 640, 687, 688, 749, 797)

*Epopterus* Chevrolat, 1844: 380. Type species, by subsequent designation of Strohecker 1953: 63: *Erotylus ocellatus* Olivier, 1791.

**Description.** Length 6.0-6.5 mm. Body long-oval, moderately convex; shiny, covered with comparatively dense, short pubescence; densely, confusedly punctured. Colour brown to black; pronotum and elytra generally with contrasting markings.

Head (Figs 38, 39) transverse, coarsely punctured. Gular sutures very short, subparallel, moderately widely separated. Eyes large, oval, prominent, coarsely faceted. Antennal grooves absent; antennal sockets visible from above. Antenna about a half of body length, 11-segmented (Fig. 92), with 3-segmented, narrow, loose, scarcely flattened club; antennomeres 3-8 elongate, but gradually shortening; antennomeres 9 and 10 triangularly produced internally. Fronto-clypeal ridge straight. Clypeus transverse, flat. Labrum (Fig. 129) strongly transverse, finely punctured, covered with dense, moderately long setae; with brushes of long setae on sides of apex; truncate apically; tormae with mesal arms recurved posteriorly; labral rods absent. Mandible (Figs 176, 177) with two, large apical teeth, and one subapical, blunt tooth; mola large, strongly sclerotized; prostheca shortly setose; submola very small, membranous. Maxilla (Fig. 225) with terminal palpomere, subcylindrical, rounded at apex. Galea moderately sclerotized, obliquely rounded apically, covered with short, sparse setae at apex; less than twice as wide as lacinia. Lacinia as long as galea, of equal breadth throughout, obliquely rounded apically; with a few, apical spines, and with long setae on inner edge. Labium (Fig. 261) with palpi distinctly separated at base; palpomeres 2 and 3 strongly transverse; terminal palpomere truncate apically. Mentum transverse, punctured, covered with short, sparse setae. Prementum transverse, sclerotized, pubescent, with ligula short and broad, roundly produced on sides of prementum; finely punctured, and moderately densely pubescent. Tentorium (Fig. 39) of *Endomychus*-type.

Prothorax. Pronotum (Fig. 315) strongly transverse, widest at base; finely bordered laterally and anteriorly; pronotal disc weakly convex; basal sulcus hardly visible or absent, lateral sulci short; anterior angles produced, blunt; posterior angles acute. Prosternal process (Fig. 316) rather broad, finely bordered, scarcely narrowing between front coxae, extends posteriorly beyond them, with weakly rounded apex. Procoxa circular in outline, its cavity externally open, internally closed; with small, oval pit near its anterior margin; trochantin concealed.

Meso- and metathorax. Mesonotum (Fig. 370) with scutellum comparatively large, transverse, heart-shaped, coarsely punctured. Mesosternum (Fig. 413) with a pair of pits at sides, near anterior margin; intercoxal process flat, as long as wide; broadly separates mesocoxae (slightly narrower than coxal diameter), not extending beyond them. Mesocoxa circular in outline, its cavity narrowly open outwardly; trochantin partially exposed. Meso-metasternal junction of straight-line type, without internal knobs. Elytron (Figs 476, 477) elongate, convex, rounded at apex, finely, densely and irregularly punctured; epipleuron narrow, incomplete apically. Metasternum (Fig. 413) transverse, weakly narrowing towards its anterior margin; with comparatively long median line; with a pair of postcoxal pits. Metacoxae transverse, widely separated. Metapleuron with one pit, at anterior part of metepisternum. Metendosternite (Fig. 525) with rather long stalk and widely separated anterior arms and tendons. Hind wing as in *Epipocus*.

Legs (Fig. 589). Trochanterofemoral attachment oblique. Femur widest near middle of its length, about twice as wide as tibia; tibia weakly widening towards tarsus, without apical spurs; in male, tibiae with characters of sexual dimorphism, e.g., fine teeth on proximal margin (Figs 590, 591). Tarsal formula 4-4-4 in both sexes; tarsomeres 1 and 2 flattened and ventrally lobed; tarsomere 3 about five times shorter than tarsomere 4 (tarsi pseudotrimerous). Claws simple. Empodium distinct, bisetose.

Abdomen (Fig. 640) with six freely articulated ventrites; ventrite 1 almost as long as four following together; ventrites 2 and 5, and 3-4 subequal in length; ventrite 6 of male broadly, arcuately emarginate apically, exposing abdominal sternite 9. Male abdominal segment 9 strongly sclerotized (Figs 687, 688), with asymmetrical lateral edges of sternite.

Aedeagus (Fig. 749) stout, comparatively long, weakly curved; strongly sclerotized, ramificate apically. Tegmen placed at base of median lobe; with tegminal plate very short, ring-shaped; parameres fused; tegminal strut reduced. Median lobe, with submembranous gonopore near apex.

Female genitalia (Fig. 797). Ovipositor sclerotized, with separated, elongate coxities; styli absent. Spermatheca moderately large, oblong-oval, submembranous; sperm duct short, slender; accessory gland very small, circular, membranous.

**Species examined.** An unnamed species from Ecuador.

**Distribution.** Central America to Argentina.

#### *Danae* Reiche, 1847

(Figs 40, 41, 93, 130, 178, 179, 226, 262, 317, 318, 371, 414, 478, 479, 526, 592, 641, 689, 690, 750, 798, 825)

*Danae* Reiche, 1847: 408. Type species, by monotypy: *Danae rufula* Reiche, 1847.

*Oediarthrus* Gerstaecker, 1858: 344. Type species, by present designation: *Oediarthrus natalensis* Gerstaecker, 1858.

*Coniopoda* Gorham, 1873b: 205. Type species, by monotypy: *Coniopoda orientalis* Gorham, 1873.

*Rhabduchus* Gorham, 1873c: 257. Type species, by original designation: *Rhabduchus denticornis* Gorham, 1873.

**Description.** Length 5.0-5.3 mm. Body (Fig. 825) elongate-oval, moderately convex; shiny, covered with dense and rather long pubescence; densely and confusedly punctured. Colour brown.

Head (Figs 40, 41) weakly transverse; moderately densely, coarsely punctured. Gular sutures short, subparallel, widely separated. Eyes large, prominent, coarsely faceted. Antennal grooves absent; antennal sockets visible from above. Antenna longer than head and thorax together, 11-segmented (Fig. 93) with 3-segmented, loose, scarcely flattened club; in male, antennomere 9 characteristically enlarged. Fronto-clypeal ridge straight. Clypeus transverse, weakly narrowing towards its apex, flat. Labrum (Fig. 130) transverse, rounded apically, sclerotized, punctured, densely setose on sides of apex; tormae elongate, with mesal arms slightly recurved posteriorly; labral rods slender, parallel-sided. Mandible (Figs 178, 179) with two apical teeth and one, moderately large subapical tooth; mola large, strongly sclerotized; prosthema large, covered with short setae on its inner edge; submola very small. Maxilla (Fig. 226) with palpomere 1 smallest; palpomere 2 twice as long as 1 and scarcely longer than palpomere 3; terminal palpomere elongate, almost as long as remaining combined, cylindrical, rounded at apex. Galea large widened at apex, covered apically with long setae, scarcely recurved towards lacinia; more than 3 × as wide as lacinia. Lacinia almost as long as galea; with a few, long spines apically, and with dense, long setae on inner edge; digitus visible. Labium (Fig. 262) with palpi moderately widely separated at base; terminal palpomere elongate, cylindrical, rounded at apex. Mentum strongly transverse, finely punctured, covered sparsely with short setae. Prementum transverse, sclerotized with ligula submembranous, expanded apically. Tentorium (Fig. 41) with anterior arms broadly fused medially, and widely divergent anteriorly; corpotentorium slender, straight, without median process.

Prothorax. Pronotum (Fig. 317) transverse, widest near middle of its length; with broad, lateral, raised margins; lateral edges densely and finely crenulate; basal sulcus distinct, with oval, deep cavity on each side; anterior angles moderately produced, blunt; posterior angles almost right-angled. Pronotal disc weakly convex. Prosternal process (Fig. 318) narrow, flat, with rounded apex; extends posteriorly beyond front coxae. Procoxa circular in outline, its cavity externally open, internally closed; trochantin concealed.

Meso- and metathorax. Mesonotum (Fig. 371) with scutellum small, transverse, rounded apically. Mesosternum (Fig. 414) almost flat, with intercoxal process elongate, moderately broadly separated mesocoxae (distinctly narrower than coxal diameter), not

extending beyond them. Mesocoxa circular in outline, its cavity outwardly open; trochantin partially exposed. Meso-metasternal junction with internal knobs. Elytron (Figs 478, 479) elongate-oval, convex; finely, densely and irregularly punctured; epipleuron narrow, incomplete apically. Metasternum (Fig. 414) transverse, weakly narrowing towards its anterior margin, weakly convex; median line a half as long as metasternum. Metacoxae transverse, widely separated. Metendosternite (Fig. 526) with moderately long stalk and widely separated anterior arms; anterior tendons long, narrowly separated.

Hind wing (Fig. 553). Anal anterior (AA) fused with cubital anterior (CuA) extends as single vein (AA+CuA) towards the back of medial field, where it is connected with reduced cubital anterior 2 (CuA 2); media posterior (MP 1+2) long, sclerotized, connected with partially reduced radius posterior (RP). Mp-CuA cross vein absent; medial bridge present; medial fleck undivided; radial cell reduced.

Legs (Fig. 592). Trochanterofemoral attachment oblique. Femur widest near middle of its length, about twice as wide as tibia, densely setose; tibia scarcely widening towards tarsus, without apical spurs. Tarsal formula 4-4-4 in both sexes; tarsomeres 1 and 2 flattened and ventrally lobed; tarsomere 3 about four times shorter than tarsomere 4 (tarsi pseudotrimerous). Claws simple. Empodium small, bisetose.

Abdomen (Fig. 641) with six freely articulated ventrites; ventrite 1 longer than three following together; ventrites 2 and 3 subequal in length. In male (Fig. 641), abdominal intercoxal process with triangular, shallow depression. Segment 9 of male as in Figs 689, 690.

Aedeagus (Fig. 750) rather stout, comparatively long, sclerotized, curved, resting on its side when retracted. Tegmen reduced; tegminal plate very short, submembranous, parameres fused; tegminal strut long, more sclerotized than tegminal plate. Median lobe with weakly sclerotized gonopore at apex. Ejaculatory duct with moderately large, bobbin-shaped gland.

Female genitalia (Fig. 798). Ovipositor weakly sclerotized, coxities elongate, with deeply divided basal parts; styli small, terminal. Spermatheca small, round, membranous; sperm duct short, slender; accessory gland very small, oval, membranous.

**Species examined.** An unnamed species from Namibia.

**Distribution.** Distributed widely in Africa, eastern Asia (incl. Japan), and eastern North America.

#### *Saula* Gerstaecker, 1858

(Figs 42, 43, 94, 131, 180, 181, 227, 263, 319, 320, 372, 415, 480, 481, 527, 554, 593, 642, 691, 692, 751, 799, 826)

*Saula* Gerstaecker, 1858: 223. Type species, by subsequent designation of Arrow 1925: 393: *Saula nigripes* Gerstaecker, 1858.

**Description.** Length 6.8–8.5 mm. Body (Fig. 826) elongate, moderately convex; shiny, covered with dense

and short pubescence; densely and confusedly punctured. Colour light to dark brown.

Head (Figs 42, 43) almost as long as wide; coarsely punctured. Gular sutures short, weakly convergent anteriorly, widely separated. Eyes large, oval, prominent, coarsely faceted. Antennal grooves absent; antennal sockets visible from above. Antenna longer than head and thorax together, 11-segmented (Fig. 94) with 3-segmented, loose, scarcely flattened club. Fronto-clypeal ridge straight. Clypeus transverse, weakly narrowing towards its apex, flat. Labrum (Fig. 131) strongly transverse, punctured, densely setose at sides of apex, emarginate apically; tormae with mesal arms recurved posteriorly; labral rods slender, weakly convergent anteriorly. Mandible (Figs 180, 181) with two apical teeth and one, moderately large, subapical tooth; mola large, strongly sclerotized; prostheca large, shortly setose; submola indistinct. Maxilla (Fig. 227) with palpomere 1 smallest; palpomere 2 twice as long as 1, and scarcely longer than palpomere 3; terminal palpomere elongate, almost as long as remaining combined, cylindrical, rounded at apex. Galea large widening towards its apex, covered apically with dense and long setae; scarcely recurved towards lacinia; more than 3 × as wide as lacinia. Lacinia weakly narrowing towards its apex, with digitus, a few apical spines, and dense setae on inner edge. Labium (Fig. 263) with palpi widely separated at base; palpomere 1 smallest; palpomeres 2 and 3 subequal; terminal palpomere elongate, cylindrical, weakly rounded apically. Mentum strongly transverse, densely punctured, covered with sparse, short setae. Prementum transverse, widest at apex, sclerotized, densely punctured; ligula short, expanded laterally, submembranous, setose. Tentorium (Fig. 43) with anterior arms broadly fused medially, and widely divergent anteriorly; corpotentorium absent.

Prothorax. Pronotum (Fig. 319) transverse, widest in apical third; lateral edges finely crenulate; basal sulcus rather distinct, lateral sulci in form of very small, oval cavities; anterior angles weakly produced, blunt; posterior angles almost right-angled. Pronotal disc weakly convex. Prosternal process (Fig. 320) rather broadly separates front coxae, extends posteriorly beyond them; flat, rounded apically. Procoxa circular in outline, its cavity externally open, internally closed; trochantin concealed.

Meso- and metathorax. Mesonotum (Fig. 372) with scutellum small, transverse, acute apically. Mesosternum (Fig. 415) with intercoxal process elongate, flat, moderately broadly separates mesocoxae (slightly narrower than coxal diameter); not extends beyond them. Mesocoxa circular in outline, its cavity outwardly open; trochantin exposed. Meso-metasternal junction with internal knobs. Elytron (Figs 480, 481) elongate-oval, convex; finely, densely and irregularly punctured; epipleuron narrow, incomplete apically. Metasternum (Fig. 415) transverse, distinctly narrowing towards its anterior margin, weakly convex; median line long. Metacoxae transverse, widely separated. Metendosternite (Fig. 527) with long stalk and widely separated anterior arms; ante-

rior tendons long, narrowly separated. Wing (Fig. 554) as in *Danae*, devoid of Mp-CuA cross vein.

Legs (Fig. 593). Trochanterofemoral attachment oblique. Femur less than twice as wide as tibia, densely setose; tibia gradually widening towards tarsus, without apical spurs. Tarsal formula 4-4-4 in both sexes; tarsomeres 1 and 2 flattened and ventrally lobed; tarsomere 3 about four times shorter than tarsomere 4 (tarsi pseudotrimerous). Claws simple. Empodium small, bisetose.

Abdomen (Fig. 642) with six freely articulated ventrites; ventrite 1 as long as two following combined; ventrites 2-3 and 4-5 subequal in length. Male abdominal segment 9 as in Figs 691, 692.

Aedeagus (Fig. 751). Median lobe short, stout, lightly sclerotized and scarcely curved, resting on its side when retracted; with internal sclerites. Ejaculatory duct with large, bobbin-shaped, accessory gland. Tegmen absent.

Female genitalia (Fig. 799). Ovipositor lightly sclerotized, with coxities reduced, divided at base; styli absent. Spermatheca large, elongate-oval, membranous, covered with very sparse, long spines; sperm duct long; accessory gland very small, elongate, membranous. Bursa copulatrix with membranous gonopores on its sides.

**Species examined.** *S. ferruginea* Gerstaecker and one unnamed species from China.

**Distribution.** Africa, Asia (incl. Japan).

#### *Stenotarsus* Perty, 1832

(Figs 44, 45, 95, 132, 182, 183, 228, 264, 321, 322, 374, 416, 472, 473, 528, 555, 594, 643, 693, 694, 752, 800)

*Stenotarsus* Perty, 1832: 112, fig. 12, pl. 22. Type species, by monotypy: *Stenotarsus brevicollis* Perty, 1832.

*Quirinus* Thomson, 1857: 157. Type species, by monotypy: *Quirinus sulcithorax* Thomson, 1857.

*Systaecha* Gorham, 1890: 132. Type species, by subsequent designation of Arrow 1920: 53: *Systaecha cyanoptera* Gorham, 1890.

*Stenotarsoides* Csiki, 1900b: 401. Type species, by present designation: *Stenotarsoides quadrimaculatus* Csiki, 1900.

**Description.** Length 5.5–6.2 mm. Body short-oval to globose, strongly but evenly convex, subhemispherical; shiny and pilose; finely, densely and confusedly punctured; often with rows of micropunctures on the elytra. Colour in most cases brown; elytra often with contrasting markings.

Head (Figs 44, 45) rather deeply retracted in prothorax, almost as long as wide. Gular sutures moderately long, subparallel, widely separated. Eyes large, oval, prominent, moderately coarsely faceted. Antennal grooves absent; antennal sockets visible from above. Antenna variable in length (generally slightly longer than head and thorax together), 11-segmented (Fig. 95) with, 3-segmented, comparatively narrow, loose, scarcely flattened club. Fronto-clypeal ridge straight. Clypeus transverse, rectangular, flat. Labrum (Fig. 132) shortly setose, with narrow submembranous, emarginate apex;

tormae elongate, with mesal arms recurved posteriorly; labral rods sclerotized, weakly divergent apically. Mandible (Figs 182, 183) with two apical teeth and one, small subapical tooth; mola transversely ridged; prostheca covered with short setae; submola small, setose, membranous. Maxilla (Fig. 228) with palpomeres 1, 2 and 3 subequal in length; terminal palpomere almost as long as 2 and 3 combined, cylindrical, narrowly rounded at apex. Galea large, weakly expanded toward its apex, densely but shortly setose apically; about twice as wide as lacinia. Lacinia almost as long as galea, of equal breadth throughout with obliquely truncate apex, covered with a few, long spines apically, and with dense setae on inner edge; digitus absent. Labium (Fig. 264) with palpi comparatively slender, distinctly separated at base; terminal palpomere elongate, cylindrical, rounded apically. Mentum transverse, punctured, covered densely with short setae. Prementum transverse, sclerotized; densely and coarsely punctured, setose; ligula distinctly lobed at sides and at the front. Tentorium (Fig. 45) of *Endomychus*-type.

Prothorax. Pronotum (Fig. 321) strongly transverse, widest at base, with broad, raised margins; basal sulcus distinct to hardly visible or absent, lateral sulci short; anterior angles produced, narrowly rounded; posterior angles right-angled or weakly acute. Pronotal disc weakly convex. Prosternal process (Fig. 322) comparatively broad, flat, with rounded or subtruncate apex; extends posteriorly beyond front coxae. Procoxa circular in outline, its cavity externally open, internally closed; trochantin concealed.

Meso- and metathorax. Mesonotum (Fig. 374) with scutellum small, transverse, rounded apically. Mesosternum (Fig. 416) with a pair of pits at sides, near anterior margin; intercoxal process transverse, with deep excavation on its front margin; moderately broadly separates mesocoxae, not extends beyond them. Mesocoxa circular in outline, its cavity outwardly open; trochantin exposed. Meso-metasternal junction of straight-line type, without internal knobs. Elytron (Figs 472, 473) oval, strongly convex; finely and irregularly punctured (in some species, with rows of micropunctures); epipleuron moderately broad, incomplete apically. Metasternum (Fig. 416) transverse, weakly narrowing towards its anterior margin, with a pair of short median lines, and two pairs of postcoxal pits. Metacoxae transverse, widely separated. Metapleuron with one pit at anterior part of metepisternum. Metendosternite (Fig. 528) with rather short stalk and widely separated anterior arms and tendons.

Hind wing (Fig. 555). Anal anterior (AA) fused with cubital anterior (CuA) extends as single vein (AA+CuA) towards the back of medial field, where it is connected with cubital anterior 2 (CuA 2); media posterior (MP 1+2) long, sclerotized, connected with partially reduced radius posterior (RP). Mp-CuA cross vein incomplete near MP; medial bridge present; medial fleck indistinctly divided; radial cell reduced.

Legs (Fig. 594). Trochanterofemoral attachment oblique. Femur widest near middle of its length, or at apex, less than twice as wide as tibia; tibia gradually widening towards tarsus, without apical spurs. Tarsal formula 4-4-4 in both sexes; tarsomeres 1 and 2 flattened and ventrally lobed; tarsomere 3 about six times shorter than tarsomere 4 (tarsi pseudotrimerous). Claws simple. Empodium distinct, bisetose.

Abdomen (Fig. 643) with six freely articulated ventrites; ventrite 1 longer than three following together; ventrites 3-5 subequal in length. Male abdominal segment 9 as in Figs 693, 694.

Aedeagus (Fig. 752) stout, comparatively long, sclerotized, curved, resting on its side when retracted. Tegmen reduced; tegminal plate very short, submembranous; parameres fused; tegminal strut long, membranous. Median lobe with weakly sclerotized gonopore at apex.

Female genitalia (Fig. 800). Ovipositor weakly sclerotized, with separated, elongate coxities (deeply divided basally); styli terminal. Spermatheca moderately large, oval, membranous; sperm duct rather short, slender, attached to connection between spermatheca and accessory gland; accessory gland about as large as spermatheca, submembranous.

**Species examined.** *S. nobilis* Gerstaecker and two unnamed species from Ecuador and Cameroon.

**Distribution.** Widely distributed in warmer regions of entire world.

#### *Perrisia* Strand, 1921

(Figs 46, 47, 96, 133, 184, 185, 229, 265, 323, 324, 375, 417, 482, 483, 529, 595, 644, 695, 696, 753)

*Perrisia* Marseul, 1868: 113 (nec *Perrisia* Rondani, 1846). Type species, by monotypy: *Lycoperdina brevis* Perris, 1864.

*Perrisia* Strand, 1921: 106. Replacement name for *Perrisia* Marseul, 1868.

**Description.** Length 3.00-3.80 mm. Body oval, moderately convex; shiny, covered with short, dense, pale pubescence; moderately coarsely, densely and confusedly punctured. Colour brown-ferruginous with antennae and legs brown.

Head (Figs 46, 47) deeply retracted in prothorax, weakly transverse. Gular sutures short, convergent anteriorly, widely separated. Middle part of ventral surface of head with fine, transverse lines - interspaces are weakly convex. Eyes moderately large, oval, prominent, coarsely faceted. Antennal grooves absent; antennal sockets visible from above. Antenna almost as long as head and thorax together, 11-segmented (Fig. 96) with, 3-segmented, narrow, loose, scarcely flattened club. Fronto-clypeal ridge straight. Clypeus transverse, convergent anteriorly, flat. Labrum (Fig. 133) covered with short setae; with submembranous truncate apex; tormae with mesal arms recurved anteriorly; labral rods slender, parallel. Mandible (Figs 184, 185) with outer edge densely setose; right mandible with two apical teeth and one, small sub-

apical tooth; left mandible weakly cleft at apex with incisor edge smooth; mola strongly sclerotized; prostheca covered with short setae; submola very small, setose, membranous. Maxilla (Fig. 229) with palpomere 2 twice as long as 1, and weakly longer than 3; terminal palpomere almost as long as 2 and 3 combined, cylindrical, rounded at apex. Galea large, expanded apically, covered with dense, short setae at apex, scarcely recurved towards lacinia; about three times as wide as lacinia. Lacinia weakly narrowing towards its apex; with a few, long, apical spines and dense setae on inner edge; digitus short, blunt. Labium (Fig. 265) with palpi rather slender, widely separated at base; palpomere 1 smallest; palpomeres 2 and 3 elongate, subequal in length; terminal palpomere, rounded apically. Mentum transverse, punctured, covered with short setae. Prementum transverse, sclerotized with ligula short, expanded laterally, weakly sclerotized, setose. Tentorium (Fig. 47) of *Endomychus*-type.

Prothorax. Pronotum (Fig. 323) strongly transverse, widest near middle of its length, with lateral raised margins; basal sulcus distinct, with oval pit on each side; lateral sulci very short; anterior angles produced, blunt; posterior angles acutely produced. Pronotal disc convex. Prosternal process (Fig. 324) comparatively broad, finely bordered, weakly rounded apically; extends posteriorly beyond front coxae. Procoxa circular in outline, its cavity externally open, internally closed; trochantin concealed.

Meso- and metathorax. Mesonotum (Fig. 375) with scutellum small, cordiform. Mesosternum (Fig. 417) with a pair of pits at sides, near anterior margin; intercoxal process elongate; widely separates mesocoxae, not extends beyond them. Mesocoxa circular in outline, its cavity outwardly open; trochantin exposed. Mesometasternal junction of straight-line type, without internal knobs. Elytron (Figs 482, 483) elongate-oval, convex; rather finely and irregularly punctured; epipleuron broad basally, incomplete at apex. Metasternum (Fig. 417) strongly transverse, slightly longer than mesosternum; weakly narrowing towards its anterior margin, with two pairs of postcoxal pits; median line absent. Metacoxae transverse, very widely separated. Metendosternite (Fig. 529) with very short stalk and widely separated anterior arms and tendons.

Hind wing vestigial - shorter and narrower than elytron.

Legs (Fig. 595). Trochanterofemoral attachment oblique. Femur subclavate, less than twice as wide as tibia; tibia weakly widening towards tarsus; tibial apex (except of outer edge) surrounded by short spines; apical spurs absent. Tarsal formula 4-4-4 in both sexes; tarsomeres 1 and 2 flattened and ventrally lobed; tarsomere 3 about five times shorter than tarsomere 4 (tarsi pseudotrimerous). Claws simple. Empodium small, bisetose.

Abdomen (Fig. 644) with six freely articulated ventrites; ventrite 1 longer than three following together; ventrites 3-5 subequal in length. Male abdominal segment 9 as in Figs 695, 696.

Aedeagus (Fig. 753) comparatively long, sclerotized, curved, resting on its side when retracted. Tegmen

reduced, with tegminal plate short, sclerotized; parameres fused; tegminal strut long, submembranous. Median lobe with large, membranous gonopore at apex.

Female genitalia – not studied.

**Species examined.** *P. brevis* (Perris), monotypic genus.

**Distribution.** Known only from Algeria.

***Danascelis*** Tomaszewska, 1999

(Figs 48, 49, 97, 134, 186, 187, 230, 266, 325, 326, 373, 418, 484, 530, 596, 597, 645, 697, 698, 754, 801)

*Danascelis* Tomaszewska, 1999: 279. Type species, by original designation: *Danascelis elongata* Tomaszewska, 1999.

**Description.** Length 2.55–2.80 mm. Body elongate, moderately convex; shiny, covered with fine, short pubescence; distinctly and densely punctured.

Head (Figs 48, 49) partially retracted in prothorax, as long as wide; moderately densely and coarsely punctured; gula, genal area and occiput with fine microsculpture. Gular sutures moderately long, weakly convergent anteriorly, widely separated. Eyes small, oval, weakly prominent, coarsely faceted. Antennal grooves absent; antennal sockets partially concealed by frons. Antenna reaches posterior pronotal margin, 11-segmented (Fig. 97), scape stout, longer than 3 following antennomeres together, pedicel elongate, antennomeres 3–8 short, transverse; last three form distinct, densely setose club. In male (Fig. 97), antennomere 9 greatly enlarged, weakly concave on its inner edge, bearing brush of long setae. Fronto-clypeal ridge straight. Clypeus weakly transverse, flat. Labrum (Fig. 134) with tormae elongate and mesal arms recurved posteriorly; labral rods slender, short, parallel. Mandible (Figs 186, 187) with single apical tooth; mola moderately large with fine, transverse ridges; prostheca covered with short setae on inner edge; submola very small. Maxilla (Fig. 230) with apical palpomere elongate, tapering, rounded apically. Galea elongate, blunt and covered densely with long setae at apex; about twice as broad as lacinia. Lacinia as long as galea, weakly narrowing towards its apex; with digitus, several subapical spines and short setae on its inner edge. Labium (Fig. 266) with terminal palpomere elongate, cylindrical, rounded apically. Mentum trapezoidal, densely punctured. Prementum weakly transverse, sclerotized; ligula submembranous, expanded apically. Tentorium (Fig. 49) with anterior arms broadly fused medially, and widely divergent anteriorly; corpotentorium weakly curved anteriorly, without median process.

Prothorax. Pronotum (Fig. 325) transverse, very narrowly bordered laterally; basal sulcus rather distinct, with double, oval, deep cavities on its sides; each cavity provided with small, oval pit. Anterior angles weakly produced, rounded; posterior angles right-angled. Pronotal disc weakly convex. Prosternum with two round, precoxal pits; intercoxal process (Fig. 326) narrow, flat, rounded apically; distinctly separates procoxae, extends posteri-

orly beyond them. Procoxa circular in outline, its cavity externally open, internally closed; trochantin concealed.

Meso- and metathorax. Mesosternum (Fig. 418) with two, oval pits on sides, near anterior margin; with longitudinal ridge and concavities on its sides; intercoxal process narrow, less than half as broad as coxal diameter. Mesocoxa circular in outline, its cavity outwardly open; trochantin exposed. Meso-metasternal junction with internal knobs. Elytron (Fig. 484) elongate, convex, with rows of dark, coarse punctures; interspaces irregularly, finely punctured; epipleuron very narrow, incomplete apically. Scutellum (Fig. 373) small, transverse, weakly acute at apex. Metasternum (Fig. 418) transverse, about 2 × as wide as long, weakly convex; with two pairs of postcoxal pits; median line absent. Metacoxae transverse, broadly separated. Metapleuron with one, oval pit in its apical part. Metendosternite (Fig. 530) with short stalk and widely separated anterior arms and tendons. Hind wing vestigial.

Leg (Fig. 597) with trochanterofemoral attachment oblique; femur swollen, excavate mesally to receive tibia; tibia subcylindrical, about half as broad as femur; without apical spurs. Tarsal formula 4-4-4 in both sexes; tarsomeres 1 and 2 weakly flattened (Fig. 596), subequal in size; tarsomere 3 slightly shorter than 1 or 2, apical tarsomere longer than remaining combined. Claws simple. Empodium small, bisetose.

Abdomen (Fig. 645) with five freely articulated ventrites; ventrite 1 longer than three following together; with two, oval, postcoxal pits and a few tear-shaped, medial punctures; ventrites 2–4 subequal in length. Male abdominal segment 9 as in Figs 697, 698.

Aedeagus (Fig. 754) with median lobe comparatively short, sclerotized, curved, resting on its side when retracted, with membranous gonopore at apex; tegmen very small, strongly reduced, ring-shaped; tegminal plate submembranous; tegminal strut short, membranous.

Female genitalia (Fig. 801) with ovipositor short, weakly sclerotized; coxities moderately large, separate, elongate, densely setose at apex; styli reduced, hardly visible, terminal. Spermatheca small, oval, membranous; sperm duct short, slender; accessory gland very small, oval, membranous.

**Species examined.** *D. elongata* Tomaszewska, monotypic genus.

**Distribution.** Known only from Pakistan.

***Lycoperdina*** Latreille, 1807

(Figs 50, 51, 98, 135, 188, 189, 231, 267, 327, 328, 376, 419, 420, 485, 486, 531, 556, 599, 600, 646, 699, 700, 755, 756, 757, 802, 827)

*Lycoperdina* Latreille, 1807: 73. Type species, by monotypy: *Galleruca bovistae* Fabricius, 1792.

*Gorgia* Mulsant, 1846: 17. Type species, by monotypy: *Silpha succincta* Linnaeus, 1767.

*Lycoperdinella* Arrow, 1920: 23 (nec *Lycoperdinella* Champion, 1913). Type species, by monotypy: *Lycoperdinella morosa* Arrow, 1920.

*Lycoperdinodes* Arrow, 1923: 485. Replacement name for *Lycoperdinella* Arrow, 1920.  
*Falsoylaia* Pic, 1945: 11. Type species, by monotypy: *Falsoylaia obscuresuturalis* Pic, 1945.

**Description.** Length 3.0–6.0 mm. Body (Fig. 827) elongate to ovate, weakly to distinctly convex; shiny, covered with fine and very short pubescence; densely but rather finely, confusedly punctured. Colour black, reddish-black, reddish-brown to light brown, sometimes with black markings on the elytra.

Head (Figs 50, 51) partially retracted in prothorax, almost circular in outline. Gular sutures short, widely separated, convergent anteriorly. Eyes large, weakly oval in outline, prominent, very coarsely faceted. Antennal grooves absent; antennal sockets visible from above. Occiput with cephalic stridulatory area (occipital file). Antenna slightly shorter than a half of body length, 11-segmented (Fig. 98) with, 2-segmented narrow, loose club; scape slightly longer than pedicel; antennomere 3 slightly shorter than pedicel; antennomeres 4–8 subequal or gradually shorter; antennomere 9 slightly longer and broader than 8, but narrower and slightly shorter than 10. Fronto-clypeal ridge weakly arcuate. Clypeus transverse, flat, narrower at apex than at base. Labrum (Fig. 135) strongly transverse, shortly setose with submembranous, emarginate apex; tormae elongate, with mesal arms recurved posteriorly; labral rods absent. Mandible (Figs 188, 189) broad, strongly concave ventrally, convex dorsally; with small apical tooth and very small, blunt subapical tooth; mola transversely ridged; prostheca covered with sparse, short setae; submola small, setose, membranous. Maxilla (Fig. 231) with terminal palpomere elongate, cylindrical, rounded at apex. Galea elongate, narrowing towards its apex, densely setose. Lacinia short and narrow, densely setose on its inner edge; digitus absent. Labium (Fig. 267) with palpomere 1 almost quadrate; palpomere 2 transverse; terminal palpomere ovate. Mentum transverse, widest in middle of its length, punctured, covered with several short setae. Prementum transverse, sclerotized, punctured, with short pubescent; ligula densely setose, expanded laterally, emarginate at apex. Tentorium (Fig. 51) of *Endomychus*-type.

Prothorax. Pronotum (Fig. 327) transverse, widest near the middle of its length, narrowly bordered laterally; anterior margin with stridulatory membrane; basal sulcus distinct, lateral sulci deep and long; anterior angles weakly to distinctly produced, acute or narrowly rounded; posterior angles right or acute; pronotal disc convex. Prosternum with a pair of pits at the front of procoxal cavities; prosternal process (Fig. 328) very narrow and short; front coxae prominent and contiguous. Procoxa circular in outline; its cavity externally open, internally closed; trochantin concealed.

Meso- and metathorax. Mesonotum (Fig. 376) sclerotized; scutellum transverse, rounded apically. Mesosternum (Fig. 419) with a pair of pits near anterior margin; intercoxal process short, narrow, carinate; narrowly separates mesocoxae, not extends beyond them, reaches

to about half of their length. Mesocoxa circular in outline, its cavity outwardly open; trochantin exposed. Mesometasternal junction with internal knob. Elytron (Figs 485, 486) elongate, convex; very densely, finely and irregularly punctured; epipleuron narrow, incomplete at apex. Metasternum (Fig. 419) transverse, weakly narrowing towards its anterior margin, with moderately long median line, with three pairs of postcoxal pits. Metacoxae weakly transverse, widely separated; femoral lines absent. Metapleuron as in Fig. 420. Metendosternite (Fig. 531) with short stalk and widely separated anterior arms and tendons. Hind wing (Fig. 556) short, with apical field reduced. Anal anterior (AA) and cubital anterior (CuA) very slender and hardly visible; media posterior (MP 1+2) long, sclerotized, connected with reduced radius posterior (RP). Mp-CuA cross vein very slender; medial bridge present; medial fleck undivided; radial cell absent.

Legs (Figs 599, 600). Trochanterofemoral attachment subheteromeroid. Femur widest at  $\frac{1}{3}$  of its apical length, about twice of the width of tibia, hardly setose; tibia and tarsus more densely setose than femur; tibia widening towards tarsus, without apical spurs. Tarsal formula 4-4-4 in both sexes; tarsomeres 1 (less) and 2 (more) flattened and ventrally lobed; tarsomere 3 about 2 times shorter than 2 and four times shorter than tarsomere 4 (tarsi pseudotrimerous). Claws simple. Empodium distinct, bisetose. In males of some species (Figs 599, 600), front and middle tibiae with characters of sexual dimorphism.

Abdomen (Fig. 646) with five freely articulated ventrites; ventrite 1 as long as three following together; ventrites 2–4 subequal in length. Male abdominal segment 9 with asymmetrical apex of sternite (Figs 699, 700).

Aedeagus (Fig. 755) stout, moderately long, heavily sclerotized, weakly curved, resting on its side when retracted. Tegmen (Figs 756, 757) placed at base of median lobe, reduced, ring-shaped with parameres fused; tegminal strut vestigial.

Female genitalia (Fig. 802). Ovipositor sclerotized, with elongate coxities, fused apically; styli absent. Spermatheca small, oval, membranous; sperm duct very short, slender, connected directly with spermatheca; accessory gland very small, circular, membranous.

**Species examined.** *L. succincta* (Linnaeus), and a few undetermined species.

**Distribution.** Widely distributed in Palaearctic, Nearctic, South Africa and Madagascar.

### *Beccariola* Arrow, 1943

(Figs 52, 53, 99, 136, 190, 191, 232, 268, 329, 330, 377, 421, 487, 488, 557, 601, 647, 701, 702, 758, 803, 828)

*Beccaria* Gorham, 1885: 521 (nec *Beccaria* Trinchese, 1870). Type species, by monotypy: *Beccaria papuensis* Gorham, 1885.

*Beccariola* Arrow, 1943: 129. Replacement name for *Beccaria* Gorham, 1885.

**Description.** Length 4.5–5.0 mm. Body (Fig. 828) short-oval, or circular in outline, strongly convex, sub-

hemispherical; surface smooth and shiny; finely and confusedly punctured. Colour from yellow to black, with contrasting markings on the elytra.

Head (Figs 52, 53) deeply retracted in prothorax, almost circular in outline. Gular sutures very short, subparallel, widely separated. Eyes large, narrowly transverse, prominent, very coarsely faceted. Antennal grooves absent; antennal sockets visible from above. Occiput with cephalic stridulatory area (occipital file). Antenna slightly shorter than a half of body length, 11-segmented (Fig. 99) with, 3-segmented, narrow, loose, flattened club; scape slightly longer than pedicel; antennomere 3 shorter or sometimes distinctly longer than pedicel; antennomeres 4–8 subequal in length. Fronto-clypeal ridge almost straight. Clypeus transverse, flat, weakly narrower at apex than at base. Labrum (Fig. 136) strongly transverse, covered with short setae; anterior edge truncate medially; tormae elongate, with mesal arms straight or recurved posteriorly; labral rods absent. Mandible (Figs 190, 191) strongly concave ventrally, convex dorsally; with one apical tooth and small subapical tooth; mola transversely ridged; prostheca covered with short setae; submola small, setose, membranous. Maxilla (Fig. 232) with terminal palpomere elongate, cylindrical, tapering, truncate at apex. Galea strongly enlarged toward its apex, densely setose apically, weakly recurved towards lacinia. Lacinia short and narrow, with long, apical and subapical spines and setae on inner edge. Labium (Fig. 268) with palpi placed close together at base; palpomere 1 very small; palpomere 2 large, strongly transverse; terminal palpomere smaller, ovate. Mentum transverse, punctured, covered with long setae. Prementum transverse, sclerotized, punctured; ligula densely setose apically, strongly lobed at sides. Tentorium (Fig. 53) of *Endomychus*-type.

Prothorax. Pronotum (Fig. 329) strongly transverse, widest at base; narrowly bordered laterally and anteriorly; anterior margin without stridulatory membrane; basal sulcus absent, lateral sulci shallow and short. Anterior angles weakly produced, blunt; posterior angles acute. Pronotal disc weakly convex. Prosternal process (Fig. 330) comparatively broad and short, excised apically (to receive anterior part of pentagonal mesosternum), not produced beyond coxae. Procoxa circular in outline; its cavity externally open, internally closed; trochantin concealed.

Meso- and metathorax. Mesonotum (Fig. 377) sclerotized; scutellum rather small, transverse, rounded apically. Mesosternum (Fig. 421) with intercoxal process transverse; broadly separates mesocoxae, not extends beyond them. Mesocoxa circular in outline, its cavity outwardly open; trochantin exposed. Meso-metasternal junction with two small internal knobs. Elytron (Figs 487, 488) oval, strongly convex, with punctures fine and irregular; (sometimes with rows of micropunctures); epipleuron broad apically, gradually narrowing towards elytral apex, complete. Metasternum (Fig. 421) transverse, weakly narrowing towards its anterior margin, with long median line, with two pairs of postcoxal pits. Metacoxae

transverse, widely separated. Metendosternite with long stalk and widely separated anterior arms. Hind wing (Fig. 557) with venation nearly complete. Anal anterior (AA) fused with cubital anterior (CuA) extends as single vein (AA+CuA) towards the back of medial field, where it is connected with cubital anterior 2 (CuA 2); media posterior (MP 1+2) long, sclerotized, connected with partially reduced radius posterior (RP). Mp-CuA cross vein incomplete near MP; medial bridge present; medial fleck divided; radial cell reduced.

Legs (Fig. 601). Trochanterofemoral attachment subheteromeroid. Femur widest near middle of its length, more than twice as wide as tibia, hardly setose; tibia and tarsus more densely setose than femur; tibia weakly widening towards tarsus, without apical spurs. Tarsal formula 4-4-4 in both sexes; tarsomeres 1 and 2 flattened and ventrally lobed; tarsomere 3 about 3 times shorter than 2, and about four times shorter than tarsomere 4 (tarsi pseudotrimerous). Claws simple. Empodium distinct, bisetose.

Abdomen (Fig. 647) with five freely articulated ventrites; ventrite 1 as long as three following together; often with femoral lines, and sometimes with small postcoxal pits; ventrites 3–5 subequal in length. Male abdominal segment 9 as in Figs 701, 702.

Aedeagus (Fig. 758) stout, moderately long, strongly sclerotized, curved, resting on its side when retracted. Tegmen reduced, placed at base of median lobe, small, ring-shaped; parameres fused; tegminal strut absent.

Female genitalia (Fig. 803). Ovipositor sclerotized, with fused coxities; styli absent. Spermatheca large, long-oval, membranous; sperm duct comparatively long, slender, connected directly with spermatheca; accessory gland small, oval, membranous.

*Species examined.* *B. orca* Heller, *B. papuensis* (Gorham) and a few undetermined species – externally.

*Distribution.* Widely distributed in Orient.

#### *Mycetaea* Stephens, 1829

(Figs 54, 55, 100, 137, 192, 193, 233, 269, 331, 332, 378, 422, 423, 489, 490, 532, 602, 648, 703, 704, 762, 763, 804, 829)

*Mycetaea* Stephens, 1829: 87. Type species, by monotypy: *Mycetaea fumata* Stephens, 1829 = *subterranea* (Fabricius), 1801. Synonymy by Strohecker, 1986: 4.

*Description.* Length 1.5–2.0 mm. Body (Fig. 829) elongate-oval, gradually narrowing from about half of the body length towards elytral apex; strongly convex; shiny, smooth, covered with rather sparse but long, suberect, pale setae. Colour light to dark brown, with antennae and legs lighter.

Head (Figs 54, 55) comparatively deeply retracted in prothorax, weakly transverse; finely and densely punctured. Gular sutures very short, weakly convergent anteriorly, widely separated. Eyes moderately large, weakly oval, prominent, coarsely faceted. Antennal grooves absent; antennal sockets visible from above. Antenna as

long as head and thorax together, 11-segmented (Fig. 100) with 3-segmented, loose, scarcely flattened club. Fronto-clypeal ridge straight. Clypeus transverse, flat, scarcely convergent anteriorly, truncate at apex. Labrum (Fig. 137) densely setose at sides of apex; rounded apically; tormae with mesal arms recurved anteriorly; labral rods slender, weakly divergent towards labral apex. Mandible (Figs 192, 193) short and moderately broad, weakly concave ventrally, convex dorsally; bifid at apex, with a few very small teeth on incisor edge; mola transversely ridged; prostheca densely setose on its inner edge; submola hardly visible. Maxilla (Fig. 233) with palpomeres 1 and 3 very short; palpomere 2 about twice as long as 1 or 3; terminal palpomere as long as remaining combined, tapering, rounded at apex. Galea moderately broad with apical setae, scarcely recurved apically toward lacinia; twice as wide as lacinia. Lacinia long, narrow, with dense, long setae on inner edge. Labium (Fig. 269) with palpomere 1 smallest; palpomeres 2 and 3 subequal in size; terminal palpomere slightly longer than wide, truncate at apex. Mentum transverse, with small, triangular, setose convexity in the middle; finely punctured, covered sparsely with short setae. Prementum as long as wide, sclerotized with ligula membranous, short and wide. Tentorium (Fig. 55) of *Endomychus*-type.

Prothorax. Pronotum (Fig. 331) strongly transverse, widest near middle of its length; with broad, raised margins; pronotal surface coarsely and sparsely punctured; lateral edges denticulate and setose; basal sulcus absent, lateral sulci in form of very short, triangular, shallow, concavities – hardly visible; anterior angles weakly produced, blunt; posterior angles almost right-angled. Pronotal disc convex. Prosternal process (Fig. 332) broad, flat, parallel-sided, with rounded apex; extends posteriorly beyond front coxae. Procoxa circular in outline; its cavity externally open, internally closed, with small rounded slit in its antero-lateral outer edge; trochantin concealed.

Meso- and metathorax. Mesonotum (Fig. 378) with scutellum very small, strongly transverse, with widely truncate apex. Mesosternum (Fig. 422) coarsely punctured, smooth, flat, with intercoxal process broadly separating mesocoxae, not extending beyond them (slightly narrower than coxal diameter). Mesosternum fused with mesoepisternum (trace of suture weakly visible). Mesocoxa circular in outline, its cavity outwardly open; trochantin concealed. Meso-metasternal junction of straight-line type. Elytron (Figs 489, 490) elongate-oval, strongly convex, with regular rows of moderately dense, coarse, dark punctures; epipleuron with outer edge crenulate, broad basally, incomplete at apex. Metasternum (Fig. 422) coarsely punctured, strongly transverse, as long as mesosternum, weakly convex; median line short. Metacoxae transverse, widely separated. Metapleuron as in Fig. 423 (metepisternum fused with metepimeron). Metendosternite (Fig. 532) with

short stalk and widely separated anterior arms and anterior tendons. Hind wing absent.

Legs (Fig. 602). Trochanterofemoral attachment oblique. Femur widest near middle of its length, more than twice as wide as tibia; tibia gradually widening towards tarsus, with two short apical spurs. Tarsal formula 4-4-4 in both sexes; tarsomere 2 weakly lobed ventrally; tarsomere 3 small but distinct, tarsomere 4 as long as remaining combined. Claws simple. Empodium small, bisetose.

Abdomen (Fig. 648) with five freely articulated ventrites; ventrite 1 slightly longer than two following together; ventrites 2–4 subequal in length. Male abdominal segment 9 lightly sclerotized (Figs 703, 704).

Aedeagus (Fig. 762) resting on its side when retracted. Median lobe sclerotized, rather long, curved. Tegminal plate (Fig. 763) submembranous, with articulated, sclerotized parameres; tegminal strut long.

Female genitalia (Fig. 804). Ovipositor weakly sclerotized, with separated, elongate coxities; styli small, terminal. Spermatheca small, membranous; sperm duct moderately long, slender; accessory gland about half as large as spermatheca, circular, membranous.

*Species examined.* *M. subterranea* (Fabricius).

*Distribution.* Europe, North America, Africa.

#### *Agaricophilus* Motschulsky, 1838

(Figs 56, 57, 101, 138, 194, 195, 234, 270, 333, 334, 379, 424, 425, 491, 492, 533, 603, 649, 705, 706, 759, 760, 761, 805, 830)

*Agaricophilus* Motschulsky, 1838: 175. Type species, by monotypy:

*Agaricophilus reflexus* Motschulsky, 1838.

*Hygrotophila* Kolenati, 1846: 56. Type species, by monotypy:

*Hygrotophila glabrata* Kolenati, 1846.

*Description.* Length 2.1–2.6 mm. Body (Fig. 830) oval, gradually narrowing from about half of the body length towards elytral apex; strongly convex (semi-globose); shiny, smooth, covered with rather sparse but long, suberect, pale setae. Colour blackish-ferruginous, with antennae, legs, sides of pronotum and broad, side margins of elytra, lighter. Whole body very coarsely and moderately densely punctured.

Head (Figs 56, 57) deeply retracted in prothorax, transverse. Gular sutures short, weakly convergent anteriorly, very widely separated. Eyes moderately large, weakly oval, prominent, coarsely faceted. Antennal grooves absent; antennal sockets visible from above. Antenna as long as head and thorax together, 11-segmented (Fig. 101) with 3-segmented, loose, scarcely flattened club. Fronto-clypeal ridge straight. Clypeus transverse, flat, scarcely convergent anteriorly, truncate at apex. Labrum (Fig. 138) densely setose at sides of apex; weakly rounded apically; tormae with mesal arms recurved anteriorly; labral rods slender, subparallel. Mandible (Figs 194, 195) weakly concave ventrally, convex dorsally; bifid at apex, with a few very small teeth on

incisor edge; mola moderately large, transversely ridged; prostheca setose on its inner edge; submola hardly visible. Maxilla (Fig. 234) with palpomeres 1 and 3 very short; palpomere 2 about twice as long as 1 or 3; terminal palpomere almost as long as remaining combined, tapering, rounded at apex. Galea moderately wide (twice as wide as lacinia) with apical setae, scarcely recurved apically towards lacinia. Lacinia long, narrow, with a few apical spines and short setae on inner edge. Labium (Fig. 270) with palpomere 1 smallest; palpomeres 2 and 3 subequal in size; terminal palpomere subquadrate, truncate at apex. Mentum transverse, with small, triangular, setose convexity in the middle; punctured, covered with sparse short setae. Prementum short, transverse, sclerotized, with ligula membranous, wide and short. Tentorium (Fig. 57) of *Endomychus*-type.

Prothorax. Pronotum (Fig. 333) strongly transverse, widest at base; with broad, raised margins; lateral edges smooth; sulci absent; anterior angles produced, acute; posterior angles almost right-angled. Pronotal disc strongly convex. Prosternal process (Fig. 334) broad, flat, bordered at sides; weakly widening towards its apex; extending to posterior margins of front coxae; truncate apically. Procoxa circular in outline; its cavity externally open, internally closed, with small rounded slit in its antero-lateral outer edge; trochantin concealed.

Meso- and metathorax. Mesonotum (Fig. 379) with scutellum small, transverse, weakly cordiform, acute apically. Mesosternum (Fig. 424) almost flat; intercoxal process with fine ridges, broadly separates mesocoxae, (as wide as coxal diameter) not extends beyond them. Mesocoxa circular in outline, its cavity outwardly open; trochantin concealed. Meso-metasternal junction of straight-line type. Elytron (Figs 491, 492) broad-oval, strongly convex, irregularly punctured; epipleuron very broad basally, gradually narrowing towards elytral apex; complete. Metasternum (Fig. 424) strongly transverse, slightly longer than mesosternum, weakly convex; with femoral lines; median line very short. Metacoxae transverse, widely separated. Metapleuron as in Fig. 425. Metendosternite (Fig. 533) with short stalk and widely separated anterior arms and anterior tendons. Hind wing reduced (shorter and narrower than elytron).

Legs (Fig. 603). Trochanterofemoral attachment subheteromeroid. Femur widest near middle of its length, more than twice as wide as tibia, densely setose; with elongate cavity on whole length of inner edge; tibia gradually widening towards tarsus, with two short apical spurs. Tarsal formula 4-4-4 in both sexes; tarsomere 1 weakly and tarsomere 2 distinctly lobed ventrally; tarsomere 3 small but distinct, tarsomere 4 almost as long as remaining combined. Claws simple. Empodium small, bisetose.

Abdomen (Fig. 649) with femoral lines; with six freely articulated ventrites; ventrite 1 slightly shorter than three following together; ventrites 2-4 subequal in length. Male abdominal segment 9 lightly sclerotized (Figs 705, 706).

Aedeagus resting on its side when retracted. Median lobe (Fig. 761) well sclerotized, long, curved. Tegmen (Figs 759, 760) with tegminal plate submembranous; parameres short, but distinct, sclerotized; tegminal strut long.

Female genitalia (Fig. 805) with ovipositor weakly sclerotized; coxities separated, elongate, covered with short, stout spines in their apical part; styli small, terminal. Spermatheca small, elongate, membranous with weakly sclerotized, oval apex; sperm duct moderately long, slender; accessory gland very small, oval, membranous.

*Species examined.* *A. reflexus* Motschulsky.

*Distribution.* Southeastern Europe.

### *Symbiotes* Redtenbacher, 1849

(Figs 58, 59, 102, 139, 203, 235, 271, 335, 336, 381, 426, 493, 535, 558, 604, 650, 707, 708, 770, 771, 806, 831)

*Symbiotes* Redtenbacher, 1849: 198. Type species, by monotypy:

*Symbiotes latus* Redtenbacher, 1849.

*Microchondrus* Wollaston, 1854: 196. Type species, by monotypy:

*Microchondrus domuum* Wollaston, 1854.

*Eponomastus* Buysson, 1891: 95. The name was proposed (unnecessarily) to replace *Symbiotes* Redtenbacher.

*Description.* Length 1.7–2.3 mm. Body (Fig. 831) elongate-oval, strongly convex; shiny, smooth, covered with moderately dense and long, suberect, pale setae; densely and moderately coarsely punctured. Colour light to dark brown.

Head (Figs 58, 59) deeply retracted in prothorax, transverse. Gular sutures short, weakly convergent anteriorly, widely separated. Eyes large, weakly oval, prominent, coarsely faceted. Antennal grooves absent; antennal sockets visible from above. Antenna as long as head and thorax together, 11-segmented (Fig. 102) with 3-segmented, long, narrow and loose club. Frontoclypeal ridge straight. Clypeus transverse, flat, parallel-sided, weakly rounded at apex. Labrum (Fig. 139) coarsely punctured, densely setose; with narrow membranous apex, weakly emarginate medially; tormae with mesal arms recurved posteriorly; labral rods slender, divergent anteriorly. Mandible (Fig. 203) weakly concave ventrally, convex dorsally; bifid at apex, with blunt, moderately large subapical tooth; mola transversely ridged; prostheca densely setose on inner edge; submola distinct. Maxilla (Fig. 235) with palpomere 1 smallest; palpomere twice longer than 3; terminal palpomere as long as remaining combined, tapering, rounded at apex. Galea moderately broad with dense, long apical setae; about twice as wide as lacinia. Lacinia elongate, with long apical hook, a few stout, apical and subapical spines, and with sparse setae on inner edge. Labium (Fig. 271) with palpi widely separated basally; palpomere 1 smallest; palpomere 2 twice as long as 1; terminal palpomere large, oval, truncate apically. Mentum transverse, sparsely but coarsely punctured, covered with long setae. Prementum weakly transverse, sclerotized, with moderately wide and short, membra-

nous ligula. Tentorium (Fig. 59) with anterior arms convergent medially, not fused, and widely divergent anteriorly; corpotentorium weakly curved.

Prothorax. Pronotum (Fig. 335) strongly transverse, widest near middle of its length, narrowly bordered laterally; with moderately broad, lateral, raised margins, extending from pronotal apex for about 0.75 its length; each raised margin provided with oval pit posteriorly; lateral edges finely denticulate and setose; basal and lateral sulci distinct, moderately deep; each side of basal sulcus provided with large, oval pit. Anterior angles weakly, abruptly produced; posterior angles right-angled. Pronotal disc convex. Prosternal process (Fig. 336) broad, weakly bordered, parallel-sided, with rounded apex; extends posteriorly beyond front coxae. Procoxa circular in outline; its cavity externally open, internally closed; trochantin concealed.

Meso- and metathorax. Mesonotum (Fig. 381) with scutellum small, strongly transverse, with widely rounded apex. Mesosternum (Fig. 426) finely bicarinate, with its middle region elongate; intercoxal process broadly separates mesocoxae (slightly narrower than coxal diameter), not extending beyond them; with two large, rounded pits on sides of anterior part of mesosternum. Mesocoxa circular in outline, its cavity widely closed outwardly by sterna; trochantin concealed. Meso-metasternal junction of straight-line type. Elytron (Fig. 493) elongate-oval, strongly convex, with oval pit near outer, anterior edge; with more or less distinct regular rows of small, dark punctures, interspaces confusedly punctured; epipleuron with outer edge crenulate, broad basally, incomplete at apex; sutural stria strongly curved outwardly near scutellum. In male, apex of elytron with hardly visible characters of sexual dimorphism (very small tubercles, illustrated in Fig. 493). Metasternum (Fig. 426) twice as wide as long, weakly convex; median line short. Metacoxae transverse, widely separated. Metendosternite (Fig. 535) with very short stalk and widely separated anterior arms and anterior tendons. Hind wing (Fig. 558) without anal lobe. Anal and cubital veins absent; media posterior (MP 1+2) long, sclerotized, connected with reduced radius posterior (RP). Medial bridge present; medial fleck undivided; radial cell reduced.

Legs (Fig. 604). Trochanterofemoral attachment oblique. Femur widest near middle of its length, more than twice as wide as tibia; tibia gradually widening towards tarsus, with two short apical spurs. Tarsal formula 4-4-4 in both sexes; tarsomeres 1-3 subequal in length, simple; tarsomere 4 as long as remaining combined. Claws simple. Empodium small, with one hair.

Abdomen (Fig. 650) with five freely articulated ventrites; ventrite 1 slightly longer than two following together; ventrites 2-4 subequal in length. Male abdominal segment 9 (Figs 707, 708) lightly sclerotized.

Aedeagus (Fig. 770) resting on its side when retracted. Median lobe (Fig. 771) weakly sclerotized, long, curved. Tegmen large, ring-like in median part, submembranous; parameres fused; tegminal strut moderately long.

Female genitalia (Fig. 806). Ovipositor lightly sclerotized, with separated, elongate coxities; styli long, terminal. Spermatheca small, elongate-oval, membranous; sperm duct long, slender; accessory gland very small, elongate, covered with long setae, membranous.

*Species examined.* *S. gibberosus* (Lucas).

*Distribution.* Europe, North America.

### *Mychothenus* Strohecker, 1953

(Figs 60, 61, 104, 140, 204, 236, 272, 337, 338, 382, 427, 428, 494, 495, 534, 559, 605, 606, 651, 807, 832)

*Mychophilus* Frivaldszky, 1877: 19 (nec *Mychophilus* Hesse, 1865). Type species, by monotypy: *Mychophilus minutus* Frivaldszky, 1877.

*Mychothenus* Strohecker, 1953: 24. Replacement name for *Mychophilus* Frivaldszky, 1877.

*Description.* Length 1.0-1.5 mm. Body (Fig. 832) oval, strongly convex; shiny, smooth, covered with moderately dense and long, suberect, pale setae; densely and moderately coarsely punctured. Colour yellowish brown to blackish brown.

Head (Figs 60, 61) deeply retracted in prothorax, weakly transverse. Gular sutures short, weakly convergent anteriorly, widely separated. Eyes large, oval, prominent, moderately coarsely faceted. Antennal grooves absent; antennal sockets visible from above. Antenna 1.5 × as long as head, 10-segmented (Fig. 104); antennomere 1 stout, oval; antennomere 2 elongate oval; 3 elongate; 4-7 almost as long as wide, shorter than antennomere 3; club 3-segmented, large. Fronto-clypeal ridge straight. Clypeus transverse, flat, weakly rounded at apex. Labrum (Fig. 140) coarsely punctured, densely setose; with very narrow, truncate, membranous apex; tormae elongate with mesal arms recurved posteriorly; labral rods absent. Mandible (Fig. 204) bifid at apex, with blunt, moderately large subapical tooth; mola transversely ridged; prostheca submembranous, with long and dense setae on its inner apical edge; submola small, membranous. Maxilla (Fig. 236) with palpomere 1 smallest; palpomere 2 slightly longer than 3; terminal palpomere almost as long as remaining combined, conical. Galea moderately broad with dense, long apical setae; about twice as wide as lacinia. Lacinia elongate, with apical hook, a few stout, subapical spines and sparse setae on inner edge. Labium (Fig. 272) with palpi widely separated basally; palpomere 1 smallest; palpomere 2 transverse; terminal palpomere large, subquadrate, truncate apically; covered with fine microsculpture. Mentum transverse, rounded apically, sparsely and finely punctured, covered with long setae. Prementum transverse, sclerotized, with ligula submembranous, wide, weakly lobed at sides. Tentorium (Fig. 61) with anterior arms convergent medially, not fused, and widely divergent anteriorly; corpotentorium curved medially.

Prothorax. Pronotum (Fig. 337) strongly transverse, widest at base, gradually narrowing anteriorly; lateral

edges with narrow (slightly broadening anteriorly) raised margins; sulci absent; basal margin sinuate, forming a short and broad lobe medially; anterior angles rounded and moderately produced anteriorly. Pronotal disc gently convex. Prosternal process (Fig. 338) with a pair of carinae in its basal part, reaching to anterior margin of sternum; moderately broad, weakly bordered laterally, broadening towards its apex, weakly rounded apically; extends shortly, beyond front coxae. Procoxa weakly oval, its cavity externally open, internally closed; trochantin concealed.

Meso- and metathorax. Mesonotum (Fig. 382) sclerotized; scutellum small, strongly transverse, pentagonal, with acute apex. Mesosternum (Fig. 427) flat; intercoxal process transverse, broadly separates mesocoxae (slightly broader than coxal diameter), not extending beyond them; with two large, oval pits on sides of anterior part of mesosternum. Mesocoxa circular in outline, its cavity widely closed outwardly; trochantin concealed. Meso-metasternal junction of straight-line type, although metasternal apex weakly curved. Elytron (Figs 494, 495) elongate-oval, strongly convex, densely punctured; humeral plates weakly prominent; epipleuron broad basally, incomplete at apex; sutural stria incomplete near scutellum. In male, apex of elytron with hardly visible characters of sexual dimorphism, in form of very small fovea. Metasternum (Fig. 427) more than twice as wide as long, weakly convex; two small postcoxal pits situated adjacent to femoral lines; median line very short. Metacoxae transverse, widely separated. Metapleuron as in Fig. 428. Metendosternite (Fig. 543) with very short stalk and very widely separated anterior arms and anterior tendons. Hind wing (Fig. 559) without anal lobe. Anal veins absent; CuA hardly visible; media posterior (MP 1+2) rather long, sclerotized, connected with vestigial radius posterior (RP). Medial bridge present; medial fleck undivided; radial cell reduced.

Legs (Figs 605, 606). Trochanterofemoral attachment oblique. Femur moderately swollen in middle of its length, more than twice as wide as tibia; tibia weakly gradually widening towards tarsus, apical spurs absent. Tarsal formula 3-3-3 in both sexes; tarsomeres elongate, simple. Claws sharply pointed and appendiculated basally. Empodium small, with one hair.

Abdomen (Fig. 651) with six freely articulated ventrites; ventrite 1 slightly shorter than three following together; ventrites 2-5 subequal in length.

Aedeagus resting on its side when retracted. Tegmen stout, ring-like in median part; parameres fused; tegminal strut moderately long. Median lobe stout, weakly curved. (Sasaji 1978).

Female genitalia (Fig. 807). Ovipositor weakly sclerotized, with coxities separated, elongate, finely sinuate on their outer apical edge; styli minute.

*Species examined.* *M. asiaticus* Sasaji.

*Distribution.* Known from southeastern Europe and Japan.

### *Micropsephodes* Champion, 1913

(Figs 62, 63, 105, 141, 205, 237, 273, 339, 340, 341, 383, 429, 430, 496, 497, 536, 560, 607, 608, 652, 709, 710, 772, 773, 774, 808, 833)

*Micropsephodes* Champion, 1913: 119. Type species, by monotypy: *Micropsephodes serraticornis* Champion, 1913.

**Description.** Length 1.5-2.0 mm. Body (Fig. 833) broadly oval, strongly convex; shiny, smooth, glabrous; densely and moderately coarsely punctured. Colour brownish black.

Head (Figs 62, 63) deeply retracted and tucked up under prothorax, not visible from above, transverse. Gular sutures short, almost parallel-sided, widely separated. Eyes large, oval, prominent, moderately coarsely faceted. Antennal grooves absent; antennal sockets visible from above. Antenna as long as head, 8-segmented (although antennomeres 3-5 fused, with weakly visible sutures) (Fig. 105); with 3-segmented, large, loosely articulated club (longer than remaining antennomeres combined). Fronto-clypeal ridge straight. Clypeus strongly transverse, flat, truncate at apex. Labrum (Fig. 141) coarsely and sparsely punctured, setose; with narrow membranous, truncate apex; tormae elongate with mesal arms recurved posteriorly; labral rods short. Mandible (Fig. 205) weakly concave ventrally, convex dorsally; bifid at apex, with blunt, moderately large subapical tooth; mola transversely ridged; prostheca with tuft of setae near mola; submola very small, membranous. Maxilla (Fig. 237) with palpomere 1 smallest; palpomere 2, twice as long as 3; terminal palpomere as long as remaining combined, ovate, truncate apically. Galea broad with long apical spines; about twice as wide as lacinia. Lacinia elongate, with only one, long, stout, apical spine. Labium (Fig. 273) with palpi narrowly separated basally, covered with fine microsculpture; palpomere 1 smallest; palpomere 2 transverse; terminal palpomere slightly longer than 2, stout, weakly rounded at apex. Mentum transverse, sparsely and finely punctured, covered with long setae. Prementum as long as wide, sclerotized, with wide and short ligula. Tentorium (Fig. 63) with anterior arms convergent medially, not fused, and widely divergent anteriorly; corpotentorium lyriform.

Prothorax. Pronotum (Fig. 339) strongly transverse, widest at base, gradually narrowing anteriorly; lateral edges narrowly bordered; sulci absent; basal margin sinuate, strongly lobed medially. Anterior angles briefly and roundly produced anteriorly. Pronotal disc convex. Prosternal process short (Figs 340, 341), very narrow, prominent, with fine median ridge; rounded apically; not extending posteriorly beyond front coxae. Procoxa weakly transverse, its cavity externally open, internally closed; trochantin partially exposed.

Meso- and metathorax. Mesonotum (Fig. 383) sclerotized; scutellum small, as long as wide, triangular, with pointed apex. Mesosternum (Fig. 429) almost flat; intercoxal process transverse, broadly separates mesocoxae

(slightly narrower than coxal diameter), not extending beyond them. Mesocoxa oval in outline, its cavity widely closed outwardly (although mesoepimeron almost reaches coxa internally – under sterna); trochantin concealed. Meso-metasternal junction of straight-line type. Elytron (Figs 496, 497) oval, strongly convex; epipleuron broad basally, gradually narrowing towards apex, complete. Metasternum (Fig. 429) almost three times as wide as long, weakly convex; median line long. Metacoxae transverse, widely separated. Metapleuron as in Fig. 430. Metendosternite (Fig. 536) with very short stalk and very widely separated anterior arms and anterior tendons. Hind wing (Fig. 560) without anal lobe; with one anal or cubital vein, which is hardly visible; media posterior (MP 1+2) long, sclerotized; radius posterior (RP) absent. Medial bridge present; medial fleck undivided; radial cell reduced.

Legs (Figs 607, 608). Trochanterofemoral attachment oblique. Femur widest near middle of its length, more than twice as wide as tibia; tibia becoming slightly broader towards tarsus, apical spurs absent. Tarsal formula 3-3-3 in both sexes; tarsomere 1, twice as long as 2, lobed ventrally, with long and stout apical spine, and a few spines on inner edge. Claws sharply pointed, with additional tooth near the middle of their length. Empodium small, with one hair.

Abdomen (Fig. 652) with six freely articulated ventrites; ventrite 1 with femoral lines; as long as three following together. Male abdominal segment 9 as in Figs 709, 710.

Aedeagus resting on its side when retracted. Tegmen (Figs 773, 774) moderately large, ring-like in anterior part; parameres small, fixed with short tegminal plate; tegminal strut membranous, long. Median lobe (Fig. 772) long, weakly curved, with membranous, elongate gonopore at apex, and slender sclerite which extends from base to apex of penis.

Female genitalia (Fig. 808). Ovipositor lightly sclerotized, with elongate, separated coxities; styli minute, terminal. Spermatheca large, oval, membranous; accessory gland small, ramificate apically, covered with long setae; sperm duct long.

**Species examined.** *M. serraticornis* Champion, monotypic genus.

**Distribution.** Known only from Guatemala and Dominican Republic.

### *Erotendomychus* Lea, 1922

(Figs 64, 65, 103, 142, 206, 238, 274, 342, 343, 384, 431, 432, 498, 499, 609, 610, 653, 711, 712, 775, 809, 834)

*Erotendomychus* Lea, 1922: 302. Type species, by monotypy: *Erotendomychus bimaculatus* Lea, 1922.

**Description.** Length 2.6–2.7 mm. Body (Fig. 834) long-oval, convex; shiny, smooth, covered with moderately dense and long, suberect, pale setae; coarsely and moderately densely punctured. Colour brownish black, elytra may have contrasting markings.

Head (Figs 64, 65) weakly transverse. Gular sutures very short, convergent anteriorly, widely separated. Eyes large, oval, moderately prominent, very coarsely faceted. Antennal grooves absent; antennal sockets visible from above. Antenna slightly shorter than head and thorax together, 11-segmented (Fig. 103) with 3-segmented, narrow and loose club. Fronto-clypeal ridge straight. Clypeus transverse, flat, almost parallel-sided, truncate apically. Labrum (Fig. 142) coarsely punctured, sparsely setose; truncate apically; with narrow membranous apex; tormae with mesal arms recurved posteriorly; labral rods absent. Mandible (Fig. 206) weakly concave ventrally, convex dorsally; bifid at apex, with blunt, large subapical tooth (looks like 3 apical teeth); mola with a few transverse ridges; prostheca densely setose on its inner edge, with tuft of setae near mola; submola very small, membranous. Maxilla (Fig. 238) covered with fine microsculpture; palpomere 1 smallest; palpomeres 2 and 3 subequal in size; terminal palpomere slightly shorter than remaining combined, subcylindrical, rounded at apex. Galea moderately broad with dense, long apical setae; about twice as wide as lacinia. Lacinia elongate, with a few apical spines and sparse setae on inner edge. Labium (Fig. 274) with palpi widely separated basally; palpomere 1 smallest; palpomeres 2 and 3 subequal in length; terminal palpomere slightly longer than wide, truncate apically. Mentum transverse, sparsely but coarsely punctured, covered with short setae. Prementum as long as wide, sclerotized, with ligula moderately short, submembranous. Tentorium (Fig. 65) with anterior arms convergent and widely fused medially, divergent anteriorly; corpotentorium curved medially.

Prothorax. Pronotum (Fig. 342) transverse, widest at base, hardly bordered laterally; sulci absent; anterior angles produced, blunt; posterior angles almost right-angled. Pronotal disc convex. Prosternal process (Fig. 343) very short and narrow, with rounded apex. Procoxa circular in outline, its cavity externally open, internally closed; trochantin concealed.

Meso- and metathorax. Mesonotum (Fig. 384) weakly sclerotized; scutellum small, cordiform, with rounded apex, sparsely setose. Mesosternum (Fig. 431) flat, intercoxal process weakly elongate, rounded and prominent basally, directed between front coxae to meet prosternum; broadly separates mesocoxae (as wide as coxal diameter), not extending posteriorly beyond them. Mesocoxa circular in outline, its cavity widely closed outwardly; trochantin concealed. Meso-metasternal junction of straight-line type. Elytron (Figs 498, 499) elongate-oval, strongly convex; epipleuron narrow, incomplete at apex. Metasternum (Fig. 431) as long as mesosternum, with large, oval postcoxal pits; weakly convex; median line absent. Metacoxae oval, very widely separated. Metapleuron as in Fig. 432. Metendosternite with very short stalk and widely separated anterior arms. Hind wing vestigial – much shorter and narrower than elytron.

Legs (Figs 609, 610). Trochanterofemoral attachment heteromeroid. Femur widest near middle of its length, about twice as wide as tibia; tibia gradually widening towards tarsus; surrounded by short and stout spines. Tarsal formula 4-4-4 in both sexes; tarsomeres almost simple to weakly pseudotrimerous. Claws finely denticulate. Empodium small, with one hair.

Abdomen (Fig. 653) with six freely articulated ventrites; ventrite 1 as long as three following together; ventrites 2-4 subequal in length. Male abdominal segment 9 (Figs 711, 712) lightly sclerotized.

Aedeagus (Fig. 775). Median lobe well sclerotized, stout, curved; resting on its side when retracted. Tegmen absent.

Female genitalia (Fig. 809). Ovipositor weakly sclerotized with two, elongate coxities; styli moderately large, terminal. Spermatheca elongate-oval, membranous with sclerotized apex; accessory gland round, membranous with internal sclerites.

**Species examined.** *E. bimaculatus* Lea and *E. lawrencei* sp. nov.

**Distribution.** Australia.

***Erotendomychus lawrencei* sp. nov.**

(Figs 64, 65, 103, 142, 206, 238, 274, 342, 343, 384, 431, 432, 498, 499, 609, 610, 653, 711, 712, 775)

**Etymology.** The species is dedicated to Dr. J.F. Lawrence, an outstanding Australian coleopterist.

**Diagnosis.** *Erotendomychus lawrencei*, the second known species of the genus, can be easily separated from the type species – *E. bimaculatus*, by the following characters: elytra without contrasting markings, decidedly less elongate and more convex; whole body more oval and more coarsely, irregularly punctured (in *E. bimaculatus* punctures finer; elytra with rows of dark micropunctures visible at least on cleared specimens); tarsi weakly pseudotrimerous (in *E. bimaculatus* tarsi simple – without ventral lobes).

**Description.** Length 3.33–3.35 mm. Body 1.83–1.87 × longer than wide; pronotum 0.58–0.59 × as long as wide; elytra 1.07–1.08 × wider than pronotum, and 2.38–2.40 × longer than pronotum.

Colour uniformly brown, or dorsal surface brownish black. Vestiture consists of sparse and moderately long hairs. Head with eyes very coarsely faceted. Scutellum weakly elongate. Elytra widest near middle of their length, thence abruptly narrowing towards their apices; strongly convex; coarsely, irregularly punctured. Metasternum with one pair of postcoxal pits. Tarsi with tarsomeres weakly pseudotrimerous. Aedeagus as in Fig. 775. Female genitalia not studied.

**Types.** Holotype (sex indet.): Australia: “15.29S 145.16E, Mt. Cook Nat. Pk., QLD, 10–12 May 1981, A. Calder & J. Feehan/ Berlesate, ANIC 731, rainforest litter.” (ANIC). Paratypes. ♂: “30.23S 152.44E, Dorrigo Nat. Pk. NSW 600 m, 14 June 1982, L. Hill/ Berlesate, ANIC

838, closed forest litter/ *Erotendomychus* sp. J.F.L. ‘93.” (ANIC). ♂: “Australia: NSW: Wiangaree SF, Brindle Ck, 740 m, 29.II–3.III.1980, subtrop. rainfor. A. Newton, M. Thayer/ berlesed from log & leaf litter.” (MIIZ, completely dissected on slide).

***Pleganophorus* Hampe, 1855**

(Figs 66, 67, 106, 143, 198, 239, 275, 344, 345, 385, 433, 500, 501, 537, 611, 654, 810)

*Pleganophorus* Hampe, 1855: 97. Type species, by monotypy: *Pleganophorus bispinosus* Hampe, 1855.

**Description.** Length about 3.6 mm. Body elongate, subparallel, convex; shiny, covered with moderately dense and short pubescence; densely and confusedly punctured. Colour dark brown.

Head (Figs 66, 67) partially retracted in prothorax, weakly transverse; coarsely punctured. Gular sutures short, convergent anteriorly, widely separated. Eyes small, oval, not prominent, minutely faceted. Antennal grooves absent; antennal sockets visible from above. Antenna stout, almost as long as head and thorax together, 4-segmented (Fig. 106); apical antennomere hugely enlarged, especially in male. Fronto-clypeal ridge straight. Clypeus strongly transverse, convergent from base to middle of its length, thence parallel, flat. Labrum (Fig. 143) truncate apically; moderately densely punctured, shortly setose; tormae with mesal arms recurved weakly anteriorly; labral rods long, slender, widely divergent anteriorly. Mandible (Fig. 198) with one apical tooth and a few small, blunt teeth on incisor edge; mola strongly sclerotized; prostheca elongate covered with short setae; submola very small. Maxilla (Fig. 239) with palpomere 1 smallest; palpomeres 2 and 3 subequal in length; terminal palpomere as long as remaining combined, cylindrical, narrowing towards apex, rounded. Galea enlarged apically, lightly sclerotized, with apical half membranous; covered densely with short setae at apex, slightly recurved towards lacinia; about 5 × as wide as lacinia. Lacinia slender, shorter than galea, densely setose at apex. Labium (Fig. 275) with palpi widely separated at base; palpomere 1 smallest, palpomere 2 transverse; terminal palpomere large, subquadrate. Mentum transverse, punctured, covered sparsely with short setae. Prementum transverse, sclerotized; ligula weakly sclerotized, finely punctured, setose, strongly lobed at sides. Tentorium (Fig. 67) with anterior arms broadly fused medially; and widely divergent anteriorly; corpotentorium straight, without median process.

Prothorax subcylindrical. Pronotum (Fig. 344) weakly transverse, convex; widest at base; lateral edges smooth; basal sulcus hardly visible with moderately large, concavity on each side; anterior angles rounded; posterior angles strongly produced, acute. Pronotal disc coarsely punctured; with short, line extending from middle of posterior margin towards middle of disc. Prosternal process (Fig. 345) very narrow between coxae (front coxae contiguous, or almost so), not extends

beyond them, rounded apically. Procoxa circular in outline, its cavity externally open, internally closed, with small rounded slit in its antero-lateral outer edge; trochantin concealed.

Meso- and metathorax. Mesonotum (Fig. 385) with scutellum moderately large, transverse, as long as wide, widely rounded apically. Mesosternum (Fig. 433) fused with mesepisternum; intercoxal process elongate, flat; narrowly separates mesocoxae, not extends beyond them. Mesocoxa circular in outline, its cavity narrowly closed outwardly; trochantin concealed. Meso-metasternal junction with internal knobs. Elytron (Figs 500, 501) elongate-oval, convex; finely, densely and irregularly punctured; humeri prominent; epipleuron very narrow, incomplete apically. Metasternum (Fig. 433) transverse, weakly narrowing towards its anterior margin, weakly convex; median line almost complete. Metacoxae transverse, widely separated. Metendosternite (Fig. 537) with very short stalk; anterior arms long, widely separated; anterior tendons short, very widely separated. Hind wing as in *Trochoideus*, devoid of Mp-CuA cross vein; medial bridge present; medial fleck undivided; radial cell reduced.

Legs (Fig. 611). Trochanterofemoral attachment oblique. Femur moderately expanded towards middle, slightly broader than tibia, finely setose; tibia scarcely widening towards tarsus; apex of tibia (except its outer edge) surrounded by short, spines; apical spurs absent. Tarsi stout; tarsal formula 4-4-4 in both sexes; tarsomeres 1, 2, 3 short, subequal in length; tarsomere 4 slightly shorter than remaining combined. Claws simple. Empodium small, bisetose.

Abdomen (Fig. 654) with six freely articulated ventrites; ventrite 1 slightly longer than two following together; 2-4 subequal in length; ventrite 5 (in female – Fig. 654) truncate in middle of its apex, and roundly produced on sides.

Aedeagus not studied.

Female genitalia (Fig. 810) – as in *Trochoideus*. Ovipositor weakly sclerotized; coxities very narrow, elongate, separated, with long setae at apex; styli absent. Sperm duct short, weakly sclerotized.

**Species examined.** *P. bispinosus* Hampe, monotypic genus.

**Distribution.** Southeastern Europe.

### *Trochoideus* Westwood, 1833

(Figs 68, 69, 107, 108, 144, 199, 200, 240, 276, 346, 347, 386, 434, 502, 503, 538, 561, 612, 616, 617, 618, 655, 713, 714, 776, 777, 778, 811, 835)

*Trochoideus* Westwood, 1833: 673. Type species, by monotypy: *Paussus cruciatus* Dalman, 1825.

*Trochoides* Chapuis, 1876: 147. (error).

*Pseudopaussus* Schulze, 1916: 292. Type species, by original designation: *Pseudopaussus monstrosus* Schulze, 1916.

**Description.** Length 3.0–4.2 mm. Body (Fig. 835) weakly elongate, moderately convex; shiny, covered with

dense and rather short pubescence; densely and confusedly punctured. Colour light to dark brown, sometimes with contrasting markings on the elytra.

Head (Figs 68, 69) partially retracted in prothorax, transverse; coarsely punctured. Gular sutures short, convergent anteriorly, widely separated. Eyes moderately large, weakly oval, prominent, coarsely faceted. Antennal grooves absent; antennal sockets visible from above. Antenna almost as long as head and thorax together, 4-segmented (Figs 107, 108); apical antennomere hugely enlarged, especially in male (Fig. 107). Fronto-clypeal ridge almost straight. Clypeus flat, transverse with sides subparallel apically. Labrum (Fig. 144) transverse, sclerotized, truncate at apex; moderately densely punctured, covered with long setae; tormae with mesal arms weakly recurved anteriorly; labral rods long, slender, widely divergent anteriorly. Mandible (Figs 199, 200) covered with moderately long setae on outer edge; with large, apical tooth and two, smaller subapical teeth; mola transversely ridged; prostheca covered with short setae on its inner edge; submola very small. Maxilla (Fig. 240) with palpomere 1 smallest; palpomere 2 twice as long as 1 or 3; terminal palpomere longer than 2 and 3 together, cylindrical, tapering, narrowly rounded at apex. Galea enlarged apically, lightly sclerotized, covered densely with short setae at apex, scarcely recurved towards lacinia; about 5 × as wide as lacinia. Lacinia much shorter than galea, weakly narrowing towards its apex, with dense, long setae at apex and on inner edge. Labium (Fig. 276) with palpi widely separated at base; terminal palpomere large, subquadrate. Mentum transverse, finely punctured, covered sparsely with short setae. Prementum transverse, sclerotized; ligula finely punctured, strongly lobed at sides. Tentorium (Fig. 69) of *Endomychus*-type.

Prothorax. Pronotum (Fig. 346) strongly transverse, widest near middle of its length; lateral edges densely and finely denticulate and setose; basal sulcus hardly visible, lateral sulci in form of shallow, triangular depressions; anterior angles rounded; posterior angles slightly produced, acute. Pronotal disc weakly convex. Prosternal process (Fig. 347) very narrow (front coxae contiguous), extends to posterior margin of coxae, rounded apically. Procoxa circular in outline, its cavity externally open, internally closed; trochantin concealed.

Meso- and metathorax. Mesonotum (Fig. 386) sclerotized; scutellum small, transverse, rounded apically. Mesosternum (Fig. 434) fused with mesepisternum; intercoxal process narrow, elongate, flat; narrowly separates mesocoxae, not extends beyond them. Mesocoxa circular in outline, its cavity narrowly closed outwardly; trochantin concealed. Meso-metasternal junction with internal knobs. Elytron (Figs 502, 503) elongate-oval, convex; finely, densely and irregularly punctured; epipleuron narrow, incomplete apically. Metasternum (Fig. 434) transverse, weakly narrowing towards its anterior margin; median line more than half as long as metasternum. Metacoxae transverse, widely separated. Metendo-

sternite (Fig. 538) with short stalk; anterior arms long, widely separated; anterior tendons short, widely separated. Hind wing (Fig. 561) with anal lobe. Anal anterior (AA) hardly visible, fused with cubital anterior (CuA) extends as single, vestigial vein (AA+CuA) towards the back of medial field; media posterior (MP 1+2) long, sclerotized, connected with reduced radius posterior (RP). Mp-CuA cross vein absent; medial bridge present; medial fleck undivided; radial cell reduced.

Legs (Fig. 612). Trochanterofemoral attachment oblique. Femur widest near middle of its length, more than twice as wide as tibia; tibia scarcely widening towards tarsus, with apex (except of its outer edge) surrounded by short, spines; tibial spurs absent. Tarsal formula 4-4-4 in both sexes; tarsomeres 1 and 2 weakly lobed ventrally; tarsomere 3 slightly shorter than tarsomere 2. Claws simple. Empodium small, bisetose. Mesotrochanters, mesotibiae and metatibiae of male with characters of sexual dimorphism (Figs 616, 617, 618).

Abdomen (Fig. 655) with six freely articulated ventrites; ventrite 1 slightly longer than two following together; ventrites 2 and 3 subequal in length. Male abdominal segment 9 as in Figs 713, 714.

Aedeagus comparatively short, weakly sclerotized, scarcely curved, resting on its side when retracted. Median lobe (Fig. 776) with internal sclerites and very small submembranous gonopore at apex. Tegmen (Figs 777, 778) with large tegminal plate and articulated parameres; tegminal strut submembranous, slender, slightly shorter than tegminal plate.

Female genitalia (Fig. 811). Ovipositor weakly sclerotized; coxities very narrow, elongate, separated, with long setae at apex; styli absent. Spermatheca large, membranous; sperm duct short, partially sclerotized; accessory gland very small, elongate, membranous.

**Species examined.** An unnamed species from Borneo (in detail), *T. desjardinsi* Guérin and one unnamed species from Madagascar (externally).

**Distribution.** Tropical regions of the world.

### *Xenomycetes* Horn, 1880

(Figs 70, 71, 109, 145, 196, 197, 241, 277, 348, 349, 387, 435, 436, 504, 505, 539, 613, 656, 715, 716, 764, 765, 766, 812, 836)

*Xenomycetes* Horn, 1880: 141. Type species, by monotypy: *Xenomycetes morrisoni* Horn, 1880.

**Description.** Length 5.0–5.5 mm. Body (Fig. 836) elongate-oval, moderately convex; shiny, covered with sparse, short pubescence; rather densely and confusedly punctured. Colour ferruginous.

Head (Figs 70, 71) partially retracted in prothorax, almost as long as wide; gular area, genae and occiput with characteristic microsculpture. Gular sutures moderately long, weakly convergent anteriorly, widely separated. Eyes large, oval, prominent, coarsely faceted. Antennal grooves absent; antennal sockets visible from above. Antenna slightly longer than head and thorax

together, 11-segmented (Fig. 109) with, 3-segmented, loose, narrow, scarcely flattened club; antennomeres 1 and 3 elongate, antennomeres 2 and 4–8 subquadrate. Fronto-clypeal ridge almost straight. Clypeus transverse, weakly narrowing towards its apex, flat. Labrum (Fig. 145) strongly transverse, covered with sparse, short setae; with broad, membranous, setose, anterior edge; tormae elongate, with mesal arms very weakly recurved posteriorly; labral rods slender, divergent anteriorly. Mandible (Figs 196, 197) with large apical tooth and one, slightly smaller subapical tooth; mola transversely ridged; prostheca covered with short setae on its inner edge; submola very small. Maxilla (Fig. 241) with palpomere 1 smallest; palpomere 2 and 3 subequal in length, slightly longer than 1; terminal palpomere as long as 2 and 3 together, cylindrical, rounded at apex. Galea moderately large, weakly widening towards its apex, with long apical setae; about twice as wide as lacinia. Lacinia almost as long as galea, weakly narrowing towards its apex, covered with a few, long apical spines, and a few long, subapical hairs; digitus visible. Labium (Fig. 277) with palpi widely separated at base; terminal palpomere subquadrate, weakly truncate at apex. Mentum transverse, finely punctured, covered sparsely with short setae. Prementum transverse, sclerotized; ligula finely punctured, covered with moderately long apical setae. Tentorium (Fig. 71) of *Endomychus*-type.

Prothorax. Pronotum (Fig. 348) weakly transverse, widest at base; widely bordered laterally and anteriorly; basal sulcus hardly visible, with very shallow depressions on its sides; anterior angles weakly produced; posterior angles almost right-angled. Pronotal disc convex. Prosternum convex, with a pair of moderately large, oval, precoxal pits. Prosternal process (Fig. 349) narrow, flat, with rounded apex; distinctly separates procoxae, extends to their posterior margins. Procoxa circular in outline, its cavity externally open, internally closed; trochantin concealed.

Meso- and metathorax. Mesonotum (Fig. 387) sclerotized; scutellum very small, transverse, rounded apically. Mesosternum (Fig. 435) strongly carinate, with a pair of oval pits on sides, near anterior margin; intercoxal process elongate, less than a half as wide as coxal diameter; narrowly separates mesocoxae, not extends beyond them. Mesocoxa circular in outline, its cavity outwardly open; trochantin partially exposed. Meso-metasternal junction with internal knobs. Elytron (Figs 504, 505) elongate, weakly truncate at apex, convex, with more or less distinct rows of dark punctures (interspaces irregularly finely punctured); epipleuron narrow, incomplete apically. Metasternum (Fig. 436) transverse, weakly convex, moderately coarsely punctured; with two pairs of oval, postcoxal pits; median line almost complete. Metacoxae transverse, widely separated. Metapleuron with one, small pit near its anterior margin. Metendosternite (Fig. 539) with short stalk and widely separated anterior arms and anterior tendons. Hind wing reduced, shorter and narrower than elytron.

Legs (Fig. 613). Trochanterofemoral attachment subheteromeroid. Femur weakly flattened, widest near middle of its length, about twice as wide as tibia; tibia scarcely widening towards tarsus, without apical spurs. Tarsal formula 4-4-4 in both sexes; tarsomeres 1 and 2 weakly flattened and ventrally lobed; tarsomere 3 distinctly smaller than tarsomere 1 or 2 (tarsi pseudotrimerous). Claws simple. Empodium small, bisetose. Male mesotibia slightly arcuate at tip.

Abdomen (Fig. 656) with five freely articulated ventrites; ventrite 1 with two pairs of postcoxal pits; longer than three following together; ventrites 2-4 subequal in length; in male (see Fig. 656), ventrite 5 with prominently elevated, elongate, median tubercle with cone-shaped tubercle on each side. Male abdominal segment 9 (Figs 715, 716) weakly sclerotized.

Aedeagus comparatively long, sclerotized, curved, resting on its side when retracted. Median lobe (Fig. 764) with small, submembranous gonopore at apex. Tegmen (Figs 765, 766) about  $2.5 \times$  shorter than median lobe; tegminal plate moderately long, sclerotized; parameres articulated; tegminal strut absent.

Female genitalia (Fig. 812). Ovipositor sclerotized, with large, separated, elongate coxities; styli small, subterminal. Spermatheca small, weakly sclerotized; sperm duct short, slender; accessory gland very small, oval, submembranous.

*Species examined.* *X. morrisoni* Horn.

*Distribution.* North America: USA.

#### *Acritosoma* Pakaluk and Ślipiński, 1995

(Figs 72, 73, 110, 146, 201, 202, 242, 278, 350, 351, 437, 506, 507, 540, 614, 615, 657, 767, 768, 769)

*Acritosoma* Pakaluk and Ślipiński, 1995: 330. Type species, by original designation: *Acritosoma elongatum* Pakaluk and Ślipiński, 1995.

**Description.** Length 1.76–1.98 mm. Body elongate to weakly ovate, convex; smooth, covered with dense and moderately long, pale hairs; distinctly, densely and confusedly punctured. Colour light to dark brown or reddish brown.

Head (Figs 72, 73) deeply retracted in prothorax, weakly transverse. Gular sutures absent. Eyes large, prominent, coarsely faceted. Antennal grooves absent; antennal sockets not visible from above. Antenna (Fig. 110) 9- or 10-segmented with 3-segmented, long, narrow and loose club; each segment of club with an apical patch of setose sensilla. Fronto-clypeal ridge arcuate. Clypeus transverse, flat, apical margin rounded. Labrum (Fig. 146) strongly transverse, coarsely punctured; with narrow submembranous apex, truncate medially; tormae with mesal arms weakly recurved posteriorly; labral rods broad, convergent, fused posteriorly. Mandible (Figs 201, 202) weakly concave ventrally, convex dorsally; bifid at apex, with large, prominent subapical tooth; mola strongly sclerotized; prostheca densely setose on its inner edge,

with tuft of setae at its base; submola distinct, membranous. Maxilla (Fig. 242) with palpomere 1 smallest; palpomeres 2 and 3 almost twice as long as 1; terminal palpomere as long as remaining combined, rounded at apex. Galea moderately broad with dense, long, stout apical setae; about twice as wide as lacinia. Lacinia elongate, with several apical and subapical spines, and with sparse setae on inner edge. Labium (Fig. 278) with palpi narrowly separated basally; palpomere 1 very small; palpomere 2 large, transverse; terminal palpomere conical. Mentum transverse, with six long setae. Prementum weakly elongate, sclerotized, with two long setae medially on apical margin, ligula moderately wide and short. Tentorium (Fig. 73) with anterior arms convergent medially, not fused, and widely divergent anteriorly; corpotentorium weakly curved, without median process.

Prothorax. Pronotum (Fig. 350) strongly transverse, widest near middle of its length, distinctly bordered laterally; anterior edge emarginate, with small median lobe; posterior edge with weak lobe medially; lateral edges weakly denticulate and setose; sulci absent; anterior angles hardly produced, blunt; posterior angles virtually right-angled. Pronotal disc convex. Prosternal process (Fig. 351) rather narrow between coxae, expanded laterally beyond them; truncate at apex. Procoxa circular in outline, its cavity closed externally and internally; trochantin concealed.

Meso- and metathorax. Mesonotum (Fig. 380) sclerotized; scutellum small, strongly transverse, truncate at apex. Mesosternum (Fig. 437) flat and smooth; intercoxal process weakly rounded apically; moderately broadly separates mesocoxae (about a half as broad as coxal diameter), reaches almost to their hind margins. Mesocoxa circular in outline, its cavity widely closed outwardly; trochantin concealed. Meso-metasternal junction of straight-line type, without internal knobs. Elytron (Figs 506, 507) elongate-oval, convex; confusedly punctured, with more or less distinct regular rows of large punctures (obvious on cleared specimens); epipleuron incomplete at apex. Metasternum (Fig. 437) twice as wide as long, weakly convex; median line moderately long (extending from posterior for about 0.75 its length); femoral lines present. Metacoxae transverse, widely separated. Metendosternite (Fig. 540) with short stalk; anterior tendons elongate, widely separate; lateral arms widely separated, each with an elongate anterior process. Hind wing without radial cell; with anal lobe; one anal vein subparallel to cubitus, almost reaching medial fleck.

Legs (Figs 614, 615). Trochanterofemoral attachment weakly heteromeroid. Femur widest near middle of its length, much more than twice as wide as tibia; tibia subcylindrical, gradually widening towards tarsus, with two short apical spurs. Tarsal formula 4-4-4 in both sexes; tarsomeres 1-3 short, simple (not lobed ventrally); tarsomere 4 longer than remaining combined. Claws with distinct tooth basally. Empodium reduced, without setae.

Abdomen (Fig. 657) with six visible ventrites; ventrite 1 longer than three following together; with broad, trun-

cate intercoxal process; femoral lines short, incomplete; ventrites 2–4 subequal in length.

Aedeagus (Figs 767, 768) with median lobe weakly curved, well sclerotized; internal sac with complex armature, median orifice ventral. Tegmen (Fig. 769) reduced, ring-shaped, parameres fused; tegminal strut elongate.

Female genitalia with ovipositor short; coxities separated, elongate, large; each with admedial ventral lobe; styli stout, subterminal, densely setose. Spermatheca small, oval, sclerotized; sperm duct rather short, attached to apex of bursa; accessory gland very small, elongate (Pakaluk and Ślipiński 1995).

**Species examined.** *A. elongatum* Pakaluk and Ślipiński.

**Distribution.** Known from Peru and Mexico.

## PHYLOGENETIC ANALYSIS

### 1. Methods

Cladistic analysis was undertaken using Hennig86 (Farris 1988). The mapping of character states and production of final cladograms saved from Hennig86 were accomplished using CLADOS (Nixon 1992).

A phylogenetic analysis was performed for 40 genera of the Endomychidae and 7 genera (representing all subfamilies) of the closely related Coccinellidae, both families being treated here as the ingroup. Within the currently recognized subfamilies of the Endomychidae, the type genus and (if available) one or more genera representing the greatest character variety, were selected and studied. Genera from the following, distantly related families of Cucujoidea: Protocucujidae, Helotidae and Brachypteridae, were chosen as the outgroups. Taxonomic placement of examined taxa follows that of Pakaluk, Ślipiński and Lawrence (1994) and Lawrence and Newton (1995).

### 2. Taxa examined for analysis

#### Outgroups.

Protocucujidae: *Ericmodes silvaticus* (Philippi).

Brachypteridae: *Kateretes* sp., from Poland.

Helotidae: *Helota* sp., from Borneo (Sarawak).

#### Ingroups.

Coccinellidae: Coccinellinae (*Coccinella septempunctata* Linnaeus); Scymninae (*Scymnus abietis* Paykull); Coccidulinae (*Coccidula rufa* (Herbst)); Chilocorinae (*Chilocorus cacti* (Linnaeus)); Epilachninae (*Epilachna vigintioctomaculata* Motschulsky); Sticholotidinae, Sukunahikonini (*Sukunahikona* sp., from Taiwan); Sticholotidinae, Carinodulini (*Carinodulina burakowskii* Ślipiński and Jadwiszczak);

Endomychidae: Holoparamecinae (*Holoparamecus* spp., from Greece and Burma); Merophysinae (*Merophysia* sp., from Rhodes; *Displotera beloni* (Wasmann)); Leiestinae (*Leiestes seminiger* (Gyllenhal), *Panamomus lewisi* Gorham, *P. brevicornis* Gorham, *Rhanidea unicolor* (Ziegler), *Phymaphora pulchella*

Newman *P. californica* Horn, *Stethorhanis vandykei* Blaisdell, *S. borealis* Blaisdell, *Panaleies decoratus* (Gorham)); Eupsilobiinae (*Microxenus laticollis* Wollaston, *Eidoreus minutus* Sharp, *Adamia mexicana* gen. et sp. nov.); Endomychinae (*Endomychus coccineus* (Linnaeus), *Endomychus* spp. from Pakistan, India, China, Japan, *Cyclotoma cingalensis* (Gorham), *C. quinquepunctata* Arrow, *Cyclotoma* sp. from Java; *Meilichius impressicollis* Strohecker, *Meilichius* sp. from Philippines, *Bolbomorphus sexpunctatus* Arrow, *Eucteanus coelestinus* Gerstaecker, *Eucteanus* sp. from India); Epipocinae (*Epipocus tibialis* (Chevrolat), *E. mutilatus* Gerstaecker, *Epopterus* sp. from Ecuador, *Danae* sp. from Namibia, *Saula ferruginea* Gerstaecker, *Saula* sp. from China, *Stenotarsus nobilis* Gerstaecker, *Stenotarsus* spp. from Ecuador and Cameroon, *Perrisina brevis* (Perris), *Danascelis elongata* Tomaszewska, *Anidrytus* sp. from Mexico, *Archipines* sp. from Peru); Lycoperdininae (*Lycoperdina succincta* (Linnaeus), *Beccariola orca* Heller, *B. papuensis* (Gorham), *Aphorista morosa* (LeConte), *Trycherus* sp. from Belg. Congo); Mycetaeinae (*Mycetaea subterranea* (Fabricius); *Agaricophilus reflexus* Motschulsky – uncertain position – former Mycetaeinae (Strohecker 1953)); Anamorphinae (*Symbiotes gibberosus* (Lucas), *Mychothenus asiaticus* Sasaji); genera incertae sedis (former Mycetaeinae, Strohecker 1953: *Micropsephodes serraticornis* Champion, *Erotendomychus bimaculatus* Lea, *E. lawrencei* sp. nov.); Pleganophorinae (*Pleganophorus bispinosus* Hampe, *Trochoideus* spp. from Borneo and Madagascar, *T. desjardinsi* Guérin); Xenomycetinae (*Xenomycetes morrisoni* Horn); Acritosomatinae (*Acritosoma elongatum* Pakaluk and Ślipiński).

### 3. Characters, discussion and polarity decisions

# 0. Head with occipital file: absent (0); present (1). The cephalic stridulatory area (occipital file) on the head is a unique character for Lycoperdininae (Figs 50, 52).

# 1. Head with antennal grooves: present (0); absent (1). The state (0), antennal grooves present, is found in all members of the outgroups. Within Endomychidae antennal grooves occur in Merophysinae, where they are long (Figs 4, 6) (extend to or beyond the posterior edge of the eye), and in Eupsilobiinae, where they are short (Figs 20, 22, 24) (extend to about the middle of the eye).

# 2. Antenna: 8–11 segmented (0); 4–5 segmented (1). The 4–5 segmented antenna is characteristic for Pleganophorinae (Figs 106–108), although there are known females of a few species of *Trochoideus*, which have antenna 7-segmented.

# 3. Fronto-clypeal ridge: absent (0); straight or weakly curved (1); strongly curved or obtusely angled (2). Fronto-clypeal ridge is absent – state (0) – in *Helota*, *Kateretes* and all Coccinellidae. All members of Endomychidae have sharply defined fronto-clypeal ridge, which is straight or weakly curved, but a strongly curved or obtusely angled ridge occurs in Merophysinae

(Figs 3, 5) and a strongly curved one in *Ericmodes* (Protocucujidae).

# 4. Labrum: visible from above (0); concealed by clypeus (1). Labrum concealed by clypeus is an autapomorphy for *Helota* in the present data set.

# 5. Mandible with mola: well-developed, large (0); absent or reduced (1). Members of Coccinellidae have mandible without mola, although *Sukunahikona* and *Carinodulina* appear to have a reduced, small mola. *Ericmodes*, *Helota*, *Kateretes* and all Endomychidae have the mola large and well-developed – state (0).

# 6. Mandible with prostheca: well-developed, only setose (0); reduced (1); with setae and apical, sclerotized, elongate projections (2). Endomychidae have mandible always with a well-developed prostheca – state (0). Within the outgroups state (0) occurs in *Ericmodes* and *Helota*, while *Kateretes* and Coccinellidae have the prostheca reduced – state (1). Polarity of this character is uncertain. The apical, sclerotized, elongate projections on the prostheca is a unique character for *Merophysia* and *Displotera* (Figs 148–151) – state (2).

# 7. Labium with mentum: flat, smooth (0); with small, triangular, setose projection placed medially (1); with large, triangular, raised area (2). Mentum flat and smooth occurs in members of the outgroups and in most Endomychidae – state (0). Some modifications occur in *Mycetaea*, *Agaricophilus* (small setose convexity placed medially – Figs 269, 270) Merophysiinae and Eupsilobiinae (large, triangular, raised area – Figs 243, 245, 252–254).

# 8. Labial palp with palpomere 2: subcylindrical or transverse (0); oval, inflated (1). Oval and inflated labial palpomere 2 – state (1) – occurs only in *Holoparamecus*, *Merophysia* and *Displotera* (Figs 243–245). The members of outgroups as well as other Endomychidae, have labial palpomere 2 transverse or elongate (subcylindrical).

# 9. Labium with prementum: transverse – at most slightly longer than mentum (0); quadrate or longer than wide – at least twice as long as mentum (1). State (1) is unique for members of the Endomychinae (Figs 255–259). The outgroups and other endomychids have the prementum transverse, at most slightly longer than mentum – state (0).

# 10. Labium with ligula: distinct, membranous or submembranous – often lobed antero-laterally (0); ligula indistinct – whole prementum evenly sclerotized (1). This character is correlated with the previous one. In Endomychinae, where the prementum is longer than wide, and at least twice as long as the mentum, the ligula is indistinct (Figs 256–259), because the whole prementum is evenly sclerotized (the only exception is *Endomychus*, which has a more or less distinct, submembranous ligula). In the outgroups and other Endomychidae, where the prementum is transverse and slightly longer than the mentum, the ligula is always distinct and most often with the antero-lateral lobes – state (0).

# 11. Maxilla with galea: well-developed (0); reduced (1). The reduced galea, is an autapomorphy for *Kateretes* in the present data set.

# 12. Maxillary palpomere 2 and 3 with membranous insertions on inner apical edges: absent (0); present (1). State (1) is characteristic for most Coccinellidae. *Sukunahikona*, *Carinodulina*, other members of the outgroups and all Endomychidae have state character (0).

# 13. Tentorium with anterior arms: separate (0); meeting medially without long process (1); meeting medially, with long process anteriorly (2). Anterior arms of tentorium are separate in *Ericmodes*, *Kateretes*, Coccinellidae, most Anamorphinae and *Acritosoma*, while anterior arms meeting medially occur in *Helota* and most Endomychidae. Polarity of this character is uncertain.

# 14. Anterior margin of pronotum with stridulatory membrane: absent (0); present (sometimes reduced) (1). The stridulatory membrane on anterior margin of the pronotum is a unique character for Lycoperdininae (Fig. 327), although it is sometimes observed to be reduced or absent (e.g. *Beccariola*).

# 15. Prosternum with antennal grooves: absent (0); present (1). The outgroups and most endomychids have the plesiomorphic state. Antennal grooves on the prosternum occur in *Merophysia* and *Displotera* (Figs 282, 284).

# 16. Procoxal cavity externally closed (0); externally open (1). Distantly related outgroups have procoxal cavities externally closed. Coccinellidae and Endomychidae have a derived condition of this character (except for *Acritosoma*, which has the plesiomorphic state – Fig. 351).

# 17. Mesosternum with intercoxal process bicarinate (boat-shaped): absent (0); present (1). The boat-shaped intercoxal process of mesosternum is a unique character for Leiestinae (Figs 392–397).

# 18. Mesocoxal cavity: open outwardly (0); narrowly closed outwardly (1); widely closed outwardly (2). The outgroups and most Endomychidae have mesocoxal cavities open outwardly – state (0). The mesocoxal cavities that are closed outwardly by sterna occur in *Holoparamecus*, Merophysiinae, Pleganophorinae (closed narrowly – Figs 389–391, 433, 434), Anamorphinae and *Acritosoma* (closed widely – Figs 426, 427, 429, 431, 437).

# 19. Mesotrochantin exposed while mesocoxal cavity open outwardly (0); mesotrochantin concealed while mesocoxal cavity open outwardly (1); mesotrochantin concealed while mesocoxal cavity closed outwardly (2). This character is correlated with the previous one. If the mesocoxal cavities are closed, the mesotrochantin is always concealed, but when the mesocoxal cavities are open, the mesotrochantin may be exposed, as in *Ericmodes*, *Kateretes* and most Endomychidae (Eupsilobiinae, Endomychinae, Epipocinae, Lycoperdininae and *Xenomycetes*) or concealed, as in *Helota*, Coccinellidae, Leiestinae and Mycetaeinae. Polarity of this character is uncertain.

# 20. Metasternum with femoral lines: absent (0); present (1). The femoral lines on the metasternum occur

in Coccinellidae and some Endomychidae, but most endomychids as well as distantly related outgroups have the metasternum without femoral lines. The distribution of the femoral lines in Cucujoidea, in general, is enigmatic, so the polarity of this character is uncertain.

# 21. Elytra covering whole abdomen (0); short, exposing 2–3 tergites (1). The short elytra, exposing 2–3 tergites occur in *Kateretes*.

# 22. Tarsal formula: 5-5-5 (or 5-5-4 in male) (0); 4-4-4 (1); 3-3-3 (2). The plesiomorphic condition occurs in distantly related outgroups. Most Coccinellidae and most Endomychidae have tarsi 4-segmented. The reduction of tarsomeres to three segments occurs within Endomychidae in *Holoparamecus*, Merophysinae and some Anamorphinae.

# 23. Tarsi 5-segmented (0); 4-segmented, simple (1); 4-segmented, distinctly pseudotrimerous (2); 3-segmented, simple (3). The 4-segmented tarsi which occur in most Endomychidae and most Coccinellidae, may be simple or pseudotrimerous. The pseudotrimerous tarsi (e.g. Fig. 584) – state (2) – is a unique character for almost all Coccinellidae and higher Endomychidae (Endomychinae, Epipocinae, Lycoperdininae and *Xenomycetes*).

# 24. Claws: simple (0); modified (1). Most Coccinellidae have claws modified, while the distantly related outgroups have claws simple – state (0). Within Endomychidae state (1) occurs only in most Anamorphinae and *Acritosoma*.

# 25. Abdomen with numbers of functional spiracles: 7 pairs (0); 6 pairs (1); 5 pairs (2). Five pairs of abdominal spiracles in the adult is generally recognized as a derived feature within the cerylonid group. The polarity of this character seems to be clear: 7 pairs of spiracles in primitive Cucujoidea, such as Protocucujidae and Helotidae – state (0); 6 pairs of spiracles in Brachypteridae – state (1); 5 pairs of spiracles in Coccinellidae and Endomychidae – state (2).

# 26. Male genital capsule formed: by abdominal segment IX and tergite VIII (0); by segment IX only (1). Both states of this character occur in members of the outgroups. A male genital capsule formed by abdominal segment IX, is found in Coccinellidae, Endomychidae and *Erimodes* (Protocucujidae). Polarity of this character is uncertain.

# 27. Sternite (IX) of male genital segment with lateral edges deeply, asymmetrically curved inwardly: absent (0); present (1). The deeply, asymmetrically curved inwardly lateral edges of the sternite of the male genital capsule is a unique character for some Epipocinae (Figs 686, 688) (*Epipocus*, *Epopterus*, *Anidrytus*)

# 28. Retracted aedeagus: with dorso-ventral position inside abdomen (0); lying on its side (1). Although the aedeagus resting on its side when retracted – state (1) – appears almost without exception in the cerylonid series, it also occurs in other cucujoid taxa (e.g. Protocucujidae). Polarity of this character is uncertain.

# 29. Aedeagus with median lobe: almost straight or curved (0); coiled (1). A coiled median lobe is characteristic for Eupsilobiinae (Figs 739, 740, 742).

# 30. Median lobe with T-shaped capsule: absent (0); present (1). A T-shaped capsule at the base of median lobe is characteristic for most Coccinellidae. Within Endomychidae it occurs in Eupsilobiinae. The distantly related outgroups, as well as most Endomychidae have the state character (0).

# 31. Median lobe with additional struts: present (0); absent (1). Additional struts on the median lobe are found in *Erimodes*, *Helota* and *Kateretes* – state (0). Coccinellidae and Endomychidae have median lobes without additional struts.

# 32. Median lobe with curled 1/3 of its basal part: absent (0); present (1). This character is unique for most Endomychinae (Figs 744–747) (except for *Endomychus*).

# 33. Ejaculatory duct of median lobe with large, bobbin-shaped gland: absent (0); present (1). This interesting structure is found only in some Epipocinae (*Danae*, *Saula* – Figs 750, 751).

# 34. Female genitalia with spiculum gastrale: present (0); absent (1). *Helota* and *Kateretes* have female genitalia with spiculum gastrale, while in *Erimodes*, Coccinellidae and Endomychidae the spiculum gastrale is absent, so the polarity of this character is uncertain.

# 35. Bursa copulatrix without infundibulum (0); with infundibulum-like structure (1); with infundibulum (2). Distantly related outgroups, as well as most Endomychidae, have the bursa copulatrix without a sclerotized infundibulum – state (0). This structure usually occurs in Coccinellidae and incidentally in Endomychidae (*Stethorhanis* – Fig. 787). The infundibulum-like structure is a unique character for Eupsilobiinae (Figs 788–790).

# 36. Ovipositor with coxities: distinct, separated (0); fused (1). Fused coxities is a unique character for Lycoperdininae (figs 802, 803).

# 37. Bursa copulatrix with sperm duct attached: directly to spermatheca (0); to broad connection between spermatheca and accessory gland (1). The sperm duct attached to the broad connection between spermatheca and accessory gland (instead of directly to the spermatheca) is an unusual character found only in most Endomychinae (*Cyclotoma*, *Meilichius*, *Bolbomorphus*, *Eucteanus* – Figs 792–795) and *Stenotarsus* (Fig. 800).

# 38. Ovipositor with deeply divided basal part of coxities: absent (0); present (1). This character is unique for some Epipocinae (*Danae*, *Saula*, *Stenotarsus* – Figs 798–800).

# 39. Pronotum with lateral raised margins: absent (0); present (1). Distantly related outgroups and most Coccinellidae, have the pronotum without lateral raised margins – state (0). These margins occur in some Epipocinae, Mycetaeinae, Anamorphinae (within Endomychidae) and in *Carinodulina* (Coccinellidae).

Table I. Data matrix used in the cladistic analyses. Character numbered as in the text "characters, discussion and polarity decisions". Characters not examined are marked with "?".

	1 1 1 1 1 1 1 1 1 2 2 2 2 2 2 2 2 3 3 3 3 3 3 3 3 3 3																																																	
	0	1	2	3	4	5	6	7	8	9	0	1	2	3	4	5	6	7	8	9	0	1	2	3	4	5	6	7	8	9	0	1	2	3	4	5	6	7	8	9										
<i>Ericmodes</i>	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0								
<i>Helota</i>	0	0	0	0	1	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0						
<i>Kateretes</i>	0	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0					
<i>Coccinella</i>	0	0	0	0	0	1	1	0	0	0	0	1	0	0	0	1	0	0	1	0	0	1	1	0	1	2	1	2	1	0	1	0	1	1	0	0	1	2	0	0	0	0	0	0						
<i>Scymnus</i>	0	0	0	0	0	1	1	0	0	0	0	1	0	0	0	1	0	0	1	0	0	1	1	0	1	2	1	2	1	0	1	0	1	1	0	0	1	0	0	0	0	0	0	0						
<i>Coccidula</i>	0	0	0	0	0	1	1	0	0	0	0	1	0	0	0	1	0	0	1	0	0	1	1	0	1	2	1	2	1	0	1	0	1	1	0	0	1	0	0	0	0	0	0	0						
<i>Chilocorus</i>	0	0	0	0	0	1	1	0	0	0	0	1	0	0	0	1	0	0	1	0	0	1	1	0	1	2	1	2	1	0	1	0	1	1	0	0	1	0	0	0	0	0	0	0	0					
<i>Epilachna</i>	0	0	0	0	0	1	1	0	0	0	0	1	0	0	0	1	0	0	1	0	0	1	1	0	1	2	1	2	1	0	1	0	1	1	0	0	1	0	0	0	0	0	0	0	0					
<i>Sukunahikona</i>	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	1	0	1	2	1	2	1	0	1	0	1	1	0	0	1	0	0	0	0	0	0	0	0					
<i>Carinodulina</i>	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	1	0	2	3	0	2	1	0	1	0	0	1	0	0	1	0	0	0	0	0	0	0	1					
<i>Holoparamesus</i>	0	1	0	1	0	0	0	0	1	0	0	0	0	1	0	0	1	0	1	2	0	0	2	3	0	2	1	0	1	0	0	1	0	0	1	0	0	1	0	0	0	0	0	0	0	0				
<i>Merophysia</i>	0	0	0	2	0	0	2	2	1	0	0	0	0	1	0	1	1	0	1	2	0	0	2	3	0	2	1	0	1	0	0	1	0	0	1	0	0	1	0	0	0	0	0	0	0	0				
<i>Displotera</i>	0	0	0	2	0	0	2	2	1	0	0	0	0	1	0	1	1	0	1	2	1	0	2	3	0	2	1	0	1	0	0	1	0	0	1	0	0	1	0	0	0	0	0	0	0	0				
<i>Leiestes</i>	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	1	0	1	0	0	1	1	0	2	1	0	1	0	0	1	0	0	1	0	0	0	0	0	0				
<i>Panamomus</i>	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	1	0	1	0	0	1	1	0	2	1	0	1	0	0	1	0	0	1	0	0	0	0	0	0				
<i>Rhanidea</i>	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	1	0	1	0	0	1	1	0	2	1	0	1	0	0	1	0	0	1	0	0	0	0	0	0				
<i>Phymaphora</i>	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	1	0	1	0	0	1	1	0	2	1	0	0	0	0	1	0	0	1	0	0	0	0	0	0				
<i>Stethorhanis</i>	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	1	0	1	0	0	1	1	0	2	1	0	1	0	0	1	0	0	1	2	0	0	0	0	0				
<i>Panaleies</i>	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	1	0	1	0	0	1	1	0	2	1	0	1	0	0	1	0	0	1	0	0	0	0	0	0	0			
<i>Microxenus</i>	0	0	0	1	0	0	0	2	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	1	0	1	1	0	2	1	0	1	1	1	1	0	0	1	1	0	0	0	0	0				
<i>Eidoreus</i>	0	0	0	1	0	0	0	2	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	1	0	1	1	0	2	1	0	1	1	1	1	0	0	1	1	0	0	0	0	0				
<i>Adamia</i>	0	0	0	1	0	0	0	2	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	1	0	1	1	0	2	1	0	1	1	1	1	0	0	1	1	0	0	0	0	0				
<i>Endomychus</i>	0	1	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	2	0	2	1	0	1	0	0	1	0	0	1	0	0	0	0	0			
<i>Cyclotoma</i>	0	1	0	1	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	2	0	2	1	0	1	0	0	1	1	0	1	0	0	1	0	0			
<i>Meilichius</i>	0	1	0	1	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	2	0	2	1	0	1	0	0	1	1	0	1	0	0	1	0	0			
<i>Bolbomorphus</i>	0	1	0	1	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	2	0	2	1	0	1	0	0	1	1	0	1	0	0	1	0	0			
<i>Eucteanus</i>	0	1	0	1	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	2	0	2	1	0	1	0	0	1	1	0	1	0	0	1	0	0			
<i>Epipocus</i>	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	2	0	2	1	1	1	0	0	1	0	0	1	0	0	0	0	0			
<i>Epopterus</i>	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	2	0	2	1	1	1	0	0	1	0	0	1	0	0	0	0	0			
<i>Danae</i>	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	2	0	2	1	0	1	0	0	1	0	1	1	0	0	0	1	1			
<i>Saula</i>	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	2	0	2	1	0	1	0	0	1	0	1	1	0	0	0	1	0			
<i>Stenotarsus</i>	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	2	0	2	1	0	1	0	0	1	0	0	1	0	0	1	1	1			
<i>Perrisina</i>	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	2	0	2	1	0	1	0	0	1	0	0	??	??	??	??	??	1			
<i>Danascelis</i>	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	2	1	0	1	0	0	1	0	0	1	0	0	0	0	0			
<i>Lycoperdina</i>	1	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	2	0	2	1	0	1	0	0	1	0	0	1	0	1	0	0	0			
<i>Beccariola</i>	1	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	2	0	2	1	0	1	0	0	1	0	0	1	0	1	0	0	0			
<i>Aphorista</i>	1	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	2	0	2	1	0	1	0	0	1	0	0	1	0	1	0	0	0			
<i>Mycetaea</i>	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	2	1	0	1	0	0	1	0	0	1	0	0	0	0	0	1		
<i>Agaricophilus</i>	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	1	1	0	2	1	0	1	0	0	1	0	0	1	0	0	0	0	1
<i>Symbiotes</i>	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	2	2	0	0	1	1	0	2	1	0	1	0	0	1	0	0	0	0	1
<i>Mychothenus</i>	0	1	0	1	0	0	0	0	0																																									

#### 4. Results

The cladistic analysis based on unordered and unweighted characters resulted in 6 most parsimonious trees (L 78, C 65, RI 87) (Figs 837–842); their Nelsen consensus tree (Fig. 843) is chosen here as the preferred tree. The successive weighting which resulted in 7 trees did not fundamentally change the topology of the trees reaching the length 428, CI 83 and RI 93 – their Nelsen consensus tree (L 83, CI 78, RI 91) is shown in Fig. 844.

The aim of the analysis, as mentioned above in section 2.1, was the resolution of three major taxonomic problems concerning: the relationship between Endomychidae and Coccinellidae; the limits of Endomychidae as a monophyletic taxon; and the limits and relationships of endomychid suprageneric taxa. The progress made in the resolution of these three problems is discussed below.

\* Close relationship between Endomychidae and Coccinellidae, as sister groups, is strongly supported by the following characters: procoxal cavity externally open (# 16,1); tarsal formula 4-4-4 (# 22,1); abdomen with 5 pairs of functional spiracles (# 25,2) and median lobe without additional struts (# 31,1).

\* The monophyly of the family Endomychidae is supported by the presence of a fronto-clypeal ridge (# 3,1), antennal grooves usually absent, although they are present in Eupsilobiinae and Merophysiinae, and tarsi 4-segmented, simple (former Endomychinae, Lycoperdininae, Epipocinae and Xenomycetinae have tarsi 4-segmented, pseudotrimerous). Thus defined, the family includes all suprageneric taxa included in the most recent classification (Pakaluk *et al.* 1994 and Lawrence and Newton 1995), plus Acritosomatinae (Pakaluk and Ślipiński 1995). Apart from accepting the subfamilies which have traditionally been used in the classification of this family, the proper placement for the former Merophysiidae and Eupsilobiinae within Endomychidae is confirmed.

The major change made here with regard to the recent classification of the Endomychidae, concerns the limits of subfamilies within the family.

\* The preferred tree supports 12 major evolutionary lineages in Endomychidae, although the relationships between suprageneric taxa are unclear based on the present data. Because of the limitation of the character matrix, the problem of the relationships between endomychid suprageneric taxa needs further attention; more research with the inclusion of more taxa and larval characters is needed.

Some tendencies of the relationships between groups of endomychid genera are shown on the cladograms. In five of the resolutions, the Eupsilobiinae are shown to be the sister group to all remaining Endomychidae, a relationship which is supported here by head without antennal grooves (# 1,1). In most of the resolutions, the former Holoparamecinae, Merophysiinae, Pleganophorinae, Anamorphinae and Acritosomatinae appear to have con-

stant tendency to form a monophyletic group, supported by mesocoxal cavities narrowly closed outwardly (# 18,1), although they are widely closed in Anamorphinae (# 18,2), and by mesotrochantin concealed while mesocoxal cavity closed outwardly (#19,2). The former subfamilies Endomychinae, Lycoperdininae, Epipocinae and Xenomycetinae, form (on 3 cladograms) a large, separate group, although not supported by an apomorphy, because the character, 4-segmented, pseudotrimerous tarsi (#23,2), which unites these taxa is shared with most Coccinellidae. There is also a serious doubt about the direct relationship between Leiestinae and Mycetinae, as shown on the five cladograms, because mesotrochantin concealed while mesocoxal cavity open outwardly (# 19,1), common for both taxa, shows a lot of homoplasy. In the light of the above mentioned facts, it seems to be most reasonable to choose, as a preferred tree, the Nelsen consensus tree, with 12 well defined, monophyletic groups of endomychid genera, treated here as the subfamilies.

The monophyly of the Endomychinae is supported by labium with prementum longer than wide – at least twice as long as mentum (# 9,1). The Anamorphinae and former Acritosomatinae form a monophyletic group, supported by mesocoxal cavity widely closed outwardly (# 18,2). The Pleganophorinae are supported by 4- or 5-segmented antenna (# 2,1). Former Holoparamecinae and Merophysiinae form a monophyletic group, recognized here as the Merophysiinae, which are defined by labial palpomere 2 oval, inflated (# 8,1). The Lycoperdininae are defined by head with occipital file (# 0,1) and ovipositor with fused coxities (# 36,1). Former Epipocinae are divided into two monophyletic subfamilies: Stenotarsinae, supported by ovipositor with deeply divided basal part of coxities (# 38,1) and Epipocinae, supported by sternite of male genital segment with lateral edges deeply, asymmetrically curved inwardly (# 27,1). Danascelinae, subfamily nov. is proposed here for *Danascelis*, which was formerly placed by the present author within an expanded Epipocinae (Tomaszewska 1999), based mainly upon the shape of the male antennal club (similar to *Danae* and *Tragoscelis*). Cladistic analysis supports *Danascelis* as a separate, monophyletic taxon, defined by two apomorphies: male antennomere 9 with a tuft of long setae in a deep concavity on the inner edge and the base of pronotum with two pairs of deep, oval cavities provided with pits. The monophyly of the Eupsilobiinae is supported by aedeagus with coiled median lobe (# 29,1) and an ovipositor with infundibulum-like structure (# 35,1). The Mycetinae are defined by a labium with the mentum provided with a small, triangular, setose convexity, placed medially. The mesosternum with a boat-shaped intercoxal process is a synapomorphy for Leiestinae. Finally, the monogeneric Xenomycetinae is defined by the male ventrite 5 which is provided with a prominently elevated, elongate, median tubercle with a cone-shaped tubercle on each side, as an autapomorphy for *Xenomycetes*.

## PROPOSED CLASSIFICATION OF ENDOMYCHIDAE

### 1. Classification of suprageneric taxa

A proposed classification of Endomychidae, according to the evolutionary lineages obtained and shown on the preferred cladogram is given below. However, the limitations of the size of the data set and the preliminary character of the analysis must be kept in mind.

1. Subfamily: Danascelinae, **subfam. nov.**
2. Subfamily: Xenomycetinae Strohecker, 1962
3. Subfamily: Endomychinae Leach, 1815
4. Subfamily: Anamorphinae Strohecker, 1953
5. Subfamily: Merophysinae Seidlitz, 1872
6. Subfamily: Lycoperdininae Redtenbacher, 1844
7. Subfamily: Stenotarsinae Chapuis, 1876
8. Subfamily: Epipocinae Gorham, 1873
9. Subfamily: Eupsilobiinae Casey, 1895
10. Subfamily: Pleganophorinae Jacquelin du Val, 1858
11. Subfamily: Mycetaeinae Jacquelin du Val, 1857
12. Subfamily: Leiestinae Thomson, 1863

### 2. Key to the subfamilies of Endomychidae

1. Head with short antennal grooves, not extending to posterior edge of eyes (Figs 20, 22, 24); aedeagus with median lobe coiled, provided with T-shaped capsule at the base (Figs 739, 740, 742) . . . . . **Eupsilobiinae**
- . Antennal grooves on head absent, or rarely long, extending beyond posterior edge of eyes (Figs 4, 6); aedeagus with median lobe almost straight or curved, T-shaped capsule absent . . . . . 2
2. Mesocoxal cavities closed outwardly by sterna (Figs 389, 390, 426) . . . . . 3
- . Mesocoxal cavities open outwardly (Figs 392, 401, 404) . . . . . 5
3. Antenna 4–5 segmented (in female rarely 7-segmented), with apical antennomere greatly enlarged (Figs 106, 107, 108) . . . . . **Pleganophorinae**
- . Antenna 7–11 segmented; apical antennomere not modified . . . . . 4
4. Labial palpomere 2 oval, inflated (Figs 243, 244, 245); mesocoxal cavities narrowly closed outwardly (Figs 389, 390, 391) . . . . . **Merophysinae**
- . Labial palp with palpomere 2 subcylindrical or transverse (Figs 271–274); mesocoxal cavities widely closed outwardly (Figs 426, 427) . . . . . **Anamorphinae**
5. Mesotrochantin concealed; procoxal cavity with oval slit antero-laterally (Figs 286, 334) . . . . . 6
- . Mesotrochantin at least partially exposed; procoxal cavity without oval slit . . . . . 7
6. Mesosternum bicarinate with intercoxal process boat-shaped (Figs 392–397); lateral sulci on pronotum strongly marked; antennal insertions not visible from above; labium with mentum flat . . . . . **Leiestinae**
- . Mesosternum almost flat (Figs 422, 424); lateral sulci on pronotum absent or hardly visible; antennal insertions visible from above; mentum with small, triangu-

- lar, setose projection, medially (Figs 269, 270) . . . . . **Mycetaeinae**
6. Tarsi 4-segmented, simple (Fig. 596); base of pronotum with two pairs of deep, oval cavities provided with pits (Fig. 325); antennomere 9 of male greatly enlarged, provided with tuft of long setae in deep concavity on inner edge (Fig. 97); body less than 3 mm length (2.50–2.80 mm) . . . . . **Danascelinae**
  - . Tarsi pseudotrimerous (Figs 582, 584); pronotum sometimes with single pits on sides of basal sulcus (Figs 303, 313, 323); antennomere 9 of male antenna rarely enlarged, but without similar tuft of setae (Fig. 93); body more than 3 mm length (3.0–14.0 mm) . . . . . 8
  8. Head with occipital file (Figs 50, 52); anterior margin of the pronotum usually with stridulatory membrane (Fig. 327); ovipositor at least partially fused (Figs 802, 803) . . . . . **Lycoperdininae**
  - . Head without occipital file, although sometimes with fine microsculpture; stridulatory membrane on the pronotum absent; ovipositor with coxities separated . . . . . 9
  9. Labium with the prementum longer than wide, at least twice as long as mentum, ligula almost always indistinct (Figs 255–259); aedeagus with median lobe usually curled along  $\frac{1}{3}$  of its basal length (Figs 744–747) . . . . . **Endomychinae**
  - . Labium with the prementum transverse, at most weakly longer than mentum (Figs 260–265, 277), ligula distinct, usually membranous; basal part of median lobe simple . . . . . 10
  10. Lateral margins of the pronotum hardly bordered; sternite (IX) of the male genital segment with lateral edges deeply asymmetrical (Figs 686, 688); median lobe heavily sclerotized, usually ramificate apically (Figs 748, 749) . . . . . **Epipocinae**
  - . Lateral margins of the pronotum distinctly bordered or/and with raised margins (Figs 317, 321); sternite (IX) of the male genital segment with lateral edges not modified (Figs 690, 696, 716); median lobe moderately sclerotized, without apical ramification (Figs 750–753, 764) . . . . . 11
  11. Pronotum usually with lateral raised margins (Figs 317, 321, 323); body covered with dense and usually long setae; ovipositor with basal part of coxities deeply divided (Figs 798–800) . . . . . **Stenotarsinae**
  - . Pronotum widely bordered laterally and anteriorly (Fig. 348); body hardly setose; basal part of coxities entire (Fig. 812); (ventrite 5 in male with characteristic tubercles (Fig. 656, mesosternum strongly carinate (Fig. 435)) . . . . . **Xenomycetinae**

## DEFINITIONS OF THE FAMILY AND SUBFAMILIES OF ENDOMYCHIDAE

Definitions for the higher-level taxa used in the classification proposed above are provided below with brief

discussion of apomorphic (A), plesiomorphic (P) and homoplastic characters (H).

All genera examined during this project, are included in the proper subfamilies. A provisional classification, based on published data and personal observations, is given for the remaining genera; probably some of them will need to be reallocated.

#### Endomychidae

Head without antennal grooves (A) – this character is common within Endomychidae, except for Eupsilobiinae which have short antennal grooves, and for *Merophysia* and *Displotera* (Merophysiinae) where long antennal grooves are present; fronto-clypeal ridge present, straight or weakly curved (A), although strongly curved or obtusely angled ridge occurs in *Merophysia* and *Displotera*; tentorium with anterior arms meeting medially (H) – this character is common within Endomychidae, except for most Anamorphinae, where the anterior arms of the tentorium are separated.

#### Danascelinae

Male antenna with antennomere 9 provided with tuft of long setae in deep concavity on inner edge (A); each side of the pronotal basal sulcus with a pair of deep, oval cavities provided with pits (A).

Note. A well defined, monophyletic taxon, proposed here as a new subfamily.

Genus included: *Danascelis* Tomaszewska.

#### Xenomycetinae

Ventrite 5 in male, with prominently elevated, elongate, median tubercle with cone-shaped tubercle on each side (A); tarsi 4-segmented, distinctly pseudotrimerous (H).

Genus included: *Xenomycetes* Horn.

#### Endomychinae

Labium with prementum quadrate, or longer than wide – at least twice as long as mentum (A); tarsi 4-segmented, pseudotrimerous (H); ligula indistinct, whole prementum evenly sclerotized (A) but a submembranous ligula is present in *Endomychus*; aedeagus with median lobe curled along 1/3 of its basal part (A); ovipositor with ejaculatory duct attached to broad connection between spermatheca and accessory gland (H) but the last two characters do not occur in *Endomychus*.

Genera included: *Endomychus* Panzer, *Cyclotoma* Mulsant, *Meilichius* Gerstaecker, *Bolbomorphus* Gorham, *Eucteanus* Gerstaecker.

#### Anamorphinae

Tentorium with anterior arms separate (H); meso-coxal cavity widely closed outwardly by sterna (A); mesotrochantin concealed (H); claws modified (H).

Note. The group includes former Anamorphinae and Acritosomatinae. The concept of the subfamily is similar to Mychotheninae (Sasaji, 1978a).

Genera included: *Symbiotes* Redtenbacher, *Erotenomychus* Lea, *Acritosoma* Pakaluk and Ślipiński (former Acritosomatinae), *Mychothenus* Strohecker, *Micropsephodes* Champion, *Anamorphus* LeConte.

Genera probably referred to Anamorphinae: *Bystodes* Strohecker, *Bystus* Guérin, *Dexialia* Sasaji,

*Dialexia* Gorham, *Idiophyes* Blackburn, *Malagaricophilus* Strohecker, *Erysma* Gorham, *Clemmus* Hampe, *Bryodryas* Strohecker, *Baeochelys* Strohecker, *Anagarricophilus* Arrow, *Geoendomychus* Lea, *Afralexia* Strohecker, *Anamycetaea* Strohecker, *Asymbius* Gorham, *Coryphus* Csiki, *Rhymbomicrus* Casey, *Parasymbius* Arrow, *Endocoelus* Gorham, *Papuella* Strohecker.

#### Merophysiinae

Labial palp with palpomere 2 oval, inflated (A); meso-coxal cavity narrowly closed outwardly (H); mesotrochantin concealed (H); tarsal formula 3-3-3 (H); tarsi 3-segmented, simple (H); pronotum with prebasal tubercles and/or carinae (A) but absent in *Merophysia* and *Displotera*; mandible with prosthema provided with apical, sclerotized, elongate projections (A); prosternum with antennal grooves (A) but the two former character do not occur in *Holoparamecus*; head with antennal grooves (H) although in *Holoparamecus* antennal grooves absent; fronto-clypeal ridge strongly curved or obtusely angled (P) – within Endomychidae, this character occurs only in *Merophysia* and *Displotera*; mentum with large, triangular, raised area (H) but in *Holoparamecus* the mentum is flat.

Note. The group includes former Holoparamecinae and Merophysiinae.

Genera included: *Holoparamecus* Curtis, *Merophysia* Lucas, *Displotera* Reitter.

Genera probably referred to Merophysiinae: *Latrapion* Rucker, *Pythlarhinus* Dajoz, *Loebliia* Dajoz, *Hexasternum* Rucker, *Cholovocera* Motschulsky, *Reitteria* Leder, *Coluocera* Motschulsky, *Evolocera* Sharp.

#### Lycoperdininae

Head with occipital file (A); tarsi 4-segmented, distinctly pseudotrimerous (H); ovipositor with fused coxities (A); anterior margin of pronotum with stridulatory membrane (A), lost in *Beccariola*.

Genera included: *Lycoperdina* Latreille, *Aphorista* Gorham, *Trycherus* Gerstaecker, *Archipines* Strohecker (former Epipocinae), *Beccariola* Arrow, *Dapsa* Latreille.

Genera probably referred to Lycoperdininae: *Hylaia* Guérin, *Ancylopus* Costa, *Encymon* Gerstaecker, *Indalmus* Gerstaecker, *Cymones* Gorham, *Haploscelis* Blanchard, *Dryadites* Frivaldszky, *Acinaces* Gerstaecker, *Amphix* Castelnau, *Cymbachus* Gerstaecker, *Polymus* Mulsant, *Mycetina* Mulsant, *Pseudindalmus* Arrow, *Parindalmus* Achard, *Engonius* Gerstaecker, *Eumorphus* Weber, *Brachytrycherus* Arrow, *Stictomela* Gorham, *Spathomeles* Gerstaecker, *Amphisternus* Germar, *Cacodaemon* Thomson, *Malindus* Villiers, *Sinocymbachus* Strohecker and Chûjô, *Callimodapsa* Strohecker, *Avencymon* Strohecker, *Amphistethus* Strohecker, *Ohtaius* Chûjô, *Chetryrus* Villiers, *Platindalmus* Strohecker, *Microtrycherus* Pic.

#### Stenotarsinae

Tarsi 4-segmented, distinctly pseudotrimerous (H); ovipositor with basal part of coxities deeply divided (A);

pronotum with lateral raised margins (H), although they are absent in *Saula*.

Genera included: *Danae* Reiche, *Saula* Gerstaecker, *Stenotarsus* Perty, *Perrisina* Strand.

Genera probably referred to Stenotarsinae: *Chondria* Gorham, *Ectomychus* Gorham, *Africansaula* Pic, *Paniegena* Heller, *Tragoscelis* Strohecker.

#### Epipocinae

Sternite (IX) of male genital segment with lateral edges deeply, asymmetrically curved inwardly (A); tarsi 4-segmented, distinctly pseudotrimerous (H); lateral edges of pronotum hardly bordered (H).

Genera included: *Epipocus* Germar, *Epopteris* Chevrolat, *Anidrytus* Gerstaecker.

Genera probably referred to Epipocinae: *Ephebus* Gerstaecker.

#### Eupsilobiinae

Head with antennal grooves (H); labium with mentum provided with large, triangular, raised area (H); metasternum with femoral lines (H); aedeagus with median lobe coiled (A); median lobe with T-shaped capsule at base (H), a unique structure within Endomychidae, but characteristic for most Coccinellidae; ovipositor with infundibulum-like structure (A).

Genera included: *Microxenus* Wollaston, *Eidoreus* Sharp, *Adamia* gen. nov.

Genera probably referred to Eupsilobiinae: *Chileolobius* Pakaluk and Ślipiński, *Ibicarella* Pakaluk and Ślipiński, *Cerasommatidia* Brèthes.

#### Pleganophorinae

Antenna 4–5 segmented (A); mesocoxal cavity narrowly closed outwardly (H); mesotrochantin concealed (H).

Note. Females of a few species of *Trochoideus* have 7-segmented antenna.

Genera included: *Pleganophorus* Hampe, *Trochoideus* Westwood.

Genera probably referred to Pleganophorinae: *Dadocerus* Arrow.

#### Mycetaeinae

Mentum with small, triangular, setose convexity, situated medially (A); mesotrochantin concealed while mesocoxal cavity open outwardly (H); pronotum with lateral raised margins (H).

Genera included: *Mycetaea* Stephens, *Agaricophilus* Motschulsky.

#### Leiestinae

Mesosternum bicarinate with intercoxal process boat-shaped (A); mesotrochantin concealed while mesocoxal cavity open outwardly (H).

Genera included: *Leiestes* Dejean, *Panamomus* Gorham, *Rhanidea* Strohecker, *Phymaphora* Newman, *Stethorhanis* Blaisdell, *Panaleies* Tomaszewska.

#### Genera incertae sedis

*Cyslemma* Dajoz, *Exysmodes* Dajoz, *Palaeoendomychus* Zhang, *Daulis* Erichson, *Daulotypus* Lea, *Atrichonota* Arrow.

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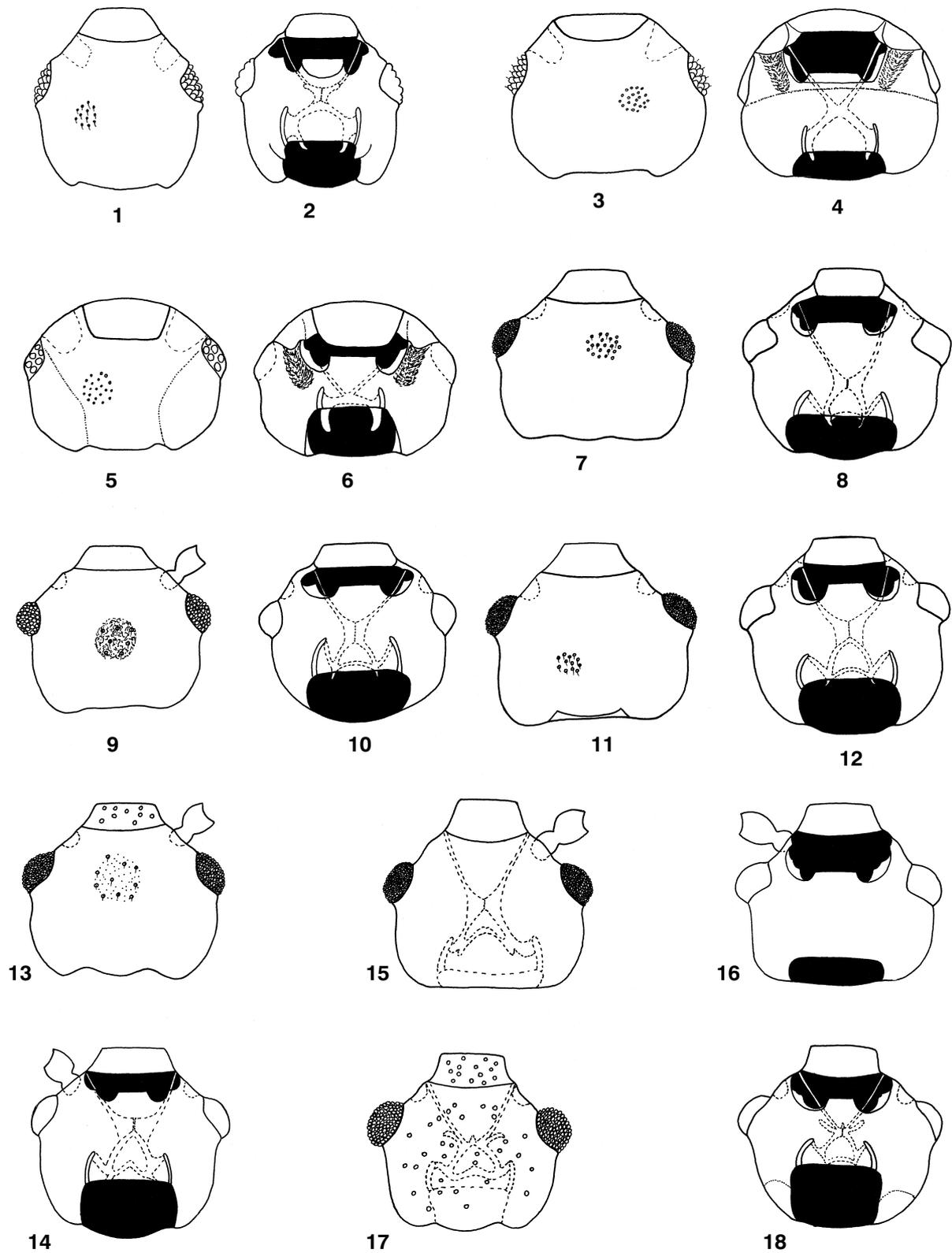
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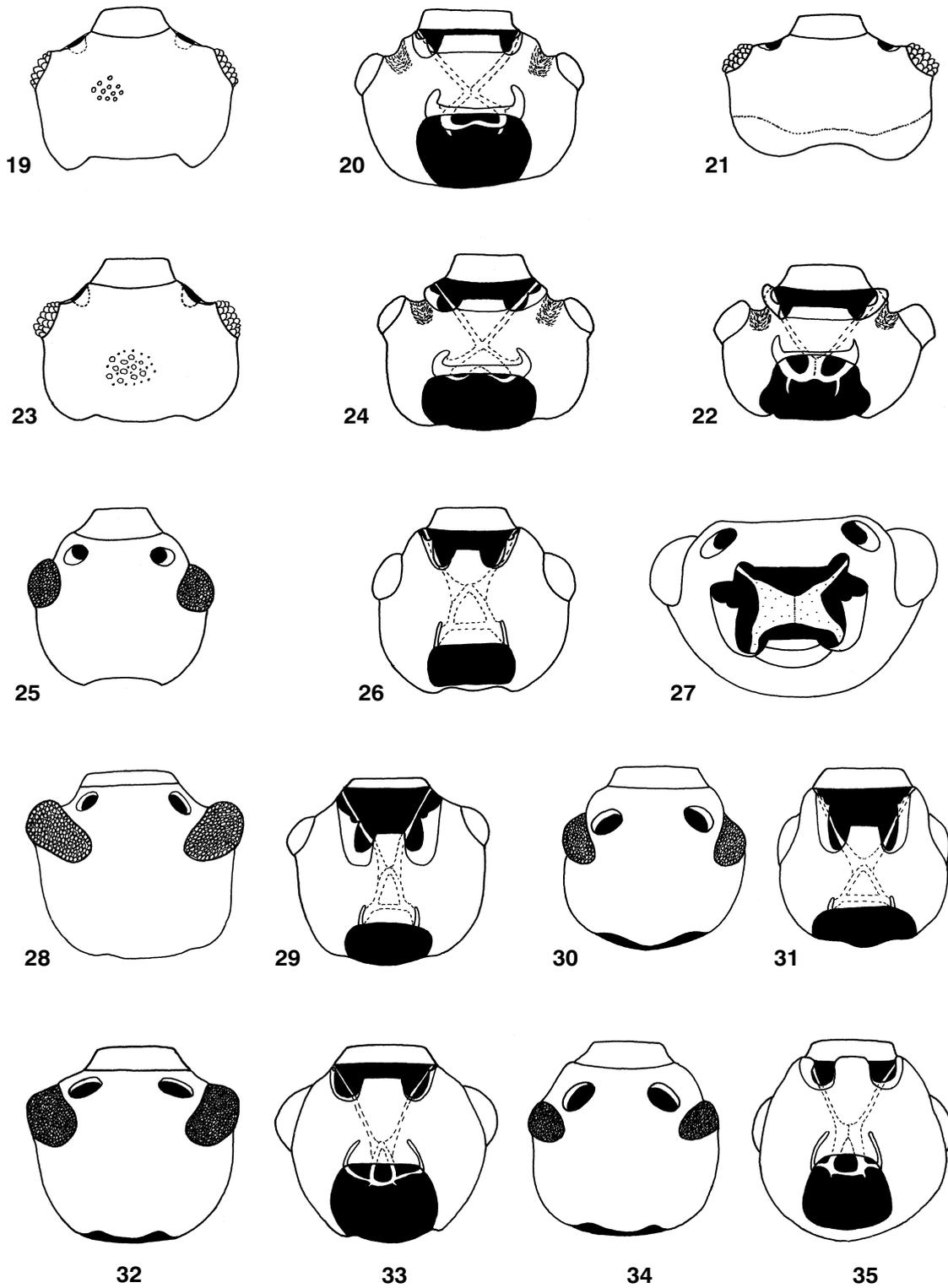
## INDEX OF GENERIC NAMES OF ENDOMYCHIDAE

Concerns the chapter: Morphology of investigated genera

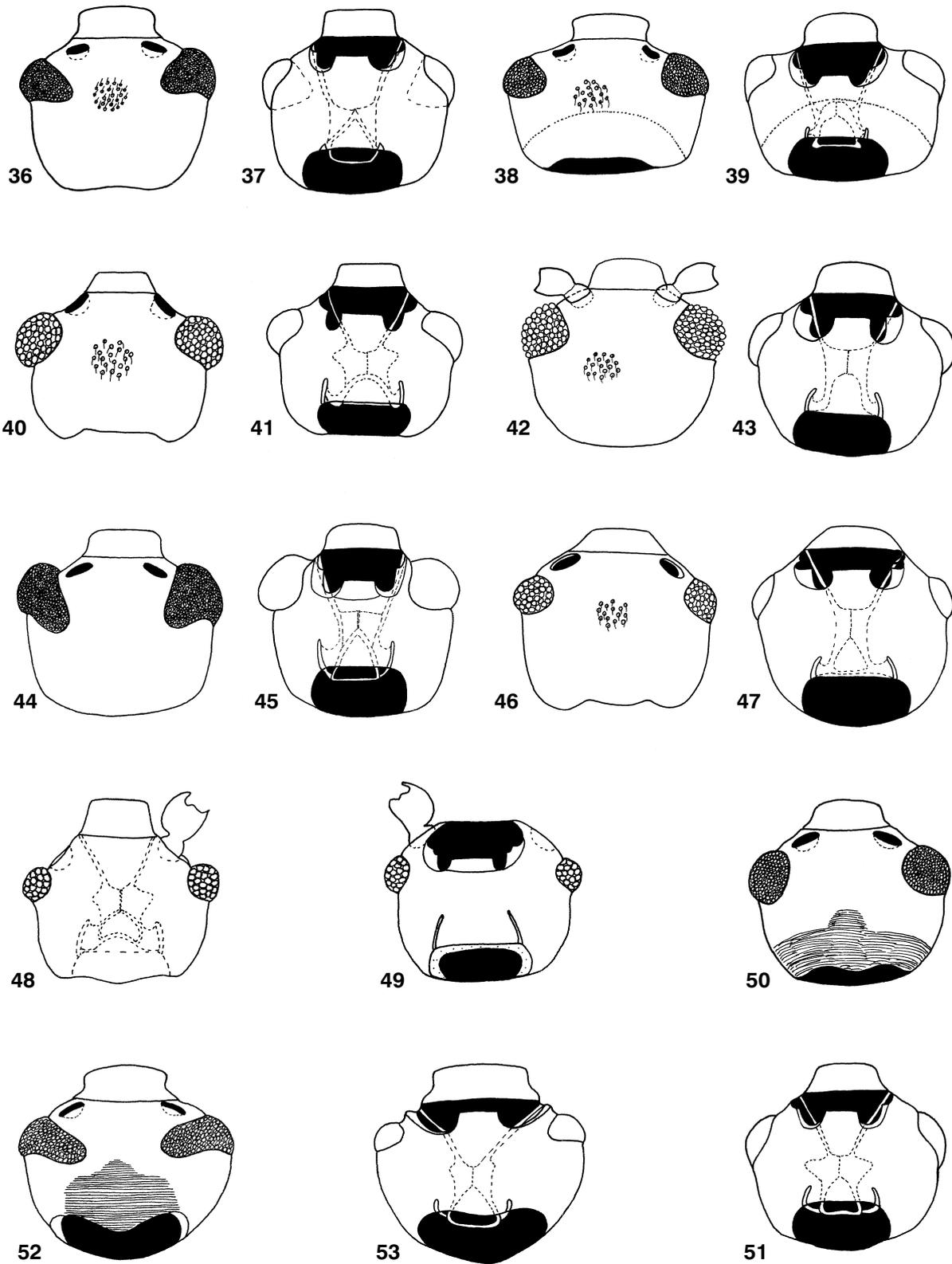
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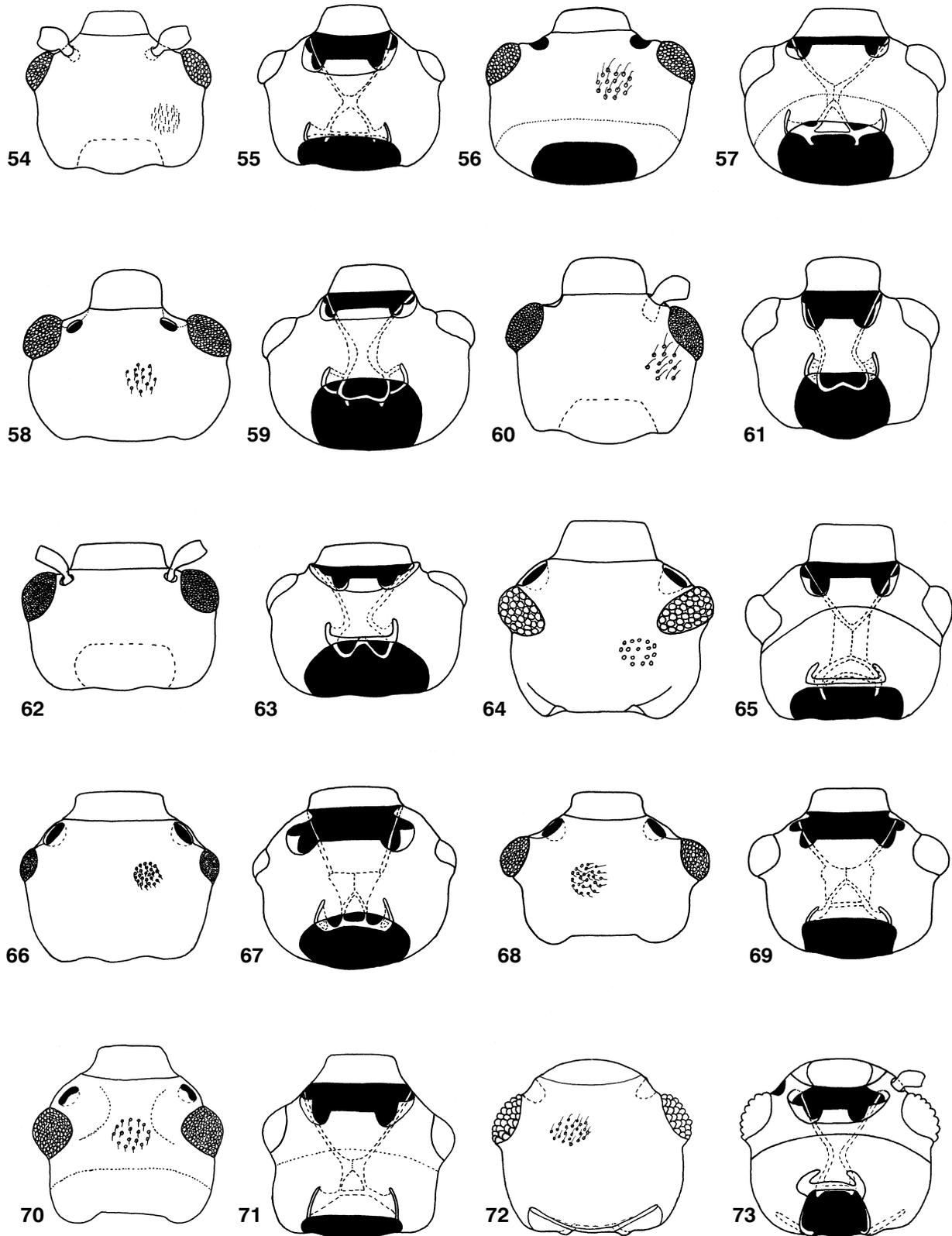
Figures 1–18. Head, dorsal and ventral: (1, 2) *Holoparamesus* sp.; (3, 4) *Merophysia* sp.; (5, 6) *Displotera beloni* Wasmann; (7, 8) *Leiestes seminiger* (Gyllenhal); (9, 10) *Panamomus lewisi* Gorham; (11, 12) *Rhanidea unicolor* (Ziegler); (13, 14) *Stethorhanis borealis* Blaisdell; (15, 16) *Phymaphora pulchella* Newman; (17, 18) *Panaleies decoratus* (Gorham).



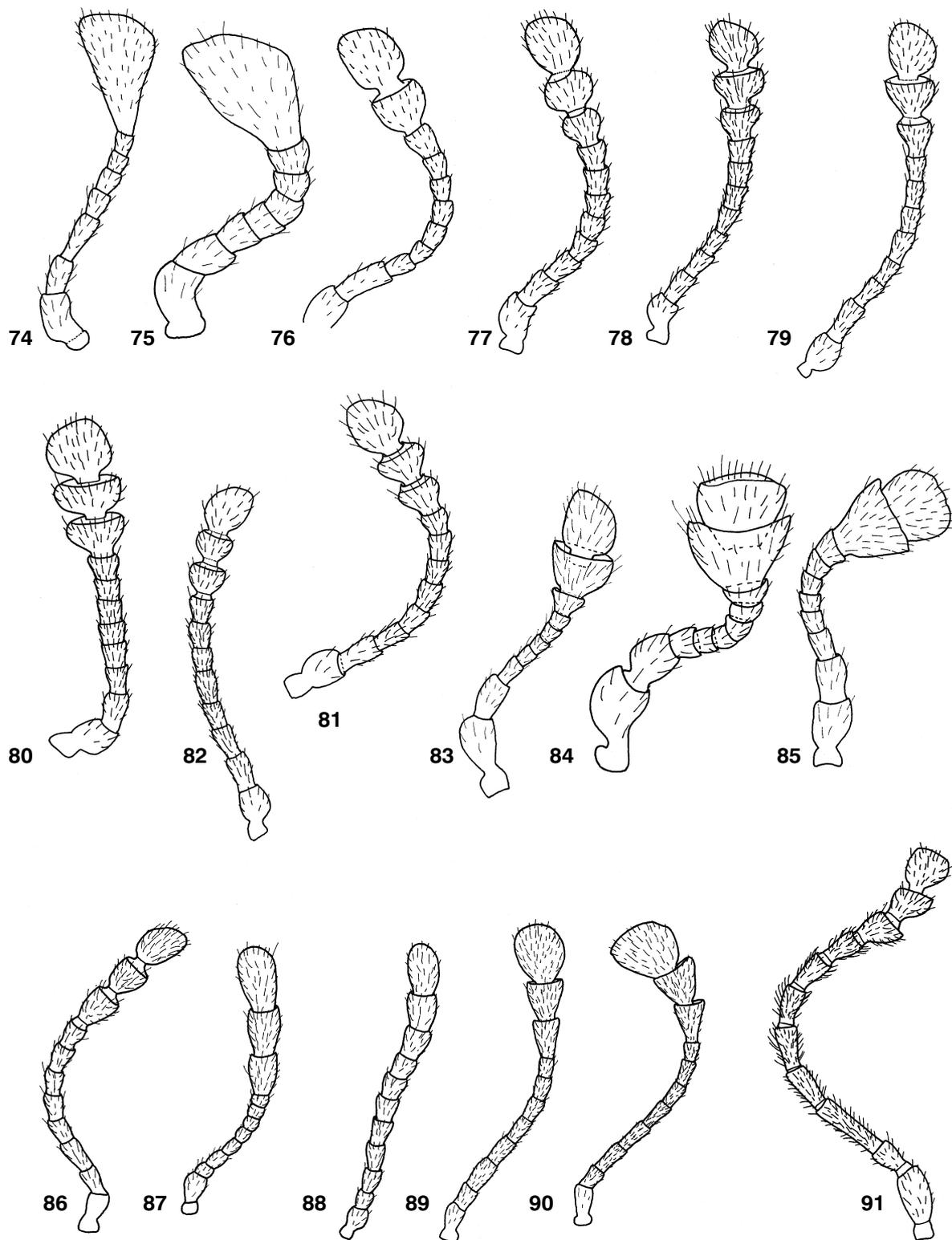
Figures 19–35. 19–26, 28–35. Head, dorsal and ventral; 27. Head, anterior view. (19, 20) *Microxenus laticollis* Wollaston; (21, 22) *Eidoreus minutus* Sharp; (23, 24) *Adamia mexicana* sp. nov.; (25, 26, 27) *Endomychus coccineus* (Linnaeus); (28, 29) *Cyelotoma* sp.; (30, 31) *Meilichius* sp.; (32, 33) *Bolbomorphus serpunctatus* Arrow; (34, 35) *Eucteanus* sp.



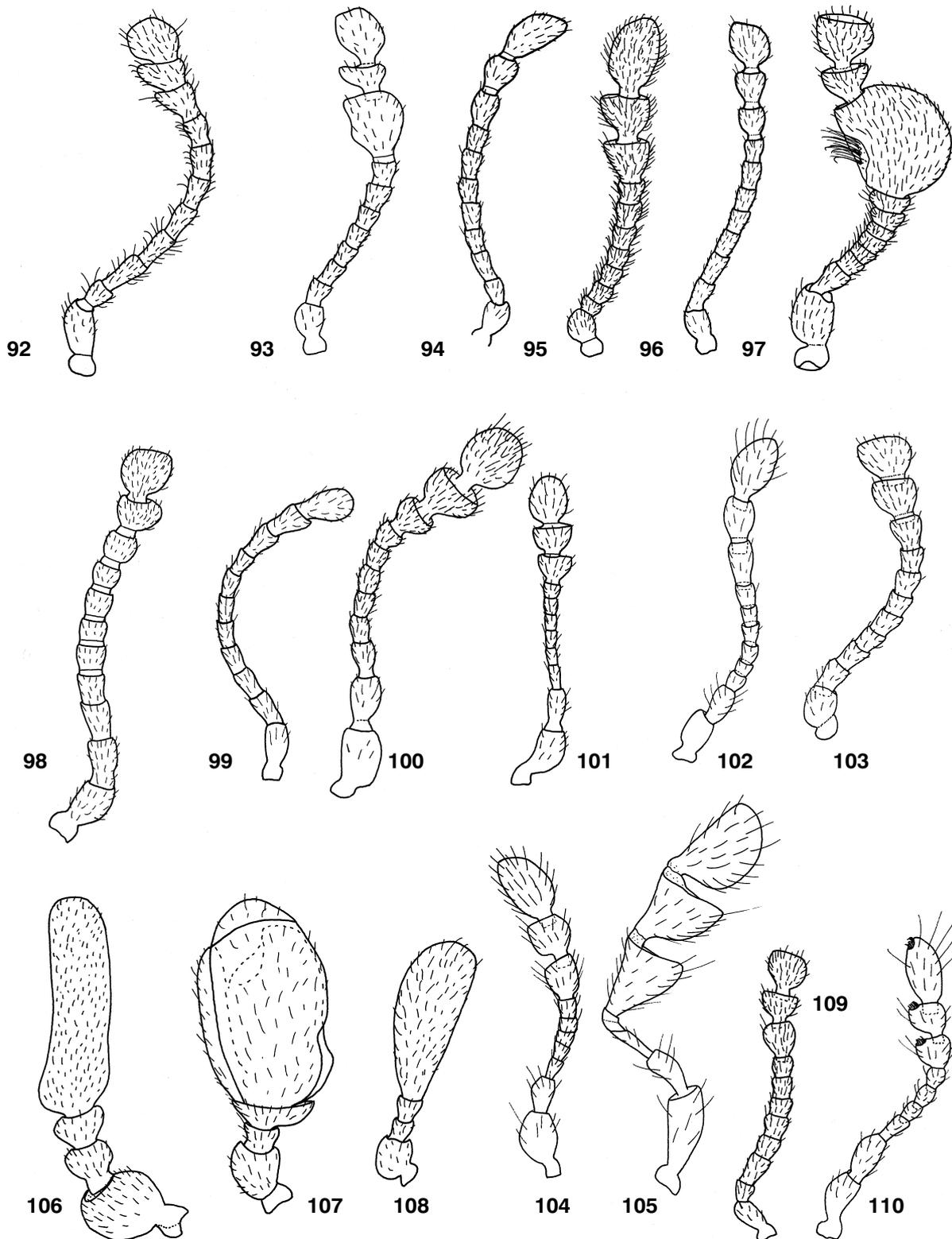
Figures 36–53. Head, dorsal and ventral: (36, 37) *Epipocus* sp.; (38, 39) *Epopteris* sp.; (40, 41) *Danae* sp.; (42, 43) *Saula* sp.; (44, 45) *Stenotarsus* sp.; (46, 47) *Perrisina brevis* (Perris); (48, 49) *Damascelis elongata* Tomaszewska; (50, 51) *Lycoperdina succincta* (Linnaeus); (52, 53) *Beccariola* sp.



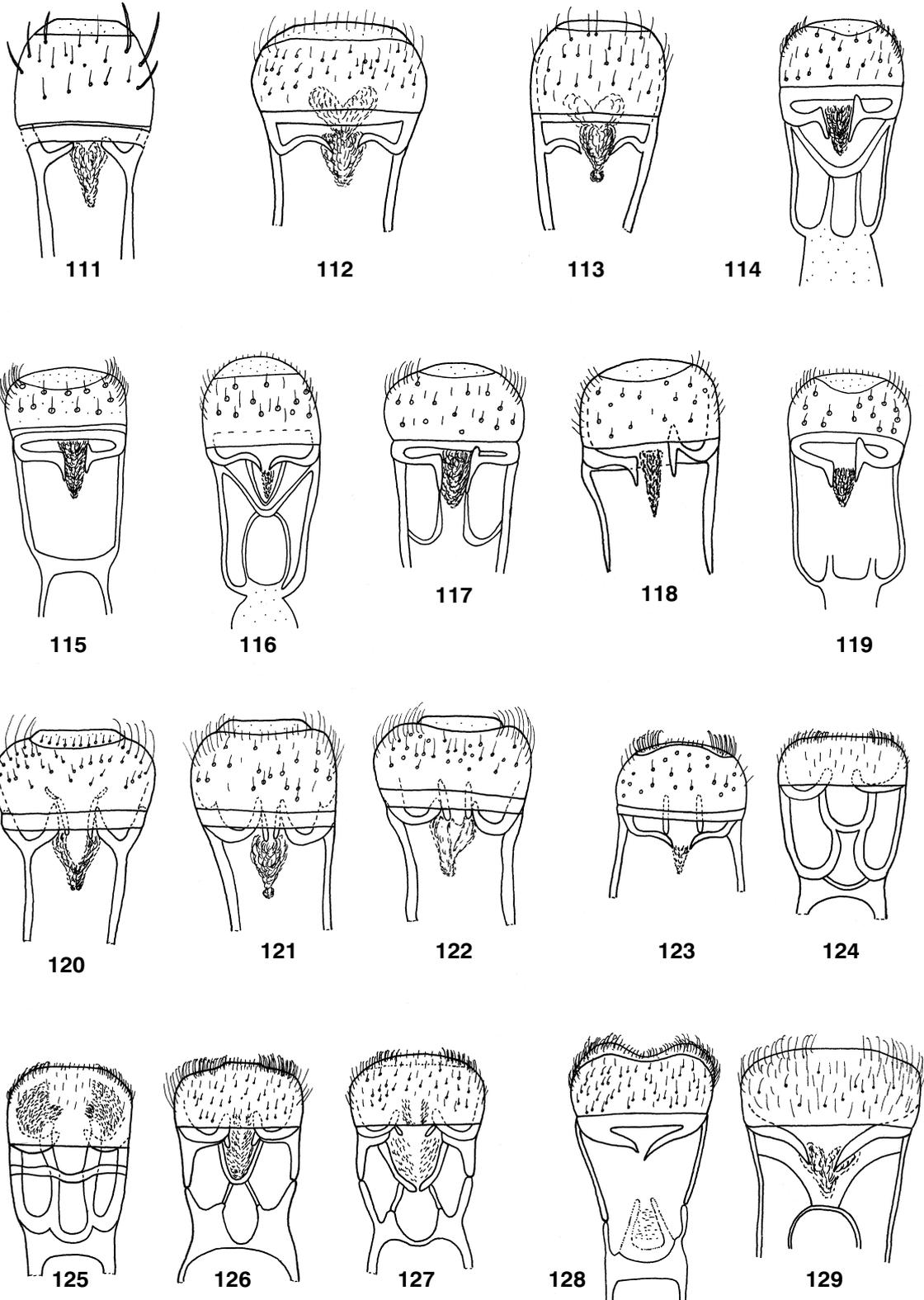
Figures 54–73. Head, dorsal and ventral: (54, 55) *Mycetaea subterranea* (Fabricius); (56, 57) *Agaricophilus reflexus* Motschulsky; (58, 59) *Symbiotes gibberosus* (Lucas); (60, 61) *Mychothenus asiaticus* Sasaji; (62, 63) *Micropsephodes serraticornis* Champion; (64, 65) *Erotendomychus lawrencei* sp. nov.; (66, 67) *Pleganophorus bispinosus* Hampe; (68, 69) *Trochoideus* sp.; (70, 71) *Xenomycetes morrisoni* Horn; (72, 73) *Acritosoma elongatum* Pakaluk and Ślipiński.



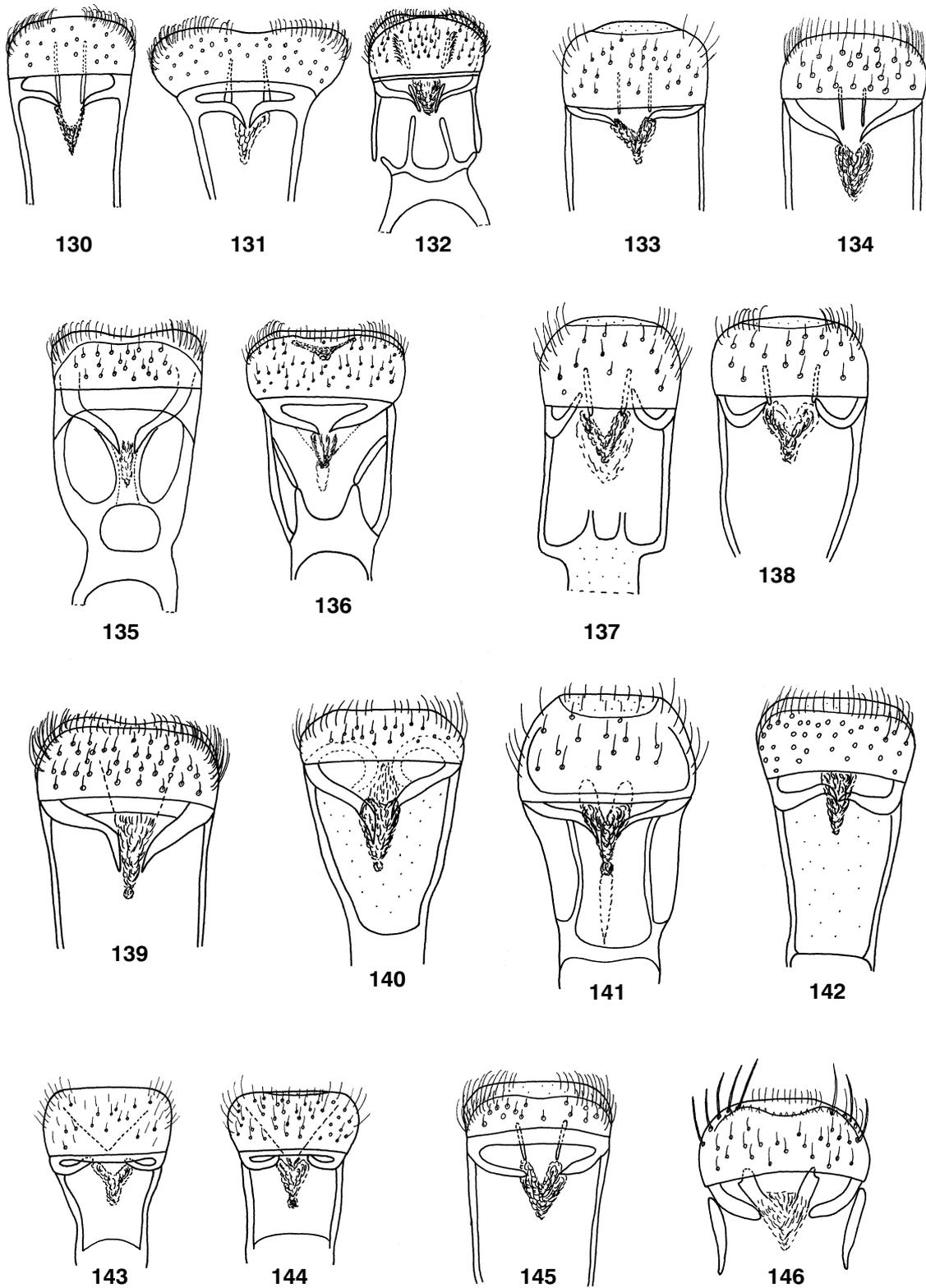
Figures 74–91. Antenna: (74) *Merophysia* sp.; (75) *Displotera beloni* Wasmann; (76) *Holoparamecus* sp.; (77) *Leiestes seminiger* (Gyllenhal); (78) *Panamomus lewisi* Gorham; (79) *Rhanidea unicolor* (Ziegler); (80) *Phymaphora putchella* Newman; (81) *Stethorhanis borealis* Blaisdell; (82) *Panaleies decoratus* (Gorham); (83) *Microxenus laticollis* Wollaston; (84) *Eidoreus minutus* Sharp; (85) *Adamia mexicana* sp. nov.; (86) *Endomychus coccineus* (Linnaeus); (87) *Cyclotoma* sp.; (88) *Meilichius* sp.; (89) *Bolbomorphus sexpunctatus* Arrow; (90) *Eucteanus* sp.; (91) *Epipocus* sp.



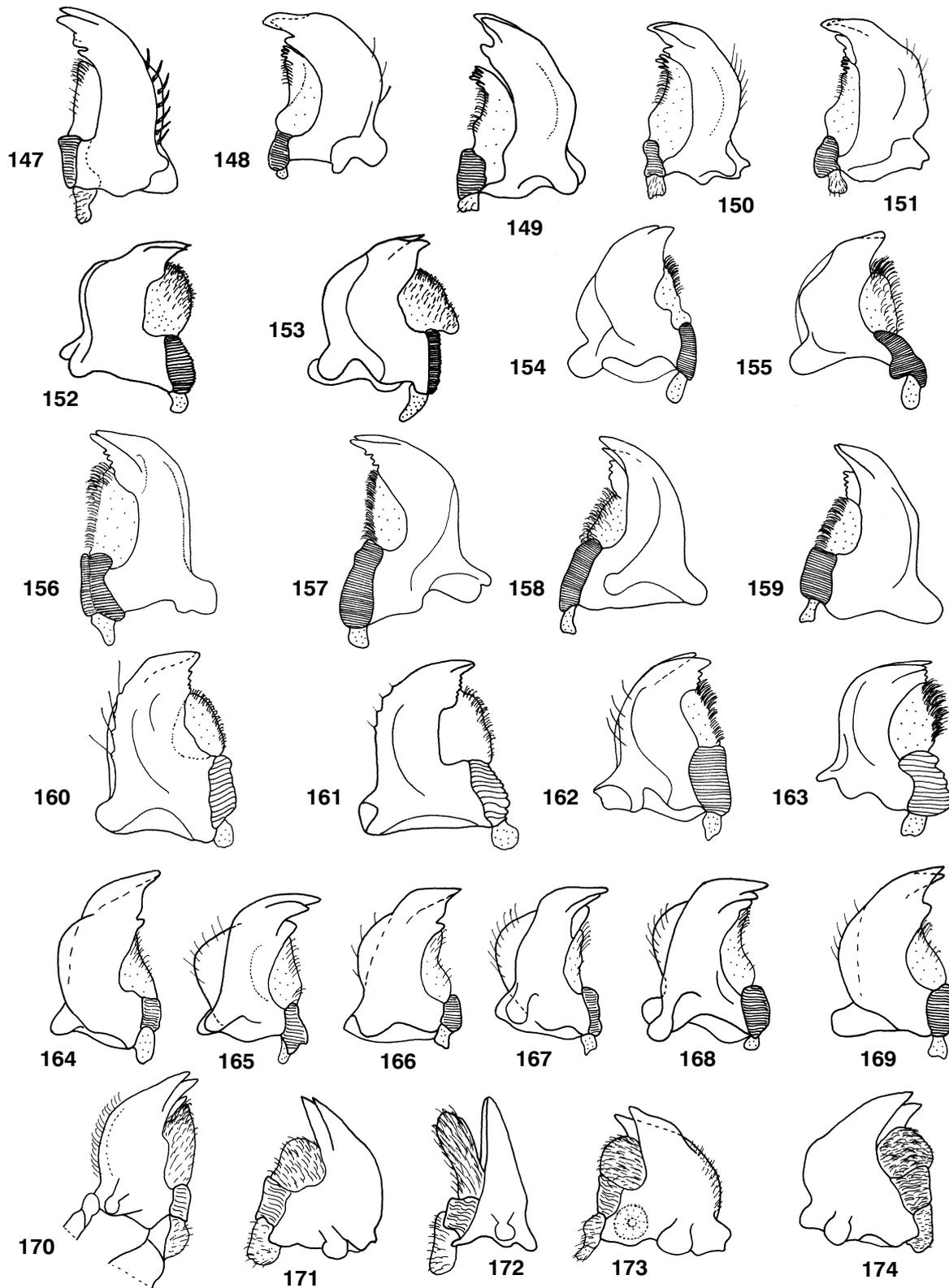
Figures 92–110. Antenna: (92) *Epopteris* sp.; (93) *Danae* sp.; (94) *Saula* sp.; (95) *Stenotarsus* sp.; (96) *Perrisina brevis* (Perris); (97) *Danascelis elongata* Tomaszewska; (98) *Lycoperdina succincta* (Linnaeus); (99) *Beccariola* sp.; (100) *Mycetaea subterranea* (Fabricius); (101) *Agaricophilus reflexus* Motschulsky; (102) *Symbiotes gibberosus* (Lucas); (103) *Erotendomychus lawrencei* sp. nov.; (104) *Mychothenus asiaticus* Sasaji; (105) *Micropsephodes seraticornis* Champion; (106) *Pleganophorus bispinosus* Hampe; (107, 108) *Trochoideus* sp.; (109) *Xenomycetes morrisoni* Horn; (110) *Acritosoma elongatum* Pakaluk and Ślipiński.



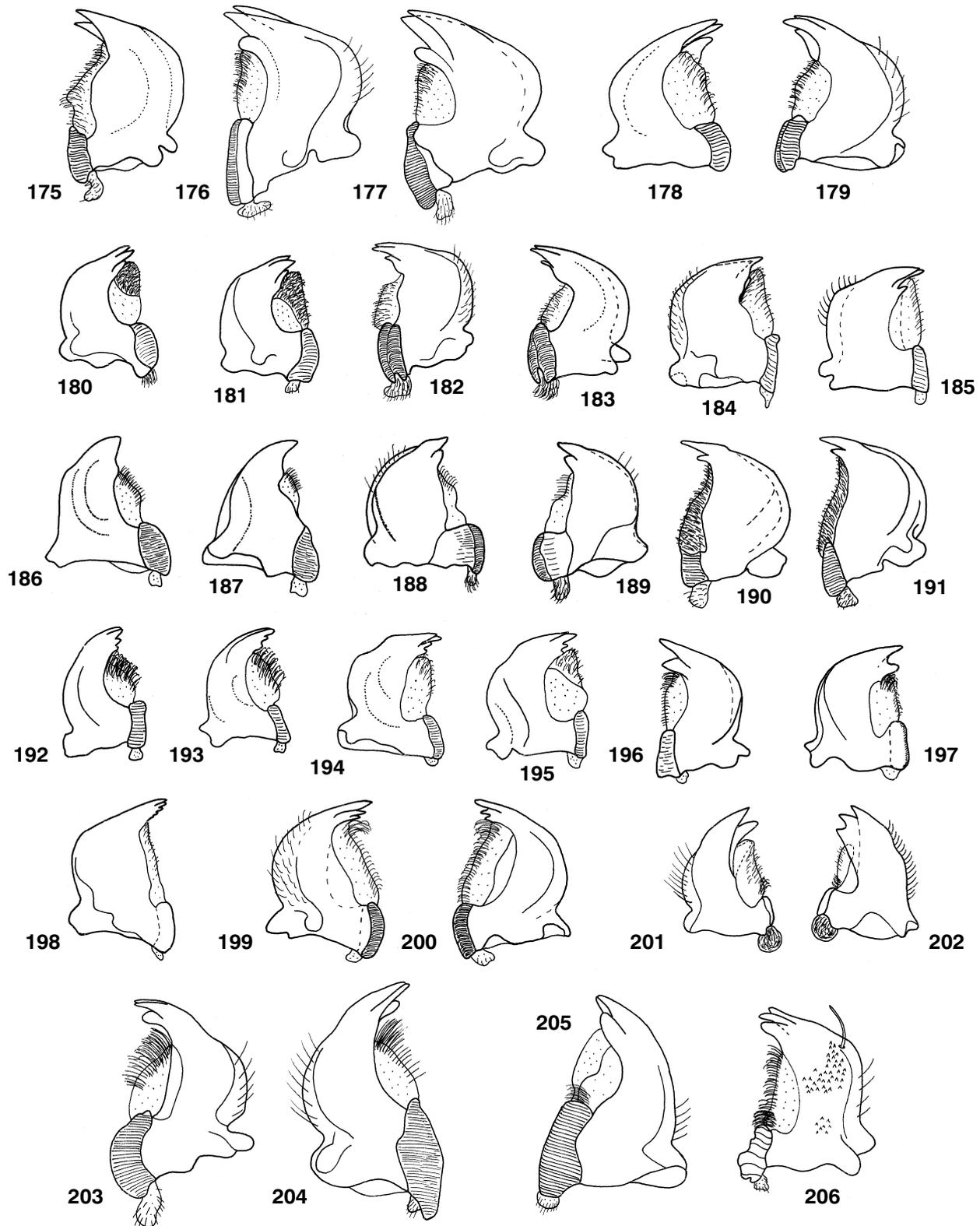
Figures 111–129. Labrum: (111) *Holoparamesus* sp.; (112) *Merophysia* sp.; (113) *Displotera beloni* Wasmann; (114) *Leiestes seminiger* (Gyllenhal); (115) *Panamomus lewisi* Gorham; (116) *Rhanidea unicolor* (Ziegler); (117) *Phymaphora pulchella* Newman; (118) *Stethorhanis borealis* Blaisdell; (119) *Panaleies decoratus* (Gorham); (120) *Microxenus laticollis* Wollaston; (121) *Eidoreus minutus* Sharp; (122) *Adamia mexicana* sp. nov.; (123) *Endomychus thoracicus* Charpentier; (124) *Cyclotoma* sp.; (125) *Meilichius* sp.; (126) *Bolbomorphus serpunctatus* Arrow; (127) *Eucteanus* sp.; (128) *Epipocus* sp.; (129) *Epopterus* sp.



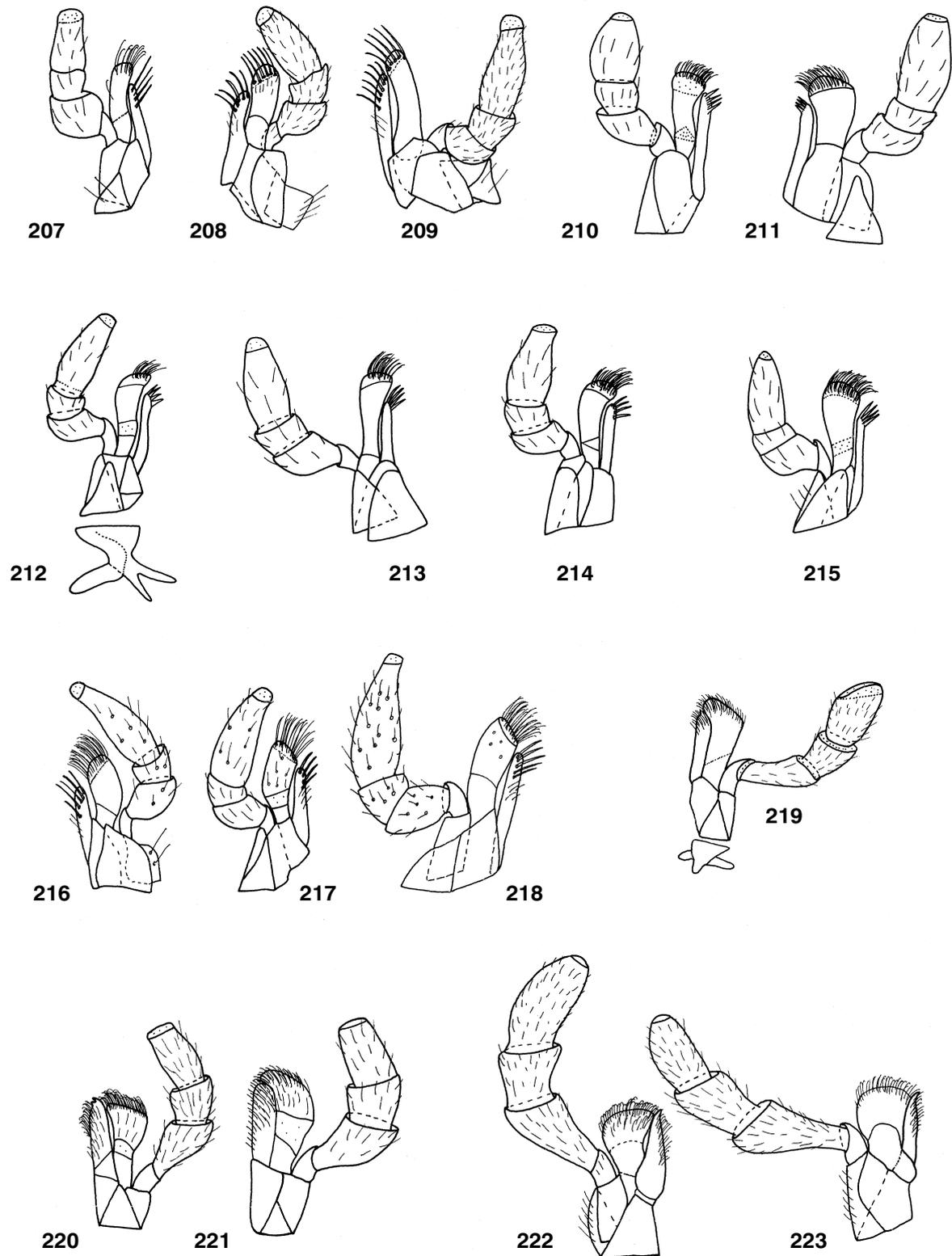
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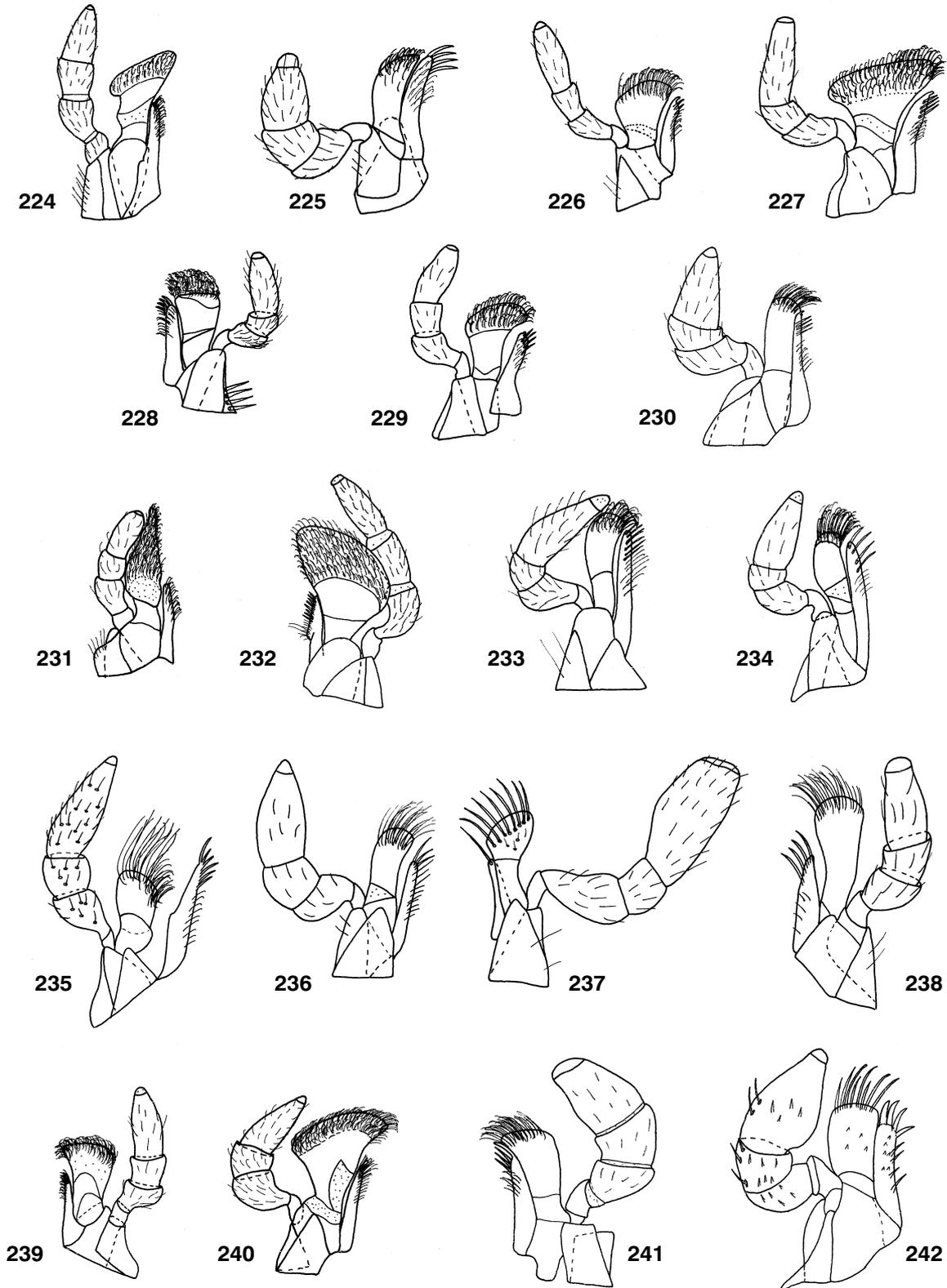
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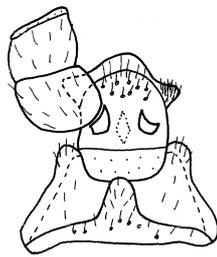
Figures 175–206. 176, 179–180, 182, 184, 187–188, 191–192, 195–196, 198, 200–201, 205–206: mandible, dorsal; 175, 177–178, 181, 183, 185–186, 189–190, 193–194, 197, 199, 202–204: mandible, ventral. (175) *Epipocus* sp.; (176, 177) *Epopterus* sp.; (178, 179) *Danae* sp.; (180, 181) *Saula* sp.; (182, 183) *Stenotarsus* sp.; (184, 185) *Perrisina brevis* (Perris); (186, 187) *Danascelis elongata* Tomaszewska; (188, 189) *Lycoperdina succincta* (Linnaeus); (190, 191) *Beccariota* sp.; (192, 193) *Mycetaea subterranea* (Fabricius); (194, 195) *Agaricophilus reflexus* Motschulsky; (196, 197) *Xenomycetes morrisoni* Horn; (198) *Pleganophorus bispinosus* Hampe (199, 200) *Trochoideus* sp.; (201, 202) *Acritosoma elongatum* Pakaluk and Ślipiński; (203) *Symbiotes gibberosus* (Lucas); (204) *Mychothemus asiaticus* Sasaji; (205) *Micropsephodes serraticornis* Champion; (206) *Erotendomychus lawrencei* sp. nov.



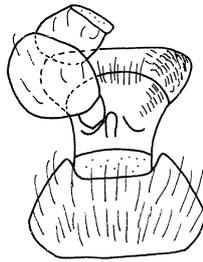
Figures 207–223. Maxilla: (207) *Holoparamecus* sp.; (208) *Merophysia* sp.; (209) *Displotera beloni* Wasmann; (210) *Leistes seminiger* (Gyllenhal); (211) *Panamomus lewisi* Gorham; (212) *Rhanidea unicolor* (Ziegler); (213) *Phymaphora pulchella* Newman; (214) *Stethorhanis borealis* Blaisdell; (215) *Panaleies decoratus* (Gorham); (216) *Microxenus laticollis* Wollaston; (217) *Eidoreus minutus* Sharp; (218) *Adamia mexicana* sp. nov.; (219) *Endomychus coccineus* (Linnaeus); (220) *Cyclotoma* sp.; (221) *Meilichius* sp.; (222) *Bolbomorphus serpunctatus* Arrow; (223) *Eucteanus* sp.



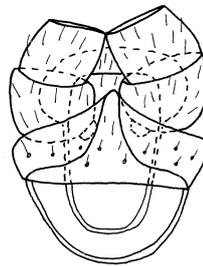
Figures 224–242. Maxilla: (224) *Epipocus* sp.; (225) *Epopterus* sp.; (226) *Danae* sp.; (227) *Saula* sp.; (228) *Stenotarsus* sp.; (229) *Perrisina brevis* (Perris); (230) *Danascelis elongata* Tomaszewska; (231) *Lycoperdina succincta* (Linnaeus); (232) *Beccariola* sp.; (233) *Mycetaea subterranea* (Fabricius); (234) *Agaricophilus reflexus* Motschulsky; (235) *Symbiotes gibberosus* (Lucas); (236) *Mychothenus asiaticus* Sasaji; (237) *Micropsephodes serraticornis* Champion; (238) *Erotendomychus lawrencei* sp. nov.; (239) *Pleganophorus bispinosus* Hampe; (240) *Trochoideus* sp.; (241) *Xenomycetes morrisoni* Horn; (242) *Acritosoma elongatum* Pakaluk and Šlipiński.



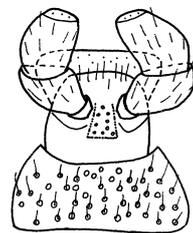
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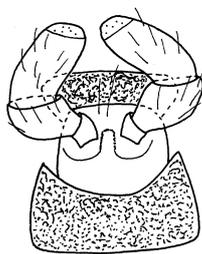
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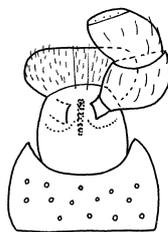
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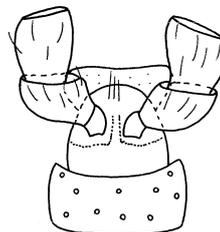
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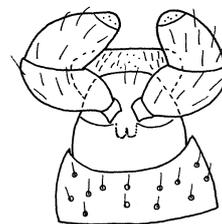
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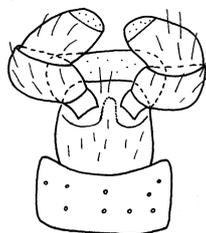
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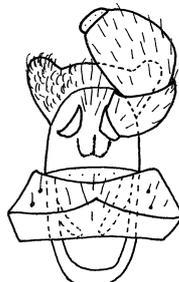
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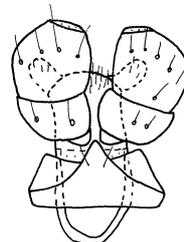
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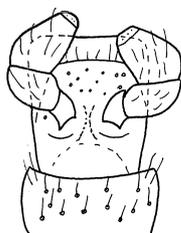
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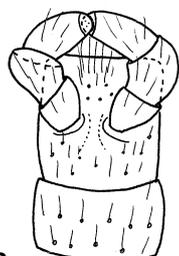
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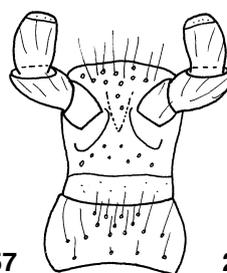
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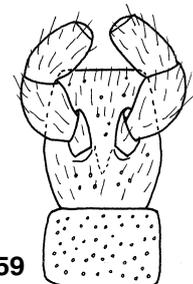
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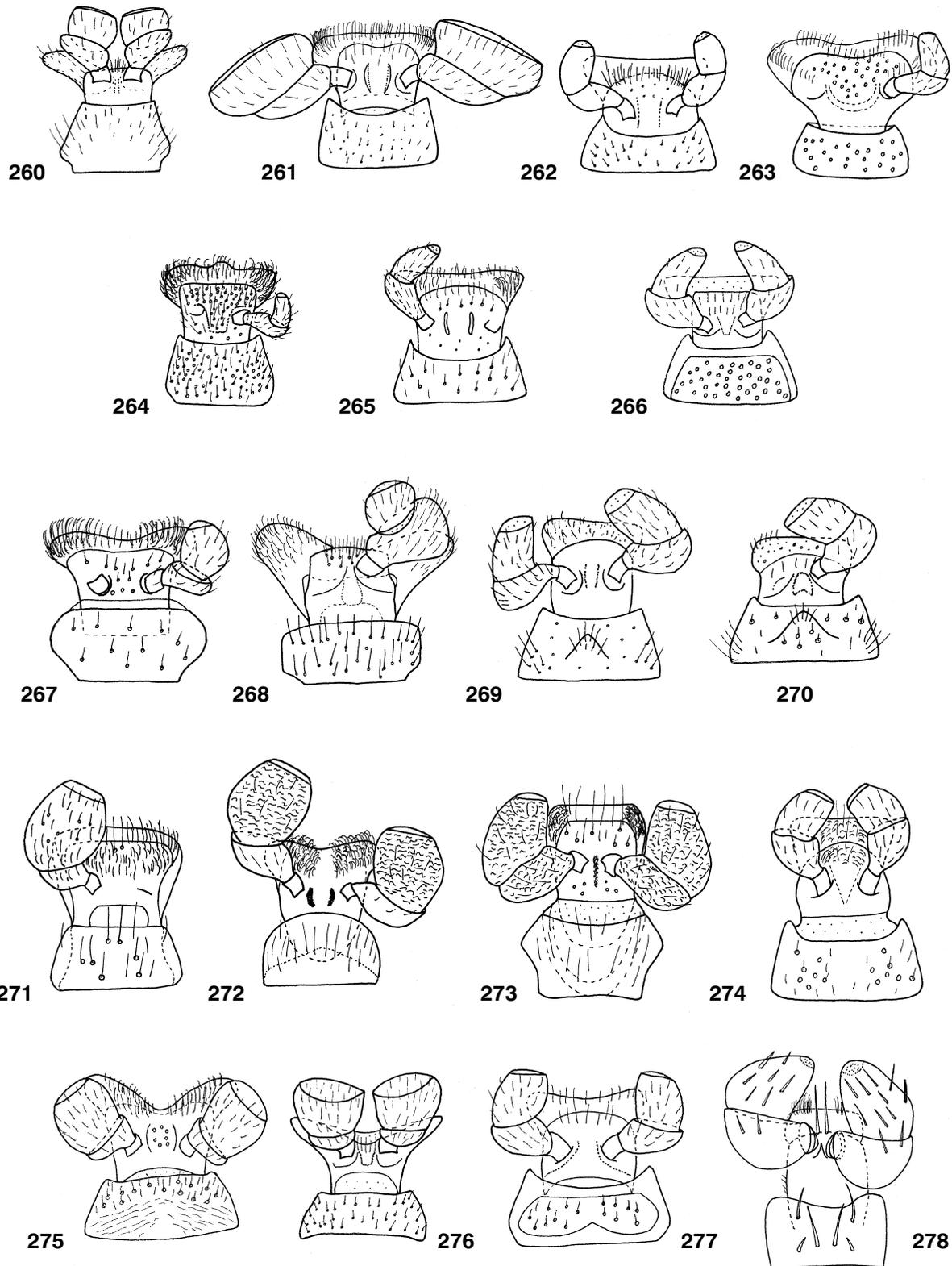


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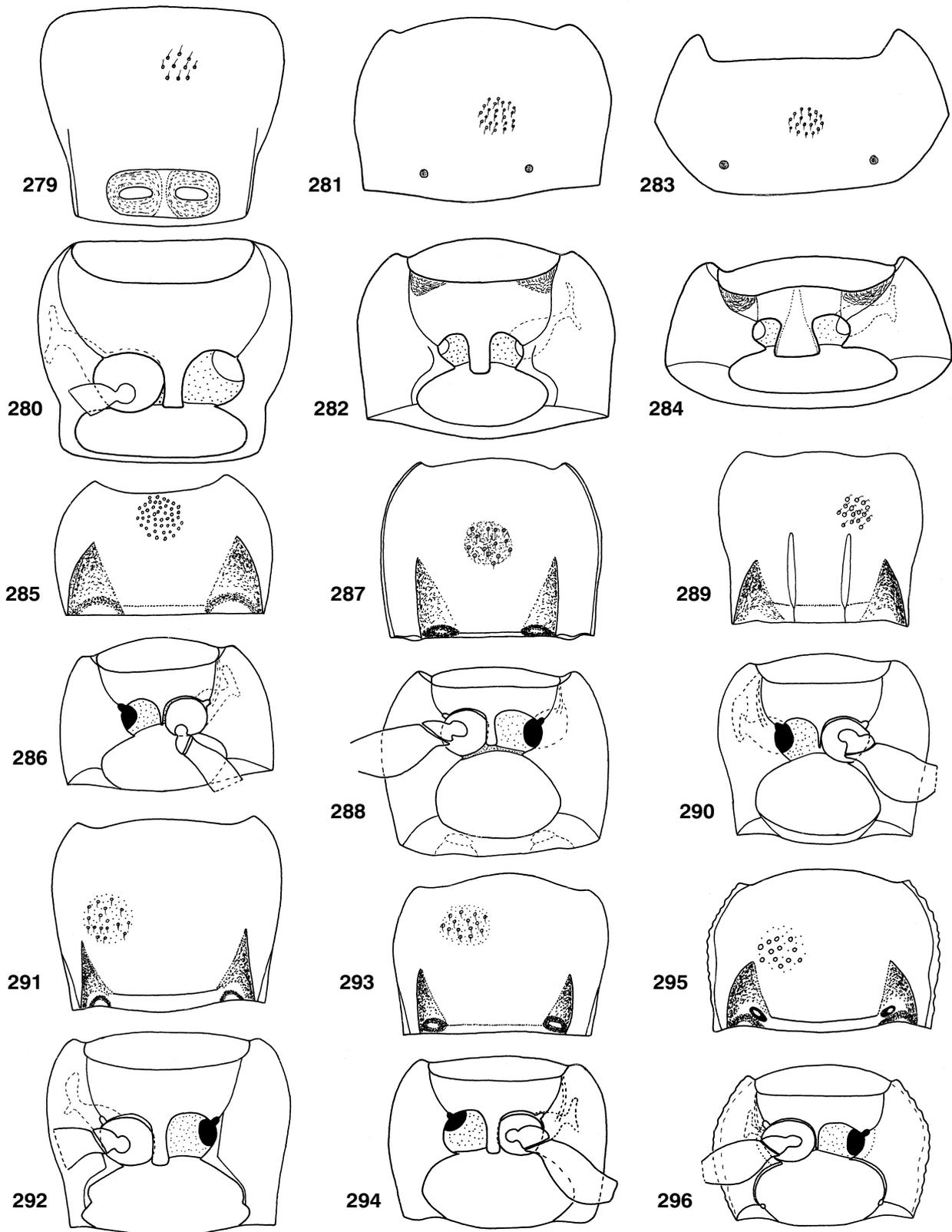


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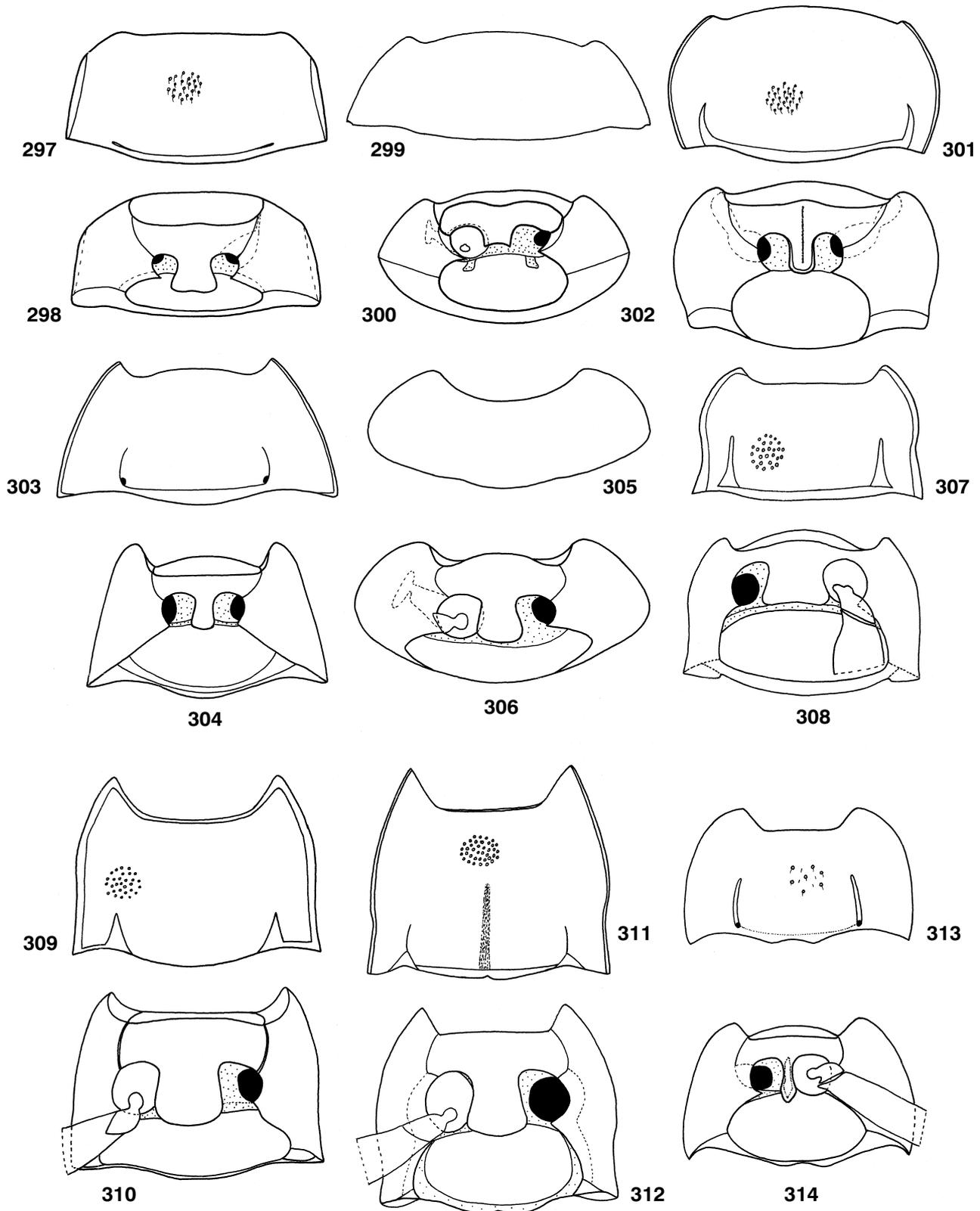
Figures 243–259. Labium: (243) *Merophysia* sp.; (244) *Holoparamesus* sp.; (245) *Displotera beloni* Wasmann; (246) *Leiestes seminiger* (Gyllenhal); (247) *Panamomus lewisi* Gorham; (248) *Rhanidea unicolor* (Ziegler); (249) *Phymaphora pulchella* Newman; (250) *Stethorhanis borealis* Blaisdell; (251) *Panaleies decoratus* (Gorham); (252) *Microxenus laticollis* Wollaston; (253) *Eidoreus minutus* Sharp; (254) *Adamia mexicana* sp. nov.; (255) *Endomychus thoracicus* Charpentier; (256) *Cyclotoma* sp.; (257) *Meilichius* sp.; (258) *Bolbomorphus serpunctatus* Arrow; (259) *Eucteanus* sp.



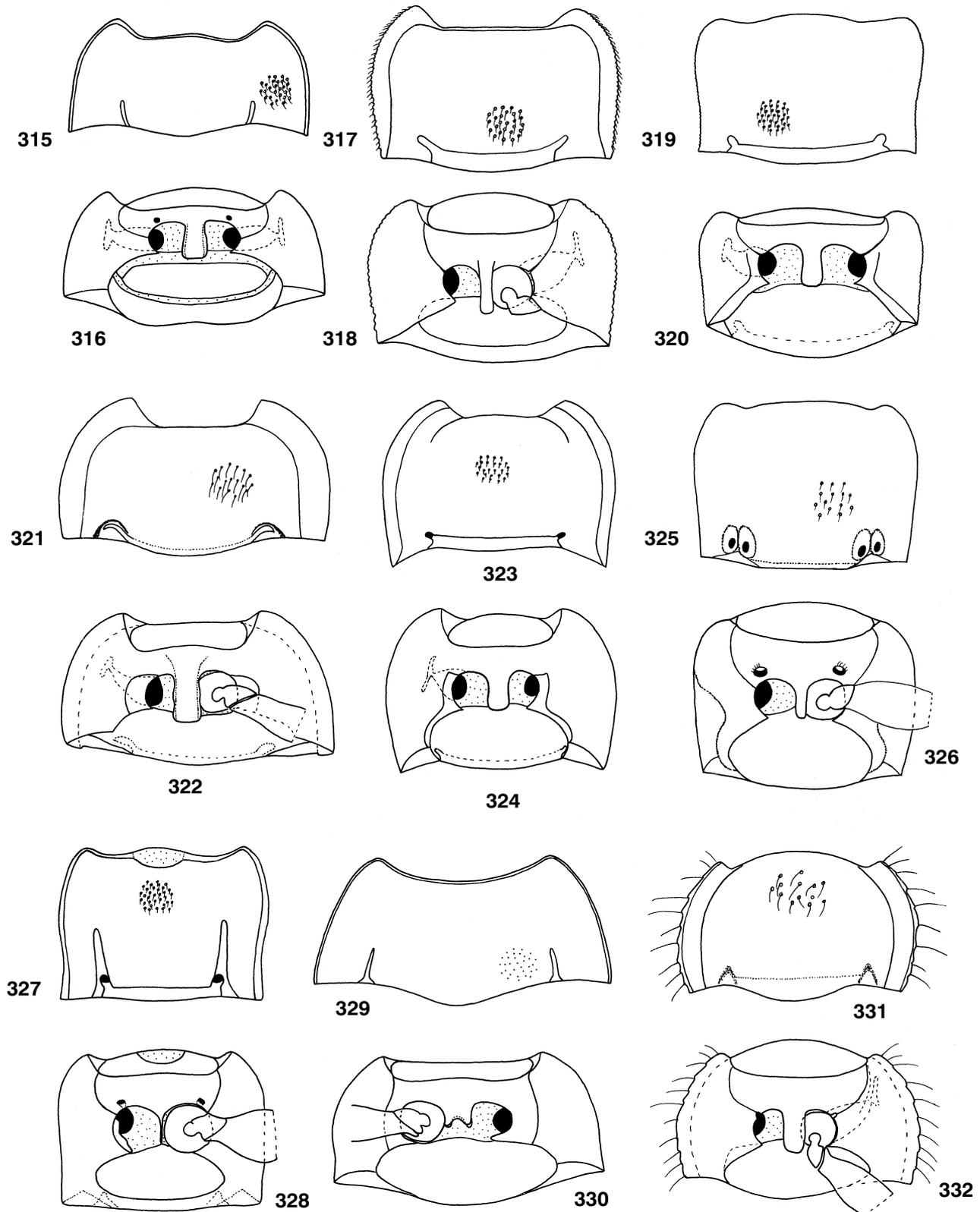
Figures 260–278. Labium: (260) *Epipocus* sp.; (261) *Epopterus* sp.; (262) *Danae* sp.; (263) *Saula* sp.; (264) *Stenotarsus* sp.; (265) *Perrisina brevis* (Perris); (266) *Danascelis elongata* Tomaszewska; (267) *Lycoperdina succincta* (Linnaeus); (268) *Beccariola* sp.; (269) *Mycetaea subterranea* (Fabricius); (270) *Agaricophilus reflexus* Motschulsky; (271) *Symbiotes gibberosus* (Lucas); (272) *Mychothenus asiaticus* Sasaji; (273) *Micropsephodes serraticornis* Champion; (274) *Erotendomychus lawrencei* sp. nov.; (275) *Pleganophorus bispinosus* Hampe; (276) *Trochoideus* p.; (277) *Xenomycetes morrisoni* Horn; (278) *Acritosoma elongatum* Pakaluk and Ślipiński.



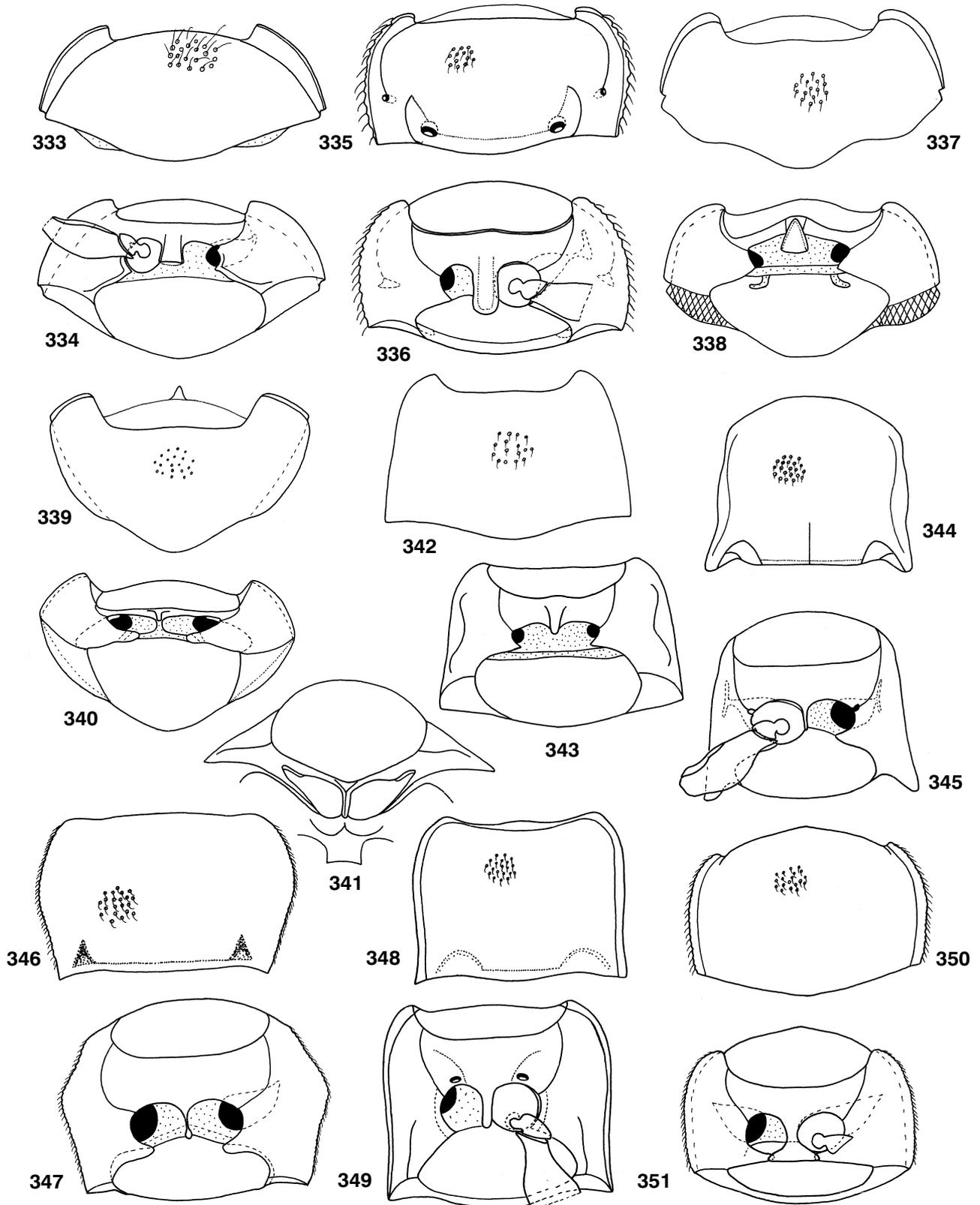
Figures 279–296. Prothorax, dorsal and ventral: (279, 280) *Holoparamesus* sp.; (281, 282) *Merophysia* sp.; (283, 284) *Displotera beloni* Wasmann; (285, 286) *Leiestes seminiger* (Gyllenhal); (287, 288) *Panamomus lewisi* Gorham; (289, 290) *Rhanidea unicolor* (Ziegler); (291, 292) *Phymaphora pulchella* Newman; (293, 294) *Stethorhanis borealis* Blaisdell; (295, 296) *Panaleies decoratus* (Gorham).



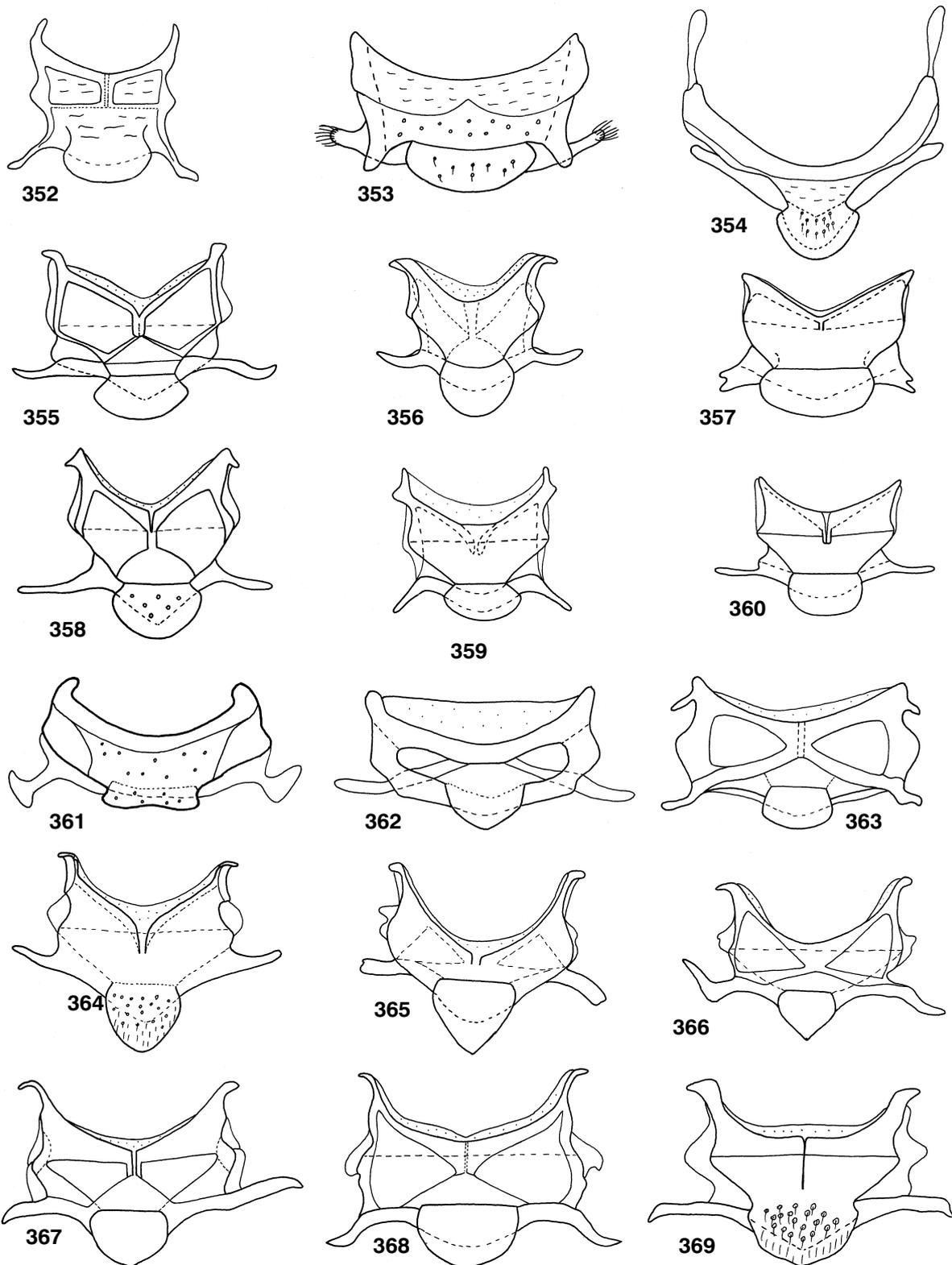
Figures 297–314. Prothorax, dorsal and ventral: (297, 298) *Microxenus laticollis* Wollaston; (299, 300) *Eidoreus minutus* Sharp; (301, 302) *Adamia mexicana* sp. nov.; (303, 304) *Endomychus coccineus* (Linnaeus); (305, 306) *Cyclotoma* sp.; (307, 308) *Meilichius* sp.; (309, 310) *Bolbomorphus serpunctatus* Arrow; (311, 312) *Eucteanus* sp.; (313, 314) *Epipoecus* sp.



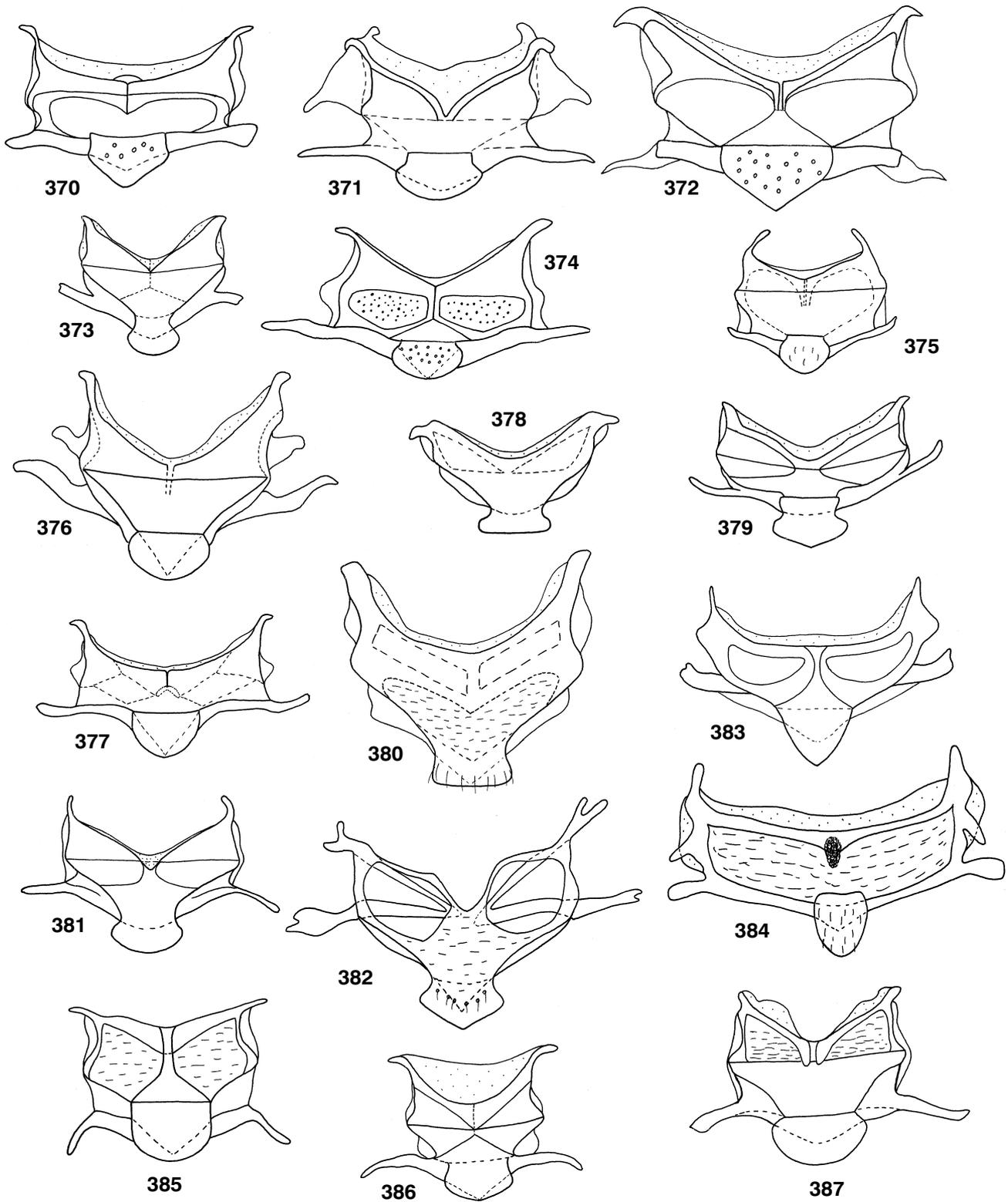
Figures 315–332. Prothorax, dorsal and ventral: (315, 316) *Epopterus* sp.; (317–318) *Danae* sp.; (319, 320) *Saula* sp.; (321, 322) *Stenotarsus* sp.; (323, 324) *Perrisina brevis* (Perris); (325, 326) *Danascelis elongata* Tomaszewska; (327–328) *Lycoperdina succincta* (Linnaeus); (329, 330) *Beccariola* sp.; (331, 332) *Mycetaea subterranea* (Fabricius).



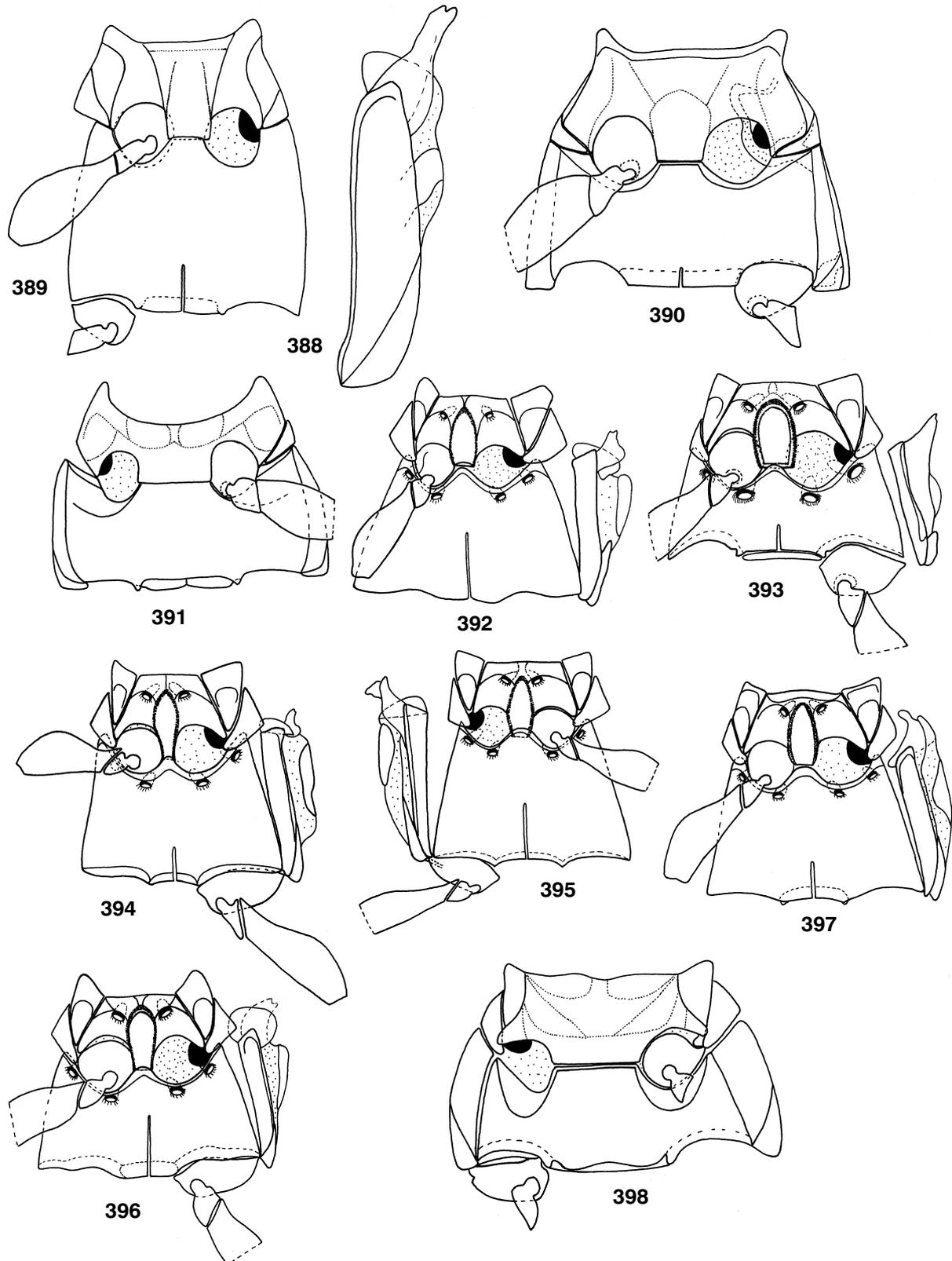
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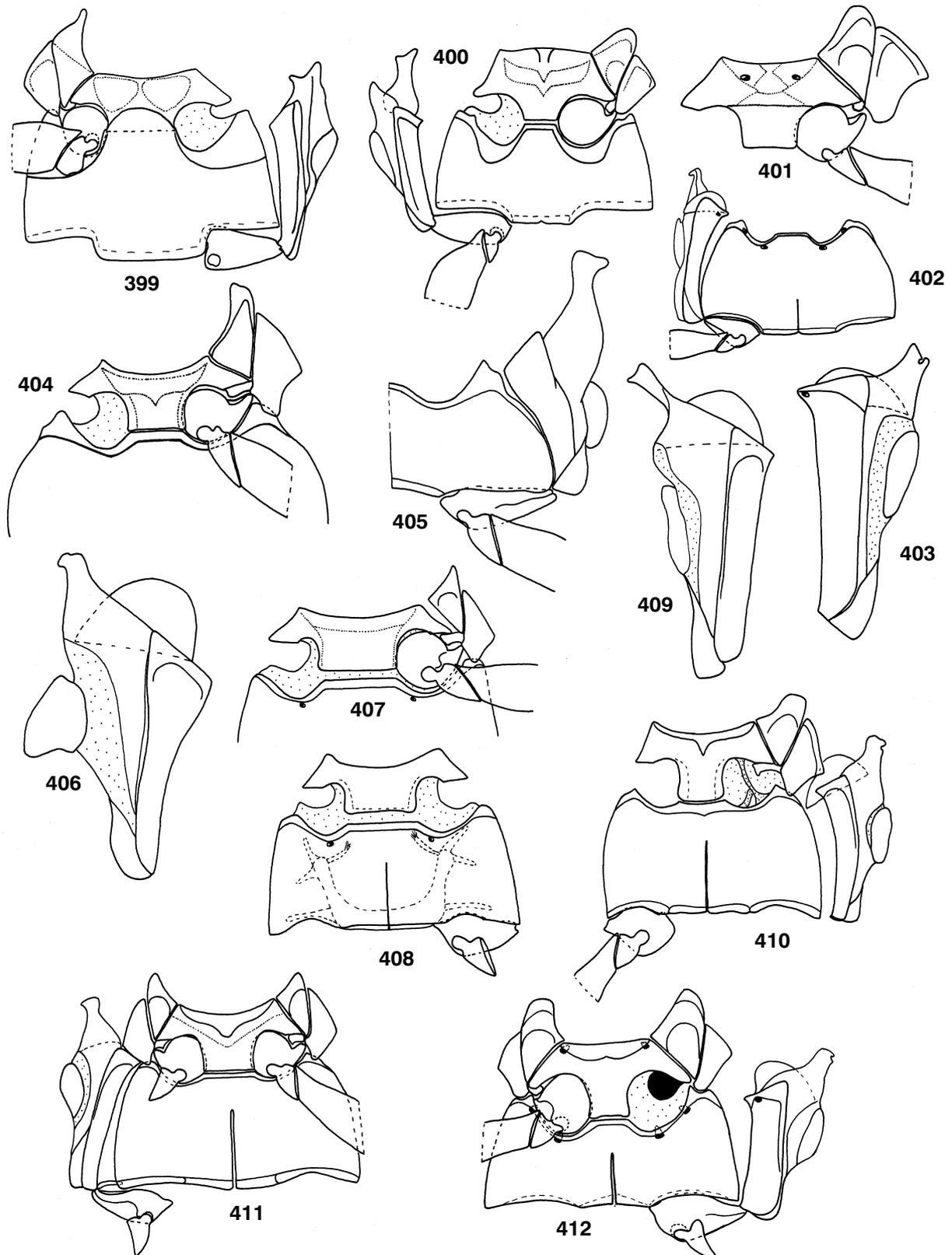
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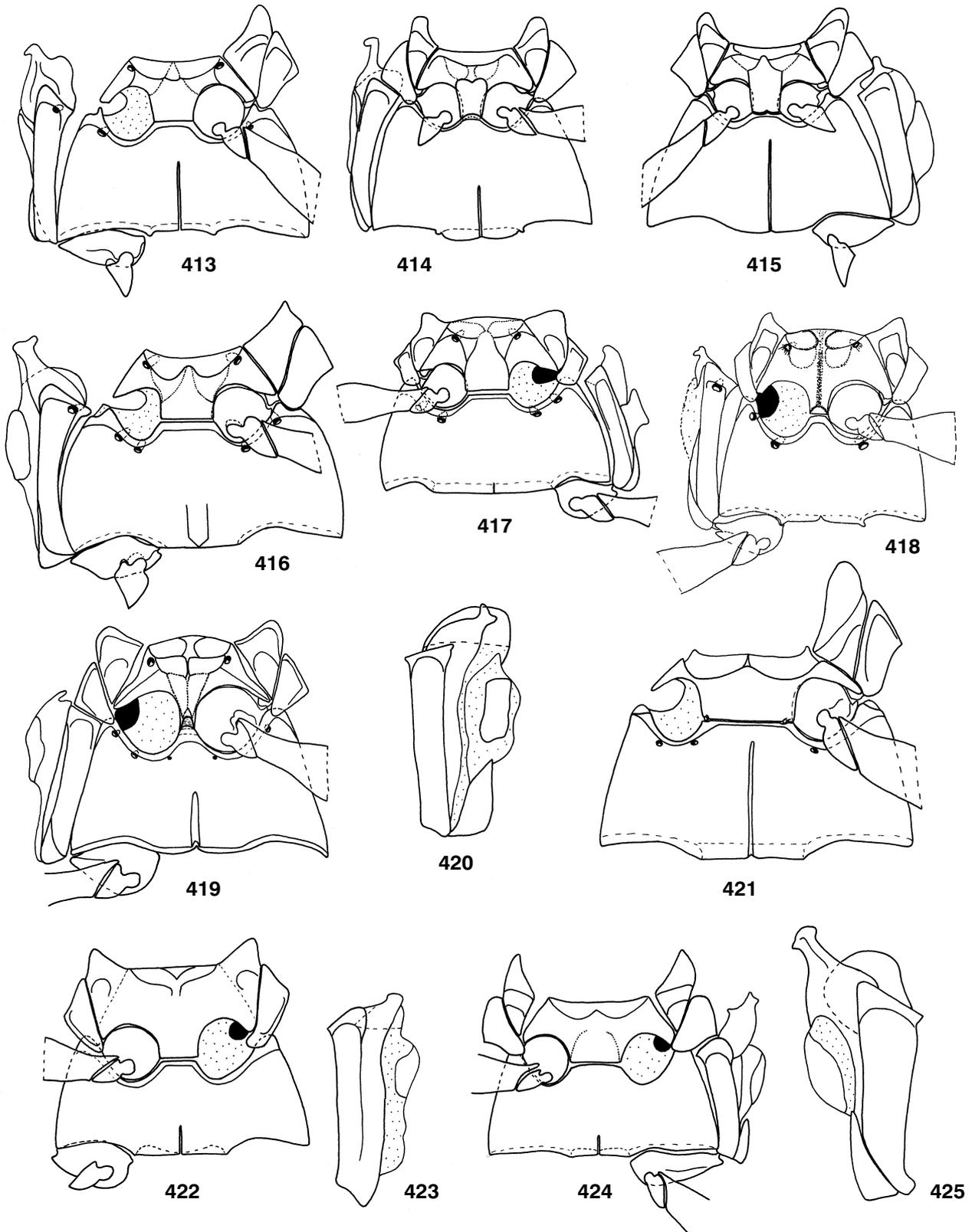
Figures 370–387. Mesonotum: (370) *Epopterus* sp.; (371) *Danae* sp.; (372) *Saula* sp.; (373) *Danascelis elongata* Tomaszewska; (374) *Stenotarsus* sp.; (375) *Perrisina brevis* (Perris); (376) *Lycoperdina succincta* (Linnaeus); (377) *Beccariola* sp.; (378) *Mycetaea subterranea* (Fabricius); (379) *Agaricophilus reflexus* Motschulsky; (380) *Acritisoma elongatum* Pakaluk and Ślipiński; (381) *Symbiotes gibberosus* (Lucas); (382) *Mychothenus asiaticus* Sasaji; (383) *Micropsephodes serraticornis* Champion; (384) *Erotendomychus lawrencei* sp. nov.; (385) *Pleganophorus bispinosus* Hampe; (386) *Trochoideus* sp.; (387) *Xenomycetes morrisoni* Horn.



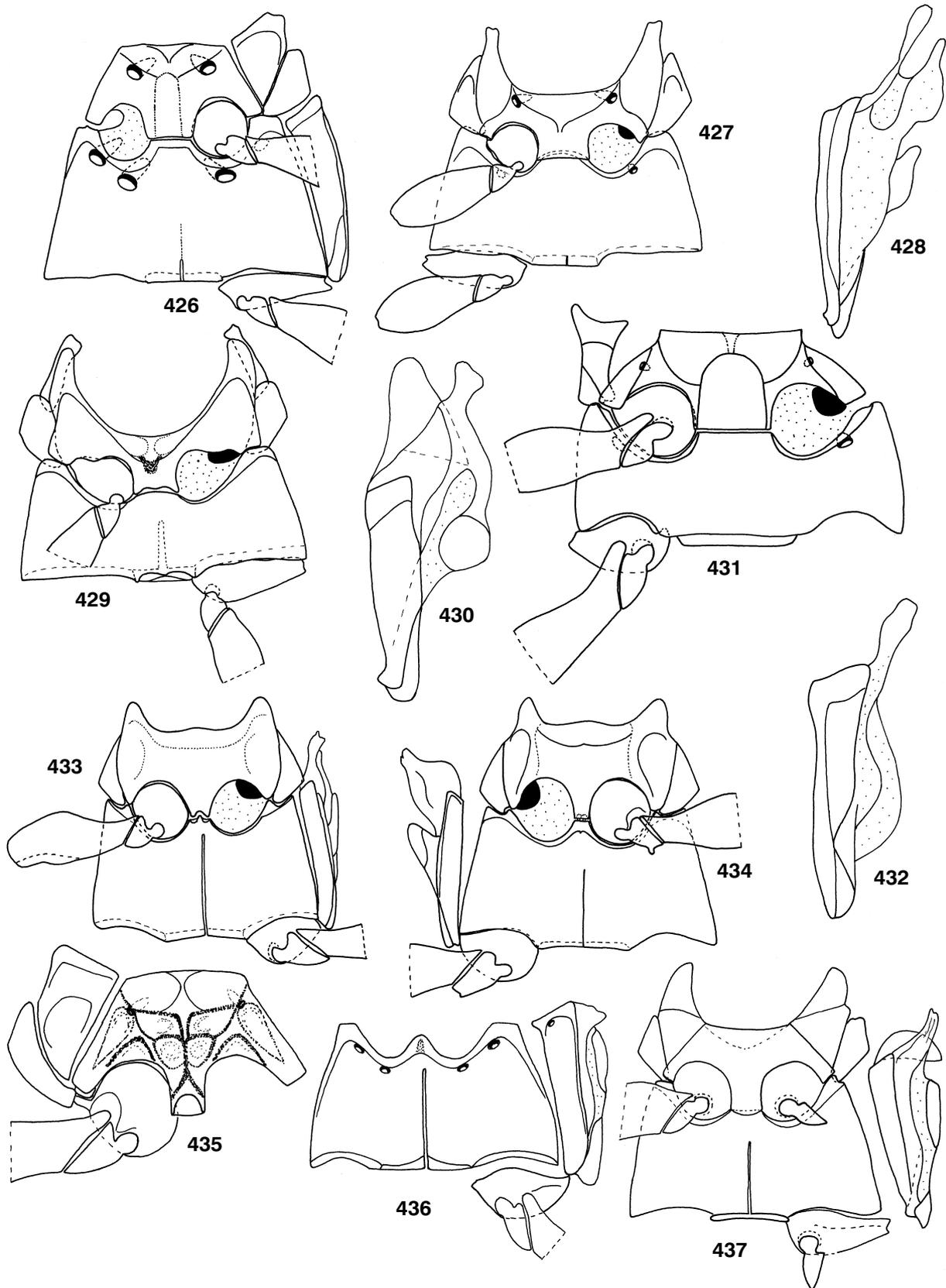
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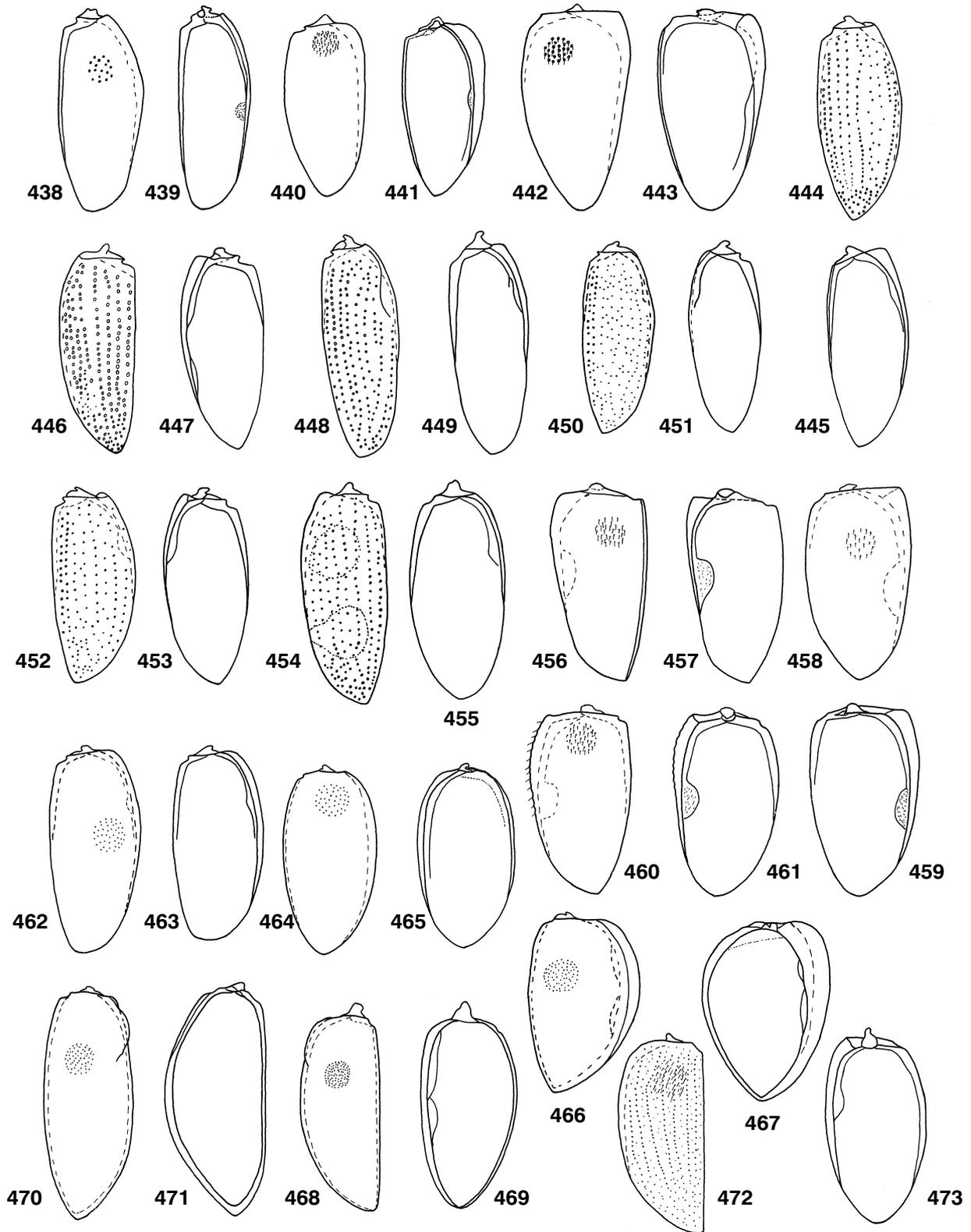
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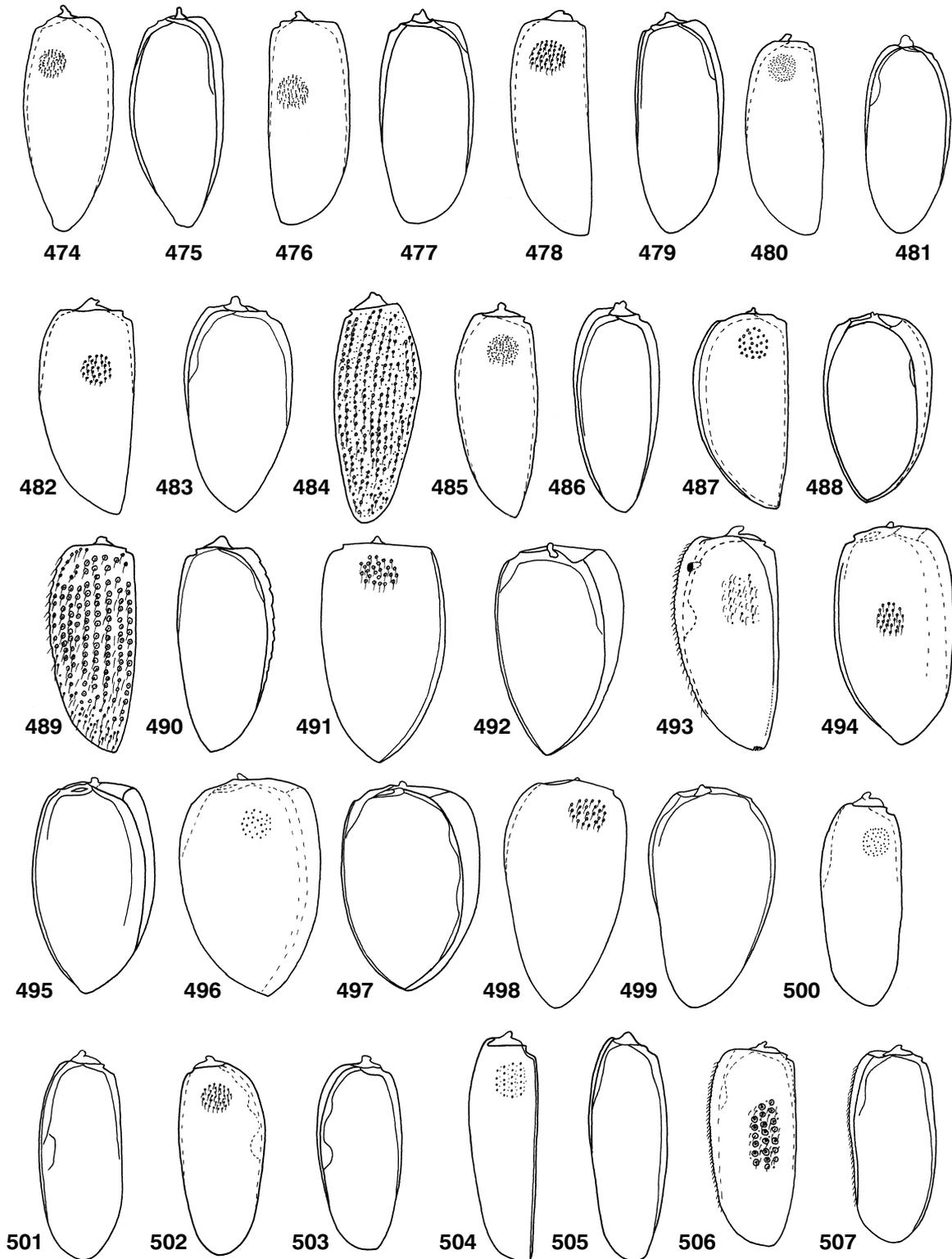
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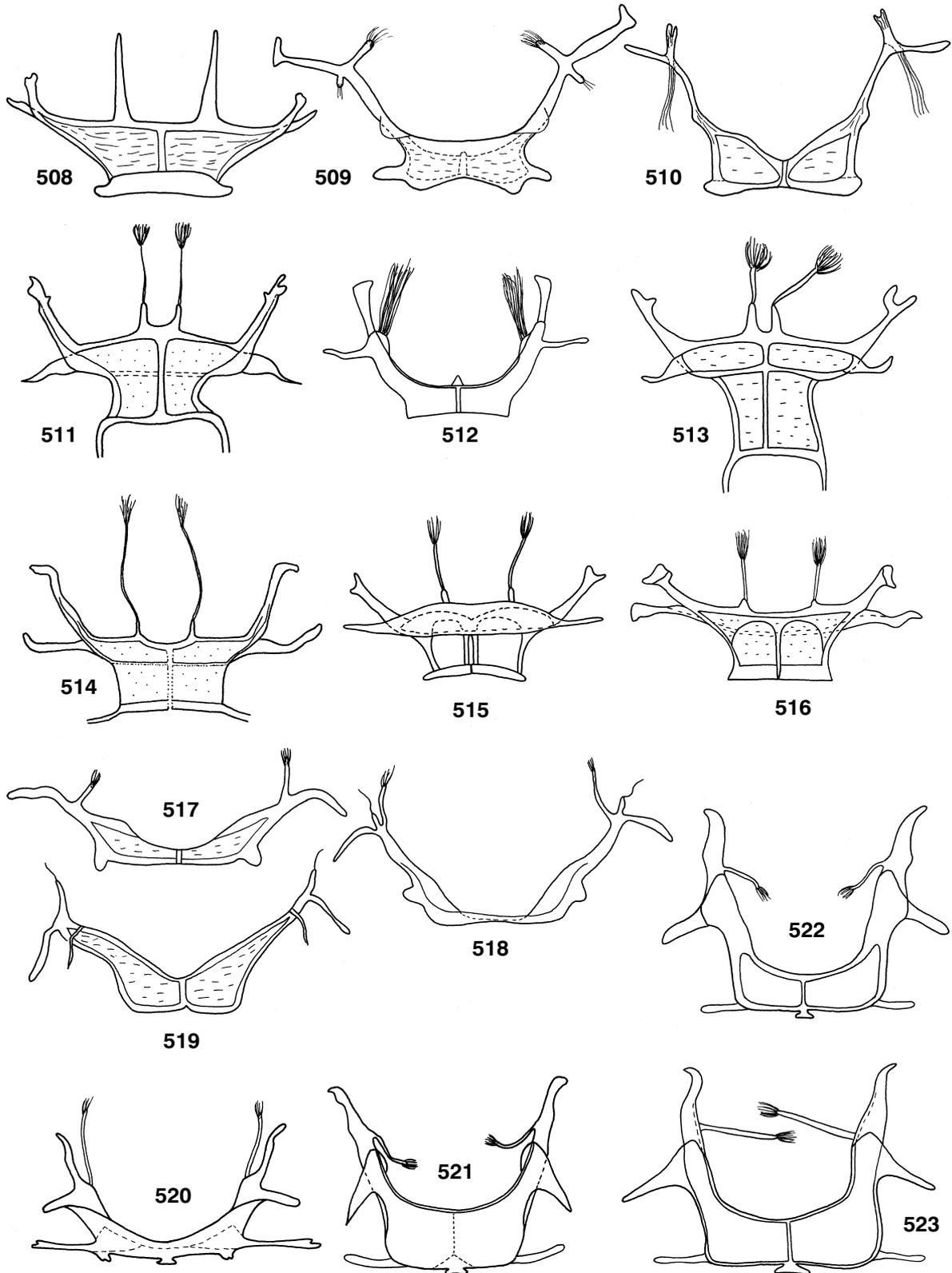
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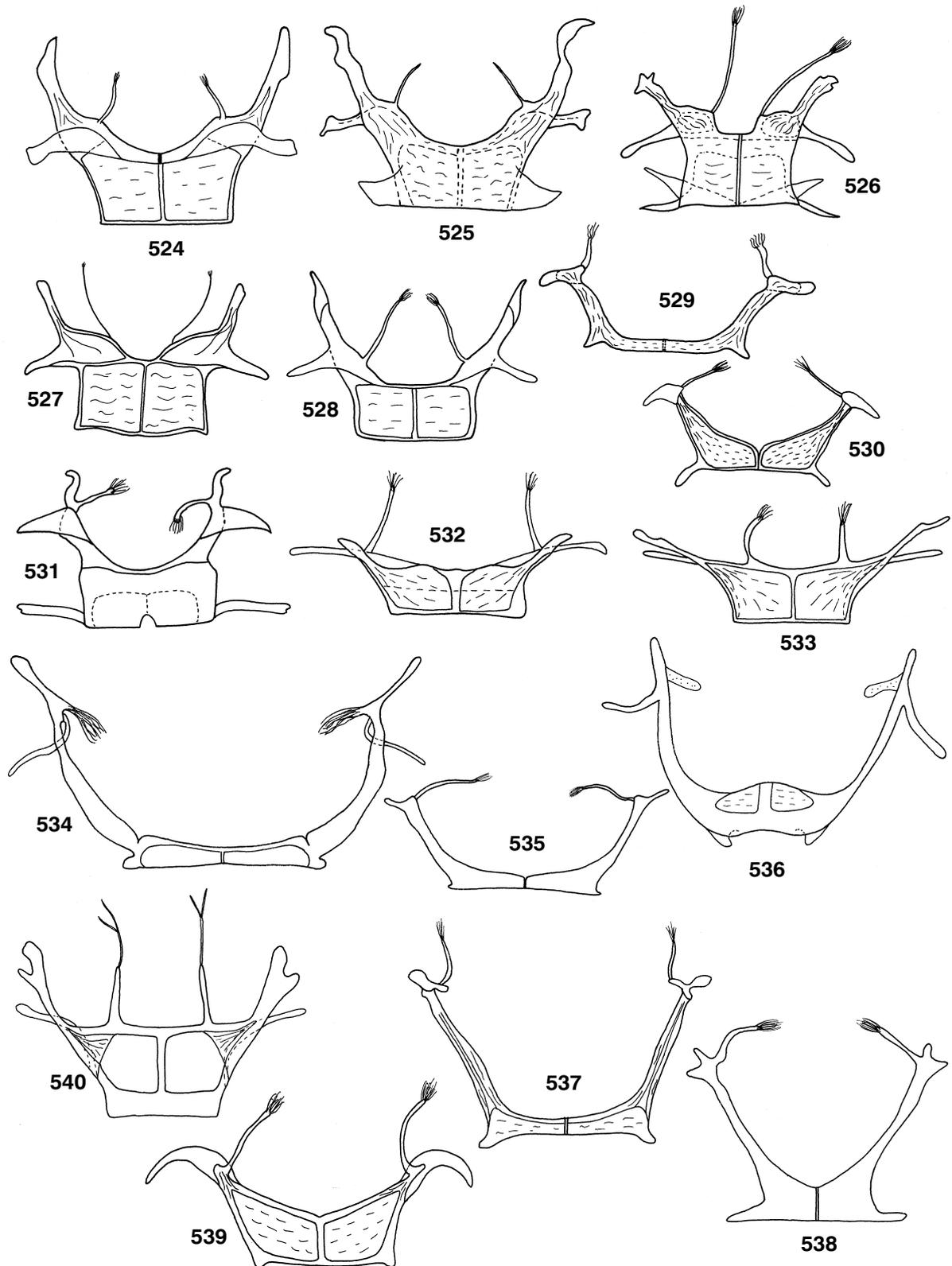
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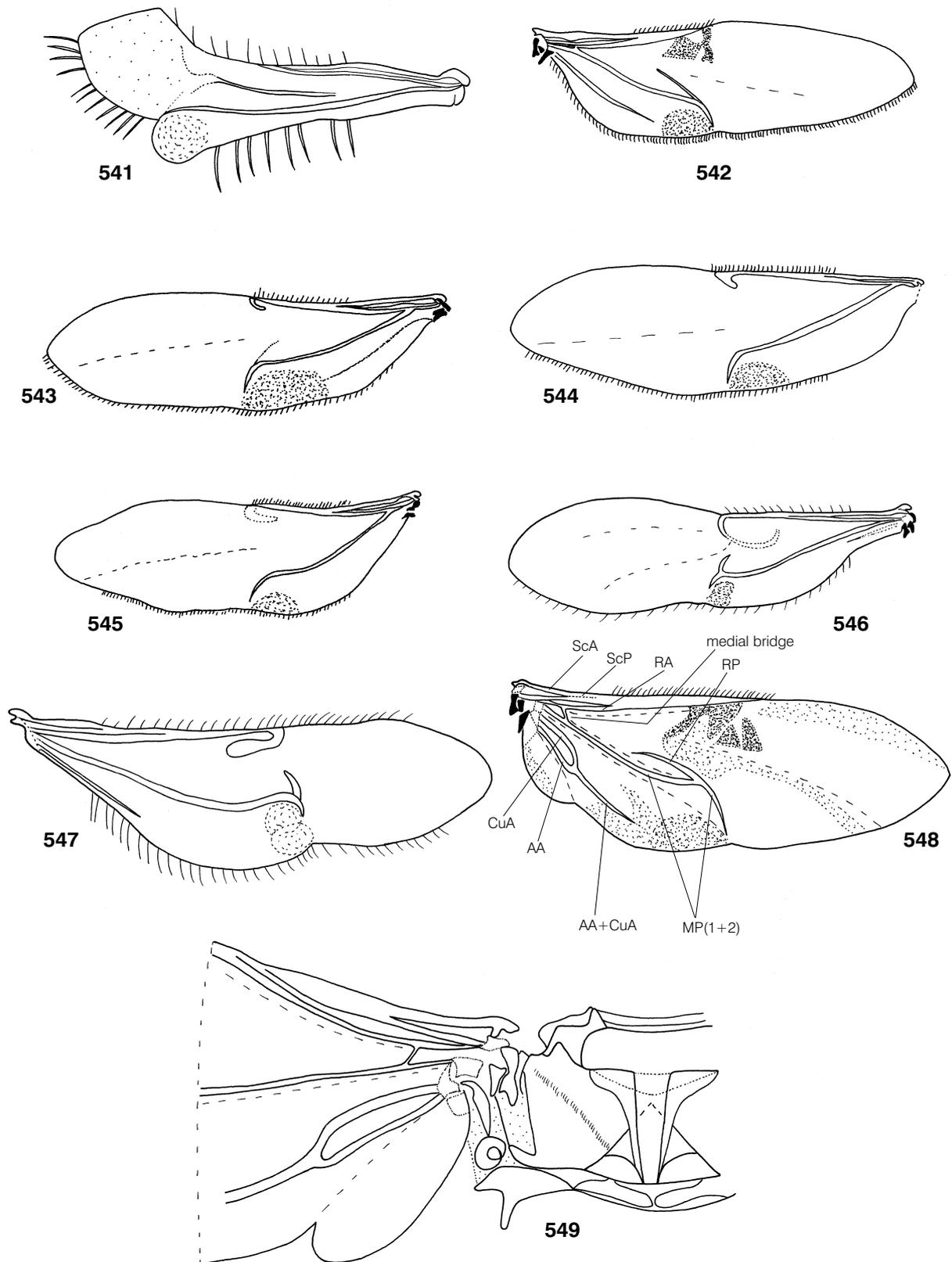
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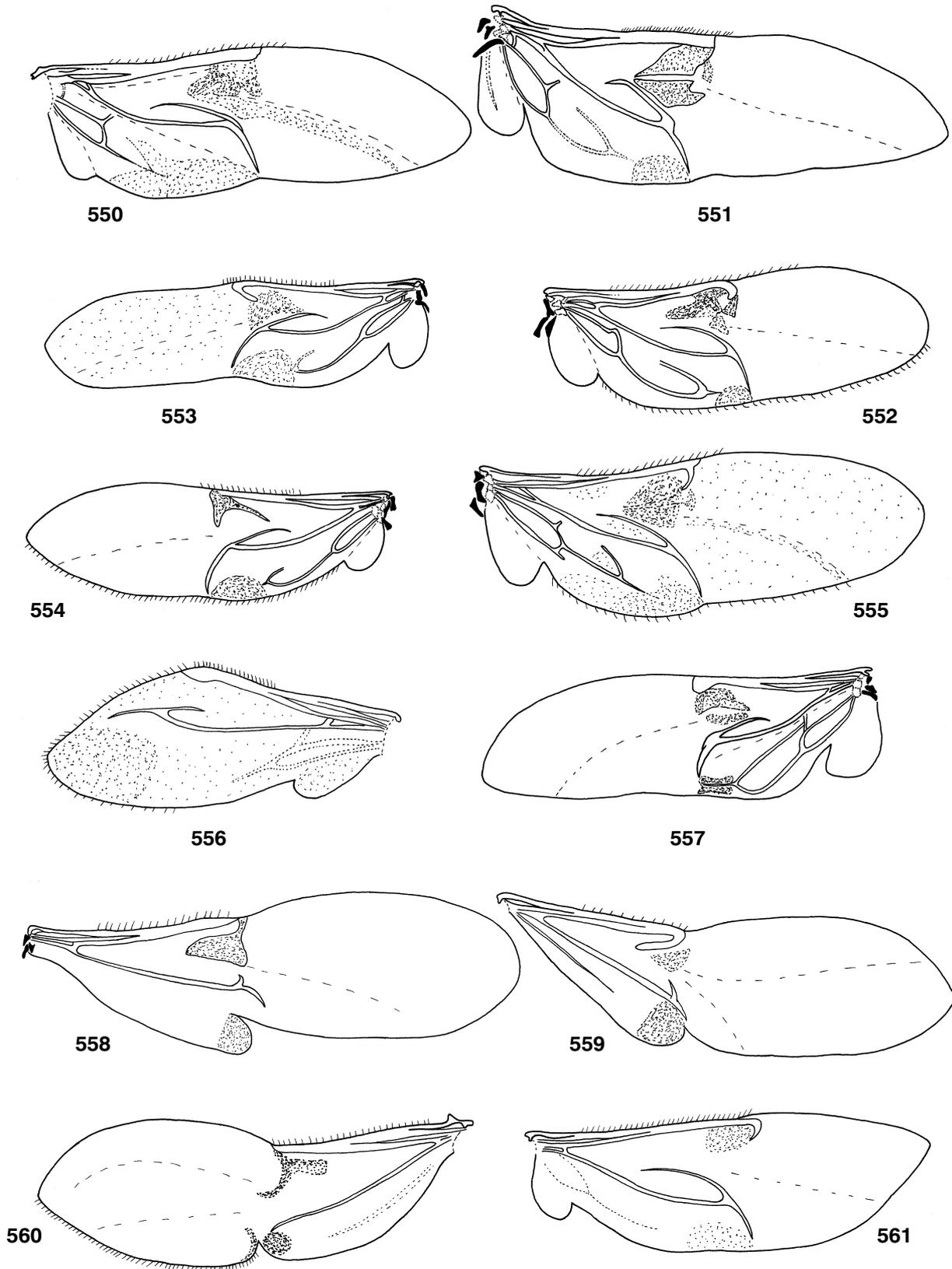
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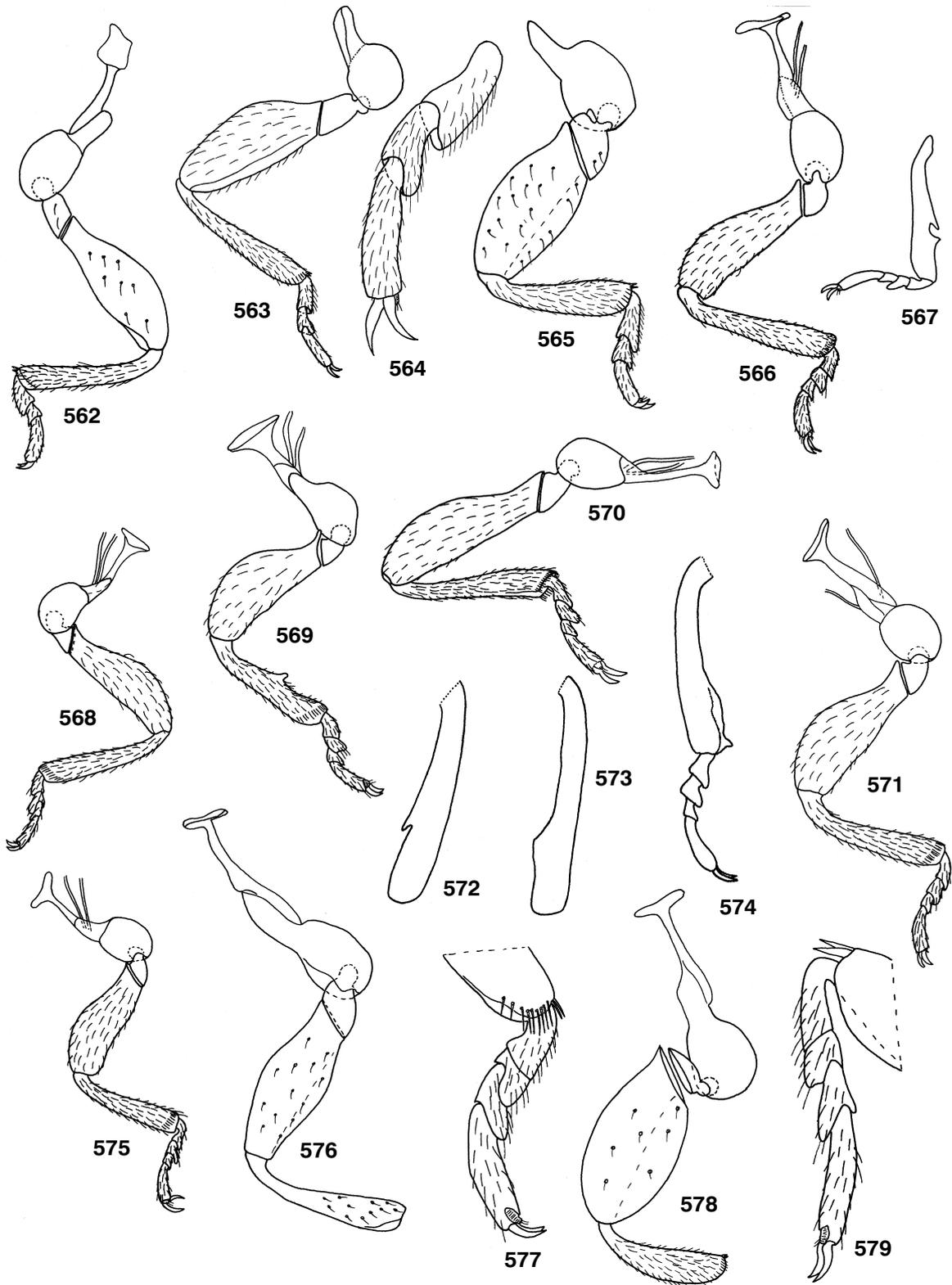
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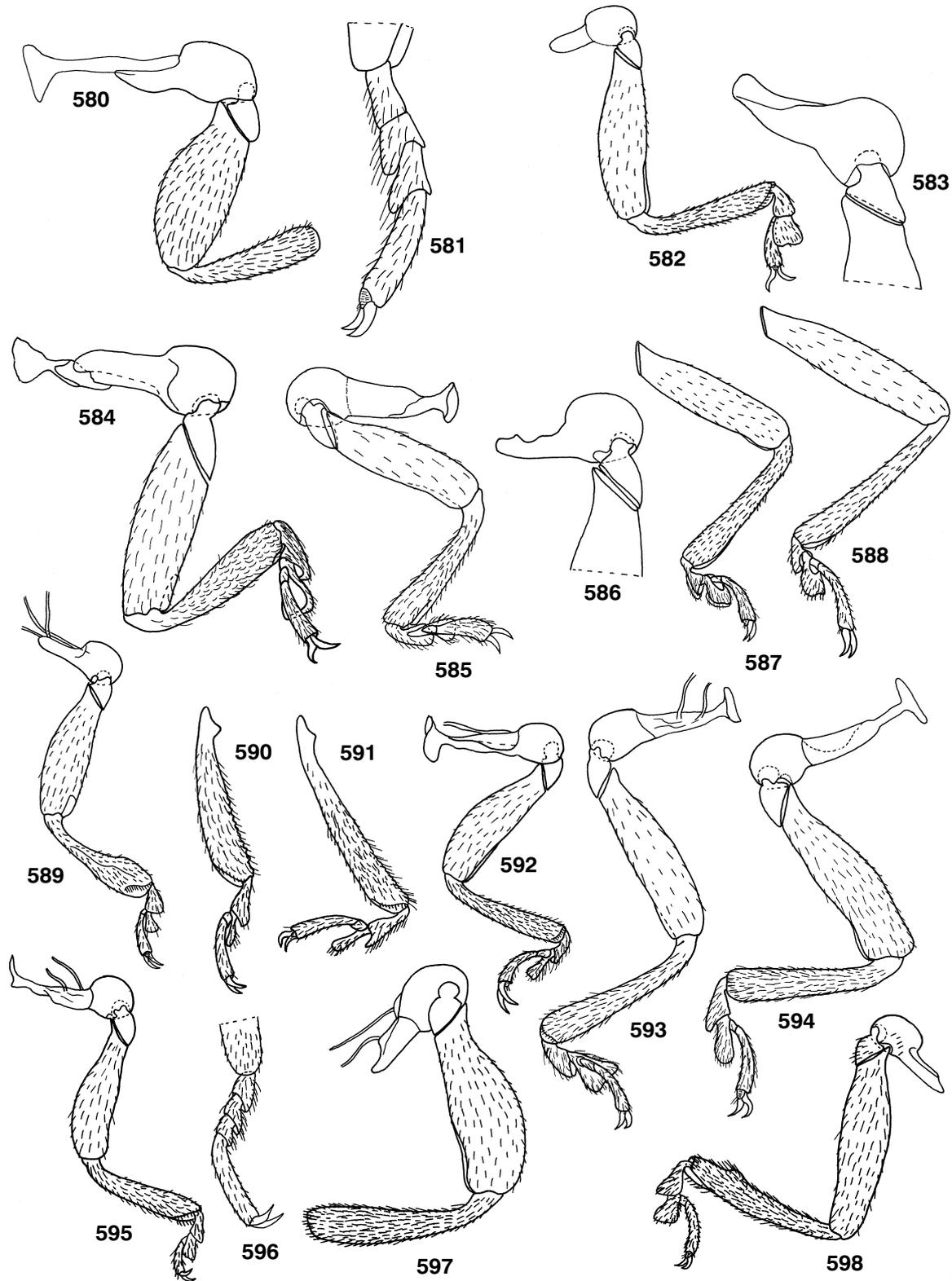
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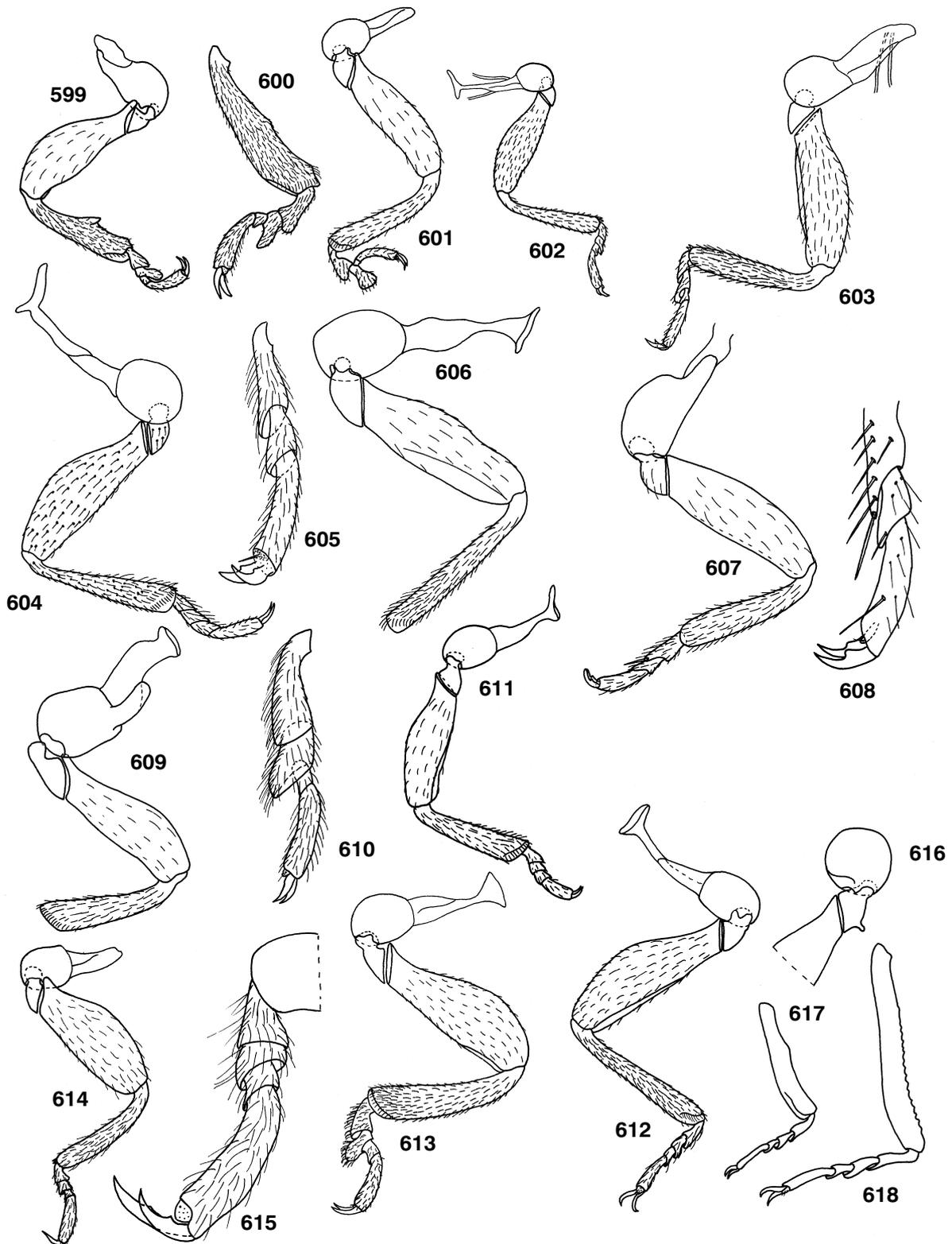
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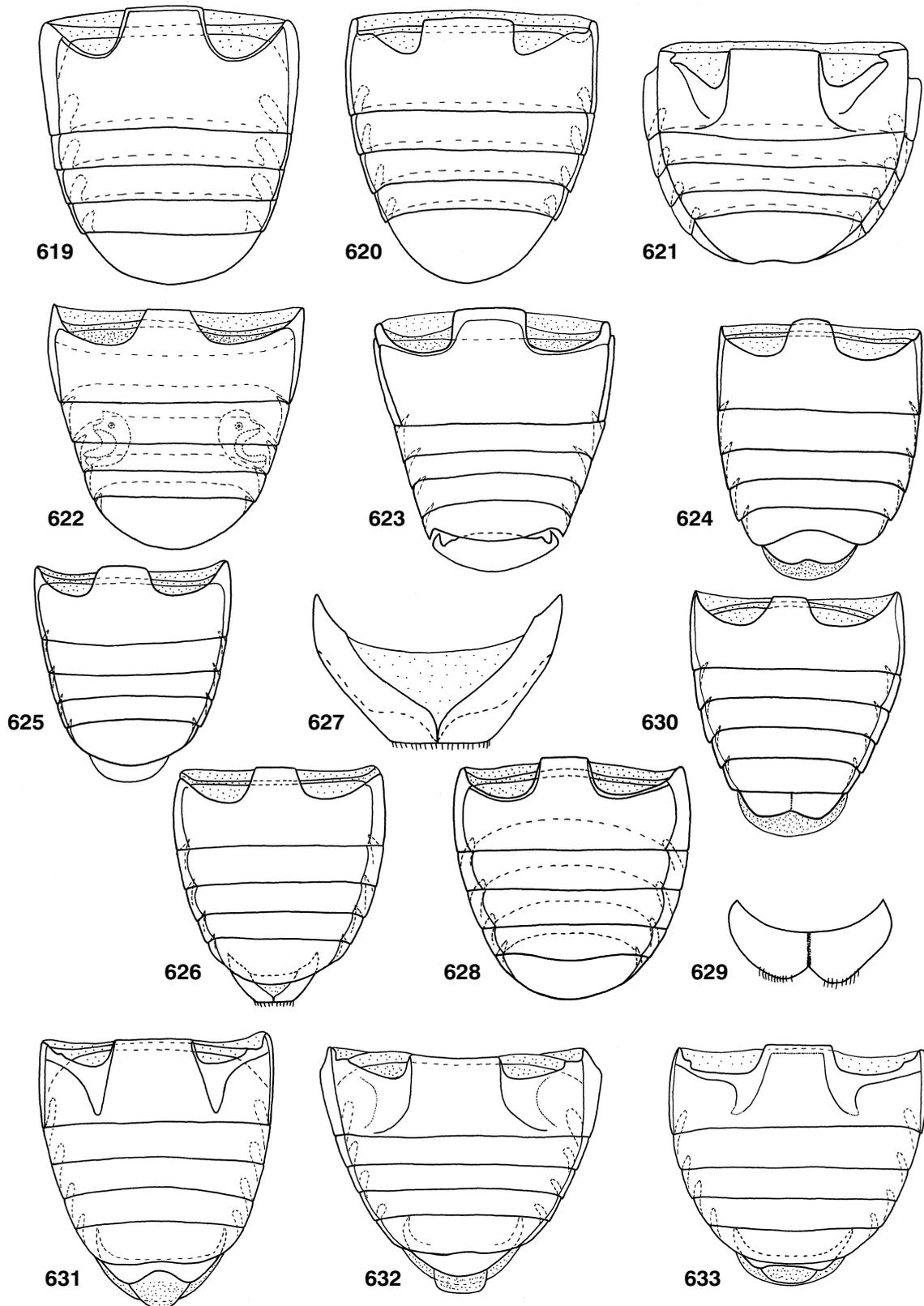
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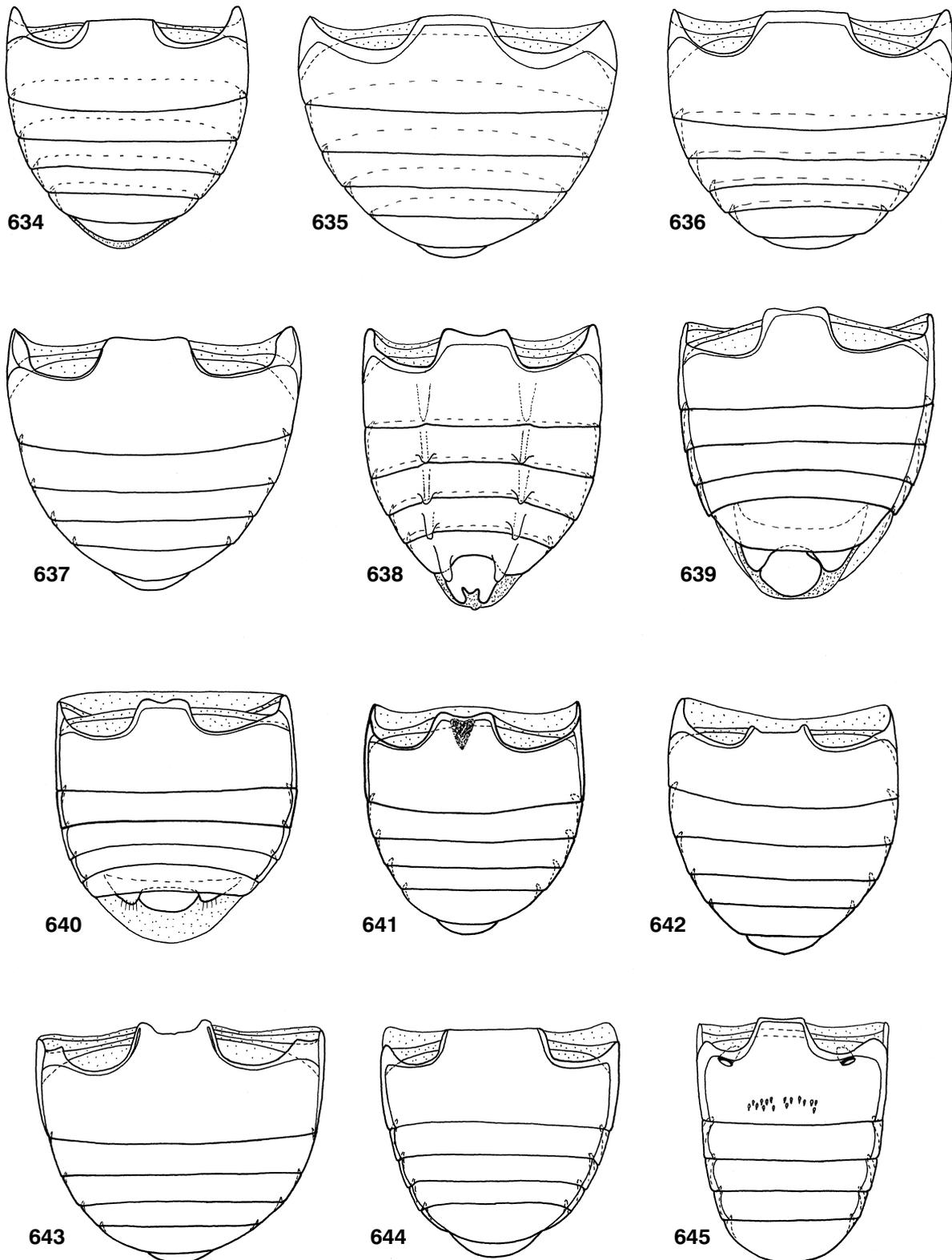
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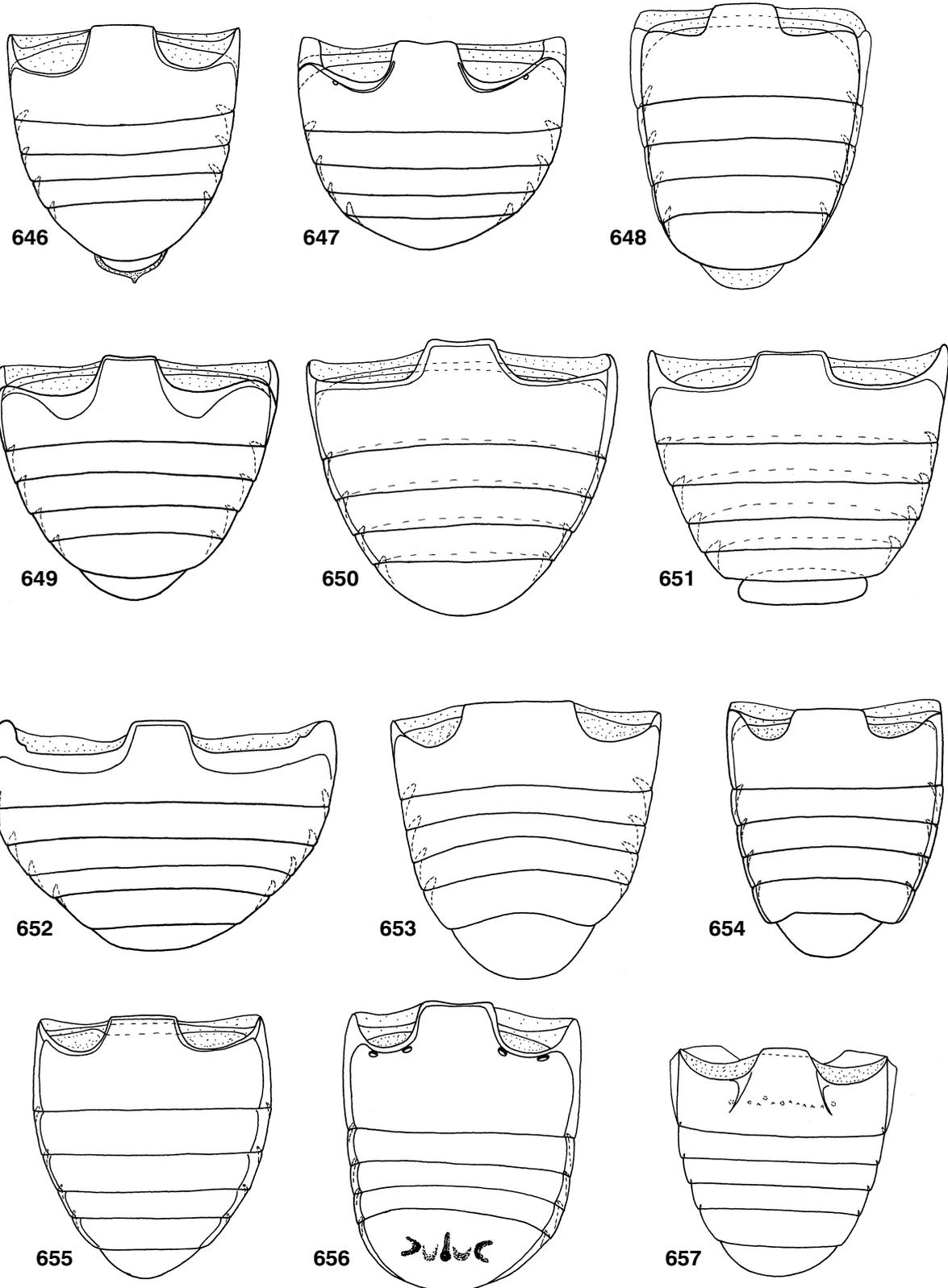
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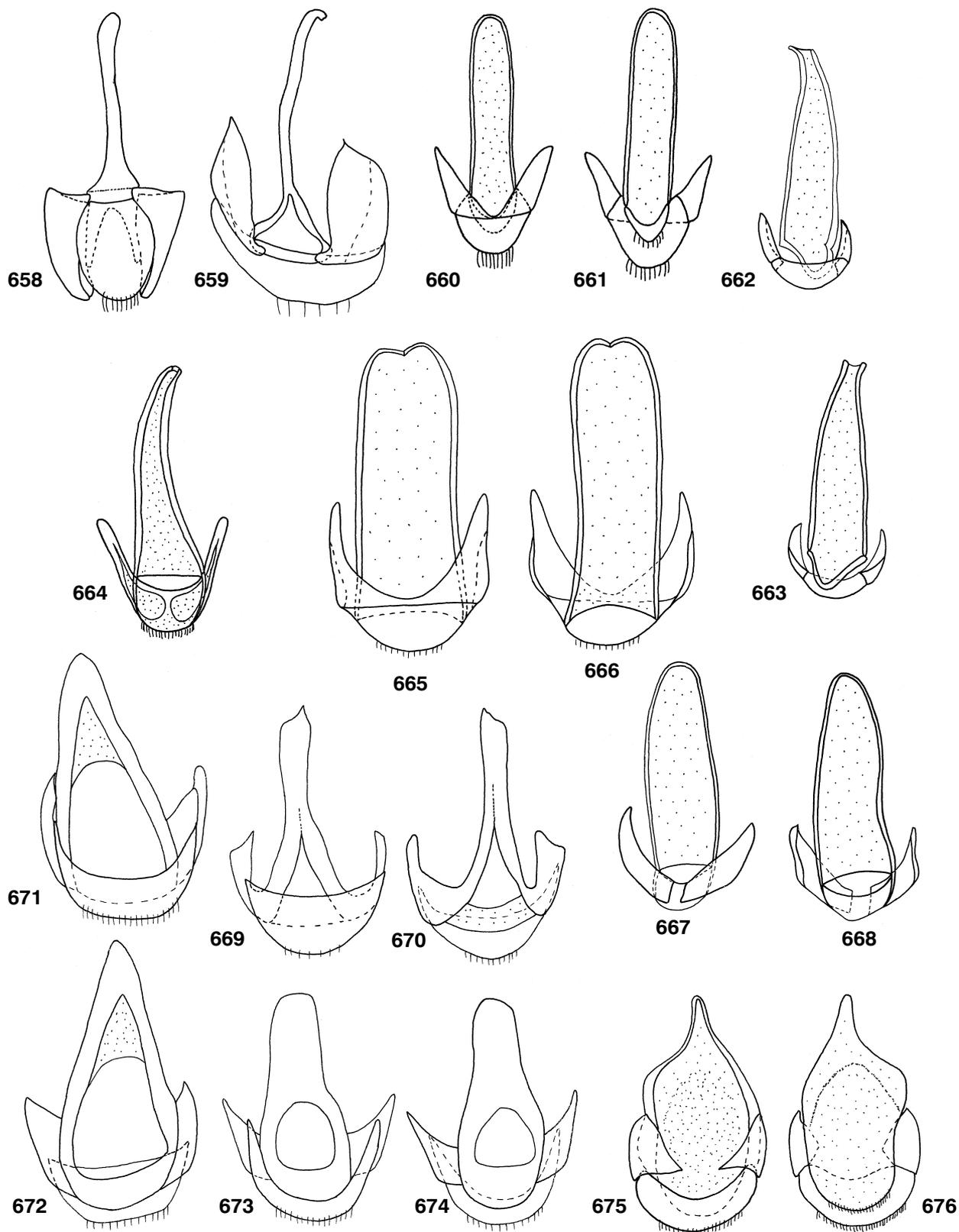
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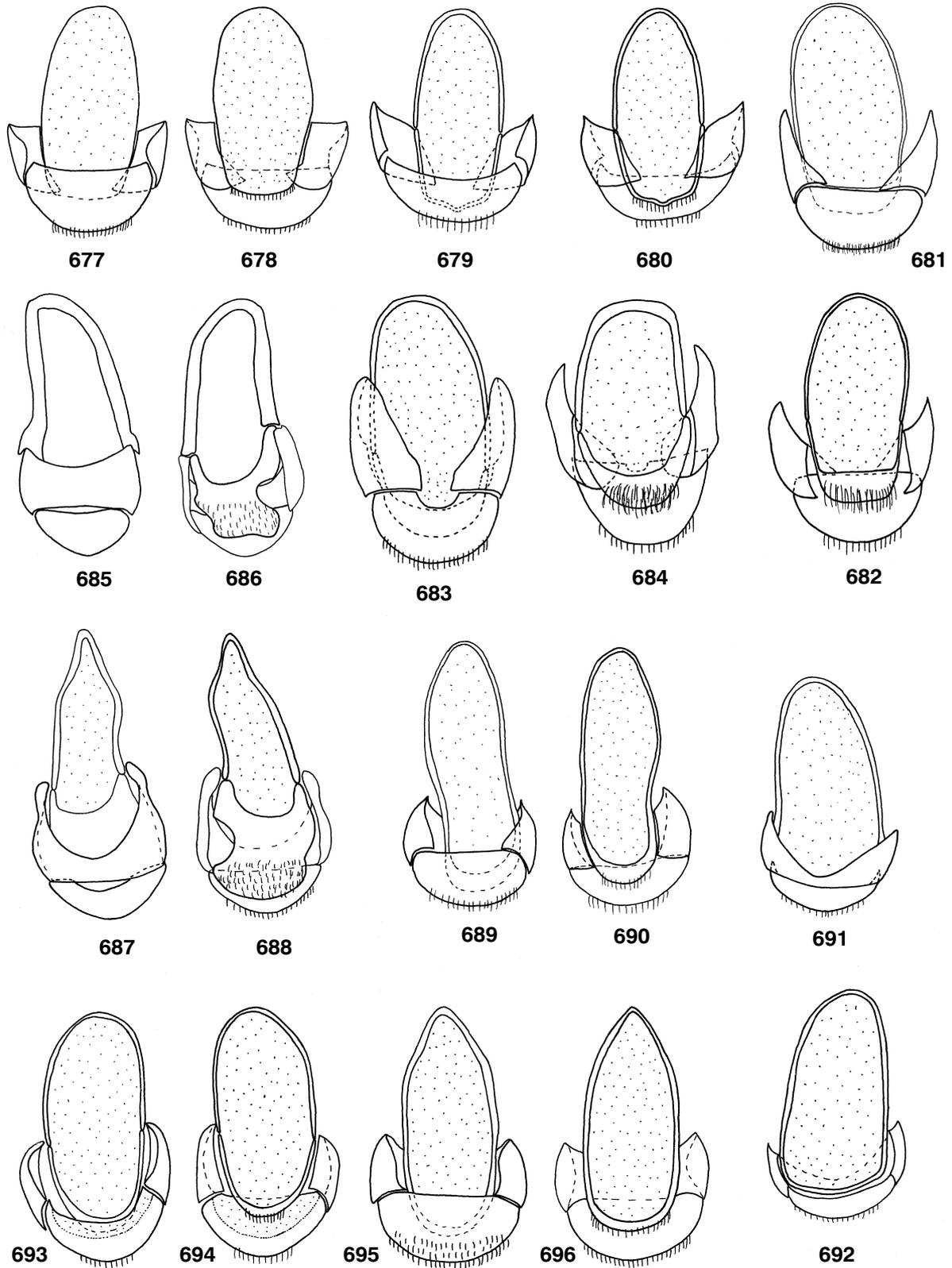
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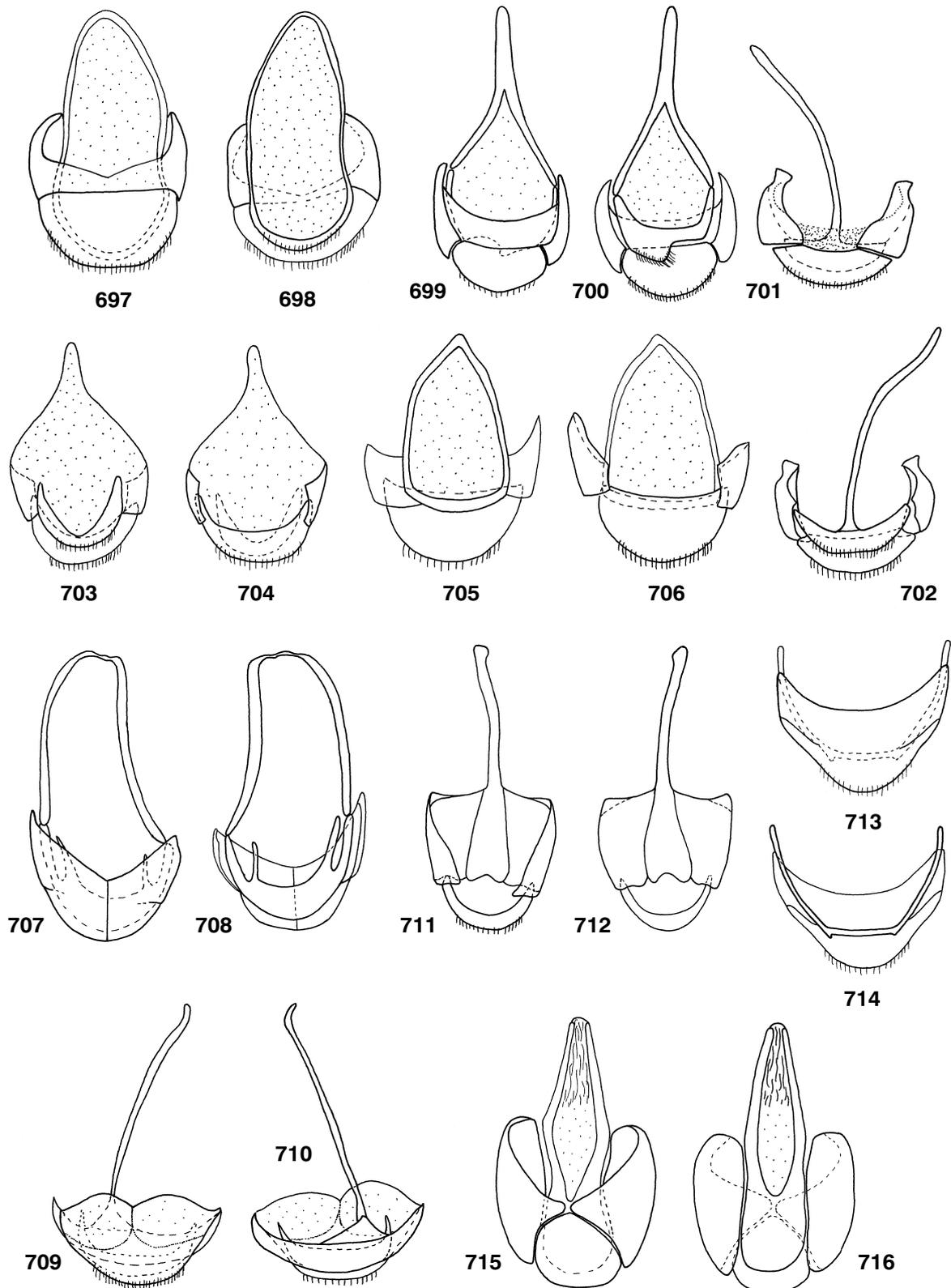
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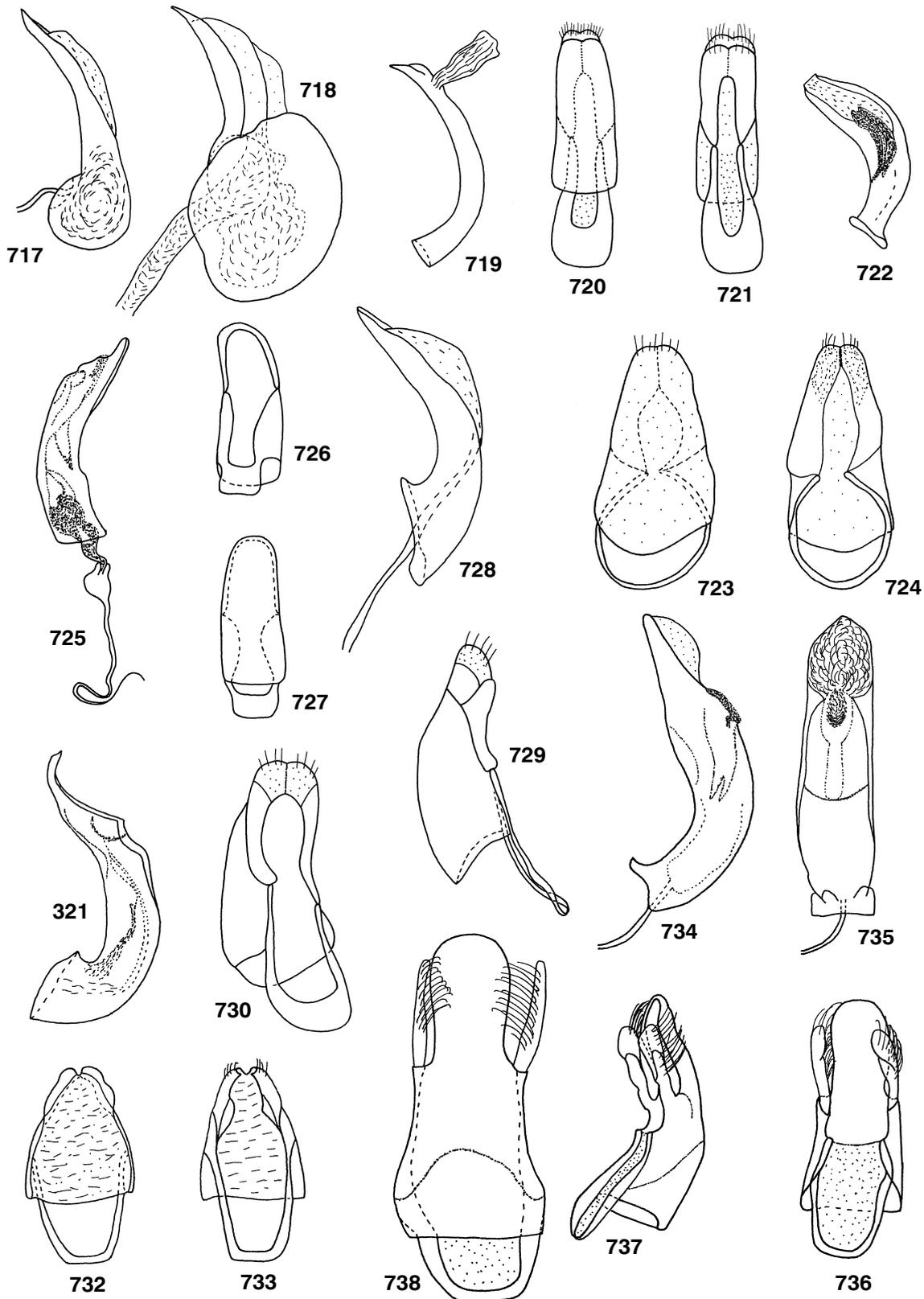
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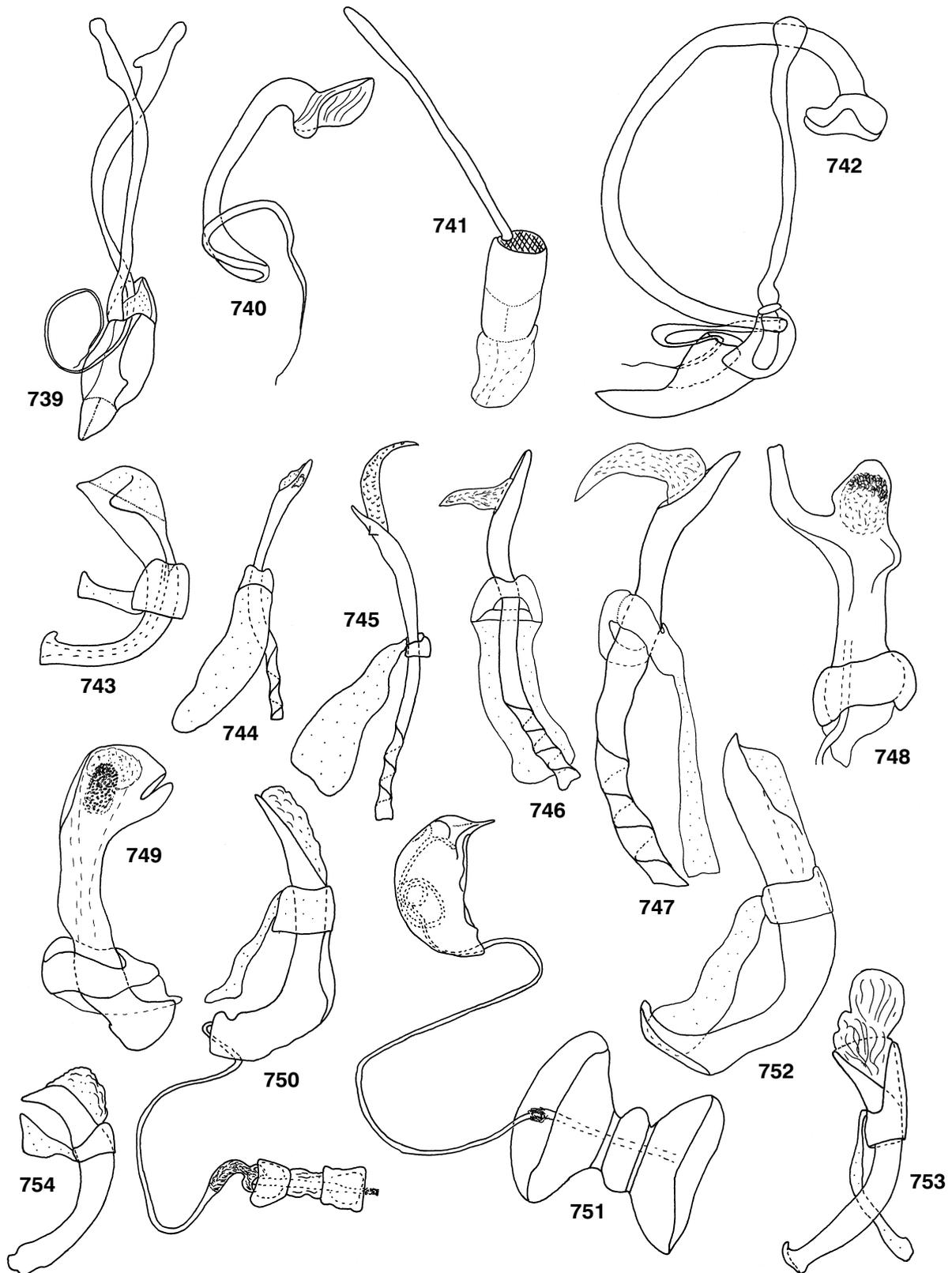
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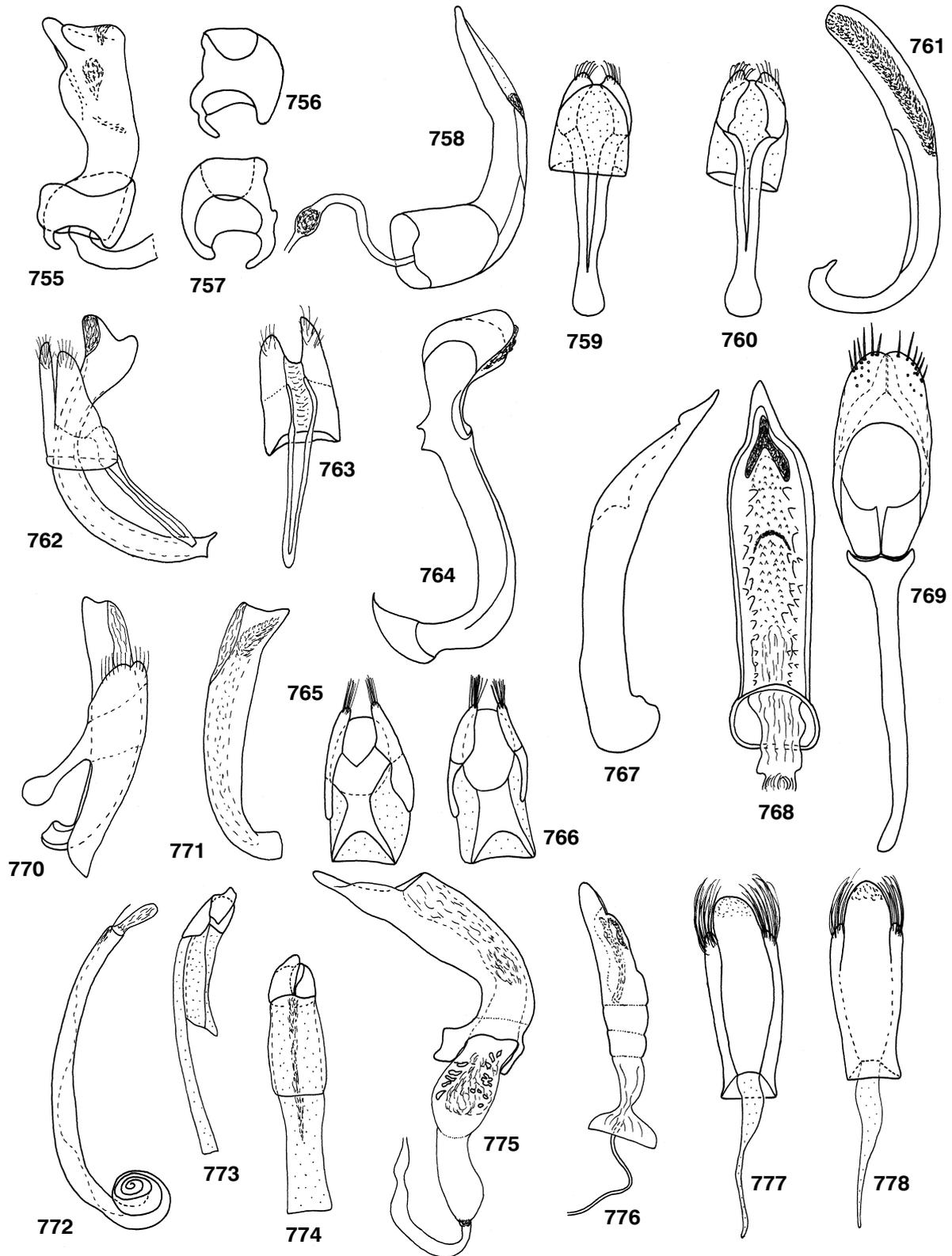
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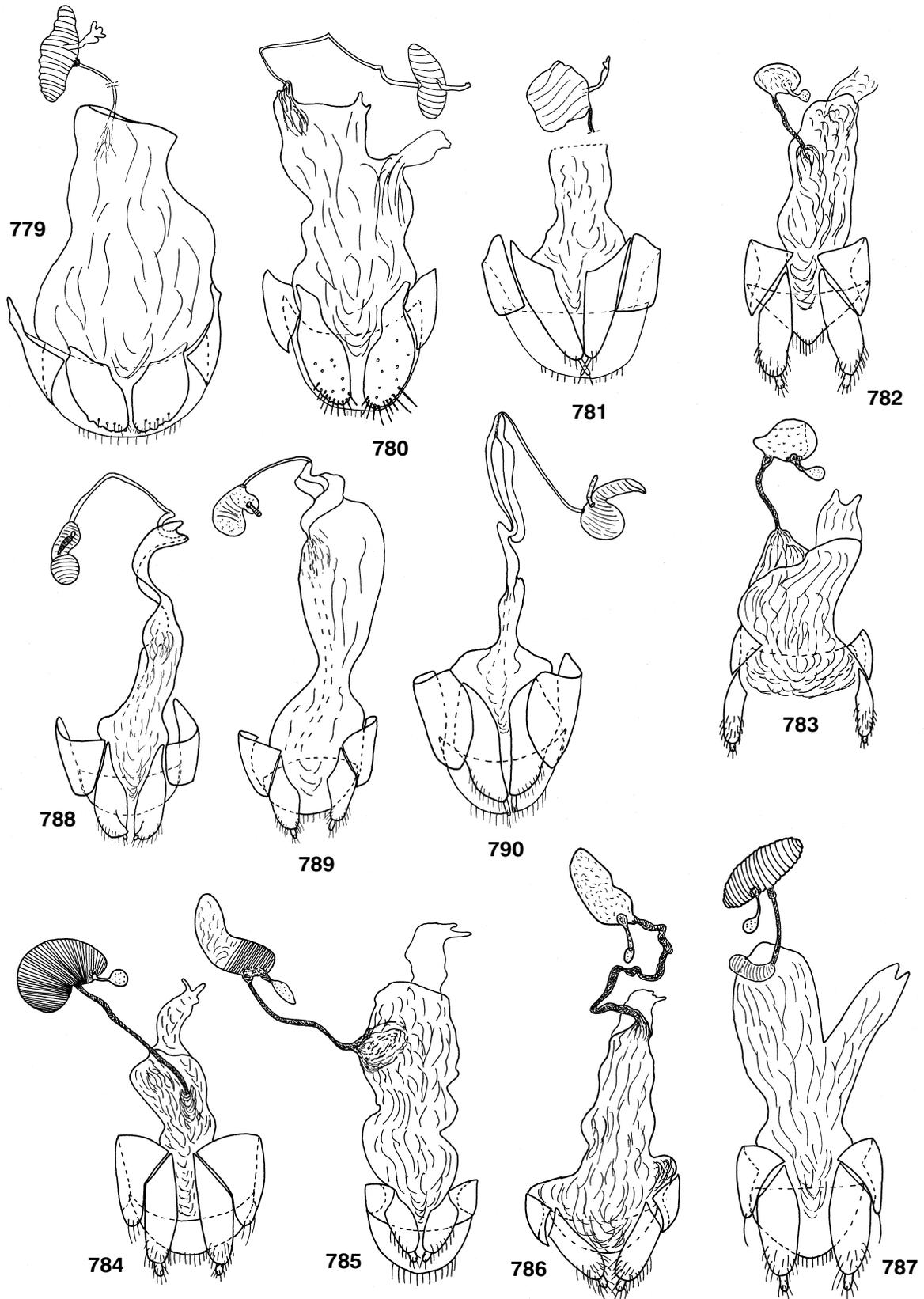
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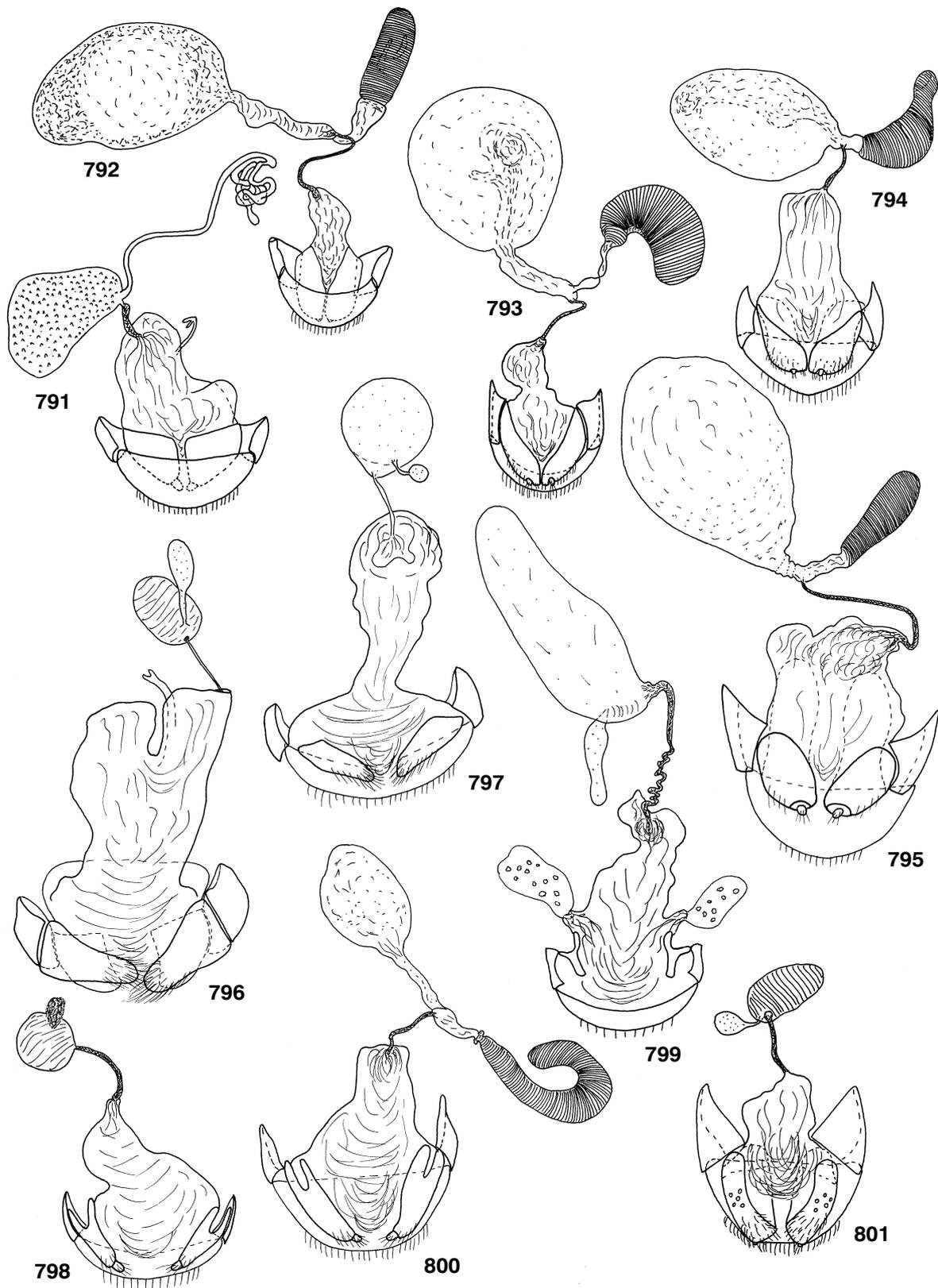
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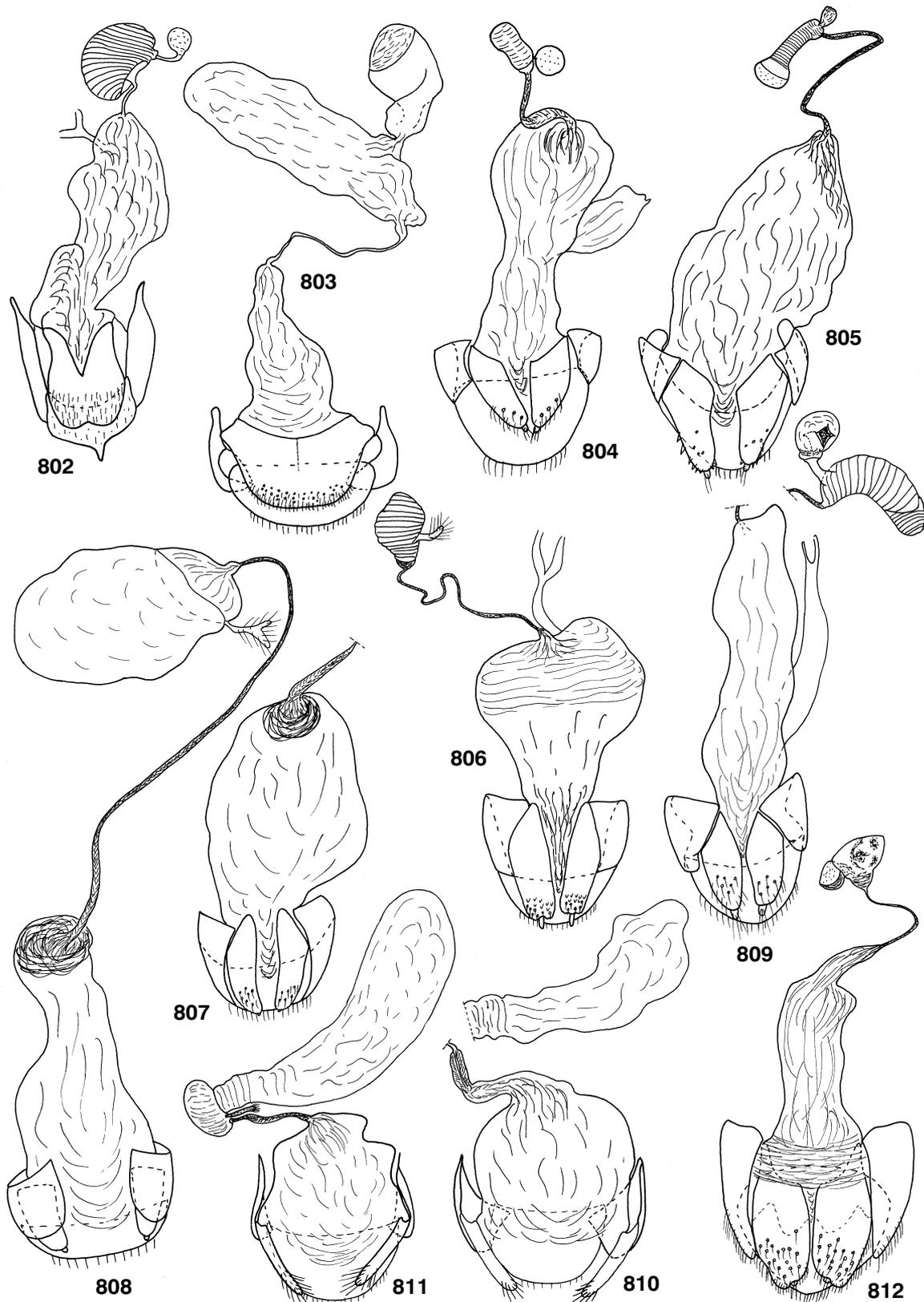
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Figures 779–790. Female genitalia, ventral: (779) *Holoparamesus* sp.; (780) *Merophysia* sp.; (781) *Displotera beloni* Wasmann; (782) *Leiestes seminiger* (Gyllenhal); (783) *Panamomus lewisi* Gorham; (784) *Phymaphora pulchella* Newman; (785) *Rhanidea unicolor* (Ziegler); (786) *Panaleies decoratus* (Gorham); (787) *Stethorhanis borealis* Blaisdell; (788) *Microzenus laticollis* Wollaston; (789) *Eidoreus minutus* Sharp; (790) *Adamia mericana* sp. nov.

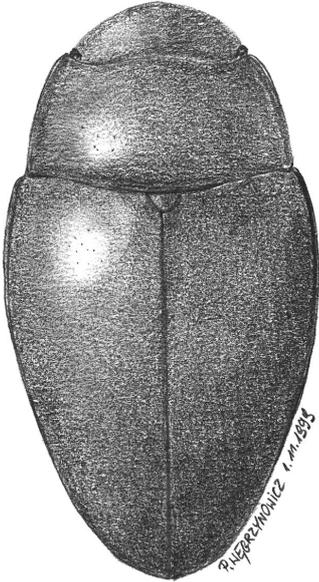


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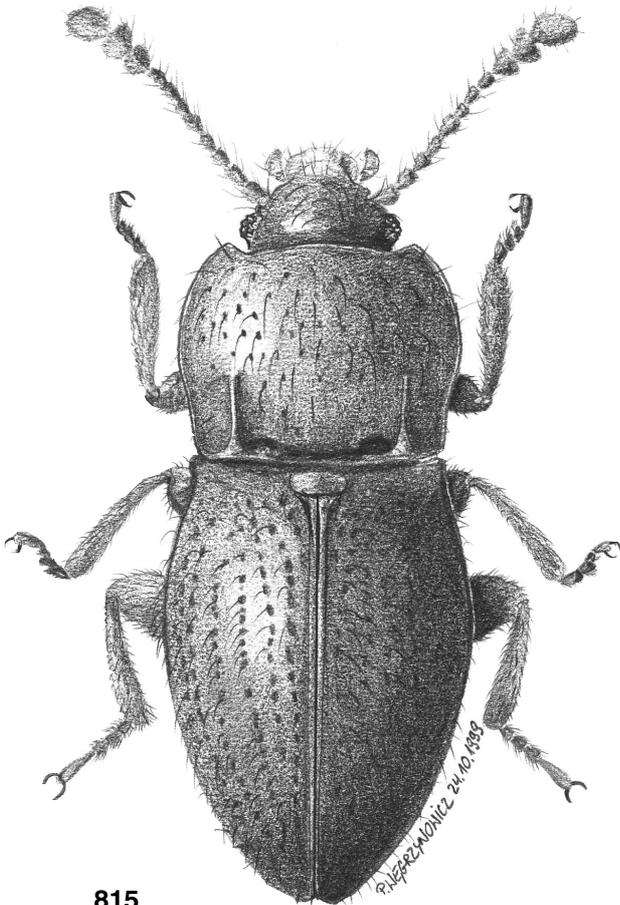
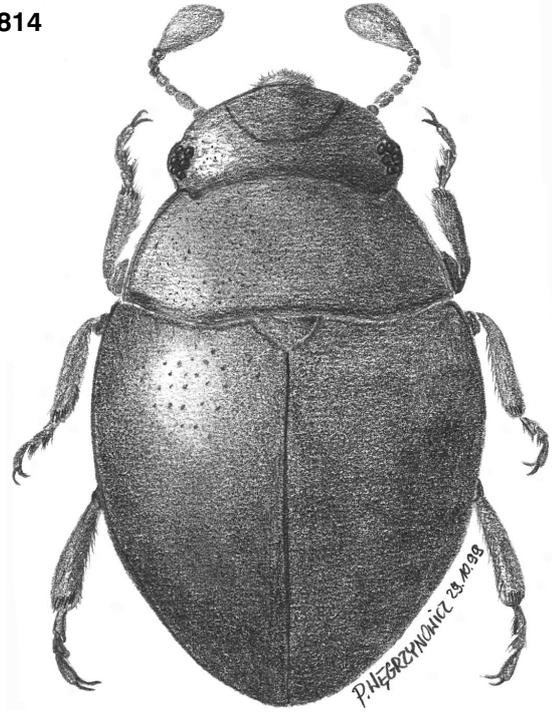


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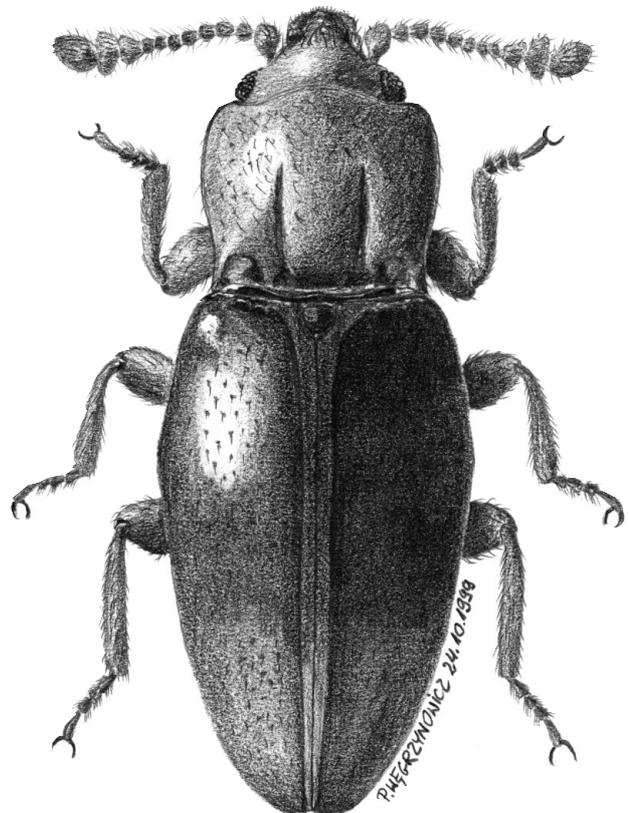
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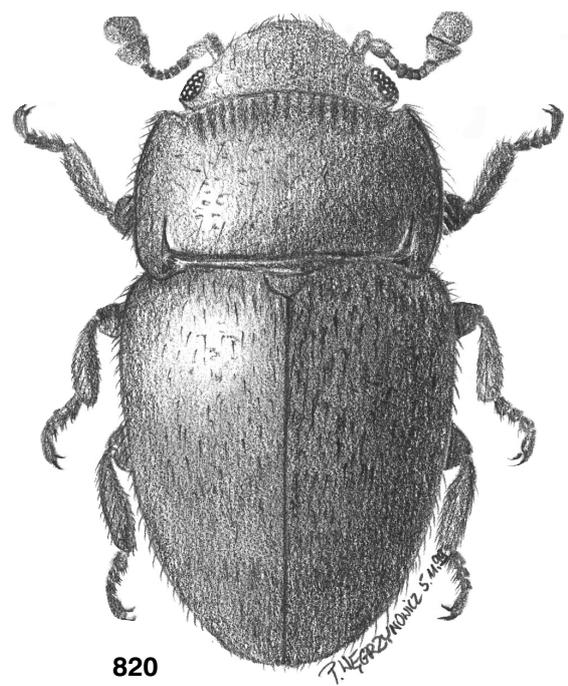
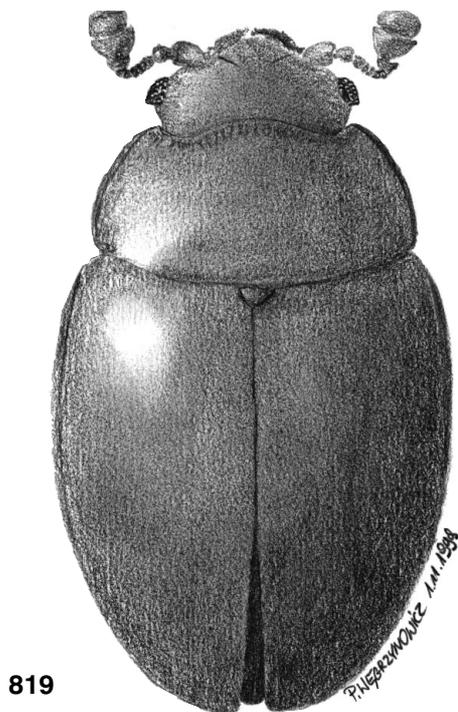
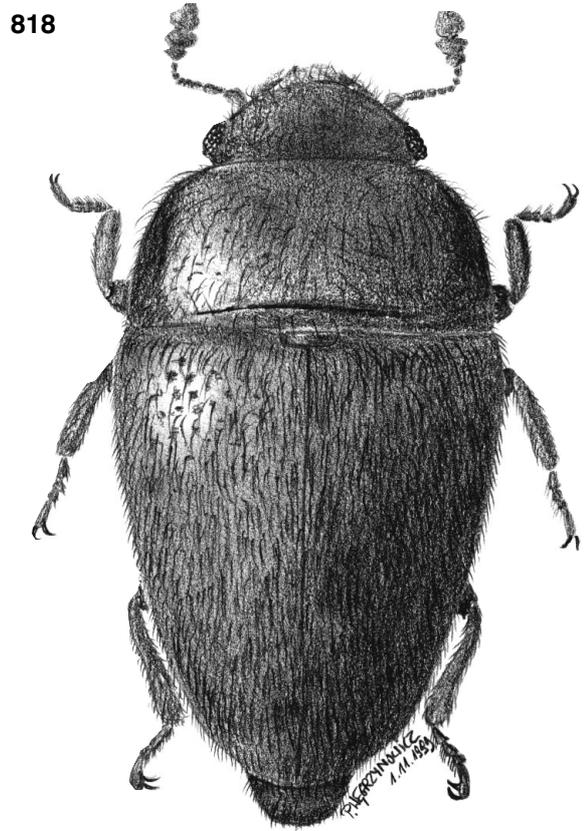
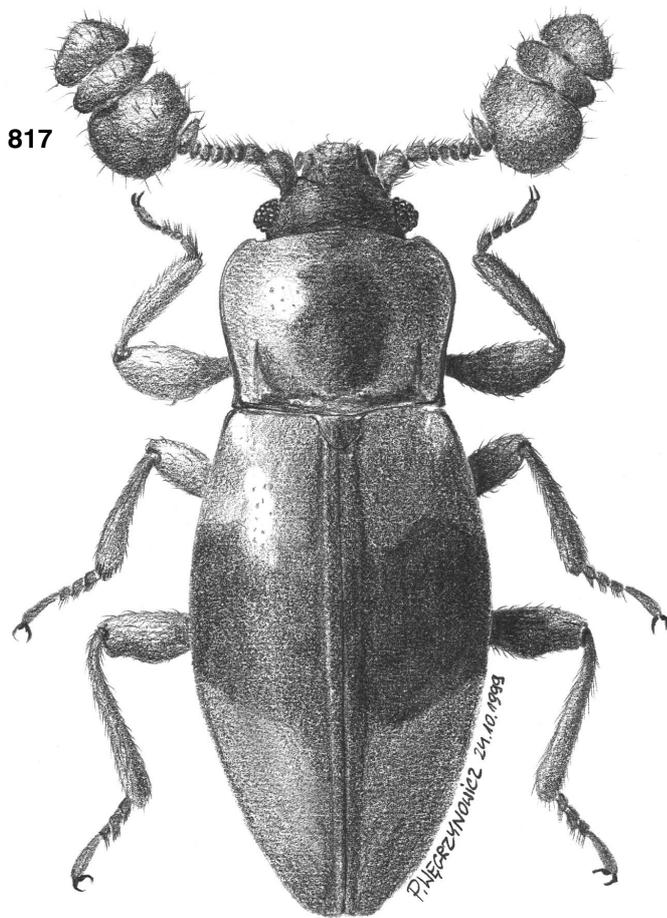


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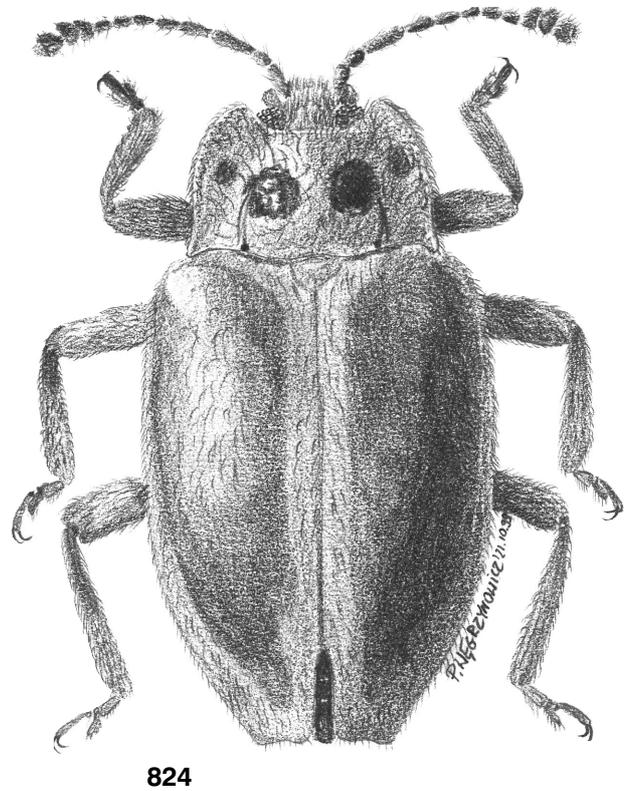
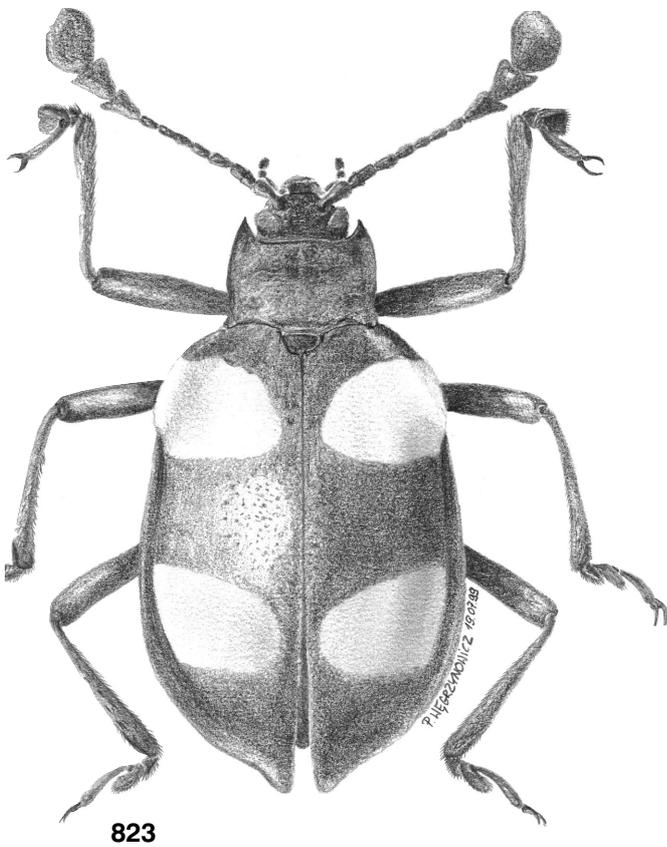
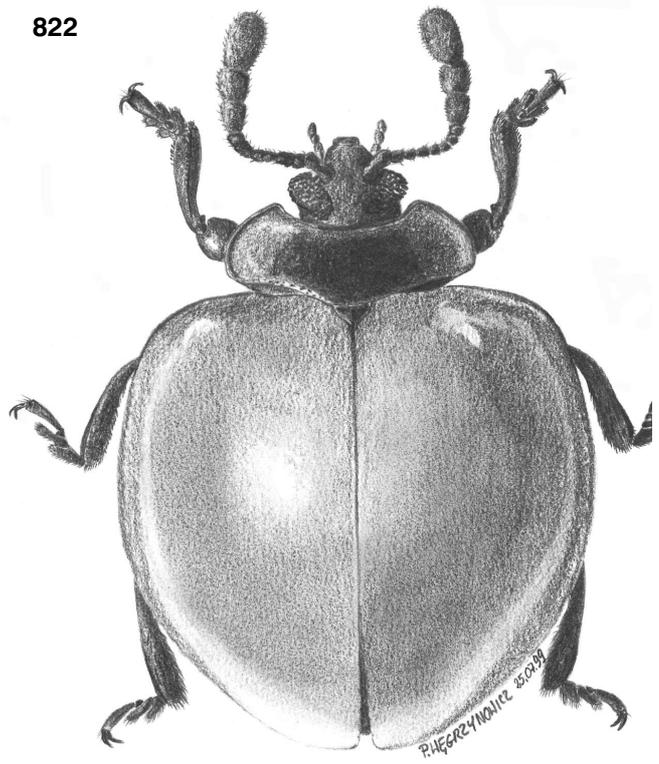
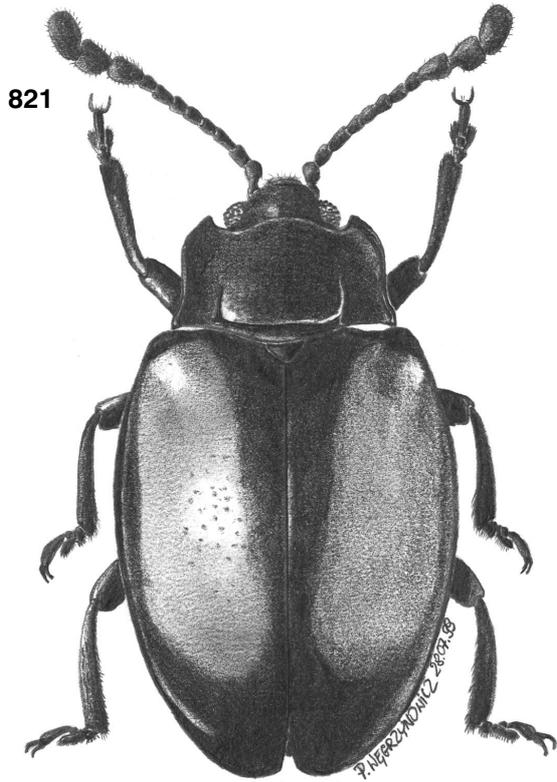


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Figures 813–816. (813) *Merophysia* sp.; (814) *Displotera beloni* Wasmann; (815) *Panamomus lewisi* Gorham; (816) *Rhanidea unicolor* (Ziegler).

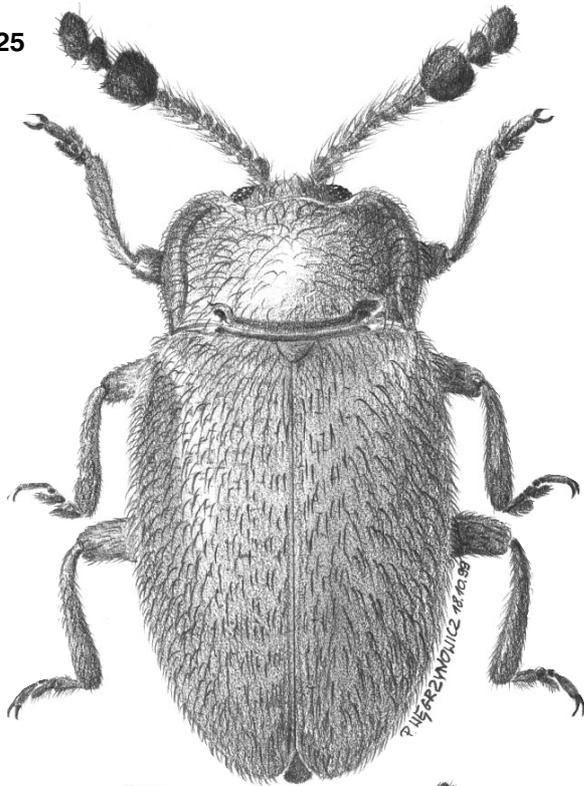


Figures 817–820. (817) *Phymaphora pulchella* Newman; (818) *Microxenus laticollis* Wollaston; (819) *Eidoreus minutus* Sharp; (820) *Adamia mexicana* sp. nov.

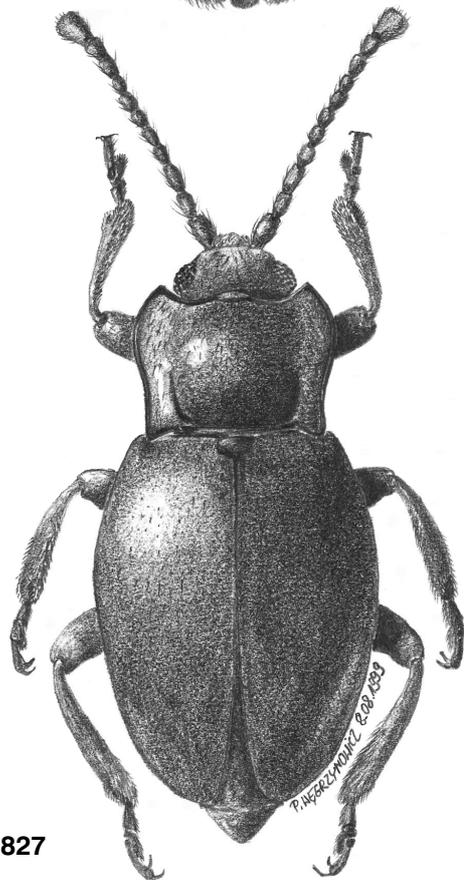
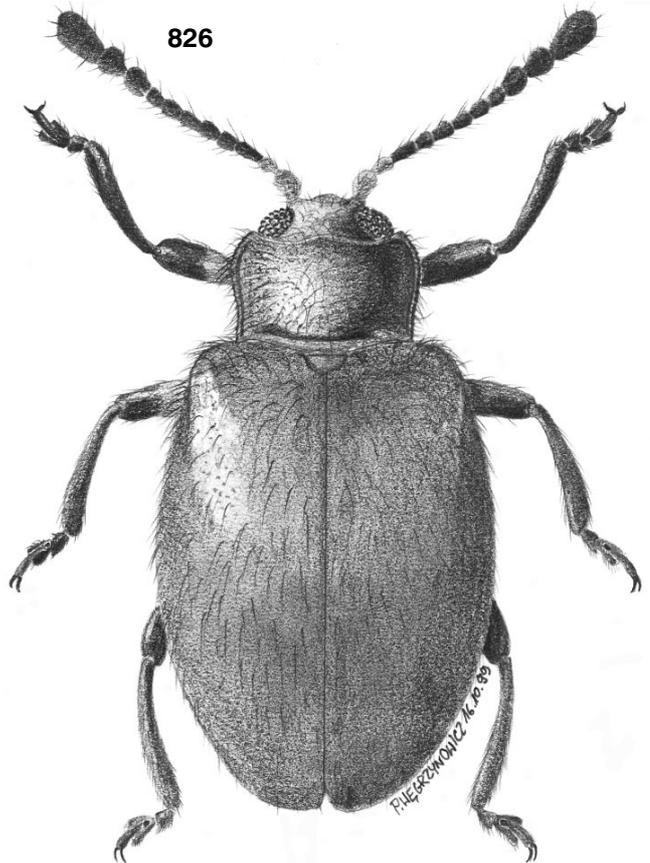


Figures 821–824. (821) *Endomychus plagiatus* (Gorham); (822) *Cyclotoma sumatrensis* (Gorham); (823) *Eucteanus coelestinus* Gerstaecker; (824) *Epipocus bifidus* Gerstaecker.

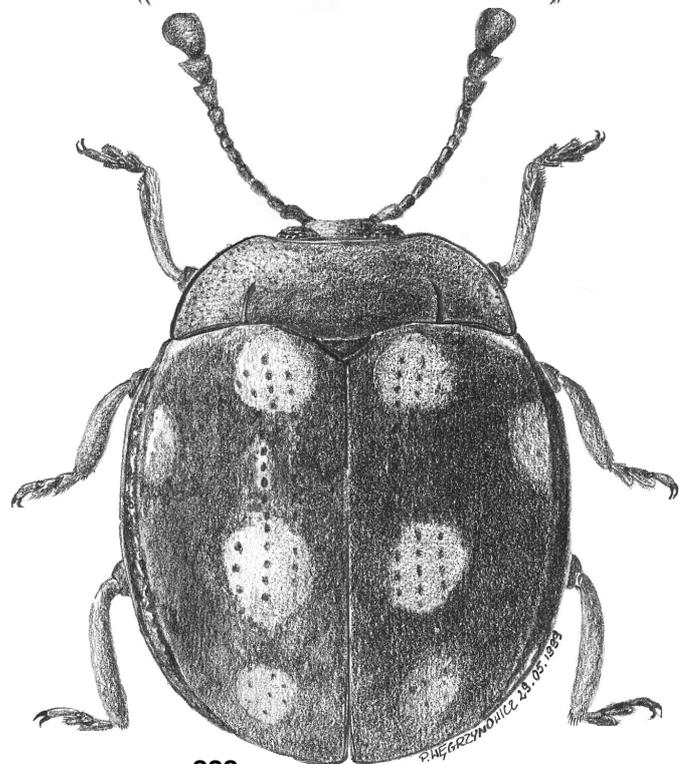
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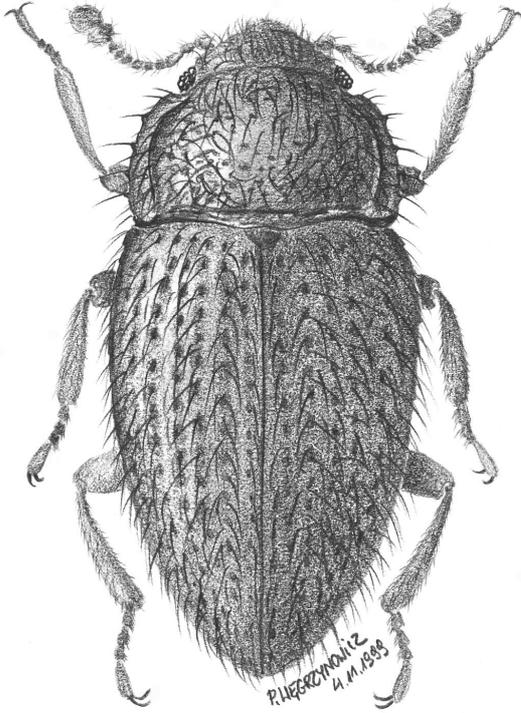
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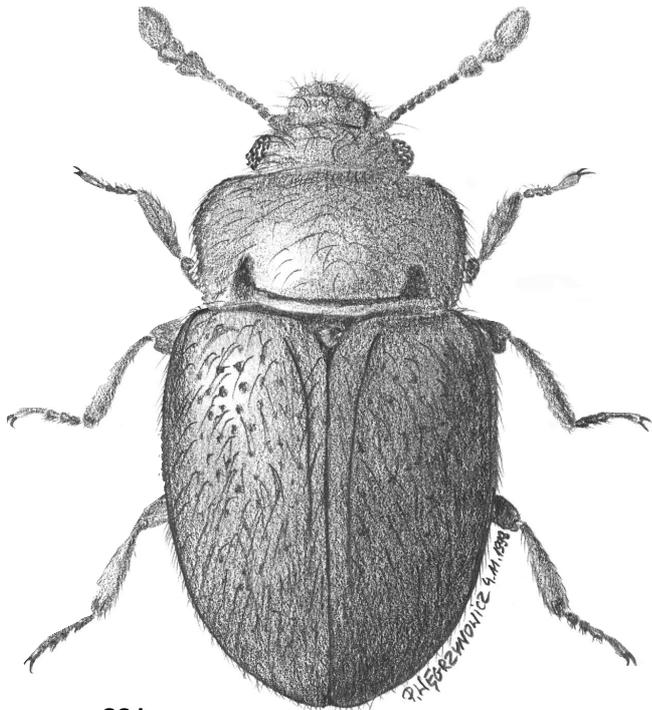
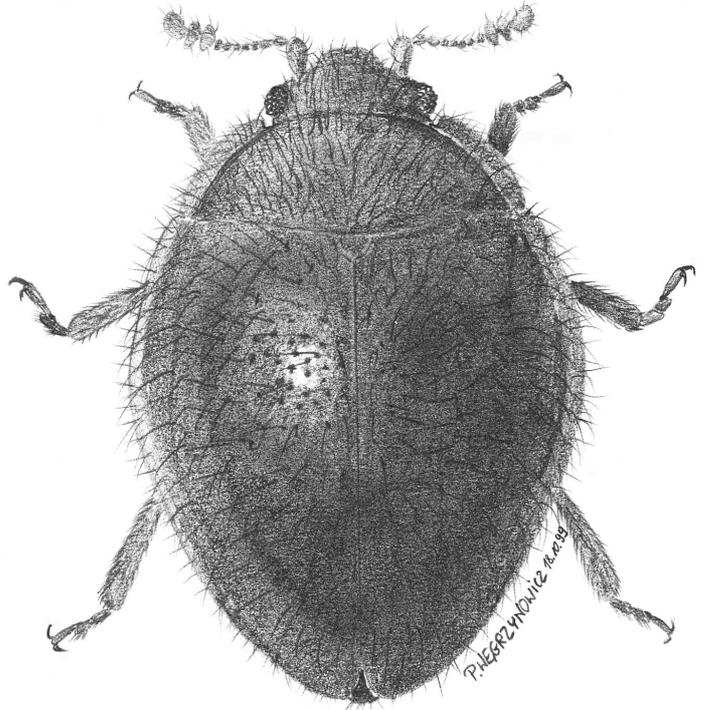
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Figures 825–828. (825) *Danae* sp.; (826) *Saula ferruginea* Gerstaecker; (827) *Lycoperdina koltzei* Reitter; (828) *Beccariola* sp.

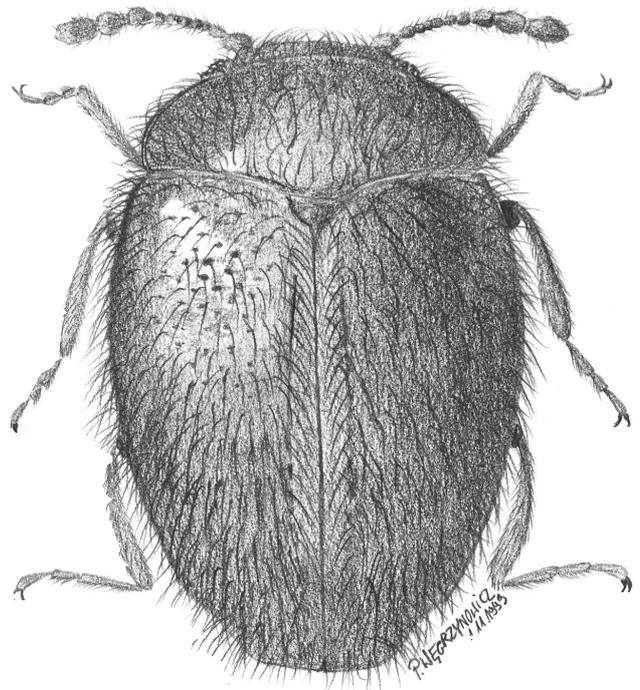
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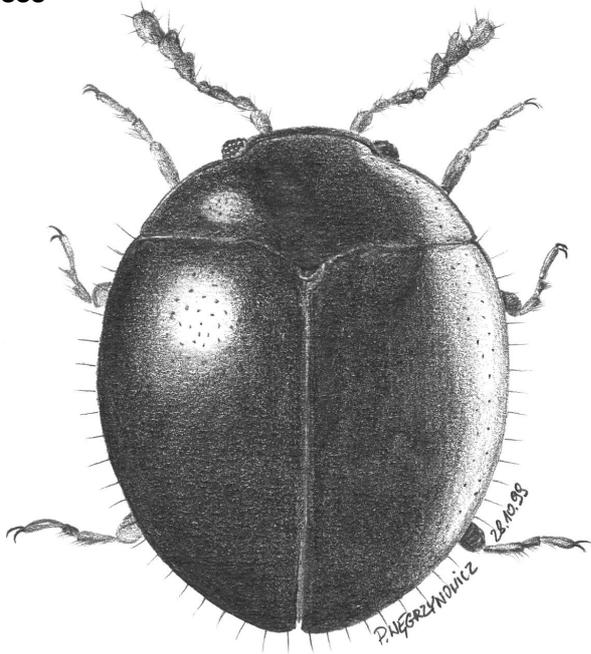
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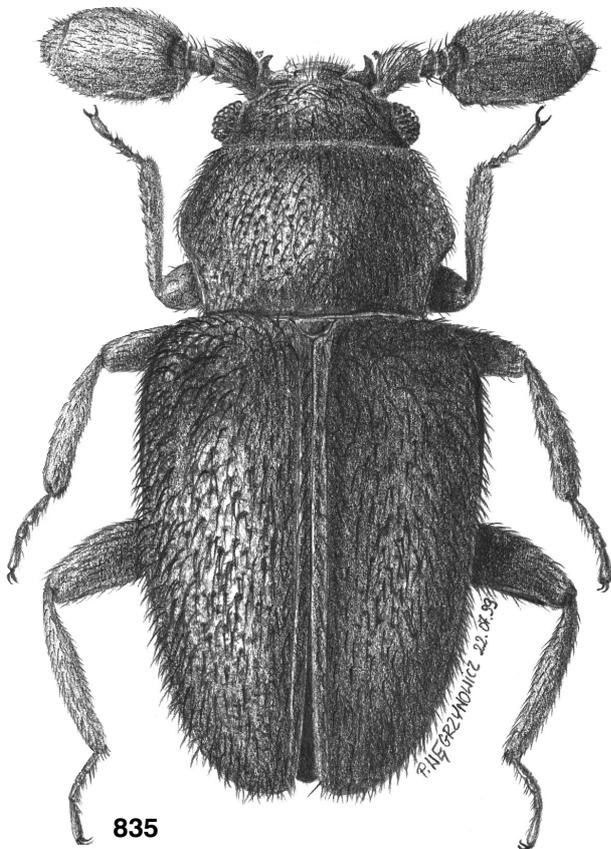
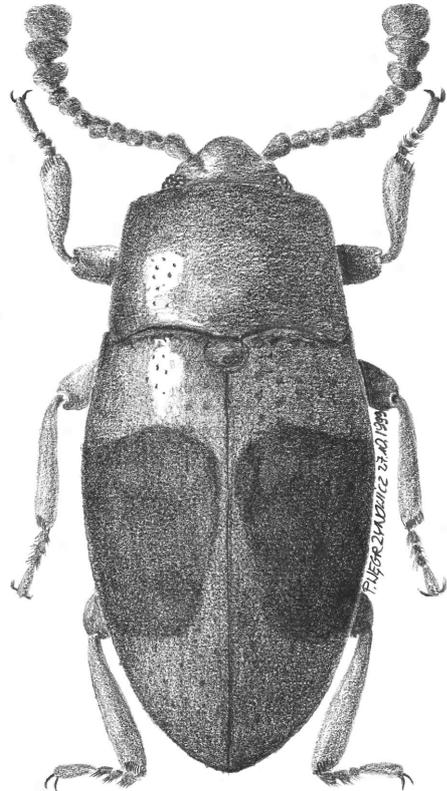
832

Figures 829–832. (829) *Mycetaea subterranea* (Fabricius); (830) *Agaricophilus reflexus* Motschulsky; (831) *Symbiotes gibberosus* (Lucas); (832) *Mychothenus asiaticus* Sasaji.

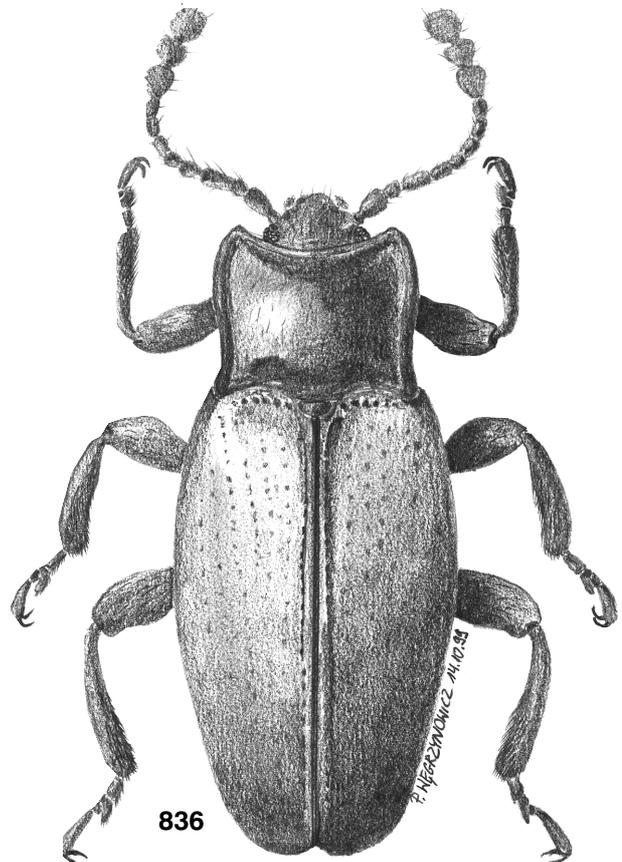
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Figures 833–836. (833) *Micropsephodes serraticornis* Champion; (834) *Erotendomychus bimaculatus* Lea; (835) *Trochoideus desjardinsi* Guérin; (836) *Xenomyctes morrisoni* Horn.

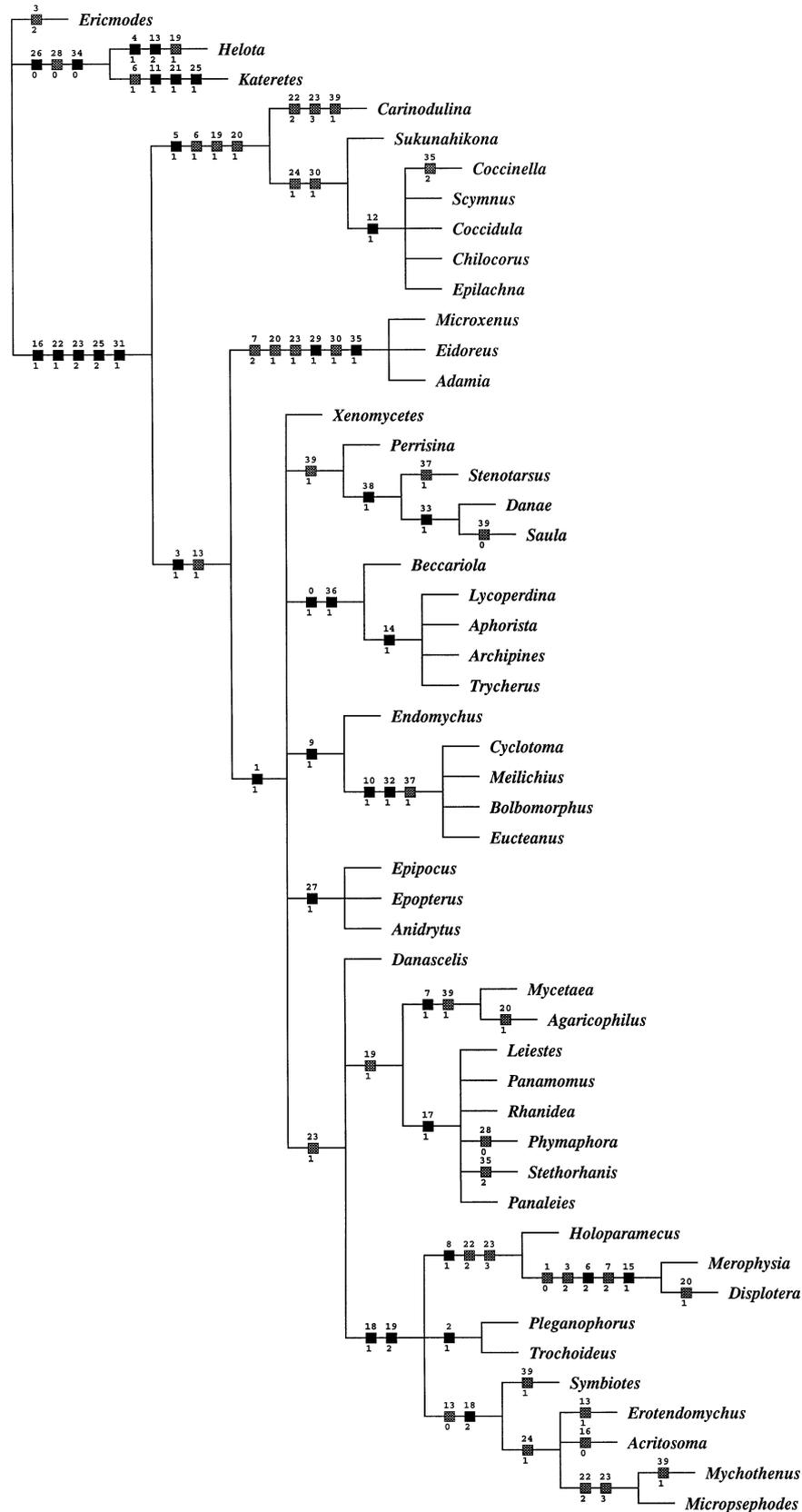


Figure 837. # 0 of 6 mhennig\* trees (L 78, CI 65, RI 87); all characters unordered; black boxes indicate synapomorphies; shaded, various degree of homoplasy.

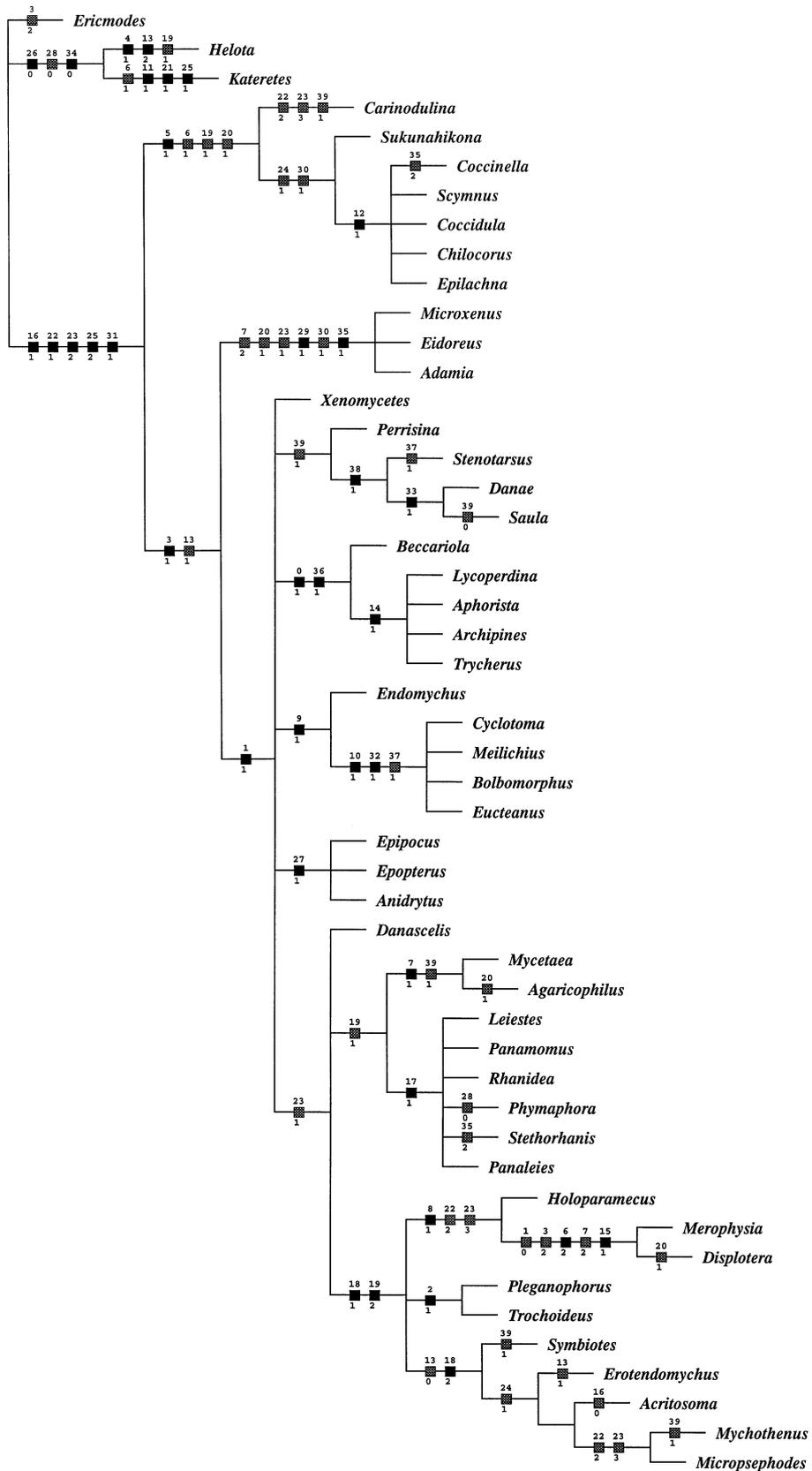


Figure 838. # 1 of 6 mhennig\* trees (L 78, CI 65, RI 87); all characters unordered; black boxes indicate synapomorphies; shaded, various degree of homoplasy.

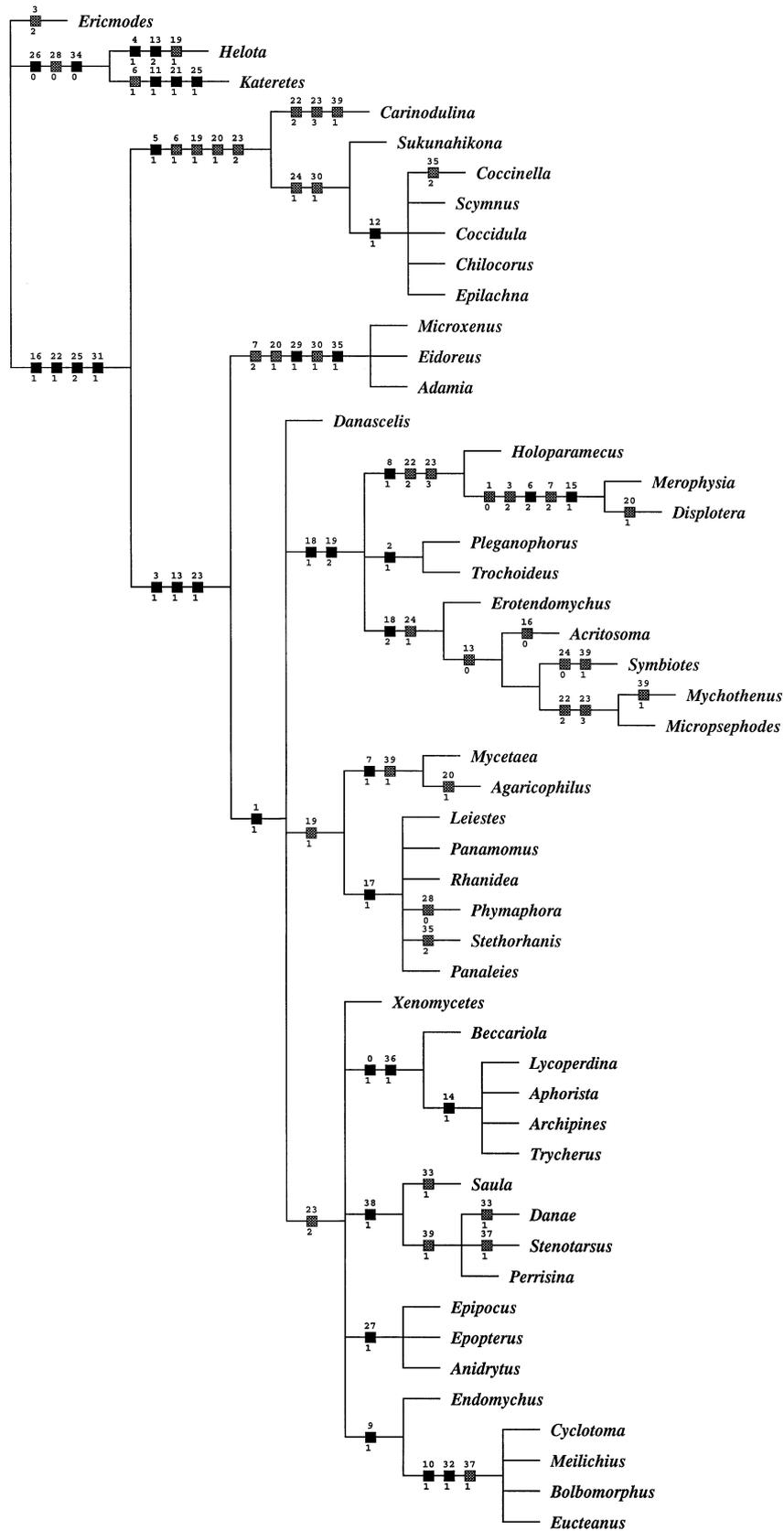


Figure S39. # 2 of 6 mhennig\* trees (L 78, CI 65, RI 87); all characters unordered; black boxes indicate synapomorphies; shaded, various degree of homoplasy.

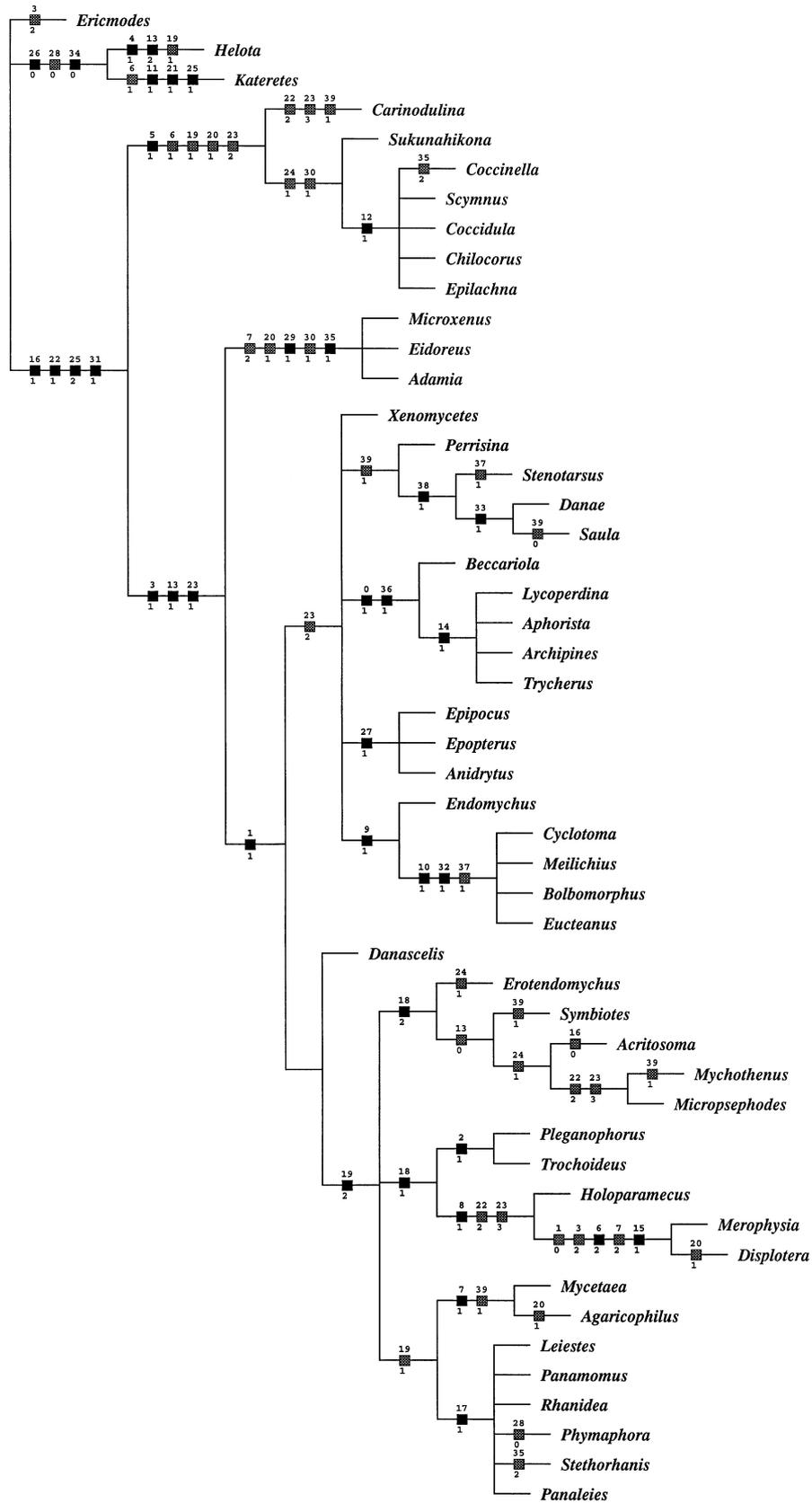


Figure 840. # 3 of 6 mhennig\* trees (L 78, CI 65, RI 87); all characters unordered; black boxes indicate synapomorphies; shaded, various degree of homoplasy.

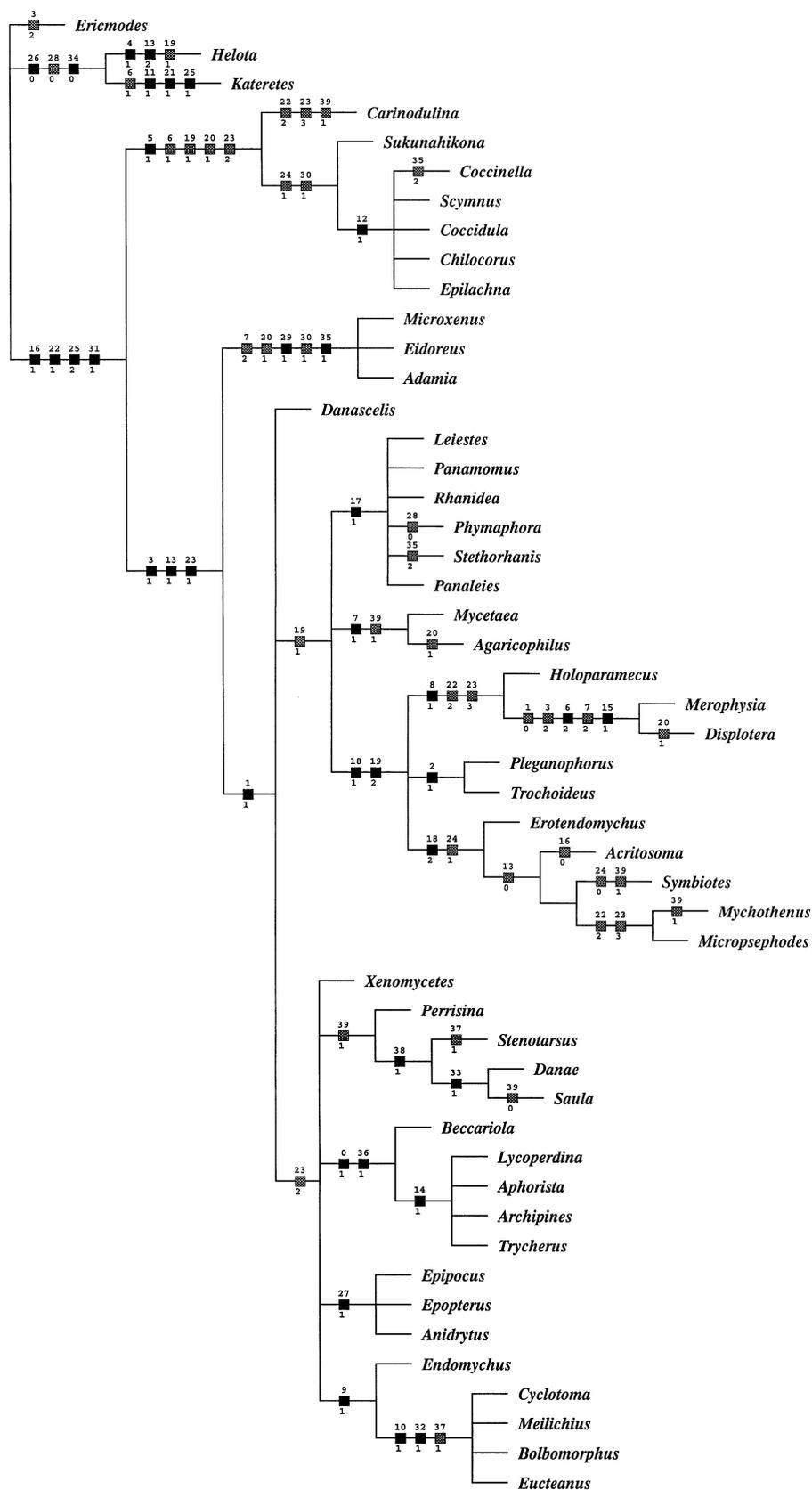


Figure 841. # 4 of 6 mhennig\* trees (L 78, CI 65, RI 87); all characters unordered; black boxes indicate synapomorphies; shaded, various degree of homoplasy.

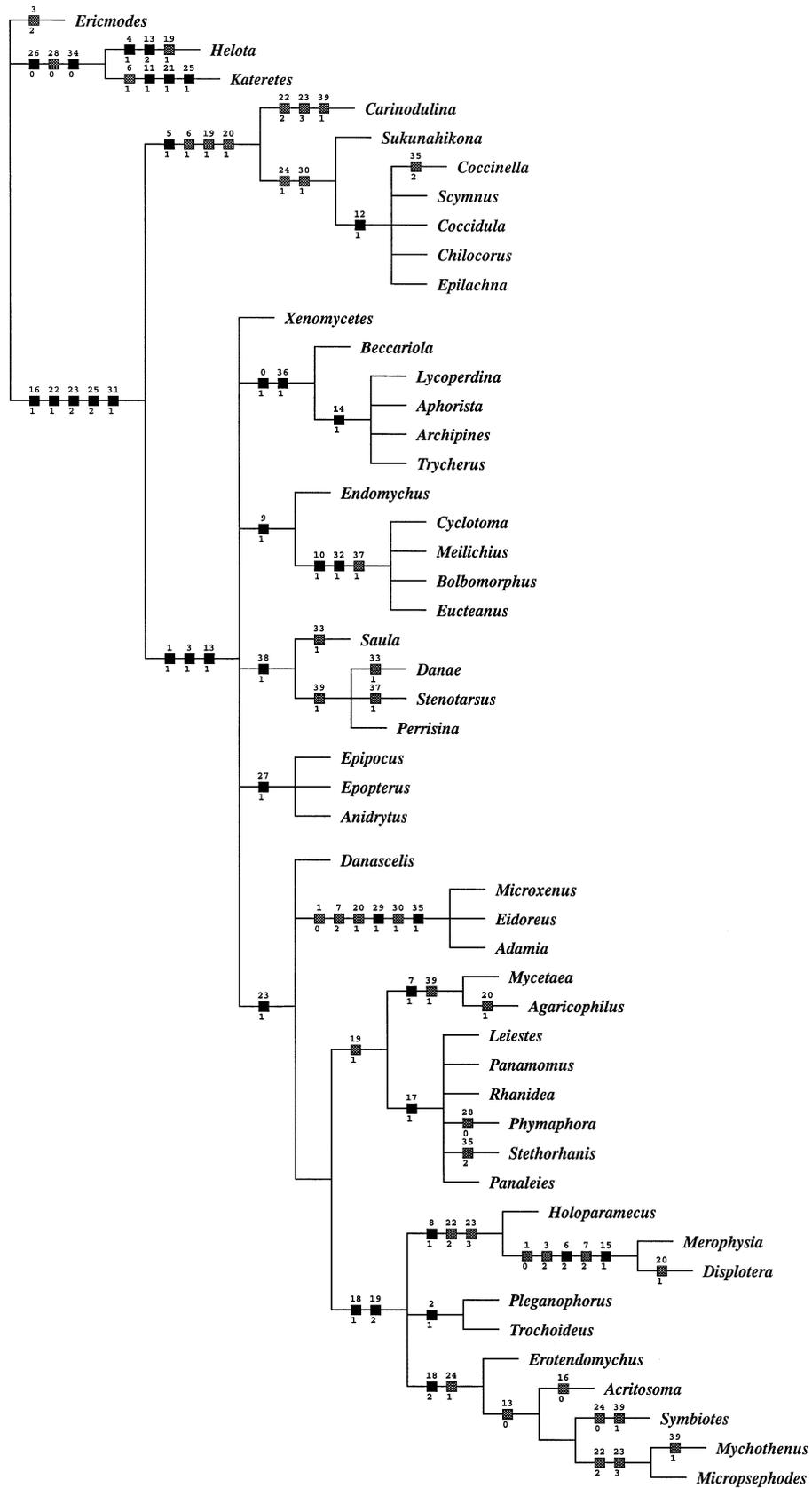


Figure 842. # 5 of 6 mhennig\* trees (L 78, CI 65, RI 87); all characters unordered; black boxes indicate synapomorphies; shaded, various degree of homoplasy.

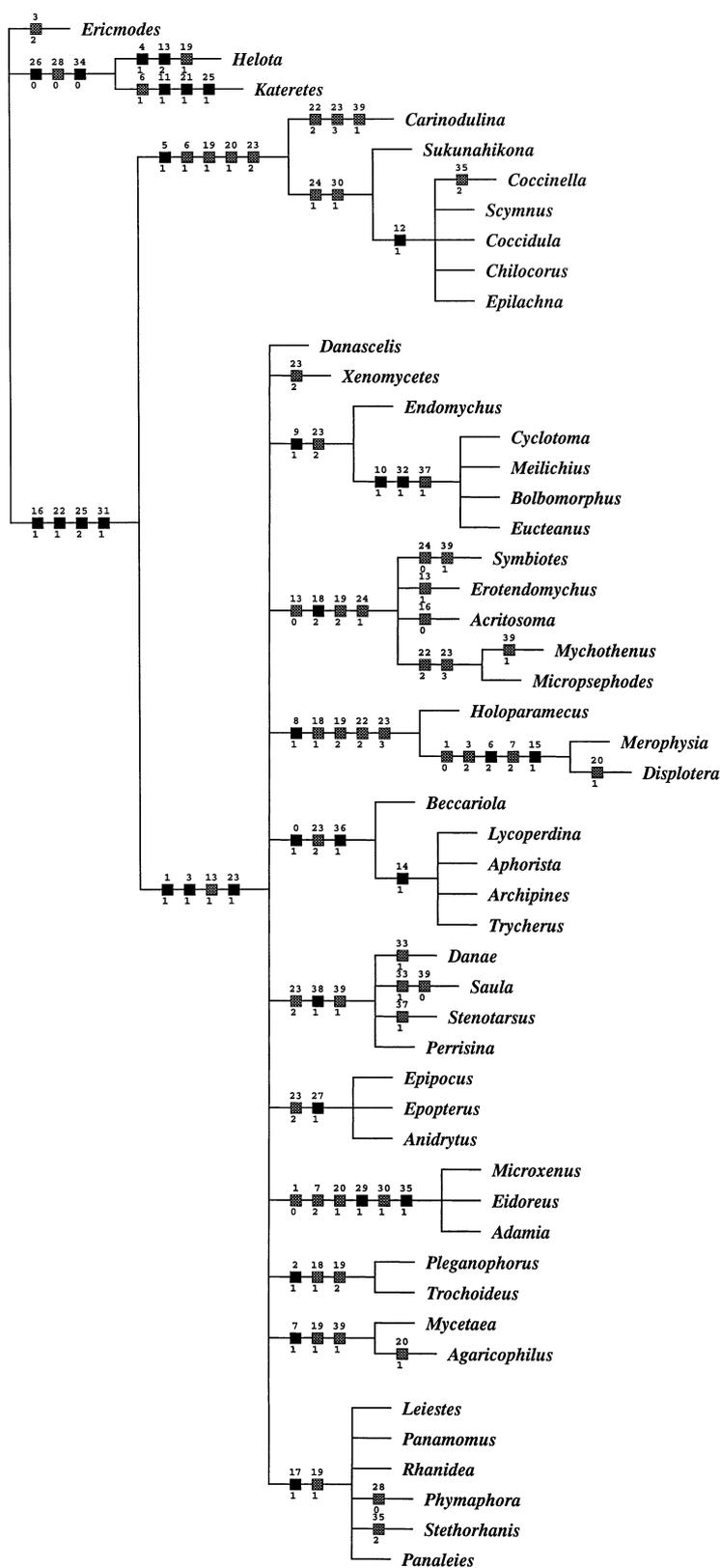


Figure 843. Preferred cladogram; Nelsen consensus tree from six mheuning\* trees (L 89, CI 57, RI 81); all charactres unordered; black boxes indicate synapomorphies; shaded, various degree of homoplasy.

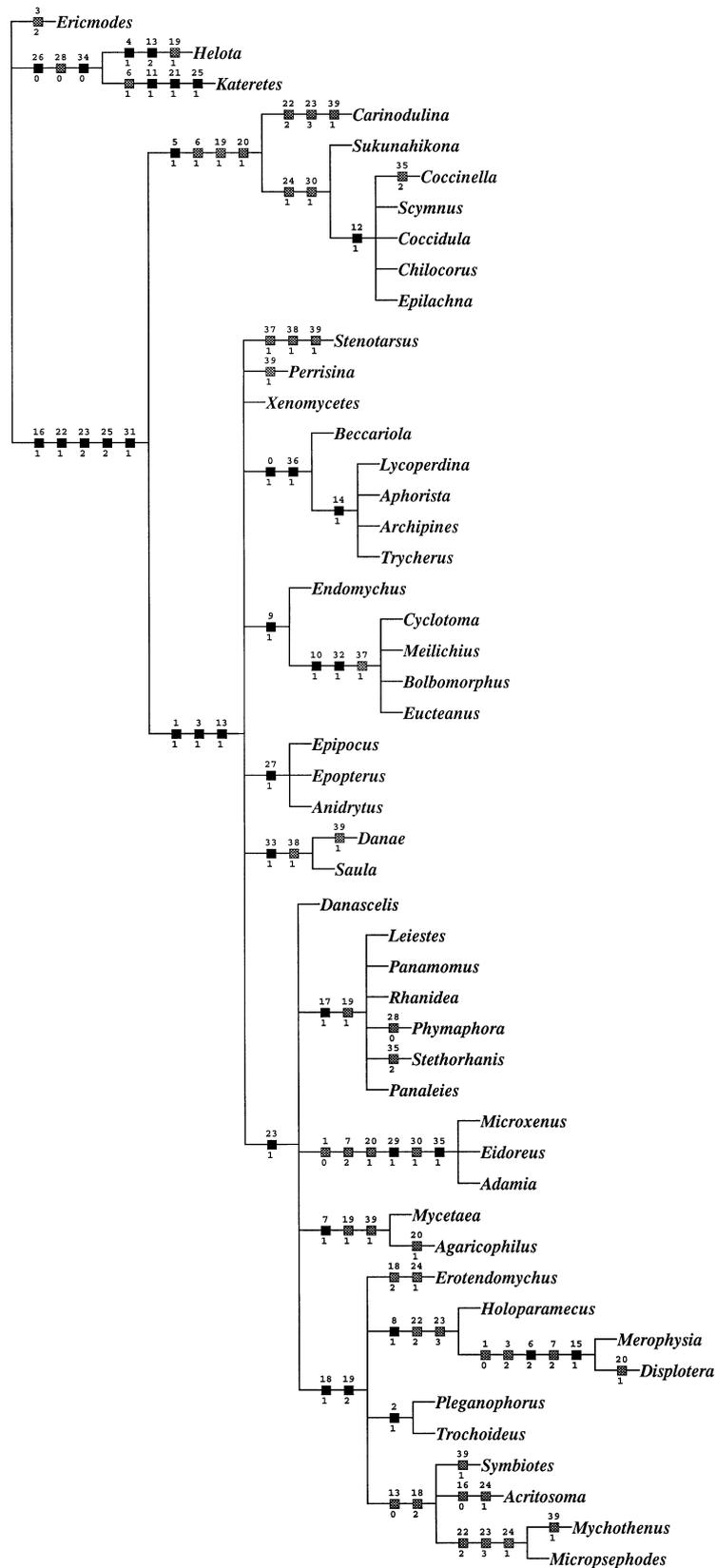


Figure 844. Nelsen consensus tree from seven mhenning\* trees, reached after successive weighting (L 83, CI 78, RI 91); black boxes indicate synapomorphies; shaded, various degree of homoplasy.