ANNALES ZOOLOGICI (Warszawa), 2011, 61(1): 1-217

PHYLOGENY OF THE COLEOPTERA BASED ON MORPHOLOGICAL CHARACTERS OF ADULTS AND LARVAE

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Abstract.— In order to infer phylogenetic relationships within the extraordinarily species-rich order Coleoptera, a cladistic analysis is performed, in which 516 adult and larval morphological characters are scored for 359 beetle taxa, representing 314 families or subfamilies plus seven outgroup taxa representing seven holometabolan orders. Many morphological features are discussed at length with accompanying illustrations, and an attempt is made to homologize these and employ a uniform set of terms throughout the order. The resulting data matrix is analyzed using the parsimony ratchet in conjunction with implied weighting. The resulting most parsimonious tree found the order Strepsiptera to be sister to Coleoptera, each of the four coleopteran suborders to be monophyletic and subordinal relationships as follows: (Archostemata + Adephaga) + (Myxophaga + Polyphaga), but without significant support for either clade. The topology of the remainder of the tree is consistent with many prior molecular and morphological analyses, with the monophyly of superfamilies Hydrophiloidea (sensu lato), Scarabaeoidea and Curculionoidea and many currently recognized families and subfamilies are well supported, with weaker support for Elateroidea, Cucujiformia and Phytophaga.

Key words.— Coleoptera, beetles, morphology, phylogeny, classification.

Introduction

Beetles (order Coleoptera) are an extraordinarily species-rich group, comprising over 360,000 described species (Bouchard *et al.* 2009), of tremendous morphological and ecological diversity with a history dating back at least to the Permian (Ponomarenko 1995). As such, beetles represent an excellent system for addressing a broad spectrum of evolutionary questions, particularly those pertaining to causes and correlates of diversification. Although many efforts have been made to explain this spectacular evolutionary radiation, relatively few attempts have been made to infer the phylogeny of beetles as a whole; of these, all recent attempts have relied on molecular data alone (Hunt *et al.* 2007, Maddison *et al.* 2009, Song *et al.*

PL ISSN 0003-4541
doi: 10.3161/000345411X576725

2010, Pons *et al.* 2010). Although sequence data is an excellent source of phylogenetic signal, it has thus far provided no conclusive resolution of the relationships among the four beetle suborders. Furthermore, few of these phylogenetic studies have incorporated a sufficiently broad taxon sampling to adequately represent the formidable diversity of Coleoptera.

This paper discusses the results of a cladistic analysis based on morphological characters of adult and larval Coleoptera, representing part of a National Science Foundation (DEB) funded project entitled "Assembling the Beetle Tree of Life" (BToL). The initial purpose of this portion of the project was 1) to develop a set of morphological characters in the adult and larval beetle that might be useful in assessing phylogenetic relationships across the order, 2) to develop a set of images illustrating many of the character states, 3) to select for analysis a group of about 350 exemplar genera, representing all major beetle groups and selected outgroups, 4) to obtain for each genus specimens suitable for DNA extraction, 5) to obtain adults and larvae (when possible) of those same genera for detailed morphological study, 6) to code each exemplar for all characters and produce a cladistic analysis of the these genera based on adult and larval morphological characters.

The ultimate goal of the BToL project is to infer the phylogeny of beetles using an extensive and carefully selected set of exemplar taxa, resulting in not only the resolution of subordinal relationships based on both morphological and molecular data but also the documentation and dissemination of a robust set of informative morphological characters for Coleoptera. The utility of this morphological data extends beyond the cladistic analysis discussed here: it will also aid future investigations of morphological evolution, insect paleontology, and molecular evolution. Uncertainty in calibration placement is one of the greatest sources of potential error in studies of divergence dating and molecular evolution rates (Ho and Phillips 2009). Thus, dating studies in particular stand to benefit from a fully-developed morphological data matrix that can be used to place fossil calibration points within the beetle tree of life. In addition to providing this morphological data in print and online, we will be making available illustrations of the characters and character states on the website MorphBank (http://www.morphbank.net).

Methods

Taxon selection

An initial list of possible exemplars was provided with advice from the leaders of different Taxonomic Working Groups (TWiGs), and efforts were made to obtain specimens for DNA extraction. An initial character list was developed by the senior author, and this was presented to the principal investigators plus members of the various working groups and other invited guests at a meeting at Montana State University (May, 2007). The advice provided at this meeting was used to further modify the character list, and subsequent versions were sent out for comment.

One criticism of the above approach is that specimens suitable for DNA extraction and analysis often belong to taxa which are known to be highly derived within their respective families (or orders in the case of outgroups), and thus characterized by a number of morphological features which would not be part of the ground plan for that taxon. Often this could not be remedied, but in some instances, a chimera was used with different taxa being used for molecular and morphological analysis. Among the outgroups, for instance, the plesiomorphic genus *Sabatinca* (Micropterygidae), rather than *Bombyx* Hübner (Bombycidae), was used to represent Lepidoptera in the morphological analysis. Chimeras were also used when the only available DNA specimens were from a taxon which could not be obtained for morphological study because of the unavailability of specimens for complete dissection.

The final taxon list includes 366 exemplar genera representing 7 outgroup families in 7 orders and 165 beetle families (Archostemata 3, Myxophaga 4, Adephaga 10, Staphyliniformia 10, Scarabaeoidea 10, Scirtoidea 4, Elateriformia 31, Derodontoidea 3, Bostrichoidea 4, Lymexyloidea 1, Cleroidea 9, Cucujoidea 34, Tenebrionoidea 28, Chrysomeloidea 7 and Curculionoidea 7). The 9 beetle families not included are Crowsoniellidae, Jurodidae, Belohinidae, Ochodaeidae, Plastoceridae, Phloiophilidae, Mauroniscidae, Tasmosalpingidae and the recently described Akalyptoischiidae (Lord *et al.* 2010). Coding was almost always based on specimens dissected and examined by the senior author, with additional input from the coauthors; however recent major descriptive works, including recent Handbook of Zoology volumes (Beutel and Leschen 2005a; Leschen *et al.* 2010) and papers cited in the taxon list, were often consulted for confirmation.

For the following taxa, the larva was coded from a specimen belonging to a different genus from the adult, although usually from the same subfamily (larval taxon in brackets): Mantispidae: *Spaminta* (Genus ?); Scarabaeidae-Scarabaeinae: *Scarabaeus* (*Onthophagus*), Dascillidae-Karumiinae: *Anorus* (*Pleolobus*), Eulichadidae: *Eulichas* (*Stenocolus*), Trogossitidae-Rentoniinae: *Rentonellum* (*Rentonium* ?), Melyridae-Melyrinae: *Melyris* (*Astylus*), Passandridae: *Catogenus* (*Taphroscelidia*), Vesperidae-Anoplodermatinae: *Sypilus* (*Midgolus*), Cerambycidae-Prioninae: *Prionus* (*Agrianome*), Cerambycidae-Lamiinae: *Tetraopes* (*Ancita*), Chrysomelidae-Bruchinae:

Caryobruchus (*Caryedon*), Urodontidae: *Urodontus* (*Urodontellus*), Curculionidae-Curculioninae: *Sympiezoscelus* (*Psepholax*).

The following larvae were coded from published descriptions and illustrations: *Eoxenos*, *Trachypachus*, *Clinidium*, *Sphaerites*, *Bolboceras*, *Hybosorus*, *Sandalus*, *Schizopus*, *Helichus*, *Cneoglossa*, *Artematopus*, *Silis*, *Malthodes*, *Euderia*, *Rentonium*?, *Taphroscelidia*, *Passandra*, *Murmidius*, *Sphaerosoma*, *Platynaspis*, *Iselma*, *Trictenotoma*, *Vesperus*, *Distenia*, *Migdolus*, *Aulacoscelis*. In some cases the published descriptions were insufficient and some characters were coded as unknown.

Larvae of the following 15 taxa are unknown: *Tetraphalerus*, *Cupes*, *Spanglerogyrus*, *Notomicrus*, *Colon*, *Diphyllostoma*, *Glaresis*, *Declinia*, *Loricaster*, *Podabrocephalus*, *Rhinorhipus*, *Telegeusis*, *Ototretadrilus*, *Dascillocyphon*, *Ostomopsis* and *Polypria*.

List of taxa

The classification used in the taxon list below and in the following discussions is based primarily on recent volumes of the Handbook of Zoology (Beutel and Leschen 2005a; Leschen *et al.* 2010; Leschen and Beutel (Coleoptera. Volume 3. Phytophaga, in preparation), with the following exceptions: Rhysodidae is considered to be a subfamily of Carabidae, the subfamilies of Dytiscidae are based on Miller (2001), Elateriformia is used in the sense of Lawence (1988) and excludes Decliniidae, Eucinetidae, Clambidae and Scirtidae (Beutel and Leschen 2005b, Lawrence and Yoshitomi 2007). Valid family-group names are those given in Bouchard *et al.* (2011); however the classification used here is slightly different. For instance, Cerambycidae: Dorcasominae is considered to be a senior synonym of Apatophyseinae, following Švácha *et al.* (1997) and Özdikmen (2008).

HOLOMETABOLA: OUTGROUPS

HYMENOPTERA: CEPHIDAE

Cephus Latreille: A+L: *C. cinctus* Norton.

MECOPTERA: PANORPIDAE

Panorpa Linnaeus: A+L: *P. helena* Byers.

LEPIDOPTERA: MICROPTERIGIDAE

Sabatinca Walker: A+L: *S. chalcophanes* (Meyrick).

RAPHIDIOPTERA: RAPHIDIIDAE

Agulla Navas: A+L: *Agulla* sp. USA: Utah, Idaho.

MEGALOPTERA: SIALIDAE

Sialis Latreille: A+L: *S. hamata* Ross. A+L: *Stenosialis australiensis* Tillyard.

NEUROPTERA: MANTISPIDAE

Spaminta Lambkin: A: *S. pavida* (Gerstaecker); L: Genus ? AUS.

STREPSIPTERA: MENGENILLIDAE

Eoxenos Peyerimhoff: A: *E. laboulbenei* Peyerimhoff; L (Literature): *E. laboulbenei* Peyerimhoff (Pohl 2002).

COLEOPTERA: ARCHOSTEMATA

OMMATIDAE: Tetraphalerinae

Tetraphalerus Waterhouse: A: *T. bruchi* Heller. L: unknown.

OMMATIDAE: Ommatinae

Omma Newman: A: *O. stanleyi* Newman, *O. mastersi* Macleay; L: *Omma* sp. AUS: Western Australia.

MICROMALTHIDAE

Micromalthus LeConte: A+L(1): *M. debilis* LeConte.

CUPEDIDAE: Priacminae

Priacma LeConte: A+L(1): *P. serrata* (Leconte).

CUPEDIDAE: Cupedinae

Cupes Fabricius: A: *C. capitatus* Fabricius; L: unknown.

Tenomerga Neboiss: A+L: *T. cinereus* (Say).

COLEOPTERA: MYXOPHAGA

LEPICERIDAE

Lepicerus Motschulsky: A+L: *L. inaequalis* Motschulsky.

TORRIDINCOLIDAE

Satonius Endrödy-Younga: A+L: *S. kurasawai* (Satô).

Torridincola Steffan: A+L: *T. rhodesica* Steffan.

Ytu Reichardt: A+L: *Y. zeus* Reichardt.

HYDROSCAPHIDAE

Hydroscapha LeConte: A: *H. natans* LeConte; L: *Hydroscapha* sp. Mexico.

SPHAERIUSIDAE

Sphaerius Waltl: A: *S. ovensensis* Oke; A+L: *Sphaerius* sp. USA: Arizona.

COLEOPTERA: ADEPHAGA

GYRINIDAE: Spanglerogyrinae

Spanglerogyrus Folkerts: A: *S. albiventris* Folkerts; L: unknown.

GYRINIDAE: Gyrininae

Macrogyrus Régimbart: A: *M. paradoxus* Regimbart, *M. oblongus* (Boisduval); L: *Macrogyrus* sp. AUS: South Australia.

Dineutus Macleay: A: *D. sublineatus* Chevrolat; L: *Dineutus* sp. AUS: Queensland.

Gyrinus Müller: A: G. *convexiusculus* Macleay; L: *G. natator* (Linnaeus) Europe.

HALIPLIDAE

Haliplus Latreille: A: *H. bistriatus* Wehnke. L: *Haliplus* sp. Canada.

Peltodytes Régimbart: A: *P. edentulus* (Leconte); L: *P. caesus* (Duftschmid).

MERUIDAE

Meru Spangler & Steiner: A+L: *M. phyllisae* Spangler & Steiner (Alarie *et al.* 2011).

ASPIDYTIDAE

Aspidytes Ribera *et al.*: A+L: *A. niobe* Ribera *et al.*

NOTERIDAE

Notomicrus Sharp: A: *N. tenellus* (Clark); L: unknown.

Noterus Clairville: A: *N. crassicornis* (Müller), *N. clavicornis* (Degeer). L: *Noterus* sp. Germany.

AMPHIZOIDAE

Amphizoa LeConte: A+L: *A. insolens* LeConte.

HYGROBIIDAE

Hygrobia Latreille: A: *H. australasiae* (Clark), *H. hermanni* (Fabricius); L: *Hygrobia* sp. AUS: Victoria.

DYTISCIDAE: Matinae

Matus Aubé: A: *M. bicarinatus* (Say), *M. ovatus* Leech; L: *Matus* sp. USA: Maryland.

DYTISCIDAE: Laccophilinae

Laccophilus Leach: A: *L. pictus* Laporte, *L. unifa-sciatus* Sharp; L: *L. sharpi* Regimbart.

DYTISCIDAE: Copelatinae

Copelatus Erichson: A: *C. distinctus* Aubé; L: *Copelatus* sp. USA: Maryland.

DYTISCIDAE: Hydroporinae

Hydroporus Clairville: A: *H. mannerheimi* Balfour-Browne; L: *H. polaris* Fall.

DYTISCIDAE: Agabinae

Agabus Leach: A: *A. seriatus* (Say); L: *A. anthracinus* Mannerheim.

DYTISCIDAE: Dytiscinae

Dytiscus Linnaeus: A: *D. circumcinctus* Ahrens, *D. marginalis* Linnaeus; L: *D. marginicollis* LeConte.

TRACHYPACHIDAE

Trachypachus Motschulsky: A: *T. gibbsi* LeConte, T. *holmbergi* Mannerheim; L (Literature): *T. holmbergi* Mannerheim (Bousquet & Goulet 1984; Arndt & Beutel 1995).

Systolosoma Solier: A+L: *S. breve* Solier.

CARABIDAE: Paussinae

Metrius Eschscholtz: A+L: *M. contractus* Eschscholtz.

Arthropterus Macleay: A+L: *Arthropterus* sp. AUS: Victoria.

CARABIDAE: Cicindelinae

Cicindela Linnaeus: A: *C. ypsilon* Dejean; L: *Cicindela* sp.

CARABIDAE: Carabinae

Calosoma Weber: A: *C. schayeri* Erichson; L: *Calosoma* sp. USA: Michigan.

CARABIDAE: Nebriinae

Nebria Latreille: A: *N. acuta* Lindroth; L: *N. brevicollis* (Fabricius).

CARABIDAE: Rhysodinae

Clinidium Kirby: A: *C. sculptile* Newman; *C. canaliculatum* (Costa); L (Literature): *C. sculptile* Newman (Böving & Craighead 1931).

Omoglymmius Ganglbauer: A+L: O. *hamatus* (LeConte).

CARABIDAE: Trechinae

Bembidion Latreille: A: *Bembidion* sp. AUS: New South Wales; L: *Bembidion* sp.: USA: Arizona.

CARABIDAE: Brachininae

Brachinus Weber: A: *B. explodens* Duftschmid; L: *Brachinus* sp. USA.

CARABIDAE: Harpalinae

Pterostichus Bonelli: A: P. *oblongopunctatus* (Fabricius); L: *Pterostichus* sp. Europe.

COLEOPTERA: POLYPHAGA

STAPHYLINIFORMIA: HYDROPHILOIDEA

HYDROPHILIDAE: Helophorinae

Helophorus Fabricius: A: *H. grandis* Illiger; L: *Helophorus* sp. USA: Michigan.

HYDROPHILIDAE: Georissinae

Georissus Latreille: A+L: *Georissus* sp. USA: Washington, California.

HYDROPHILIDAE: Spercheinae

Spercheus Illiger: A+L: *S. platycephalus* Macelay.

HYDROPHILIDAE: Hydrophilinae

Tropisternus Solier: A: *T. ellipticus* (LeConte); L: *Tropisternus* sp. USA: Arizona.

HYDROPHILIDAE: Sphaeridiinae

Andoytpus Spangler: A+L: *A. ashworthi* Spangler.

SPHAERITIDAE

Sphaerites Duftschmid: A: *S. glabratus* (Fabricius); L (Literature): *S. glabratus* (Fabricius) (Nikitsky 1976; Newton 1991).

SYNTELIIDAE

Syntelia Westwood: A+L: *S. histeroides* Lewis.

HISTERIDAE: Dendrophilinae

Bacanius LeConte: A+L: *B. punctiformis* (LeConte).

HISTERIDAE: Saprininae

Euspilotus Lewis: A: *E. scissus* (LeConte); L: *Euspilotus* cf. *assimilis* (Paykull) USA: Texas.

HISTERIDAE: Histerinae

Hister Linnaeus: A+L: *H. nomas* Erichson.

STAPHYLINIFORMIA: STAPHYLINOIDEA

HYDRAENIDAE: Hydraeninae

Hydraena Kugelann: A+L: *Hydraena* sp. UK: Scotland

HYDRAENIDAE: Ochthebiinae

Meropathus Enderlein: A: *M. chuni* Enderlein. L: *Meropathus* sp. New Zealand: Southland.

Ochthebius Leach: A: *Ochthebius* (*Asiobates*) sp. USA: California; L: *Ochthebius* sp. USA: California.

PTILIIDAE: Ptiliinae

Nossidium Erichson: A: *Nossidium* sp. USA: California; L: *Nossidium* sp. Panama.

PTILIIDAE: Acrotrichinae

Acrotrichis Motschulsky: A+L: *Acrotrichis* sp. USA: Arizona.

AGYRTIDAE: Necrophilinae

Necrophilus Latreille: A+L: *N. hydrophiloides* Guérin-Méneville.

AGYRTIDAE: Pterolomatinae

Apteroloma Hatch: A+L: *A. tenuicorne* (LeConte).

LEIODIDAE: Camiarinae

Agyrtodes Portevin: A: *A. tasmanicus* Zwick; L: *A. atropos* (Blackburn).

LEIODIDAE: Coloninae

Colon Herbst: A: *Colon* sp. AUS: New South Wales; L: unknown.

LEIODIDAE: Leiodinae

Anisotoma Panzer: A+L: *A. basalis* (LeConte).

LEIODIDAE: Cholevinae

Prionochaeta Horn: A+L: *P. opaca* (Say).

SILPHIDAE: Silphinae

Necrophila Kirby & Spence. A+L: *N. americana* (Linnaeus).

SILPHIDAE: Nicrophorinae

Nicrophorus Fabricius: A: *N. tomentosus* Weber; L: *N. vespillo* (Linnaeus).

STAPHYLINIDAE: Glypholomatinae

Glypholoma Jeannel: A: *G. pustuliferum* Jeannel, *G. rotundulum* Thayer & Newton; L: *G. pustuliferum* Jeannel.

STAPHYLINIDAE: Omaliinae

Paraphloeostiba Steel: A+L: *P. gayndahensis* (Macleay).

STAPHYLINIDAE: Tachyporinae

Leucotachinus Coiffait & Saiz: A+L: *Leucotachinus* sp. Chile.

STAPHYLINIDAE: Scaphidiinae

Scaphidium Olivier: A: S. *punctipenne* Macleay; L: *Scaphidium* sp. AUS: Queensland.

STAPHYLINIDAE: Osoriinae

Renardia Motschulsky: A+L: *Renardia* spp. USA: Utah, California.

STAPHYLINIDAE: Scydmaeninae

Palaeostigus Newton: A+L: *P. bifoveolatus* (Boheman).

Adrastia Broun: A+L: *A. clarkei* (Franz).

Euconnus Thomson: A: *Euconnus* sp. AUS: New South Wales; L: *Euconnus* sp. USA: Florida.

STAPHYLINIDAE: Staphylininae

Creophilus Leach: A+L: *C. erythrocephalus* (Fabricius).

SCARABAEIFORMIA: SCARABAEOIDEA

PLEOCOMIDAE

Pleocoma LeConte: A: *P. linsleyi* Hovore, *P. behrensi* LeConte; L: *P. linsleyi* Hovore.

GEOTRUPIDAE: Bolboceratinae

Bolboceras Kirby: A: *B. liebecki* (Wallis); L (Literature): *B. simi* (Wallis) (Ritcher 1966).

GEOTRUPIDAE: Taurocerastinae

Taurocerastes Philippi: A+L: *T. patagonicus* Philippi.

GEOTRUPIDAE: Geotrupinae

Geotrupes Latreille: A: *G. splendidus* (Fabricius); L: *G. spiniger* Marsham.

DIPHYLLOSTOMATIDAE

Diphyllostoma Fall. A: *Diphyllostoma* sp. USA: California. Female unknown. Larva unknown.

LUCANIDAE: Nicaginae

Nicagus LeConte: A+L: *N. obscurus* (LeConte).

LUCANIDAE: Aesalinae

Aesalus Fabricius. A: *A. scarabaeoides* (Panzer); L: *A. ulanowskii* Ganglbauer.

LUCANIDAE: Ceratognathinae

Ceratognathus Westwood: A: *C. niger* Westwood, *C. westwoodi* Thomson; L: *Ceratognathus* sp. AUS: Australian Capital Territory.

LUCANIDAE: Lucaninae

Lucanus Scopoli: A: *L. capreolus* (Linnaeus); L: *Lucanus* sp. USA: Nebraska.

PASSALIDAE: Passalinae

Passalus Fabricius: A: *P. interstitialis* Eschscholtz; L: *P. punctiger* (Serville).

GLARESIDAE

Glaresis Erichson: A: *G. ecostata* Fall; L: unknown.

TROGIDAE

Trox Fabricius: A+L: *T. aequalis* (Say).

HYBOSORIDAE: Hybosorinae

Hybosorus Macleay. A: *H. illigeri* Reiche; L (Literature): *H. orientalis* West (Ritcher 1966).

GLAPHYRIDAE

Lichnanthe Burmeister: A: *L. rathvoni* (Leconte); L: *L. vulpina* (Hentz).

SCARABAEIDAE: Aphodiinae

Aphodius Illiger. A+L: A. *fimetarius* (Linnaeus).

SCARABAEIDAE: Scarabaeinae

Scarabaeus Linnaeus: A: *S. deludens* Strassen; *Onthophagus* Latreille: L: *Onthophagus gazella* (Fabricius).

SCARABAEIDAE: Melolonthinae

Rhopaea Erichson. A+L: *R. magnicornis* Blackburn.

SCARABAEIDAE: Dynastinae

Dynastes Macleay: A+L: *D. tityus* (Linnaeus).

SCARABAEIDAE: Cetoniinae

Cetonia Fabricius: A+L: *C. aurata* (Linnaeus).

SCIRTIFORMIA: SCIRTOIDEA

DECLINIIDAE

Declinia Nikitsky *et al.*: A: *D. relicta* Nikitsky *et al.*; L: unknown.

EUCINETIDAE

Nycteus Latreille: A+L: *N. infumatus* (LeConte).

CLAMBIDAE: Acalyptomerinae

Acalyptomerus Crowson: A: *A. asiaticus* Crowson, A. *herbertfranzi* Endrody-Younga; L: *A. asiaticus* Crowson.

CLAMBIDAE: Calyptomerinae

Calyptomerus Redtenbacher: A: *C. dubius* (Marsham), *C. oblongus* Mannerheim; L: *C. dubius* (Marsham).

CLAMBIDAE: Clambinae

Clambus Fischer von Waldheim: A: *C. simsoni* Blackburn; L: *Clambus* sp. AUS: Victoria.

Loricaster Mulsant & Rey: A: *L. bioculatus* Endrödy-Younga, *L. rotundus* Grigarick & Schuster; L: unknown.

SCIRTIDAE

Cyphon Paykull: A+L: *Cyphon* sp. USA: California.

Veronatus Sharp: A: *Veronatus* spp. New Zealand; L: *V. longipalpus* Sharp.

Amplectopus Sharp: A: *Amplectopus* sp. New Zealand; L: unknown.

ELATERIFORMIA: DASCILLOIDEA

DASCILLIDAE: Dascillinae

Dascillus Latreille: A: *D. cervinus* (Linnaeus); L: *D. davidsoni* LeConte.

DASCILLIDAE: Karumiinae

Anorus LeConte: A: *A. piceus* LeConte; *Anorus* sp. USA: Nevada; L: *Pleolobus* sp. Chile.

RHIPICERIDAE

Sandalus Knoch: A: *Sandalus* spp. Mexico, Colombia; L (Literature): *Sandalus niger* Knoch (Craighead 1921).

ELATERIFORMIA: BUPRESTOIDEA

BUPRESTIDAE: Schizopodinae

Schizopus LeConte: A: *S. laetus* LeConte; L (Literature): *Schizopus* sp. (Rees 1941).

BUPRESTIDAE: Julodinae

Julodis Eschscholtz: A: *J. cirrosa* (Schönherr); L: *J. variolaris* (Pallas).

BUPRESTIDAE: Polycestinae

Acmaeodera Eschscholtz: A: *Acmaeodera* sp. USA: California; L: *A. pubiventris yumae* Knull.

BUPRESTIDAE: Buprestinae

Buprestis Linnaeus: A: *B. langi* Mannerheim; L: *B. viridisuturalis* Nicolay & Weiss.

BUPRESTIDAE: Agrilinae

Agrilus Curtis: A: *A. hypoleucus* Gory & Laporte; L: *Agrilus* sp. USA: Arizona.

ELATERIFORMIA: BYRRHOIDEA
(incl. Dryopoidea)

BYRRHIDAE: Byrrhinae

Simplocaria Stephens: A: *S. semistriata* (Fabricius); L: *Simplocaria* sp. Poland.

BYRRHIDAE: Syncalyptinae

Microchaetes Hope: A: *Microchaetes* sp. AUS: New South Wales; L: *Microchaetes* sp. AUS: Tasmania.

ELMIDAE: Larainae

Lara LeConte: A+L: *L. avara* LeConte.

ELMIDAE: Elminae

Optioservus Sanderson: A: *O. quadrimaculatus* (Horn); L: *Optioservus* sp. USA: Michigan.

DRYOPIDAE

Helichus Erichson: A: *Helichus* sp. USA: Arizona; L (Literature): *Helichus suturalis* LeConte (Ulrich 1987).

LUTROCHIDAE

Lutrochus Erichson: A: *Lutrochus* sp. USA: Arizona; L: *Lutrochus luteus* LeConte.

LIMNICHIDAE: Limnichinae

Byrrhinus Motschulsky. A+L: *Byrrhinus* sp. AUS: Queensland.

HETEROCERIDAE

Heterocerus Fabricius: A: *H. fenestratus* (Thunberg); L: *Heterocerus* sp. Poland.

PSEPHENIDAE: Eubrianacinae

Eubrianax Kiesenwetter: A: *Eubrianax edwardsi* (LeConte); L: *Eubrianax* sp. Kenya.

PSEPHENIDAE: Psepheninae

Psephenus Haldeman: A+L: *P. herricki* DeKay. USA: New York, New Jersey, Kentucky.

CNEOGLOSSIDAE

Cneoglossa Guérin-Méneville: A: *Cneoglossa* spp. Costa Rica, Guatemala; L (Literature): *Cneoglossa edsoni* Costa *et al.* (Costa *et al.* 1999).

PTILODACTYLIDAE: Anchytarsinae

Anchycteis Horn: A+L: *A. velutina* Horn.

PTILODACTYLIDAE: Ptilodactylinae

Ptilodactyla Illiger: A: *P. angustata* Horn; L: *Ptilodactyla* sp. USA: Tennessee.

PODABROCEPHALIDAE

Podabrocephalus Pic: A (male): *P. sinuaticollis* Pic; L: unknown.

CHELONARIIDAE

Chelonarium Fabricius: A: *Chelonarium* sp. Argentina; L: *Chelonarium* sp. Malaysia: Sabah.

EULICHADIDAE

Eulichas Jakobson: *Eulichas* sp. A: Malaysia: Perak. *Stenocolus* LeConte: L: *S. scutellaris* LeConte.

CALLIRHIPIDAE

Callirhipis Latreille: A: *C. cardwellensis* Blackburn; L: *Callirhipis* sp. AUS: Queensland.

ELATERIFORMIA: ELATEROIDEA
(including Cantharoidea)

ARTEMATOPODIDAE

Macropogon Motschulsky: A: *M. testaceipennis* Motschulsky; L: *Macropogon* sp. USA: New Hampshire.

Artematopus Perty: A: *Artematopus* spp. Brazil, Colombia. L (Literature): *A. discoidalis* Pic (Costa *et al.* 1985, 1988).

RHINORHIPIDAE

Rhinorhipus Lawrence: A: *R. tamborinensis* Lawrence; L: unknown.

BRACHYPSECTRIDAE

Brachypsectra LeConte: A+L: *B. fulva* LeConte.

CEROPHYTIDAE

Cerophytum Latreille: A: *C. pulsator* (Haldeman); L: *C. elateroides* (Latreille).

EUCNEMIDAE: Anischiinae

Anischia Fleutiaux: A: *A. stupenda* Fleutiaux, *A. bicolor* Lawrence, *A. kuscheli* Lawrence; L: *A. kuscheli* Lawrence.

EUCNEMIDAE: Melasinae

Melasis Olivier: A: *M. buprestoides* (Linnaeus), *M. pectinicornis* Melsheimer, *M. ruficornis* Horn; L: *M. pectinicornis* Melsheimer.

EUCNEMIDAE: Macraulacinae

Onichodon Newman: A+L: *O. canadensis* (W. J. Brown).

THROSCIDAE

Aulonothroscus Horn: A: *Aulonothroscus* sp. AUS: New South Wales; L: *Aulonothroscus* ? sp. USA: Vermont.

ELATERIDAE: Lissominae

Lissomus Dalman: A: *Lissomus* sp. French Guiana; L: *Lissomus* sp. Panama.

ELATERIDAE: Cebrioninae

Selonodon Latreille: A+L: *S. floridensis* Galley.

ELATERIDAE: Elaterinae

Ampedus Dejean: A: *A. sanguineus* (Linnaeus); L: *Ampedus* sp. Russia.

ELATERIDAE: Cardiophorinae

Paracardiophorus Schwarz: A: *P. assimilis* Carter; L: *Paracardiophorus* sp. AUS: Australian Capital Territory.

DRILIDAE

Drilus Olivier: A+L: *Drilus* sp. South Africa:.

OMALISIDAE

Omalisus Geoffroy: A+L: *O. fontisbellaquei* (Fourcroy).

LYCIDAE

Dictyoptera Latreille: A+L: *D. aurora* (Herbst).

Lycus Fabricius: A: *Lycus* sp. USA: Arizona; L: *L. sanguineus* Gorham.

TELEGEUSIDAE

Telegeusis Horn: A: *T. debilis* Horn; L: unknown.

PHENGODIDAE: Phengodinae

Phengodes Illiger: A: *P. frontalis* LeConte; L: *Phengodes* sp. USA: Michigan.

PHENGODIDAE: Mastinocerinae

Cenophengus LeConte: A: *C. debilis* LeConte; L: Genus ? sp. Brazil.

RHAGOPHTHALMIDAE

Rhagophthalmus Motschulsky: A: *R. scutellatus* Motschulsky; L (Literature): *Rhagophthalmus ohbai* Wittmer (Kawashima *et al.* 2010).

LAMPYRIDAE: Ototretinae

Ototretadrilus Pic: A (male): *Ototretadrilus* sp. Indonesia: Java. L: unknown.

LAMPYRIDAE: Pterotinae

Pterotus LeConte: A+L: *P. obscuripennis* LeConte.

LAMPYRIDAE: Lampyrinae

Ellychnia Blanchard: A: *E. californica* Motschulsky; L: *Ellychnia* sp. USA: California.

Pyrocoelia Gorham: A+L: *P. praetexta* E. Olivier.

OMETHIDAE: Matheteinae

Matheteus LeConteL A+L: *M. theveneti* LeConte.

CANTHARIDAE: Silinae

Silis Charpentier: A: *Silis nitidula* (Fabricius), *Silis* sp. USA: California; L (Literature): *S. ruficollis* (Fabricius) (Fitton 1975).

CANTHARIDAE: Malthininae

Malthodes Kiesenwetter: A: *M. fuscus* (Waltl), *M. minimus* (Linnaeus); L (Literature): *Malthodes* spp. (Fitton 1975).

CANTHARIDAE: Chauliognathinae

Chauliognathus Hentz: A+L: *C. lugubris* (Fabricius).

DERODONTIFORMIA: DERODONTOIDEA

DERODONTIDAE: Derodontinae

Derodontus LeConte: A+L: *D. maculatus* (Melsheimer), *D. esotericus* Lawrence.

DERODONTIDAE: Laricobiinae

Laricobius Rosenhauer: A: *L. rubidus* LeConte, *L. erichsoni* Rosenhauer; L: *L. nigrinus* Fender.

Nothoderodontus Crowson: A: *N. chilensis* Lawrence, *N. darlingtoni* Lawrence, *N. gourlayi* Crowson; L: *N. gourlayi* Crowson

NOSODENDRIDAE

Nosodendron Latreille: A: *N. unicolor* Say; L: *Nosodendron* sp. AUS: Queensland.

JACOBSONIIDAE

Derolathrus Sharp: A: *Derolathrus* sp. AUS: New South Wales, Norfolk Island; L: *D. atomus* Sharp.

Saphophagus Sharp: A+L: *S. minutus* Sharp.

BOSTRICHIFORMIA: BOSTRICHOIDEA

DERMESTIDAE: Dermestinae

Dermestes Linnaeus: A: *D. ater* Degeer; L: *D. maculatus* Degeer.

DERMESTIDAE: Orphilinae

Orphilus Erichson: A+L: *O. subnitidus* LeConte.

DERMESTIDAE: Megatominae

Anthrenus Geoffroy: A: *A. scrophulariae* (Linnaeus); L: *A. verbasci* (Linnaeus).

ENDECATOMIDAE

Endecatomus Mellié: A+L: *E. rugosus* (Randall).

BOSTRICHIDAE: Bostrichinae

Apatides Casey: A+L: *A. fortis* LeConte.

BOSTRICHIDAE: Dinoderinae

Rhyzopertha Stephens: A+L: *R. dominica* (Fabricius).

BOSTRICHIDAE: Lyctinae

Lyctus Fabricius: A: *L. brunneus* (Stephens); L: *Lyctus* sp. AUS: Northern Territory.

BOSTRICHIDAE: Euderiinae

Euderia Broun: A: *E. squamosa* Broun; L (Literature): *E. squamosa* Broun (Crowson 1961).

PTINIDAE: Ptininae

Ptinus Linnaeus: A: *P. clavipes* Panzer; L: *Ptinus* sp. New Zealand.

PTINIDAE: Anobiinae

Stegobium Motschulsky: A+L: S. *paniceum* (Linnaeus).

CUCUJIFORMIA: LYMEXYLOIDEA

LYMEXYLIDAE: Melittommatinae

Melittomma Murray: A+L: *M. pervagum* (Olliff).

LYMEXYLIDAE: Atractocerinae

Atractocerus Palisot de Beauvois: A+L: *A. brasiliensis* Lepeletier & Audinet-Serville.

CUCUJIFORMIA: CLEROIDEA

TROGOSSITIDAE: Thymalinae

Thymalus Latreille: A: *Thymalus* sp. Nepal; L: *T. marginicollis* Chevrolat.

TROGOSSITIDAE: Rentoniinae

Rentonellum Crowson: A: *Rentonellum* sp. NZ; L (Literature): *Rentonium* ? sp. (Crowson 1966).

TROGOSSITIDAE: Lophocaterinae

Eronyxa Reitter: A: *E. angusta* (Casey); L: *E. expansa* (Van Dyke)

Grynoma Broun: A+L: *Grynoma* spp. New Zealand.

TROGOSSITIDAE: Trogossitinae

Acalanthis Erichson: A: *A. quadrisignatus* Erichson, *A. mirabilis* Reitter; L: *Acalanthis* sp. Chile.

Temnoscheila Westwood: A: *T. coerulea* Olivier, *T. chlorodia* (Mannerheim); L: *Temnoscheila* sp. USA: Arizona.

CHAETOSOMATIDAE

Chaetosoma Westwood: A+L: *C. scaritides* Westwood.

METAXINIDAE

Metaxina Broun: A+L: *M. ornata* Broun.

THANEROCLERIDAE

Isoclerus Lewis: A: *I. rumcajs* Kolibac, *I. gerstmeieri* Kolibac; L: *Isoclerus* sp. AUS: Queensland.

CLERIDAE: Tillinae

Cymatodera Grey: A: *C. californica* Horn, *Cymatodera* sp. USA: Texas; L: *C. balteata* LeConte.

CLERIDAE: Clerinae

Trichodes Herbst: A: *T. balteatus* LeConte; *T. ornatus* Say.

CLERIDAE: Korynetinae

Necrobia Olivier: A+L: *N. rufipes* (Degeer).

ACANTHOCNEMIDAE

Acanthocnemus Perris: A+L: *A. nigricans* (Hope).

PHYCOSECIDAE

Phycosecis Pascoe: A+L: *P. litoralis* Pascoe.

PRIONOCERIDAE

Idgia Laporte: A+L: *Idgia* spp. Taiwan, Indonesia, India.

MELYRIDAE: Melyrinae

Melyris Fabricius: A: *M. abdominalis* (Fabricius), *Melyris* sp. Zaire; L: *Astylus* Moseley: *Astylus* sp. Chile

MELYRIDAE: Dasytinae

Listrus Motschulsky: A+L: *Listrus* sp. USA: California.

MELYRIDAE: Malachiinae

Collops Erichson: A: *Collops* sp. USA: California, Mexico; A+L: *Collops* sp. USA: California.

CUCUJIFORMIA: CUCUJOIDEA

BOGANIIDAE

Paracucujus Sen Gupta & Crowson: A+L: *P. rostratus* Sen Gupta & Crowson.

BYTURIDAE: Byturinae

Byturus Latreille: A+L: *B. tomentosus* (Degeer).

Xerasia Lewis: A: *X. griscescens* (Jayne), *X. meschniggi* (Reitter); L: *X. griscescens* (Jayne).

BYTURIDAE: Platydascillinae

Dascillocyphon Everts: A: *Dascillocyphon* sp. Malaysia: Malay Peninsula; L: unknown.

HELOTIDAE

Helota Macleay: A: *Helota* sp. Sumatra. L: *H. thoracica* Ritsema.

PROTOCUCUJIDAE

Ericmodes Reitter: A+L: *Ericmodes* sp. Chile.

SPHINDIDAE: Protosphindinae

Protosphindus Sen Gupta & Crowson: A+L: *S. chilensis* Sen Gupta & Crowson.

SPHINDIDAE: Sphindinae

Sphindus Megerle in Dejean: A+L: *S. americanus* LeConte.

BIPHYLLIDAE

Diplocoelus Guérin-Méneville: A+L: *D. rudis* (LeConte), *D. fasciatus* (Macleay).

EROYTLIDAE: Pharaxonothinae

Pharaxonotha Reitter: A+L: *P. kirschi* Reitter, *P. floridan*a (Casey).

EROTYLIDAE: Languriinae

Languria Latreille: A+L: *L. mozardi* Latreille, *L. bicolor* (Fabricius).

EROTYLIDAE: Cryptophilinae

Toramus Grouvelle: A+L: *Toramus* sp. Panama.

EROTYLIDAE: Erotylinae

Dacne Latreille: A+L: *D. picta* Crotch, D. *quadrimaculata* (Say).

Pselaphacus Percheron: A: *P. signatus* Guérin-Méneville, *Pselaphacus* sp. Panama; L: *Pselaphacus* sp. Peru.

MONOTOMIDAE: Rhizophaginae

Rhizophagus Herbst: A: *R. minutus* Mannerheim, *R. sculpturatus* Manerheim; L: *Rhizophagus* sp. USA: Western Australia.

MONOTOMIDAE: Monotominae

Bactridium LeConte: A+L: *B. ephippigerum* (Guérin-Méneville).

HOBARTIIDAE

Hobartius Sen Gupta & Crowson: A: *H. chilensis* Tomaszewska & Ślipiński; A+L: *H. eucalypti* (Blackburn).

CRYPTOPHAGIDAE: Cryptophaginae

Cryptophagus Herbst: A: *C. cellaris* (Scopoli); A+L: *C. lycoperdi* (Scopoli).

Chiliotis Reitter: A+L: *Chiliotis* sp. Chile.

CRYPTOPHAGIDAE: Atomariinae

Atomaria Stephens: A+L: *A. lewisi* Reitter.

AGAPYTHIDAE

Agapytho Broun: A+L: *A. foveicollis* Broun.

PRIASILPHIDAE

Priasilpha Broun: A+L: *P. obscura* Broun.

PHLOEOSTICHIDAE

Hymaea Pascoe: A: *H. magna* Sen Gupta & Crowson; L: *Hymaea* sp. AUS: Tasmania.

SILVANIDAE: Brontinae

Uleiota Latreille: A+L: *U. planata* (Linnaeus), *U. dubia* (LeConte).

SILVANIDAE: Silvaninae

Oryzaephilus Ganglbauer: A+L: *O. surinamensis* (Fauvel), *O. mercator* (Fauvel).

CUCUJIDAE

Cucujus Fabricius: A+L: *C. clavipes* Fabricius.

MYRABOLIIDAE

Myrabolia Reitter: A+L: *Myrabolia* sp. AUS: New South Wales, Australian Capital Territory. Tomaszewska and Ślipiński (2008).

CAVOGNATHIDAE

Taphropiestes Reitter: A+L: *T. pullivora* (Crowson). Ślipiński and Tomaszewska (2010).

LAMINGTONIIDAE

Lamingtonium Sen Gupta & Crowson: A+L: *L. binnaburrense* Sen Gupta & Crowson. *L. thayerae* Lawrence & Leschen.

PASSANDRIDAE

Catogenus Westwood: A: *C. decoratus* Newman, *C. rufus* (Fabricius); *Taphroscelidia* Crotch: L (Literature): *Taphroscelidia linearis* (LeConte) (Böving & Craighead 1931).

Passandra Dalman: A: *P. fasciata* (Gray), *P. heros* (Fabricius); L (Literature): *P. trigemina* (Newman) (Gravely 1916).

PHALACRIDAE: Phaenocephalinae

Phalacrinus Blackburn: A+L: *Phalacrinus* spp. AUS: Australian Capital Territory, South Australia.

PHALACRIDAE: Phalacrinae

Olibrus Erichson: A+L: *O. aeneus* (Fabricius).

PROPALTICIDAE

Propalticus Sharp: A: *P. doddi* John; L: *Propalticus* sp. AUS: Queensland.

LAEMOPHLOEIDAE

Laemophloeus Dejean: A+L: *L. biguttatus* (Say)

CYCLAXYRIDAE

Cyclaxyra Broun: A+L: *C. politula* (Broun). Gimmel *et al.* (2009).

KATERETIDAE

Amartus LeConte: A+L: *A. rufipes* LeConte.

NITIDULIDAE: Carpophilinae

Carpophilus Stephens: A: *C. hemipterus* (Linnaeus); L: *C. mutilatus* Erichson.

NITIDULIDAE: Meligethinae

Meligethes Stephens: A+L: *Meligethes* sp. USA: California.

NITIDULIDAE: Nitidulinae

Stelidota Erichson: A: *S. geminata* (Say), *Stelidota* sp. Panama; L: *Stelidota* sp. Panama.

NITIDULIDAE: Cillaeinae

Brachypeplus: Erichson: A+L: *B. planus* Erichson, *Brachypeplus* sp. AUS: Queensland

NITIDULIDAE: Cryptarchinae

Glischrochilus Reitter: A+L: *Glischrochilus sp.* USA: Tennessee, Vermont.

SMICRIPIDAE

Smicrips LeConte: A+L: *Smicrips* sp. USA: FL, AZ; Panama.

BOTHRIDERIDAE: Xylariophilinae

Xylariophilus Pal & Lawrence: A+L: *X. honoratus* Pal & Lawrence.

BOTHRIDERIDAE: Teredinae

Teredolaemus Sharp: A+L: *T. leae* (Grouvelle).

BOTHRIDERIDAE: Bothriderinae

Bothrideres Erichson: A: *B. montanus* Horn, *Bothrideres* sp. Mexico; L: *Bothrideres bipunctatus* (Gmelin).

CERYLONIDAE: Euxestinae

Hypodacnella Ślipiński: A: *H. tasmaniae* (Lea); L: *Hypodacnella* sp. AUS: Queensland.

CERYLONIDAE: Ostomopsinae

Ostomopsis Scott: A: *O. solitaria* Scott, *Ostomopsis* sp. New Caledonia; L: unknown.

CERYLONIDAE: Murmidiinae

Murmidius Leach: A: *M. ovalis* (Beck); L (Literature): *M. ovalis* (Beck) (Böving & Craighead 1931).

CERYLONIDAE: Ceryloninae

Philothermus Aubé: A+L: *Philothermus* sp. Mexico.

ALEXIIDAE

Sphaerosoma Samouelle: A: *S. sparsum* Reitter, *Sphaerosoma* sp. Croatia; L (Literature): *S. algiricum* Reitter (Peyerimhoff 1913).

DISCOLOMATIDAE

Aphanocephalus Wollaston: A: *Aphanocephalus* sp. AUS: SA; L: *Aphanocephalus* sp. AUS: Queensland.

Discoloma Erichson: A+L: *Discoloma* sp. Brazil.

ENDOMYCHIDAE: Merophysiinae

Holoparamecus Curtis: A: *Holoparamecus* sp. Panama; L: *Holoparamecus* sp. USA: FL.

ENDOMYCHIDAE: Anamorphinae

Bystus Guérin-Méneville: A+L: *Bystus* sp. Panama.

ENDOMYCHIDAE: Endomychinae

Endomychus Panzer: A+L: *E. coccineus* (Linnaeus).

ENDOMYCHIDAE: Epipocinae

Epipocus Germar: A+L: *E. subcostatus* Gorham.

COCCINELLIDAE: Microweiseinae

Delphastus Casey: A+L: *D. pusillus (*LeConte).

COCCINELLIDAE: Coccinellinae

Rhyzobius Stephens: A+L: *Rhyzobius* sp. AUS: Australian Capital Territory.

Stethorus Weise: A: *S. vagans* Blackburn; L: *S. nigripes* Kapur.

Rodolia Mulsant: A: *R. cardinalis* (Mulsant); L: *R. simplicipennis* Blackburn.

Platynaspis Redtenbacher: A: *P. capicola* Crotch, *Platynaspis* sp. Greece; L (Literature): *P. luteorubra* Goeze (Korschefsky 1934); *Platynaspidius maculosus* (Weise) (Sasaji 1992).

Harmonia Mulsant: *H. conformis (*Boisduval).

Epilachna Dejean: A+L: *Epilachna* sp. AUS: New South Wales.

CORYLOPHIDAE: Periptyctinae

Periptyctus Blackburn: A: *P. kosciuszko* Tomaszewska & Ślipiński; L: *Periptyctus* sp. AUS: New South Wales.

CORYLOPHIDAE: Corylophinae

Holopsis Broun: A: *Holopsis* spp. Chile, AUS: Australian Capital Territory; L: *Holopsis* spp. AUS: Australian Capital Territory, New Zealand.

Orthoperus Stephens: A+L: *O. scutellaris* LeConte.

Clypastraea Haldeman: A: *C. lunata* (LeConte), *Clypastraea* spp. Brazil, Mexico; L: *Clypastraea* sp. Mexico.

LATRIDIIDAE: Latridiinae

Eufallia Muttkowski: A+L: *E. seminivea* (Motschulsky).

LATRIDIIDAE: Corticariinae

Corticaria Marshall: A: *C. ferruginea* Marsham, *Corticaria* sp. USA: California; L: *Corticaria* sp. USA: California.

CUCUJIFORMIA: TENEBRIONOIDEA

MYCETOPHAGIDAE: Mycetophaginae

Mycetophagus Hellwig: A+L: *M. punctatus* Say.

MYCETOPHAGIDAE: Bergininae

Nesolathrus Scott: A+L: *Nesolathrus* sp. AUS: Queensland.

ARCHEOCRYPTICIDAE

Enneboeus Waterhouse: A+L: *E. barrocolorado* Merkl, *E. ovalis* Waterhouse, *Enneboeus* sp. Mexico.

PTEROGENIIDAE

Histanocerus Motschulsky. A+L: *Histanocerus* spp. Malaysia: Sabah, Pahang.

CIIDAE: Sphindociinae

Sphindocis Fall: A+L: *S. denticollis* Fall.

CIIDAE: Ciinae

Cis Latreille: A+L: *C. vitulus* Mannerheim.

TETRATOMIDAE: Tetratominae

Tetratoma Fabricius: A+L: *T. fungorum* Fabricius.

TETRATOMIDAE: Penthinae

Penthe Newman: A+L: *P. obliquata* (Fabricius).

TETRATOMIDAE: Eustrophinae

Eustrophopsis Champion: A+L: *E. bicolor* (Fabricius).

MELANDRYIDAE: Melandryinae

Orchesia Latreille: A+L: *O. cultriformis* Laliberté.

Phloiotrya Stephens: A: *P. rufipes* (Gyllenhal); L: *P. vaudoueri* Mulsant.

MORDELLIDAE

Mordella Linnaeus: A: *M. atrata* Melsheimer; L: *Mordella* sp. USA: Arizona.

RIPIPHORIDAE: Pelecotominae

Pelecotoma Fischer: A: *P. fennica* (Paykull), *P. flavipes* Melsheimer; L: *P. fennica* Paykull.

RIPIPHORIDAE: Ripidiinae

Rhipidioides Riek: A+L: *R. helenae* Riek.

ZOPHERIDAE: Colydiinae

Colydium Fabricius: A: *C. ferrugineum* Reitter; L: *Colydium* sp. Poland.

Pristoderus Hope: A: *P. antarcticus* White; L: *Pristoderus* sp. AUS: Australian Capital Territory; L: *P. saccharatus* (Pascoe).

ZOPHERIDAE: Zopherinae

Hyporhagus Thomson: A+L: *H, gilensis* Horn; *Hyporhagus* sp. Brazil.

Pycnomerus Erichson: A+L: *P. fuliginosus* Erichson.

Phellopsis LeConte: A: *P. obcordata* (Kirby), *P. porcata* (LeConte); L: *P. obcordata* (Kirby).

ULODIDAE

Dipsaconia Pascoe: *D. pyritosa* Pascoe.

Meryx Latreille: A+L: *M. rugosa* Latreille.

PROMECHEILIDAE

Parahelops Waterhouse: A: *P. darwini* Waterhouse, *Parahelops* sp. Argentina; L: *Parahelops* sp. Chile.

Sirrhas Champion: A: *S. limbatus* Champion, *S. variegatus* Lawrence; L: *S. variegatus* Lawrence.

CHALCODRYIDAE

Chalcodrya Redtenbacher: A+L: *C. variegata* Broun.

TRACHELOSTENIDAE

Trachelostenus Solier: A+L: *T. inaequalis* Solier.

TENEBRIONIDAE: Lagriinae

Adelium Kirby: A+L: *Adelium* sp. AUS: Victoria.

Statira Serville: A+L: *Statira* spp. Brazil, Mexico, Panama.

TENEBRIONIDAE: Phrenapatinae

Dioedus LeConte: A+L: *Dioedus* sp. AUS: Queensland.

TENEBRIONIDAE: Zolodininae

Tanylypa Pascoe: A+L: *T. morio* Pascoe.

TENEBRIONIDAE: Pimeliinae

Coelus Eschscholtz: A: *C. ciliatus* Eschscholtz; L: *Coelus* sp. USA: California.

TENEBRIONIDAE: Tenebrioninae

Leaus Matthews & Lawrence: A+L: *L. tasmanicus* Matthews & Lawrence.

Tribolium Macleay: A+L: *T. confusum* Jacquelin Du Val.

TENEBRIONIDAE: Diaperinae

Diaperis Müller: *D. maculata* Olivier.

PROSTOMIDAE

Prostomis Latreille: A+L: *P. intermedius* Blackburn.

SYNCHROIDAE

Synchroa Newman: A+L: *S. punctata* Newman.

STENOTRACHELIDAE: Cephaloinae

Cephaloon Newman: A+L: *C. ungulare* LeConte.

OEDEMERIDAE: Polypriinae

Polypria Chevrolat. A: *Polypria cruxrufa* Chevrolat, *Polypria* sp. Argentina; L: unknown.

OEDEMERIDAE: Calopodinae

Calopus Fabricius: A: *C. angustus* LeConte, *C. serraticornis* (Linnaeus); L: *C. serraticornis* (Linnaeus)

OEDEMERIDAE: Oedemerinae

Ditylus Fischer von Waldheim: A: *D. gracilis* (LeConte); L: *Ditylus* sp. Canada: British Columbia.

MELOIDAE: Eleticinae

Iselma Haag-Rutenberg: A: *I. flavipennis* Haag-Rutenberg, *I. lanuginosa* Kaszab; L (Literature): *I. flavipennis* Haag-Rutenberg, *I. pallidipennis* Haag-Rutengerg (Bologna *et al.* 2001).

MELOIDAE: Meloinae

Epicauta Dejean: A: *E. pardalis* LeConte; L (first instar): *E. apache* Pinto.

MYCTERIDAE: Eurypinae

Lacconotus Leconte: A+L: *L. pinicola* Horn.

MYCTERIDAE: Hemipeplinae

Hemipeplus Latreille: A+L: *H. marginipennis* (LeConte).

BORIDAE

Boros Herbst: A+L: *B. schneideri* (Panzer), *B. unicolor* Say.

TRICTENOTOMIDAE

Trictenotoma Gray: A+L: *T. childreni* Gray; L (Literature): *T. childreni* Gray (Gahan 1908).

PYTHIDAE

Ischyomius Chevrolat: A+L: *I. chevrolatii* Champion.

Pytho Latreille: A+L: *P. niger* Kirby.

PYROCHROIDAE: Pilipalpinae

Morpholycus Lea: A: *M. costipennis* Lea; L: *M. apicalis* (Malceay).

PYROCHROIDAE: Pedilinae

Pedilus Fischer: A: *P. canaliculatus* (LeConte), *P. labiatus* Say; L: *Pedilus* spp. USA: Virginia, Wisconsin, Arizona.

PYROCHROIDAE: Pyrochroinae

Pyrochroa Geoffroy: A+L: *P. coccinea* (Linnaeus).

SALPINGIDAE: Othniinae

Elacatis Pascoe: A+L: *E. delusa* Pascoe, *E. lugubris* (Horn), *E. umbrosus* (LeConte)

SALPINGIDAE: Prostominiinae

Ocholissa Pascoe: *O. nigricollis* Grouvelle, *O. humeralis* Fairmaire; L: *Ocholissa* sp. Christmas Island, Indian Ocean.

SALPINGIDAE: Inopeplinae

Euryplatus Motschulsky: A+L: *E. dimidiatus* Waterhouse.

SALPINGIDAE: Salpinginae

Salpingus Illiger: A+L: *S. viridiaeneus* (Randall), *S. pallipes* (Boheman).

ANTHICIDAE?: Lagrioidinae

Lagrioida Fairmaire & Germain: A+L: *L. australis* Champion.

ANTHICIDAE?: Ischaliinae

Ischalia Pascoe: A: *I. costata* (LeConte), *I. indigacea* Pascoe, *I. vancouverensis* Harrington; L: *I. vancouverensis* Harrington.

ANTHICIDAE: Lemodinae

Lemodes Boheman: A: *L. coccinea* Boheman; L: *Lemodes* sp. AUS: New South Wales, VIC.

ANTHICIDAE: Anthicinae

Anthicus Paykull: A: *A. nanus* LeConte; L: *A. lutulentus* Casey.

ADERIDAE

Syzeton Blackburn: A+L: *Syzeton* sp. AUS: Australian Capital Territory, NSW.

SCRAPTIIDAE: Anaspidinae

Anaspis Geoffroy: A: *A. atrata Champion*; L: *Anaspis* sp. Poland.

SCRAPTIIDAE: Scraptiinae

Scraptia Latreille: A: *Scraptia* sp. AUS: TAS; L: *Scraptia* sp. AUS: Australian Capital Territory.

TENEBRIONOIDEA: FAMILY?

Rhizonium Sharp: A+L: *R. antiquum* Sharp.

CUCUJIFORMIA: CHRYSOMELOIDEA

OXYPELTIDAE

Oxypeltus Blanchard: A: *O. quadrispinosus* Blanchard; L (Literature): *O. spinosus* Blanchard (Švácha & Danilevsky 1987).

VESPERIDAE: Vesperinae

Vesperus Dejean: A: *V. strepens* (Fabricius); L (Literature): *V. xatari* Dufour, *V. strepens* (Fabricius) (Švácha & Danilevsky 1987).

VESPERIDAE: Anoplodermatinae

Sypilus Guérin-Méneville: A: *S. orbignyi* Guérin-Méneville; *Migdolus* Westwood: L (Literature): *Migdolus fryanus* Westwood (Švácha & Danilevsky 1987).

DISTENIIDAE

Distenia Lepeletier & Audinet-Serville in Latreille: A: *D. undata* (Fabricius); L (Literature): *Distenia gracilis* Blessing (Švácha & Danilevsky 1987).

CERAMBYCIDAE: Parandrinae

Parandra Latreille: A+L: *P. brunnea* (Fabricius).

CERAMBYCIDAE: Prioninae

Prionus Fabricius: A: *P. laticollis* (Drury); *Agrianome* Thomson: L: *Agrianome spinicollis* (Macleay).

CERAMBYCIDAE: Lepturinae

Rutpela Nakane & Ohbayashi: A+L: *R. maculata* (Poda).

CERAMBYCIDAE: Dorcasominae

Apatophysis Chevrolat: A: *A. kashmiriana* Semenow, *A. caspica* Semenow; L: *A. barbara* Lucas.

CERAMBYCIDAE: Cerambycinae

Phoracantha Newman: A: *P. semipunctata* (Fabricius); L: *Phoracantha* sp. AUS: Australian Capital Territory.

CERAMBYCIDAE: Lamiinae

Tetraopes Dalman in Schoenherr: A: *T. tetrophthalmus* (Forster); *Ancita* Thomson: L: *Ancita marginicollis* (Boisduval)

MEGALOPODIDAE: Palophaginae

Palophagus Kuschel: A+L: *Palophagus bunyae* Kuschel. *Palophagoides* Kuschel: A+L: *P. vargasorum* Kuschel;

ORSODACNIDAE: Aulacoscelidinae

Aulacoscelis Duponchel & Chevrolat: A: *A. vogti* Monrós, A. *candezei* Chapuis; L (Literature): *A. appendiculata* Cox & Windsor (Cox & Windsor 1999).

CHRYSOMELIDAE: Bruchinae

Caryobruchus Bridwell: A: *C. gleditsiae* (Linnaeus), *Caryobruchus* sp. Panama; *Caryedon* Schoenherr: L: *Caryedon serratus* (Olivier).

CHRYSOMELIDAE: Criocerinae

Crioceris Geoffroy: A+L: *C. asparagi* (Linnaeus).

CHRYSOMELIDAE: Cassidinae

Cephaloleia Chevrolat: A+L: *C. belti* Baly.

CHRYSOMELIDAE: Chrysomelinae

Chrysomela Linnaeus: A: *C. populi* Linnaeus; L: *C. scripta* Fabricius.

CHRYSOMELIDAE: Galerucinae

Diabrotica Chevrolat: A: *D. undecimpunctata* Jacoby; L: *D. balteata* LeConte.

CHRYSOMELIDAE: Cryptocephalinae

Neochlamisus Karren: A: *N. gibbosus* (Fabricius); L: *N. bebbianae* (W. J. Brown).

CUCUJIFORMIA: CURCULIONOIDEA

NEMONYCHIDAE: Nemonychinae

Nemonyx Redtenbacher: A+L: *N. lepturoides* (Fabricius).

NEMONYCHIDAE: Rhinorhynchinae

Rhynchitomacerinus Voss: A+L: *R. kuscheli* (Voss).

ANTHRIBIDAE: Urodontinae

Urodontus Louw: A: *U. mesemoides* Louw; *Urodontellus* Louw: L: *Urodontellus lilii* (Fahraeus).

ANTHRIBIDAE: Anthribinae

Toxonotus Lacordaire: A+L: *T. fascicularis* (Schoenherr).

BELIDAE: Oxycoryninae

Oxycraspedus Kuschel: A+L: *O. cornutus* Kuschel. *Rhopalotria* Chevrolat: A: *R. mollis* (Sharp); L (Literature): *R. mollis* (Sharp) (May 1993).

BELIDAE: Belinae

Rhinotia Kirby: A+L: *R. bidentatus* (Donovan).

CARIDAE

Car Blackburn: A+L: *C. condensatus* Blackburn.

ATTELABIDAE: Rhynchitinae

Merhynchites Sharp: A+L: *M. bicolor* (Fabricius).

BRENTIDAE: Eurhynchinae

Eurhynchus Kirby: A: *E. laevior* (Kirby); L (Literature): *E. laevior* (Kirby) (Oberprieler 2000).

BRENTIDAE: Brentinae

Cylas Latreille: A+L: *C. formicarius* (Fabricius).

CURCULIONIDAE: Dryophthorinae

Sphenophorus Schönherr: A+L: *S. brunnipennis* (Germar).

CURCULIONIDAE: Molytinae

Tranes Schönherr: A+L: *T. lyterioides* (Pascoe). *Sympiezoscelus* Waterhouse: A: *S. spencei* Waterhouse; *Psepholax* White: L: *Psepholax granulatus* Broun.

CURCULIONIDAE: Curculioninae

Curculio Linnaeus: A: *C. bicruciatus* (Motschulsky); L: *Curculio* sp. USA: California.

CURCULIONIDAE: Scolytinae

Dendroctonus Erichson: A: *D. valens* LeConte; L: *Dendroctonus* sp. USA: Arizona.

CURCULIONIDAE: Platypodinae

Platypus Herbst: A: *P. australis* Chapuis; L: *Platypus* sp. AUS: Tasmania.

Although the vast majority of the above taxa belong to the same genus as the species being used to obtain DNA, several belong to another genus in the same family group; these chimeras are as follows (DNA material in brackets): *Spaminta* (*Plega*), *Sabatinca* (*Bombyx*), *Eoxenos* (*Mengenilla*), *Stenocolus* (*Eulichas*), *Chiliotis* (*Micrambina*), *Rhipidioides* (*Pirhidius*), *Dipsaconia* (*Syrphetodes*), *Syzeton* (*Aderus*?), *Caryobruchus* (*Bruchus*?). A number of taxa were also coded for morphological characters, although DNA material was still unavailable when this paper was submitted; these include *Omma*, *Ytu*, *Aesalus*, *Ceratognathus*, *Acalyptomerus*, *Calyptomerus*, *Amplectopus*, *Artematopus*, *Rhinorhipus*, *Onichodon*, *Endecatomus*, *Melittomma*, *Byturus*, *Lamingtonium*, *Meligethes*, *Discoloma*, *Periptyctus*, *Nesolathrus*, *Dioedus*, *Diaperis* and *Ischalia*.

Character selection

Developing a character list to be used to assess phylogenetic relationships across an entire order involves a number of problems. Although important comparative morphological works covering the entire order, such as Böving and Craighead (1931) and Emden (1942) on larvae or Forbes (1926) on hind wing folding, were published in the early 20th Century and incorporated into the keys and discussions found in Crowson's first major works (1955, 1960), along with his own studies on the metendosternite (Crowson 1938, 1944), cladistic analyses involving a wide selection of taxa across the order were virtually non-existent until the recent work of Beutel and Haas (2000), which included 28 beetle genera (27 families and most superfamilies) and four neuropteroid outgroups.

Some morphological characters traditionally used to define suborders, series or superfamilies involve internal anatomical features requiring special techniques for preservation and examination. Two examples are the type of attachment of Malpighian tubules to the hind gut (Poll 1932, Stammer 1934, Saini 1964) and the fine structure of the ommatidial rhabdom (Wachmann 1977, Caveney 1986). The normal type of cryptonephridial Malpighian tubules (with tubules attached independently) and an ommatidium with an open rhabdom are both restricted to the series Cucujiformia, while a modified type of cryptonephridism (with tubules attached at a single point) is a characteristic of Bostrichoidea, which also have a fused rhabdom. Musculature is another important system utilized in a number of recent works, including Beutel and Haas (2000), Beutel *et al.* (2007) and Ge *et al.* (2007). In the first of these on relationships of the beetle suborders, about a third of the characters were based on thoracic musculature. Published studies utilizing the above characters have been based invariably on a relatively small selection of exemplars, and constraints on time, appropriately preserved specimens, expertise and equipment prevented their use in the present study.

Most modern phylogenetic studies based on morphological characters have involved subsets of the order, such as Adephaga (Beutel 1992, 1995a, 1997; Miller 2001), Myxophaga (Beutel 1999a, Beutel *et al.* 1999), Staphyliniformia (Newton and Thayer 1995; Hansen 1997; Beutel and Molenda 1997; Beutel and Komarek 2004; Beutel and Leschen 2005c; Bernhard *et al.* 2009), Elateriformia (Lawrence 1988; Beutel 1995b; Lawrence *et al.* 1995; Costa *et al.* 1999; Caterino *et al.* 2005), Cucujoidea (Leschen *et al.* 2005), Chrysomeloidea (Reid 1995) or Curculionoidea (Morimoto 1962; Kuschel 1995; Marvaldi and Morrone 2000; Marvaldi *et al.* 2006). These taxon-limited character sets were useful to clarify relationships within particular groups, and a number of them were included in our character set; but homoplasies sometimes resulted when they were applied to taxa in other groups.

Characters chosen for this study had to be of the type observable in cleared and dissected museum specimens, and the initial source was a series of characters originally developed for interactive keys to adult and larval Coleoptera published by Lawrence *et al.* (1999a, 1999b). Many of these, such as length-width ratios, while useful for identification, were apparently inappropriate for phylogenetic analyses, but the utility of others remains untested. Additional characters were taken from some of the group-specific studies mentioned above or suggested by members of the BToL TWiGs. Four adult character sets have been used extensively here which were either lacking or treated rather superficially in Lawrence *et al.* (1999b) and Beutel and Haas (2000): hind wing (38 characters), abdomen (37), and male genitalia (20) and female genitalia (19). Although excellent comparative studies of female genitalia have been published for Adephaga (Liebherr and Will 1998; Miller 2001), few studies have been made in Polyphaga, except for the early work of Tanner (1927). Characters of the internal female tract were not included due to difficulties in making reasonable dissections with all ducts intact and especially in determining homologies throughout the order.

Characters involving the hind wing and genitalia presented certain problems when dealing with outgroup taxa. In the case of the hind wing, many important features are associated with folding and unfolding and had to be coded as inapplicable for all outgroups, where transverse folding does not occur. Genitalic characters of both sexes were difficult to code for outgroups, because comparative studies of holometabolan genitalia (e.g., Aspöck 2002; Aspöck and Aspöck 2008; Vilhelmsen 2000, 2001) almost never include Coleoptera.

Although we tried to include characters that were considered to be "good" phylogenetic indicators, we were well aware of the fact that the usefulness of such characters only reflected their ability to produce cladograms that were not in conflict with current preconceived notions. The final character set includes 516 characters: 344 based on adults and 172 on larvae.

Character list and notes

Terminology (general)

Orientation. The beetle body is always considered to be in normal walking position, so terms like "above" or "higher plane" always refer to true dorsal, and the term "inclined" in C161 is equivalent to "anteriorly elevated". This statement is necessary, since in descriptions some workers describe a beetle on its back, thus reversing the above terms.

Conventions. In the notes, character numbers have a "C" prefix and states an "S" prefix. Summaries of occurrence refer only to exemplars in this study unless stated otherwise.

Head and mouthparts

The major regions of the head are not always very clear cut in Coleoptera, and usage may vary from author to author. Occipital here refers to the region directly in front of the occipital foramen, usually up to the posterior edges of the eyes, while vertex is the region between the eyes. There is never a clear cut division between the vertex and the frons, the latter extending in front of the eyes and often forming ridges over the antennal insertions. Likewise, the frons and clypeus are not clearly separated except when there is a distinct frontoclypeal suture. General terminology for mouthparts is shown in Fig. 34A.

1. Head

1. not completely concealed from above by pronotum.
2. completely concealed from above by pronotum (Fig. 42A).

2. Head at base

1. declined less than 45 degrees.
2. declined at least 45 degrees (Fig. 1A).

This refers to the declination of the head at its base and relative to the prothorax. It should not be confused with the declination of the vertex from about the beginning of the eyes, anterior declination of the frontoclypeus or distortion of the prothorax, so that the head is attached ventrally. S2 is often accompanied by the shortening of the prosternum in front of the coxae (C117) or in some cases excavation of the prosternum (C120) to receive the head in repose.

3. Head behind eyes

1. not or gradually constricted laterally, without temples (Figs 2B, 4B).
2. abruptly constricted laterally to form distinct temples and narrower neck (Figs 3D, 38B).

S2 excludes a constriction immediately behind the eye, where no temple is formed (e.g., Fig. 2B) or any gradual narrowing where a well defined temple cannot be measured.

4. Temple

1. less than 0.25 times as long as eye as seen from above (Fig. 38B).
2. 0.25 to 1.0 times as long as eye as seen from above (Fig. 38A).
3. longer than eye as seen from above (Fig. 3D). Inapplicable when C3 = S1.

5. Posterodorsal edge of head capsule above occipital foramen

1. not or barely emarginate.
2. with single emargination (Fig. 37D).
3. with two small emarginations or incisions within a larger emargination.
4. with two emarginations (Figs 2B, 37C).

In S3 a line connecting the lateral edges of the larger emargination does not meet the cuticular process separating the two smaller emarginations. If it does so then it is considered as S4.

6. Median occipital endocarina

1. absent (Fig. 4B) or less than 0.2 times as long as greatest head width behind eyes.
2. at least 0.2 times as long as greatest head width behind eyes (Figs 2C, 39G).

The median occipital endocarina begins at the edge of the occipital foramen and extends anteriorly.

7. Occipital region

1. without stridulatory file.
2. with single stridulatory file (Fig. 4D).
3. with paired stridulatory files (Figs 4B, 4E).

Under lower magnifications stridulatory files usually appear to be shiny areas just in front of the occipital foramen. Among the included exemplars, a single file (S2) occurs only in *Myrabolia*, while paired files (S3) are found in one cryptophagid (*Atomaria*) and two erotylids (*Dacne* and *Pharaxonotha*). Paired files and single files occur in a number of other Erotylidae, and single files may also occur in Tasmosalpingidae, lycoperdinine Endomychidae and some cassidine Chrysomelidae.

8. Length of occipital region

1. less than 0.25 times as long as greatest head width behind eyes.
2. 0.25 to 0.5 times as long as greatest head width behind eyes.
3. more than 0.5 times as long as greatest head width behind eyes (Fig. 4H).

Length of the occipital region is the distance between a line joining the posterior edges of the eyes and a line tangential to the posterior edge of the head capsule.

9. Elevated transverse occipital ridge

1. absent.
2. present, but not abutting anterior edge of pronotum.
3. closely appressed to and abutting anterior edge of pronotum concealing neck region (Figs 38C, 38D).

This ridge must be elevated above the head surface behind it, as seen in lateral view; it may be rounded or sharply carinate. The ridge abuts the anterior edge of the pronotum, so that the neck is not obvious (S3) in cholevine Leiodidae, Clambidae, Mordellidae and anaspidine Scraptiidae.

10. Low transverse occipital carina

1. absent.

2. present (Figs 3E, 6C).

The areas on either side of this carina are on the same plane. This has been called the vertexal line by Leschen (2003).

11. Vertex

1. not or slightly declined.

2. strongly declined, vertical or inflexed (Figs 1D, 1F).

Declination of the vertex begins at or near the posterior edges of the eyes. This does not refer to the declination of the entire head (C2).

12. Ocelli

1. three.

2. two (Fig. 2A).

3. one (Figs 2E, 42C).

4. none (Fig. 3D).

S1 occurs in *Cephus*, *Panorpa* and *Agulla* among the outgroups and also in the unusual genus *Sikhotealinia* (Jurodidae), doubtfully placed in Archostemata, but unavailable for this study. Paired ocelli (S2) occur in *Sabatinca* among the outgroups and also in the hydraenid genera *Ochthebius* and *Meropathus,* the staphylinid genera *Paraphloeostiba* and *Glypholoma*, and all Derodontidae. A single median ocellus (S3) occurs in the dermestid genera *Orphilus* and *Anthrenus*. The significance of ocelli in beetles and the possibility that they are part of the ground-plan of Coleoptera have been discussed by Leschen and Beutel (2004).

13. Eyes

1. at least slightly protuberant, extending laterally beyond sides of head as seen from above (Figs 3A, 4G, 6E).

2. not at all protuberant, outline continuous with sides of head (Figs 4F, 4H, 7C).

S2 eyes occur in many Hydradephaga, but in most beetles eyes are at least slightly protuberant.

14. Eyes

1. undivided (Figs 1D, 1E).

2. divided into upper and lower parts (Figs 7A, 7C).

S2 is a synapomorphy uniting the taxa of Gyrinidae, but it also occurs in the scarabaeoid genera *Bolboceras*, *Geotrupes* and *Scarabaeus*, in clambine Clambidae, and in the cerambycid genus *Tetraopes*.

15. Vertical eye diameter

1. less than 1.25 times greatest horizontal eye diameter (Fig. 1E).

2. at least 1.5 times greatest horizontal eye diameter (Figs 1C, 1D).

Vertical and horizontal are independent of the angle of the head to the main body axis.

16. Anterior or mesal eye emargination

1. absent or less than 0.2 times eye width on either side of emargination (Figs 1D, 5B).

2. at least 0.2 times eye width on either side of emargination (Fig. 7B).

17. Interfacetal setae

1. absent (Figs 2C, 3F, 4G).

2. slender and shorter than diameter of eye facet (Fig. 4A).

3. slender and at least as long as diameter of eye facet (Figs 6A, 6B, 39C).

4. stout and at least as long as diameter of eye facet.

18. Ommatidium

1. not of exocone type, without expanded corneal lens.

2. of exocone type with expanded corneal lens (Fig. 54E).

S2 should be visible in cleared specimens with rough sections, since the corneal lens is large and extends proximally; however coding for most groups was based on the work of Caveney (1986). Distinction was not made between acone and eucone, since the crystalline cone dissolves during clearing and its preservation requires special histological techniques. Exocone eyes are known in *Pleocoma*, Dascillidae, most members of the superfamilies Byrrhoidea and Elateroidea (excluding Lutrochidae, Dryopidae and Eucnemidae) and many Bostrichoidea. The condition never occurs in Cucujiformia.

19. Antennal socket

1. not located within fossa (Fig. 1E).

2. located within broad, saucer-like fossa (Fig. 3F).

The countersunk antennal fossa must at least partly and usually entirely encircle the socket. If just the area below the socket is concave, this is considered to be part of the subantennal groove (C24). S2 occurs in Gyrinidae, *Sandalus*, *Aulonothroscus* and *Lissomus*.

20. Antennal socket

1. not located within eye emargination (Fig. 2B).

2. located within eye emargination (Fig. 7B).

21. Antennal socket

1. not or only slightly raised (Fig. 2F).

2. distinctly raised (Figs 1F, 7B).

Raised antennal sockets are characteristic of Cerambycidae and the related families Oxypeltidae, Vesperidae and Disteniidae, but S2 also occurs in some elateriform taxa, such as Rhipiceridae, Eulichadidae, Callirhipidae, Cerophytidae, Omalisidae, Lycidae, and a few tenebrionoids (e.g., *Rhipidioides*, *Pristoderus*, *Meryx*, *Calopus*).

22. Antennal sockets

1. not completely concealed by frontal ridges, at least partly visible in dorsal or frontal view (Figs 2B, 4C, 4F, 4G).

2. completely concealed from above or in front by frontal ridges (Figs 1E, 2A, 41B).

In S1, the socket itself (with the antenna removed) must be at least partly visible from directly above the head or in frontal view if the head is somewhat declined.

23. Antennal sockets separated by

1. less than 1.5 times diameter of a socket (Figs 2D, 39C).

2. at least 1.5 times diameter of socket (Fig. 6D).

Narrowly separated antennal sockets occur in the outgroups *Panorpa* and *Spaminta*, in the families Haliplidae, Callirhipidae, Cerophytidae, Omalisidae, Lycidae, Rhagophthalmidae and Lampyridae, in the cantharid genus *Malthodes*, the cryptophagid genus *Atomaria*, *Rhipidioides* and *Ischalia* among the Tenebrionoidea and the chrysomelid genus *Diabrotica*.

24. Subantennal groove

1. absent (Fig. 1E).

2. present between eye and mouth cavity (Fig. 3F).

3. extending below or behind eye (Fig. 7F).

The subantennal groove begins immediately beneath the antennal socket; it is shiny and separates the edge of the eye from the mouth cavity. It is often relatively short, forming a housing for the scape (S2), but in some groups it may extend beyond the lower edge of the eye or well behind the eye (S3).

25. Median frontoclypeal groove

1. absent (Fig. 4A).

2. present (Figs 2D, 2F).

The median frontoclypeal groove is found in a number of chrysomeloids, some basal curculionoids, and a few other unrelated genera; it is usually relatively deep and well-defined and, unlike the midcranial suture (C29), it is not connected to the frontoclypeal suture.

26. Frontoclypeal region at midline

1. not or only slightly, gradually declined (Fig. 1E).

2. strongly and abruptly declined but not forming sharp carina.

3. forming sharp, transverse carina (Figs 1B, 3F).

Although an abruptly declined frontoclypeal region is characteristic of some family-group taxa, especially in Scarabaeoidea and Elateriformia, this region is highly variable in Elateridae, where all three states occur.

27. Frontoclypeal suture

1. absent or incomplete (Figs. 3A, 4C).

2. distinct and complete (Figs 2A, 3B, 4A).

If there is a vague transverse impression in the frontoclypeal region, the taxon is coded as lacking a suture.

28. Frontoclypeal suture

1. straight, very slightly curved or curved or angulate at sides only.

2. moderately to strongly, evenly curved (Figs 3B, 4A).

3. angulate at middle (Fig. 2A, 37G).

Inapplicable when C27 = S1.

29. Midcranial suture

1. absent.

2. present (Fig. 37G).

This median suture or line is called the dorsomedian suture by Beutel & Leschen (2005c) and may be homologous to what is called the epicranial suture in some other orders. When it occurs in Polyphaga, it is usually associated with what is generally called the frontoclypeal suture, but the homologies here are unclear. Among the exemplars, it occurs in the outgroup *Sialis*, in *Hygrobia*, several Hydrophilidae, *Bacanius* among the Histeridae, the staphylinoid genera *Agyrtodes* and *Nicrophorus*, the scarabaeoid *Geotrupes* and the genus *Chrysomela*.

30. Clypeus

1. not subdivided (Fig. 37G).

2. subdivided into membranous (or hyaline) anterior part (anteclypeus) and sclerotized posterior part (postclypeus), the latter not necessarily separated from frons (Figs 37C, 38A).

In Tenebrionidae (see Aalbu *et al.* 2002) and possibly elsewhere, the anteclypeus is referred to as a "clypeolabral membrane", which may or may not be concealed beneath the edge of the clypeus.

31. Length of muzzle or rostrum

1. less than width of clypeus or frontoclypeus (Fig. 2F).

2. greater than width of clypeus or frontoclypeus (Fig. 1C).

The length of the muzzle or rostrum is the distance between a line connecting the anterior edges of the eyes and the anterior edge of the clypeus or frontoclypeus. Although a very long rostrum is found only in Curculionoidea and in the outgroup *Panorpa*, the rostrum is longer than wide in scattered other taxa, including *Tetraphalerus*, *Rhinorhipus*, *Lycus*, *Paracucujus*, *Salpingus* and *Caryobruchus*.

32. Labrum

1. completely membranous or well sclerotized and freely movable with strip of basal membrane between it and clypeus (Figs 7A, 37C, 38B).

2. connate with clypeus but separated from it by complete line or groove at its base.

3. partly or completely fused to clypeus, without or with incomplete line or groove at its base (Figs 3A, 37D).

In S1 the clypeus or anteclypeus usually overlaps the base of the labrum, which is more or less movable. In S2 the two sclerites are on the same plane and abut one another, so that the labrum is not movable; this condition was found in the genera *Arthropterus*, *Syntelia*, *Creophilus*, *Chauliognathus*, *Cucujus*, *Parandra* and *Urodontus*, while a partly or completely fused labrum (S3) occurs in *Panorpa*, *Eoxenos*, *Omma*, *Micromalthus*, *Pleocoma*, *Diphyllostoma*, *Ceratognathus*, *Lucanus*, *Sandalus*, *Chelonarium*, *Atractocerus*, *Helota*, *Glischrochilus*, *Rhipidioides*, *Sypilus*, and all Curculionoidea, except Nemonychidae and Anthribidae.

33. Labrum

1. not concealed beneath clypeus (Figs 7A, 38B).
2. concealed beneath clypeus and not visible externally (Figs 5D, 18F, 37A).

The labrum in S2 is usually free but often membranous, and not visible beyond the edge of the clypeus. This occurs in *Andotypus*, the scarabaeid genera *Aphodius*, *Scarabaeus*, *Dynastes* and *Cetonia*, *Chelonarium*, *Rhinorhipus*, *Onichodon* and *Malthodes* among the Elateriformia, the cucujoid taxa *Paracucujus*, *Diplocoelus*, Monotomidae, *Murmidius* and *Discoloma* and the zopherid genus *Hyporhagus*.

34. Base of labrum

1. on same plane as apex.
2. on lower plane than apex forming deep groove between clypeus and labrum (Fig. 40A).

S2 occurs in Byrrhidae, *Aulonothroscus* and elaterid exemplars, except *Selonodon*.

35. Labral apex

1. narrowly rounded to acute.
2. broadly rounded or angulate (Fig. 7A).
3. truncate.
4. emarginate (Fig. 38B).
5. trilobed.

36. Antennae

1. more or less pubescent (Fig. 42D).
2. glabrous or with few very short, fine hairs only (Fig. 8A, 8B).

S2 occurs primarily in aquatic Myxophaga, Adephaga and Elmidae, but it also occurs in *Tetraphalerus* and *Passandra*.

37. Number of antennomeres

1. more than twelve.
2. twelve.
3. eleven (Figs 8B, 37C, 38E).
4. ten (Figs 37D, 39E, 42D).
5. nine (Fig. 8A).
6. eight.
7. seven.
8. six.
9. four (Fig. 35A).

The majority of beetles have 11-segmented antennae (S3), and scattered taxa throughout the order, including most Scarabaeoidea, have the number reduced to 10 (S4). Antennae are 9-segmented (S5) in *Torridincola* and *Ytu*, Hydrophilidae (except *Spercheus*), some Histeridae, Hydraenidae, *Aphodius* and *Scarabaeus*, *Acalyptomerus*, *Aphanocephalus*, *Bystus*, *Delphastus*, *Platynaspis* and *Orthoperus*. Eight-segmented antennae (S6) occur in *Hydroscapha*, *Gyrinus*, *Dineutus*, *Loricaster*, *Helichus*, *Rodolia* and *Sphenophorus*, while those with seven antennomeres (S7) occur only in *Spercheus* among the exemplars. Six-segmented antennae (S8) occur in *Eoxenos* and *Platypus*, and those with four antennomeres (S9) only in *Lepicerus*. An increase to 12 antennomeres (S2) is known in Phengodidae, *Rhagophthalmus* and the cerambycid genus *Prionus*, while multisegmented antennae (S1) are found in most of the outgroups.

38. Antennal flagellum

1. filiform or moniliform, antennomeres more or less equal in width and elongate or subquadrate (Figs 1A, 8B).
2. incrassate or clavate, antennomeres gradually increasing in width towards apex (Figs 8A, 8D).
3. serrate to flabellate, most antennomeres (but usually not apical one) asymmetrically expanded to form rami (Figs 35C, 35G, 39H).
4. capitate, with one or more apical antennomeres distinctly wider and/or longer than preceding ones (Figs 8E, 37E, 39E, 42D).
5. perfoliate, most antennomeres more or less equal in width but distinctly wider than long (Fig. 43A).

All of the first four antennal types occur widely throughout the order, although S3 is characteristic of most Elateriformia and S4 is the dominant type in Hydrophiloidea, Histeroidea, basal Staphylinoidea, Scarabaeoidea, Cucujoidea and Curculionoidea. Perfoliate antennae (S5) occur only in *Arthropterus* and *Diaperis* among the exemplars.

39. Antennal rami in male

1. beginning on antennomere 3 or 2 (Figs 35G, 39H).
2. beginning on antennomere 4.
3. beginning on antennomere 5.
4. beginning on antennomere 6.

Inapplicable when C38 = S1, S2, S4 or S5.

40. Antenna

1. not geniculate or elbowed, pedicel not forming angle with scape (Figs 38E, 42D).
2. distinctly geniculate or elbowed, pedicel forming distinct angle with scape (Figs 7F, 37B).

Geniculate refers to the articulation of the pedicel to the scape and not to the shape of the scape. S2 occurs in *Syntelia*, Histeridae, *Palaeostigus*, *Aesalus*, *Lucanus*, *Scarabaeus*, *Uleiota*, *Holopsis*, *Clypastraea* and Curculionidae among the exemplars.

41. Antennal scape

1. shorter than pedicel (Fig. 39F).
2. 1 to 3 times as long as pedicel (Figs 3D, 4F, 4H, 42D).

3. more than 3 times as long as pedicel (Figs 37B, 37D).

42. Antennal scape

1. as long as wide or shorter than wide (Figs 7A, 8A).
2. 1 to 3 times as long as wide (Figs 2A, 2D, 4F).
3. more than 3 times as long as wide (Figs 4H, 7F, 37B).

43. Scape

1. parallel-sided or only slightly curved (Fig. 4F).
2. distinctly bent (Fig. 37B).
3. ovoid to subglobular or subtriangular (Figs 7A, 8A).
4. consisting of two distinct parts.

Most character states occur widely throughout the order, but S4 is known only in *Aspidytes* and Noteridae.

44. Pedicel

1. not partly enclosed within scape.
2. partly enclosed within apex of scape (Fig 7A).

A partial enclosure of the pedicel by the scape (S2) is known in *Satonius*, Gyrininae, *Aspidytes*, *Arthropterus* and *Collops*.

45. Apical three or four antennomeres

1. without periarticular grooves.
2. with periarticular grooves filled with sensilla (Fig. 8E).

Periarticular grooves are known in Leiodidae and Boridae.

46. Number of apical antennomeres abruptly enlarged to form club

1. five or more (Fig. 43C).
2. four (Fig. 38E).
3. three (Figs 3B, 8C, 42D).
4. two (Fig. 39E).
5. one (Fig. 35A).
6. none.

47. Antennal club

1. not 5-segmented or with second club segment subequal to or larger than first one.
2. 5-segmented with second club segment smaller than first and third (Figs 8E, 38F).

Inapplicable when C46 = S6. S2 occurs in most Leiodidae and in the hobartiid genus *Hydnobioides*.

48. Antenna

1. without cupule.
2. with glabrous cupule (Figs 37C, 37F, 43C).
3. with pubescent cupule.

Inapplicable when C46 = S6. The cupule, as used here, includes but is not restricted to the functional cupule playing a role in the respiration of aquatic hydrophilids and hydraenids. Any cup-like antennomere immediately preceding the club (e.g. that in Silphidae) is also considered to be a cupule.

49. Antennal club

1. not or only slightly asymmetrical (Figs 3B, 39E).
2. distinctly asymmetrical with serrate, pectinate or flabellate segments (Figs 37D, 37E).
3. distinctly asymmetrical with lamellate or cupuliform segments (Fig. 8F).

Inapplicable when C46 = S6. The difference between S2 and S3 is mainly in the width of the rami. S3 clubs are found primarily in Scarabaeoidea, but that in *Nicrophorus* has also been coded as S3.

50. Antennomeres comprising antennal club

1. loosely articulated (Figs 3B, 8C).
2. tightly articulated forming compact club (Fig. 37B).

Inapplicable when C46 = S6.

51. Terminal antennomeres

1. without enlarged sensilla or compound sensoria.
2. with enlarged sensilla (sensoria or sensory vesicles) (Fig. 8G).
3. with compound, multi-pronged sensoria.

This usually refers to antennomeres comprising the club, but may also apply to most antennomeres. Enlarged sensilla, which are usually simple but may be forked (S2), occur in *Nossidium*, *Orphilus* and the Corylophidae. Multi-pronged sensilla (S3) were noted in *Cis* and *Diaperis*.

52. Mandible

1. not more than 2 times as long as basal width (Fig. 10H).
2. more than 2 times as long as basal width (Fig. 10F).

53. Mandible

1. visible in lateral view (Fig. 8F).
2. not visible in lateral view (Fig. 7D).

S2 is correlated with endognathy or with highly reduced mandibles. Those of some scarabaeoids may have massive bases but highly reduced apices, which are not externally visible.

54. Mandible

1. not flattened and lamellar.
2. flattened and lamellar (Fig. 41D).

55. Mandible

1. not inserted within deep socket.
2. inserted within deep socket (Figs. 12A, 12E).

S2 occurs in most Curculionoidea, but not in Nemonychinae, Urodontinae, Scolytinae or Platypodinae.

56. Basal mandibular width

1. greater than width of antennal scape.
2. not greater than width of antennal scape.

S2 mandibles include those which are highly reduced (e.g., Psephenidae or Chelonarium) or those which are elongate with a slender base (e.g., Lycidae, Lampyridae).

57. Mandibular apex

1. neither broadly rounded nor truncate.

2. broadly rounded or truncate (Figs 10D, 41D).

58. Mandibular apex

1. simple, not subdivided (Fig. 10A, 10F).

2. divided into two lobes or sharp teeth (Fig. 10B).

3. divided into three lobes or sharp teeth.

4. divided into more than three lobes or sharp teeth.

59. Mandibular apex in apical view

1. narrow, apical edge strongly oblique or parallel with plane of movement or multiple teeth, if present, obliquely oriented and not in same plane (Figs 38A, 40D).

2. broad, apical edge more or less perpendicular to plane of movement or multiple teeth, if present, on same plane (Figs 10G, 12A, 17A, 18F).

60. Incisor edge of mandible

1. without fixed lobes or teeth (Fig. 10F).

2. with one fixed lobe or tooth.

3. with two or more fixed lobes, teeth or serrations (Fig. 38A).

61. Articulated, sclerotized process on inner subapical edge of mandible

1. absent.

2. present on both mandibles (Fig. 10H).

3. present on one mandible only (Fig. 43F).

The presence of an articulated, sclerotized process on both mandibles (S2) occurs in Hydraenidae, Clambidae and *Byrrhinus*. A similar process on one mandible only (S3) is restricted to Myxophaga.

62. Dorsal surface of mandible

1. without cavity.

2. with glabrous cavity.

3. with setose cavity (Figs 3C, 10C).

A glabrous cavity (S2) occurs in our exemplars of Phloeostichidae and Silvanidae but may be somewhat reduced in the latter family. A setose cavity (S3) is characteristic of *Omma*, *Rhinorhipus*, Boganiidae, Sphindidae and Megalopodidae: Palophaginae. The possible functions of these cavities have been discussed by Grebennikov & Leschen (2010). Sen Gupta & Crowson (1966) hypothesized that mandibular cavities function as mycangia, and in the family Sphindidae, whose members feed exclusively on spores of Myxomycetes, this is probably the case. However, the function of the mandibular cavities in other groups is yet to be determined.

63. Dorsal surface of mandible

1. without tubercle or ridge.

2. with tubercle fitting into depression on lateral edge of clypeus (Figs 3C, 5C, 11G)

3. with ridge fitting against lateral edge of clypeus.

4. with projection fitting into depression at base of labrum.

5. with ridge fitting against lateral edge of labrum.

Some attempt has been made here to distinguish between the various ways in which the mandibles in closed position interlock with the clypeus or labrum. A mandibular tubercle fitting into a clypeal depression (S2) occurs in Sphindidae, Hobartiidae and Phloeostichidae among the Cucujoidea, but also in the staphylinid genus *Scaphidium*, and a similar tubercle fitting into a labral depression (S4) occurs in *Hydraena* and Ptiliidae (Betz *et al.* 2003). A dorsal ridge fits against the lateral edge of the clypeus (S3) in some Histeridae, *Rhinorhipus* and *Orphilus*, or the lateral edge of the labrum (S5) in rhysodine Carabidae, *Hister* and some Elateriformia. This interlocking of the mandible with clypeus or labrum is sometimes associated with the presence of a dorsal mandibular cavity, which is concealed when the mandibles are in closed position (see C62).

64. Mandibular mola

1. present (Figs 10B, 10D).

2. absent (Fig. 10F).

The mola in both adult and larval mandibles refers to a basal processing area, which is often armed with ridges, tubercles or asperities and interacts with the mola on the opposite mandible to process food particles (fragmenting them or compacting them into a bolus which is passed into the gut). The mola is absent in adults of all outgroups and all Archostemata and Adephaga; within the Polyphaga the mola is absent in *Syntelia* and *Hister*, Silphidae and some Staphylinidae, Scirtidae, Dascilloidea, Buprestoidea, some Byrrhoidea, most Elateroidea, some Bostrichoidea, many Cleroidea, several Cucujoidea and most Chrysomeloidea and Curculionoidea, but in very few Tenebrionoidea.

65. Prostheca

1. well developed, usually membranous and fringed with hairs (Fig. 38A).

2. reduced, often only a fringe of short hairs.

3. absent.

The prostheca in both adult and larval mandibles lies just distad of the mola and in adults it usually consists of a membranous lobe, often lined with short setae. In adult mandibles the prostheca may be coded as present (either S1 or S2) even when there is no mola, but this is not the case for larval mandibles (see Larval Mandibles, C395, C397).

66. Mandibular bases

1. in contact when mandibles in closed position (Fig. 5C).

2. not in contact when mandibles in closed position (Figs 3F, 37D).

67. Mesal corner of mandibular base

1. without pubescent process.

2. with pubescent process not longer than mandible (Fig. 10G).

3. with pubescent process (pharyngeal process) longer than mandible (Fig. 41E).

Although a short pubescent process may occur in this position in a number of taxa, a very long one capable of conveying food through the rostrum is characteristic of most curculionoids.

68. Maxillary lobes

1. consisting of galea and lacinia (Figs 9B, 9E, 34A, 58C).

2. consisting of galea only.

3. consisting of lacinia only.

4. consisting of mala or apparent fusion of galea and lacinia (Fig. 9G).

5. absent.

It is often difficult to determine if a single maxillary lobe is galea, lacinia or the two combined (= mala) without studying musculature. When there is some doubt as to the nature of a single lobe it has been coded as S4.

69. Galea or mala

1. rounded or truncate and pubescent or setose (Figs 41A, 58D).

2. with one or more stout spines or teeth, with or without pubescence (Fig. 9C).

3. with one or more membranous, setose acute lobes.

4. palpiform and subglabrous (Figs 9E, 34A, 58C).

5. falciform or styliform (Fig. 9A).

70. Lacinia

1. moderately long, extending beyond middle of galea, not much narrower than galea (Figs 34A, 58C).

2. moderately long, extending beyond middle of galea, but much narrower than galea.

3. short, not extending beyond middle of galea.

4. apparently absent, highly reduced or completely fused to galea (Fig. 9H).

71. Lacinia

1. with tridentate apical or subapical uncus.

2. with bidentate apical or subapical uncus (Fig. 9B).

3. with unidentate apical or subapical uncus (Figs 58C, 58D).

4. without uncus Fig. 41A).

The uncus is located at or very near the apex of the lacinia; it is unarticulated and usually larger or more heavily sclerotized than the various spines that may line the laciniar apex; it is more obvious when subdivided.

72. Maxillary palps

1. elongate, projecting anterolaterally, usually extending well beyond apex of galea (Figs 9E, 9H).

2. short, not projecting, usually shorter than galea or extending only slightly beyond its apex (Fig. 12E).

S2 characterizes the Curculionoidea, excluding Nemonychidae and Anthribidae.

73. Number of maxillary palpomeres

1. five.

2. four (Figs 9A, 9E, 9H).

3. three (Fig. 12E).

4. one.

Five maxillary palpomeres (S1) occurs only in the outgroups *Cephus*, *Panorpa* and *Sabatinca*. Four palpomeres (S2) occurs in the vast majority of beetle taxa, with a reduction to three (S3) in the corylophid genus *Holopsis* and in several Curculionoidea. A single palpomere (S4) occurs only in the outgroup *Eoxenos* and in the highly specialized ripiphorid genus *Rhipidioides*.

74. Apical maxillary palpomere

1. not or only slightly shorter or narrower than preapical palpomere (Fig. 34A).

2. distinctly shorter and narrower than preapical palpomere (palp awl-like) (Fig. 9A).

75. Apical maxillary palpomere

1. cylindrical to fusiform (narrowed at both ends) or conical (narrowed apically) (Figs 9B, 9G, 34A).

2. slightly expanded and truncate apically (Fig. 41A).

3. strongly expanded and squarely to obliquely truncate apically, triangular to securiform or cultriform (Figs 11F, 42B).

Both securiform and cultriform terminal palpomeres have two sides unequal and the apical side strongly oblique; cultriform appears to be an extreme type of securiform.

76. Apical maxillary palpomere

1. without distinct patch of projecting sensilla.

2. with group of projecting sensilla located on surface.

3. with group of projecting sensilla located within deep cavity (Figs 9F, 11A, 11F).

S2 and S3 refer to the more or less projecting sensilla on the surface in Cupedidae (S2) or in a deep cavity in Micromalthidae and Ommatidae (S3), not to the flattened and inset sensilla which are relatively common but often very difficult to see except with the SEM (Honomichl 1980).

77. Ligula

1. not emarginate, truncate to acute (Figs 11B, 11E).

2. shallowly emarginate.

3. deeply emarginate or bilobed (Fig. 9D).

4. multilobed.

5. absent.

The divided or bilobed ligula may represent the basal condition, the lobes being homologous to the paraglossae. A truncate or slightly emarginate ligula may project laterally, but this is not considered to be a bilobed condition.

78. Number of labial palpomeres

1. four.
2. three (Figs 10E, 11B).
3. two.
4. one.
5. none (Fig. 41H).

Four labial palpomeres (S1) occur in the outgroup *Cephus*, and the labial palps are entirely absent (S5) in the outgroup *Eoxenos*, the zopherid genus *Pristoderus* (and a few related Notogean genera) and the highly derived ripiphorid genus *Rhipidioides*. Three labial palpomeres (S2) occur in almost all Coleoptera, with reductions to two or one (S3 and S4) in *Panorpa* among the outgroups, in the myxophagan genera *Lepicerus* and *Satonius*, *Julodis* and *Acmaeodera* among the Buprestidae, the elateroid genera *Telegeusis* and *Cenophengus*, and several groups of Cucujoidea and Curculionoidea.

79. Articulations of labial palps

1. located on ventral surface of prementum and visible from below (Figs 10E, 11B).
2. located on ventral surface of prementum but concealed from below by mentum (Figs 11E, 12A).
3. located on dorsal surface of prementum and concealed from below.
4. located within pits or grooves and concealed from below.

80. Apical labial palpomere

1. cylindrical to fusiform (narrowed at both ends) or conical (narrowed apically) (Figs 10E, 11B).
2. slightly expanded and apically truncate (Fig. 11D).
3. strongly expanded and squarely to obliquely truncate apically, subtriangular to securiform or cultriform.

81. Mentum

1. less than 0.5 times as long as wide (Fig. 5A).
2. 0.5 to 1.0 times as long as wide (Fig. 10E).
3. longer than wide (Figs 5E, 11E).

82. Mentum or postmentum

1. widest at or near base (Fig. 10E).
2. widest at about middle (Fig. 5A).
3. widest at or near apex (Figs 11C, 11E).

83. Apex of mentum or postmentum

1. convex (Fig. 10E).
2. subtruncate (Fig. 5A).
3. shallowly to moderately emarginate or biemarginate (Fig. 11E).
4. very deeply emarginate or biemarginate, enclosing prementum (Figs 34A, 40B, 41F).
5. fused to prementum.

Although S1–S3 are widely distributed, S4 is found almost exclusively in Adephaga, with a similar condition occurring in Passalidae and Heteroceridae. S5 was observed in the scarabaeid genus *Cetonia* and in the latridiid genera *Corticaria* and *Eufallia*.

84. Mentum

1. not enclosed by lateral lobes of submentum.
2. enclosed by lateral lobes of submentum (Fig. 40F).

S2 occurs only in Passandridae and parandrine Cerambycidae.

85. Mentum

1. separated from submentum or gulamentum by suture.
2. fused to submentum or gulamentum.

The mentum is fused to the submentum or gulamentum in all curculionoids, but also in *Sabatinca*, *Ytu*, *Spanglerogyrus*, *Notomicrus*, *Amphizoa*, *Arthropterus*, the Rhysodinae, the elateriform genera *Sandalus*, *Lycus*, *Cenophengus*, *Ellychnia*, *Pyrocoelia*, *Silis* and *Malthodes*, and the tenebrionoid genera *Chalcodrya*, *Epicauta* and *Ischalia*.

86. Subgenal ridges

1. absent.
2. present (Fig. 7E).

Subgenal ridges extend from the ventral mandibular condyles posteriorly and more or less separate the gena from the hypostoma or postgena on each side. In Scirtidae these ridges lie against the procoxae when the head is in resting position and the area between the ridges is concave. Subgenal ridges occur in *Lepicerus*, *Declinia*, *Nycteus*, Clambidae, Scirtidae, *Lara*, Ptilodactylidae, *Podabrocephalus*, *Chelonarium*, *Callirhipis*, Artematopodidae, *Anischia*, *Aulonothroscus* and Elateridae.

87. Gulamentum

1. less than 0.33 times as long as head length as seen from above.
2. 0.33 to 0.67 times as long as head length as seen from above (Fig. 5E).
3. more than 0.67 times as long as head length as seen from above (Figs 7E, 7F).

The gulamentum is defined as the gula combined with the submentum, or the distance from the base of the mentum to the posterior edge of the head, as seen from below.

88. Median gular endocarina (between gular sutures)

1. absent.
2. present.

This endocarina lies between the gular sutures and is NOT homologous to the single gular invagination or fusion of the posterior tentorial arms when the gular sutures are fused together. It may also be very short and has been called a gular apodeme. This endocarina occurs mainly in Adephaga, but is also found in the hydraenid genera *Hydraena* and *Ochthebius*.

89. Gular sutures

1. separated for their entire lengths (Figs 5F, 7E).

2. partly or completely fused together (Figs 7F, 39G).

3. absent.

The gular sutures are considered to begin at the posterior tentorial pits and extend posteriorly to the edge of the head capsule. Any sutures or grooves extending anterad of the tentorial pits are not considered to be gular sutures (see C90 and C91). Partly or completely fused gular sutures characterize most Cuculionoidea, but also occur in *Agulla* and in scattered polyphagan taxa.

90. Submentum or anterior part of gulamentum

1. without longitudinal or oblique grooves.

2. with paired longitudinal or oblique grooves extending anteriorly from posterior tentorial pit or pits to base of submental peduncle (Figs 7E, 12C).

S2 sutures are equivalent to the subgenal sutures (and apparently the hypostomal-labial sutures) of Lyal (1995).

91. Submentum or anterior part of gulamentum

1. without longitudinal, subparallel grooves.

2. with subparallel, longitudinal grooves not connected to gular suture or sutures.

S2 sutures are equivalent to the occipital sutures of Lyal (1995) and occur in most curculionoids.

92. Tentorium

1. with anterior arms slender, not mesally expanded.

2. with anterior arms expanded mesally to form laminatentoria, sometimes meeting at midline (Figs 38B, 55H).

3. without anterior arms.

When the laminatentoria meet broadly at the midline, the resulting structure may be referred to as an anterior tentorial bridge.

93. Corpotentorial bridge

1. straight.

2. singly arched (Fig. 39B, 55H).

3. doubly arched.

4. with anterior process.

5. incomplete or absent.

The corpotentorial bridge or corpotentorium is a term used by Stickney (1923) and MacGillivray (1923) and is sometimes referred to as the posterior tentorial bridge or just tentorial bridge. An anteriorly projecting mesal process on the bridge characterizes members of the family Cerylonidae, but a similar structure occurs in some Adephaga, the staphylinoid genera *Meropathus*, *Apteroloma* and *Prionochaeta*, *Nosodendron*, several cucujoid families, including most Nitidulidae, and the tenebrionoid genus *Cephaloon*.

94. Lateral cervical sclerites on each side

1. at least 0.15 times as long as head width behind eyes, often subdivided (Fig. 55B).

2. less than 0.15 times as long as head width behind eyes, not subdivided.

3. absent.

Although lateral cervical sclerites are absent in all Archostemata, Myxophaga and Adephaga, they occur in five of the outgroups and in basal members of all major polyphagan lineages. Within the Polyphaga, they have been reduced in size or lost a number of times.

Prothorax

As in other flying insects, the prothorax in Coleoptera is usually smaller and more simplified than the wing-bearing mesothorax and metathorax, with the pleuron usually relatively small (except in Archostemata and Adephaga, where it forms a substantial portion of the thoracic wall) and in Polyphaga completely internal. The pleuron, when present, is never subdivided, and the trochantin in both Myxophaga and Polyphaga appears to be completely fused to the pleuron. The entire area in front of and between the procoxae, as well as a portion of each procoxal cavity is referred to as prosternum Although it is possible that the true sternum has been invaginated and fused with sub-coxal elements as in the meso- and metathorax, no trace can be found of a discrimen or katepisternal suture. Terminology for the fore legs is given in Figs 34C and 34D.

95. Sides of prothorax

1. not explanate.

2. laterally horizontally explanate (Figs 13B, 20C).

3. obliquely to vertically explanate.

96. Sides of prothorax

1. with complete lateral carinae separating disc from hypomeron on each side (Figs 15A, 15C, 16A, 16B, 19A).

2. with incomplete lateral carinae not extending to anterior edge (Fig. 16D).

3. with incomplete lateral carinae not extending to posterior edge.

4. with incomplete lateral carinae, extending to neither anterior nor posterior edge.

5. without lateral carinae, disc continuous with hypomera or hypomera absent (Figs 16F, 22D).

The lateral pronotal carinae are often referred to as the lateral margins of pronotum. A margin is considered here to be a raised edge or bead, not just an edge. Also, because the pronotum extends ventrally as a hypomeron, it cannot be considered the lateral edge of the pronotum. It could also be referred to as the lateral edge of the prothorax or of the pronotal disc.

97. Lateral pronotal carina

1. not forming continuous curve with anterior edge of pronotal disc (Fig. 15C).

2. forming continuous curve with anterior edge of pronotal disc (Figs 20C, 40E).

Inapplicable when C96 = S5. If there is an abrupt change in the curvature of the lateral carina when it extends mesally, it is coded as S1. This state occurs in most Clambidae, *Eubrianax*, *Cneoglossa*, *Chelonarium*, Lampyridae, *Silis*, *Chauliognathus*, *Holopsis*, *Clypastraea* and *Eustrophopsis*.

98. Lateral pronotal carina

1. on different plane than anterior edge of pronotal disc.

2. on same plane as anterior edge of pronotal disc (coplanar) (Fig. 40E).

Inapplicable when C96 = S5. In a subset of those taxa coded as 97,2, the lateral pronotal carinae are coplanar with the anterior edge.

99. Lateral pronotal carina

1. without distinct bead (Figs 15A, 16B).

2. with distinct bead (Figs 15C, 16A).

Inapplicable when C96 = S5.

100. Edge of lateral pronotal carina

1. simple or minutely crenulate (Fig. 15C).

2. finely denticulate (Fig. 20F).

3. coarsely dentate (Fig. 14E).

4. with two or more lobes.

Inapplicable when C96 = S5.

101. Anterolateral portion of pronotum

1. without glandular pore or callosity.

2. with glandular pore or pores only.

3. with glandular pore or pores on callosity (Figs 15E, 15F).

The callosity is a flattened thickening of the cuticle which contains one or more gland openings; it is usually located at the anterior end of the lateral pronotal carina, but may be at the anterolateral corner of the pronotal disc. Glandular pores only occur in *Laricobius*, *Languria*, *Pselaphacus*, *Discoloma*, *Caryobruchus* and *Neochlamisus*, while those located on callosities are known in *Malthodes* and *Cryptophagus* among the exemplars, but also occur in boganiine Boganiidae (Crowson 1990). The details of the pronotal glands in Erotylidae have been discussed by Drilling *et al.* (2010).

102. Anterior pronotal angles as viewed from above

1. not produced forward, rounded or angulate (Figs 14B, 15A, 20A).

2. produced forward and broadly rounded (Fig. 13B).

3. produced forward and narrowly rounded (Figs 13F, 20B).

4. produced forward and acute (Figs 16E, 55A).

The anterior pronotal angle refers to the anterolateral corner of the pronotum, which is not necessarily angular but may be rounded or variously produced.

103. Posterior pronotal angles as viewed from above

1. absent or broadly rounded (Fig. 14D).

2. obtuse to right (Figs 13B, 55A).

3. slightly to moderately acute but not produced (Figs 15C, 20A).

4. strongly produced posteriorly or posterolaterally and acute or narrowly rounded (Fig. 18F, 19B, 44H).

The posterior pronotal angle refers to the posterolateral corner of the pronotum, which is not necessarily angular but may be rounded or variously produced.

104. Posterior pronotal angles

1. not embracing elytral humeri.

2. embracing elytral humeri.

In most cases of S2 the pronotal angles extend just beyond the humeri, but in others they may be received in humeral impressions. This state is well known in Elateridae and some related groups, but occurs in scattered other taxa.

105. Posterior edge of pronotum

1. more or less straight, evenly rounded or slightly concave (Fig. 17C).

2. distinctly sinuate, angulate or variously lobed (Figs 15C, 18C, 19C).

State 2 usually represents part of a pro-mesothoracic interlocking mechanism, the various lobes or sinuations fitting against the anterior edges of the scutellum and elytra. They are always lost in those forms which have become soft-bodied, usually in connection with the shortening of adult life or development of a chemical defense system and aposematic coloration.

106. Posterior edge of pronotum

1. not crenulate.

2. crenulate (Figs 14A, 19C).

Crenulations along the posterior edge of the pronotum, another part of the pro-mesothoracic interlocking mechanism, occur in our exemplars representing the families Rhipiceridae, Buprestidae, Ptilodactylidae, Eulichadidae, Callirhipidae and Chelonariidae; however this feature varies in all of these families except for the last two.

107. Pronotal disc

1. without sublateral carinae.

2. with short, sublateral carinae on posterior angles only.

3. with sublateral carinae mesad of posterior angles and not extending to middle of pronotum.

4. with sublateral carinae mesad of posterior angles and extending at least to middle of pronotum (Fig. 40D).

All sublateral pronotal carinae begin at the posterior edge of the disc.

108. Posterior, sub-basal portion of pronotal disc

1. without paired impressions.

2. with pair of broad, shallow impressions.

3. with pair of small, well defined impressions or pits (Fig. 19D).

109. Mesolateral portions of pronotum

1. without deep pits formed by internal apodemes.

2. with deep pits formed by internal apodemes (Fig. 22D).

S2 is characteristic of many Anthicidae, but a similar feature occurs in *Rhizonium*.

110. Ventral or lateral portion of prothorax on each side

1. with notopleural and pleurosternal sutures (notum and sternum completely separated by pleuron) (Fig. 44M).

2. with notosternal, pleurosternal and notopleural sutures (notum and sternum abutting anteriorly) (Fig. 44K).

3. with notopleural suture only (pleuron and sternum completely fused) (Fig. 44L).

4. with complete notosternal suture only (pleuron internalized) (Figs 16B, 18A, 44B).

5. with incomplete notosternal suture or without sutures (Fig. 22D).

S1 occurs in all outgroups and in those Coleoptera having a well-developed external propleural wall (e.g., *Priacma*, Lepiceridae, Sphaeriusidae and Hydroscaphidae); *Declinia* is also coded as having S1, although the anterior extension of the trochantinopleuron barely separates notum from sternum. In S2 the notopleural and pleurosternal sutures meet just before the anterior edge, forming a very short notosternal suture where notum abuts sternum; this is characteristic of *Tetraphalerus*, Cupedinae, Torridincolidae, and almost all Adephaga. In the genus *Omma* and in the rhysodine genera *Clinidium* and *Omoglymmius*, the pleuron and sternum have fused so that only the notopleural suture remains (S3). S4 represents the common condition throughout the suborder Polyphaga, in which the pleuron has become internalized and notum and sternum are separated by the notosternal suture. This suture, however may be further reduced or lost altogether (S5), so that notum and sternum are solidly fused. This occurs sporadically throughout Polyphaga and also in the Strepsiptera and the archostematan family Micromalthidae. The presumed notosternal suture of the polyphagan family Hydraenidae was shown to be a secondary external ridge by Beutel and Jäch (1995).

111. Anterior portion of hypomeron

1. without antennal impression or anteriorly opening antennal pocket.

2. with shallow antennal impression (Figs 17F, 19F).

3. with anteriorly opening antennal pocket (Figs 15D, 17C).

A shallow antennal impression (S2) occurs in *Lepicerus*, *Spercheus*, *Aesalus*, *Scarabaeus*, *Orphilus* and *Clypastraea*, while an anteriorly opening pocket (S3) characterizes *Hister*, *Hydraena*, *Ochthebius*, *Anthrenus* and *Murmidius*.

112. Pronotal hypomeron

1. without antennal grooves or subsurface pockets.

2. with lateral antennal groove (Fig.19B).

3. with mesal antennal groove (Fig. 20A).

4. with deep antennal pocket extending beneath the surface of hypomeron (Figs 12F, 17B, 17D).

Lateral antennal grooves (S2), lying just below the lateral pronotal carinae, occur only in *Onichodon* among the exemplars, but are common in the family Eucnemidae. Mesal grooves (S3) occur in *Bacanius*, *Acalyptomerus*, Byrrhidae, *Aulonothroscus*, *Delphastus* and *Hyporhagus*. A deep antennal pocket extending beneath the hypomeral surface (S4) occurs only in the exemplar genus *Lissomus*, but is also found in members of the elaterid subfamily Thylacosterninae (Figs 17B, 17D).

113. Pronotal hypomeron

1. without crural impression.

2. with crural impression (Figs 20F, 21F).

A crural impression accommodates at least part of the fore leg, and, unlike an antennal cavity, it is located on the posterior part of the hypomeron.

114. Procoxal cavities

1. absent, procoxae not countersunk.

2. well developed, procoxae distinctly countersunk (Figs 14C, 14D).

3. secondarily reduced (Fig. 22B).

The term coxal cavity is somewhat of a misnomer, since it represents a cuticular counter-sunk housing for the coxa, which is visible when the leg is removed by tearing the joining membrane. The cavity in this sense includes, not only the true cavity joining the hemocoel of the leg with that of the body, but in addition cuticular rests extending from the sternum and in some Polyphaga a broad or narrow connection to the notum (e.g., C138, S2 and S3). There are no procoxal cavities in the outgroups, including Strepsiptera, but they occur in most Coleoptera. However, in several lineages which have evolved soft-bodied adults the cavities may be secondarily reduced or virtually absent. The latter forms (e.g., *Micromalthus*, many soft-bodied Elateroidea, *Atractocerus*, Prionoceridae, some malachiine Melyridae and Ripiphoridae) have been coded as S3.

115. Propleuron or propleurotrochantin

1. extending to anterior edge of prothorax, completely separating notum and sternum (Fig. 44A, 44E, 44J).

2. extending well in front of procoxae but not reaching anterior edge of prothorax (Figs 44D, 44G, 44I).

3. extending only slightly beyond anterior edge of procoxal cavity (Fig. 44B).

4. not extending beyond anterior edge of procoxal cavity (Figs 44C, 44F).

5. solidly fused to notum.

S1, where the notopleural and pleurosternal sutures are completely separate, occurs in the outgroups and in *Priacma*, *Lepicerus*, *Hydroscapha* and *Sphaerius*. S2, where the notopleural and pleurosternal sutures meet anteriorly, so there is a short notosternal suture, occurs in Ommatidae, Cupedinae, Torridincolidae, and all Adephaga. S3 refers to a rare condition in which the propleurotrochantin extends just slightly beyond the coxal cavity (e.g., in *Declinia*, *Laricobius* and *Derodontus*). S4 is the norm for Polyphaga and S5 occurs in *Micromalthus* and some Polyphaga.

116. Propleuron or propleurotrochantin

1. extending behind procoxa (Figs 44A, 44D, 44E, 44G, 44J).

2. not extending behind procoxa (Fig. 44B, 44C, 44F).

The propleuron extends well behind the coxal cavity (S1) in Archostemata, Myxophaga and Adephaga and may extend mesally to close the cavity from behind in some Carabidae. This is never the case in Polyphaga, where any closure of the procoxal cavities is accomplished by mesal projections of the pronotal hypomeron.

117. Lateral portion of prosternum in front of middle of procoxal cavity or procoxal base

1. less than 0.5 times as long as mid length of cavity or coxal base at that point (Figs 18A, 18B, 19F, 21B).

2. 0.5 to 2 times as long as mid length of cavity or coxal base at that point (Figs 13C, 19E, 20B).

3. more than 2 times as long as mid length of cavity or coxal base at that point (Figs 12F, 13E, 18C, 18F, 21A).

The prosternum is very short in front of the coxae (S1) in most of the outgroups, *Lepicerus* and *Sphaerius* among the Myxophaga, Gyrinidae, some Dytiscidae, *Spercheus* and *Tropisternus*, *Sphaerites*, *Acrotrichis*, Leiodidae, *Nicrophorus*, a few staphylinids, most Scarabaeoidea, all Scirtoidea, most of the soft-bodied Elateroidea ("cantharoids"), *Laricobius*, *Nosodendron*, most Bostrichoidea, and scattered taxa among the Cucujiformia. A relatively elongate prosternum (S3) occurs in *Agulla*, Ommatidae and Cupedidae, Rhysodinae, *Renardia*, some Buprestidae, *Helichus*, *Podabrocephalus*, *Brachypsectra* and *Cerophytum*, Eucnemidae and Elateridae (except *Selonodon*), Jacobsoniidae, a number of Cucujoidea, including Monotomidae, Bothrideridae and Cerylonidae, a number of Tenebrionoidea and *Phoracantha*. The remainder of the taxa fall into the intermediate category (S2).

118. Prosternum in front of coxae

1. without paired lines or carinae (Figs 13C, 18A).

2. with paired lines or carinae extending anteriorly from sides of prosternal process onto body of sternite (Figs 13F, 39A).

Paired lines or carinae on the prosternum (S2) occur in Torridincolidae, Haliplidae, Histeridae, *Aesalus*, *Declinia*, *Microchaetes*, *Optioservus*, Artematopodidae, *Anischia*, *Aulonothroscus*, *Dacne*, *Pselaphacus*, *Chiliotis*, *Hypodacnella*, *Murmidius*, *Bystus*, *Rhyzobius*, *Rodolia*, *Periptyctus*, *Orthoperus*, *Hyporhagus*, *Neochlamisus* and *Sympiezoscelus*, those of the last taxon representing the sides of the rostral canal.

119. Prosternal "chin-piece"

1. absent (Fig. 13C).

2. apically truncate (Fig. 14A).

3. apically rounded (Figs 17A, 17C).

The chin piece is an anterior extension of the prosternum beneath the head; its infolded edge acts as a head rest. In some groups (e.g. Byrrhidae) there is no anteriorly produced chin-piece, but there may be an extensive head rest (Fig. 16C).

120. Anterior edge of prosternum

1. not abruptly excavate at middle.

2. abruptly excavate at middle (Figs 18B, 18D).

An abrupt anterior prosternal excavation (S2) occurs in *Georissus*, *Anchycteis*, *Chelonarium*, *Callirhipis*, *Pelecotoma*, *Vesperus* and *Sympiezoschelus*.

121. Prosternal process

1. complete and continuous, extending at least to posterior edge of coxa (Figs 13B, 13C).

2. complete but externally interrupted, forming an apparently separated apical piece (Figs 14C, 39I).

3. incomplete, ending before posterior edge of coxa, or absent (Figs 14D, 22B).

An interrupted prosternal process (S2) is deeply concave at middle, so that there is a short anterior portion, often acute, and a disconnected posterior portion, which is often called the "sternellum" and which may be joined to or sometimes fused with the hypomeral postcoxal projections. This condition occurs in almost all curculionoids, although in some of these (e.g., *Toxonotus* and *Sphenophorus*), the two pieces are contiguous, but always separated by a narrow groove, while in *Sympiezoscelus* the anterior portion of the prosternal process is obliterated by the prosternal groove which receives the rostrum.

122. Portion of prosternal process extending behind coxae

1. absent (Fig. 21A).

2. less than 0.2 times as long as shortest diameter of procoxal cavity.

3. 0.2 to 0.5 times as long as shortest diameter of procoxal cavity.

4. more than 0.5 times as long as shortest diameter of procoxal cavity (Figs 13C, 18F, 19B).

In Elateridae, Eucnemidae and Cerophytidae the posterior extension of the prosternal process is referred to as the prosternal spine and fits into a deep mesoventral cavity.

123. Prosternal process in lateral view

1. not or only slightly curved (Figs 15B, 18A).

2. moderately strongly, evenly or sinuately curved from base to apex (Figs 13B, 22C).

3. straight or slightly curved basally but gradually elevated near apex (Fig. 18F).

4. straight or slightly curved basally but strongly and abruptly elevated or notched near apex.

124. Prosternal process in ventral view

1. not expanded apically (Figs 13C, 15B, 17F).

2. slightly or gradually expanded apically (Figs 12C, 18B, 20A, 22A).

3. distinctly and abruptly expanded apically (Figs 13F, 16E, 19A, 19E).

125. Apical edge of prosternal process in ventral view

1. acute or narrowly rounded (Figs 14A, 14D, 18A, 18F, 21A).

2. broadly rounded, angulate or truncate (Figs 12C, 13C, 20A).

3. emarginate or cleft (Fig. 13F, 20F).

126. Prosternal process

1. not or only slightly extending beyond anterior edge of mesoventrite (Figs 15B, 21A).

2. extending well beyond anterior edge of mesoventrite but not abutting or exceeding anterior edge of metaventrite (Figs 12D, 18F, 25B).

3. abutting or exceeding anterior edge of metaventrite (Fig. 22A).

S1 and S2 are both widely distributed throughout the order, although the former is found in all Archostemata, most Myxophaga, Scarabaeoidea, soft-bodied Elateriformia and Tenebrionoidea and most Curculionoidea and the latter in most Scirtoidea and the more compact or solidly-built Elateriformia and Tenebrionoidea. Those taxa with the process abutting or exceeding the anterior edge of the metaventrite (S3) include Haliplidae, Aspidytidae, Noteridae, *Hygrobia*, Dytiscidae, *Agrilus*, *Helichus*, *Paracardiophorus*, *Trictenotoma* and *Neochlamisus*.

127. Procoxae

1. not or slightly projecting below prosternum.

2. projecting well below prosternum (Figs 20E, 22B, 22E).

128. Visible portion of procoxa

1. distinctly transverse and subcylindrical (Figs 14A, 15B, 18B).

2. subconical to elongate (Fig. 22E).

3. more or less globular (Figs 13C, 16E, 18C, 44H).

129. Concealed extension of procoxa

1. absent or less than 0.2 times as long as exposed portion of procoxa (Fig. 44F, 44H).

2. 0.2 to 0.67 times as long as exposed portion of procoxa (Fig. 44C).

3. more than 0.67 times as long as exposed portion of procoxa (Fig. 41I).

130. Propleurocoxal articular area

1. well developed, at least half as long as remainder of procoxa (Fig. 42E).

2. well developed but less than half as long as remainder of procoxa.

3. highly reduced or absent (Fig. 44H).

131. Procoxa

1. without distinct lamina or plate (may be carinate).

2. with distinct lamina or plate (Fig. 43B).

A procoxal lamina or plate (S2) occurs in Ommatidae, Cupedidae, *Satonius*, *Gyrinus*, *Meru*, *Noterus*, *Laccophilus*, *Declinia*, *Acalyptomerus*, *Amplectopus*, *Microchaetes*, *Byrrhinus*, Artematopodidae, *Lissomus*, *Orphilus* and *Anthrenus*.

132. Secondary mesal procoxal articulation

1. absent.

2. formed by procoxal knob and prosternal fossa (Fig. 44G).

3. formed by prosternal knob or tongue and procoxal fossa or groove (Figs 13A, 21B).

A secondary articulation involving a projection of the procoxa fitting into a lateral fossa on the prosternal process (S2) occurs in *Spanglerogyrus*, *Meru*, Haliplidae, *Aspidytes*, Noteridae, *Amphizoa*, Trachypachidae, Carabidae (except *Arthropterus*), *Euspilotus*, *Microchaetes*, *Lissomus*, *Stegobium*, *Chiliotis*, *Tanylypa* and *Prionus*. The S3 type of articulation, in which a lateral projection of the prosternal process fits into an impression of the procoxa is known in *Cerophytum* and *Orphilus* among the exemplars, but also occurs in some eumolpine Chrysomelidae.

133. Protrochantin

1. free from pleuron (Figs 44E, 44G).

2. fused to pleuron forming pleurotrochantin (Fig. 42E).

3. apparently absent.

A free protrochantin (S1) occurs in all outgroups, except *Eoxenos*, all Archostemata except *Micromalthus* and all Adephaga. The trochantin is absent (S3) in *Eoxenos* and *Micromalthus*, and apparently fused to the pleuron forming a pleurotrochantin (S2) in all Myxophaga and Polyphaga.

134. Protrochantin or propleurotrochantin

1. exposed (Figs 14A, 18B, 21C, 44E).
2. concealed (Figs 19A, 20A,44G, 44H).

Except for some Gyinidae, the protrochantin in Adephaga is free (133,1) but concealed (134,2). The prothoracic trochantin is free (133,1) and exposed (134,1) in most outgroups and in Archostemata (except *Micromalthus*, where it appears to be absent). The propleurotrochantin is exposed in Myxophaga and in a number of Polyphaga which appear to be basal within this clade, and also in many soft-bodied Elateroidea, Cleroidea and Tenebrionoidea, where the condition may be secondary. A concealed pleurotrochantin (134,2) occurs in a few Hydrophilidae; *Syntelia*; Histeridae; *Nossidium* in Ptiliidae; a few Staphylinidae (including Scydmaeninae); Scarabaeoidea (except *Pleocoma*, *Diphyllostoma* and *Nicagus*); *Optioservus* in Elmidae; *Ptilodactyla* among the Ptilodactylidae; all of the well sclerotized Elateroidea; Jacobsoniidae; most Bostrichoidea; the cleroid genera *Isoclerus*, *Cymatodera* and *Phycosecis*; a number of Cucujoidea (including Erotylidae, Silvanidae, Passandridae and almost all of the cerylonid series); many groups of Tenebrionoidea (e.g., Ciidae, Melandryidae, Zopheridae, Ulodidae, Promecheilidae, Tenebrionidae, Mycteridae and Salpingidae); the chrysomeloid genera *Oxypeltus*, *Sypilus*, *Distenia*, *Phoracantha* and *Crioceris*; and all Curculionoidea.

135. Exposed portion of propleurotrochantin

1. moderately large and abutting sternum and notum (Fig. 21E, 44F).
2. usually more slender and abutting neither sternum nor notum (Figs 21B, 22B).

Inapplicable when C133 = S1. The exposed portion of the pleurotrochantin in Polyphaga varies considerably in size, shape and degree of freedom of movement, but in general it is relatively small and freely movable or sometimes highly reduced or fused to the notum. In those taxa coded as having S1, the trochantin is somewhat larger, abutting the sternum and notum and forming part of the wall of the prothorax. This condition occurs in Myxophaga, *Declinia*, *Nycteus*, Buprestidae, *Helichus*, *Byrrhinus*, Artematopodidae and *Rhinorhipus*.

136. Propleurotrochantin

1. not attached to notum (Figs 44C, 44F).
2. attached to notum (Fig. 44H).

Inapplicable when C133 = S1. The attachment of the pleurotrochantin is a slender one, which is internal and at the notosternal junction. It is probably not a true fusion, but does appear to restrict movement. The character is difficult to code and may have been miscoded in some cases.

137. Procoxal cavities externally

1. broadly open (Figs 13C, 14A, 14D, 18B, 20B).
2. narrowly open (Figs 13D, 13E).
3. narrowly closed (Figs 15B, 17E, 20E).
4. broadly closed (Figs 14C, 16E, 21D, 39I).

138. Procoxal cavities internally

1. open (Figs 13E, 20B).
2. closed by slender bar (Figs 13C, 14B, 21F).
3. broadly closed (Figs 14D, 19F, 21D).

139. Procoxal cavities

1. contiguous or separated by less than 0.25 times shortest diameter of coxal cavity (Figs 14C, 20E).
2. separated by 0.25 to 0.75 times shortest diameter of procoxal cavity (Fig. 13D).
3. separated by more than 0.75 times shortest diameter of procoxal cavity (Figs 13F, 17F, 18C).

140. Anterolateral edge of procoxal cavity

1. without narrow extension (Fig. 13C, 13D).
2. with narrow extension (Figs 14B, 19F).

This extension is a result of the notum and sternum (Polyphaga) or notum and pleuron being slightly separated for a short distance.

141. Postcoxal projections of propleuron or pronotal hypomeron

1. absent or very short and usually rounded, angulate or truncate (Fig. 18A, 18B).
2. moderately long and acute (Fig. 17C).
3. meeting prosternal process (Figs 13B, 13F, 20E, 39D).
4. meeting opposing postcoxal projection (Figs 14C, 20D, 39I).
5. fused to opposing postcoxal projection.
6. fused to opposing postcoxal projection and to apex of prosternal process (Figs 14F, 18E).

S1 to S3 occur widely throughout the order. S4 is known in *Chalcodrya*, *Palophagus*, *Crioceris*, *Rhinotia*, *Car*, Brentidae, *Sphenophorus* and *Tranes*. The meeting of the postcoxal projection with the prosternal process may be of several types, which have not been distinguished here; the two may abut, overlap or be joined by a condylar joint, as in Fig. 39D. Fusion of the postcoxal projections (S5 and S6) occurs only in Curculionoidea and the latridiid genus *Eufallia*.

142. Paired anterior prothoracic defensive glands

1. absent.
2. present.

Prothoracic defense glands have evolved independently in *Hygrobia* and Dytiscidae, some Tenebrionidae, and the melyrid genus *Collops*.

Pterothorax

The pterothorax comprises the two wing-bearing segments or mesothorax and metathorax, although the term usually refers only to the ventral portions of thoraces: mesoventrite, mesanepisterna, mesepimera, metaventrite, metanepisterna and metepimeron, plus the associated endosternites, coxae and trochantins (when present). Pterothoracic terminology is given in Figs 32A–C.

143. Scutellum

1. exposed but elytra absent.
2. visible between elytral bases as scutellar shield (Figs 23A, 23B, 23C).
3. concealed by elytral bases.

In almost all Coleoptera a portion of the mesoscutellum is visible externally as a scutellar shield, which lies between and usually interlocks with the anteromesal portions of the elytra (S2). Only in the outgroups, which lack elytra, is the entire mesoscutellum visible (S1). The scutellar shield is secondarily concealed beneath the elytral bases (S3) in only a few of our exemplars (*Meru*, *Haliplus*, *Bacanius*, *Euconnus* and *Derolathrus*), although the state occurs in a number of other taxa not included in this study.

144. Anterior edge of scutellar shield

1. not or only slightly or gradually elevated (Fig. 23C).
2. distinctly and abruptly elevated (Figs 23A, 23B).

Inapplicable if C143 = S1 or S3. The scutellar shield is the externally visible portion of the mesoscutellum, which lies between and usually interlocks with the anteromesal portions of the elytra. In many beetles, the anterior edge is abruptly elevated, so that the body of the shield is on a higher plane than the anterior portion of the mesoscutellum (S2). This condition occurs in *Omma*, Cupedidae, Torridincolidae, the adephagan genera *Noterus* and *Amphizoa*, Hydrophilidae, *Sphaerites*, Histeridae, the scarabaeoid genus *Aesalus*, *Declinia*, *Nycteus*, Clambidae (except *Clambus*), Scirtidae, Dascillidae, *Sandalus*, Buprestidae (except *Julodis* and *Acmaeodera*), Byrrhoidea (except Psephenidae and *Cneoglossa*), *Artematopus*, *Rhinorhipus*, *Brachypsectra*, *Cerophytum*, Eucnemidae (except *Melasis*), *Aulonothroscus*, Elateridae (except *Selonodon*), Derodontidae, *Nosodendron*, *Orphilus*, *Anthrenus*, *Rhyzopertha*, *Lyctus*, *Thymalus*, *Acalanthis*, *Isoclerus*, *Cymatodera*, *Pharaxonotha*, *Languria*, *Toramus*, Cryptophagidae, *Agapytho*, *Priasilpha*, *Hymaea*, Silvanidae, *Passandra*, *Cyclaxyra*, Bothrideridae, Cerylonidae (except *Hypodacnella*), Discolomatidae, Coccinellidae, *Periptyctus*, *Eufallia*, *Cis*, Zopheridae, *Dipsaconia*, *Dioedus*, *Diaperis*, *Distenia*, *Neochlamisus*, *Toxonotus*, *Rhinotia*, *Car*, *Tranes* and *Curculio*.

145. Anterior edge of scutellar shield

1. simple (Fig. 23C).
2. notched (Fig. 23A).
3. biemarginate (Fig. 23D).
4. crenulate (Fig. 23B).

Inapplicable if C143 = S1 or S3. Modifications of the anterior edge of the scutellar shield are part of the promesothoracic interlocking system, often correlated with modifications of the posterior edge of the pronotum. Among the exemplars, a notched anterior edge (S2) occurs in Ptilodactylidae, a biemarginate one (S3) in *Neochlamisus*, and a crenulate one (S4) in *Chelonarium* and *Callirhipis*.

146. Scutellar shield posteriorly

1. narrowly rounded or acute (Figs 23A, 23B).
2. broadly rounded to obtusely angulate (Figs 23C, 23F).
3. truncate (Fig. 23E).
4. emarginate (Fig. 23D).
5. biemarginate.

Inapplicable if C143 = S1 or S3.

147. Mesoscutum

1. without stridulatory file.
2. with stridulatory file (Fig. 23F).

The mesothoracic stridulatory file occurs on the anterior (concealed) portion of the mesotergum lying beneath the posterior edge of the pronotum. In some cases the file may be divided into two parts by a smooth longitudinal line. This file occurs in Disteniidae, Cerambycidae (except Parandrinae and Prioninae), Megalopodidae (*Palophagus*), and Nemonychidae (*Rhynchitomacerinus*).

148. Mesothoracic wings in male

1. forming part of flight mechanism.
2. highly modified to form elytra or halteres.

S1 occurs in all outgroups, except *Eoxenos*.

149. Elytral apices

1. meeting at midline, conjointly rounded to narrowly acute (Fig. 35A).
2. meeting at midline, squarely or obliquely truncate (Fig. 35B).
3. independently rounded, truncate or emarginate, separated by distinct gap (Fig. 35C).
4. independently acute, separated by distinct gap.

Inapplicable when C148 = S1. S2, S3 and S4 are usually associated with exposure of abdominal tergites (C150, S2 and S3).

150. Elytra

1. concealing all abdominal tergites or exposing part of one only.
2. exposing at least one complete tergite and sometimes part of second one (Fig. 35B).
3. exposing two or more complete tergites (Fig. 35C).

Inapplicable when C148 = S1. The exposure of two or more complete tergites (S3) occurs in *Micromalthus*, *Hydroscapha*, *Sphaerites*, *Hister*, *Acrotrichis*, *Nicrophorus*, Staphylinidae (except *Scaphidium* and Scydmaeninae), *Lichnanthe*, *Telegeusis*, Phengodidae, *Ototretadrilus*, *Atractocerus*, *Carpophilus*, *Brachypeplus*, *Orthoperus*, *Rhipidioides* and *Euryplatus*.

151. Sides of elytra anteriorly

1. without interlocking tongue.
2. with interlocking tongue.

Inapplicable when C148 = S1. The lateral interlocking tongue may be homologous to the "schiza" of fossil schizophoroids (Ponomarenko 1969). This does not include the frictional surfaces which anchor the elytra to the metepimeron in many beetles (Gorb 1998). In at least some Carabidae the internal ridge is much longer, extending almost to the apex.

152. Elytra

1. without window punctures.
2. with window punctures (Fig. 43E).

Inapplicable when C148 = S1. Window punctures are large, somewhat quadrate and deep with a translucent floor. Although they are often considered to occur only in Archostemata, very similar punctures may be found in the elytra of *Rhinorhipus*, *Omalisus*, Derodontidae, and some Lycidae, and smaller deep, translucent punctures occur in some members of other families.

153. Elytral punctures

1. irregularly aligned or with a few vaguely defined rows (Fig. 24F).
2. with more than 5 distinct puncture rows (Fig. 43E).
3. with more than 5 distinct striae (Fig. 43H).

Inapplicable when C148 = S1.

154. Number of puncture rows or striae, excluding scutellary striole

1. more than twelve.
2. twelve.
3. eleven.
4. ten.
5. nine.
6. eight.
7. seven.
8. six.

Inapplicable when C148 = S1 or C153 = S1.

155. Elytral scutellary striole

1. present.
2. absent.

Inapplicable when C148 = S1. The scutellary striole is a short stria or puncture row in the immediate vicinity of the scutellum.

156. Elytral apices, when closed

1. without exposed sutural flange.
2. with exposed sutural flange (Fig. 24A).

Inapplicable when C148 = S1. An exposed sutural flange at the elytral apex (S2) occurs in *Rhinorhipus*, Cryptophagidae, *Priasilpha*, *Hymaea*, *Taphropiestes* and Passandridae.

157. Elytral apex

1. without ventral interlocking tongue.
2. with ventral interlocking tongue (Fig. 24C, 24E).

Inapplicable when C148 = S1. A ventral interlocking tongue at the elytral apex (S2) occurs in *Tetraphalerus*, Rhysodinae, *Georissus*, *Microchaetes*, Artematopodidae, *Teredolaemus* and *Pycnomerus*.

158. Elytral epipleuron

1. not or gradually narrowed and complete to apex (Figs 24B, 24D).
2. gradually narrowed and incomplete.
3. abruptly narrowed but complete to apex.
4. abruptly narrowed and incomplete.
5. apparently absent.

Inapplicable when C148 = S1. An epipleuron is not considered to be complete unless it reaches the midline. Truncate elytra always have incomplete epipleura.

159. Mesoventrite

1. separated by complete sutures from mesanepisterna (Figs 32A, 32B, 32C).
2. partly or completely fused to mesanepisterna (Fig. 58A).

The term mesoventrite refers to the sclerite formerly called mesosternum, following recent works by Lawrence (1999), Beutel & Haas (2000) and Lawrence *et al.* (1999b, 2010a). Mesanepisternum refers to the anterior portion of the mesepisternum, however for practical purposes this includes the entire mesepisternum in Coleoptera; the mesokatepisterum exists as a separate sclerite in a few Archostemata only, and then it is rarely visible externally. The paired mesanepisterna are usually separated by complete sutures from the mesoventrite, but partial or complete fusion occurs in various taxa. Partial or complete fusion of the mesoventrite to the mesanepisternum on each side of it (S2) occurs in scattered taxa throughout the order and may vary within some families.

160. Mesanepisterna

1. distinctly separated at midline.
2. very narrowly separated, meeting or broadly joined at midline (Figs 45D, 45E).

In most Coleoptera, the mesanepisterna are well separated from one another anteriorly, and the mesoventrite between them is anteriorly truncate. In various polyphagan taxa, however, the two sclerites may be very narrowly separated, contiguous or broadly joined at the midline, so that the mesoventrite is anteriorly subacute or rounded (S2). This condition occurs in Hydrophilidae (except *Georissus*), *Podabrocephalus*, *Apatides*, Lymexylidae, *Necrobia*, *Penthe*, *Mordella*, *Sirrhas*, *Cephaloon*, *Polypria*, *Calopus*, Meloidae, *Lacconotus*, *Pytho*, Pyrochroidae, *Salpingus*, *Lagrioida*, Anthicidae and Scraptiidae.

161. Paired procoxal rests on anterior edge of mesoventrite

1. absent (Fig. 27E).
2. horizontal or slightly inclined (Figs 27F, 45F).
3. moderately to strongly inclined or vertical (Figs 12B, 26B, 26D, 42H).

Paired procoxal rests are always somewhat concave for reception of convex procoxae. This character refers only to the rests on the anterior edge of the mesoventrite, not to their lateral extensions onto the mesanepisterna, nor those situations in which the entire body of the mesoventrite is biconcave and acts as a pair of coxal rests (see C171).

162. Broad prothoracic rest (peduncle) on anterior edge of mesothorax

1. absent.
2. present, fitting within prothoracic foramen (Fig. 45A).

This type of rest for the entire hind portion of the prothorax occurs in taxa with broadly closed procoxal cavities and a relatively large prothorax which is capable of rotating on the peduncle. The anterior portions of the mesoventrite and mesanepisterna in this case are often relatively smooth. This condition occurs in some Carabidae, several Staphyliniformia, all Scarabaeoidea (except *Pleocoma*), Derodontidae (except *Laricobius*), *Saphophagus*, most Bostrichidae, a number of cleroids, cucujoids, tenebrionoids and chrysomeloids, and most Curculionoidea; it never occurs in Scirtoidea or Elateriformia.

163. Anterior edge of mesoventrite at midline

1. on same plane as metaventrite.
2. on different plane than metaventrite (Fig. 26A, 26E).

The anterior edge of the mesoventrite at the midline excludes the paired procoxal rests, if present.

164. Anterior edge of mesoventrite

1. without median prosternal rest.
2. with median prosternal rest, abutting upper (concealed) surface of prosternal process (Figs 41G, 45G).

The prosternal rest is a flattened platform, often subtriangular, on which the prosternal process rests and is not an impression or cavity. S2 may also apply to the raised area immediately preceding the deep mesoventral cavity in those elateroids exhibiting the "clicking" behavior, but this seems to vary in its development within Elateridae.

165. Mesanepisternum and mesepimeron

1. separated by pleural suture and underlying pleural ridge (Fig. 46B).
2. more or less fused together, without pleural ridge.

The fusion of mesanepisternum and mesepimeron and complete loss of the pleural ridge is characteristic of Cerophytidae and Eucnemidae, but also occurs in *Eoxenos*, *Meru* and *Eufallia*.

166. Mesepimeron

1. more or less triangular or trapezoidal, widest laterally (Fig. 28G).
2. slender and parallel-sided.

The reduction of the mesepimeron to form a slender, parallel-sided structure (S2) was used by Beutel (1992, 1997) to distinguish certain groups within Carabidae, but it occurs in some other Adephaga and sporadically in Polyphaga.

167. Mesothoracic discrimen

1. present (Figs 35E, 45B, 45C, 46B).
2. absent (Fig. 45F).

The mesothoracic discrimen is a median line representing the invagination of the true mesosternum forming the mesendosternite (C182), which in most groups consists of two independent apodemes, rather than a single fork-like structure. The mesothoracic discrimen occurs in all outgroups, Archostemata (except *Micromalthus*), Gyrinidae, most Scirtoidea, Dascillidae, Buprestidae (except *Agrilus*), several byrrhoids, *Callirhipus* and *Artematopus*.

168. Mesokatepisternal suture

1. present.
2. represented by internal ridge only.
3. absent.

This structure, which is serially homologous to the metakatepisternal suture (C187), is apparently present in a few Archostemata and Adephaga, but it is not easy to see. There is rarely any external indication but there may be an internal ridge which does not appear to cross the discrimen like its counterpart in the metathorax.

169. Mesoventral cavity for reception of prosternal process

1. absent (Fig. 45F).
2. small to moderately large but shallow (Figs 25E, 26B, 27F, 45C).
3. large and deep (Fig. 45G).

The presence of a depression or cavity for the reception of the prosternal process is relatively widely distributed, but very rare in Tenebrionoidea and found only in one exemplar (*Chrysomela*) among the Phytophaga. A large and deep cavity (S3) occurs in *Meru*, Haliplidae, *Matus* and *Laccophilus* among the Adephaga, in Buprestidae, except *Schizopus* (which has a shallow cavity), in several byrrhoids, and in *Artematopus*, *Cerophytum*, Eucnemidae, *Aulonothroscus* and Elateridae among the Elateroidea.

170. Mesoventral cavity

1. not extending posteriorly behind anterior edges of mesocoxal cavities (Figs 25E, 27F, 35E).

2. extending posteriorly behind anterior edges of mesocoxal cavities (Fig. 45G).

171. Anterior portion of mesoventrite (in front of mesoventral process)

1. without median tumescence or carinae separating paired impressions.

2. with median tumescence, carina or paired carinae separating large pair of impressions (Fig. 45E).

In some taxa that lack the distinct paired procoxal rests at the anterior edge of the mesoventrite (C161 = S1), the main portion of the ventrite is tumid or carinate along the midline, forming a pair concavities which may act as procoxal rests, especially in conglobate forms (e.g. Clambidae) or those with relatively large and projecting procoxae. This occurs in *Calosoma* among the adephagan exemplars, and is of scattered occurrence within Polyphaga.

172. Mesoventral process

1. extending to or beyond anterior edge of metaventrite (Figs 26D, 27C, 27E).

2. extending behind middle of mesocoxae but not reaching metaventrite (Fig. 45D).

3. not extending behind middle of mesocoxae Figs 45H, 46C).

4. absent (Fig. 46A).

173. Apex of mesoventral process

1. divided, forming paired lobes (Figs 25E, 35E, 45C, 45H).

2. undivided, narrowly rounded or acute (Fig. 45D, 46C).

3. undivided, broadly rounded or truncate (Fig. 26C, 27C, 42H).

4. undivided, concave or biconcave (Figs 26E, 27D).

Inapplicable when C172 = S4. The apex of the mesoventral process is considered to form paired lobes (S1) only when a discrimen is present (C167 = S1); this condition occurs in all outgroups, except *Cephus* and *Eoxenos*, Ommatidae and Cupedidae, Gyrinidae, *Declinia*, *Nycteus*, *Loricaster*, *Cyphon*, *Veronatus*, *Dascillus*, *Psephenus*, Ptilodactylidae and *Callirhipis*.

174. Mesocoxae

1. not strongly projecting.

2. strongly projecting (Fig. 45D).

175. Mesocoxa

1. without secondary mesal articulation.

2. with mesal articulation consisting of mesoventral knob and coxal fossa (Fig. 27B).

3. with mesal articulation consisting of metaventral tongue and coxal groove (Fig. 27D).

4. with mesal articulation consisting of coxal knob and mesoventral fossa.

5. with mesal articulation consisting of coxal knob and metaventral fossa (Fig. 22A).

6. with mesal articulation consisting of metaventral knob and coxal fossa.

Several different types of secondary mesocoxal articulations have evolved in various beetle families, but within the present data set the character is not very useful, except for uniting the two genera of Haliplidae, which have S5, as does *Orphilus*. The S2 type of articulation occurs in *Toxonotus*, S3 in *Dermestes*, S4 *Cicindela* and *Phoracantha*, and S6 in *Matus*.

176. Mesotrochantin

1. exposed (Fig. 12B, 26A, 45E, 46A).

2. concealed or absent (Figs 27E, 45F, 45G).

177. Mesotrochantin

1. setose (Fig. 46A).

2. glabrous (Fig. 26A).

178. Mesocoxal cavities

1. absent, mesocoxae not countersunk.

2. moderately deep, and completely demarcated mesally and posteriorly by sharp ridge (Figs 26A, 45E–G).

3. shallow and not completely demarcated mesally and posteriorly by sharp ridge (Fig. 45D).

4. secondarily reduced, not or only barely impressed.

The formation of coxal cavities is considered to be a coleopteran autapomorphy, and their absence (S1) occurs only in the outgroups. Secondary reduction to form shallow cavities not completely demarcated by a sharp ridge (S3) have evolved mainly in Ommatidae and Cupedidae, some Staphylinidae, and scattered soft-bodied Elateroidea, Cleroidea and Tenebrionoidea, while extreme reduction and virtual loss of the cavities (S4) occurs in *Micromalthus*, most soft-bodied Elateroidea, Lymexylidae, *Idgia*, *Rhipidioides* and *Ischalia*.

179. Mesocoxal cavities

1. circular to slightly transverse and not or only slightly oblique (Fig. 26C).

2. strongly transverse and not or only slightly oblique (Fig. 45E).

3. strongly transverse and strongly oblique (Fig. 26F).

180. Mesocoxal cavities

1. contiguous or separated by less than 0.25 times shortest diameter of coxal cavity (Figs 45A, 45D, 45H).

2. separated by 0.25 to 0.75 times shortest diameter of coxal cavity (Fig. 27B).

3. separated by more than 0.75 times shortest diameter of coxal cavity (Figs. 26B, 26D, 26E, 45B).

181. Mesocoxal cavity bordered by

1. mesoventrite, mesanepisternum, mesepimeron, metanepisternum and metaventrite.

2. mesoventrite, mesanepisternum, mesepimeron and metaventrite (Fig. 45C).

3. mesoventrite, mesepimeron, metanepisternum and metaventrite (Figs 32A, 35E, 45H).

4. mesoventrite, mesepimeron and metaventrite (Fig. 45D).

5. mesoventrite, mesanepisternum and metaventrite.

6. mesoventrite, metanepisternum and metaventrite.

7. mesoventrite and metaventrite (Figs 27F, 28E, 28G, 45A, 45F, 45G).

Mesocoxal cavities with S1 to S6 are normally referred to as "laterally open", and S7 as "laterally closed". S2, S4 and S7 are the most commonly encountered conditions. S1 occurs in Ommatidae, *Micromalthus*, *Priacma*, Myxophaga (except *Lepicerus*), *Dytiscus*, *Veronatus*, *Amplectopus* and *Derodontus*, and S3 in *Cupes*, *Tenomerga*, *Spanglerogyrus*, *Amphizoa*, *Matus*, *Hydroporus*, *Agabus*, *Cicindela*, *Paraphloeostiba*, *Declinia*, *Nycteus*, Clambidae (except *Acalyptomerus*), *Schizopus*, Byrrhidae, *Lutrochus*, *Lycus*, *Ellychnia*, *Nothoderodontus*, *Necrobia*, *Epicauta* and *Parandra*. S5 was found only in *Hydraena*, *Nossidium*, *Atractocerus* and Discolomatidae, and S6 in *Aspidytes* and *Georissus*.

182. Mesendosternal arms

1. contiguous or fused at base.

2. separated by less than 2 times basal diameter of one arm.

3. separated by at least 2 times basal diameter of one arm (Fig. 54G).

The mesendosternal arms are more or less contiguous or fused together (S1) only in the outgroups and in the genus *Omma*, and they are most often distinctly separated (S3). Relatively narrowly separated arms (S2) occur in *Tetraphalerus*, *Cupes*, Gyrinidae, *Peltodytes*, *Amphizoa*, *Dytiscus*, *Systolosoma*, *Nebria*, *Tropisternus*, *Andotypus*, *Necrophilus*, several scarabaeoids, *Nycteus*, *Amplectopus*, *Dascillus*, *Sandalus*, *Callirhipis* and scattered taxa among the remaining superfamilies except Cucujoidea and Curculionoidea.

183. Internal portions of mesothorax and metathorax within mesocoxal cavities

1. separated from one another by membrane (Fig. 45H).

2. separated from one another by suture or line.

3. solidly fused, without suture.

Inapplicable when C178 = S1. The common condition in Polyphaga and Myxophaga is for the meso- and metathoracic portions of each mesocoxal cavity to be solidly fused together, with (S2) or without (S3) a separating suture. The separation of the two sclerites by a thin membranous joint (S1) occurs in all Archostemata and Adephaga, and the condition was previously thought to occur only in those suborders (Beutel and Haas 2000) or to be secondarily derived in a few polyphagan families but not part of the polyphagan ground plan (Ge *et al.* 2007). However, the occurrence of S1 in Agyrtidae, *Prionochaeta*, *Paraphloeostiba*, *Declinia*, most Clambidae, Scirtidae, *Anorus*, *Simplocaria*, Artematopodidae, *Rhinorhipus*, Derodontidae, *Nosodendron*, *Acanthocnemus*, *Paracucujus*, *Pharaxonotha*, *Hobartius*, *Agapytho*, *Hymaea*, *Cucujus*, *Taphropiestes* and *Laemophloeus* does not support that hypothesis.

184. Mesoventral and metaventral processes

1. distinctly separated from one another or absent (Figs 45A, 45D, 45H).

2. meeting at point or abutting (Figs 26B).

3. overlapping with mesoventrite ventrad of metaventrite.

4. overlapping with metaventrite ventrad of mesoventrite.

5. joined by monocondylic ball and socket fitting.

6. joined by dicondylic ball and socket fitting (Figs 27F, 45F).

7. solidly fused together but separated by suture or line.

8. solidly fused together with no separation.

185. Mesometaventral junction at midline

1. exposed or absent.

2. concealed by prosternal process (Fig. 40C).

3. concealed by metaventral process (Fig. 22A).

4. concealed by head.

The mesometaventral junction is usually exposed (S1), but may be concealed by prosternal or metaventral process or by the head (in some conglobate forms). The junction is concealed by the prosternum (S2) in *Aspidytes*, *Notomicrus*, *Hygrobia*, Dytiscidae (except *Matus* and *Laccophilus*), *Helichus*, *Tricenotoma* and *Neochlamisus*, and by the metaventrite (S3) in Haliplidae, *Matus* and *Laccophilus*. Concealment of the junction by the head (S4) occurs in *Calyptomerus* and *Clambus*.

186. Metaventrite

1. without postcoxal lines or crural impressions.

2. with one pair of straight, slightly curved or sinuate postcoxal lines (Figs 12D, 26B, 45F).

3. with two pairs of straight or curved postcoxal lines.

4. with one pair of recurved postcoxal lines usually delimiting crural impressions (Fig. 26D).

5. with single, curved postcoxal line.

The term metaventrite is equivalent to metasternum, as used by most coleopterists, including Crowson (1955, 1981), but the true nature of this ventral plate lying immediately behind and usually between the mesocoxal cavities was first elucidated by Ferris (1940), Campau (1940) and Matsuda (1960), and recently revived by Lawrence (1999), Lawrence *et al.*

(1999b), Beutel and Haas (2000) and Lawrence *et al.* (2010a), who proposed the term metaventrite for the compound structure consisting of paired metapre-episterna (subcoxal elements) anteriorly and paired metakatepisterna posteriorly. The true metasternum has been invaginated along the midline forming the discrimen (C188). The dividing line between pre-episterna and katepisterna or the katepisternal suture (C187) is often obliterated laterally or entirely, and the discrimen may be shortened or lost entirely in various groups.

Metaventral lines occur on the metaventrite in a number of different groups, usually extending posteriorly or posterolaterally from the hind edges of the mesocoxal cavities and often serving either to block the movement of femora or to delimit crural impressions into which femora may be fitted. Recurved lines delimiting crural impressions (S4) are probably the most common type, ocurring in *Satonius*, *Scaphidium*, *Amplectopus*, several elateriform families, *Nosodendron*, *Anthrenus*, *Cyclaxyra*, and several cucujoid families belonging to the cerylonid series. Straight or slightly curved lines (S2) are known in *Arthropterus*, *Hydraena*, *Nossidium*, *Saphophagus*, *Dermestes*, *Endecatomus*, *Thymalus*, several cucujoid families, *Hyporhagus* and *Chrysomela*. Double lines (S3) occur in *Torridincola*, *Ytu*, Histeridae and *Anischia*, while a single curved, postcoxal line (S5), extending behind both mesocoxal cavities, occurs in *Calyptomerus*, *Clambus*, *Rentonellum* and *Bystus*.

187. Metakatepisternal suture

1. crossing midline and extending at least half way across ventrite on each side (Figs 42H, 45B, 45H, 46D).
2. crossing midline but extending less than half way across ventrite on each side (Figs 35E, 45C).
3. absent or not crossing midline (Fig. 45G).

This is often referred to as the transverse metasternal suture, but has been shown to represent the division between the paired pre-episterna and paired katepisterna (see C186). In some taxa there may be relatively long transverse grooves immediately in front of the metacoxae, but these either do not extend to the midline or curve posteriorly to meet the posterior edge of the ventrite. It is not at all certain that these are remnants of the metakatepisternal suture and so they have been coded as S3.

188. Metathoracic discrimen

1. at least 0.8 times as long as metaventrite excluding metaventral process (Fig. 45B).
2. less than 0.8 times as long as metaventrite excluding metaventral process (Fig. 45A).
3. absent.

As in the mesothorax, the metathoracic discrimen represents the invagination of the true metasternum; unlike the mesothoracic discrimen, this structure is present in most families and often moderately long. The metathoracic discrimen is absent in *Sphaerius*, *Helophorus*, *Georissus*, *Spercheus*, *Bacanius*, all Staphylinoidea (except *Scaphidium*), *Diphyllostoma*, *Aesalus*, *Passalus* and *Trox* among the scarabaeoids, *Clambus* and *Loricaster*, *Onichodon*, *Aulonothroscus*, Jacobsoniidae, *Rhyzopertha* and *Lyctus*, Lymexylidae, the trogossitid genera *Rentonellum*, *Eronyxa* and *Grynoma*, *Lamingtonium*, *Cyclaxyra*, *Meligethes*, several members of the cerylonid series, a few Tenebrionoidea (including all Salpingidae), *Eurhynchus* and *Curculio*.

189. Major portion of metapleuron

1. vertical and more or less perpendicular to long axis of body.
2. horizontal and more or less parallel to long axis of body.

S1 occurs in all outgroups except *Eoxenos*. The horizontal and more or less longitudinal alignment of the metepimeron and metanepisternum (S2) occurs in Strepsiptera and in all Coleoptera.

190. Exposed portion of metanepisternum

1. less than 2.5 times as long as its greatest width (Fig. 25E).
2. 2.5 to 5.0 times as long as its greatest width (Fig. 45C).
3. more than 5.0 times as long as its greatest width (Figs 45F, 45G).

Meru, *Bacanius*, *Euconnus*, *Aphanocephalus*, *Discoloma* and *Eufallia* are all coded as inapplicable for this character, because the metanepisternum is either fused to the metaventrite (*Meru*) or is very slender and completely concealed.

191. Metepimeron

1. at least partly exposed.
2. concealed (Fig. 25B).

In Coleoptera, most of the metepimeron is concealed by the elytral epipleuron with only a small posterior portion visible. In *Cupes*, *Tenomerga*, *Sphaerius*, many Adephaga, and at least some taxa in most polyphagan superfamilies, this portion of the metepimeron is also concealed (S2).

192. Metatrochantin

1. externally visible (Figs 32A, 45H).
2. completely concealed or absent.

An externally visible metatrochantin occurs in all outgroups, except *Eoxenos* and in the coleopterous families Cupedidae and Ommatidae. In all other Coleoptera it has been reduced to an internal muscle disc.

193. Angle formed at midline by horizontal line and line tangential to anterior edge of metacoxa

1. less than 30 degrees.
2. at least 30 degrees (Figs 25A, 25E, 45D).

194. Metacoxa

1. not longer at middle than adjacent portion of metaventrite.

2. longer at middle than adjacent portion of metaventrite (Figs 25A, 25E).

The metacoxa is longer than the adjacent metaventrite (S2) in the outgroups (except *Agulla* and *Eoxenos*) and in Gyrinidae, Haliplidae, *Aspidytes*, Noteridae, *Hygrobia*, Dytiscidae, Trachypachidae, *Metrius*, *Pterostichus*, *Taurocerastes*, *Glaresis*, *Nycteus*, *Clambus*, *Lycus*, *Mordella*, *Adelium* and *Coelus*. In the hydradephagan families this is connected with the enlargement of metacoxae and formation of swimming legs, while in some other taxa (e.g., *Metrius*, *Adelium*, *Coelus*) it is correlated with the absence of hind wings.

195. Transverse extent of metacoxa

1. less than 2 times as long as longitudinal extent (Fig. 25B, 25E, 45H).

2. 2 to 3 times as long as longitudinal extent.

3. more than 3 times as long as longitudinal extent (Fig. 25D).

The transverse extent refers to the longest transect which is more or less perpendicular to the long axis of the body; in the case of the metacoxa this would be at the anterior end.

196. Metacoxae

1. contiguous or separated by less than 0.2 times transverse diameter of one coxa (Fig. 45G, 45H).

2. separated by 0.2 to 0.5 times transverse diameter of one coxa (Fig. 45F).

3. separated by more than 0.5 times transverse diameter of one coxa (Figs 25B, 58A).

197. Exposed portions of metacoxae

1. extending laterally to meet elytra or sides of body (Figs 35E, 45A, 45B, 45G).

2. not extending laterally to meet elytra or sides of body (Figs 26C, 27F, 45F).

S1 is the plesiomorphic state, occurring in almost all outgroups and Archostemata, *Lepicerus*, *Sphaerius*, almost all Hydradephaga, *Arthropterus*, most Hydrophilidae and Scarabaeoidea, Scirtoidea, most Elateriformia, Derodontidae, *Nosodendron*, most Cleroidea a few scattered groups of Cucujoidea and Tenebrionoidea, and *Palophagus* and *Phoracantha* among the chrysomeloids. S2 occurs in *Cephus*, *Micromalthus*, Torridincolidae, *Hydroscapha*, Carabidae (except *Arthropterus*), *Helophorus*, *Georissus*, Histeroidea, most Staphylinoidea, some Scarabaeoidea, a few Elateriformia (including Psephenidae and Ptilodactylidae), some Bostrichoidea, a few Cleroidea and most Cucujoidea, Tenebrionoidea and Phytophaga.

198. Metacoxae

1. more or less movable.

2. completely immobile but separated from metaventrite by complete suture (Fig. 25A).

3. partly or completely fused to metaventrite, suture incomplete or absent.

Immobile metacoxae (S2) occur mainly in Hydradephaga and Trachypachidae, but also occur in the tenebrionoid genera *Orchesia* and *Mordella* in connection with metacoxal modifications for jumping or “tumbling”, respectively. Carabid metacoxae are capable of limited movement. Complete fusion of the metacoxae (S3) occurs in *Eoxenos*, *Meru* and *Notomicrus*.

199. Metacoxae mesally

1. completely free from one another.

2. more or less connate (Fig. 25A).

Mesally connate metacoxae (S2) occur in most of the taxa in which C198 = S2 or S3.

200. Metacoxal plates

1. well developed and more or less uniform (about as wide laterally as mesally) (Figs 25C, 25E, 35E).

2. well developed mesally but weakly developed or absent laterally (Fig. 25D).

3. weakly developed (Fig. 25A).

4. absent.

Although all outgroups lack metacoxal plates, the excavation of the metacoxae to form at least weak coxal plates appears to occur in taxa usually considered to be basal within the order. These plates are well-developed at least mesally (S1 and S2) in Cupedidae, Myxophaga, some Hydradephaga, most Carabidae, a few staphylinoids (including *Necrophilus*), *Declinia*, *Nycteus*, Clambidae and *Cyphon* among the scirtoids, a number of elateriforms, *Nothoderodontus*, *Nosodendron* and several bostrichoids. Weakly developed metacoxal plates (S3) occur in Ommatidae, some Gyrinidae, *Meru*, *Hygrobia*, *Laccophilus*, a few carabids like *Cicindela* and *Brachinus*, several staphylinoids, *Veronatus* and *Amplectopus* among the scirtoids, a number of Elateriformia, including most soft-bodied groups, *Derodontus*, *Laricobius*, Lymexylidae and the cucujoid genus *Helota*. Within Coleoptera, the plates are completely absent (S4) in *Micromalthus*, some Gyrinidae, most Dytiscidae, *Arthropterus*, *Clinidium*, Hydrophilidae, Histeroidea, Hydraenidae, most Leiodidae, *Necrophila*, *Scaphidium*, Scydmaeninae, *Creophilus*, all Scarabaeoidea, *Cerophytum*, *Anischia*, Dictyoptera, Phengodidae, Cantharidae, Jacobsoniidae, *Endecatomus*, Bostrichidae, *Ptinus*, all Cleroidea, Tenebrionoidea, Chrysomeloidea and Curculionoidea, and all Cucujoidea, except *Helota*. The reduction or loss of plates in Gyrinidae and Dytiscidae is correlated with the development of swimming legs.

201. Metacoxal plates

1. concealing no ventrites.

2. concealing most of first ventrite (Figs 25C, 25E).

3. concealing most of first three ventrites (Fig. 25F).

Inapplicable when C200 = S4. Metacoxal plates conceal most of the first ventrite (S2) in Clambidae and most of the first three ventrites (S3) in Haliplidae.

Metendosternite

This structure, which is often referred to as the metafurca, is formed by the invagination of the true metasternum and serves as an attachment for several muscles, including promotors and remotors of the metacoxae, metatrochanteral depressors and a pair of slender muscles attached to the mesothoracic furcal arms. This has been an important character complex in Coleoptera because of Crowson's two classic comparative studies (1938, 1944) and his use of metendosternal characters in later studies on beetle phylogeny and classification (1955, 1960). The muscles have been discussed by Larsén (1966) and Beutel and Haas (2000).

202. Metendosternite: stalk

1. at least twice as long as wide (Figs 47D, 47G, 54G).
2. between one and two times as long as wide (Fig. 54C).
3. shorter than wide or absent (Fig. 58A).

The reduction or loss of the stalk (S3) occurs widely, but especially in those taxa in which the metacoxae have become widely separated.

203. Metendosternite: lateral arms

1. short or absent (Figs 47D).
2. moderately to very long (distinctly longer than their maximum width) (Figs 46E, 47B, 47G, 54G).

The lateral arms of the metendosternite are usually moderately long and often extend anterolaterally. Short lateral arms (S1) are most commonly found in Archostemata, Adephaga and Elateriformia, rarely in Staphyliniformia or Scarabaeiformia and never in Cucujiformia.

204. Metendosternite: laminae

1. well developed and broad (Figs 47C, 47H, 54C).
2. moderately well developed but narrow.
3. absent or only barely protruding from arms (Figs 47B, 47G, 54G).

Laminae are flattened projections arising near the bases of the lateral arms; they are usually somewhat disc-like but may be slender in some taxa. They are almost entirely restricted to Cucujiformia, although slender laminae appear to be present in the megalopteran outgroup and in the staphyliniform genus *Sphaerites*.

205. Metendosternite: ventrolateral processes

1. absent or weakly developed.
2. strongly developed, protruding prominently from stalk (Fig. 47F).

Ventrolateral processes arise from the junction of the stalk and lateral arms and project more or less posteriorly. Well developed ventrolateral processes (S2) occur in Ommatidae, Cupedidae, *Hygrobia*, *Cicindela*, *Declinia*, *Calyptomerus*, *Clambus*, Scirtidae, *Cneoglossa*, *Eulichas*, *Callirhipis*, *Rhinorhipus*, *Brachypsectra*, *Matheteus*, *Laricobius*, Dermestidae, *Eronyxa* and *Idgia*. The broad, subtriangular structures in this vicinity in *Cicindela* may not be homologous to those in other groups.

206. Metendosternite: anterior process

1. at least as long as wide (Figs 47D, 54G).
2. shorter than wide (Figs 47B, 47F).
3. absent (Fig. 47G).

The anterior process extends forward from the bases of the frontal arms and may be short and broad to long and narrow; in some groups it is deeply emarginate anteriorly and more or less divided into two lobes (see C207-S2); the two anterior tendons usually arise from this process. An elongate anterior process (S1) is found in a number of Archostemata, Adephaga and Scarabaeoidea and is particularly common in Elateriformia.

207. Metendosternite: anterior tendons

1. more or less approximate (separated by less than 5 times a basal width) (Figs 47D, 54G).
2. moderately to widely separated but located on either side of deep anterior emargination (Fig. 46E, 47E).
3. widely separated (by at least 5 times a basal width) and located at apex of anterior process (Fig. 47B, 47C).
4. located on lateral arms or not apparent (Fig. 47G).

The deep anterior emargination with tendons on each side of it (S3) is particularly common in Adephaga, but occurs in some taxa within most groups.

Hind wing

Hind wing terminology and assessment of veinal homologies are based mainly on Kukalová-Peck and Lawrence (1993, 2004). This system of nomenclature differs from those of Forbes (1922), Balfour-Browne (1944), Crowson (1955), Hamilton (1972), Ponomarenko (1972), Brodsky (1994), Zherikhin and Gratshev (1995), Hörnschemeyer (1998, 2005) and Fedorenko (2009).

Although wing morphology has been discussed in some detail in the first two references above, some changes in nomenclature given on the last page of the 2004 paper and based in part on the paper by Haas and Kukalová-Peck (2001) have been overlooked by some authors, and minor modifications (particularly in the medial field) have resulted from more recent studies by JFL (see Lawrence *et al.* 2010a).

Two important and consistent landmarks in the beetle wing are the **anterior wing strut** or **radial bar** (ScP plus RA-RA_{1+2}) and the **posterior wing strut** or **medial bar** (MP_{1+2}), the two being joined sub-basally by a short, spring-like **medial bridge** and usually loosely joined apically by a series of cross-veins and sometimes cells. Another important landmark is the **anal fold,** which separates the ano-jugal lobe (usually referred to as the anal lobe) from the remainder of the wing. To aid in descriptions, the hind wing has been divided into five major regions or **fields**, shown for an hypothetical polyphagan in Kukalová-Peck and Lawrence 1993, Figs 12A, B). The **apical field** lies between the ends of the two wing struts and the wing apex; it almost always contains various folds and often contains apical extensions of RP and sometimes RA, but in some wings it may be entirely membranous or contain one or more non-homologizable sclerites only. The **radial field** is the region between the bases of the two wing struts, which contains one or two longitudinal folds only, and the **central field** lies between this and the apical field and contains pivotal folds and the **triangular folding area** characteristic of Archostemata, Myxophaga and Adephaga. The **medial field** is the region between the posterior wing strut and the anal fold, which contains a complex of interconnected veins arising from MP_{3+4}, Cu and AA_{3+4}, plus one or two longitudinal folds. Finally, the **anal field** coincides with the anal lobe and lies between the anal fold and the wing base, containing AP_{3+4}, sometimes AP_{1+2}, and occasionally a remnant of the jugal vein. Some of the terms applied to the beetle hind wing are given in Figs. 32D and 33A–C.

Many of the features of the beetle hind wing, including the reinforced radial cross-veins and R-M loop, are special structures involved in wing folding and they are lost in a number of derived polyphagan wings. In order to distinguish between the loss of these features and their absence in outgroups in which transverse folding does not occur, their absence in outgroups has been coded as inapplicable.

208. Hind wing: radial bar (anterior wing strut)

1. with moderately to very long bending zone but without and not followed by sclerotized hinge or folding point (Fig. 50A).
2. with bending zone followed by sclerotized hinge beyond end of bar (Fig. 49C).
3. with moderately long bending zone followed by folding point beyond end of bar (Figs 47A, 52C, 53E).
4. with very short bending zone near its apical end (Figs 53A, 53B).
5. without bending zone, but with hinge or fold proximad of radial cell or end of bar (Figs 36A, 53C, 54B).
6. without bending zone or hinge proximad of radial cell or end of bar (Figs 48A, 51C, 52A).

Bending zones occur in the radial and medial bars of many beetle wings and consist of a region which is selectively weakened by flattening or asymmetrical crimping, so that it is capable of bending in one direction only. These zones are critical to wing folding and unfolding in Archostemata, Myxophaga, Adephaga and a number of polyphagan groups, since the rotation of the wing bars in one direction allows their apical regions to bend towards one another, and reversing the rotation locks them in a straight position. The wing folding mechanism has been discussed in detail by Schneider (1978), Kukalová-Peck & Lawrence (1993, 2004), Haas & Beutel (2001) and Haas (2006). Note that Schneider, Haas and Beutel define the bending zone in a particular way, so as to exclude the short bending zone in Archostemata (see below). Haas (2006) thus assumes that the bending zone arose after the splitting off of modern Archostemata. We disagree with this hypothesis and consider the long bending zone to have arisen in the earliest of the true beetles, and a shortening of this zone or its conversion into a sharp hinge to represent secondary modifications.

Long radial bending zones in the absence of any hinges or folding points along the entire anterior wing margin (S1) are characteristic of almost all Adephaga (in *Meru* and possibly in some minute adephagans not among the exemplars, the bending zone may be reduced (S4). A bending zone followed by a sclerotized hinge beyond the end of the radial bar (S2) occurs in Hydrophilidae, *Sphaerites* and *Syntelia* and in all Scarabaeiformia, but has been lost in Histeridae. A moderately long bending zone followed by a **folding point** (where a transverse fold meets the anterior wing margin) (S3) occurs in some basal polyphagans, such as Agyrtidae, most Scirtoidea, *Nosodendron* and several bostrichoids, as well as the melyrid *Collops*. In Archostemata and Myxophaga, the bending zone is very short and almost hinge-like (S4) and a similar condition occurs in *Meru* and in Clambidae. The bending zone is absent, but a hinge is present proximad of the radial cell or the end of the radial bar (S5) in Silphidae and Staphylinidae. In the remaining groups of Polyphaga, the radial bar has neither bending zone nor hinge (S6), although folding points or occasionally a hinge may occur distad of the radial bar.

209. Hind wing: apical field

1. with one or more distinct veins (branches of RA and/or RP), sometimes with additional sclerites (Figs 33B, 33C, 48C, 49B, 50C).
2. without distinct veins, sometimes with transverse or oblique linear sclerites which are not obvious veinal remnants (Figs 32D, 33A, 48A).

The oblique linear sclerites present in Elateridae and some related groups may well be remnants of RP (S1), which have becomes straightened and detached in connection with the shortening of the apical field;

however these are coded as S2. The numerous slender lines occurring in the apical field in some Staphyliniformia and Scarabaeiformia are secondary thickenings of the membrane and are considered neither vein remnants nor linear sclerites.

210. Hind wing: post-radial sclerite

1. absent (Figs 33A, 33B, 33C, 48A, 49A, 50C).
2. present (Figs 48B, 49B).

The post-radial sclerite refers to a relatively small heavily pigmented sclerite located just beyond the radial cell in some Polyphaga. It occurs widely and almost exclusively in Cucujiformia, and its presence in *Tropisternus* and *Heterocerus* is probably homoplasious.

211. Hind wing: RA_{1+2} and RA_{3+4}

1. not rejoining at or near anterior wing margin (Figs 33B, 48C, 50A, 50B).
2. rejoining at or near anterior wing margin, usually forming radial cell (Figs 32D, 33A, 33C, 48A, 49B).

S2 refers to the condition in almost all Polyphaga, where RA_{1+2} and RA_{3+4} recombine after a short distance, thus pinching off a cell of a unique type found only in this suborder, the radial cell. In Archostemata, Myxophaga and Adephaga and apparently in the polyphagan family Clambidae, this secondary union does not occur. A cell may occur in this region formed by two radial cross-veins in some Archostemata and Adephaga; this was referred to as the brachial cell by Atkins (1963). The condition in Clambidae is problematic and difficult to interpret because of extreme size reduction in this family (0.7–2 mm). It is notable that Crowson (1955) placed the genus *Calyptomerus* Redtenbacher (although not the remaining Clambidae) in the suborder Myxophaga; however he later refuted this (Crowson 1960). In a number of Polyphaga, the radial cell may be secondarily reduced or lost, either by the obliteration of the base of the cell or by the secondary fusion of RA_{1+2} and RA_{3+4} with the closure of the lumen (see C212); however they are still coded as having S2.

212. Hind wing: radial cell

1. complete (Figs 33A, 33C, 35D, 51A, 51B, 51C).
2. with proximal side (base of RA_{3+4}) incomplete.
3. with proximal side (base of RA_{3+4}) absent (Fig. 52A).
4. highly reduced or absent (Figs 36A, 50C).

Inapplicable when C211 = S1. In S3, the posterior and apical walls of the cell, where RA_{3+4} meets the radial bar, is still intact, whereas in S4, these are missing.

213. Hind wing: apical side of radial cell

1. straight (Figs 35D, 51C).
2. curved (Fig. 51B).
3. angulate.

Inapplicable when C211 = S1.

214. Hind wing: RA_{3+4}

1. divided by triangular folding area (Figs 50A, 50B).
2. not divided by triangular folding area.

The triangular folding area is equivalent to the pivotal folding area in Archostemata, Adephaga and Myxophaga: C plus D of Forbes (1926) or B, as used by Fedorenko (2009). In almost all Polyphaga, this area is clearly subdivided and never crosses RA_{3+4}, however, the wings in Clambidae, although highly reduced, appear to be similar in this respect to the other three suborders and these taxa have been coded as S1.

215. Hind wing: RA_{3+4}

1. complete and well sclerotized (Figs 32D, 33A, 33C).
2. incomplete or very lightly sclerotized where crossed by triangular folding area (Fig. 50B).
3. incomplete basally or absent.

216. Hind wing: cross-vein r1

1. complete (Figs 33B, 48C).
2. incomplete (Fig. 53A).
3. absent.

There are never more than four reinforced radial cross-veins in beetles and r1 is the most basal of these. Cross-vein r2 occurs only in *Omma* and is incomplete in that taxon, while r3 and r4 are widely distributed. Cross-vein r1 is complete (S1) in most Archostemata and Adephaga and incomplete (S2) in Torridincolidae. In *Cupes*, this cross-vein connects RA to RP, while in most other Archostemata and Adephaga it connects RA_{3+4} to RP.

217. Hind wing: radial cell

1. less than 1.75 times as long as wide (Figs 49A, 51A).
2. 1.75 to 3 times as long as wide (Figs 49B, 51C).
3. more than 3 times as long as wide (Fig. 48A).

Inapplicable when C211 = S1.

218. Hind wing: basal edge of radial cell

1. more or less straight and perpendicular to long axis of wing (Figs 32D, 51B, 51C).
2. moderately to strongly oblique, but straight (Figs 48A, 48B, 35D).
3. distinctly curved or bowed (Fig. 51A).

Inapplicable when C211 = S1.

219. Hind wing: inner posterobasal angle of radial cell

1. right or obtuse (Figs 48A, 51B, 51C).
2. acute (Fig. 48B)

Inapplicable when C211 = S1.

220. Hind wing: cross-vein r3

1. more or less perpendicular to long axis of wing (Fig. 50B).
2. moderately to strongly oblique (Figs 49A, 51C).

3. more or less parallel to long axis of wing (Figs 33A, 48A).

4. absent (Fig. 51A).

Cross-vein r3 has been previously misinterpreted as a vein (the radial recurrent) by some authors because it has a tendency to become longitudinally oriented in various polyphagan wings, in which the radial and medial fields have become elongate and the apical field very short. The cross-vein is more or less perpendicular to the long wing axis (S1) in Ommatidae and Cupedidae and moderately to strongly oblique (S2) in Gyrininae and a wide variety of polyphagan taxa. The longitudinally oriented cross-vein (S3) is also widely distributed among Polyphaga, but often found in elateriform taxa with elongate bodies. Cross-vein r3 is absent (S4) in *Micromalthus*, all Myxophaga, most Adephaga, most Staphyliniformia and Scarabaeoidea, and various taxa within the other superfamilies.

221. Hind wing: cross-vein r3

1. arising from radial cell well away from r4 (Figs 32D, 33A, 51C).

2. arising from radial cell very close to or at same point as r4 (Figs 33C, 52C).

3. fused at base with r4.

Inapplicable when C211 = S1 or 220 = S4. When cross-vein r3 has fused at base with r4, it often appears to be absent (C220-S4), but r4 appears to be abruptly bent and a stub of r3 may be visible.

222. Hind wing: cross-vein r4

1. more or less complete (Figs 48A, 51B, 51C).

2. incomplete (Fig. 49C).

3. absent.

223. Hind wing: cross-vein r4

1. without apically projecting spur.

2. with apically projecting spur (Fig. 49B).

This apical spur appears to be a veinal remnant. In many groups there is a pigment patch crossing r1, but that is a different feature which is not included in the character set. Among the exemplars, the spur occurs in the cleroid genus *Listrus* and in a few genera of Cucujoidea, Chrysomeloidea and Curculionoidea.

224. Hind wing: basal portion of RP

1. complete to or close to origin (Figs 35D, 50B).

2. incomplete basally but moderately long (Figs 51B, 51C).

3. very short (Figs 51A, 52C).

4. absent (Fig. 50C).

The basal portion of RP is that portion basad of cross-vein r4, the oblongum cell or the beginning of the R-M loop. In most beetles the basal section has been obliterated probably as a result of the formation of the medial bridge connecting RA with MP. In a few taxa (e.g., *Satonius*, *Declinia*), RP is more or less complete and has been coded as S1, but it has been partly obliterated beyond the base.

225. Hind wing: R-M loop

1. moderately to very broad and rounded or truncate (Figs 48B, 48C, 49A, 49B, 52C).

2. moderately broad but forming acute angle (Fig. 48A, 51B, 51C).

3. forming narrowly acute angle (Figs 49C, 52A).

4. absent (Figs 50C, 53C).

The R-M loop usually refers to the normally curved connection between RP and MP_{1+2} in Polyphaga; however it is homologous to the outer edge of the oblongum cell in Archostemata, Adephaga and Myxophaga. It is normally broadly rounded or truncate, but may be acute or absent, especially in Staphyliniformia. This is the functional equivalent to the radial loop, which may involve the radial or brachial cell.

226. Hind wing: apical portion of RP (apicad of R-M loop)

1. well developed and consisting of more than one branch (Figs 48C, 49B, 49C, 50A, 51B).

2. well developed but consisting of single branch (Fig. 49A).

3. absent or vaguely indicated (Figs 48A, 51A, 51C, 52C).

227. Hind wing: MP_{1+2}

1. without bending zone or hinge.

2. with moderately long bending zone (Figs 47A, 53E).

3. with very short bending zone or hinge near apical end (Figs. 36B, 48C, 53A).

The medial bending zone is never as strong as the radial bending zone in Archostemata or Staphyliniformia and more likely to be selectively weakened by flattening, rather than by crimping. A moderately long and weak bending zone (S2) occurs in a few groups of basal Polyphaga. The very short bending zone or medial hinge (S3) occurs in Archostemata, Myxophaga, Adephaga and Clambidae.

228. Hind wing: oblongum cell

1. about as long as wide or with long axis parallel with long axis of wing (Figs 36C, 53A).

2. with long axis perpendicular to long axis of wing (Figs 48C, 50A, 50B).

3. absent (Figs 33A, 33C).

The oblongum cell is formed by the joining of RP with MP_{1+2} by a pair of radio-medial cross-veins. It occurs in all Archostemata, Myxophaga and Adephaga, but with a weakened or obliterated apical wall in *Micromalthus* and *Hydroscapha* (coded as S3 in the latter). It is also present in the clambid genus *Calyptomerus*.

229. Hind wing: medial spur

1. extending to or nearly to wing margin (Figs 48A, 49C, 51B).

2. moderately long but ending well before wing margin.

3. a very short stub (Fig. 48C).
4. absent (Fig. 50A).

The medial spur is an extension of MP_{1+2} beyond the end of the R-M loop or the posterior end of the oblongum cell.

230. Hind wing: medial spur

1. not curved posteriorly (Figs 48C, 50B. 51B).
2. curved posteriorly (Figs 48A, 49B, 52A).

The spur is short and never curved posteriorly in Archostemata, Myxophaga or Adephaga; in Polyphaga it is quite variable, but often curved posteriorly and extending to the wing margin.

231. Hind wing: medial embayment

1. absent (Fig. 51B).
2. present (Fig. 49B).

An embayment is any emargination in the wing margin, and the medial embayment is that which lies at or beyond the end of the medial spur.

232. Hind wing: number of free veins in medial field

1. five or rarely six (Figs 33A, 33C, 48A, 50B, 51B).
2. four (Figs 33B, 48C, 49C, 50A).
3. three (Fig. 49B).
4. two (Fig. 48B).
5. one (Fig. 50C).
6. none (Fig. 36C).

As indicated above the medial field is that portion of the wing between MP_{1+2} and the anal fold. The maximum number of free veins in this field has been referred to by Crowson (1955) as the "number of anal veins in the main group". The maximum number is almost always five (MP_3, MP_4, CuA_2, AA_3 and AA_4, but in some Dermestidae (e.g., *Attagenus*) and in the buprestid genus *Julodis*, there may be six, with CuA_{3+4} extending to the wing margin instead of meeting AA_3 to close off the wedge cell. Commonly, MP_{3+4} does not fork apically, so that there are only four free veins in the field. There are almost never more than four free veins in Archostemata and Adephaga, in spite of the relatively large size of many taxa; in the former group MP_{3+4} never forks, while in the latter CuA_2 is always absent. Extra veins or cells may occur occasionally in this field, but in all cases known to us, these are individual variants (often in one wing only). Because the branches of MP, Cu and AA in this field anastomose in various ways, the number of free veins are often reduced and in some wings, especially those of very small beetles, they may disappear altogether.

233. Hind wing: basal medio-cubital cross-vein

1. absent.
2. joining MP and Cu (Fig. 50A).
3. joining MP_{3+4} and CuA (Fig. 50B).

This brace is usually broken in the middle by a fold. S2 occurs in most Adephaga and a few Polyphaga, while S3 occurs only in Archostemata.

234. Hind wing: binding patch anterad of MP_{3+4}

1. absent.
2. present (Fig. 49B).

Binding patches in the median field apparently assist in the folding process by allowing the wings to adhere to one another and/or to binding patches beneath the elytral apices. This anterior patch is also called a medial fleck and was formerly called the subcubital fleck (based on previously used veinal terminology). Sometimes the fleck is apparently divided into two parts (an illusion formed by a change in direction of its constituent microtrichia) or is bisected by a vein. This type of binding patch is widely distributed throughout Cucujoidea and Tenebrionoidea. It also occurs in some groups of Chrysomeloidea (e.g., Orsodacninae, a few Cerambycidae, most Spilopyrinae and Eumolpinae, and at least some Chrysomelinae and Hispinae), but only in *Palophagus* among the exemplars.

235. Hind wing: binding patch posterad of MP_{3+4}

1. absent.
2. present (Fig. 54D).

Posteriorly located binding patches occur only in the adephagan families Aspidytidae, Noteridae, Amphizoidae, Dytiscidae and Trachypachidae.

236. Hind wing: MP_{3+4}

1. with basal connection and sometimes sub-basal cross-vein (Fig 48C, 50B).
2. with sub-basal cross-vein and basal spur (Figs 32D, 35D, 48A).
3. with sub-basal cross-vein but no basal spur (Fig. 50A).
4. with neither sub-basal cross-vein nor basal spur.
5. absent (Figs 36C, 50C).

MP_{3+4} appears to separate from MP_{1+2} at various points in different groups, but in most cases this is not the position of the original fork, but rather a subsequent cross-vein, a basal spur often extending proximad from this cross-vein (S3) indicating that the original connection has been severed.

237. Hind wing: CuA_{1+2} or CuA_1

1. joining MP_{3+4} (Figs 35D, 48C, 51C).
2. joining MP_4 (Figs 32D, 48A, 50B).
3. not joining MP or absent (Figs 48B, 49C, 50C).

The cubital system is often connected with MP by a cross-vein representing CuA_1 or in some cases CuA_{1+2} (CuA_1 having been incorporated into MP). This is coded as S1 if the CuA cross-vein joins MP_{3+4} before the MP_3-MP_4 fork and S2 if it joins MP_4 after the fork.

238. Hind wing: CuA_{3+4}

1. meeting AA3 to close off wedge cell (Figs 48A, 50B, 51B).
2. present but not meeting AA3 (Fig. 49A).
3. absent (Figs 49B, 49C, 50A, 52C).

Except for the outgroups, S2 occurs only *Julodis*, although as indicated above a similar situation occurs in the dermestid genus *Attagenus*.

239. Hind wing: length of wedge cell

1. at least 0.25 times greatest width of wing (Figs 48C, 51B, 51C).
2. less than 0.25 times greatest width of wing (Fig. 52B).

Inapplicable when C238 = S2 or S3.

240. Hind wing: apex of wedge cell

1. squarely truncate (Figs 32D, 48A, 48C).
2. obliquely truncate (Fig. 51C).
3. acute (Fig. 51B).

Inapplicable when C238 = S2 or S3. When the wedge cell is more or less truncate (S1 and S2), CuA_{1+2} arises from the anterodistal corner and AA_3 from the posterodistal corner. With an acute wedge cell (S3), CuA_{1+2}, if present arises subapically and AA_3 apically.

241. Hind wing: anal lobe

1. well developed (Figs 48C, 51B).
2. highly reduced or absent (Figs 36C, 53A).

The anal lobe refers to the area basad of the anal fold and is equivalent to the ano-jugal lobe. It is not necessary for this lobe to be delimited by an anal embayment; although in some previous works the term anal lobe was used only when a notch-like anal embayment was present (Fig. 32D, Anal Notch).

242. Hind wing: anal embayment

1. absent or gradual and shallow.
2. abrupt and notch-like, usually deep (Figs 32D, 36A, 51A, 52A).

S3 is widely distributed but usually occurs in wings which are relatively small.

243. Hind wing: AA_4

1. not joining anal fold posteriorly.
2. joining anal fold posteriorly (Figs 35D, 52C).
3. absent.

S2 occurs in *Declinia*, Scirtidae and some Adephaga.

244. Hind wing: AP_{3+4}

1. forked to form AP_3 and AP_4 (Figs 48C, 50B, 52C).
2. not forked (Figs 48A, 49C, 51B).
3. absent (Fig. 52A).

AP_{3+4} is usually the only vein in the anal field, although a short AP_{1+2} and/or a short jugal remnant are occasionally present. AP_{3+4} forks to form AP_3 and AP_4 in all Archostemata (except *Micromalthus*) and in Trachypachidae, *Dascillus* and *Sandalus*.

245. Hind wing: long fringe hairs

1. absent.
2. lining posterior margin only.
3. lining most or all of wing margin (Figs 36C, 53A, 53D).
4. restricted to basal portions of anterior and posterior wing margins.
5. restricted to anal lobe.

Well developed fringe hairs occur in a number of very small beetles and appear to increase the wing surface and allow the beetles to be carried as aerial plankton.

Legs

246. Profemoral antenna cleaner

1. absent.
2. present.

A profemoral antenna cleaner occurs in *Aspidytes*, *Noterus* and *Laccophilus*.

247. Protibial antenna cleaner

1. absent.
2. present (Figs 30F, 30G, 34C).

The protibial antenna cleaner appears to define the Geadephaga (Trachypachidae plus Carabidae), but has been lost in the highly modified *Arthropterus*.

248. Number of protibial spurs

1. two (Figs 30F, 30G).
2. one (Fig. 34D).
3. none.

Protibial spurs may be reduced to one or lost in a number of groups, but it is often difficult to observe smaller ones when occurring along with a setal fringe, making this character prone to observational errors.

249. Protibial spurs

1. both apical.
2. apical and subapical (Figs 30F, 30G, 34C).

S2 occurs in most derived taxa of Carabidae, except those which have lost one or both spurs.

250. Mesotibia

1. not strongly widened.
2. strongly widened at or near apex.
3. strongly widened well before apex (Fig. 30D).

251. Outer edge of mesotibia

1. without fixed lobes or teeth.
2. with fixed lobes or teeth (Fig. 43D).

252. Spiniform setae on outer edge of mesotibia

1. absent.
2. moderately long and slender (Fig. 31B).
3. short and stout (Fig. 31C).

253. Outer apical or subapical edge of mesotibia

1. without antenna cleaner.
2. with antenna cleaner (Fig. 30C).

The mesotibial antenna cleaner occurs in *Distenia* and *Tetraopes* among our exemplars. Antenna cleaners on the meso- and metatibiae (Fig. 30B) also occur in some eumolpine Chrysomelidae, but these have a different structure and are certainly not homologous.

254. Outer apical angle of mesotibia

1. simple or slightly produced, angulate or rounded.
2. with one or more straight or outwardly facing teeth.
3. with rounded or angulate lobe or process, sometimes bearing spiniform setae (Fig. 31F).
4. with inwardly projecting or hooked spine (uncus) (Figs 31A, 31E).

255. Inner apical angle of mesotibia

1. not or slightly produced.
2. distinctly produced forming tooth (mucro) (Fig. 31E).

256. Mesotibial spurs

1. two (Figs 30D, 30E).
2. one.
3. none (Fig. 43D).

257. Mesotibial spurs

1. glabrous (Fig. 30E).
2. pubescent (with hair-like microtrichia) (Fig. 30A).
3. serrate or pectinate (Fig. 31G).

258. Metatibial spurs

1. two.
2. one.
3. none.

259. Tarsal formula

1. 5-5-5 in both sexes.
2. 5-5-5 in female and 5-5-4 in male.
3. 5-5-4 in both sexes.
4. 5-4-4 in male and 4-4-4 in female.
5. 5-4-4 in both sexes.
6. 4-4-4 in both sexes or 3-4-4 in male only.
7. 3-3-3 in both sexes.
8. 1-1-1 in both sexes (Fig. 35A).

260. Basal mesotarsomere

1. not much shorter than tarsomere 2.
2. much shorter than tarsomere 2.

261. Mesotarsomeres in female

1. without ventral lobes.
2. with ventral lobes on 1 and 2 or 2 only.
3. with ventral lobes on 1, 2 and 3 or 2 and 3 only.
4. with ventral lobes on 1, 2, 3 and 4 or 2, 3 and 4 only.
5. with ventral lobe on 3 only.
6. with ventral lobe on 4 only (Fig. 43I).

262. Ventral mesotarsal lobes

1. not membranous.
2. membranous.

263. Penultimate mesotarsomere

1. not much shorter than preceding tarsomere and not enveloped by its ventral lobe.
2. much shorter than preceding tarsomere but not enclosed by its ventral lobe.
3. simple, much shorter than preceding tarsomere and encompassed by its ventral lobe.

S3 includes the pseudotetramerous tarsi characteristic of most Chrysomeloidea and Curculionoidea; however, tarsi in a number of other beetle groups are hardly separable from those of the phytophagous families, and conversely some Phytophaga have tarsi which must be coded as S1 (e.g., *Cephaloleia*, which has 4-4-4 tarsi with the penultimate one lobed, or *Parandra,* which lacks tarsal lobes) or S2 (e.g., *Sipylus*, *Platypus*).

264. Mesopretarsal claws

1. simple.
2. toothed or bifid.
3. serrate or pectinate (Fig. 31I).

265. Mesopretarsal claws

1. without ventral appendages.
2. with membranous or lightly sclerotized, usually pubescent appendages.
3. with heavily sclerotized, blade-like or bristle-like appendages.

266. Empodium

1. well developed and visible between pretarsal claws (Fig. 31H, 31I).
2. reduced and not visible between claws or absent.

A number of smaller beetle species may have empodia but they are not usually visible between the claws at low magnifications; these have all been coded as S2. This and the next character are prone to observational errors.

267. Number of setae on empodium

1. none.
2. two.
3. three or more (Fig. 31H).

Abdomen

The term **ventrite** is often misused in descriptions and keys. A ventrite is one of the sternites that are visible when the metacoxae are in place and that make up the more heavily sclerotized portion of the beetle abdomen. Thus the tautological “visible ventrite” is incorrect. These are numbered using Arabic numerals beginning with the first one which is at least partly visible from below, while the true sternites are numbered using Roman numerals. In Fig. 34E, this convention was not used; ventrites are numbered V1–V5, sternites S3–S9 and tergites T1–T10.

268. Abdominal ventrites in male

1. nine (sternites I to IX).
2. eight (sternites II to IX) (Fig. 56A).
3. seven (sternites II to VIII) (Fig. 56B).
4. seven (II to VII plus IX).
5. seven (sternites III to IX).

6. six (sternites II to VII) (Figs 29E, 43G).
7. six (sternites III to VIII) (Fig. 28D).
8. five (sternites III to VII) (Figs 25D, 29H, 34E).
9. three (Fig. 56L).

Normally in beetles there are only five ventrites, which are numbered with Arabic numerals and correspond to abdominal sternites III to VII (S8: most Archostemata, *Torridincola*, *Ytu* and most Polyphaga); or sternite VIII may also be visible (S7: a variety of polyphagan groups). Those taxa having six ventrites including sternites II to VII (S6) include *Lepicerus*, *Satonius*, most Adephaga and a few Polyphaga (e.g., *Sphaerites*, *Pleocoma* and *Passalus*). Four ventrites occur in none of our exemplars, although some Aderidae appear to have four ventrites because of the almost complete obliteration of the suture between ventrites 1 and 2. S10 (three ventrites) is known only in the myxophagan genus *Sphaerius*. The occurrence of seven ventrites (S3–S5) is less common, occurring mainly in those Adephaga with sternite VIII exposed and various soft-bodied taxa like *Micromalthus*, *Atractocerus* and *Rhipidioides*, several staphyliniforms and scarabaeiforms, and a few neotenic Elateroidea. Eight ventrites (S2) occurs in *Cephus*, *Panorpa*, *Hydroscapha*, *Ochthebius* and most of the neotenic Elateroidea, while nine ventrites (S1) occurs only in outgroups, but is also known in various larviform females.

269. Basal abdominal ventrites connate

1. none (Figs 28D, 56A).
2. two (Figs 29A, 54F).
3. three (Figs 29E, 29F, 34E, 43G).
4. four (Figs 25D, 29H).
5. five or more.

This character is sometimes difficult to code, especially when the freedom of movement of ventrites varies gradually from base to apex. However in most groups two or more basal ventrites are more or less solidly fused, while those distad of them are freely movable. The fusion of two basal ventrites (S2) occurs in *Lepicerus*, *Satonius* and in various polyphagan taxa. In most Adephaga the first three ventrites are solidly fused together (S3) and the suture between ventrites 1 and 2 is often almost obliterated; in addition to Adephaga, S3 occurs in *Declinia*, *Amplectopus*, a variety of Byrrhoidea, *Rhinorhipus*, *Anischia*, *Anthrenus*, *Ptinus* and a number of Tenebrionoidea. S4 occurs in Cerophytidae, most Elateridae, a few tenebrionoids, Anthribidae and *Merhynchites* of the Attelabidae. A number of Scarabaeoidea, Artematopodidae, most Eucnemidae and Throscidae have S5, as does the zopherid genus *Pristoderus*.

270. Abdominal ventrite one

1. on same plane as ventrites two and three (Figs 29D, 29H).
2. on same plane as ventrite two but on lower plane than ventrite three.
3. on lower plane than ventrite two.

271. Abdominal sternite II

1. more or less evenly sclerotized or membranous.
2. more heavily sclerotized laterally than mesally.
3. more heavily sclerotized mesally than laterally.

This character is seen only with metacoxae removed.

272. Abdominal sternite II

1. distinctly separated from sternite III by suture.
2. partly fused to sternite III (incomplete suture).
3. completely fused to sternite III (no suture).

273. Abdominal sternite II

1. with distinct intercoxal process.
2. with low carina only.
3. without median partition.

274. Metacoxal cavities

1. absent, metacoxae not countersunk.
2. well defined, completely limited posteriorly by carina (Fig. 54F).
3. secondarily reduced, without or with incomplete posterior carina (Fig. 55C).

275. Abdominal sternite III

1. with intercoxal process (Fig. 54F).
2. without intercoxal process.

276. Ventrite 1 at about midpoint between midline and lateral edge of abdomen

1. not visible.
2. shorter than ventrite 2 at same point (Fig. 29B).
3. 1.0 to 1.5 times as long as ventrite 2 at same point (Fig. 29H).
4. more than 1.5 times as long as ventrite 2 at same point (Figs 25B, 29C).

277. Basal abdominal ventrite

1. continuous across base of abdomen (Figs 28D, 29A).
2. divided into two parts by metacoxae (Fig. 29E).
3. divided into three parts by metacoxae.
4. visible only between metacoxae.

278. Basal abdominal ventrite

1. without postcoxal lines or crural impressions (Fig. 54F).
2. with a pair of straight or slightly curved postcoxal lines (Figs 25B, 28A, 28B, 29D, 29G).
3. with a pair of strongly recurved postcoxal lines usually delimiting crural impressions (Fig. 28C, 29I).

The postcoxal lines on ventrite 1 usually begin at the base of the intercoxal process and extend posteriorly, sometimes reaching the posterior edge of the ventrite; occasionally a second pair of postcoxal lines may be present between the intercoxal process and the lateral edge of the ventrite, as in Biphyllidae (Fig. 28B).

279. Abdominal tergites III to VII
1. not flanked by articulated paratergites (Fig. 34E).
2. flanked by one or two pairs of articulated paratergites on three or more segments.

S2 occurs in various Staphylinidae (*Glypholoma*, *Leucotachinus* and *Creophilus* among the exemplars).

280. Patches wing-folding microtrichia on tergite VIII
1. absent (34E).
2. present.

Spicule patches are known to occur on at least some abdominal terga in a large number of taxa across all of the suborders, but are more common in smaller beetles. These have been discussed in detail by Hammond (1979) and apparently allow movements of abdominal segments to assist in the wing-folding process.

281. Patches of wing-folding microtrichia on tergite VII
1. absent (Fig. 34E).
2. present.

282. Patches of wing-folding microtrichia on tergite VI
1. absent (Fig. 34E).
2. present (Fig. 56G).

283. Patches of wing-folding microtrichia on tergite V
1. absent (Fig. 34E).
2. present (Fig. 56G).

284. Patches of wing-folding microtrichia on tergite IV
1. absent (Fig. 34E).
2. present (Fig. 56G).

285. Patches of wing-folding microtrichia on tergite III or tergites II and III
1. absent (Fig. 34E).
2. present (Fig. 56G).

286. Glandular openings on tergites I to VIII
1. absent.
2. present (Fig. 42G).

S2 occurs only in the family Cantharidae.

287. Tergite VII and sternite VII
1. separated by membrane or a distinct suture (Fig. 34E).
2. solidly fused, without or with incomplete suture between them.

288. Abdominal intersegmental membranes
1. without pattern of minute sclerites.
2. with brick-wall-like pattern of minute sclerites (Fig. 55C).
3. with minute sclerites of other shapes.

Minute sclerites in the intersegmental membranes occur mainly in Staphylinoidea, but a similar condition was found in the buprestid genus *Acmaeodera* and in two cleroids.

289. Tergite VIII in male dorsally
1. not concealed by tergite VII (Fig. 34E).
2. concealed by tergite VII.

290. Tergite VIII in female dorsally
1. not concealed by tergite VII.
2. concealed by tergite VII.

291. Sternite VIII in male ventrally
1. not concealed by sternite VII.
2. concealed by sternite VII.

292. Sternite VIII in female ventrally
1. not concealed by sternite VII.
2. concealed by sternite VII.

293. Functional spiracles on abdominal segment VIII
1. present in pleural membrane or between fused tergite and sternite (Fig. 34E).
2. present on sternite.
3. present on tergite or laterotergites (Figs 60A, 60E).
4. absent (Fig. 45I).

The absence of functional eighth spiracles is a synapomorphy of Cucujiformia, but loss of these spiracles also occurs in *Sabatinca* and *Eoxenos* among the outgroups, *Meru* (in which all spiracles appear to be lacking), most Hydrophilidae, all histeroids, *Colon*, *Rhopaea* and *Cetonia* among the scarabaeoids, the clambid genera *Acalyptomerus* and *Calyptomerus*, *Declinia*, all Scirtidae, a number of Byrrhoidea, *Melasis* and *Aulonothroscus* among the elateroids, *Nosodendron* and *Lyctus*.

294. Spiracles on segment VIII
1. not enlarged, similar to anterior spiracles (Fig. 34E).
2. enlarged, modified and posteriorly oriented (Figs 60A, 60E).

The eighth spiracles are somewhat enlarged and more or less posteriorly oriented in Myxophaga, but also in *Aspidytes* and *Clambus*.

295. Functional spiracles on abdominal segment VII
1. present in pleural membrane or between fused tergite and sternite (Fig. 34E).
2. present on sternite (Fig. 45I).
3. present on tergite or laterotergites.
4. absent (Fig. 56G).

296. Functional spiracles on abdominal segment VI
1. present in pleural membrane or between fused tergite and sternite (Fig. 34E).
2. present on sternite (Fig. 45I).
3. present on tergite or laterotergites.
4. absent.

297. Functional spiracles on abdominal segment V
1. present in pleural membrane or between fused tergite and sternite (Fig. 34E).
2. present on sternite (Fig. 45I).
3. present on tergite or laterotergites.
4. absent.

298. Abdominal sternite VIII

1. without gland cells and reservoir complex at anterior edge.

2. with gland cells and reservoir associated with median projection on anterior edge (Figs 55C, 58K).

S2 occurs in *Paraphloeostiba* and *Glypholoma*.

299. Sternite VIII and tergite VIII in male

1. separated on each side by sutures.

2. solidly fused at least at base.

300. Tergite VIII in male

1. not completely divided by median suture (similar to Fig. 60E).

2. completely divided by median suture (Fig. 60A).

301. Anterior edge of sternite VIII in male

1. without median strut.

2. with median strut (Fig. 56F).

The anterior strut in males is sometimes referred to as the spiculum relictum.

302. Anterior edge of sternite VIII in male

1. without lateral struts.

2. with lateral struts (Fig. 60A).

303. Posterior edge of sternite VIII in male

1. not or shallowly emarginate.

2. deeply emarginate.

304. Paired subapical abdominal defensive gland openings

1. absent.

2. opening between segments VIII and IX.

3. opening between segments VII and VIII.

4. opening behind abdominal tergite VIII.

S2 occurs only in *Adelium*, while S3 is found in some genera of Tenebrionidae. S4 apparently occurs in all Adephaga.

Abdominal apex

The structure of the abdominal apex in both male and female Coleoptera has been the subject of much dispute. Crowson (1955, 1981) considered the beetle abdomen to consist of nine segments, segments X and XI of many other insect orders having been completely lost. The proctiger, which lies just above the anus, was considered to be tergite IX, and the paraprocts (in both sexes) to be laterotergites IX. The presence of an undivided tergite immediately preceding the proctiger was interpreted as a secondary fusion of the two laterotergites. This interpretation was followed by Hieke (1966) based on musculature; however that author later (Hieke 1971) recognized the existence of a tenth tergite in various Scarabaeoidea. Wanat (2007) in his recent detailed study of genitalic alignment in Coleoptera (particularly Phytophaga), considered the proctiger to be tergite IX, and also suggested that the tegmen itself might be homologous to segment X.

In the present work the proctiger is considered to be homologous to segment X in both sexes, following Hieke (1971), Lawrence and Newton (1982), Lawrence and Britton (1991, 1994), Beutel and Lawrence (2005) and Lawrence *et al.* (2010a). A well-developed proctiger and an undivided tergite IX (C307 = S1 and C309 = S1) occur in a number of beetle families which are considered to occupy a basal position within the order (see C307), which makes it less likely to be a secondarily derived condition, as suggested by Crowson (above).

Male

305. Anteroventral edge of segment IX in male

1. with broadly rounded, angulate, truncate or emarginate subgenital plate (Figs 34E, 56D).

2. with narrowly rounded to acute subgenital plate (Fig. 56E)

3. with single median strut or spiculum gastrale (Fig. 56C).

4. with paired independent, divergent or subparallel lateral struts (laterotergites) (Fig. 60A).

5. completely membranous.

The anteroventral portion of segment IX in the male is often considered to be sternal in origin, but in most cases it consists partly or entirely of anterior protrusions of the laterotergites, which fuse together and to the sternite to form a **subgenital plate**. In many taxa the plate becomes more or less membranous and only the sclerotized edges remain. The anterior edge of the subgenital plate may be broadly rounded, angulate, truncate or emarginate (S1), but in some taxa it is narrowly rounded or acute (S2) or more often drawn out to form a median strut or **spiculum gastrale** (S3). Some workers consider any anterior projection to be a spiculum, but we define the spiculum here as a slender strut.

306. Posterior edge of sternite IX in male

1. without projecting mesal lobe.

2. with projecting mesal lobe or tegmenite (Fig. 56C).

A posteriorly projecting, apically setose lobe on sternite IX in Oedemeridae was referred to as the tegmenite by Arnett (1949, 1951). It has been coded as present in a few other tenebrionoid families and several cleroids and cucujoids as well, but it is not at all certain if all of these conditions are homologous. The tegmenite appears to be derived from the main sternal plate of segment IX, when a portion of this projects posteriorly and usually is cut off by membrane from the remainder of sternite.

307. Tergite IX in male

1. simple and undivided (sometimes with median endocarina) (Fig. 42F).

2. divided by longitudinal suture.

3. divided into two separated laterotergites (Figs 56E, 60A).

4. completely membranous.

An undivided ninth tergite (S1) is widely distributed throughout Archostemata, Myxophaga, Adephaga, Staphyliniformia, Scarabaeoidea and Elateriformia and Bostrichoidea, but relatively uncommon in Cucujiformia, while the distinct separation into laterotergites (S3) occurs in some members of Myxophaga, Adephaga, Staphyliniformia and Scarabaeiformia and most Cucujiformia. In Derodontidae and a few other scattered groups, the tergite is divided by a longitudinal suture (S2), and in *Oxypeltus* tergite IX is completely membranous.

308. Posterior edge of tergite IX in male

1. truncate.

2. shallowly emarginate (Figs 34E, 58G).

3. deeply emarginate (Figs 42F, 58E, 58F).

Inapplicable when C307 = S4 or S5 and when C309 = S2 or S3.

309. Tergite X (proctiger) in male

1. well developed and free (Figs 34E, 42F, 58E, 58F, 58G).

2. partly fused to tergite IX.

3. completely fused to tergite IX.

310. Tergite X (proctiger) in male

1. lightly to moderately heavily sclerotized, without baculi (Figs 34E, 58E, 58F).

2. sclerotized laterally with broad or narrow mesal membranous strip.

3. membranous or lightly sclerotized with paired longitudinal baculi.

4. completely membranous.

The proctiger is the sclerite lying just above the anal opening and considered here to be homologous to Tergite X.

Aedeagus

The terminology applied to the male genitalia has varied over the years and at least two sets of terms are currently in use. In the present work we are using those discussed briefly in Lawrence *et al.* (2010a). Aedeagus is used here to refer to the phallobase, parameres and penis and not to the penis alone. Also, penis is used instead of median lobe and parameres instead of lateral lobes.

311. Phallobase

1. at least partly sclerotized and usually ventrad of penis (sometimes rotated 90 or 180 degrees) (Figs 55F, 57A, 58H, 59D, 60A).

2. forming ring or sheath partly or completely surrounding penis (cucujiform type) (Figs 56K, 59A).

3. membranous or slender and strap-like, so that parameres appear to be articulated with penis (Figs. 55G, 58E).

4. absent or possibly fused to base of penis.

The cucujiform type of aedeagus (S2) in which the phallobase forms a ring or sheath surrounding the penis occurs throughout the Series Cucujiformia, although with a series of reductions and modifications, while most other beetles have some modification of the trilobate type (S1). S3, which occurs in Adephaga and Staphylinoidea, differs from the trilobate type in that the phallobase is highly reduced or membranous and the parameres appear to be articulated directly with the penis. S4 refers to those outgroups which appear to have no homologue of the phallobase.

S1 and S2 are based on the hypothesis first presented by Crowson (1955) that all of the aedeagal types in Coleoptera may be derived from the trilobate type with parameres articulated to the phallobase which lies beneath the penis. The cucujiform type is assumed to have evolved by the enveloping of the penis by the phallobase with the parameral attachment becoming dorsal. The so-called cucujoid or ring-type is a further modification involving the reduction in the body of the phallobase; however there is no clear separation between this and the cleroid or sheath-type. The tenebrionoid type may be derived directly from the sheath-type with the elimination of the ventral part of the phallobase, so that the entire tegmen (= phallobase plus its attached parameres) comes to lie dorsad of the penis. In some cases, the tenebrionoid type may resemble the original trilobate type, especially when a subsequent rotation occurs. Further modifications of the cucujoid type involving reduction of the tegmen occur within the Phytophaga. S3 and S4 may be derived directly from a trilobate type by a reduction and/or membranization of the phallobase, and other specialized aedeagi, which involve the formation of a parameral tube completely enveloping the penis (C314 = S3; the histeroid or buprestoid types used in Lawrence *et al* 1999b), are also derivable directly from the trilobate type.

This is a highly variable complex of structures and very difficult to code. Although the Crowson hypothesis has been used as a basis for delimiting characters and states below, the authors recognize the inadequacies of the system to explain all the known genitalic types. One of the major difficulties is the apparent 180æ rotation of the aedeagus, especially within the Cucujiformia. This may be due to a rotation of the aedeagus when everted (as in the Tenebrionidae), but Wanat (2007) has recently proposed the independent evolution of three types of abdominal apex with 1) neither segment IX nor the tegmen rotated (most superfamilies, plus Coccinellidae), 2) segment IX not rotated but tegmen rotated (some basal cucujoids, including Cucujidae and Byturidae), or 3) both segment IX and tegmen rotated (Nitidulidae, Cryptophagidae, Chrysomeloidea and Curculionoidea).

312. Parameres

1. attached to posterior or distal edge of phallobase (Figs 57A, 57G).

2. arising proximad of distal edge of phallobase (phallobase and parameres overlapping) (Fig. 57J).

3. attached directly to penis (phallobase apparently absent) (Figs 41C, 55G).

4. fused to phallobase, visible as projecting lobes or apparently absent (Fig. 60A).

5. absent (when phallobase also absent).

According to Wanat (2007) the parameres of Phytophaga and at least some cucujoids are not homologous to those of other groups, since they arise from the membrane between the anus and the dorsal wall of the tegmen, and not from the membrane between the ventral wall of the tegmen and the penis (aedeagus of Wanat). He suggested that the term parameroids be used for these structures.

313. Parameres

1. not joined to penis at base.

2. joined to penis at base (Figs 57D, 57J).

Although the parameres or parameral struts may be closely joined to the base of the penis or to basal penile struts, the two may not be solidly fused. It is more likely that they are joined by a tendon. It is also possible that other taxa not coded as S2 have hyaline connections between the parameres and penis, so that the two are not really independent.

314. Articulated parameres

1. free from one another at base (sometimes contiguous or with parameral struts which fuse together near base of penis (Figs 57A, 57B, 57G)

2. completely fused together ventrally, joined by continuous bridge at or near base (Fig. 57J).

3. fused together ventrally and dorsally and forming tube surrounding penis (Figs 57E, 57I).

4. broadly fused together to form parameral plate or apicale, which may be cleft to deeply emarginate (Figs 57F, 57H).

Inapplicable when C312 = S4 or S5. S2 refers to the condition in most Bostrichoidea (although not in *Dermestes*) where the phallobase overlaps and is joined by membrane to the parameres and the latter are joined together ventrally by a slender bridge. The formation of a parameral tube (S3) occurs in Histeridae and closely related families, but also in a few scarabaeoids, most Buprestidae and a few other unrelated taxa. The dorsal parameral plate or apicale (S4) is a characteristic of Tenebrionoidea, although this plate may be deeply excavate and resemble the trilobate type in some groups. The fusion of articulated parameres also occurs in *Creophilus*, *Clambus* and a few Cucujoidea.

315. Paired accessory lobes on parameral plate or apicale

1. absent.

2. articulated (Fig. 57H).

3. fixed.

Articulated accessory lobes on the apicale (S2) occur in the exemplar genera *Boros*, *Pytho*, *Trictenotoma*, *Morpholycus, Euryplatus* and *Salpingus*, but they are also found in some other groups of Tenebrionoidea and may be present or absent within the family Aderidae. The apicale in *Orchesia* is unique in being trilobed, with the lateral lobes fixed (S3).

316. Phallobase

1. symmetrical.

2. asymmetrical (Fig. 58H).

317. Anterior edge of phallobase or tegmen

1. without struts (Fig. 58B).

2. with single strut (Fig. 56K).

3. with paired lateral struts.

4. with single strut and opposing paired struts (Fig. 59A).

5. with slender strut and opposing broad strut.

The single tegminal strut (S2) is sometimes called a manubrium. Paired struts (S3) occurs only in the bostrichoid genus *Apatides* and the cucujoid genus *Propalticus*, and S5 only in the Phalacridae. S4 refers to the “double tegmen” described by Crowson (1964) for certain Cleroidea, but a very similar condition occurs in the cucujoid families Biphyllidae and Byturidae.

318. Anterior edge of phallobase or tegmen

1. not or only slightly emarginate.

2. with deep emargination.

319. Penis

1. not divided into dorsal and ventral lobes (Figs 57C, 58H).

2. divided into smaller dorsal lobe (tectum) and larger ventral lobe (pedon) (Fig. 56H).

3. divided into longer dorsal lobe and short ventral lobe (trigonium) (Fig. 59D).

4. divided into long slender dorsal lobe and equally long, broader ventral lobe.

5. divided into short, broad dorsal lobe and longitudinally divided ventral lobe (Fig. 55F).

6. divided into longer dorsal lobe and slightly shorter, slender and acute ventral lobe.

Division of the penis into a smaller tectum and larger pedon (S2), is characteristic of basal Phytophaga, but the penis is further modified in a number of derived groups in both Chrysomeloidea and Curculionoidea. The occurrence of a short ventral lobe or trigonium (S3) is characteristic of Dascillidae, Psephenidae and Cneoglossidae and occurs in some Scirtidae and Buprestidae. State 5 appears to be restricted to *Pleocoma*, although Crowson (1971) noted the resemblance of this type of penis to that of Dascillidae. S4 and S6 occur in scattered taxa. The character is probably not very informative, except within the Chrysomeloidea and Curculionoidea.

320. Penis

1. not divided into basal and apical sections.

2. divided into basal and apical sections (Fig. 58I).

The division of the penis into well-defined basal and apical sections occurs in several groups of Cucujoidea (e.g., Priasilphidae and Agapythidae), but was also noted in the chrysomelid genus *Neochlamisus* among the exemplars and characterizes most members of the chrysomelid subfamily Eumolpinae.

321. Penis

1. well sclerotized.

2. basally sclerotized and apically membranous (except for endophallic structures).

3. more or less membranous except for paired longitudinal baculi.

4. entirely membranous (except for endophallic structures).

322. Anterior edge of penis

1. without struts (Fig. 56J).

2. with paired struts (Figs 57C, 58H).

3. with single strut (Fig. 56I).

323. Endophallus

1. entirely membranous.

2. with sclerotized endophallic armature (Figs 56I, 56J).

324. Ejaculatory duct

1. without sperm pump.

2. with sperm pump.

Female

325. Tergite VIII in female

1. undivided (Fig. 60E).

2. partly divided (with apical cleft).

3. divided into two lateral sclerites by median line or suture (Fig. 60B).

4. divided into two lateral sclerites by strip of membrane.

326. Sternite VIII in female

1. not divided into two parts.

2. divided into two parts (Figs 60C, 60G).

The complete division of sternite VIII into two parts occurs in Adephaga and in Myxophaga, excluding *Sphaerius* and *Hydroscapha*. The two halves of sternite VIII are referred to as coxosternites by most Adephaga specialists, but Deuve (1988) considered them to be laterotergites of segment VIII (according to Deuve the sternal plate is lacking in segments VIII and IX in the ground-plan of pterygote insects).

327. Anterior edge of sternite VIII in female

1. without median strut.

2. with fixed median strut (spiculum ventrale), usually forked at base (Fig. 59C).

3. with articulated median strut (spiculum ventrale) never forked at base (Fig. 59E).

328. Spiculum ventrale

1. elongate and slender (Fig. 59E).

2. short and truncate or apically forked.

329. Anterior edge of sternite VIII in female

1. without lateral struts.

2. with paired lateral struts (Figs 59C, 60B, 60D, 60G).

Ovipositor

The ovipositor is composed of segments IX and X, although the latter is variously reduced in some groups. There have been several sets of terms used for the ovipositor in beetles. The terminology used here is that given in Lawrence *et al.* (2010a) and based partly on Tanner (1927), but also on papers by Mikoleit (1973), Bils (1976), Burmeister (1976, 1980, 1990), Liebherr and Will (1998) and Miller (2001), which differ in detail but consider the main portion of the beetle ovipositor to consist of limb-based gonocoxites and gonostyli attached to ventrolateral extensions of laterotergites IX, which, in turn, usually lie on either side of tergite X; sternite IX is considered to be either absent or represented by a ventral linear sclerite lying between the laterotergites. Another commonly used system of terms for the beetle ovipositor is based on the concept of Snodgrass (1935) and followed by Lindroth and Palmen (1970) and Matsuda (1976) that the appendage-based ovipositor of other insect groups has become completely lost in Coleoptera. The structures referred to here as gonocoxites are called hemisternites and are considered to have been secondarily derived from sternite IX. This term has been used in recent years in works dealing with Lucanidae (Holloway 1960, 2007) and Curculionoidea (Holloway 1982; Kuschel 1989, Zimmerman 1994).

We consider tergite X (proctiger) to be present in many groups of beetles, where it lies immediately above and anterior to the anal opening; however it is sometimes completely membranous or mainly membranous but reinforced by paired longitudinal struts or baculi. Tergite IX is complete in a small number of taxa (see below), but usually divided into paired laterotergites or paraprocts, which may extend ventrally to form the base of the ovipositor. The paraprocts are often supported by longitudinal baculi, each of which may articulate with a horizontal or oblique baculum on the proximal lobe of the gonocoxa. This articulation is an important landmark which articulates with laterotergite IX in a number of other insect orders, suggesting that the proximal lobe of the coxite (or base of an undivided coxite) is homologous to the gonangulum described by Scudder (1961, 1971). This proximal coxital lobe has been referred to as a valvifer by Tanner (1927) and Crowson (1981). The distal coxital lobe is usually more slender and often has a gonostylus attached at or near its apex.

In some ovipositors, the paraprocts are located laterad and slightly dorsad of the coxites and the entire ovipositor is short and broad, but in a number of beetle lineages the ovipositor has become very long and narrow, mainly by the elongation of the paraprocts and usually the proctiger, which lies in between them. In other groups the coxites have become heavily sclerotized with the styli reduced (sometimes represented by a tuft of setae only) or lost altogether. In a few groups the entire apparatus becomes highly reduced and membranous.

330. Tergite IX in female

1. not divided into two parts, articulating apically with tergite X (Fig. 55E).
2. completely divided into two parts (paraprocts) which lie on either side of tergite X (Figs 34B, 55D, 60B, 60E).

331. Tergite X (proctiger) in female

1. more or less evenly sclerotized, without paired longitudinal baculi (Figs 55D, 55E, 60B, 60E).
2. sclerotized laterally with broad mesal membranous strip.
3. membranous to moderately sclerotized with paired longitudinal baculi (Fig. 34B).
4. membranous and apparently absent.

The female proctiger, sometimes referred to as the epiproct (McHugh *et al.* 1998), is considered here to be homologous to Tergite X.

332. Ovipositor

1. present, at least coxites well defined (Fig. 34B).
2. absent, segments IX and X membranous.
3. absent but segments IX and X well developed.

Almost all Coleoptera have some type of ovipositor, although it may consist of short coxites only. The entire abdominal apex has become membranous in Heteroceridae, Oxypeltidae and platypodine Curculionidae. In the outgroups *Panorpa* and *Eoxenos* and in the larviform females of Phengodidae, the ovipositor is lacking but apical abdominal segments are complete, while in the larviform *Rhagophthalmus* female (Fig. 54A) a short ovipositor with styli is present, but segments IX and X are well developed.

333. Ovipositor

1. shorter than wide Figs 60C, 60G).
2. less than 2 times as long as wide.
3. at least 2 times as long as wide (Figs. 59B, 59G, 59H).

334. Paraproct

1. shorter than gonocoxite (Figs. 60B, 60G).
2. not more than 1.5 times as long as gonocoxite.
3. more than 1.5 times as long as gonocoxite (Figs 59B, 59F, 59G, 59H).

335. Paraprocts

1. without baculi (Fig. 55D).
2. with baculi (Figs 59B, 59F).

Baculi are longitudinal struts usually located at the ventral edges of the paraprocts in elongate ovipositors.

336. Gonocoxites

1. glabrous or with few setae only.
2. distinctly setose (Fig. 60G).

337. Gonocoxites

1. undivided (Fig. 59J, 60C, 60G).
2. divided into proximal and distal lobes.
3. divided into three or more lobes (Fig. 59B).

The proximal or basal lobe of the gonocoxite is often called the valvifer, but is probably homologous to the gonangulum, since it is usually articulates with the paraproct or laterotergite IX.

338. Gonocoxites

1. separated from paraprocts (Figs 59B, 59F).
2. at least partly fused to paraprocts.

This is often impossible to determine in highly derived ovipositors with membranous paraprocts.

339. Gonocoxites

1. without baculi.
2. with paired transverse or oblique basal baculi (Figs 59B, 59F).
3. with paired longitudinal baculi.
4. with paired oblique and longitudinal baculi.

This is the basal baculum, which usually articulates with the paraproctal baculum, suggesting that the base of the coxite or basal coxital lobe is homologous to the gonangulum. In *Languria*, the entire basal lobe is sclerotized and pigmented, but it still articulates with the paraproctal baculum.

340. Base of gonocoxite

1. situated mesad or ventrad of paraproct (Figs 55D, 60B, 60G).
2. situated distad of paraproct (Figs 34B, 59B, 59F, 59H).

341. Distal portion of gonocoxite

1. not more heavily sclerotized than proximal portion.
2. more heavily sclerotized than proximal portion.

342. Gonostyli

1. moderately to well developed and palpiform (Figs 34B, 55D, 59B, 59F).
2. highly reduced and palpiform.
3. highly reduced and button-like.
4. reduced to patch of setae or absent (Figs 59H, 59J, 60C, 60F, 60G).

343. Gonostyli

1. attached apically (Fig. 34B).

2. attached subapically (Fig. 55D, 59F).

344. Rectum

1. without six cuticular rings.

2. with six cuticular rings (Fig. 35F).

This has been seen in some Scirtoidea only, but it may occur elsewhere, since the rectum is sometimes lost in dissection.

Larva

345. Larva: body (as viewed from above)

1. elongate and not widest at middle.

2. oblong to broadly ovate, widest at middle (Figs 72D, 72E).

346. Larva: body in cross-section

1. not strongly flattened.

2. strongly flattened.

347. Larva: body as viewed from side

1.not or only slightly curved ventrally (Figs 72A–C, 72E).

2. strongly curved ventrally (Figs 67B, 73G).

348. Larva: most abdominal terga

1. not or only slightly extending laterally beyond sterna.

2. extending laterally well beyond sterna (Fig. 64D).

349. Larva: dorsal vestiture

1. without modified setae.

2. with pubescent setae (more or less irregularly lined with fine, hair-like microtrichia) (Fig. 31D).

3. with spicisetae sometimes combined with hastisetae.

4. with apically expanded, frayed or subdivided setae.

5. with flattened or scale-like setae (Fig. 67E).

350. Larva: head

1. not or only slightly declined (prognathous) (Figs 72A, 72C).

2. moderately to strongly declined (hypognathous) (Figs 67B, 72E).

3. distinctly elevated (hyperprognathous) (Fig. 64E).

The hyperprognathous head (S3) characterizes various predaceous larvae, such as those of Carabidae, Hydrophilidae, Histeridae, Brachypsectridae and Drilidae.

351. Larva: head

1. protracted or slightly retracted (Figs 66F, 67B).

2. strongly retracted (Figs 64A, 66E) .

352. Larva: head

1. not concealed from above by prothorax.

2. concealed from above by prothorax.

353. Larva: posterior edge of head capsule at middle (as seen from above)

1. not or shallowly emarginate.

2. moderately to deeply emarginate (Figs 61F, 64I, 73B).

354. Larva: dorsal surface of head capsule

1. without serrate, scale-like cuticular modifications.

2. with serrate, scale-like cuticular modifications.

S2 occurs in Torricincolidae, *Sphaerius* and *Hydroscapha*.

355. Larva: epicranial stem

1. absent (Figs 61A, 61B, 61F, 73B).

2. not more than 0.33 times as long as greatest head width (Fig. 64H).

3. more than 0.33 times as long as greatest head width (Figs 63A, 65A).

This is the median ecdysial line, which forks to form the two frontal arms. In some cases there is no stem on the head and the two arms appear to arise from one or two points at the posterior edge of the head.

356. Larva: frontal arms

1. lyriform (Fig. 61B).

2. V-shaped or U-shaped (Figs 61A, 63A, 65A, 69E, 83B).

3. absent.

Frontal arms are paired ecdysial lines sometimes referred to as frontal lines or frontal sutures. The epicranial stem and frontal arms combined are sometimes called the epicranial suture.

357. Larva: bases of frontal arms

1. contiguous (Figs 65A, 69E, 73E).

2. distinctly separated (Fig. 83B).

It is likely that the ecdysial lines on the head meet at some point in the cervical region where they connect up with the median ecdysial line on the pronotum. In S2 heads they are well separated at the base of the head but abruptly curve mesally and meet just behind the head.

358. Larva: dorsal endocarina on head

1. absent (Fig. 73E).

2. single, lying beneath epicranial stem only.

3. single, extending anteriorly between frontal arms (Fig. 69E).

4. single, epicranial suture not evident (Fig. 64I).

5. double, lying beneath frontal arms (at least basally) (Fig. 61F).

6. double, not connected with frontal arms.

7. Y-shaped, lying beneath epicranial stem and frontal arms.

8. Y-shaped, lying between frontal arms.

9. Y-shaped, ecdysial lines not evident.

10. V-shaped, ecdysial lines not evident.

The word "beneath" here refers to the internal surface of the head capsule, not ventral direction. Externally the endocarina is usually seen as a slight thickening of the ecdysial line; in a cleared head it may be "felt" with a micropin.

359. Larva: dorsal endocarina on head

1. ending well before clypeus (Fig. 69E).

2. extending to clypeus or almost so (Fig. 64I).

A long endocarina approaching or meeting the clypeus occurs in Cupedidae and some members of the Buprestidae, Cleroidea and Chrysomeloidea.

360. Larva: number of stemmata on each side

1. more than 20.
2. seven.
3. six (Figs 65H, 66D, 71G, 72E).
4. five (Fig. 66F).
5. four.
6. three.
7. two.
8. one (Figs 66E, 83C).
9. none.

Stemmata, as used here, includes those structures without distinct lenses (eye spots).

361. Larva: multiple stemmata on each side

1. well separated (Figs 65H, 72E).
2. forming two tight clusters.
3. forming single tight cluster (Fig. 72A).
4. forming tight cluster beneath single lens.

Inapplicable when C360 = S8 or S9.

362. Larva: multiple stemmata

1. not located on single lateral projection.
2. located on single lateral projection.

Inapplicable when C360 = S8 or S9. S2 occurs in Torridincolidae and Priasilphidae.

363. Larva: frontoclypeal suture

1. absent, incomplete or vaguely indicated without internal epistomal ridge (Fig. 61B).
2. complete and more or less distinct with internal epistomal ridge (Figs 74A, 77D).

In a number of larvae, the anterior part of the frontoclypeal region may be hyaline, forming a distinctly demarcated region possibly homologous to the anteclypeus in adults. The line of demarcation between the sclerotized and hyaline portions of the clypeus is sometimes misinterpreted as a frontoclypeal suture.

364. Larva: labrum

1. separated from head capsule by complete suture (Figs 61B, 83B).
2. partly fused to head capsule, suture incomplete (Fig. 73E).
3. completely fused to head capsule, suture absent (Figs 61H, 63F, 68B, 85C, 74F).

Partial fusion of the labrum to the head capsule (S2) occurs in *Necrophila* (Silphidae), *Nycteus* (Eucinetidae) and Dascillidae and has evolved five or six times in Cucujoidea. Complete fusion characterizes the Adephaga, Hydrophiloidea, some Staphylinidae (including Scydmaeninae and *Creophilus*) and most Elateroidea, and also occurs in two outgroups, the *Priacma* first instar, *Hydroscapha*, *Cyphon*, *Sandalus*, *Nosodendron*, several families of Cucujoidea, the tenebrionoid genera *Rhipidioides* and *Ischalia*, and the chrysomeloid groups Oxypeltidae and Palophaginae (Megalopodidae).

365. Larva: labral tormae

1. present (Fig. 63A, 65G).
2. absent.

Tormae differ from epipharyngeal rods (C367) in extending posteriorly from the posterolateral portions of the labrum.

366. Larva: labrum or clypeolabrum

1. symmetrical.
2. asymmetrical (Fig. 73E).

367. Larva: paired epipharyngeal rods

1. absent.
2. present (Fig. 62M).

Epipharyngeal rods, often called labral rods, are longitudinal, subparallel sclerites lying on either side of the midline and not attached to the posterolateral corners of the labrum. They characterize the larvae of a number of Curculionoidea, but are also found in Endecatomidae, some Dermestidae and *Eustrophopsis* in the tenebrionoid family Tetratomidae.

368. Larva: nasale

1. absent.
2. consisting of single, simple lobe (Figs 61H, 74F).
3. consisting of bidentate or tridentate lobe.
4. consisting of multidentate lobe or several lobes or teeth.

The nasale is sometimes used as a synonym of clypeolabrum, but as used here it is a distinct anterior mesal projection of the clypeolabrum, sometimes subdivided to form two to several teeth.

369. Larva: paranasal lobes

1. absent.
2. present (Fig. 61H).

Paranasal lobes usually refer to anterior projections lying on either side of the nasale, but the term could apply to any paramedian lobes on the frons, clypeus or frontoclypeus.

370. Larva: number of antennomeres

1. more than five.
2. five.
3. four (Figs 64H, 74F).
4. three (Figs 76B, 77D).
5. two (Figs 64F, 66E).
6. one (Figs 75D, 77E).
7. none.

The usual number of antennomeres in larval beetles is three (S4). Four-segmented antennae (S3) occur in three outgroups, Ommatidae, most Cupedidae, all Adephaga, a few staphylinoids and several scarabaeoids, while five antennomeres (S2) are known only in *Aphodius* (plus in at least some larvae of *Distocupes* Neboiss). S1 occurs only in larvae of Scirtidae and is normally considered to be a highly derived or autapomorphic feature. The possibility exists, however, that this type of larval antenna has been retained from a pre-coleopteran ancestor with multi-annulate antennae. Reduction in the number of antennomeres to two or one occurs in various groups, including first-instar *Priacma* (later instars are unknown), all Myxophaga, and scattered polyphagan taxa. Only the outgroup *Eoxenos* lacks larval antennae.

371. Larva: antenna

1. less than 0.2 times as long as greatest head width (Fig. 76A).
2. 0.2 to 0.5 times as long as greatest head width (Figs 73B, 73E).
3. more than 0.5 times greatest head width.

372. Larva: antennal sockets

1. located on surface, slightly raised or slightly retracted.
2. located beneath frontal ridges.
3. located within deep cavities.

S2 occurs in a few members of both Adephaga and Polyphaga, while S3 is known only in Eucnemidae and a few Phytophaga.

373. Larva: antennal socket separated from mandibular articulation

1. by membrane or strip of cuticle less than 0.5 diameter of socket.
2. by strip of cuticle between 0.5 and 1.5 times diameter of socket.
3. by strip of cuticle more than 1.5 times diameter of socket (Fig. 85A).

374. Larva: antennal sensorium

1. located on preapical antennomere or antennomere preceding multi-annulate flabellum (Fig. 76B).
2. located on apical antennomere (Fig. 66E).
3. absent.

The antennal sensorium is a large sensillum or complex of sensilla normally located on the preapical antennomere of beetle larvae; it has also been called sensory appendage or sensory appendix. The sensorium may be located on the apical antennomere (S2) in those antennae which have lost the true apical antennomere and are thus 2-segmented or which have lost the apical and basal antennomeres and are 1-segmented.

375. Larva: antennal sensorium on preapical antennomere located

1. anterad or mesad of apical antennomere (Fig. 61H).
2. posterad or laterad of apical antennomere (Fig. 63A).
3. dorsad of apical antennomere.
4. ventrad of apical antennomere (Figs 61F, 76B).

376. Larva: antennal sensorium

1. less than 0.5 times as long as apical antennomere (Figs 62F, 63A).
2. 0.5 to 1.0 times as long as apical antennomere (Figs 61B, 61F).
3. longer than apical antennomere.

377. Larva: shape of antennal sensorium

1. conical, palpiform or acorn-shaped (Figs 61A, 61B, 61F, 76B).
2. setiform (with narrowly acute apex).
3. dome-like or C-shaped (Figs 66E, 74F).
4. complex (consisting of two or more elements) (Fig. 62G).

378. Larva: sensorium on preapical antennomere

1. arising at same level as apical antennomere.
2. arising well basad of apical antennomere (Fig. 64J).

Larval mandibles

The mandibles constitute an important suite of characters for both identification and phylogenetic analysis, but terminology has varied and homologies are often uncertain. When a basal processing area or mola is present, the major features are somewhat clear cut, with the prostheca lying just distad of the mola and the incisor edge between the mola and the mandibular apex. When the basal mola is absent, however, the mesal edge of the mandibular base may have one or more structures of uncertain homology. In this work (as in Lawrence 1991, Lawrence & Britton 1991 or Lawrence *et al*. 1999a) a prostheca is defined as a structure accompanying the basal mola. Sometimes, basomesal projections of the mandible may represent a reduced mola (as is probably the case in some Coccinellidae), but often they appear to be either unique features or possibly relicts of early mandibular appendages. **Note** that C391–C394 below all refer to basal mandibular features which only occur in the absence of a mola.

379. Larva: mandibles

1. not endognathous.
2. endognathous.

380. Larva: mandible

1. not more than 2.5 times as long as basal width (Figs 80H, 80I, 81A).
2. more than 2.5 times as long as basal width (Figs 81H, 84C).

381. Larva: mandible

1. not consisting of pair of longitudinal blades of dual origin.
2. consisting of pair of longitudinal blades, one of which is of clypeal origin (Fig. 65E, 66E).

This is an autapomorphy of the family Lycidae (*Dictyoptera* and *Lycus*).

382. Larva: mandibles

1. opposable, at least slightly curving mesally at apex and meeting or crossing when closed (Figs 77A, 77B, 82G).

2. non-opposable, straight or curving laterally at apex (Figs 65E, 73F).

383. Larva: mandible

1. without groove or perforation.

2. with open or partly closed groove.

3. with internal perforation, open only at base and apex (Figs 74B, 81H, 84C).

The bipartite mandible of Lycidae is coded as having an open groove. Internally perforate mandibles occur in several adephagan taxa, as well as in the elateroid families Brachypsectridae, Drilidae, Phengodidae, Rhagophthalmidae and Lampyridae.

384. Larva: mandible

1. without accessory ventral process.

2. with accessory ventral process (Figs 78F, 80G–I).

The accessory ventral process, sometimes referred to as an accessory ventral condyle or ventral crushing tubercle, is located on the ventral surface of the mandibular base somewhat laterad of the mesal edge; it is usually rounded and projects mesally. It occurs in *Hydroscapha*, most Scarabaeoidea and Scirtoidea, Dascillidae, Derodontidae, *Nosodendron*, *Orphilus*, and a number of Cucujoidea.

385. Larva: mandibular apex

1. not subdivided (Figs 75C, 79C, 85C).

2. bidentate or bilobed (Figs 76A, 77E, 80E).

3. tridentate or trilobed (at least on one mandible) (Figs 75B, 75D, 75E, 82F).

4. multidentate or multilobed (Figs 77C, 77F, 79A, 82A).

386. Larva: mandibular apex in apical view

1. narrow, orientation of single apical lobe or placement of multiple lobes or teeth parallel to or oblique to plane of movement of mandible (Figs 74B, 75A, 77E, 85C).

2. broad, orientation of single apical lobe or placement of multiple apical lobes perpendicular to plane of movement of mandible (Figs 75B, 75E, 82F).

387. Larva: incisor edge of mandible (mesal edge basad of apical teeth or lobes)

1. without subapical teeth, serrations or lobes (Figs 62C, 79A).

2. with articulated, complex subapical lobe (Figs 78I, 81D, 82D).

3. with fixed, simple subapical tooth or retinaculum (Figs 62B, 62N, 64H).

4. with fixed, bifurcate or complex retinaculum (Fig. 76C).

5. with two or more subapical teeth, serrations or retinacula (Figs 78A, 78F, 79H, 80G, 81E, 82B).

The incisor edge is the cutting edge of the mandible, lying between the apex and the prostheca, the mola or other basal or sub-basal armature. The articulated, complex subapical lobe (S2) is located just proximad of the apex; it may be attached to the membranous prostheca and was considered to be part of the prostheca by Beutel *et al.* (1999). S3 refers to a variety of more or less acute, fixed processes, from the large retinaculum of mandibles which lack a basal mola (e.g., many Adephaga, Staphyliniformia, Scarabaeiformia, Elateroidea or Cleroidea) to small subapical teeth in mandibles often having a basal mola, while S4 is a specific type of large retinaculum with two lobes (also occurring in scattered groups).

388. Larva: mesal surface of mandibular base

1. with well developed, basal mola (Figs 74A, 78E, 80D, 80E, 81F, 82E).

2. with reduced, basal or sub-basal mola (Figs 78B, 78G, 79F, 79H, 80C, 80F).

3. without mola (Figs 77F, 79A, 82C).

The sub-basal mola (S2) often represents a reduced basal mola, but in some cases it may represent a newly formed feature.

389. Larva: mandibular molae

1. symmetrical (Figs 77A, 82H).

2. asymmetrical (Figs 81B, 81C, 82F, 82G).

Asymmetrical larval molae (S2) are characteristic of many Tenebrionoidea and Scarabaeoidea.

390. Larva: mesal surface of mandibular base

1. without brush of hairs.

2. with brush of hairs (Figs 78D, 79D, 81H).

A basal brush of hairs may occur with or without a basal mola.

391. Larva: mesal surface of mandibular base

1. without fixed, rigid, hyaline process.

2. with fixed, rigid, simple, hyaline process (occasionally on one mandible only).

3. with fixed, subdivided or complex hyaline process (lacinia mobilis) (Fig. 62D).

4. with fixed, rigid, simple hyaline process and apically complex hyaline process.

The features indicated here, as well as those in C392, C393 and C394, occur in place of, rather than in addition to, a mola. S2 is usually a narrow, acute hyaline process similar to the prostheca, which accompanies the mola in a number of taxa (see C395, C397). S3 refers to a fixed hyaline process which is apically subdivided or complex, as opposed to several simple hyaline processes joined only at the base (see C392); both types are found in Cleroidea but occur elsewhere as well. The combination of simple and complex hyaline processes (S4) occurs only in the cucujoid genera *Taphropiestes* and *Myrabolia*.

392. Larva: mesal surface of mandibular base
1. without two to five hyaline processes.
2. with two to five hyaline processes, sometimes joined at base (Fig. 82C).
3. with two to five hyaline processes associated with a sclerotized tooth (Fig. 62A).

393. Larva: mesal surface of mandibular base
1. without membranous lobe.
2. with membranous lobe (Figs 79B, 79E).

394. Larva: mesal surface of mandibular base
1. without articulated process.
2. with articulated process (Figs 62O, 81G).

395. Larva: mandibular mola
1. accompanied by distal prostheca (Figs 62C, 77A, 80B, 80G–I, 81F).
2. not accompanied by distal prostheca (Figs 74A, 78C, 78G, 80D, 81A, 81B, 81C, 82G).

396. Larva: mandibular mola
1. without sub-basal lobe.
2. with sub-basal lobe (Figs. 62P, 78B, 80F).

397. Larva: mandibular prostheca
1. a rigid, hyaline process with acute apex (Figs 77A, 80B).
2. a rigid, hyaline process with obtusely angulate apex (Figs 62C, 80A).
3. two rigid, hyaline processes.
4. a broad, membranous lobe, usually setose.
5. a bifid, serrate or multidentate process (Fig. 80G).
6. a group of two or more simple or complex hairs (Figs 79G, 80H).
7. a group of fringed membranes (Fig. 77B).
8. a rigid, acute process accompanied by brush of hairs (Fig. 74C).
9. an articulated process and transparent spot (Fig. 78F).

The apically acute prostheca (S1) occurs in a number of cucujoid families, but also in Clambidae, several staphylinoid groups and the outgroup *Panorpa*. S2 occurs in Derodontidae as well as in Erotylidae and a few other cucujoid families. S3 appears to be an autapomorphy of the *Clypastraea* larva, and S4 (membranous lobe) occurs in Myxophaga, but also in *Orphilus*, *Endecatomus*, lyctine and dinoderine Bostrichidae, and the endomychid genus *Epipochus*. The bifid, serrate or multidentate prostheca (S5) is known in Hydraenidae and Cryptophagidae. A group of simple or complex hairs (S6), including both comb-hairs and forked hairs characterizes *Xerasia*, Nosodendridae and Biphyllidae. Fringed membranes (S7) characterize Nitidulidae, and an acute process accompanied by a brush of hairs (S8) may be found in larvae of *Necrophilus*, Eucinetidae and Clambidae. The articulated process accompanied by a transparent area (S9) characterizes the larval mandible of Dascillidae.

Larval ventral mouthparts

The ventral mouthparts include the paired maxillae and the labium, which are often closely associated forming the maxillolabial complex and may be retracted so that they lie in an emargination usually referred to as the hypostomal cavity or sinus.

398. Larva: ventral mouthparts
1. not retracted (articulations of mandibles and maxillae at same level) (Figs 61C, 61E).
2. slightly retracted (distance between mandibular and maxillary articulations less than 0.5 times mid width of stipes).
3. moderately retracted to deeply retracted (distance between mandibular and maxillary articulations at least 0.5 times mid width of stipes) (Figs 61D, 61I, 73C).

In most beetle larvae the ventral mouthparts are at least slightly retracted, with the maxillary articulations lying well behind the mandibular articulations. Non-retracted ventral mouthparts with the mandibular and maxillary attachments at the same level (S1) are characteristic of Adephaga and Hydrophiloidea, but also occur in three of the outgroups, in some Buprestidae, in a number of cucujoid families and in Meloidae.

399. Larva: maxillae and labium
1. completely separated at base or joined by maxillary articulating area (Figs 62K, 63B, 77C, 83A).
2. joined together to form maxillolabial complex but separated by complete sutures (Figs 68G, 76E, 76F).
3. joined together to form maxillolabial complex, with maxillolabial sutures incomplete (Fig. 74B).
4. joined together to form solid maxillolabial complex, maxillolabial sutures absent (Fig. 75B).

The consolidation of the maxillolabial complex by the partial or complete fusion of various elements has occurred several times in Coleoptera. S1 occurs not only in larvae with protracted mouthparts and completely separated maxillae and labium, but also in those with retracted mouthparts where the maxillae are relatively freely movable but each is joined at base to the labium by a more or less membranous articulating area. S2 represents a step in the consolidation of the maxillae and labium where the two elements are in close association but separated by complete sutures; it occurs in several outgroups, in Haliplidae and rhysodine Carabidae among the Adephaga and in a number of Elateriformia and Cucujiformia. S3 occurs in *Agrilus* (Buprestidae), Brachypsectridae, Eucnemidae, and the genera *Dictyoptera* (Lycidae), *Phalacrinus* (Phalacridae) and *Tetraopes* (Cerambycidae). Complete fusion to form a solid maxillolabial complex

(S4) occurs in Elmidae, Chelonariidae, *Lycus* (Lycidae) and *Rodolia* (Coccinellidae).

400. Larva: cardo
1. separated by suture from stipes.
2. completely fused to stipes.

401. Larva: cardo
1. undivided (sometimes with internal ridge)
2. externally divided into two or occasionally three parts.

402. Larva: cardo
1. transverse or slightly oblique (Fig. 61C).
2. strongly oblique or longitudinal (Fig. 73C).

Rotation of the cardines, so that they come to be almost longitudinally oriented (S2) occurs in several groups, but is particularly noticeable in larvae of Elateroidea and those of the cucujoid family Nitidulidae.

403. Larva: cardines
1. well separated from each other by labium.
2. closely approximate or contiguous (Figs 62E, 75D).
3. completely fused together but separated from stipites and labium.
4. fused together with stipites and labium (Fig. 75B).
5. completely fused with postmentum forming transverse basal sclerite.

404. Larva: stipes (or cardo plus stipes if the two are not separated by suture)
1. shorter than wide.
2. 1 to 2 times as long as wide (Fig. 83A).
3. more than 2 times as long as wide (Fig. 65B).

405. Larva: maxillary articulating area
1. present (Figs 83A, 85D).
2. absent (Fig. 68G).

406. Larva: maxilla
1. with articulated galea and fixed or articulated lacinia (Figs 61I, 62H, 74D, 75E).
2. with articulated galea only (Figs 68G, 74E, 84C).
3. with fixed galea and lacinia (Fig. 76B).
4. with fixed lacinia only.
5. with mala (fusion of galea and lacinia) (Figs 77F, 84B).
6. without apical lobes.

In some instances, a single maxillary lobe can be reasonable identified as galea, lacinia or a fusion of the two (mala) based on location and structure, but in others this is impossible without studying muscle attachments. In this case, the taxon is codes as S5.

407. Larva: maxilla
1. without laciniar spine.
2. with one or more than one laciniar spine.

408. Larva: outer apical angle of galea or mala
1. without complex fringe.
2. with complex fringe (Fig. 6F).

The galeal fringe occurs in both larvae and adults in Jacobsoniidae and in several staphylinoids. Those illustrated here are taken from adults.

409. Larva: apex of galea or mala
1. rounded (Fig. 84A).
2. truncate (Fig. 84F).
3. falcate (Fig. 62L).
4. stylet-like (Fig. 73F).

410. Larva: apex of mala
1. cleft (Fig. 62K).
2. not cleft (Fig. 84A).

411. Larva: apex of mala
1. without pedunculate setae.
2. with one or more pedunculate setae.

A pedunculate seta usually consists of a single seta at the end of an elongate peduncle, but sometimes there may be more than one seta on a single peduncle.

412. Larva: inner apical angle of mala
1. simple.
2. with one or more teeth or stout spines (Figs 62K, 63C, 84F).
3. with discrete lobe or uncus (sometimes subdivided or subapical) (Fig. 84B).

S3 includes the subapical lobe characteristic of most nitidulid larvae.

413. Larva: mala dorsally
1. without subapical accessory lobe.
2. with subapical accessory lobe.

This accessory lobe is located on the dorsal surface of the mala and is not visible ventrally. It is considered here to be a derived feature of the family Ciidae, although it is possible that it represents a laciniar remnant.

414. Larva: number of maxillary palpomeres, excluding palpifer
1. three or four (Figs 61G, 62L).
2. two.
3. one.
4. none.

The basal number of palpomeres in Coleoptera appears to be three, but in numerous taxa the palpifer is articulated and segment-like. Four-segmented maxillary palps are known in *Agulla* among the outgroups and in some Scirtidae.

415. Larva: apical maxillary palpomere
1. without complex tripartite apical sensorium.
2. with complex tripartite apical sensorium.

The tripartite sensorium appears to be a synapomorphy of Hydraenidae + Ptiliidae.

416. Larva: maxillary palpifer
1. segment-like, with inner and outer edges more or less equal, and usually articulated at base (Fig. 61G).

2. shelf-like, with outer side much longer than inner side, and usually fixed at base (Figs 62K, 63B).

3. apparently absent.

417. Larva: galea or mala arising

1. at stipital apex near base of palpifer or palp (Figs 63B, 63C).

2. at or near apex of palpifer (Fig. 61G).

This character has been misinterpreted by various authors, including Lawrence (1991) and Lawrence *et al.* (1999a). The articulated and segment-like palpiger in a number of Adephaga and Elateriformia was considered to be the basal palpomere, and the galea attached to the apex of the palpiger in Sialidae, Trachypachidae and Hydrophiloidea was treated as a neoformation independently evolved in three lineages, along with the disappearance of the true apical maxillary lobes. It now seems apparent to us that the classic interpretations of Böving and Craighead (1931) and Emden (1942) were correct and that the galea in the above taxa has migrated to the apex of the segment-like palpifer.

418. Larva: maxillolabial complex

1. not fused to epicranium.

2. enclosed within hypostomal cavity and solidly fused to epicranium on each side.

In the family Eucnemidae the maxillolabial complex is deeply retracted, as it is in related members of the Elateroidea, but it has lost its mobility and is firmly attached to the head capsule on each side.

419. Larva: labium consisting of

1. prementum, mentum and submentum or gulamentum (Fig. 61D).

2. prementum and postmentum (often fused with gula) (Fig. 62E).

3. single labial plate.

420. Larva: labium

1. without trident-shaped sclerite.

2. with trident-shaped sclerite.

This characteristic ligular sclerite is found in the genus *Car* and in all exemplars of Curculionidae. It also occurs in some Brentidae (e.g., *Tanaos* Schoenherr and *Nanophyes* Schoenherr).

421. Larva: sides of postmentum or mentum

1. not expanded laterally, exposing maxillary bases.

2. expanded laterally and partly or completely concealing maxillary bases (Figs 61D, 76D).

In Scirtidae, Cneoglossidae and some taxa of Psephenidae and Ptilodactylidae, there is a well-developed maxillary articulating area, but this is more or less concealed by a lateral expansion of the postmentum or mentum.

422. Larva: ligula

1. as long as or longer than labial palp.

2. shorter than labial palp but at least as long as basal palpomere (Figs 61D, 62J, 85D).

3. shorter than basal palpomere (Fig. 63B).

4. absent (Fig. 62I).

423. Larva: ligula

1. undivided (Fig. 75A).

2. consisting of two distinct lobes (Figs 73D, 74C).

424. Larva: wedge-shaped ligular sclerome

1. absent.

2. present (Figs 74D, 75D, 77D).

The wedge-shaped ligular sclerome is characteristic of all archostematan larvae but a similar structure also occurs in the polyphagan family Callirhipidae.

425. Larva: ligula

1. without papillae or microvilli.

2. with papillae or microvilli.

426. Larva: number of labial palpomeres (excluding palpiger)

1. three.

2. two.

3. one (Fig. 73C).

4. none or non-articulated remnant only.

427. Larva: labial palpiger

1. well developed and segment-like.

2. reduced and shelf-like.

3. apparently absent.

428. Larva: labial palps separated by

1. less than 1.2 times width of basal palpomere.

2. 1.2 to 3 times width of basal palpomere.

3. more than 3 times width of basal palpomere.

429. Larva: hypopharyngeal sclerome

1. absent.

2. consisting of transverse bar only.

3. consisting of single sclerite shaped like molar tooth (usually irregularly concave) (Figs 62J, 62K, 84A).

4. consisting of more than one sclerite (Fig. 73D).

430. Larva: hypopharyngeal bracon

1. present, forming bridge to head capsule on each side (Fig. 62M).

2. absent.

The hypopharyngeal bracon is a sclerotized but hyaline bridge joining the hypopharynx to the ventral mandibular articulation on each side. It is usually, but not always, present when the ventral mouthparts are strongly retracted and appears to serve as a brace for the labium-hypopharynx.

431. Larva: hypopharyngeal bracon

1. without apodemal plates connected by transverse hypopharyngeal muscle.

2. with pair of mesally directed apodemal plates (muscle discs) connected by transverse hypopharyngeal muscle.

S2 characterizes Agyrtidae and Leiodidae.

432. Larva: oral cavity
1. not blocked.
2. blocked by hairs and/or meeting of cibarial walls (Figs 74E, 75F, 76C).

This refers to a combination of features associated with liquid feeding and extraoral digestion and is not restricted to the presence of a "preoral filter apparatus" discussed by Beutel and Leschen (2005c). S2 occurs in Adephaga, Hydrophilidae, Histeroidea, Scydmaeninae, *Creophilus* and all Elateroidea.

433. Larva: gena
1. without anterior rounded protuberance bearing long seta.
2. with anterior rounded protuberance bearing long seta.

S2 occurs in Hydraenidae, Ptiliidae, Agyrtidae and Leiodidae.

434. Larva: hypostomal rods
1. subparallel or slightly converging.
2. diverging (Fig. 62M).
3. absent (Figs 61D, 65F, 65G).

Hypostomal rods are said to be present only when they extend posterad of maxillary articulations. Their origin is actually at the ventral mandibular articulations, and when the ventral mouthparts are retracted, they may line the sides of the hypostomal cavity; however they cannot be seen unless they extend behind the maxillary articulations.

435. Larva: ventral epicranial ridges
1. absent.
2. present (Figs 76E, 77C, 83A).

Ventral epicranial ridges originate just laterad of the ventral mandibular articulations and extend posteriorly flanking the hypostomal rods or lateral edges of the hypostomal cavity; they are not sclerotized rods but rather the edges of a countersunk housing for the ventral mouthparts or maxillolabial complex.

436. Larva: gular region
1. absent (labium contiguous with cervical membrane) (Figs 64G, 66C).
2. not more than 0.5 times as long as head length as seen from above (Figs 65F, 66D, 66F).
3. more than 0.5 times as long as head length as seen from above (Figs 65B, 67C).

437. Larva: gular sutures
1. separate.
2. partly or completely fused together (Fig. 65B).
3. absent.

438. Larva: median length of gula
1. less than 0.33 times as long as greatest width.
2. 0.33 to 0.99 times as long as greatest width.
3. at least as long as greatest width.

439. Larva: tentorial bridge
1. present (Fig. 62M).
2. absent.

440. Larva: thickness of tentorial bridge at midline
1. less than 0.1 times greatest head width.
2. 0.1 to 0.2 times greatest head width (Fig. 62M).
3. more than 0.2 times greatest head width.

441. Larva: cervical sclerites
1. absent.
2. present (Fig. 67B).

442. Larva: paired dorsal gland openings
1. absent.
2. present on thorax and most abdominal segments (Fig. 72B).
3. present on abdominal segments I to VI or VII (Fig. 67E).
4. present on abdominal segments I and VIII.

443. Larva: prothorax
1. not or only slightly wider than abdomen.
2. much wider than abdomen (Fig. 64A, 64B)

444. Larva: prothorax
1. not longer than mesothorax and metathorax combined.
2. longer than mesothorax and metathorax combined (Figs 64A, 64B).

445. Larva: thoracic terga
1. without long, lateral processes.
2. with long, lateral processes (Fig. 65D).

446. Larva: thoracic terga
1. without patches of asperities.
2. with patches of asperities on one or more terga.

447. Larva: thoracic terga
1. without rows of asperities.
2. with transverse rows of asperities on one or more terga.

448. Larva: tergal ampullae
1. absent.
2. present on some thoracic and abdominal segments (Fig. 69D).
3. present on some abdominal segments only.

449. Larva: protergum
1. without sclerotized plate.
2. with single sclerotized plate.
3. with more than one sclerotized plate.

450. Larva: mesotergum and metatergum
1. without sclerotized plates or with single plate on each.
2. with two or more sclerotized plates on one or both.

451. Larva: prothoracic presternum
1. entire or not clearly delimited (Figs 68F, 68G).
2. divided into two parts by longitudinal suture.
3. divided into three parts by longitudinal sutures.
4. divided into three parts by Y-shaped suture.

452. Larva: prothoracic venter

1. without supporting rods.
2. with paired supporting rods (Fig. 73F).
3. with single median supporting rod (Fig. 64A).

Paired supporting rods (S2) occur in Cerophytidae, Throscidae and in the eucnemid genera *Anischia* and *Melasis*, and a single rod (S3) occurs in Buprestidae (except *Schizopus*) and in *Lamingtonium* and *Cyclaxyra*.

453. Larva: number of segments in mesothoracic leg (including pretarsus)

1. six (Fig. 69B).
2. five (Figs. 64J, 68F, 69F).
3. four.
4. three.
5. two (Fig. 66C, 69G).
6. one.
7. none.

Six-segmented legs (S1) occur in *Agulla*, *Sialis*, *Omma*, *Micromalthus*, Cupedidae and all Adephaga, and those with five segments (S2) occur in Myxophaga and almost all Polyphaga. The number of leg segments is reduced to four (S3) in *Panorpa*, *Sabatinca*, Mantispidae Genus ? and *Eoxenos* among the outgroups, and in *Georissus*, *Euderia*, *Agrianome*, *Phoracantha*, *Crioceris* and *Cephaloleia*. Three-segmented legs (S4) are known in *Cephus*, *Sandalus*, Passandridae, *Palophagus* and *Car* and those with two segments (S5) in *Bolboceras*, *Scarabaeus*, *Mordella*, *Toxonotus*, *Eurhynchus* and *Cylas*. *Anischia* and *Rhynchitomacerinus* have one-segmented legs (S6), and legs are absent (S7) in Buprestidae, *Melasis*, *Onichodon*, *Tetraopes*, *Urodontus*, Belidae, *Merhynchites* and all Curculionidae.

454. Larva: mesocoxae separated by

1. less than shortest basal coxal diameter (Fig. 68F).
2. 1 to 4 times shortest basal coxal diameter.
3. more than 4 times shortest basal coxal diameter.

Inapplicable when C453 = S7.

455. Larva: mesothoracic leg

1. less than 0.25 times as long as greatest width of mesothorax (Fig. 69D).
2. at least 0.25 times as long as greatest width of mesothorax (Figs 67B, 71A, 85D).

Inapplicable when C453 = S7.

456. Larva: vestiture of thoracic legs

1. consisting of fine setae only.
2. including some stout spines or pegs (Fig. 68F).

Inapplicable when C453 = S7.

457. Larva: apical segment of mesothoracic leg

1. acute or subdivided.
2. rounded or truncate.

Inapplicable when C453 = S7. The apex of the mesothoracic leg is rounded or truncate (S2) in *Eoxenos*, *Bolboceras*, *Scarabaeus*, *Cetonia*, *Anischia*, *Mordella*, *Pelecotoma*, *Palophagus*, *Caryedon*, *Rhynchitomacerinus*, *Toxonotus*, *Eurhynchus* and *Cylas*.

458. Larva: mesocoxal stridulatory file

1. absent.
2. present.

Inapplicable when C453 = S7. A stridulatory file is present on the mesocoxa in Pleocoma, Geotrupidae, Lucanidae and Passalidae.

459. Larva: number of movable pretarsal claws

1. two.
2. one.
3. none.

Inapplicable when C453 = S7. Paired tarsal claws (S1) occur in *Agulla*, *Sialis* and Mantispidae Genus ? among the outgroups and in most Archostemata and Adephaga. A single pretarsal claw (S2) occurs in *Cephus*, *Panorpa* and *Sabatinca* among the outgroups, *Priacma* (first instar only known), Myxophaga, Haliplidae, *Arthropterus*, Rhysodinae, *Bembidion*, *Brachinus*, and almost all Polyphaga. Among those larvae with legs, a pretarsal claw is absent (S3) in *Eoxenos*, *Bolboceras*, *Scarabaeus*, *Anischia*, *Mordella*, *Pelecotoma*, *Palophagus*, *Caryedon*, *Rhynchitomacerinus*, *Toxonotus*, *Eurhynchus* and *Cylas*.

460. Larva: pretarsal claw

1. without basal tooth.
2. with basal tooth.

Inapplicable when C453 = S7. A basal pretarsal tooth occurs in *Sabatinca*, *Agulla*, *Satonius*, *Acrotrichis*, and several genera of Coccinellidae and Chrysomelidae.

461. Larva: number of pretarsal setae on single claw

1. three or more.
2. two.
3. one.
4. none.

Inapplicable when C453 = S7. The single pretarsal claw usually bears 2 setae (S2), but three or more setae (S1) occur in *Taurocerastes*, *Lucanus*, *Lichnanthe*, *Cetonia*, Dascillidae and Cantharidae. Reduction to a single seta (S3) occurs in a number of groups, including *Sabatinca*, *Lepicerus*, Torridincolidae, *Hydroscapha*, *Sandalus*, most families in the dryopoid complex, *Derolathrus*, *Ptinus*, all Cleroidea, various cucujoid families including Byturidae, Biphyllidae, Passandridae, Phalacridae, some Nitidulidae, and all members of the cerylonid series, a few tenebrionoids and chrysomeloids and the genus *Car*. Pretarsal setae are absent (S4) in *Cephus*, *Panorpa*, *Sphaerius*, *Arthropterus*, Rhysodinae and scattered polyphagan taxa.

462. Larva: paired pretarsal setae on single claw

1. lying side by side or obliquely situated.
2. lying in row, one distal to the other.

Inapplicable when C453 = S7 or when C461 = S3 or S4.

463. Larva: pretarsal pulvillus

1. absent.
2. present.

Inapplicable when C453 = S7. A pretarsal pulvillus (S2) occurs in the chrysomelid genera *Crioceris*, *Chrysomela* and *Diabrotica*.

464. Larva: metathoracic leg

1. not much shorter than mesothoracic leg.
2. much shorter than mesothoracic leg (Figs 64F, 64G).

Inapplicable when C453 = S7. A shortened metathoracic leg (S2), which acts as a stridulatory plectrum, occurs in *Taurocerastes*, *Geotrupes* and *Passalus*.

465. Larva: length of abdomen without terminal appendages

1. less than 2 times length of thorax (Figs 71B, 72E).
2. at least 2 times length of thorax (Figs 72A, 72C).

466. Larva: lateral abdominal tergal processes

1. absent.
2. present on most segments (Figs 65D, 68C).

467. Larva: abdominal terga

1. without patches of asperities.
2. with patches of asperities on one or more segments (Figs 68D, 73G).

468. Larva: abdominal terga

1. without rows of asperities.
2. with single transverse row of asperities.
3. with incomplete or complete ring of asperities on each side (Fig. 63D).
4. with longitudinal row of asperities on each side.

A single transverse row of tergal asperities (S2) occurs in Rhysodinae, *Sphaerites*, *Stegobium*, *Byturus*, *Murmidius*, *Pristoderus*, *Phellopsis*, *Chalcodrya* and *Diaperis*. Tergal asperities form curved or ring-like rows (S3) in *Hymaea*, *Laemophloeus*, *Hyporhagus* and *Lacconotus*, and longitudinal rows of asperities are found in larvae of *Syntelia* and *Trictenotoma*.

469. Larva: abdominal tergum III

1. without transverse folds.
2. divided by transverse sulcus to form two transverse folds (Fig. 73G).
3. divided by two transverse sulci to form three transverse folds (Fig. 67B).
4. divided by three or more transverse sulci to form four or more transverse folds (Fig. 68A).

470. Larva: long unsegmented lateral abdominal gills

1. absent.
2. present on segments I to IX (Fig. 71A).

S2 occurs only in Gyrinidae.

471. Larva: long segmented lateral abdominal gills

1. absent.
2. present (Fig. 67A).

S2 occurs in Torridincolidae and in the outgroup *Sialis*.

472. Larva: abdominal sterna

1. without patches of asperities.
2. with patches of asperities on one or more segments.

S2 occurs in *Melasis*, *Lamingtonium*, *Cyclaxyra*, *Phellopsis*, *Calopus*, *Trictenotoma* and *Cephaloleia*.

473. Larva: abdominal sterna

1. without rows of asperities.
2. with rows of asperities on one or more segments.

S2 occurs in *Spherties*, *Syntelia*, *Hymaea*, *Laemophloeus* and *Lacconotus*.

474. Larva: paired ventral prolegs

1. absent.
2. present on two to several abdominal segments.

Ventral prolegs are known in the outgroup genus *Panorpa*, in the histerid genus *Bacanius* and in Oedemeridae, but they occur on different segments.

475. Larva: ventral abdominal ambulacral warts

1. absent.
2. present.

Ventral ambulacral warts occur on the larval abdomen of *Omma* and *Tenomerga* among the Archostemata, a few Histeridae (*Hister*) and Zopheridae (*Hyporhagus*), and several groups of Chrysomeloidea.

476. Larva: ventral abdominal gill tufts

1. absent.
2. present (Figs 67C, 72C).

Ventral abdominal gill tufts occur in the larvae of Hygrobiidae, Eulichadidae and Psephenidae (Psepheninae and Eubrianacinae only).

477. Larva: dorsal, balloon-like tracheal gills

1. absent.
2. present (Figs 71B, 72D).

Balloon-like tracheal gills occur on the thorax and abdominal segments I and VIII in *Hydroscapha* and on abdominal segments I–VIII in *Sphaerius*.

478. Larva: tergum VIII

1. without median processes.
2. with posteriorly or posterodorsally projecting median process (Fig. 67C).

S2 occurs in the adephagan families Hygrobiidae, Noteridae, Amphizoidae and Dytiscidae, and in the polyphagan family Nosodendridae. This process almost always bears a pair of spiracles at the apex and serves as a siphon, but these spiracles have apparently been lost in Hygrobiidae in conjunction with the development of ventral gill tufts.

479. Larva: abdominal apex

1. without respiratory chamber.
2. with respiratory chamber (Fig. 85B).

The respiratory chamber is formed from terga VIII and IX and encloses a pair of enlarged spiracles. It is found only in the hydrophilid subfamilies Spercheinae, Sphaeridiinae and Hydrophilinae (excluding *Berosus* Leach), and in the family Scirtidae.

480. Larva: segment IX at midline and excluding appendages

1. less than 0.5 times as long as segment VIII.
2. 0.5 to 1.5 times as long as segment VIII.
3. more than 1.5 times as long as segment VIII (Fig. 65D).

481. Larva: tergum IX

1. not forming articulated plate.
2. forming articulated plate (Figs 65D, 69H, 70B, 70G).

Tergum IX forms an articulated plate in *Brachypsectra*, in the cucujoid genera *Uleiota*, *Cucujus*, *Propalticus* and *Laemophloeus* and in the tenebrionoid genera *Prostomis*, *Lacconotus*, *Hemipeplus*, *Boros*, *Morpholycus*, *Pyrochroa* and *Euryplatus*.

482. Larva: tergum IX

1. entirely dorsal (Figs 63E, 63I, 71A, 71G).
2. extending onto ventral surface or entirely ventral (Figs 69H, 70A, 70C).

S1 is strongly correlated with a dorsally exposed tenth segment (C500) and S2 with the posterior extension of tergum IX to form paired urogomphi (C484) or a median process (C485). Both states are widely distributed throughout the order, but S1 is found in all Adephaga, except for *Peltodytes* and members of the dytiscoid group and also in the highly specialized larvae of *Metrius* and *Arthropterus*. It is common in the Staphyliniformia and Scarabaeiformia.

483. Larva: surface of tergum IX

1. flat or convex.
2. concave, usually surrounded by sharp circular carina or series of teeth.

This modification of tergum IX has occurred independently in a number of beetle groups, probably as a means of preventing a predator from grasping the abdominal apex or blocking the entrance to a burrow. Among our exemplars, it occurs in *Microchaetes*, *Anchycteis*, *Stenocolus*, Artematopodidae, Lymexylidae, *Acalanthis*, *Chaetosoma*, *Sphindocis*, *Sirrhas*, *Trachelostenus*, *Dioedus* and *Leaus*.

484. Larva: paired urogomphi on tergum IX

1. absent (Figs 67E, 72A, 72B, 72E).
2. basally articulated (Figs 64C, 67F).
3. fixed (Figs 70E, 70I).

The term urogomphi refers to a variety of paired processes at or near the posterior edge of tergum IX. They have probably evolved numerous times within the order. Basally articulated and apparently musculated urogomphi may be homologous in Torridincolidae, Hydradephaga and possibly Staphyliniformia, but probably not in Carabidae. Fixed urogomphi are extremely variable and have probably evolved in a number of groups where larvae live in enclosed spaces or dense substrates, where they serve to anchor the hind body so that the larva may quickly move backwards through its burrow. Those in various Elateridae result from the development of a deep posterior emargination in tergum IX, while in many groups they represent a hook-like extrusions of the tergum.

485. Larva: posterior edge of tergum IX

1. without median process.
2. drawn out to form acute, median process.
3. drawn out to form narrowly truncate or bifurcate median process (Figs 83E, 83F).
4. with large, dehiscent, apically rounded process (Fig. 69C).
5. with rounded lobe between urogomphi
6. with single median tooth between urogomphi (Fig. 70I).

Tergum IX is drawn out at the apex to form an acute process (S2) in *Lepicerus* and the elaterid genus *Ampedus*. S3 occurs in the archostematan families Micromalthidae and Cupedidae, as well as in the larva of *Mordella* and the apparent larva of *Rentonium*. The large, dehiscent process (S4) is characteristic of all scraptiine Scraptiidae. S5 occurs in the bothriderid genus *Xylariophilus* and S6 in the trogossitid subfamily Lophocaterinae (including *Eronyxa* and *Grynoma*).

486. Larva: urogomphi

1. not subdivided.
2. subdivided forming two or more segments (Fig. 64C).

Inapplicable when C484 = S1. Subdivided urogomphi (S2) occur in Aspidytidae, *Helophorus*, Histeridae and their relatives and several groups of Staphylinoidea.

487. Larva: urogomphi

1. not bifurcate.
2. bifurcate (Figs 63G, 71F).

Inapplicable when C484 = S1. Bifurcate urogomphi are relatively common, occurring among our exemplars in the elaterid genus *Lissomus*, Lamingtoniidae, the nitidulid genera *Brachypeplus* and *Glischrochilus*, the pythid genus *Ischyomius*, the pyrochroid genus *Pedilus*, and the salpingid genera *Ocholissa* and *Salpingus*.

488. Larva: urogomphi

1. without accessory processes.

2. with accessory processes, teeth or spines (Figs 69A, 70E).

Inapplicable when C484 = S1. Accessory processes on the urogomphi are subapical and either mesal or lateral. Among our exemplars they occur in the carabid genus *Calosoma*, *Derodontus* (Derodontidae), *Thymalus* (Trogossitidae) and a number of cucujoid and tenebrionoid larvae.

489. Larva: urogomphi in dorsal view

1. more or less straight and parallel (Figs 67F, 70B, 70G).

2. more or less straight and diverging (Fig. 70F).

3. straight or bowed with apices converging (Fig. 70A).

Inapplicable when C484 = S1.

490. Larva: urogomphi in lateral view

1. straight or only slightly curved (Fig. 67C).

2. distinctly curved upwards (Figs 63I, 67D).

Inapplicable when C484 = S1. S1 urogomphi include those characteristic of active, surface-dwelling larvae and commonly found in Adephaga, Hydrophilidae, Histeroidea and Staphylinoidea; however a number of other homoplasious projections on tergum IX have also been coded as S1. The S2 type of urogomphi, which curve upwards and may be recurved, usually function to anchor a larva in a burrow or within a relatively closed substrate; they are characteristic of most larvae of Cleroidea, Cucujoidea and Tenebrionoidea.

491. Larva: urogomphi

1. without pregomphi.

2. with one pair of pregomphi (Fig. 71F).

3. with more than one pair of pregomphi (Fig. 69A).

Inapplicable when C484 = S1. Pregomphi are located at or near the base of the main pair of urogomphi and are usually somewhat smaller. The term applies to a second pair of projections (S2), which occur in *Pharaxonotha*, *Rhizophagus*, *Hobartius*, *Cucujus*, *Lamingtonium*, several Nitidulidae, *Teredolaemus*, *Tetratoma* and *Dipsaconia*, but more than two may occur on tergum IX (S3) in *Ericmodes*, *Dacne*, *Pytho* and *Elacatis*.

492. Larva: urogomphi

1. without pit between them.

2. with single pit between them (Fig. 69A).

3. with two pits between them (Fig. 70A, 70B, 70D).

Inapplicable when C484 = S1. A single pit lies between the urogomphi in the phloeostichid genus *Hymaea*, various genera of Zopheridae, and the tenebrionoid genera *Synchroa*, *Calopus*, *Pytho*, *Elacatis*, *Anthicus* and *Anaspis*. Two interurogomphal pits (S3) occur in *Lacconotus*, *Boros* and the pyrochroid genera *Morpholycus*, *Pedilus* and *Pyrochroa*.

493. Larva: sternum IX

1. partly or entirely exposed.

2. completely concealed and apparently absent (Fig. 67F).

Sternum IX is concealed in *Lepicerus*, *Amphizoa*, *Hygrobia*, *Laccophiluls*, *Callirhipis*, Silvanidae, *Olibrus*, *Adelium* and *Statira*.

494. Larva: base of sternum IX

1. simple or finely spiculate.

2. with one asperity on each side (Figs 66B, 67D).

3. with two to six asperities on each side (Fig. 70F).

4. with more than six asperities on each side, usually forming continuous row (Fig. 70C).

The occurrence of two or more asperities at the base of sternum IX is characteristic of the larvae of several groups of Tenebrionoidea. A single pair of asperities (S2) occurs in Synchroidae, *Pedilus* (Pyrochroidae), *Salpingus* (Salpingidae) and *Lagrioida* (Anthicidae) among our exemplars. Two to six asperities on each side (S3) characterizes larvae of *Calopus* (Oedemeridae) and the salpingid genera *Ocholissa* and *Euryplatus*. A continuous basal row of asperities is known in Trictenotomidae, the pythid genera *Ischyomius* and *Pytho*, the pyrochroid genera *Morpholycus* and *Pyrochroa*, and the salpingid genus *Elacatis*.

495. Larva: apex of sternum IX

1. without row of asperities.

2. with transverse row of asperities (Fig. 69H).

S2 occurs only in *Sphindocis* (Ciidae) and in Prostomidae.

496. Larva: sternum IX

1. not U-shaped with horns or teeth.

2. U-shaped with apicolateral horns or teeth (Figs 70A, 70H).

The U-shaped ninth sternum (S2) occurs in larvae of *Anischia* (Eucnemidae) and in the tenebrionoid families Mycteridae and Boridae.

497. Larva: sternum IX

1. not enclosed by sternum VIII.

2. partly to almost completely enclosed by sternum VIII (Fig. 70H).

This refers to the partial enclosure of the sternum laterally, not its concealment (see C493). This condition occurs in *Eubrianax*, *Nosodendron*, *Laemophloeus*, *Aphanocephalus*, Mycteridae, *Boros*, *Morpholycus*, *Pyrochroa* and *Euryplatus*.

498. Larva: segment X

1. not forming ventrally-hinged operculum.

2. forming ventrally-hinged operculum without hooks (Fig. 83D).

3. forming ventrally-hinged operculum bearing pair of hooks (Fig. 66A).

A ventrally-hinged operculum not bearing hooks (S2) occurs in the families Dryopidae and Chelonariidae, while that bearing a pair of hooks (S3) occurs in Hydroscaphidae, Lutrochidae and Elmidae. The non-homologous, dorsally-hinged operculum was not included among the characters, since it is an autapomorphy of the family Callirhipidae.

499. Larva: abdominal apex

1. without paired longitudinally oval lobes or pads separated by groove.
2. with paired, narrow, longitudinally oval lobes or pads separated by groove.
3. with paired, moderately broad, longitudinally oval lobes or pads separated by groove.

S2 refers to a characteristic feature of soft-bodied larvae of most Bostrichoidea (excluding Dermestidae); this slender, longitudinally subdivided structure lies below the anal opening (appearing anterior due to the strong curvature of the abdominal apex). The pads referred to in S3 are broader pads lying on either side of the anus in larvae of Lucanidae.

500. Larva: segment X

1. distinct and visible in dorsal view (Figs 63E, 63I, 71A, 71G).
2. concealed in dorsal view by tergum IX but visible in ventral view (Figs 67E, 69H).
3. completely concealed or more or less fused to sternum IX.

The degree of exposure of segment X from above is considered to be independent of the degree of curvature of the body.

501. Larva: segment X

1. not forming cylindrical or conical, movable pygopod.
2. forming cylindrical or conical, movable pygopod (Fig. 63I).

502. Larva: segment X

1. without paired pygopods or lobes.
2. with pair of cylindrical or conical pygopods which are shorter than wide.
3. with pair of cylindrical or conical pygopods which are at least as long as wide (Fig. 63E).
4. with pair of globular lobes (Figs 83E, 83F).

Elongate pygopods (S3) occur in *Ytu*, *Brachinus*, *Paracardiophorus*, *Paracucujus*, and the tenebrionid genera *Tanylypus*, *Leaus* and *Tribolium*, and globular lobes (S4) in *Micromalthus* and *Tenomerga*.

503. Larva: segment X

1. without osmoregulatory papillae.
2. with several osmoregulatory papillae (Fig. 73A).

These consist of tubular, finger-like protrusions without asperities and are easily distinguished from holdfast organs (C504) and gill-tufts (C508). S2 is known in the exemplar genera *Cyphon*, *Cneoglossa* and *Anchycteis*.

504. Larva: segment X

1. without asperate, eversible holdfast organs.
2. with multitubular, asperate, eversible, holdfast organs (Fig. 65C).
3. with simple, globular or cylindrical, asperate, eversible holdfast organs.

Multitubular holdfast organs (S2) are known in *Panorpa*, the staphylinid genera *Scaphidium* and *Renardia* and in known larvae of Lampyridae, while the simple holdfast organs occur in Agyrtidae and in the leiodid genus *Agyrtodes*. These structures may also serve as grooming organs, especially in Lampyridae, whose larvae often must contend with slime produced by their molluscan prey.

505. Larva: anal region

1. posteriorly or terminally oriented (Figs 63E, 63I).
2. posteroventrally oriented (Figs 67D, 73A).
3. ventrally oriented (Figs 70C, 70H).

The anal region is considered to be posteroventrally or ventrally oriented (S2 and S3) only when tergum IX extends onto the ventral surface. A terminal anal region (S1) may appear posteroventral in larvae which are slightly to strongly curved ventrally, but these will still be coded as having a terminal anus unless tergum IX is produced onto the ventral surface.

506. Larva: anal opening

1. simple, more or less circular.
2. strongly transverse (Fig. 70A)
3. vertical, bordered by lateral lobes.
4. Y-shaped or T-shaped, bordered by three lobes.
5. complex, bordered with more than three lobes (Fig. 66B).

507. Larva: anal hooks not associated with operculum

1. absent.
2. one on each side.
3. two on each side (Fig. 71A).
4. three or more on each side (Fig. 73A).

A tenth segment with one pair of anal hooks not associated with a ventral operculum (S2) occurs in the staphylinoid families Hydraenidae and Ptiliidae and in most Limnichidae, including our exemplar *Byrrhinus*. A pair of hooks on each side of segment X (S3) is characteristic of Gyrinidae, and three or more hooks on each side (S4) occurs in Sphaeriusidae, the byrrhoid families Cneoglossidae and Ptilodactylidae, *Atractocerus* (Lymexylidae) and the tenebrionoid genera *Chalcodrya* (Chalcodryidae) and *Coelus* (Tenebrionidae).

508. Larva: anal gill tufts

1. absent.
2. present (Fig. 66A).

Each gill tuft consists of a number of slender processes. Anal gill tufts occur in our exemplars from the byrrhoid families Lutrochidae and Elmidae, but they are also known in the genus *Hyphalus* (Limnichidae).

Larval spiracles

The larval spiracles, unlike those of the adult, vary considerably in structure. The states described here apply to spiracles on both the thorax (C509) and abdomen (C511), which in the vast majority of larvae are of the same type. In Scirtidae and some Byrrhoidea, thoracic or anterior abdominal spiracles may be reduced, and in a very few cucujiform larvae, the thoracic spiracles may be annular-biforous, whiled the abdominal ones are annular. The annular spiracles (S1) may vary in shape from circular to narrowly elongate, but the perimeter or peritreme lacks accessory openings of any kind. In some cases the peritreme may be somewhat crenulate. S2 and S3 spiracles have one or two adjacent accessory openings respectively, and S4 spiracles have several to many accessory openings distributed around the peritreme. The biforous or bilabiate spiracle (S5) has paired openings similar to those in S3, but these two openings replace, rather than supplement, the original opening, which collapses and becomes scar-like after the old spiracular lining and trachea are withdrawn during ecdysis. In a cribriform spiracle (S6) a sieve plate replaces the old spiracular opening and a spiracular scar is also present (see C512). The annular-cribriform spiracle (S7) is a term coined here referring to a condition in which the normal annular opening remains adjacent to a type of sieve plate and does not collapse and form a spiracular scar. This type of spiracle was referred to as cribriform by Kasap & Crowson (1976) and as uniforous by LeSage (1982, 1984). The cribriform and biforous spiracle types are associated with the elateroid type of ecdysial process described by Hinton (1947, 1967), while the annular-biforous and annular-cribriform types are associated with the normal type of ecdysis. S8 spiracles, if present, may be recognized by the reduced size, blocked openings and usually collapsed tracheae.

509. Larva: thoracic spiracles

1. annular.
2. annular-uniforous (unicameral).
3. annular-biforous (bicameral)
4. annular-multiforous (multicameral).
5. biforous (bilabiate).
6. cribriform.
7. annular-cribriform
8. reduced and non-functional or absent.

The thoracic spiracle is usually located on the mesothorax or between the mesothorax and metathorax or on a mesothoracic laterotergite; in a few groups it has migrated onto the prothorax. For discussion of character states, see above under **Larval Spiracles**.

510. Larva: thoracic spiracles

1. not at ends of spiracular tubes.
2. at ends of spiracular tubes (Fig. 71G).

The spiracular opening may be slightly elevated in some taxa coded as S1, but the elevations should be at least as long as wide to be coded as S2.

511. Larva: anterior abdominal spiracles

1. annular (Fig. 68E).
2. annular-uniforous (unicameral).
3. annular-biforous (bicameral) (Fig. 71C).
4. annular-multiforous (multicameral).
5. biforous (bilabiate) (Figs 71D, 84E).
6. cribriform (Figs 67G, 71E, 84D).
7. annular-cribriform (Fig. 63H).
8. reduced and non-functional or absent.

For discussion of character states, see above under **Larval Spiracles**. The annular (S1) and annular-biforous (S3) are the two most common types of spiracle in beetle larvae. The annular spiracle occurs in most of the outgroups, all Archostemata, almost all Adephaga and Myxophaga, most Staphylinoidea, all Scirtoidea, Jacobsoniidae, most Bostrichoidea, Lymexylidae and a wide variety of Cucujiformia. Annular-biforous or bicameral spiracles occur in the myxophagan genus *Lepicerus*, the adephagan family Haliplidae, helophorine and georissine Hydrophilidae, Histeridae and related families, *Necrophilus* and *Anisotoma* among the Staphylinoidea, the dascilloid genus *Sandalus*, Derodontidae and Nosodendridae, and an equally wide variety of Cucujiformia. The annular-uniforous type (S2) is relatively uncommon, occurring in a few bostrichoids, the cucujoid genera *Lamingtonium* and *Laemophloeus*, and several curculionoids, as is the annular-multiforous type (S4), which occurs in the tenebrionid genus *Diaperis*, Oedemeridae, *Pedilus* (Pyrochroidae), Disteniidae and *Parandra* and *Rutpela* among the Cerambycidae. The biforous or bilabiate spiracle (S5) occurs in *Taurocerastes* and *Trox* among the Scarabaeoidea, *Schizopus* of the Buprestoidea and in almost all Byrrhoidea and all Elateroidea. True cribriform spiracles, involving a spiracular scar, occur in most Scarabaeoidea, Dascillidae, most Buprestidae and Heteroceridae. The outgroup genus *Panorpa* has also been coded as having this state, but it appears to be of a different type in which the spiracular scar is located at the center of the sieve plate. S7 (annular-cribriform) has developed in a few cleroids (only *Grynoma* among our exemplars) and in the tenebrionoid family Promecheilidae (= Perimylopidae; see Lawrence *et al.* 2010c), the tenebrionid genus *Leaus* and the mycterid genus *Hemipeplus*.

512. Larva: spiracular scar

1. absent.

2. adjacent to but detached from paired openings or cribriform plate (Figs 67G, 71D, 71E, 84E).

3. in the center of cribriform plate

The spiracular scar is associated with the elateroid type of ecdysial process discussed by Hinton (1947, 1967) and marks the location of the opening through which the trachea of the previous instar has been withdrawn during ecdysis. The scar usually lies adjacent to the paired spiracular openings, but in those Scarabaeoidea with C-shaped cribriform plates, the scar is partly surrounded by the cribriform plate, resembling the type found in Mecoptera, which occurs in the center of the plate (S3).

513. Larva: abdominal spiracles

1. not placed at ends of spiracular tubes.

2. all placed at ends of spiracular tubes (Fig. 71G).

3. placed at ends of spiracular tubes on segment VIII only.

4. placed at ends of spiracular tubes on segments I and VIII

Spiracles may be slightly elevated, but spiracular tubes should be at least as long as wide to be coded as S2, S3 or S4. Although spiracular tubes occur in a number of beetle larvae, those occurring only on segment VIII (S3) are known only in *Lamingtonium* among our exemplars and those on I and VIII (S4) are found only in *Hydroscapha*.

514. Larva: spiracles on segment VIII

1. functional and about same size as others on abdomen.

2. reduced and non-functional or absent.

3. much larger than others on abdomen.

4. only functional pair on abdomen.

5. one of two functional pairs on abdomen (the other being on segment I).

The spiracles on segment VIII are reduced and non-functional or absent (S2) in the outgroup *Sialis*, in the adephagan families Gyrinidae, Haliplidae and Hygrobiidae, in *Clambus* (Clambidae) and *Rhipidioides* (Ripiphoridae: Ripidiinae). In the Sialidae and Gyrinidae, this is associated with the presence of lateral gills, in Haliplidae with the presence of long tracheal gills (*Peltodytes*) or microtracheal gills (*Haliplus*) and in Hygrobiidae with the presence of ventral gill tufts. The enlargement of the eighth spiracles (S3) occurs in Aspidytidae, Noteridae, Dytiscidae and Amphizoidae, where it is correlated with posterodorsal displacement and the development of a spiracular siphon; however this enlargement also occurs in lyctine Bostrichidae, Lamingtoniidae, Pterogeniidae and bruchine Chrysomelidae. In those Hydrophilidae with a spiracular chamber (Spercheinae, Sphaeridiinae and Hydrophilinae), in Scirtidae and in psephenine and eubrianacine Psephenidae, only the eighth spiracles are functional (S4), while in *Hydroscapha* and *Meru*, only the spiracles on segments I and VIII are functional (S5).

515. Larva: spiracles on segment VIII

1. lateral or dorsolateral.

2. posterolateral and facing posteriorly.

3. dorsal, often near midline and facing posteriorly (Fig. 83D).

4. at end of posteriorly projecting siphon (Fig. 85E).

Spiracles on segment VIII are usually laterally placed, but in various groups, they have migrated towards the posterior edge of the segment with the openings facing posteriorly (S2). The spiracles have moved towards the midline (S3) in the adephagan families Meruidae, Aspidytidae and Amphizoidae, in those hydrophilids which have a spiracular chamber, in Scirtidae and Dryopidae, and in the cucujiform genera *Diplocoelus* and *Sphenophorus*. In the adephagan families Noteridae and Dytiscidae and in *Nosodendron*, spiracles are also located posteriorly near the midline, but segment VIII has been expanded posteriorly to form an elongate process with the spiracles at its apex (S4).

516. Larva: spiracular closing apparatus

1. present (Fig. 71C).

2. absent (Fig. 71D).

The closing apparatus, consisting of a sclerotized bar attached to the trachea proximad of the spiracular chamber, appears to be homologous throughout the order. The closing apparatus associated with the cribriform spiracles of some Scarabaeoidea has been discussed by Lotz (1962) and Hinton (1967) and presumably occurs in all Trogidae, Lucanidae, Passalidae and Glaphyridae. In cleared dissections, it was not possible to see a cuticular bar of the type associated with the closing apparatus in other beetles. It is possible that the scarabaeoid type is not homologous with the normal type.

Cladistic methods

The characters listed above were scored for 366 taxa, 351 of which included larval data (Table 1). All characters were treated as multistate and unordered. Of the 188,856 character states coded, 3,630 were scored as unknown (?) and 12,194 inapplicable (-). The cladistic analysis of the data was performed using the parsimony ratchet (Nixon 1999) as implemented in the program TNT (Goloboff *et al.* 2008), using the "xmult" strategy (scripted commands: rss css fuse 20 frift 20 ratchet 100 replic 100; bbreak: tbr safe nofillonly;). Xmult is a heuristic search method that uses tree drifting and fusing (Goloboff 1999) as well as tree bisection and reconnection. Implied weighting (Goloboff 1993) was used to reduce the effects of homoplasy; searches with implied weights were repeated using concavity constants (k) from 1–24. Character fit showed no substantial change for values of k greater than 18; therefore, this value was used for the final searches. In order to ensure thorough exploration of the treespace, this analysis was repeated four times from different random seeds. Support for the resulting topology was assessed under implied weighting (as used in the heuristic search), with 1000 replications of symmetric resampling (P = 33). The choice of analytical methods and the problems of dealing with a large dataset with a high incidence of homoplasy will be discussed in a future work (Seago *et al.*, in preparation).

Character state changes were reconstructed using the"trace all changes" option in MacClade v4.08 (Maddison and Maddison 2005), including unambiguous changes only. Character state changes supporting the numbered nodes discussed in the text are listed in Table 2.

Results and discussion

The initial heuristic search (xmult) found 10,000+ most parsimonious trees with a length of 18,936 steps. Subsequent searches using implied weighting (K = 18) resulted in the tree shown in Cladograms 2–5, and a summary of major groups is given in Cladogram 1. Coleoptera (node 1), Archostemata (node 76), Adephaga (node 102), Myxophaga (node 17), Ptiliidae + Hydraenidae (node 82), Bostrichoidea (excluding Dermestidae) (node 86), Hydrophiloidea (including Histeroidea) (node 21), Scarabaeoidea (node 100), and Curculionoidea (node 15) were strongly supported, but support values for deeper nodes were not statistically significant. Most well-supported nodes were found at the family and subfamily levels (e.g., Rhysodinae, Trachypachidae, Haliplidae, Gyrinidae, Torridincolidae, Clambidae, Agyrtidae, Scydmaeninae, Histeridae, Ptinidae, Dascillidae, Byrrhidae, Buprestidae, Psephenidae, Artematopodidae, Elateridae, Eucnemidae, Derodontidae, Scirtidae, Discolomatidae, Coccinellidae, Lymexylidae, Phalacridae and Curculionidae). Character state changes supporting the 102 labelled nodes on Cladograms 2–5 are given in the Table 2.

As shown in the summary tree (Cladogram 1), Strepsiptera is sister to Coleoptera, the four coleopteran suborders are each monophyletic and subordinal relationships are given as (Archostemata + Adephaga) + (Myxophaga + Polyphaga), but without significant support for either clade. This appears to be a unique 4-taxon statement, but seven others have been published. The traditional one proposed by Crowson (1955, 1960), supported by Beutel and Haas (2000), and based on morphological characters is Archostemata (Adephaga (Myxophaga + Polyphaga), while Polyphaga (Archostemata (Myxophaga + Adephaga) was proposed by Kukalová-Peck and Lawrence (1993, 2004) based on hind wing characters alone. Among the more recent analyses based on molecular data, however, the following have also been proposed: Archostemata + Myxophaga + (Adephaga + Polyphaga) (Shull *et al.* 2001), Archostemata (Myxophaga (Adephaga + Polyphaga) (Caterino *et al.* 2002), (Archostemata + Myxophaga) (Adephaga + Polyphaga) (Hunt *et al.* 2007, Maddison *et al.* 2009), (Myxophaga + Adephaga) (Archostemata + Polyphaga) (Song *et al.* 2010, Pons *et al.* 2010) and Polyphaga (Adephaga (Archostemata + Myxophaga) (McKenna and Farrell 2010).

Within the Archostemata, neither Ommatidae nor Cupedidae is monophyletic, Ommatinae forming a clade with Cupedinae and Tetraphalerinae with Priacminae, while Micromalthidae is sister to the remaining taxa. Adephaga forms a highly supported clade, but its internal topology is weakly supported, except for Amphizoidae + Hygrobiidae + Dytiscidae. Geadephaga, as currently defined, is non-monophyletic, with Trachypachidae sister to Hydradephaga and Carabidae in four basal lineages: *Arthropterus* (Paussinae), Cicindelinae, most Carabidae and *Metrius* (Paussinae). Gyrinidae and Haliplidae are two terminals in a clade also containing Noteridae, Aspidytidae and Meruidae. This contradicts the results of most recent analyses, both morphological and molecular (Shull *et al.* 2001, Ribera *et al.* 2002, Balke *et al.* 2005, 2008; Beutel *et al.* 2006, Hunt *et al.* 2007, Beutel *et al.* 2008, Maddison *et al.* 2009, Dressler and Beutel 2010), where Gyrinidae is sister to the remaining Hydradephaga, Haliplidae sister to Hydradephaga excluding Gyrinidae, and Trachypachidae either basal to or well within a geadephagan clade.

Of the currently recognized polyphagan superfamilies (Lawrence and Newton 1995, Beutel and Leschen 2005a, Leschen *et al.* 2010), Hydrophiloidea, Scarabaeoidea, Buprestoidea, Elateroidea, Bostrichoidea, Lymexyloidea, Chrysomeloidea and Curculionoidea are monophyletic; however Buprestoidea is nested within one of the two byrrhoid clades and Lymexyloidea within the largest of the tenebrionoid clades (see below). Staphylinoidea, Scirtoidea, Dascilloidea, Byrrhoidea and Derodontoidea each form two distinct clades, Cucujoidea and Tenebrionoidea form five clades each, and Cleroidea, although primarily monophyletic, is sister to Cucujoidea 3 (node 52), while the trogossitid genus *Thymalus* and subfamily Rentoniinae belong to two different cucujoid clades.

The basal positions of the superfamilies Scirtoidea (*sensu* Beutel and Leschen 2005a) and Derodontoidea (*sensu* Leschen *et al.* 2010) within the suborder Polyphaga were suggested by Crowson (1959, 1960), Lawrence and Newton (1982), Lawrence (1999, 2001) and Lawrence and Yoshitomi (2007), and this was first supported by molecular data when Caterino *et al.* (2002) found that exemplar genera *Eucinetus* Germar (Eucinetidae) and *Laricobius* (Derodontidae) formed two clades sister to the remainder of the Polyphaga based on 18S rDNA. A similar position for one or both of these groups was found by Shull *et al.* (2001), Hunt *et al.* (2007), Maddison *et al.* (2009), Song *et al.* (2010) and Pons *et al.* (2010). Scirtoidea are now known to be more common in Jurassic beds than they were previously thought to be (Kirejtshuk and Ponomarenko 2010). In the present tree, the scirtoid family Clambidae is sister to the remaining Polyphaga, while the rest of the scirtoids (Decliniidae, Scirtidae and Eucinetidae) form a clade with Nosodendridae and Derodontidae, which is sister to the series Cucujiformia. This unusual placement of Clambidae could be an artifact produced, for instance, by small size and highly compacted body form; however clambid wings, in spite of their small size, exhibit some unusual features found only in Myxophaga, Adephaga and Archostemata. Forbes (1926) placed Clambidae, along with Lepiceridae, Hydroscaphidae and Sphaeriusidae, in the suborder Adephaga based on wing folding, and Crowson (1955) placed *Calyptomerus* (as Calyptomeridae) in his new suborder Myxophaga, although he later (1960) returned it to Clambidae in Polyphaga. Although Kukalová-Peck and Lawrence (1993) figured the wings of the clambid genera *Calyptomerus*, *Acalyptomerus* and *Sphaerothorax* Endrödy-Younga, they underestimated the importance of some features. All three genera (as well as *Clambus*) have a sharp bending zone or hinge in MP1+2, as in Adephaga, Myxophaga and Archostemata, but the *Calyptomerus* wing also has distinct oblongum cell, which occurs in no polyphagan. The remaining members of the superfamily Scirtoidea, as presently defined, have none of these features. The small derodontoid family Jacobsoniidae, not included in any previous analyses, formed two clades sister to part of the Staphylinoidea. Crowson (1959, 1960) placed Jacobsoniidae in his Dermestoidea, along with Derodontidae, Nosodendridae and Dermestidae, but he called attention to staphylinoid-like hind wings (highly reduced venation), a well-developed but concealed abdominal sternite II (apparently plesiomorphic within Coleoptera) and a fringe-like attachment to the larval galea also occurring in Ptiliidae and some Hydraenidae.

The Staphylinoidea form the second and third basal polyphagan clades: Staphylinidae (including Scydmaeninae) + Silphidae and Ptiliidae + Hydraenidae + Agyrtidae + Leiodidae, with the two jacobsoniid clades at the base of the latter. In this cladogram Scydmaeninae is sister to the remaining Staphylinidae plus Silphidae, but Grebennikov and Newton (2009) have presented evidence that the group is more closely related to Staphylininae and related subfamilies.

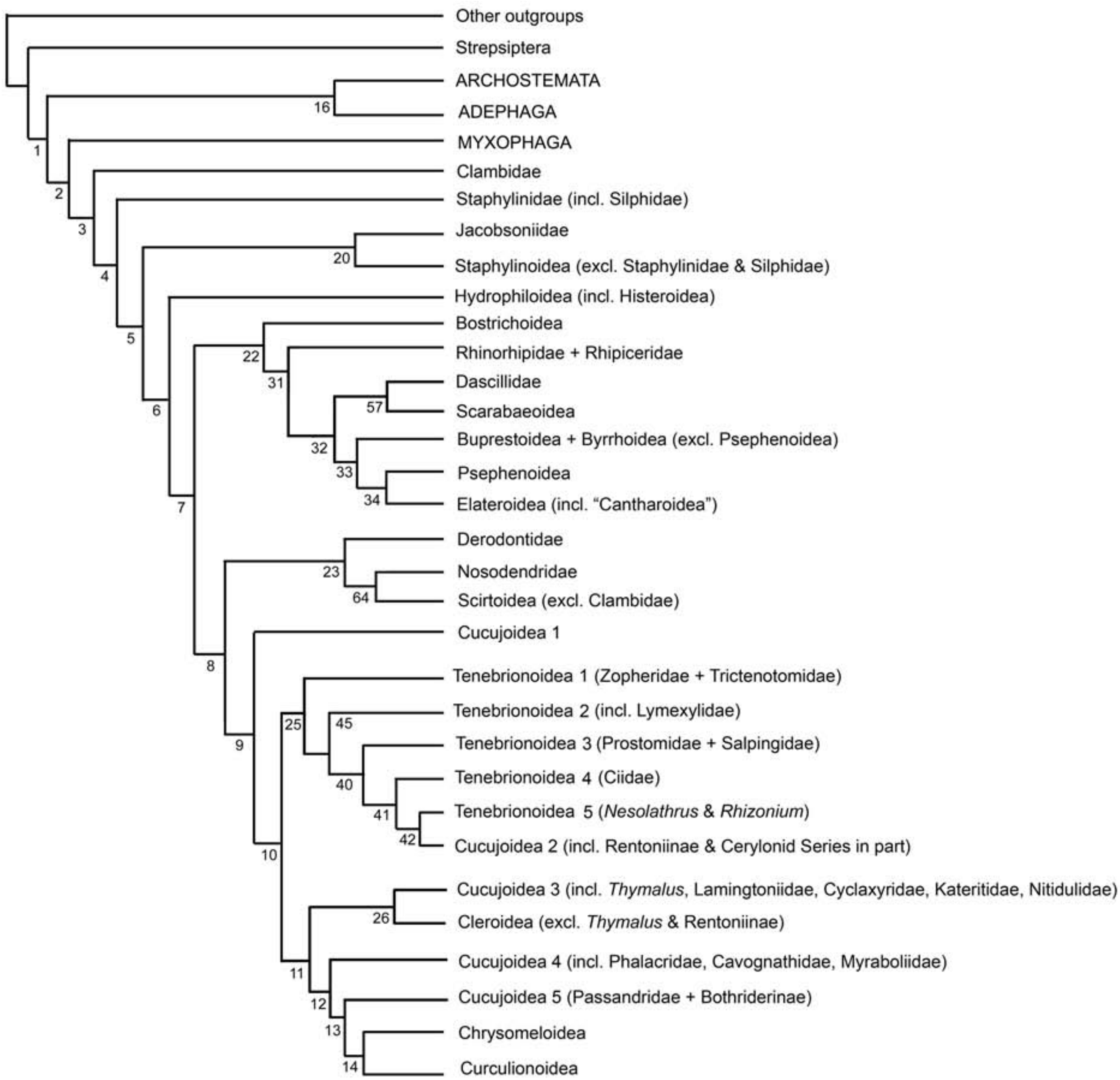
The second staphylinoid clade includes the well-supported clades Hydraenidae + Ptiliidae and Leiodidae + Agyrtidae, although agyrtids are nested within leiodids here. The superfamily Hydrophiloidea is monophyletic, as are the families of the former "Histeroidea" (Sphaeritidae + Synteliidae + Histeridae), but as in some other morphological and molecular studies (Beutel 1999b, Bernhard *et al.* 2009) the histeroids nest among the subfamilies of Hydrophilidae. The superfamily Hydrophiloidea is often considered to be related to both Staphylinoidea and Scarabaeoidea, forming the group Haplogastra (or Staphyliniformia *sensu lato*); this concept was supported by Scholtz *et al.* (1994) and Hansen (1997) based on morphology, by Caterino *et al.* (2005) based on a combination of morphology and 18S rDNA data, and Song *et al.* (2010) based on a large molecular dataset. A relationship between Hydrophiloidea and Scarabaeoidea was also weakly supported in a morphological analysis by Beutel and Leschen (2005c). Haplogastra is not supported in the tree by Hunt *et al.* (2007), where Staphylinoidea, Hydrophiloidea and Scarabaeoidea form several clades sister to ((Bostrichoidea + Elateriformia) + Cucujiformia), nor in our tree, where Hydrophiloidea forms a clade sister to the remaining Polyphaga (excluding Clambidae, Staphylinoidea and Jacobsoniidae) and within this Scarabaeoidea forms a clade sister to most of the Elateriformia. Dascilloidea form one clade including Rhinorhipidae (whose relationships are still in doubt), sister to Scarabaeoidea + Elateriformia, and one sister to Scarabaeoidea. Dascilloidea form one clade including Rhinorhipidae (whose relationships are still in doubt), sister to Scarabaeoidea + Elateriformia, and one sister to Scarabaeoidea. Crowson (1960, 1971) proposed a clade consisting of Dascilloidea and Scarabaeoidea, which was sister to Elateriformia, based in large part on larval morphology plus similarities in the aedeagi of Pleocomidae and Dascillidae, and this was followed by Lawrence and Newton (1982).

Bostrichoidea (including Dermestidae) is monophyletic and is sister to the Scarabaeoidea + Elateriformia. This position of bostrichoids at the base of a scarabaeoid-elateriform clade is in conflict with the concept of Bostrichiformia (Crowson 1955, 1960; Lawrence & Newton 1982, 1995; Leschen *et al.* 2010), in which bostrichoids and derodontoids form one or two clades sister to Cucujiformia. A sister-group relationship between Bostrichoidea and Elateriformia (but not Scarabaeoidea) was found by Hunt *et al.* (2007). In our tree, the Derodontoidea (excluding Jacobsoniidae) plus the Scirtoidea (excluding Clambidae) are sister to Cucujiformia.

The series Elateriformia has been variously defined, as pointed out by Beutel and Leschen (2005b). Elateriformia in a restricted sense (excluding Scirtoidea, Dascilloidea and Rhinorhipidae) is monophyletic in our tree; however Byrrhoidea, as delimited by Lawrence and Newton (1995) and Beutel and Leschen (2005b), is not. The byrrhoid families form two clades, the first of which (58) consists of Byrrhidae, Heteroceridae, Lutrochidae, Elmidae, Limnichidae and Dryopidae, plus Buprestidae (which is in a subclade with Limnichidae and Dryopidae) and is sister to a second clade (59) plus Elateroidea (*sensu lato*) (35). This second byrrhoid clade contains Cneoglossidae, Psephenidae, Eulichadidae, Chelonariidae, Callirhipidae and Ptilodactylidae, and is equivalent to the superfamily Psephenoidea, as defined by Lawrence (1988). Crowson (1982) suggested that Buprestidae may have affinities with Elmidae and Dryopidae, and Lawrence (1988) included Buprestidae within Byrrhoidea.

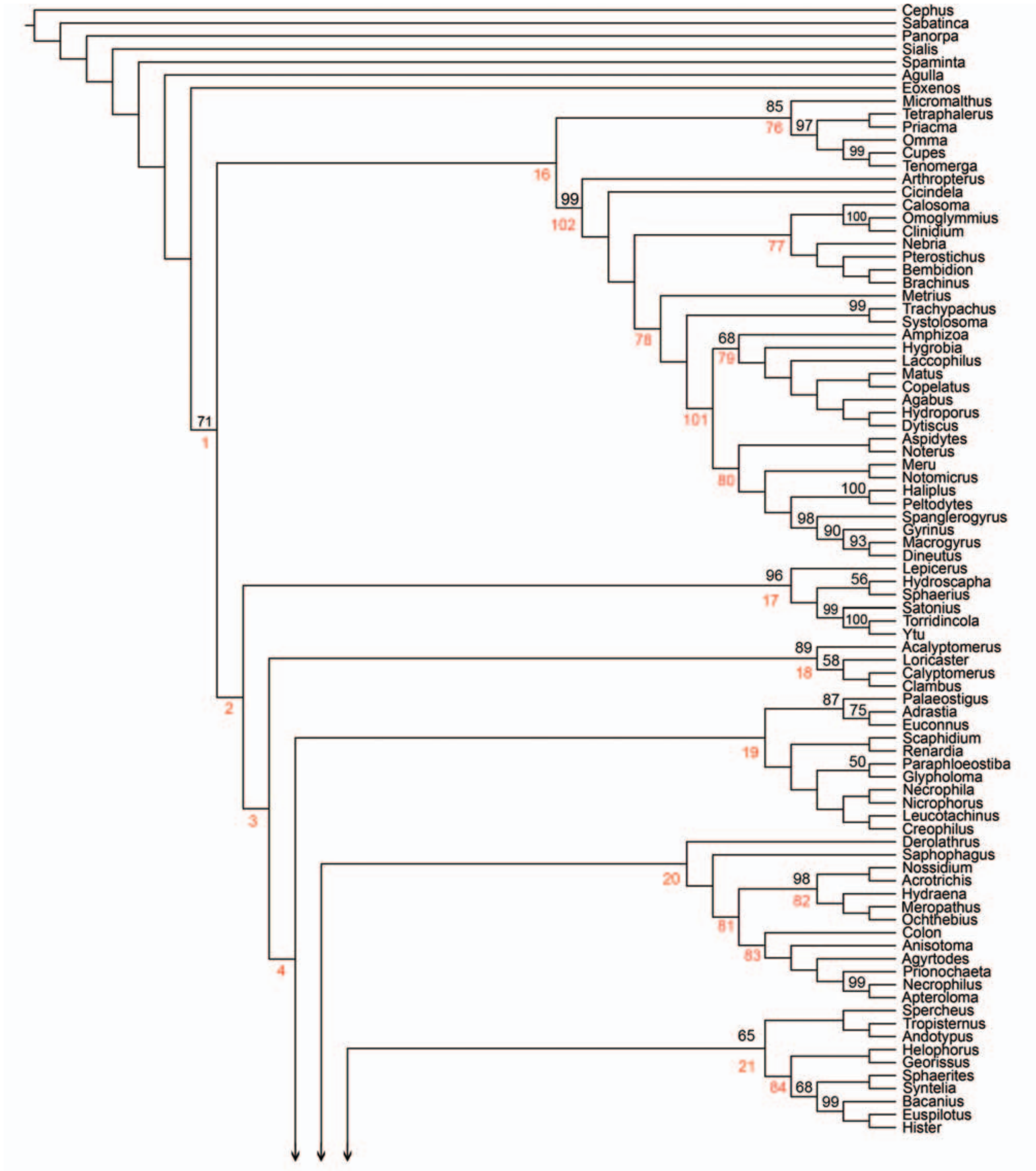
Elateroidea in the broad sense, including those taxa formerly included in Cantharoidea, forms a monophyletic group with the family Artematopodidae sister to the remaining taxa. This broad definition of Elateroidea was proposed by Lawrence and Newton (1982) and Lawrence (1988) recognized the same group but with the addition of Rhinorhipidae, which was found to be outside the group by Lawrence *et al.* (1995). A monophyletic Elateroidea (including Cantharoidea) has been strongly supported in several works, particularly those of Bocakova *et al.* (2007), Bocak *et al.* (2008) and Bocak and Kundrata (2011), but also by Hunt *et al.* (2007), Sheffield *et al.* (2009), Song *et al.* (2010) and Pons *et al.* (2010) with far smaller taxon samples. The position of Podabrocephalidae within

Cladogram 1. Summary of coleopteran relationships at the suborder and superfamily level, based on morphological characters. Suborders other than Polyphaga are indicated by uppercase type. Numbers after superfamily names indicate clades discussed in the text.

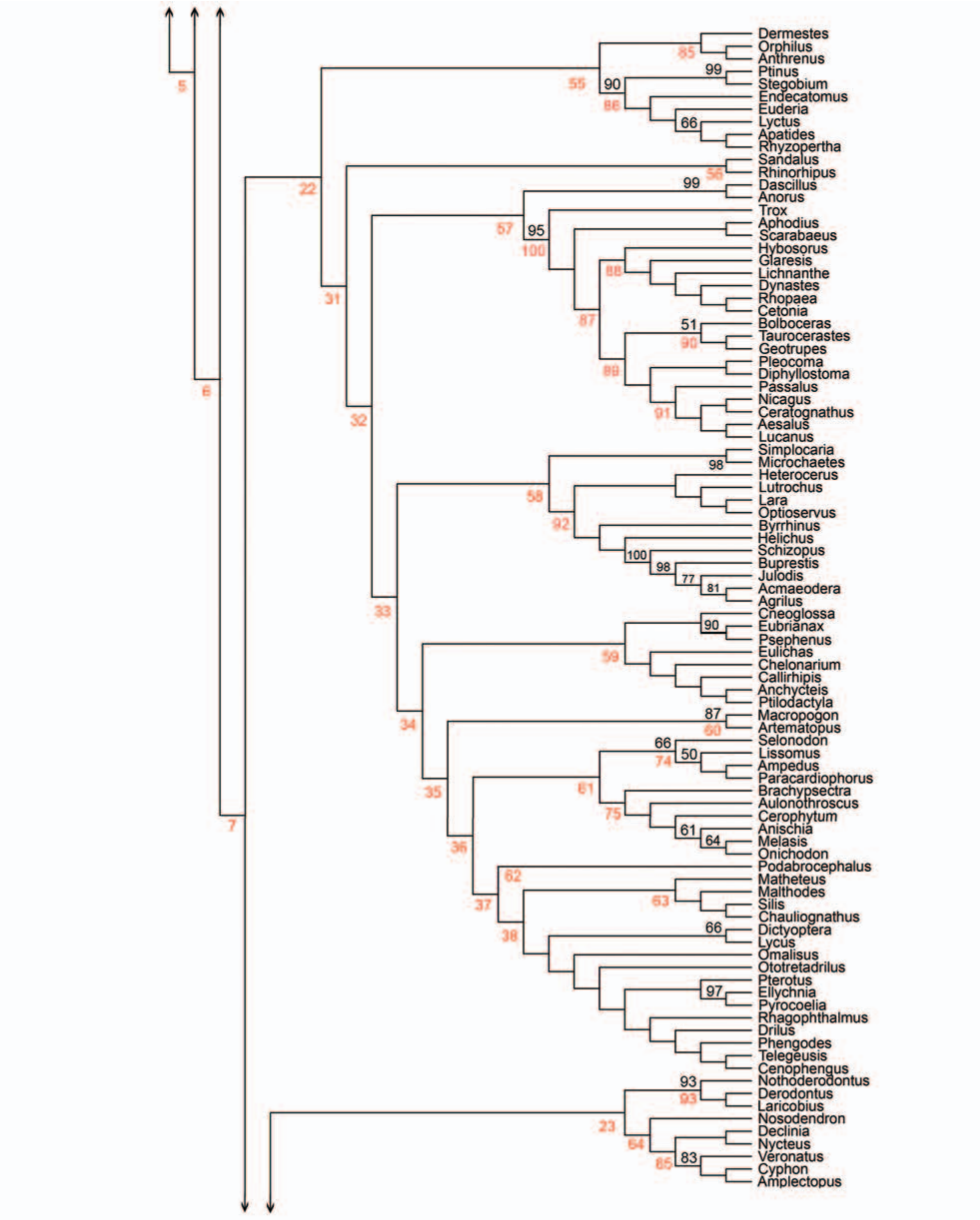


Cladograms 2–5. Relationships of Coleoptera, based on parsimony analysis of adult and larval morphological characters. Red numbers below nodes indicate clades discussed in the text; black numbers above nodes are support values determined by symmetric resampling.

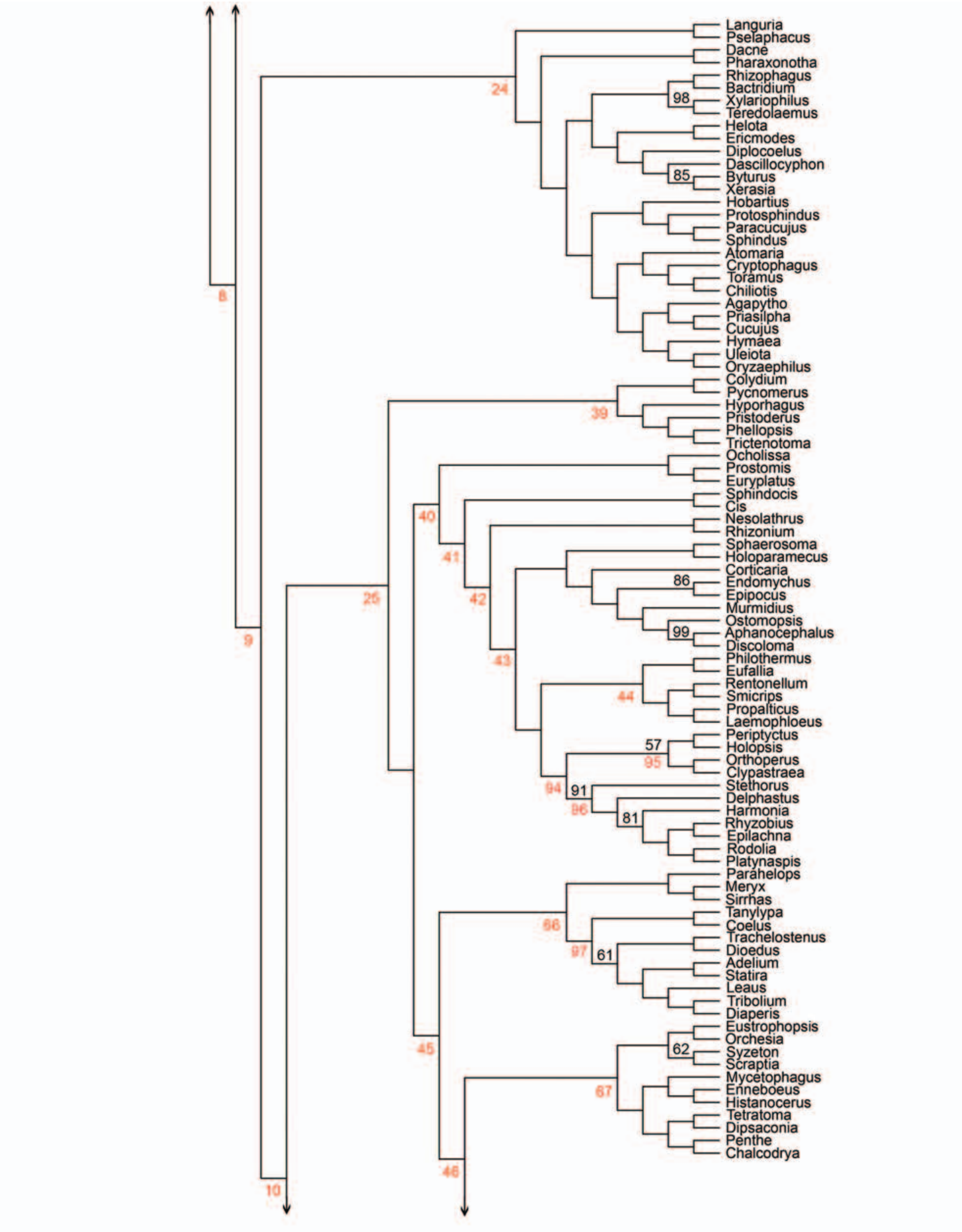
Cladogram 2.



Cladogram 3.


Dermestes
Orphilus
Anthrenus
Ptinus
Stegobium
Endecatomus
Euderia
Lyctus
Apatides
Rhyzopertha
Sandalus
Rhinorhipus
Dascillus
Anorus
Trox
Aphodius
Scarabaeus
Hybosorus
Glaresis
Lichnanthe
Dynastes
Rhopaea
Cetonia
Bolboceras
Taurocerastes
Geotrupes
Pleocoma
Diphyllostoma
Passalus
Nicagus
Ceratognathus
Aesalus
Lucanus
Simplocaria
Microchaetes
Heterocerus
Lutrochus
Lara
Optioservus
Byrrhinus
Helichus
Schizopus
Buprestis
Julodis
Acmaeodera
Agrilus
Cneoglossa
Eubrianax
Psephenus
Eulichas
Chelonarium
Callirhipis
Anchycteis
Ptilodactyla
Macropogon
Artematopus
Selonodon
Lissomus
Ampedus
Paracardiophorus
Brachypsectra
Aulonothroscus
Cerophytum
Anischia
Melasis
Onichodon
Podabrocephalus
Matheteus
Malthodes
Silis
Chauliognathus
Dictyoptera
Lycus
Omalisus
Ototretadrilus
Pterotus
Ellychnia
Pyrocoelia
Rhagophthalmus
Drilus
Phengodes
Telegeusis
Cenophengus
Nothoderodontus
Derodontus
Laricobius
Nosodendron
Declinia
Nycteus
Veronatus
Cyphon
Amplectopus

Cladogram 4.


Languria
Pselaphacus
Dacne
Pharaxonotha
Rhizophagus
Bactridium
Xylariophilus
Teredolaemus
Helota
Ericmodes
Diplocoelus
Dascillocyphon
Byturus
Xerasia
Hobartius
Protosphindus
Paracucujus
Sphindus
Atomaria
Cryptophagus
Toramus
Chiliotis
Agapytho
Priasilpha
Cucujus
Hymaea
Uleiota
Oryzaephilus
Colydium
Pycnomerus
Hyporhagus
Pristoderus
Phellopsis
Trictenotoma
Ocholissa
Prostomis
Euryplatus
Sphindocis
Cis
Nesolathrus
Rhizonium
Sphaerosoma
Holoparamecus
Corticaria
Endomychus
Epipocus
Murmidius
Ostomopsis
Aphanocephalus
Discoloma
Philothermus
Eufallia
Rentonellum
Smicrips
Propalticus
Laemophloeus
Periptyctus
Holopsis
Orthoperus
Clypastraea
Stethorus
Delphastus
Harmonia
Rhyzobius
Epilachna
Rodolia
Platynaspis
Parahelops
Meryx
Sirrhas
Tanylypa
Coelus
Trachelostenus
Dioedus
Adelium
Statira
Leaus
Tribolium
Diaperis
Eustrophopsis
Orchesia
Syzeton
Scraptia
Mycetophagus
Enneboeus
Histanocerus
Tetratoma
Dipsaconia
Penthe
Chalcodrya
8
9
10
24
98
85
39
25
40
41
42
43
86
99
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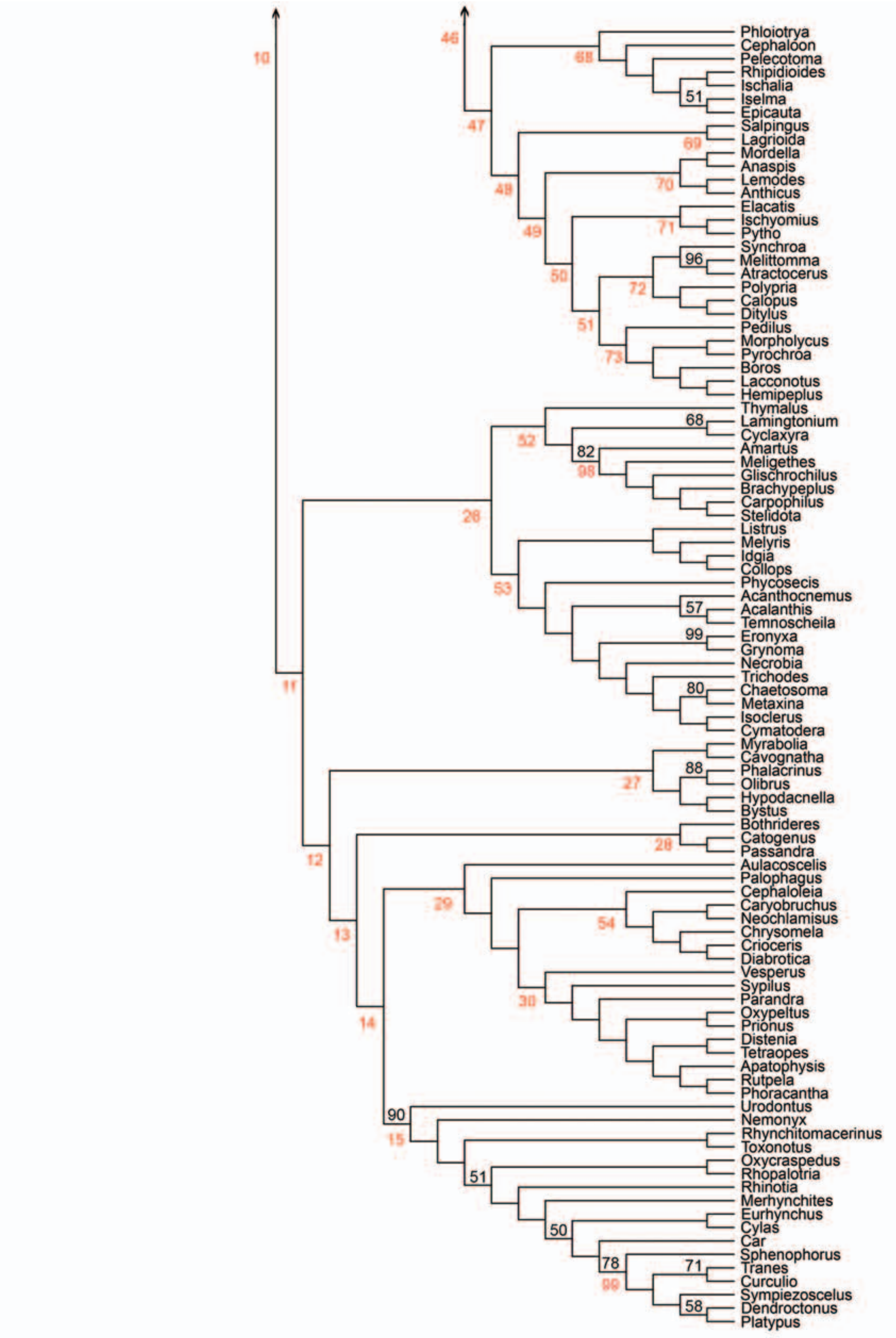
Cladogram 5.


Phloiotrya
Cephaloon
Pelecotoma
Rhipidioides
Ischalia
Iselma
Epicauta
Salpingus
Lagrioida
Mordella
Anaspis
Lemodes
Anthicus
Elacatis
Ischyomius
Pytho
Synchroa
Melittomma
Atractocerus
Polypria
Calopus
Ditylus
Pedilus
Morpholycus
Pyrochroa
Boros
Lacconotus
Hemipeplus
Thymalus
Lamingtonium
Cyclaxyra
Amartus
Meligethes
Glischrochilus
Brachypeplus
Carpophilus
Stelidota
Listrus
Melyris
Idgia
Collops
Phycosecis
Acanthocnemus
Acalanthis
Temnoscheila
Eronyxa
Grynoma
Necrobia
Trichodes
Chaetosoma
Metaxina
Isoclerus
Cymatodera
Myrabolia
Cavognatha
Phalacrinus
Olibrus
Hypodacnella
Bystus
Bothrideres
Catogenus
Passandra
Aulacoscelis
Palophagus
Cephaloleia
Caryobruchus
Neochlamisus
Chrysomela
Crioceris
Diabrotica
Vesperus
Sypilus
Parandra
Oxypeltus
Prionus
Distenia
Tetraopes
Apatophysis
Rutpela
Phoracantha
Urodontus
Nemonyx
Rhynchitomacerinus
Toxonotus
Oxycraspedus
Rhopalotria
Rhinotia
Merhynchites
Eurhynchus
Cylas
Car
Sphenophorus
Tranes
Curculio
Sympiezoscelus
Dendroctonus
Platypus

Elateroidea and sister to the remaining soft-bodied groups is in conflict with current concepts and might be due to the extremely modified adult male and the lack of knowledge concerning females or larvae. Although *Podabrocephalus* was first considered to be a member of the Malacodermata or Cantharoidea (Pic 1913, 1930), Wittmer (1969) suggested that the genus might be in the byrrhoid family Ptilodactylidae (following advice by R. A. Crowson) and this was supported by Lawrence *et al.* (2010b) based on tarsi, wing venation, connate basal abdominal ventrites and lack of functional eighth spiracles.

The major polyphagan group, Cucujiformia (node 9), is monophyletic and contains three major clades: Cucujoidea 1 (node 24), Tenebrionoidea 1–5 and Cucujoidea 2 (node 25), and Cucujoidea 3–5, Cleroidea and Phytophaga (node 11). The superfamily Lymexyloidea, normally placed at the base of Cucujiformia, is located well within Tenebrionoidea 1, as part of a minor clade also containing Synchroidae and Oedemeridae. In the cladogram produced by Hunt *et al.* (2007) Lymexylidae was in a clade with both Cleroidea and Tenebrionoidea, and a close relationship between Lymexylidae and Tenebrionoidea was also found by Levkaničová (2009). As can be seen in Cladogram 1, tenebrionoid taxa belong to several clades, the most derived of which is sister to Cucujoidea Clade 2 (node 43) (including the major part of the cerylonid series). The superfamily Cleroidea is polyphyletic, with most of its members forming a clade (node 53) sister to Cucujoidea Clade 3 (node 52), but two groups of Trogossitidae, the peltine genus *Thymalus* and the subfamily Rentoniinae, belong to different cucujoid clades (nodes 52 and 44, respectively). In a recent reclassification of Trogossitidae by Kolibáč (2006), both groups belong to a tribe Thymalini in the subfamily Peltinae. The inclusion of Cleroidea within Cucujoidea has been supported in morphology-based cladograms by Beutel and Pollock (2000), Beutel and Ślipiński (2001) and Leschen *et al.* (2005), as well as in various molecular phylogenies, such as those of Hunt *et al.* (2007), Buder *et al.* (2008) and Marvaldi *et al.* (2009).

Of the five cucujoid clades, the largest is Cucujoidea Clade 1 (node 24), which contains most of the "basal" cucujoid families treated by Leschen *et al.* (2005), in addition to two genera belonging to two closely related subfamilies of Bothrideridae (Xylariophilinae and Teredinae), usually placed in the cerylonid series. Cucujoidea Clade 2 (node 43), contains the other members of the cerylonid series except *Hypodacnella* and *Bystus*, which are in Cucujoidea Clade 4 (node 27), and *Bothrideres*, which is in Cucujoidea Clade 5 (node 28). Robertson *et al.* (2008) found the cerylonid series to be monophyletic, but only Bothriderinae and Ceryloninae were represented among the exemplars. Of the remaining cucujoid clades, Cucujoidea Clade 3 (node 52) includes Nitidulidae, Kateretidae, Lamingtoniidae and Cyclaxyridae, as well as the trogossitid genus *Thymalus*, and is sister to the major part of Cleroidea (node 53), while Cucujoidea Clade 4 (node 27) (Phalacridae, Cavognathidae, Myraboliidae, *Bystus* from Endomychidae: Anamorphinae and *Hypodacnella* from Cerylonidae: Euxestinae) and Cucujoidea Clade 5 (node 28) (Passandridae and Bothrideridae: Bothriderinae) are sister to the Phytophaga (node 14). The placement of Passandridae and Bothriderinae in the same clade is interesting, since both have ectoparasitic larvae; however, previous morphological (Leschen *et al.* 2005, Thomas 1984) and molecular (Hunt *et al.* 2007, Robertson *et al.* 2008) analyses place passandrids close to Phalacridae, Laemophloeidae and some other cucujoid families, but never in the cerylonid series where Bothriderinae is always placed (see Burckhardt and Ślipiński 2010 and Ślipiński *et al.* 2010). Among those cucujoid and cleroid families represented by more than one exemplar, some such as Melyridae, Monotomidae, Byturidae, Silvanidae, Phalacridae, Nitidulidae, Discolomatidae, Corylophidae, Coccinellidae, were found to be monophyletic, but Trogossitidae, Cleridae, Erotylidae, Sphindidae, Bothrideridae, Cerylonidae, Endomychidae and Latridiidae were either paraphyletic or polyphyletic based on this data set.

All families of Tenebrionoidea belong to a single clade (node 25) containing 5 subclades, one of which, Tenebrionoidea Clade 5, is sister to Cucujoidea Clade 2 (most of the cerylonid series plus Smicripidae, Laemophloeidae, Propalticidae and the trogossitid subfamily Rentoniinae). The two genera comprising Tenebrionoidea Clade 5 consist of very small beetles recently placed in Tenebrionoidea. *Nesolathrus* has 3-3-3 tarsi and was originally placed in Latridiidae, but was moved to Mycetophagidae by Lawrence and Leschen (2010) based on both adult and larval characters. *Rhizonium* is a New Zealand endemic related to the widely distributed *Aprostomis* Grouvelle and doubtfully placed in Tenebrionoidea but not assigned to a family (Lawrence *et al.* 2010d). Tenebrionoidea Clade 4 contains only the family Ciidae, which has also been somewhat doubtfully included in the superfamily. Although once considered to be cleroid (Böving and Craighead 1931), the Ciidae are usually considered to be basal tenebrionoids. In cladograms produced by Buder *et al* (2008) based on 18S and COI, the family was either sister to Nitidulidae or at the base of the cucujoid-tenebrionoid assemblage. Tenebrionoidea Clade 1 (node 45) contains most of the families, while Tenebrionoidea Clade 2 (node 39) contains Zopheridae plus Trictenotomidae and Tenebrionoidea Clade 3 (sister to node 41) includes Prostomidae and the salpingid subfamilies Prostominiinae and Inopeplinae. Within the major clade, Tenebrionoidea Clade 1 (node 45), relationships are somewhat confusing and monophyly was not recovered for the following polytypic families: Mycetophagidae, Tetratomidae, Melandryidae, Ripiphoridae, Ulodidae, Promecheilidae, Zopheridae, Pyrochroidae, Salpingidae and Scraptiidae. There have been few cladistic analyses of Tenebrionoidea involving more than a few exemplars. That of Beutel and Friedrich (2005) was based on larval morphology alone and had very low resolution, while the molecular phylogeny of Buder *et al.* (2008) contained only nine families. Two larger data sets of more than 150 species in at least 20 families and based on sequence data are those of Hunt *et al.* (2007) and Levkaničová (2009). In both, Tenebrionoidea is monophyletic and contains the superfamily Lymexyloidea.

Phytophaga (node 14), Chrysomeloidea (node 29) and Curculionoidea (node 15) are all monophyletic, but with significant support only for the last. This is concordant with the molecular cladogram by Marvaldi *et al.* (2009). The chrysomeloid clade (node 29) shows Aulacoscelidinae (Orsodacnidae) and Palophaginae (Megalopodidae) branching off first, and the combined cerambycoid families forming a clade (node 30) sister to Chrysomelidae. Although the two vesperid groups (Vesperinae and Anoplodermatinae) form basal clades, both Oxypeltidae and Disteniidae are within the Cerambycidae clade. This disagrees with works by Švácha and Danilevsky (1987) and Švácha *et al.* (1997). Within the Curculionoidea, monophyly of three families, Nemonychidae, Anthribidae and Belidae, was not recovered, with five basal clades consisting of Anthribidae: Urodontinae, Nemonychidae: Nemonychinae, Nemonychidae: Rhinorhynchinae + Anthribidae: Anthribinae, Belidae: Oxycoryninae, and Belidae: Belinae. This is, however, weakly supported, and in conflict with most recent works on curculionoid phylogeny (Kuschel 1995; Marvaldi and Morrone 2000, Marvaldi *et al.* 2002, 2006, 2009; McKenna *et al.* 2009). The largest weevil family, Curculionidae, is supported as monophyletic.

These results suggest that utility of morphological characters is surprisingly robust, in spite of the extreme diversity of form exhibited by both larvae and adults and the resulting homoplasy in the data set, the impact of which was reduced by the use of implied weighting. Subordinal and many superfamilial relationships were resolved, and a number of groupings were consistent with recent molecular results. Homoplasy is still a major problem with morphological characters, although this might be reduced by a careful reexamination and redefinition of character states. A serious challenge in performing morphological analyses of the entire order Coleoptera – strongly divergent in so many ways from other Holometabola – is the inapplicability of many characters to the necessary outgroups, leaving the polarities of those characters potentially ambiguous, or at least not rooted by the outgroups.

The tendency for taxa with soft-bodied paedomorphic adults clustering together was partly overcome, in that the soft-bodied elateroids or "cantharoids" came out in the same clade (node 35) as Artematopodidae, Brachypsectridae, Cerophytidae, Eucnemidae, Throscidae and Elateridae, and did not cluster with soft-bodied cleroids or lymexyloids. They are, however, part of the same elateroid subclade (node 37), along with *Podabrocephalus*, which, as noted above, may belong elsewhere. Molecular evidence (Bocakova *et al.* 2007, Bocak *et al.* 2008) suggests that these "cantharoid" families belong to several clades interspersed with non-neotenic elaterids, throscids and eucnemids. Small body size could also be responsible for some unexpected placements, and the obvious example would be Clambidae; however the position of Clambidae was not significantly supported by any characters associated with body size reduction.

Another tendency found in some groups within our cladogram is for taxa usually considered "basal" or sister to the remaining members of their clade to belong to the most derived subclade. This is true of the Gyrinidae and Haliplidae within Adephaga, Silphidae within Staphylinidae, Agyrtidae within Leiodidae, and Geotrupidae and Pleocomidae within Scarabaeoidea. This may be a result of reversal of character polarity, so that symplesiomorphies are uniting these terminals. If combined morphological and molecular analyses are able to support stable relationships among the suborders – neither having done so alone to date – it may then be possible to perform more robust morphological analyses within individual suborders, using the appropriate other suborders as outgroups.

Although morphological data may be challenging to code and – like molecular data – subject to long-branch attraction and other effects of homoplasy, they clearly remain valuable for resolving phylogenetic relationships, particularly in groups where molecular sequence data is scarce or available loci evolve too rapidly (leading to saturation) or too slowly (providing inadequate signal). Recent studies (Lopardo *et al* 2010, Seago *et al* 2011) have shown that morphological data can be highly effective in resolving basal divergences that molecular data cannot. We expect to find similar results when these data are combined with nuclear and mitochondrial genomic data in the final BtoL analysis.

ACKNOWLEDGMENTS

A major portion of this research was conducted with the aid of a National Science Foundation Grant (Division of Environmental Biology) # 0531768. ATOL: Collaborative Research: Assembling the Beetle Tree of Life (1 Oct. 2005–30 Sept. 2010). Principal Investigator: Brian Farrell. A. Marvaldi's research was also supported by CONICET, through PIP grants # 5766 and # 00162. Field work of MKT and AFN was partly supported by a National Science Foundation PEET grant (0118749). Various portions of this project were also supported by a NSF PEET grant DEB-0417180 to J. V. McHugh and by several grants from the Australian Biological Resources Study to AS. Field work of JFL in Chile was supported by NSF grant DEB 0445413 to E. T. Arias and K. W. Will. Many of the scanning electron micrographs (particularly those of larvae) were taken by E. Seling at Harvard University with support to two of the authors (JFL and AFN) from NSF Research Grant 7502606, while others were taken by E. Hines, E. Brooks, H. Escalona and others using the CSIRO Electron Microscopy facility at the Black Mountain site in Canberra. All authors acknowledge support from and research facilities of their respective institutions.

The following institutions and individuals are gratefully acknowledged for providing specimens for dissection, literature or advice: Y. Alarie, Biology Department, Laurentian University, Sudbury, Ontario, Canada; E. Arias, Essig Museum, University of California, Berkeley, CA, USA; Australian National Insect Collection, CSIRO Entomology (now Ecosystem Sciences), Canberra (R. Oberprieler, T. A. Weir, H. Escalona), Australia; M. Balke, Zoologische Staatsammlung München, Germany; C. L. Bellamy, Plant Pest Diagnostic Laboratory, California Department of Food and Agriculture, Sacramento, CA, USA; R. G. Beutel, Institut für spezielle Zoologie und Evolutionsbiologie, Friedrich-Schiller-Universität, Jena, Germany; Bohart Museum, University of California at Davis, Davis, CA, USA (L. Kimsey); M. Bologna, Dipartimento di Biologia, Università Roma, Rome, Italy; M. Branham, University of Florida, Gainesville, FL, USA; California Department of Food and Agriculture, Sacramento, CA, USA (C. Bellamy); Charles A. Triplehorn Insect Collection, Ohio State University, Columbus, OH, USA (N. F. Johnson, L. Musetti); D. J. Clarke, Field Museum of Natural History and University of Illinois at Chicago, Chicago, IL, USA; Division of Entomology, University of Nebraska State Museum, Lincoln, NE, USA (M. L. Jameson, B. Ratcliffe); Essig Museum of Entomology, University of California, Berkeley, CA, USA (C. Barr, W. Shepard, E. Arias, K. Will); Field Museum of Natural History, Division of Insects, Chicago, IL USA; Florida State Collection of Arthropods, Florida Department of Agriculture and Consumer Services, Gainesville, FL, USA (P. E. Skelley); N. Guthrie, Department of Wildlife and Conservation, Wanneroo, WA, Australia; Insect Research Collection, Department of Entomology, University of Wisconsin-Madison, Madison, WS, USA (D. K. Young); Instituto Argentino de Investigaciones de Zonas Aridas, Entomología, Mendoza, Argentina (M. Chani-Posse, G. E. Flores, F. C. Ocampo, S. A. Roig); C.-F. Lee, Academia Sinica, Taipei, Taiwan; D. R. Maddison, Department of Zoology, Oregon State University, Corvallis, OR, USA; J. V. McHugh, Department of Entomology, University of Georgia, Athens, GA, USA; Montana State University, Bozeman, MT, USA (M. A. Ivie, R. Miller); Museum and Institute of Zoology, Polish Academy of Sciences, Warsaw (D. Iwan, W. Tomaszewska); Museum of Comparative Zoology, Harvard University, Cambridge, MA, USA (P. D. Perkins, D. McKenna, B. Farrell); New Zealand Arthropod Collection, Landcare Research, Auckland, New Zealand (R. A. Leschen); J. Nunn, Dunedin, New Zealand; S. B. Peck, Department of Biology, Carleton University, Ottawa, Canada; M. A. Perotti, University of Reading, UK; K. Philips, Department of Biology, Western Kentucky University, Bowling Green, KY, USA; H. Pohl, Universität Rostock, Rostock, Germany; D. Pollock, Department of Biology, Eastern New Mexico University, Portales, NM, USA; Queensland Museum, Brisbane, Qld, Australia (C. Lambkin, G. Thompson, G. Monteith, F. Turco); C. A. M. Reid, The Australian Museum, Sydney, Australia; J. Růžička, Department of Ecology, Faculty of Environmental Sciences, Czech University of Life Sciences, Prague, Czech Republic; Snow Entomological Collections, Division of Entomology, University of Kansas, Lawrence, KS, USA (Z. Falin, G. Byers); A. Solodovnikov, Zoological Musuem, Natural History Museum of Denmark, Copenhagen, Denmark; P. Švácha, Institute of Entomology, Czech Academy of Sciences, České Budějovice, Czech Republic; United States Department of Agriculture Systematic Entomology Laboratory and Smithsonian Institution, Washington, DC, USA (T. Erwin, D. Furth, G. Hevel, A. Konstantinov, L. Roberts, W. Steiner, N. Vandenberg); M. G. Volkovitsh, Zoological Institute, Russian Academy of Sciences, St. Petersburg, Russia; M. F. Whiting, Department of Biology, Brigham Young University, Provo, UT, USA; A. Wild, Department of Entomology, University of Illinois, Urbana-Champaign, IL, USA.

A. Hastings (CSIRO Ecosystem Sciences) is gratefully acknowledged for her artwork and graphics skills. Thanks are given to Field Museum interns J-C. Martínez, G. Brilmyer and G. Krause for imaging and for difficult specimen disarticulations. Several of the color images of prothoraces were modified from original line drawings by Hlavac (1975), those of male and female abdominal apices of Torridincolidae from original line drawings by Reichardt & Vanin (1976, 1977), and those of metendosternites from original line drawings by Crowson (1938, 1944, 1955). JFL would like to express his sincere gratitude to his wife, Rachel, who put up with him for the past five years during the grueling task of coding, and to three colleagues who taught him, each in their own way, how to interpret and utilize morphological features of Coleoptera: T. F. Hlavac, J. Kukalová-Peck and the late R. A. Crowson. We are indebted to R. A. B. Leschen and W. Tomaszewska for reviewing an earlier version of this manuscript.

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Received: 8 March, 2011
Accepted: 20 March, 2011

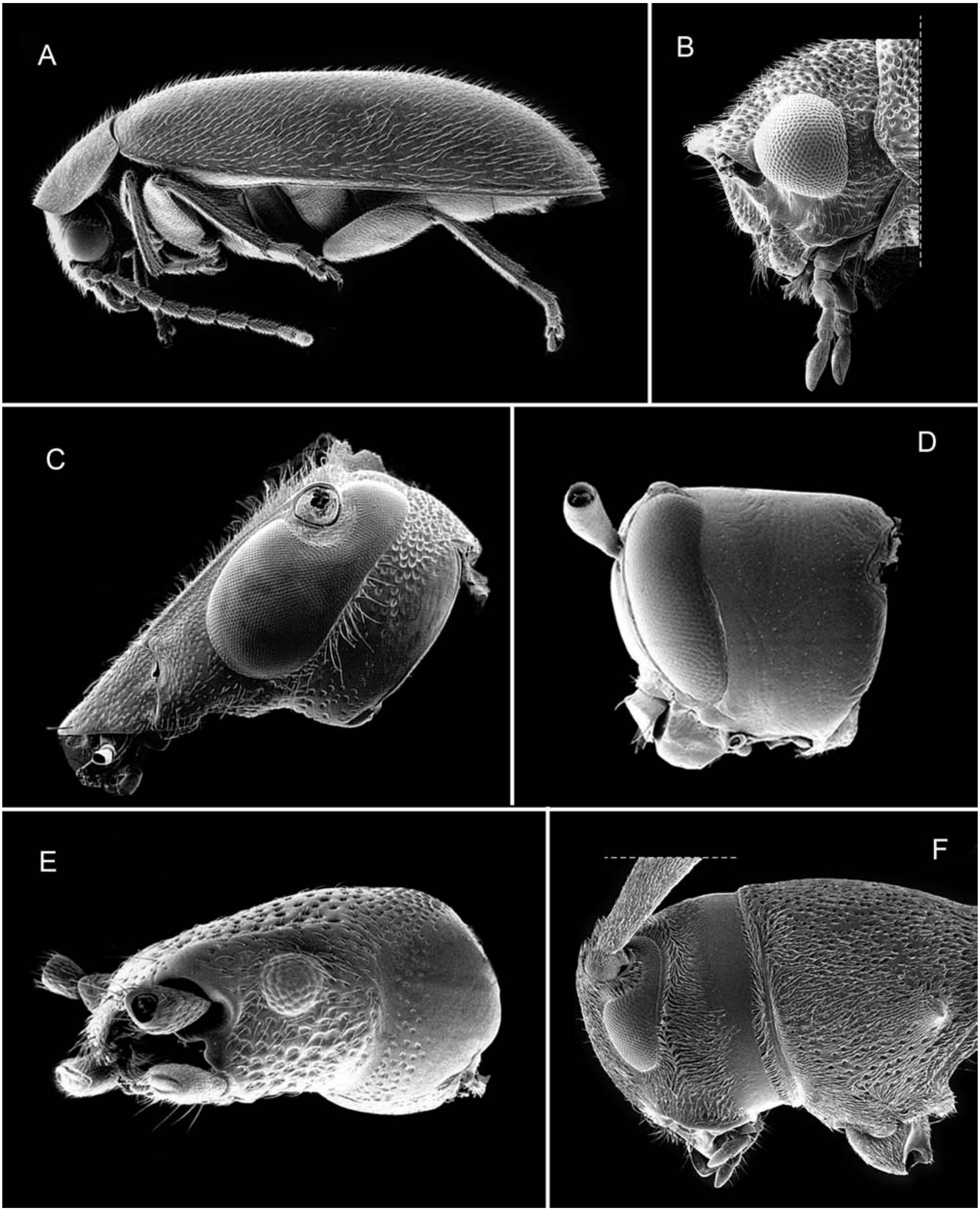


Figure 1. Adult Coleoptera. (A) *Pseudomicrocara variabilis* Armstrong (Scirtidae), habitus, lateral; (B–F). Heads, lateral. (B) *Rousia dumbrelium* Calder (Elateridae). (C) *Hesthesis* sp. (Cerambycidae). (D) *Aspidimorpha* sp. (Chrysomelidae). (E) *Laena* sp. (Tenebrionidae). (F) *Dectes* sp. (Cerambycidae).

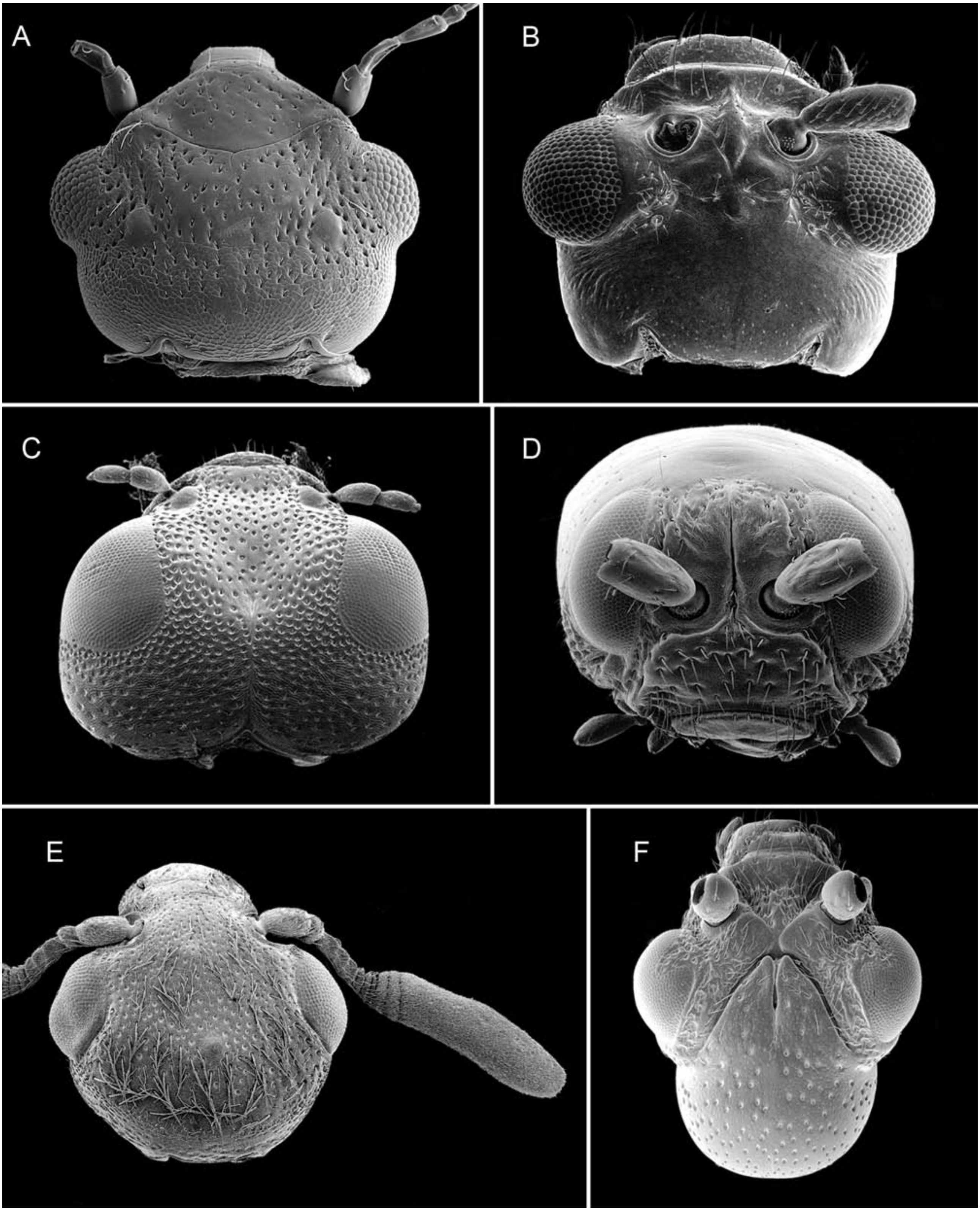


Figure 2. Adult Coleoptera heads. (A) *Glypholoma pecki* Thayer & Newton (Staphylinidae), dorsal. (B) *Cryptophagus cellaris* (Scopoli) (Cryptophagidae), dorsal. (C) *Castiarina* sp. (Buprestidae), dorsal. (D) *Chelymorpha* sp. (Chrysomelidae), anterodorsal. (E) *Attagenus pellio* (Linnaeus) (Dermestidae), dorsal. (F) *Crioceris asparagi* (Linnaeus) (Chrysomelidae).

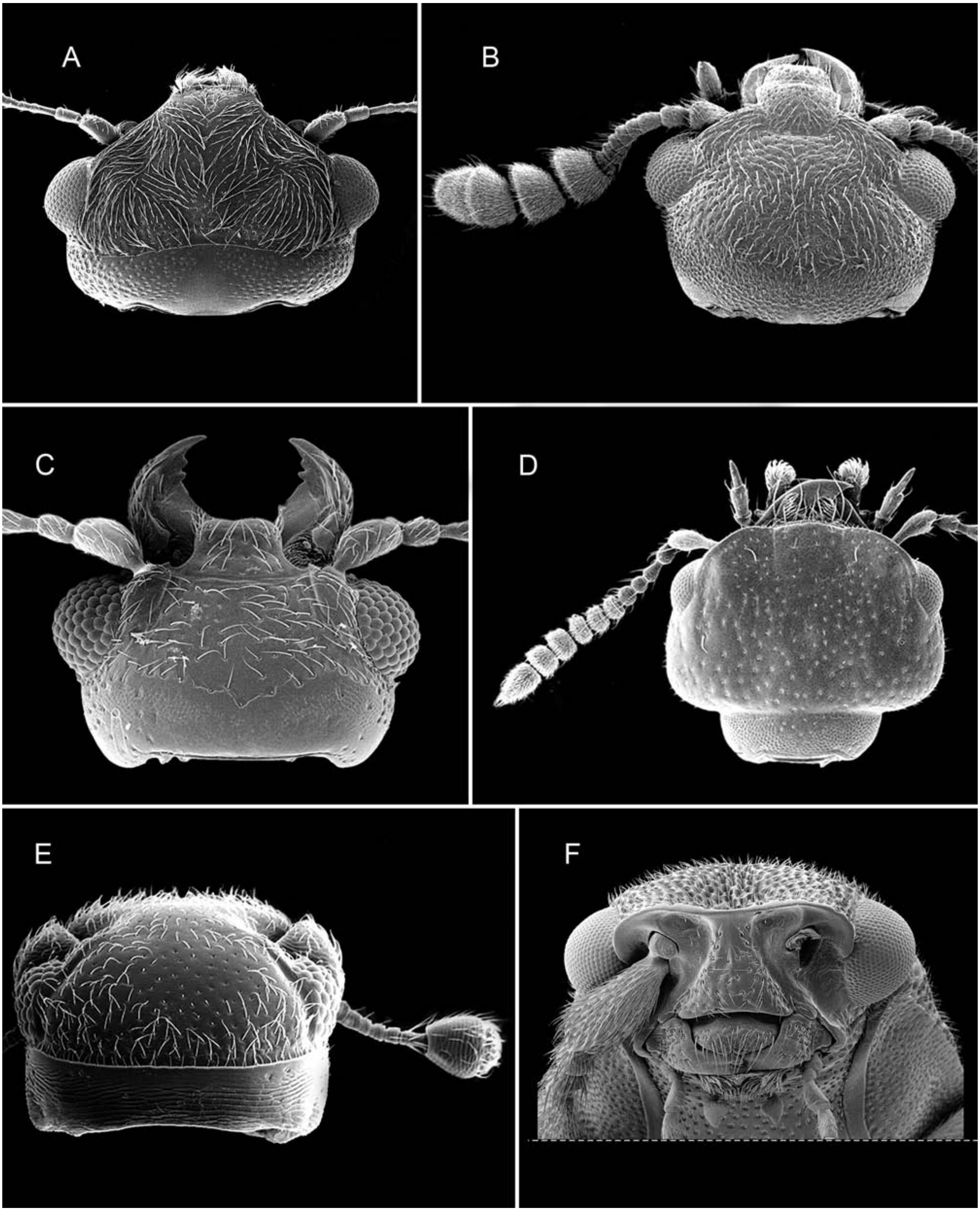


Figure 3. Adult Coleoptera heads. (A) *Cryptarcha australis* Reitter (Nitidulidae), dorsal. (B) *Notopisenus boleti* Nikitsky & Lawrence (Tetratomidae), dorsal. (C) *Boganium* sp. (Boganiidae), dorsal. (D) *Anotylus* sp. (Staphylinidae), dorsal. (E) *Murmidius ovalis* (Beck) (Cerylonidae), dorsal. (F) *Rousia dumbrelium* Calder (Elateridae), anterior.

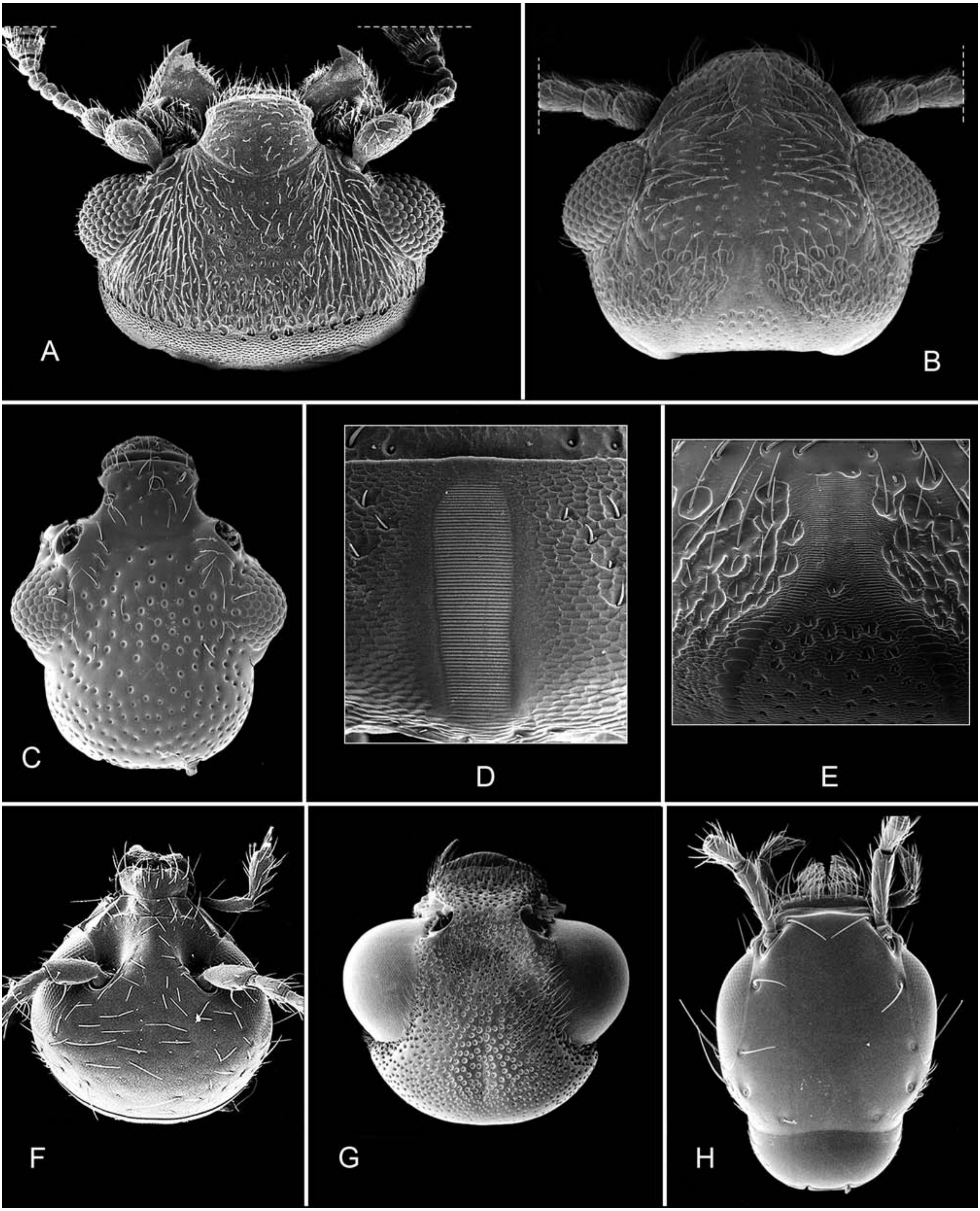


Figure 4. Adult Coleoptera heads. (A) *Sphindus americanus* LeConte (Sphindidae), dorsal. (B) *Cnecosa insueta* (Crotch) (Erotylidae), dorsal. (C) *Hymaea succinifera* Pascoe (Phloeostichidae), dorsal. (D) *Leucohimatium arundinaceum* (Forskål) (Erotylidae), occipital region, dorsal, with single stridulatory file. (E) *Cnecosa insueta* (Crotch) (Erotylidae), occipital region, dorsal, with paired stridulatory files. (F) *Aleochara* sp. (Staphylinidae), dorsal. (G) *Ennometes* sp. (Callirhipidae), dorsal. (H) *Quedius* sp. (Staphylinidae), dorsal.

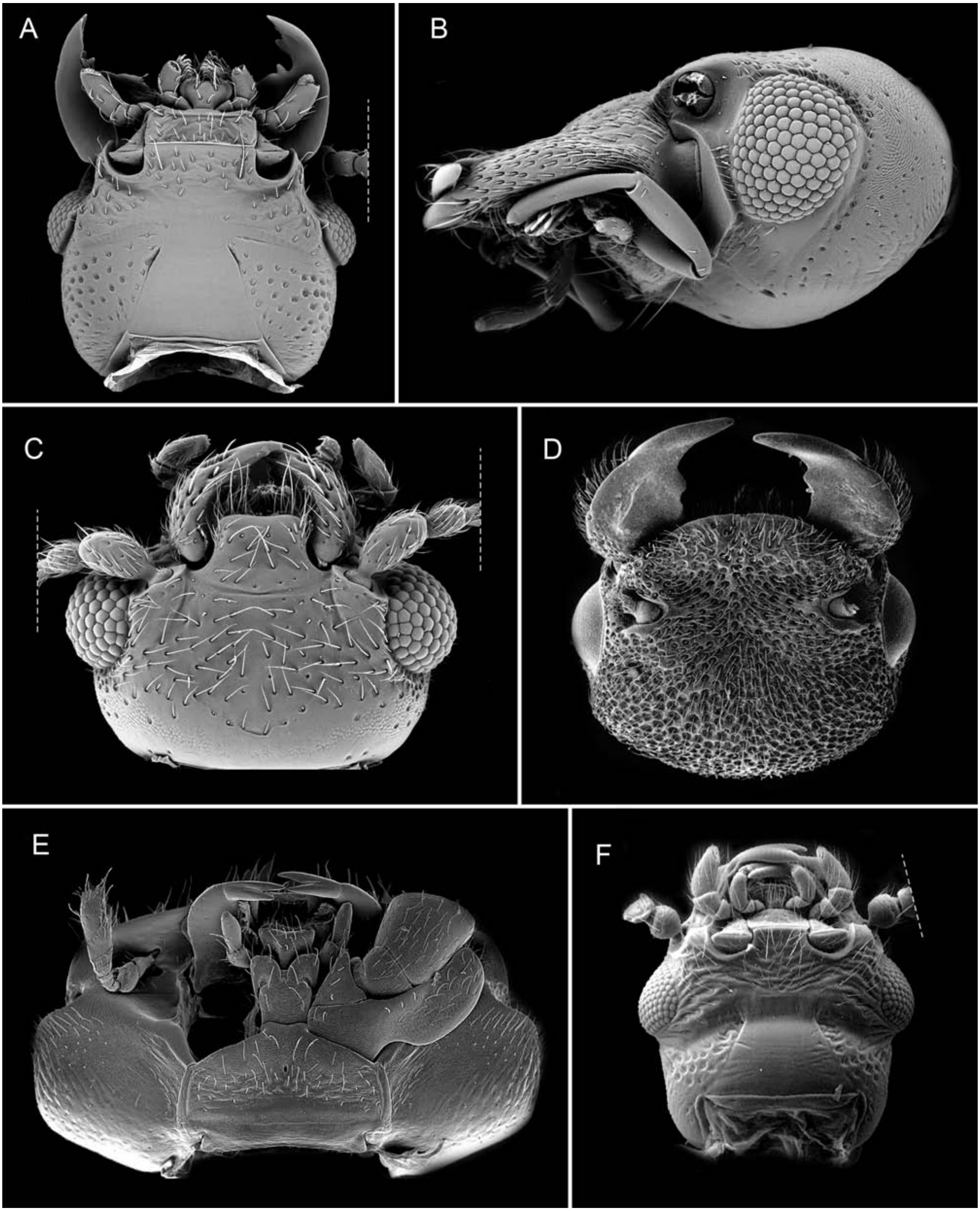


Figure 5. Adult Coleoptera heads. (A) Genus ? sp. (Salpingidae), ventral. (B) *Paracucujus rostratus* Sen Gupta & Crowson (Boganiidae), lateral. (C) *Boganium* sp. (Boganiidae), dorsal. (D) *Hemiops* sp. (Eucnemidae), dorsal. (E) *Platynaspis* sp. (Coccinellidae), ventral. (F) *Rhizonium antiquum* Sharp (Family ?), ventral.

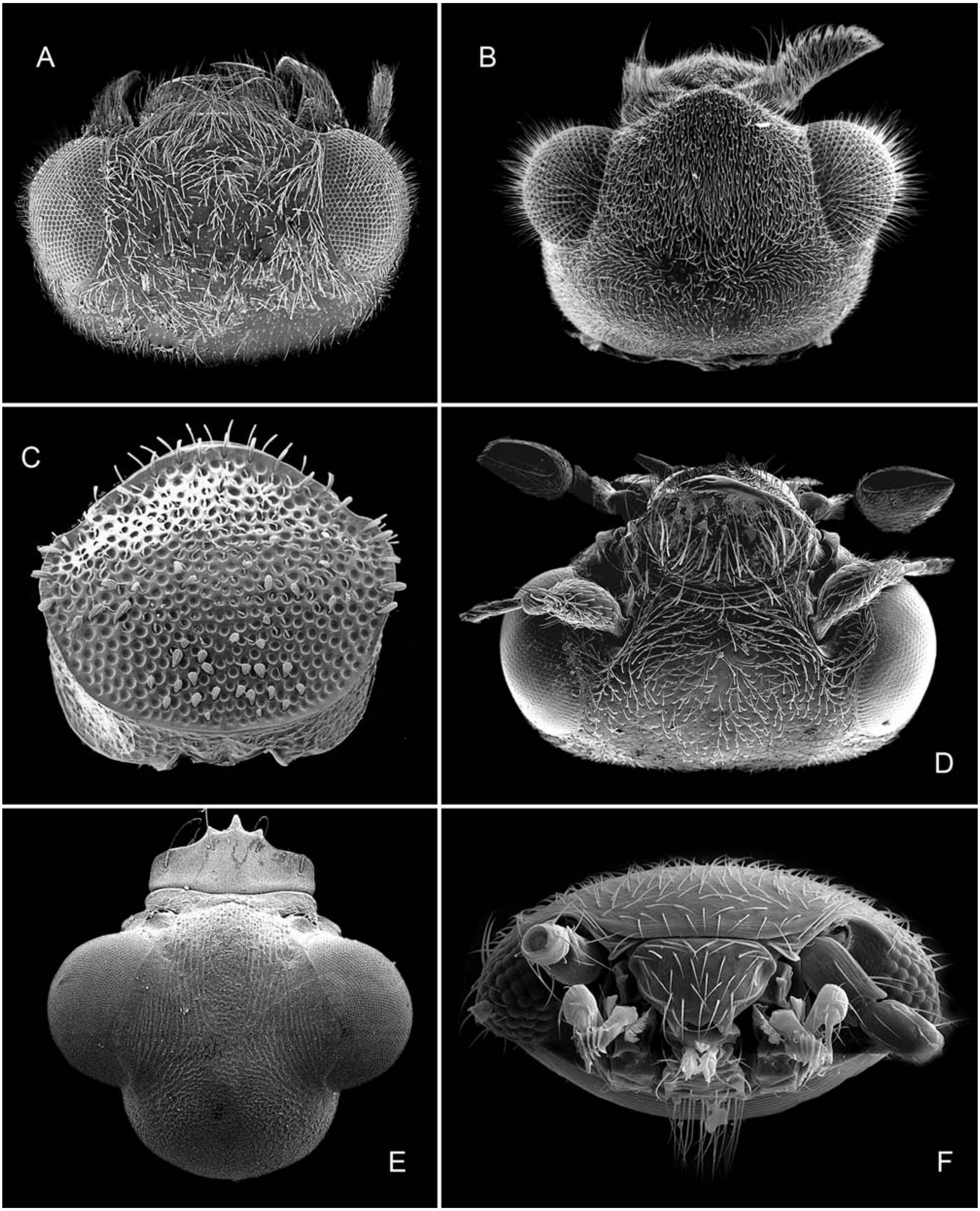


Figure 6. Adult Coleoptera heads. (A) *Rodolia* sp. (Coccinellidae), dorsal. (B) *Pelonomus* sp. (Dryopidae), dorsal. (C) *Microchaetes* sp. (Byrrhidae), dorsal. (D) *Epilachna* sp. (Coccinellidae), anterodorsal. (E) *Cicindela* sp. (Carabidae), dorsal. (F) *Acrotrichis* sp. (Ptiliidae), anterior.

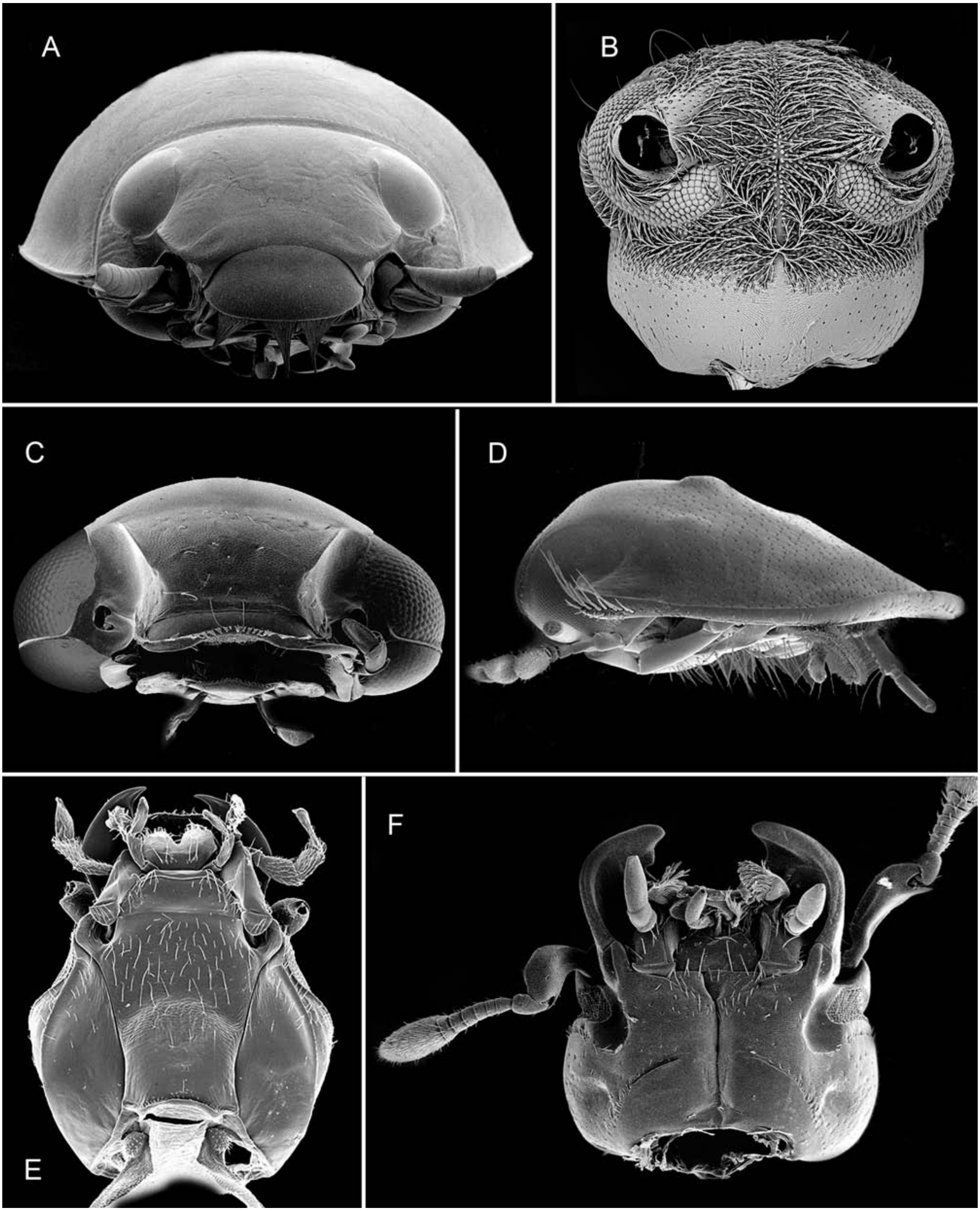


Figure 7. Adult Coleoptera heads. (A) *Macrogyrus* sp. (Gyrinidae), anterior. (B) *Sybra* sp. (Cerambycidae), dorsal. (C) *Spanglerogyrus albiventris* Folkerts (Gyrinidae), anterior. (D) *Acrossidius tasmaniae* (Hope) (Scarabaeidae), anterolateral. (E) *Pseudomicrocara* sp. (Scirtidae), ventral. (F) *Platysoma* sp. (Histeridae), ventral.

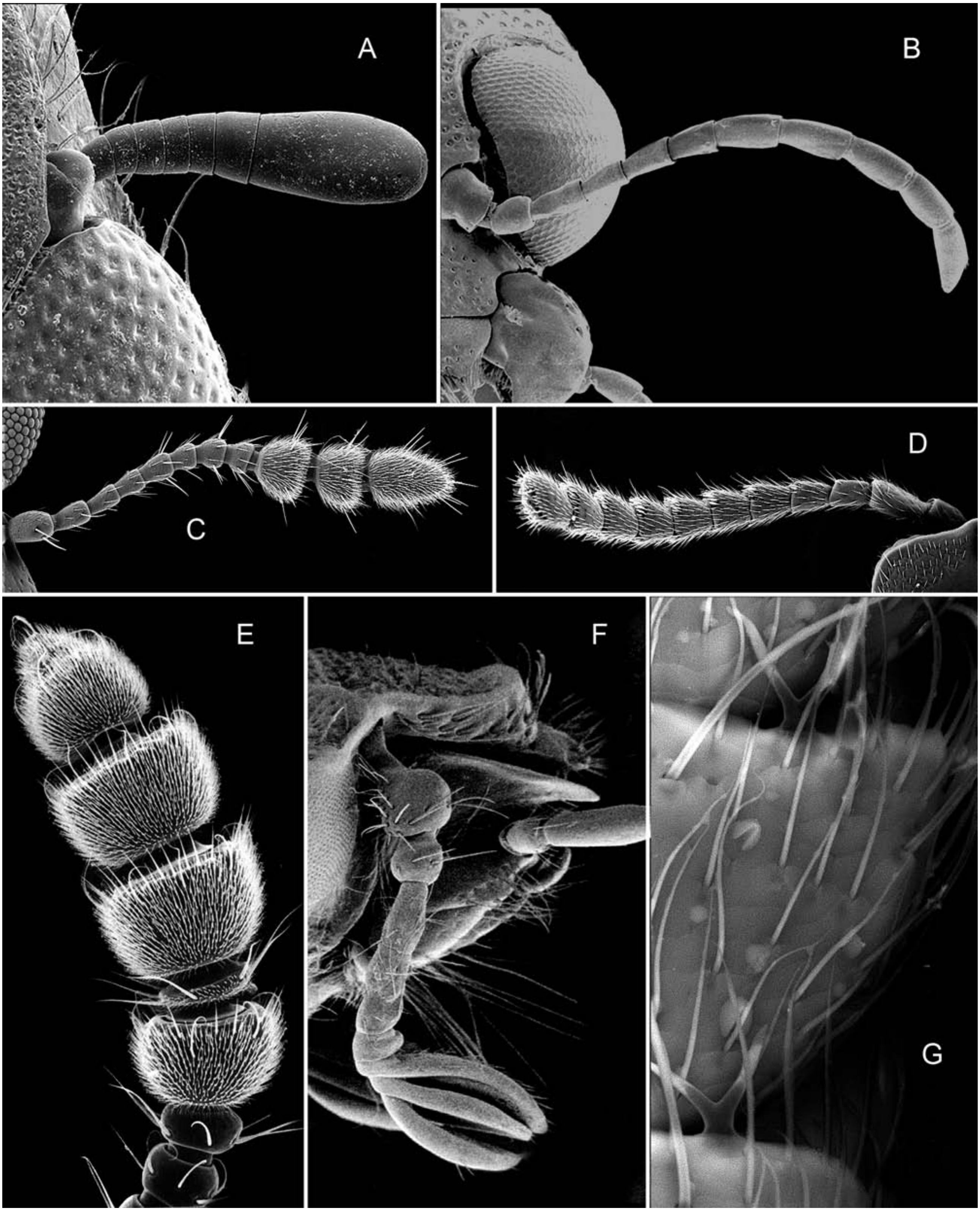


Figure 8. Adult Coleoptera antennae. (A) *Ytu zeus* Reichardt (Torridincolidae). (B) *Haliplus* sp. (Halilpidae). (C) Genus ? sp. (Salpingidae). (D) *Eucinetus* sp. (Eucinetidae). (E) *Macrohydnobius crestonensis* (Hatch) (Leiodidae), club only. (F) *Phyllopertha horticola* (Linnaeus) (Scarabaeidae). (G) *Peripytctus* sp. (Corylophidae), preapical antennomere only.

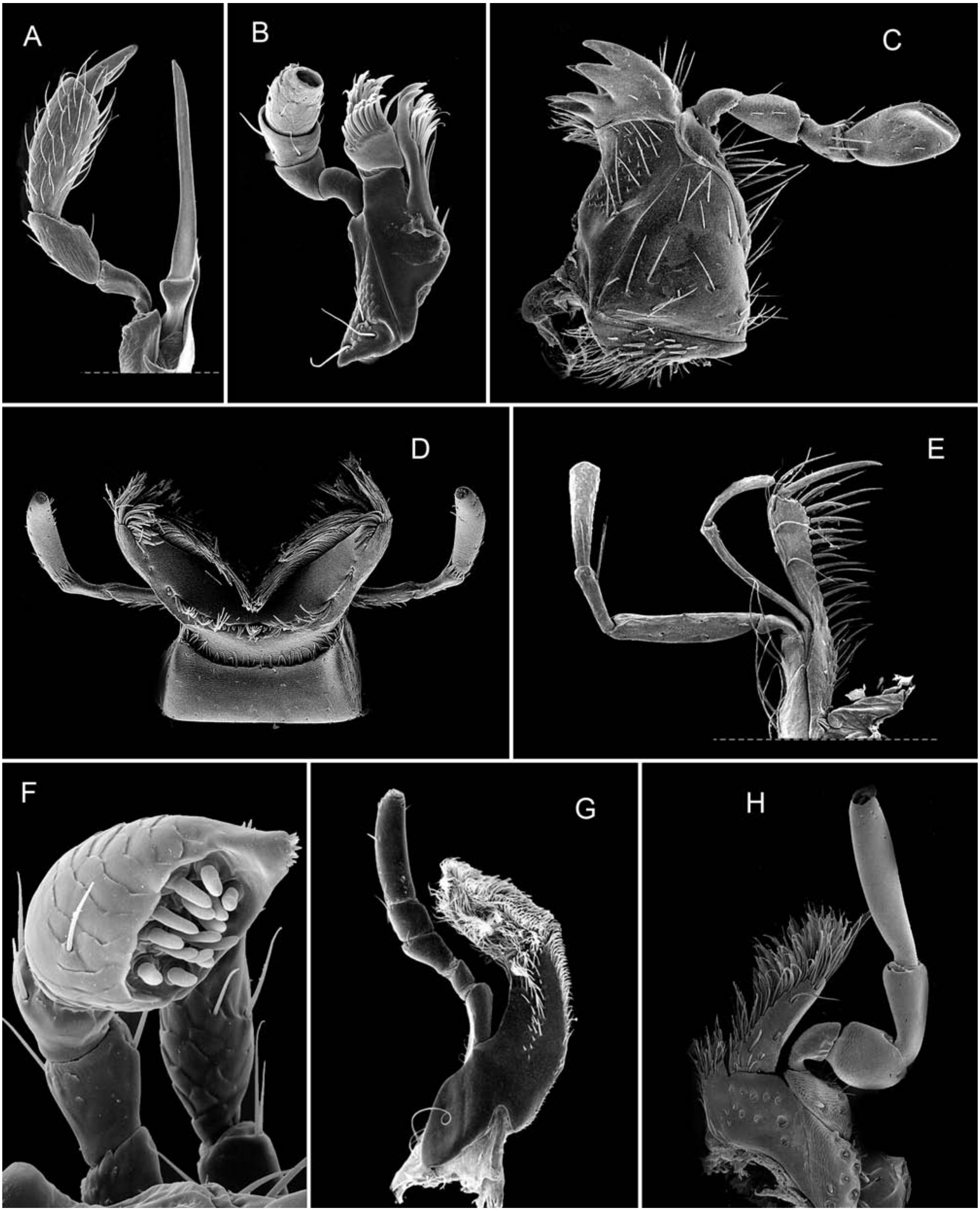


Figure 9. Adult Coleoptera ventral mouthparts. (A) *Glyptolopus* sp. (Cerylonidae), maxilla. (B) *Chiliotis* sp. (Cryptophagidae), maxilla. (C) *Phyllopertha horticola* (Linnaeus) (Scarabaeidae), maxilla. (D) *Passandra* sp. (Passandridae), labium. (E) *Cicindela* sp. (Carabidae), maxilla. (F) *Micromalthus debilis* LeConte (Micromalthidae), apical maxillary palpomere. (G) *Glischrochilus* sp. (Nitidulidae), maxilla. (H) *Ceratognathus niger* Westwood (Lucanidae), maxilla.

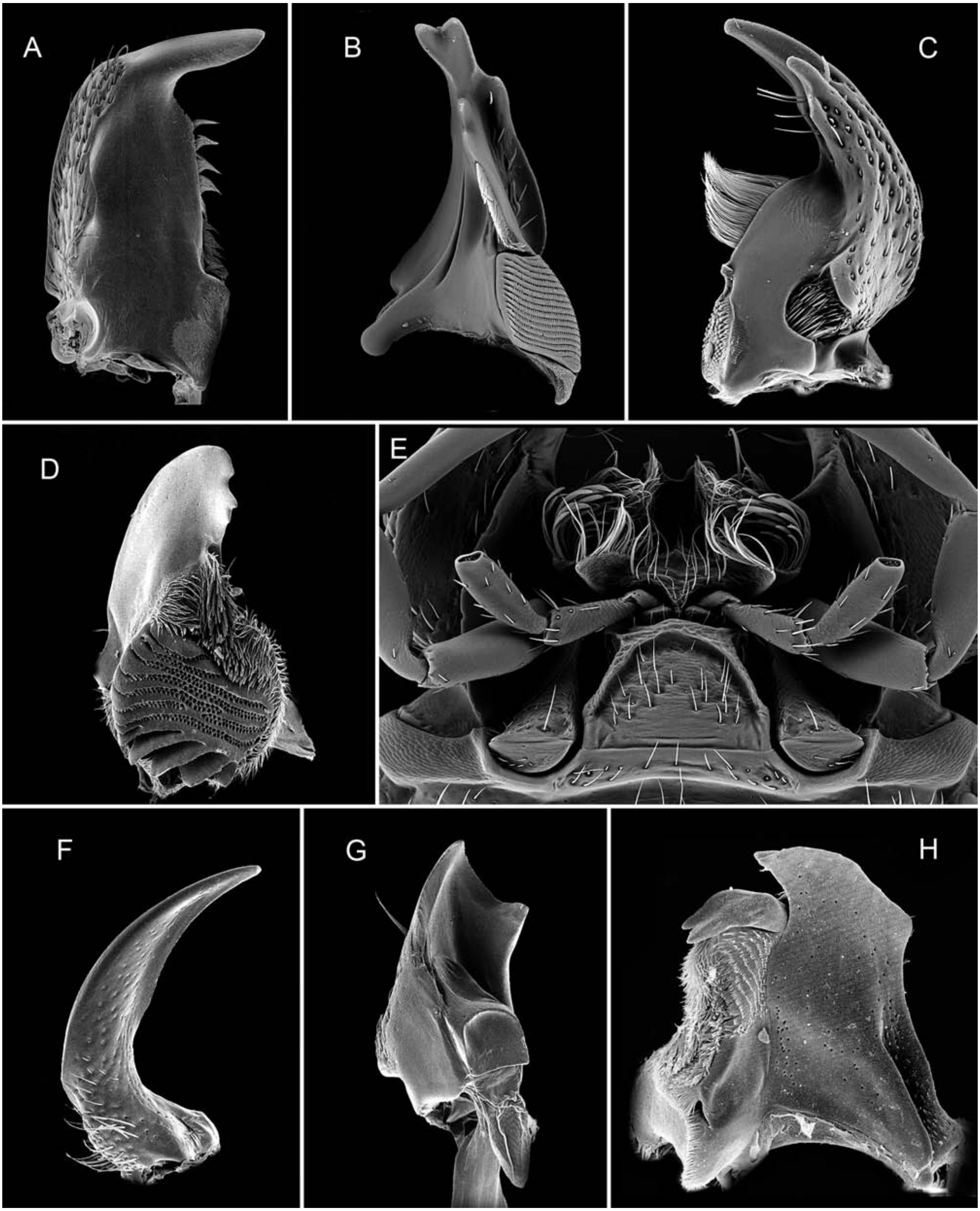


Figure 10. Adult Coleoptera mouthparts. (A) *Eulichas* sp. (Eulichadidae), mandible, dorsal. (B) Genus ? (Salpingidae), mandible, mesal. (C) *Paracucujus rostratus* Sen Gupta & Crowson (Boganiidae), mandible, dorsal. (D) *Phyllopertha horticola* (Linnaeus) (Scarabaeidae), mandible, mesal. (E) *Paracucujus rostratus* Sen Gupta & Crowson (Boganiidae), labium. (F) *Phengodes* frontalis Leconte (Phengodidae), mandible, dorsal. (G) *Euparius* sp. (Anthribidae), mandible, mesal. (H) *Meropathus* sp. (Hydraenidae), mandible, ventral.

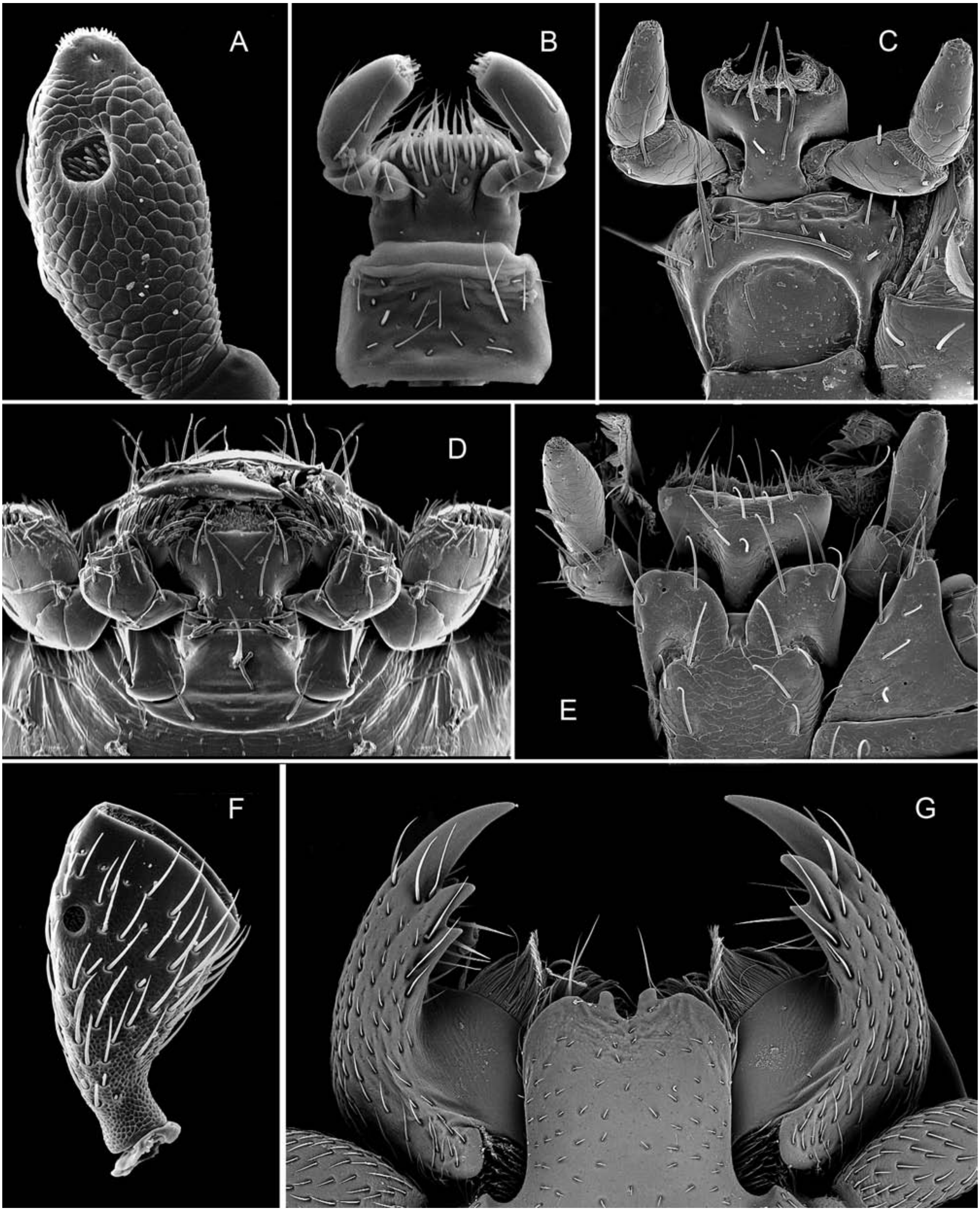


Figure 11. Adult Coleoptera mouthparts. (A) *Tetraphalerus* sp. (Ommatidae), apical maxillary palpomere. (B) *Rhizonium antiquum* Sharp (Family ?), labium. (C) *Rhyzobius* sp. (Coccinellidae), labium. (D) *Sphaerosoma* sp. (Alexiidae), maxillae & labium. (E) *Aspidimerus* sp. (Coccinellidae), labium. (F) *Omma rutherfordi* Lawrence (Ommatidae), apical maxillary palpomere. (G) *Paracucujus rostratus* Sen Gupta & Crowson (Boganiidae), mandibles, dorsal.

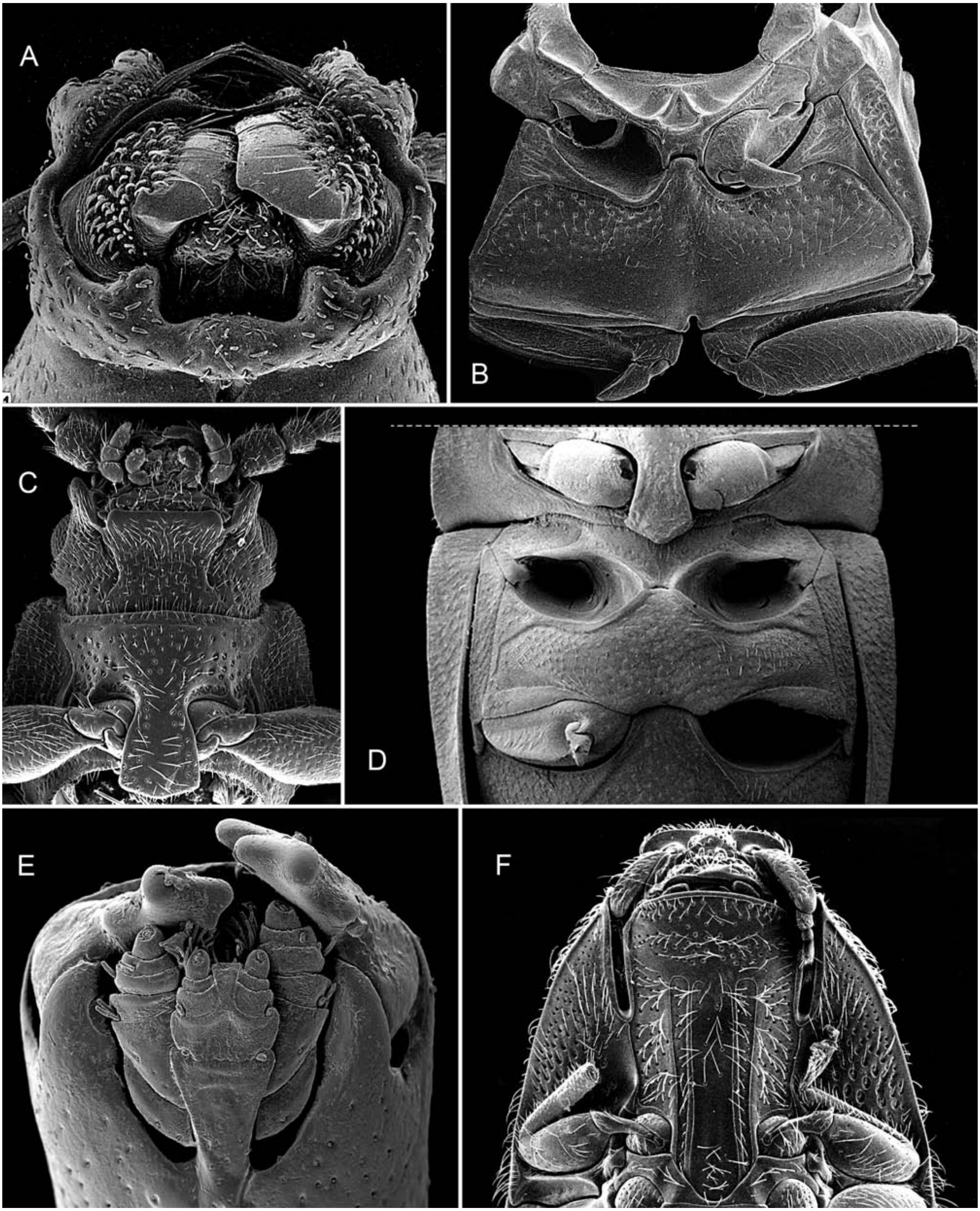


Figure 12. Adult Coleoptera. (A) *Talaurinus typicus* Macleay, mouthparts, anteroventral. (B) *Thymalus* sp. (Trogossitidae), pterothorax, ventral. (C) *Taphropiestes* sp. (Cavognathidae), head and prothorax, ventral. (D) *Thalycrodes* sp. (Nitidulidae), prothorax and pterothorax, ventral. (E) *Car* sp. (Caridae), mouthparts, ventral. (F) *Drapetes vicinus* Fleutiaux (Elateridae), head and prothorax, ventral.

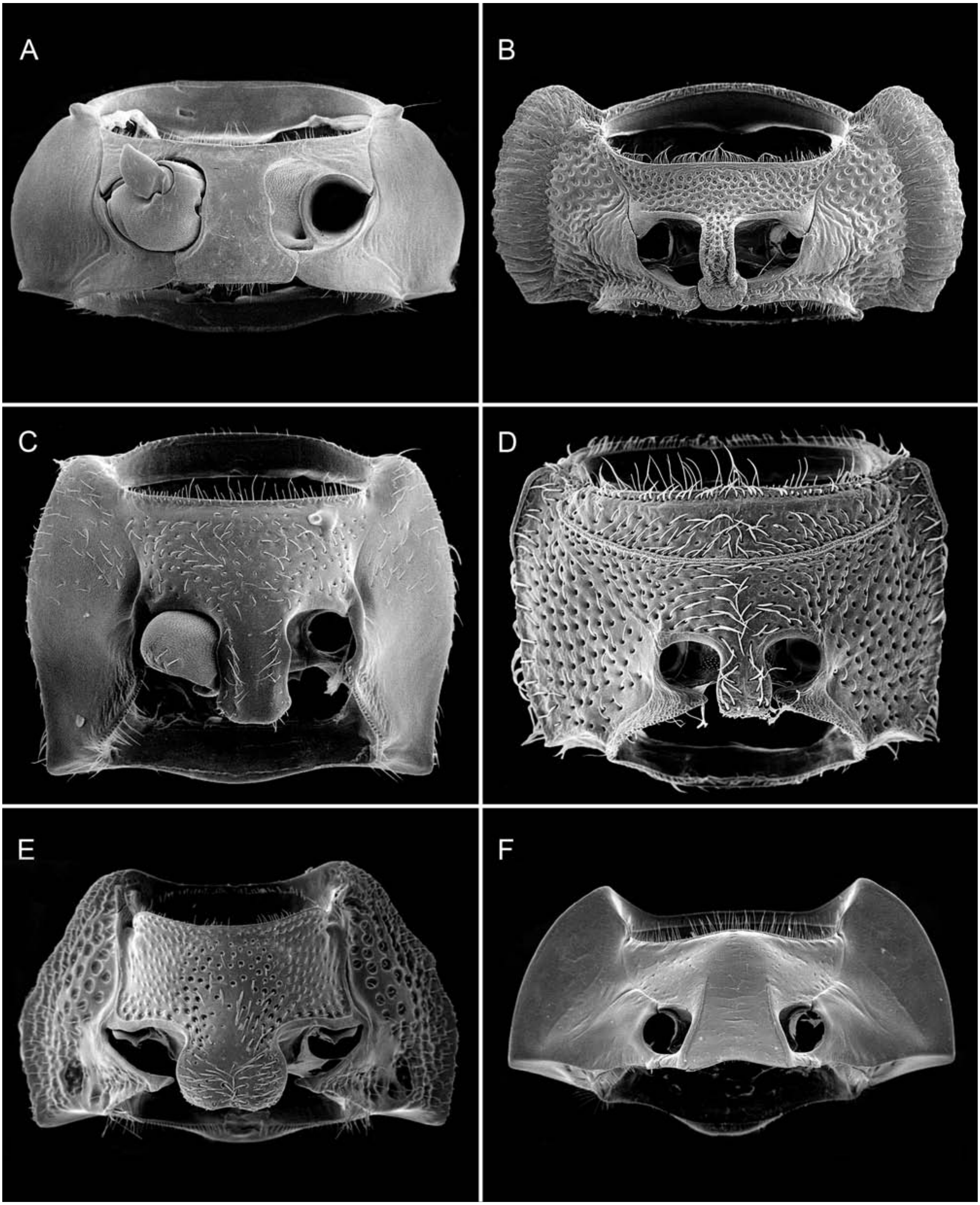


Figure 13. Adult Coleoptera prothoraces, ventral. (A) *Rhyparida* sp. (Chrysomelidae). (B) *Eleates depressus* (Randall) (Tenebrionidae). (C) *Cryptothylypterus pteropilosus* Leschen & Lawrence (Cryptophagidae). (D) *Leucohimatium arundinaceum* (Forskål) (Erotylidae). (E) *Priasilpha obscura* Broun (Priasilphidae). (F) *Aulacochilus* sp. (Erotylidae).

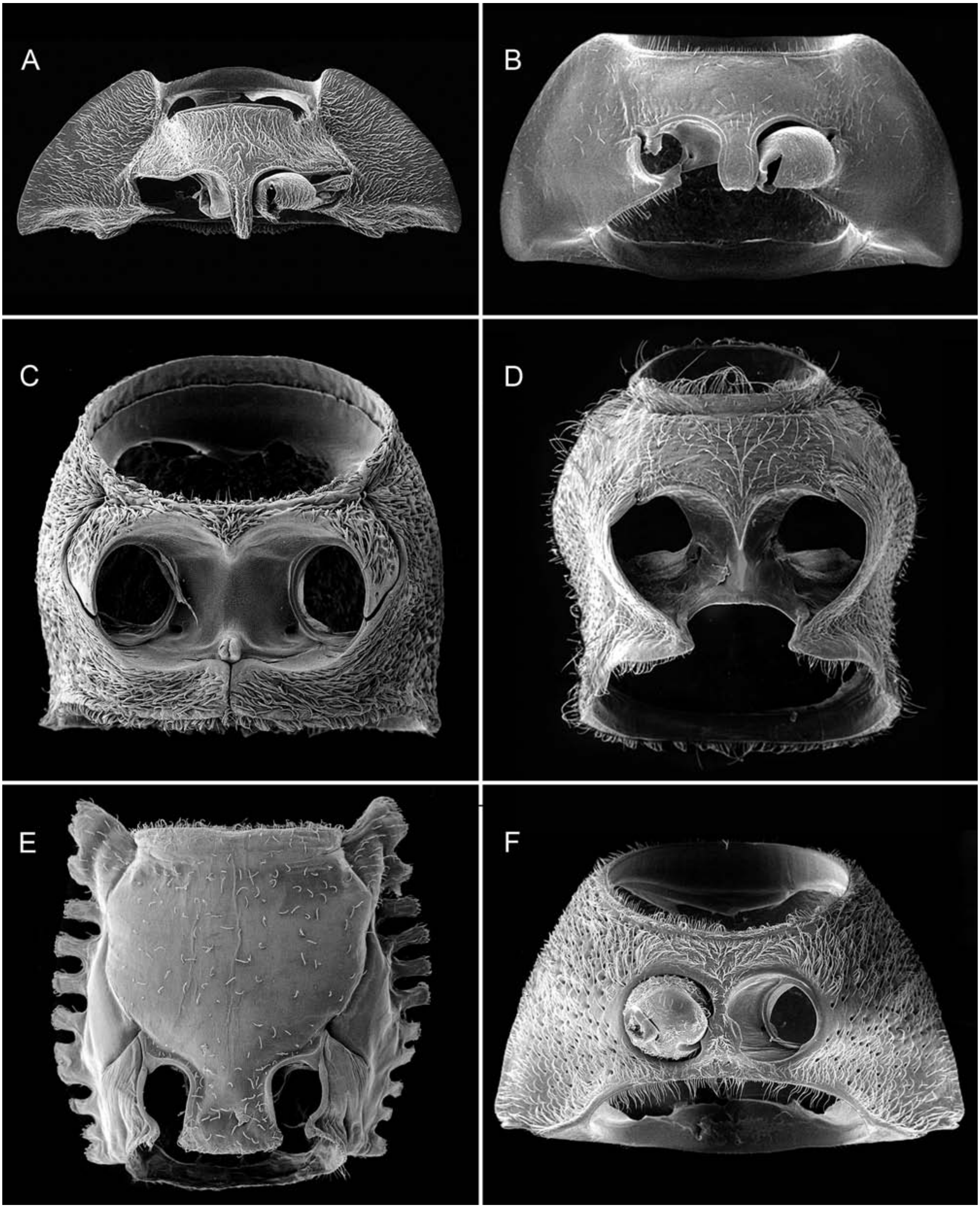


Figure 14. Adult Coleoptera prothoraces, ventral. (A) *Sclerocyphon* sp. (Psephenidae). (B) *Filicivora chilensis* (Philippi & Philippi). (C) *Ithycerus noveboracensis* (Forster) (Brentidae). (D) *Pergetus campanulatus* (Leconte) (Anthicidae). (E) *Brontopriscus* sp. (Silvanidae). (F) *Araecerus coffeae* (Fabricius) (Anthribidae).

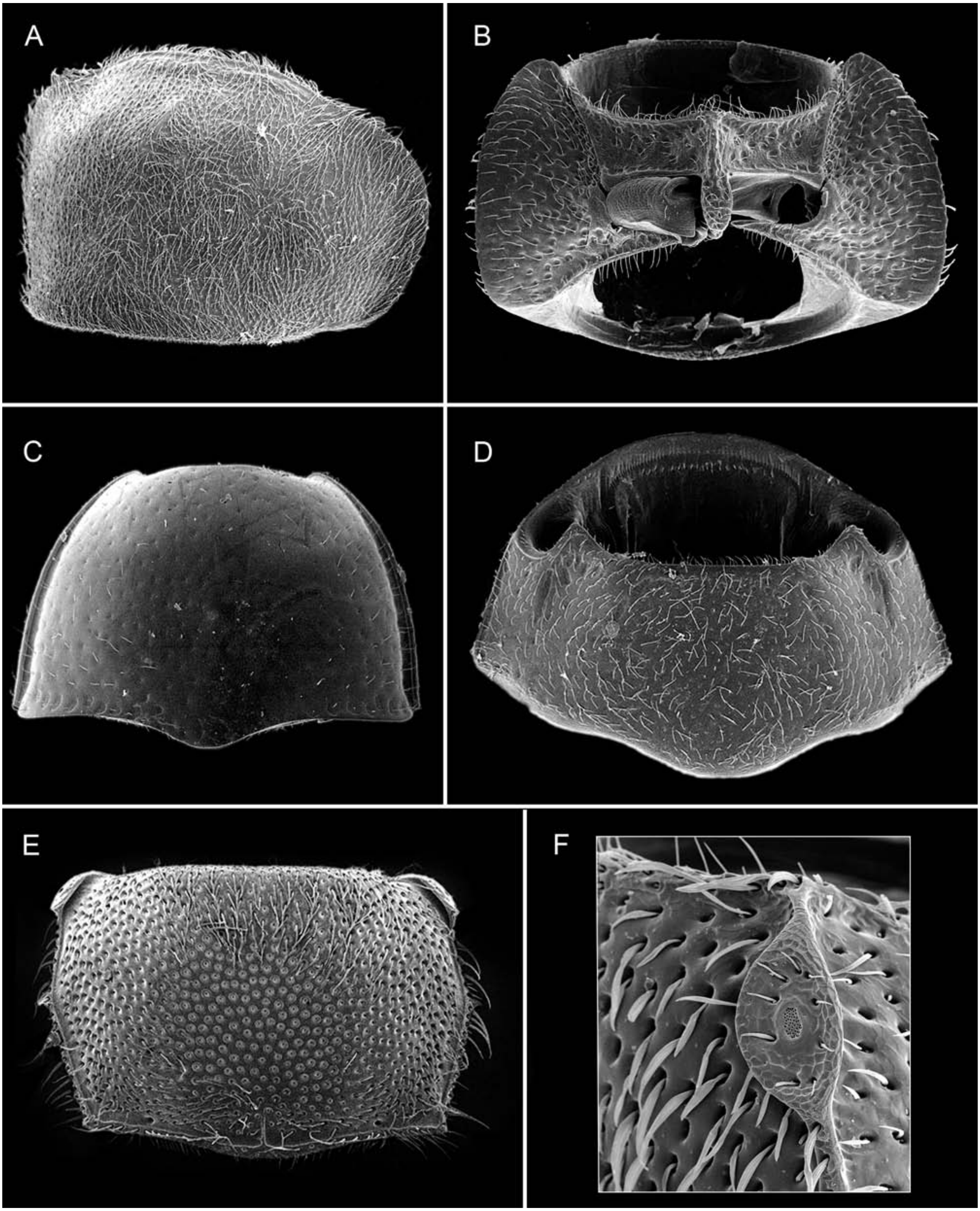


Figure 15. Adult Coleoptera prothoraces. (A) *Ernobius mollis* (Linnaeus) (Ptinidae), posterodorsolateral. (B) *Cis* sp. (Ciidae), ventral. (C) *Mychocerus discretus* (Casey) (Cerylonidae), dorsal. (D) *Murmidius ovalis* (Beck) (Cerylonidae), dorsal. (E) *Cryptophagus cellaris* (Scopoli) (Cryptophagidae), dorsal. (F) Same, anterior pronotal angle, lateral.

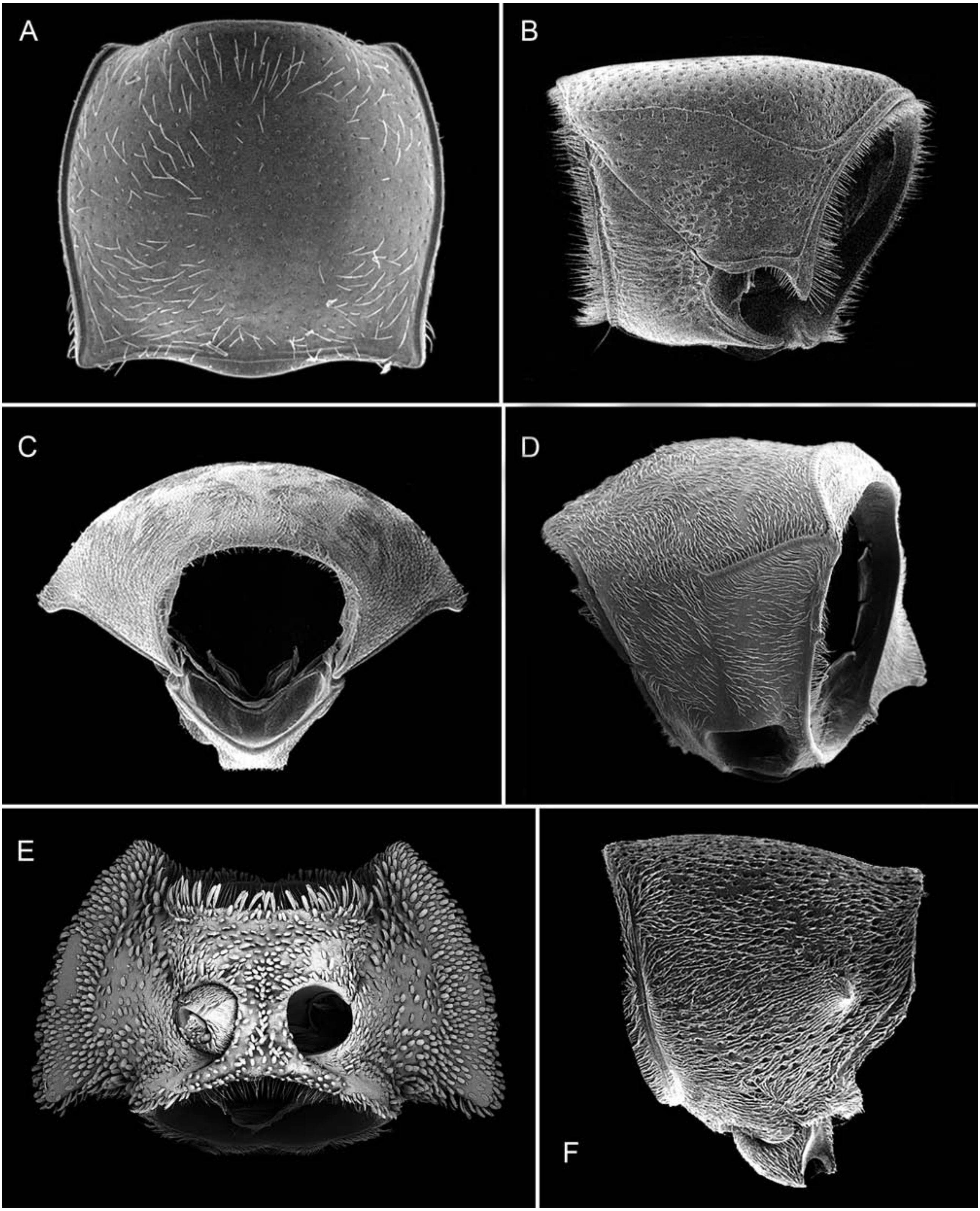


Figure 16. Adult Coleoptera prothoraces. (A) *Cryptothelypterus pteropilosus* Leschen & Lawrence (Cryptophagidae), dorsal. (B) *Synercticus heteromerus* Newman (Boridae), lateral. (C) *Byrrhus* sp. (Byrrhidae), anterior. (D) *Euparius* sp. (Anthribidae), ventrolateral. (E) *Ulodes* sp. (Ulodidae), ventral. (F) *Dectes* sp. (Cerambycidae), lateral.

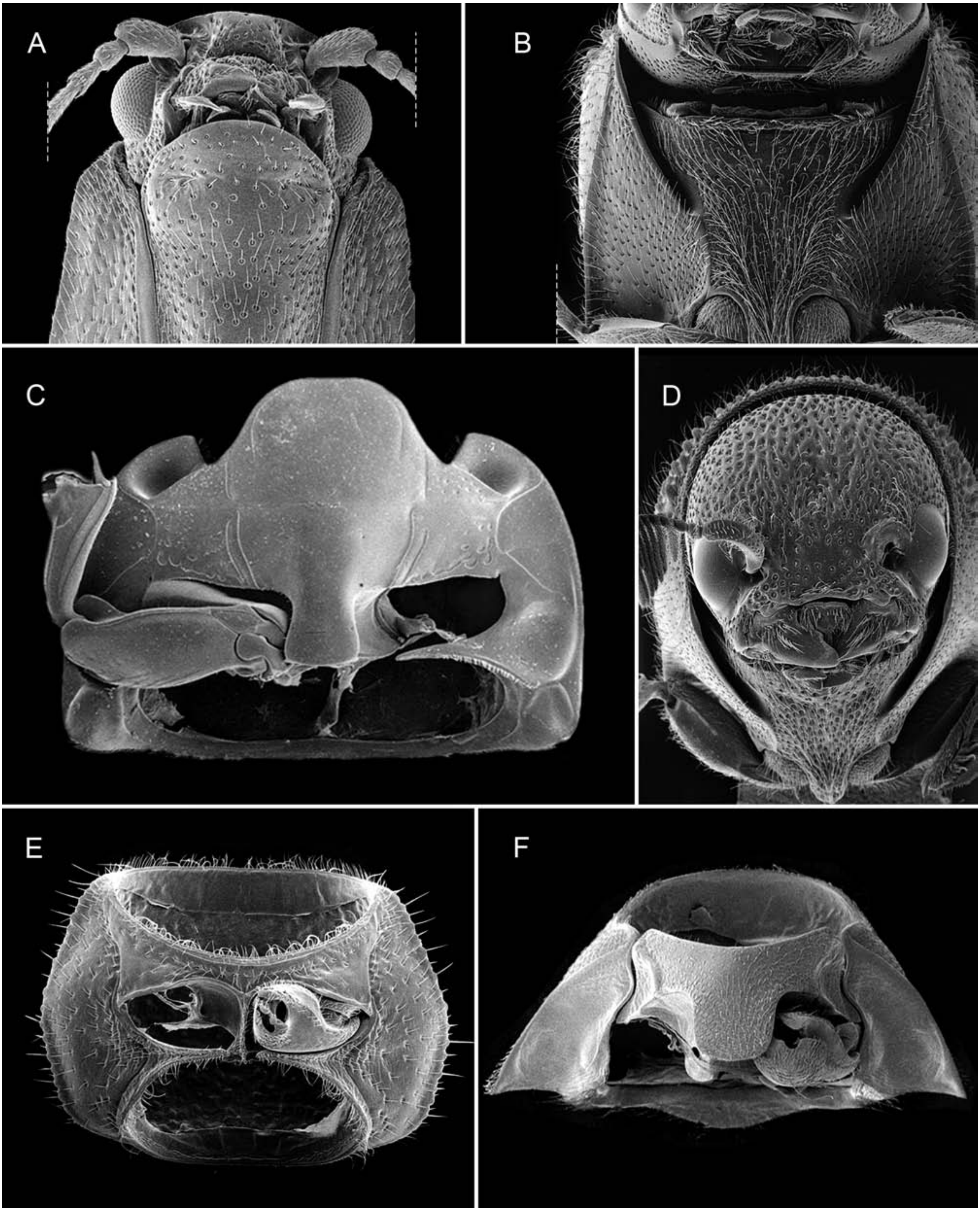


Figure 17. Adult Coleoptera. (A) *Parasaphes* sp. (Elateridae), head and prothorax, ventral. (B) *Cussolenis mutabilis* (Bonvouloir) (Elateridae), prothorax, ventral. (C) *Platysoma* sp. (Histeridae), ventral. (D) *Cussolenis mutabilis* (Bonvouloir) (Elateridae), head and prothorax, anterior. (E) *Necrobia rufipes* (Degeer) (Cleridae), prothorax, ventral. (F) *Byrrhus* sp. (Byrrhidae), prothorax, ventral.

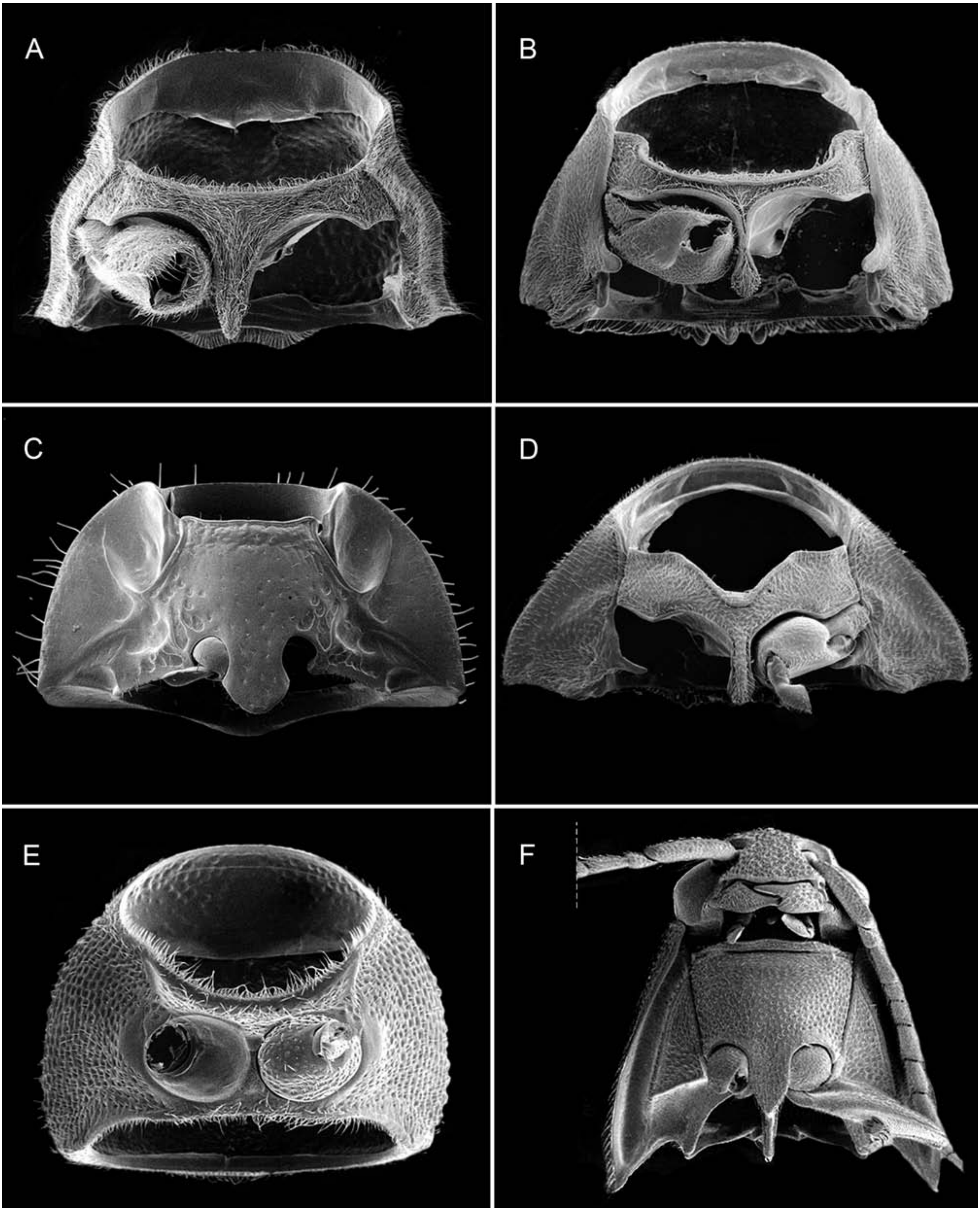


Figure 18. Adult Coleoptera prothoraces, ventral. (A) *Lara avara* LeConte (Elmidae). (B) *Araeopidius monachus* (LeConte) (Ptilodactylidae). (C) *Mychocerus discretus* (Casey) (Cerylonidae). (D) *Drupeus laetabilis* Lewis (Ptilodactylidae). (E) *Hylurgops* sp. (Curculionidae). (F) *Fornax* sp. (Eucnemidae), with attached head.

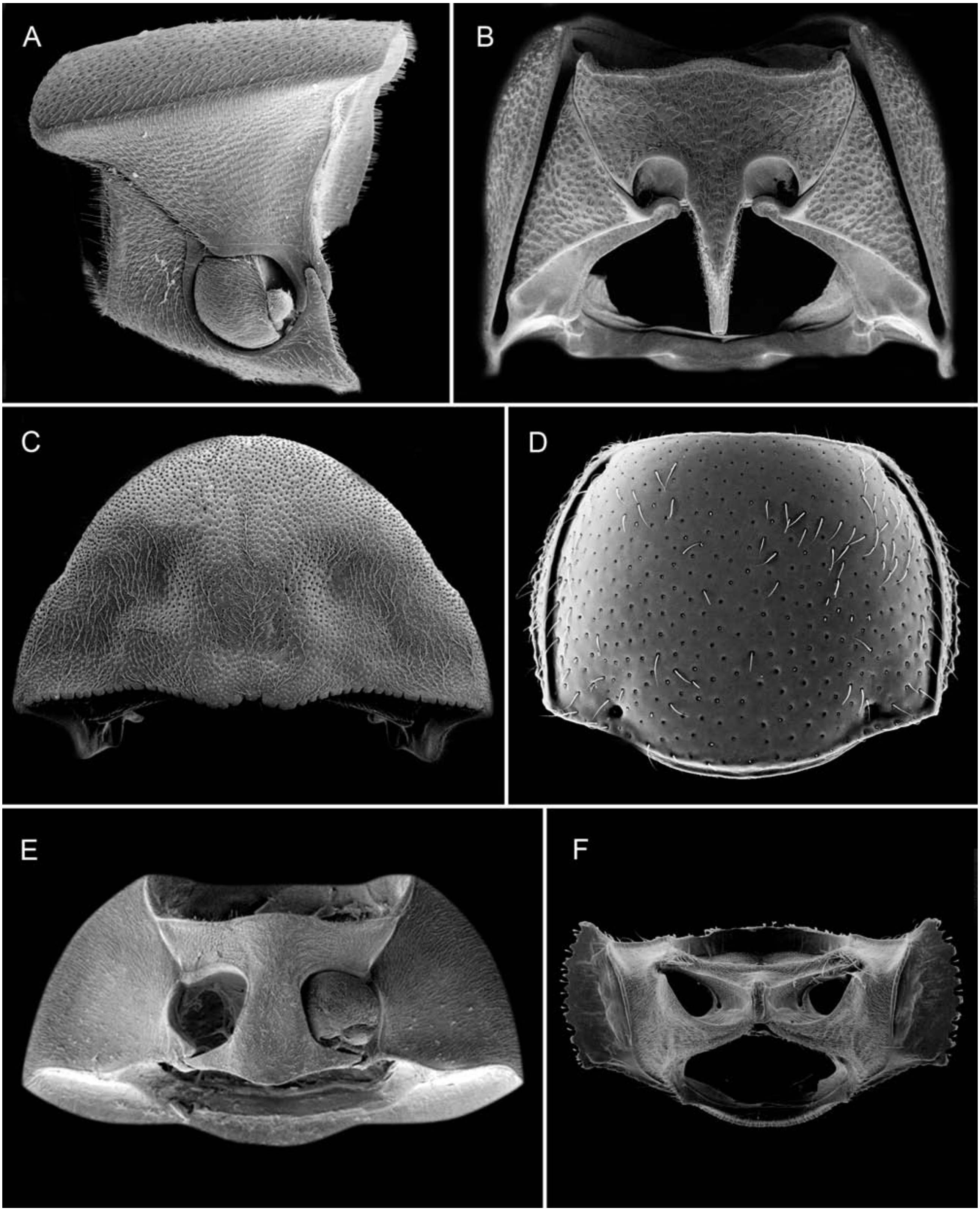


Figure 19. Adult Coleoptera prothoraces. (A) *Archeocrypticus topali* Kaszab (Archeocrypticidae), lateral. (B) *Galbites* sp. (Eucnemidae), ventral. (C) *Callirhipis reticulata* Lea (Callirhipidae), dorsal. (D) *Carinodulina* sp. (Coccinellidae), dorsal. (E) *Enneboeus* sp. (Archeocrypticidae), ventral. (F) *Spercheus platycephalus* Macleay (Hydrophilidae), ventral.

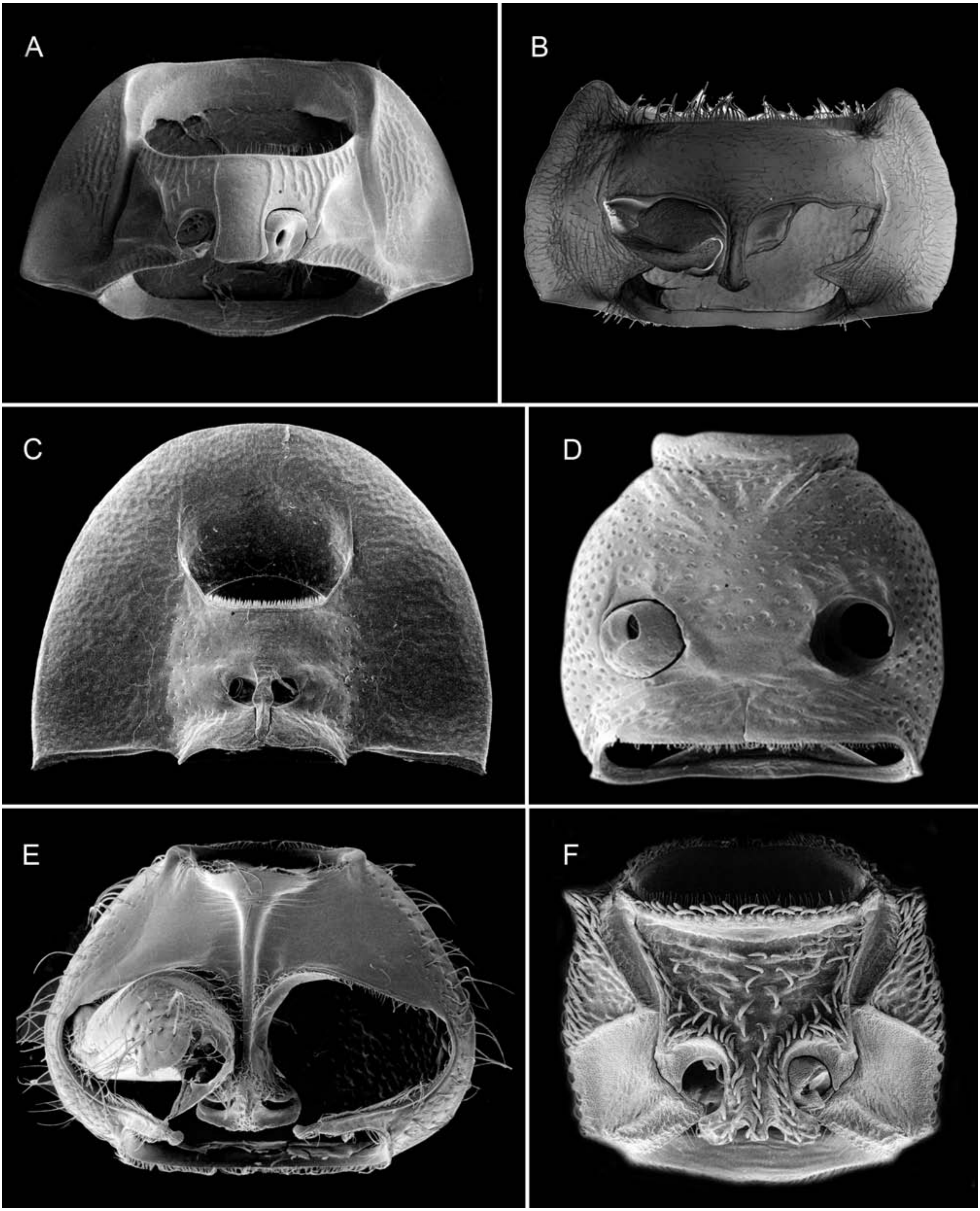


Figure 20. Adult Coleoptera prothoraces, ventral. (A) *Hyporhagus punctulatus* LeConte (Zopheridae). (B) *Grynocharis quadrilineata* (Melsheimer) (Trogossitidae). (C) *Cossyphus* sp. (Tenebrionidae). (D) *Cossonus* sp. (Curculionidae). (E) *Diphyllostoma* sp. (Diphyllostomatidae). (F) *Latometus* sp. (Zopheridae).

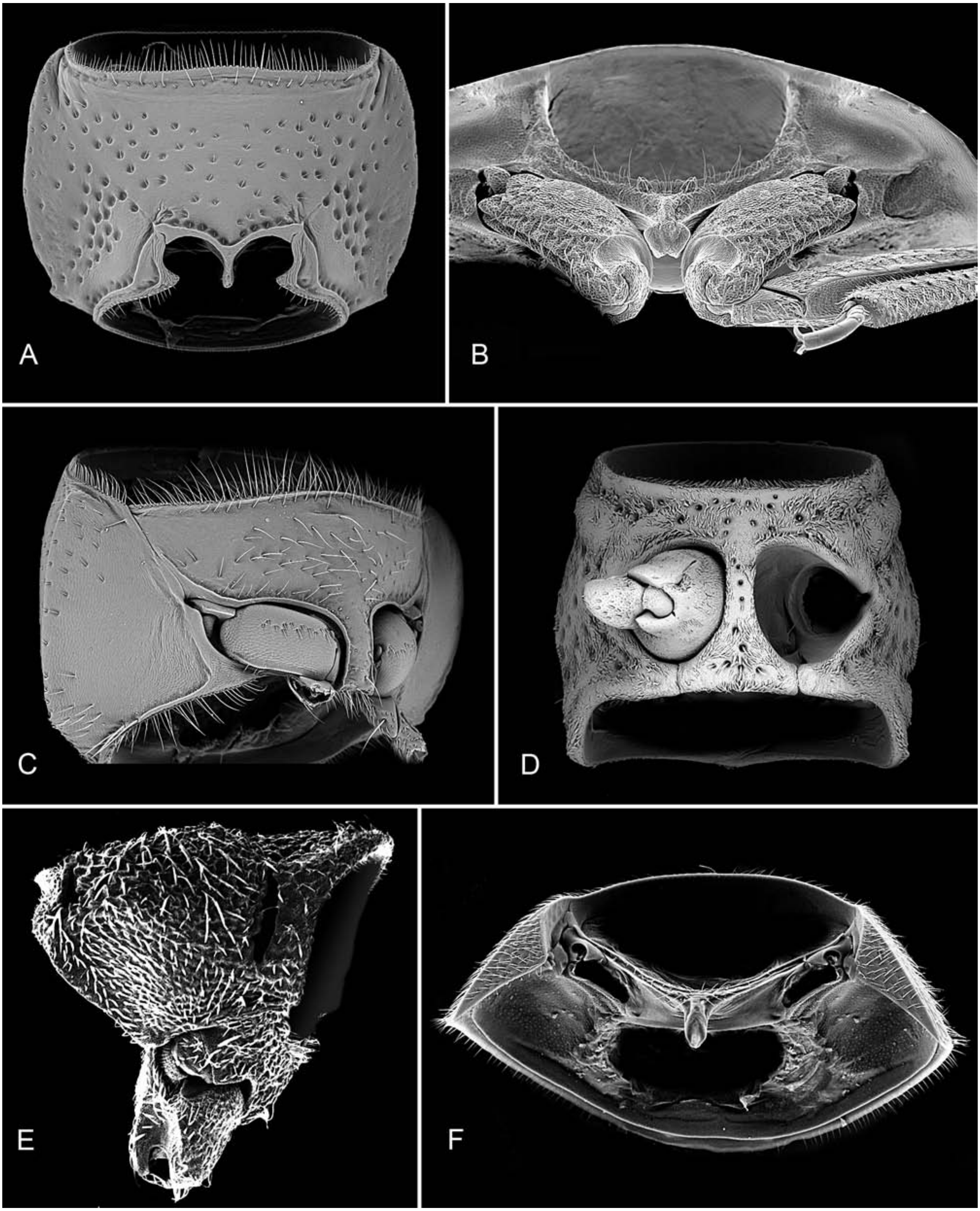


Figure 21. Adult Coleoptera prothoraces. (A) Genus ? sp. (Salpingidae), ventral. (B) *Orphilodes australis* Lawrence & Slipinski (Dermestidae), ventral. (C) *Paracucujus rostratus* Sen Gupta & Crowson (Boganiidae), ventrolateral. (D) *Apomecyna* sp. (Cerambycidae), ventral; (E) *Rhinorhipus tamborinensis* Lawrence (Rhinorhipidae), lateral. (F) *Eucinetus* sp. (Eucinetidae), ventral.

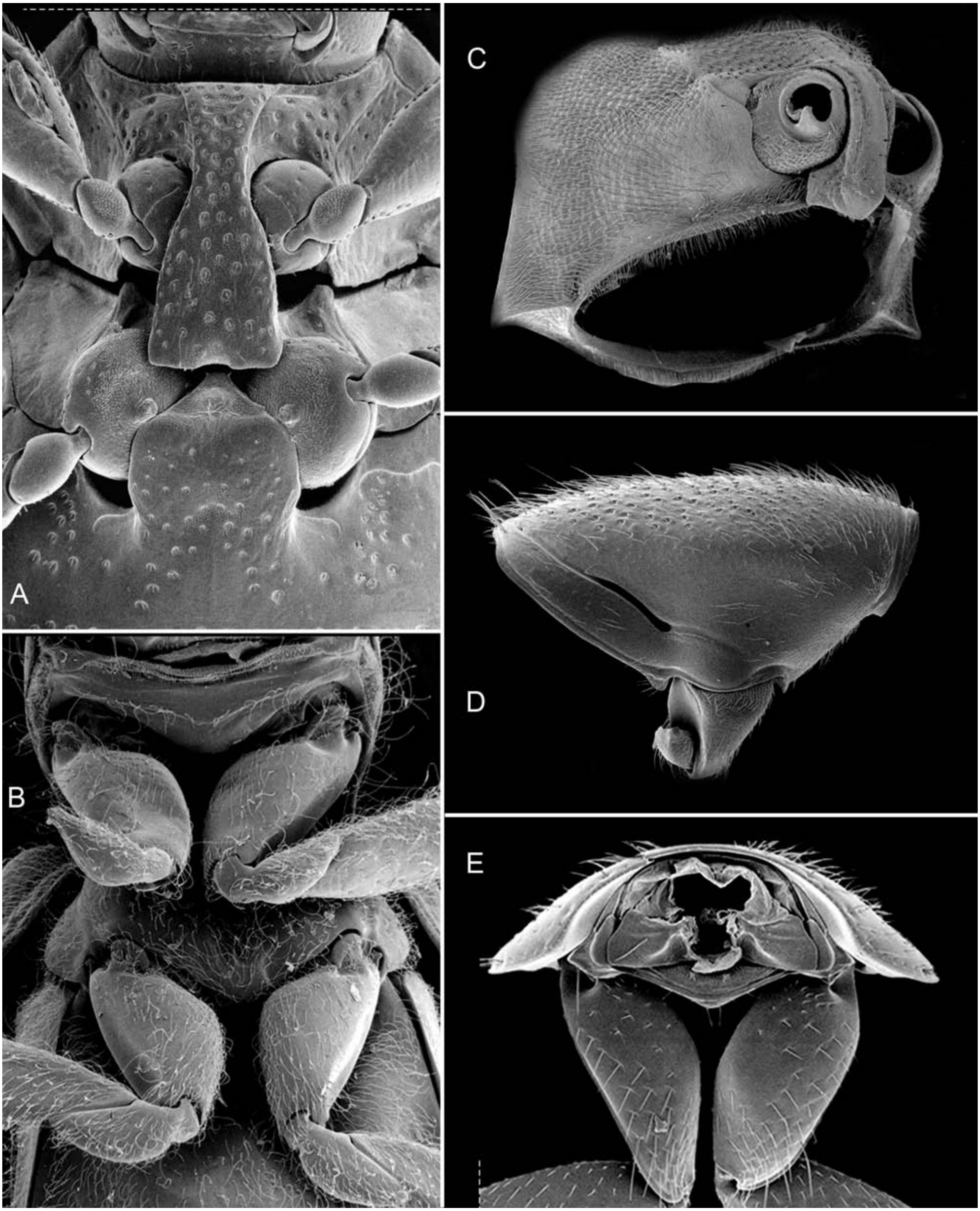


Figure 22. Adult Coleoptera. (A) *Haliplus* sp., prothorax and part of pterothorax, ventral. (B) *Balanophorus* sp. (Melyridae), prothorax and mesothorax, ventral. (C) *Lepispilus* sp. (Tenebrionidae), prothorax, posteroventrolateral. (D) *Macratria* sp. (Anthicidae), prothorax, lateral. (E) *Aleochara* sp. (Staphylinidae), prothorax, anterior.

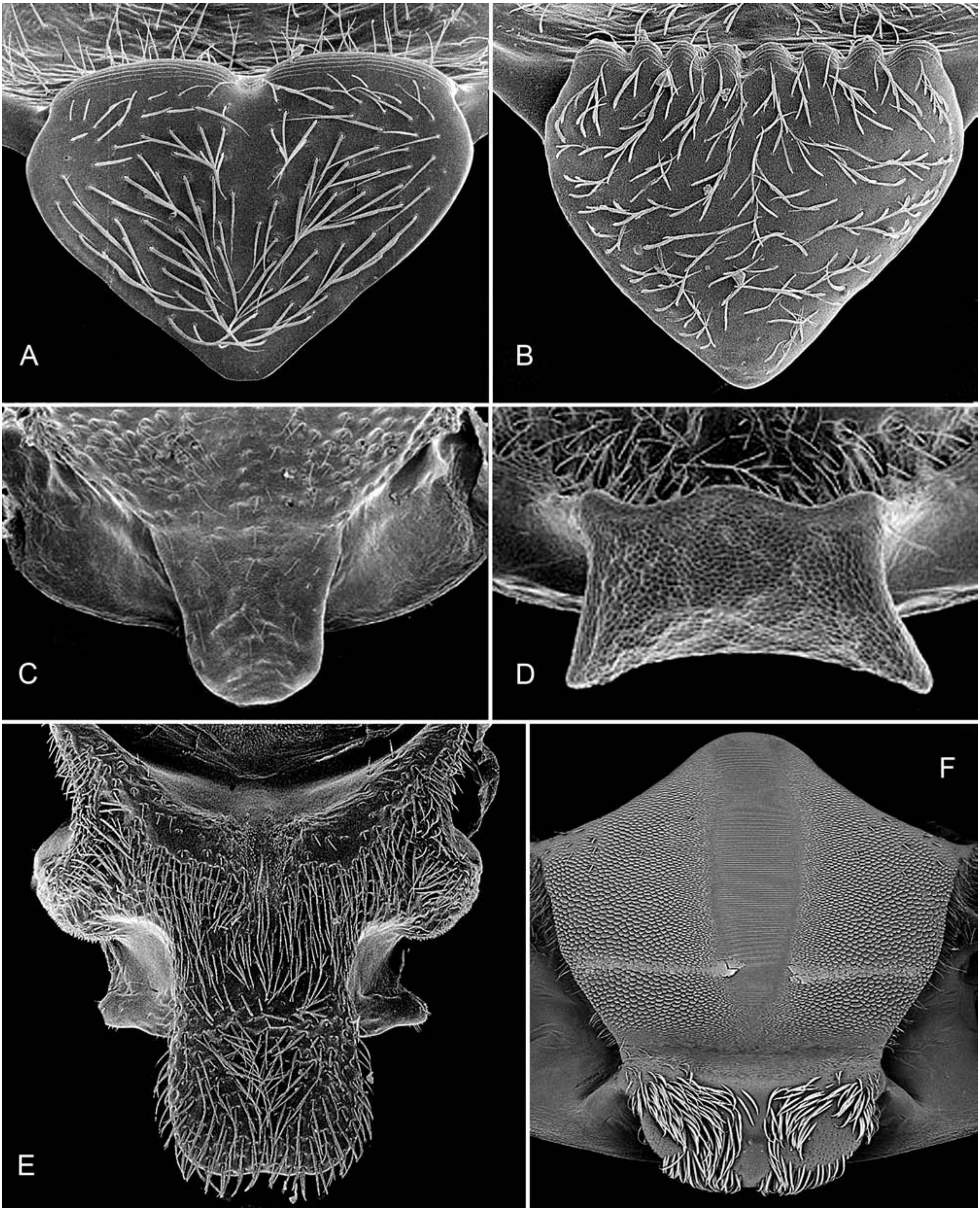


Figure 23. Adult Coleoptera scutellar shields (with or without mesoscutum). (A) *Ptilodactyla* sp. (Ptilodactylidae). (B) *Sclerocyphon* sp. (Psephenidae). (C) *Callidium violaceum* (Linnaeus) (Cerambycidae). (D) *Neochlamisus* sp. (Chrysomelidae). (E) *Euctenia* sp. (Ripiphoridae). (F) *Temnosternus* sp. (Cerambycidae) with stridulatory file.

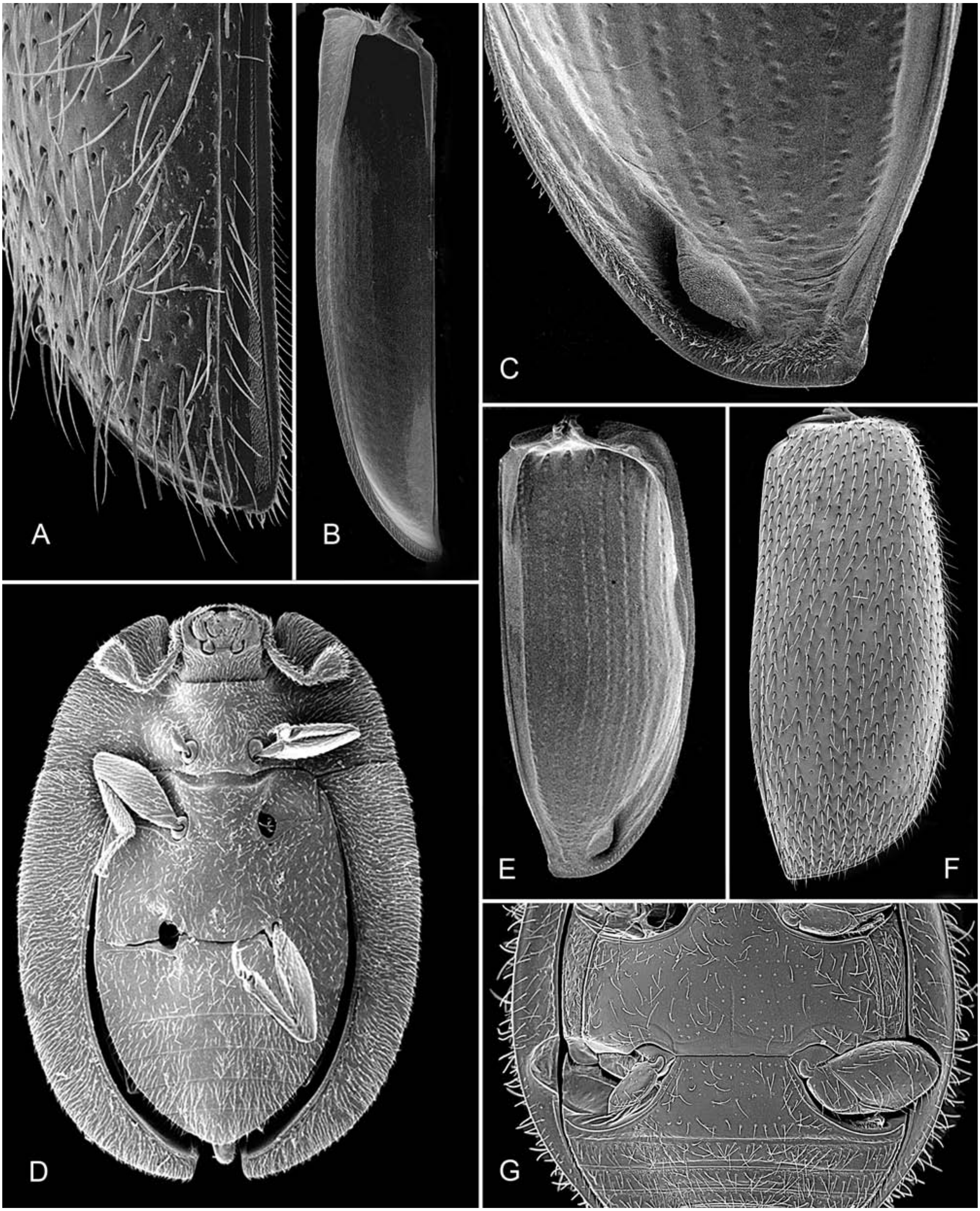


Figure 24. Adult Coleoptera. (A) *Cryptophagus cellaris* (Scopoli) (Cryptophagidae), apex of left elytron, dorsal. (B) *Pharaxonotha kirschi* Reitter (Erotylidae), right elytron, ventral. (C) *Byrrhus* sp. (Byrrhidae), apex of elytron, ventral. (D) *Discoloma* sp. (Discolomatidae), habitus, ventral. (E) *Byrrhus* sp. (Byrrhidae), left elytron, ventral. (F) *Boganium* sp. (Boganiidae), right elytron, dorsal. (G) *Serangium* sp. (Coccinellidae), pterothorax and part of abdomen, ventral.

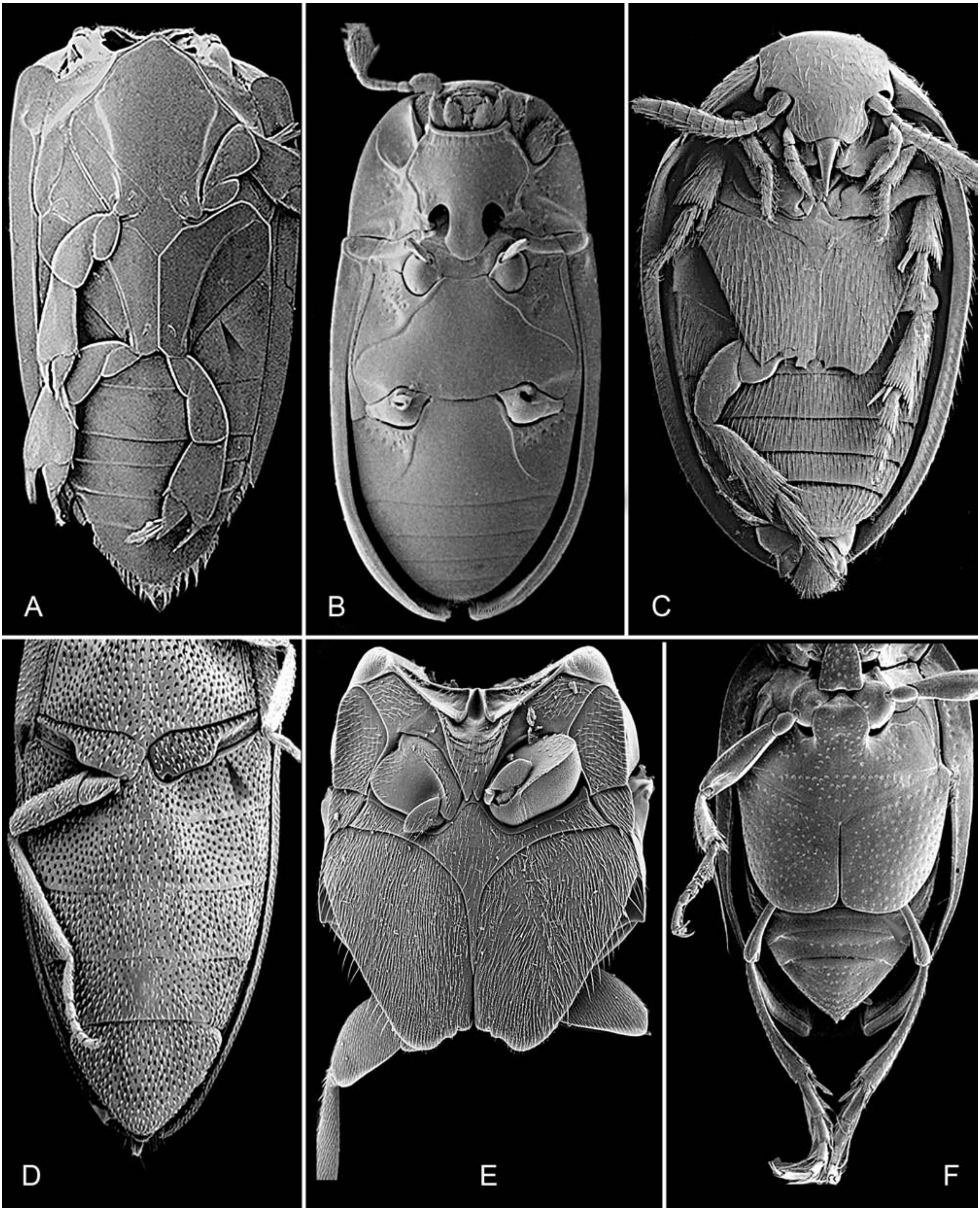


Figure 25. Adult Coleoptera. (A) *Macrogyrus* sp. (Gyrinidae), pterothorax, ventral. (B) *Mychocerus* sp. (Cerylonidae), habitus, ventral. (C) *Jentozkus* sp. (Eucinetidae), habitus, ventral. (D) *Agrypnus* sp. (Elateridae), abdomen and part of metathorax, ventral. (E) *Eucinetus* sp. (Eucinetidae), pterothorax, ventral. (F) *Haliplus* sp. (Haliplidae), pterothorax and abdomen, ventral.

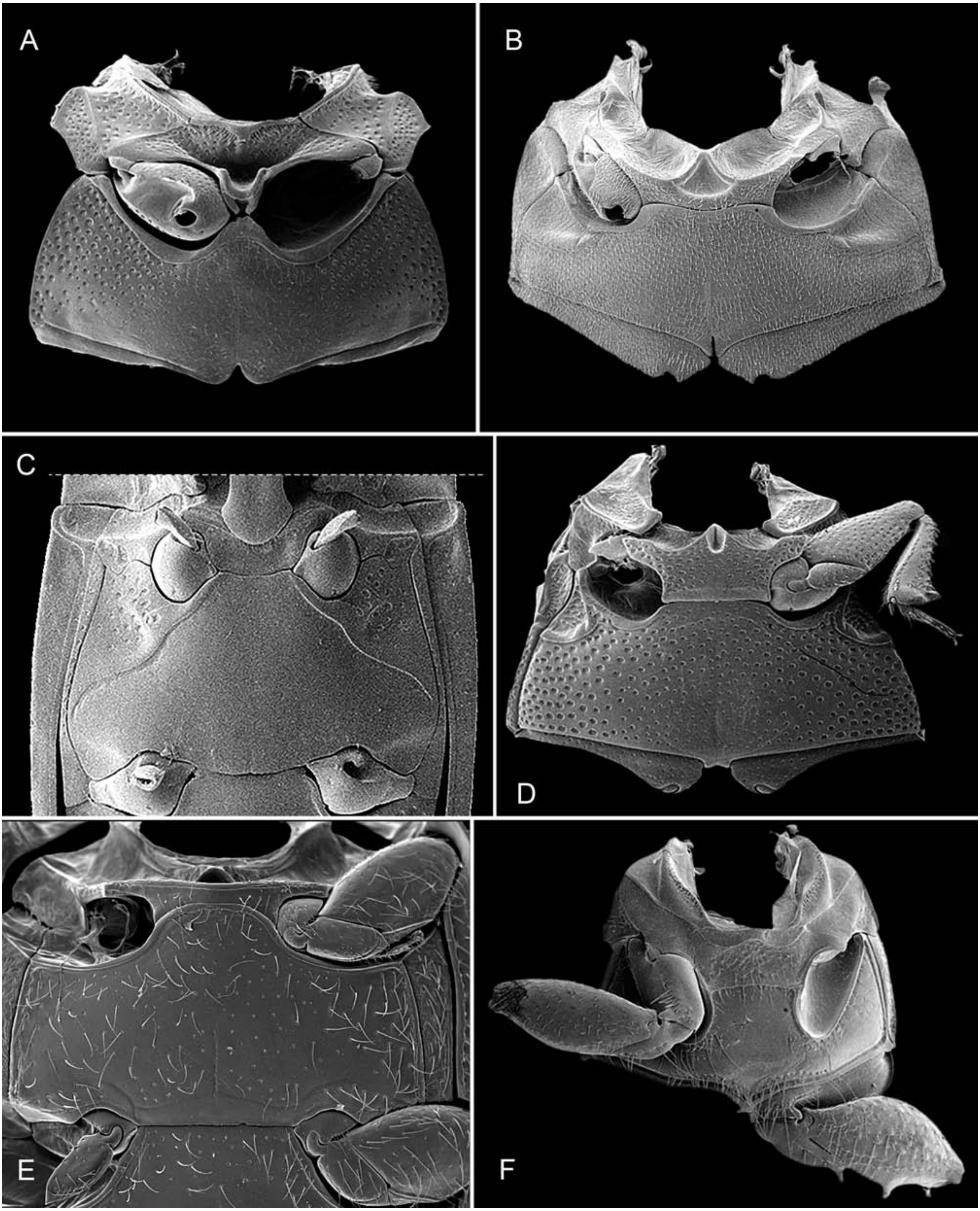


Figure 26. Adult Coleoptera pterothoraces, ventral. (A) *Diaperis maculata* (Olivier) (Tenebrionidae). (B) *Byrrhus* sp. (Byrrhidae). (C) *Mychocerus* sp. (Cerylonidae). (D) *Nosodendron unicolor* Say (Nosodendridae). (E) *Serangium* sp. (Coccinellidae). (F) *Dietta* sp. (Leiodidae).

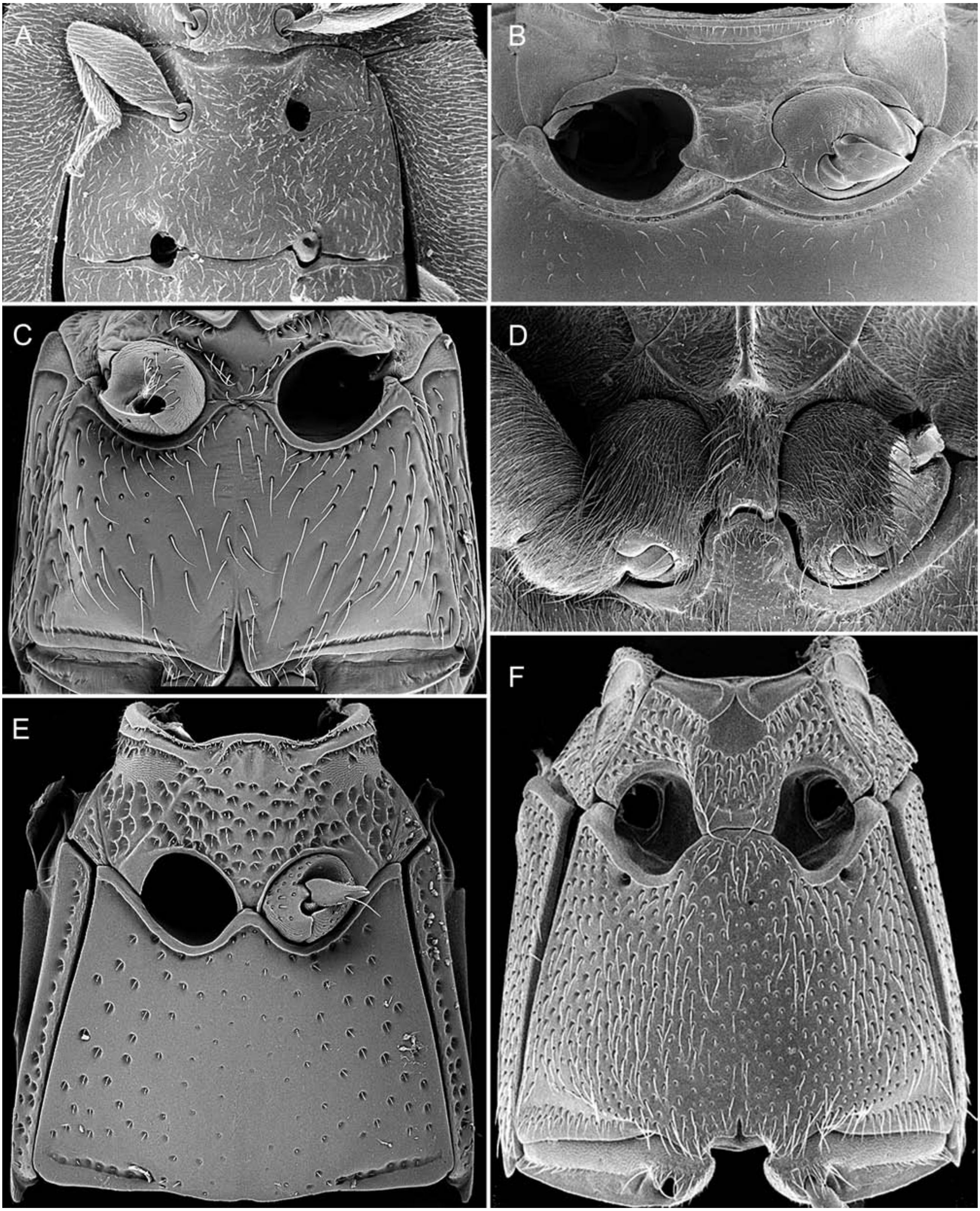


Figure 27. Adult Coleoptera pterothoraces, ventral. (A) *Discoloma* (Discolomatidae). (B) *Rhyparida* sp. (Chrysomelidae). (C) *Athertonium* sp. (Boganiidae). (D) *Dermestes ater* Degeer (Dermestidae). (E) Genus ? sp. (Salpingidae). (F) *Cryptophagus cellaris* (Scopoli) (Cryptophagidae).

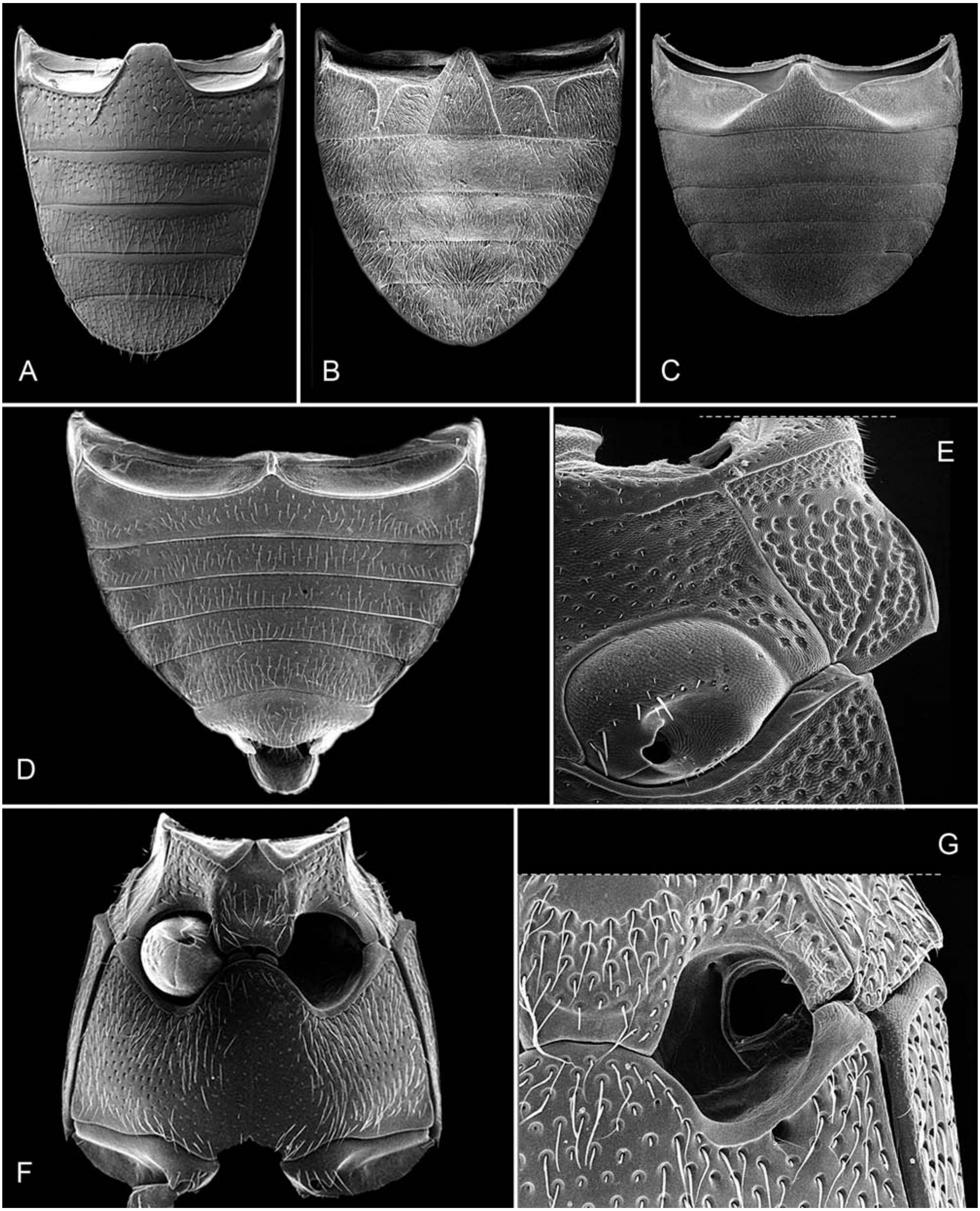


Figure 28. Adult Coleoptera. (A)–(D) Abdomens, ventral. (A) *Cryptophilus* sp. (Erotylidae). (B) *Diplocoelus fasciatus* (Macleay) (Biphyllidae). (C) *Byrrhus* sp. (Byrrhidae). (D) *Anisotoma* sp. (Leiodidae). (E)–(G) Pterothoraces, ventral. (E) *Corticeus* sp. (Tenebrionidae). (F) *Cryptothelypterus* (Cryptophagidae). (G) *Cryptophagus cellaris* (Scopoli) (Cryptophagidae).

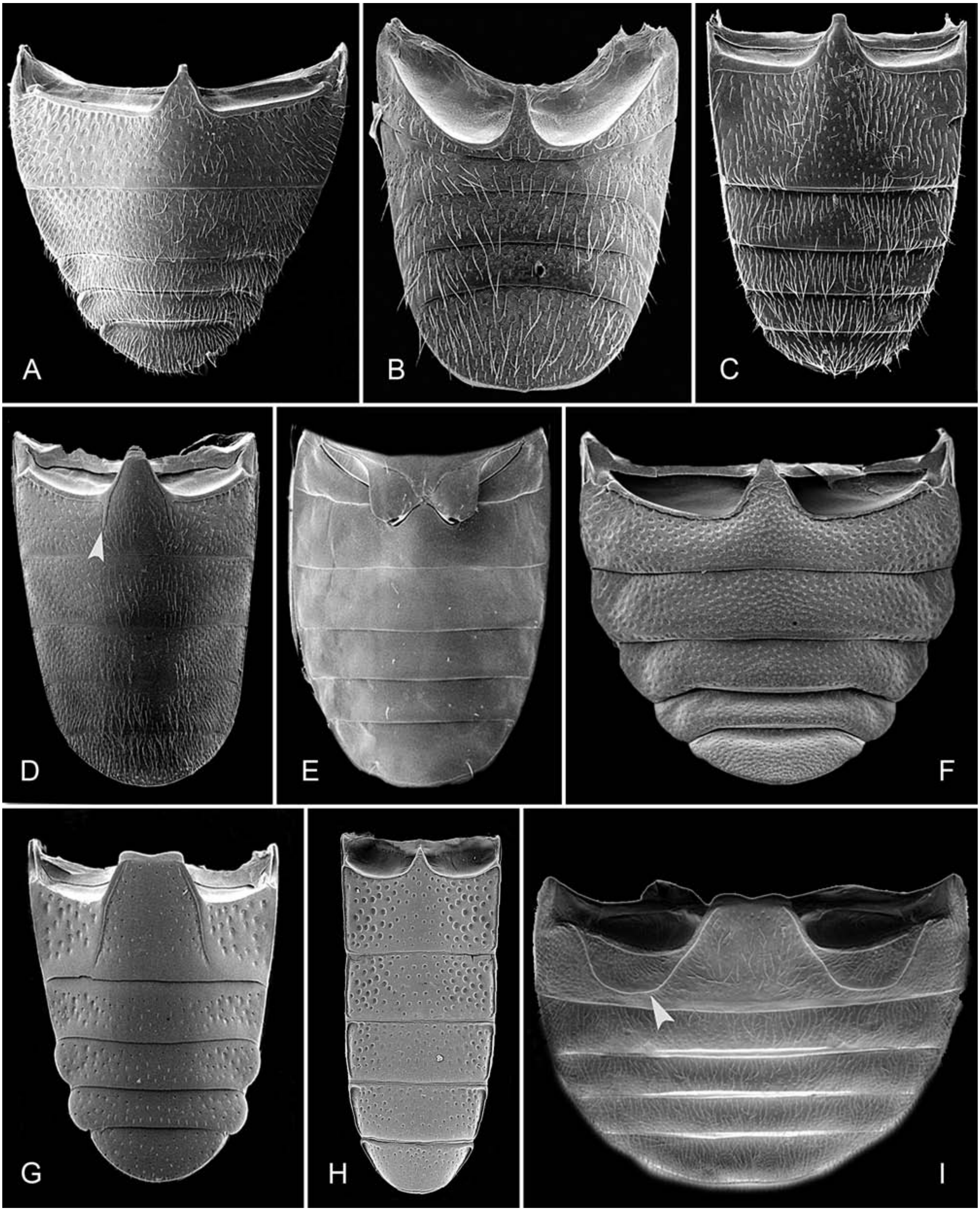


Figure 29. Adult Coleoptera abdomens, ventral. (A) *Pterogenius nietneri* Candèze. (B) *Platypus* sp. (Curculionidae). (C) *Myrabolia* sp. (Myraboliidae). (D) *Cnecosa insueta* (Crotch) (Erotylidae). (E) *Amblytelus* sp. (Carabidae). (F) *Eleates depressus* (Randall) (Tenebrionidae). (G) *Metacerylon minutum* (Carter) (Cerylonidae). (H) Genus ? sp. (Salpingidae). (I) Genus ? sp. (Coccinellidae).

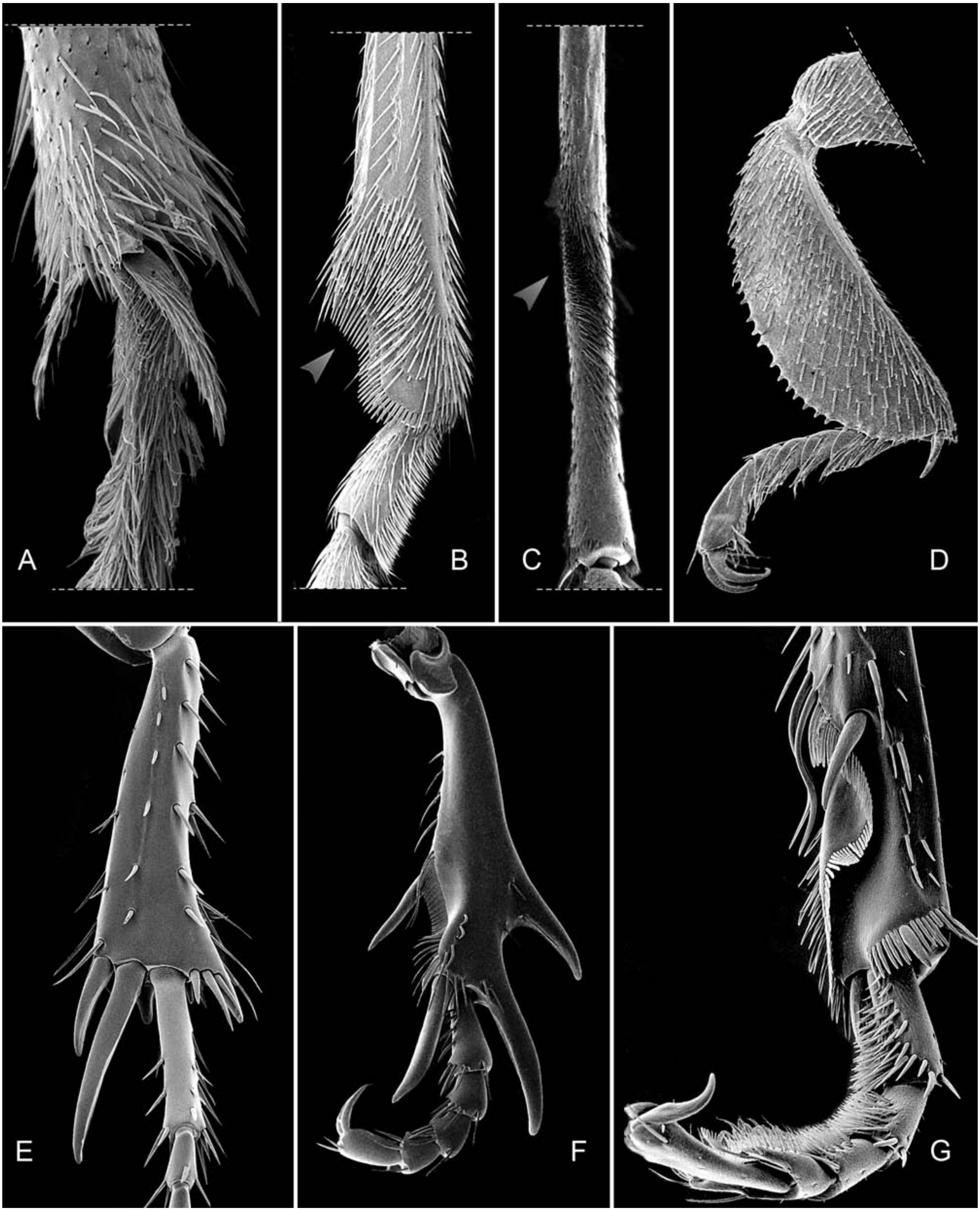


Figure 30. Adult Coleoptera tibiae and tarsi. (A) *Scraptia* sp. (Scraptiidae). (B) *Rhyparida* sp. (Chrysomelidae, mesotibia. (C) *Typodryas* sp. (Disteniidae), mesotibia. (D) *Byrrhus* sp. (Byrrhidae). (E) *Ataenius picinus* Harold. (Scarabaeidae). (F) *Carenum* sp. (Carabidae), protibia. (G) *Amblytelus* sp. (Carabidae), protibia.

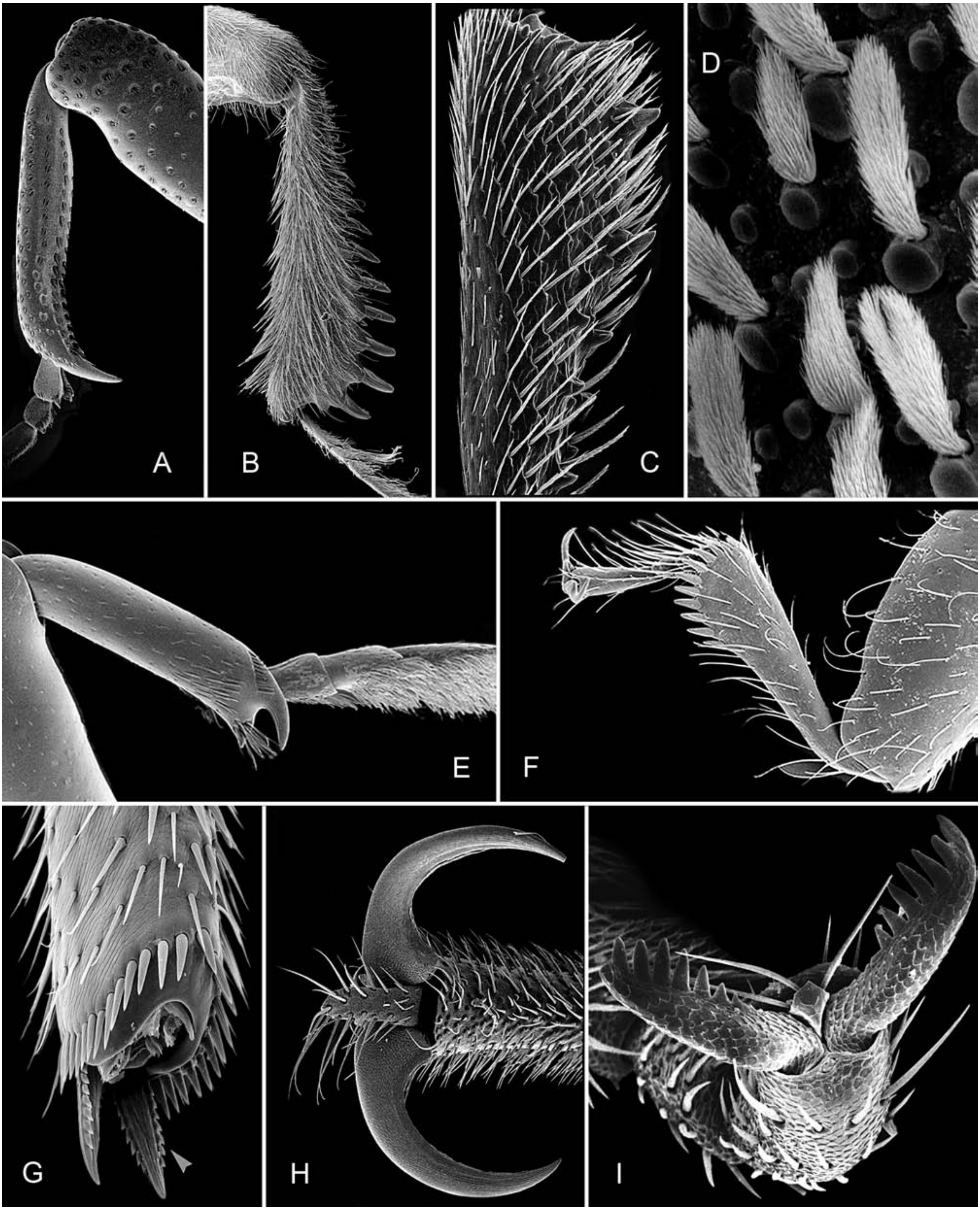
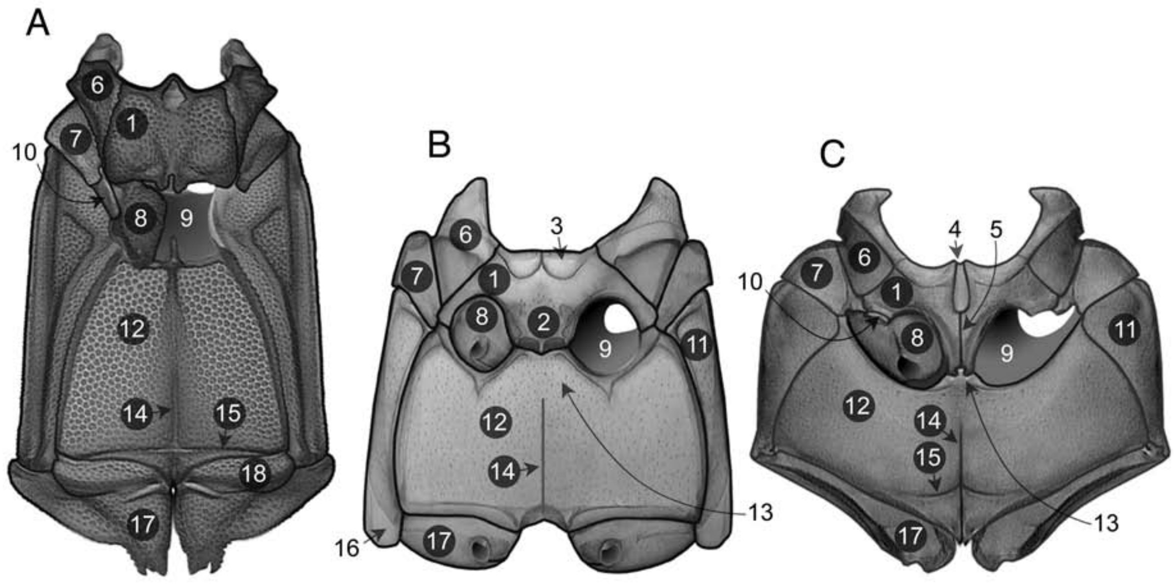


Figure 31. (A)–(C) Adult Coleoptera tibiae. (A) *Cosmopolites sordidus* (Germar) (Curculionidae), protibia. (B) *Heterocerus* sp. (Heteroceridae) protibia. (C) *Hylurgops* sp. (Curculionidae), mesotibia. (D) *Austrolichas monteithi* Lawrence & Stribling (Ptilodactylidae), larva, portion of abdominal cuticle. (E) *Tyrpetes* sp. (Curculionidae), adult mesotibia and tarsus. (F) *Rhopalodontus* sp. (Ciidae), adult tibia and tarsus. (G) *Filicivora chilensis* (Philippi & Philippi) (Mycetophagidae), adult tibial apex. (H) *Callirhipis reticulata* Lea (Callirhipidae), adult pretarsus. (I) *Rhinorhipus tamborinensis* Lawrence (Rhinorhipidae), adult pretarsus.



1. Mesoventrite
2. Mesoventral Process
3. Procoxal Rest
4. Mesoventral Cavity
5. Mesothoracic Discrimen
6. Mesanepisternum
7. Mesepimeron
8. Mesocoxa
9. Mesocoxal Cavity
10. Mesotrochantin
11. Metanepisternum
12. Metaventrite
13. Metaventral Process
14. Metathoracic Discrimen
15. Metakatepisternal Suture
16. Metepimeron
17. Metacoxa
18. Metatrochantin

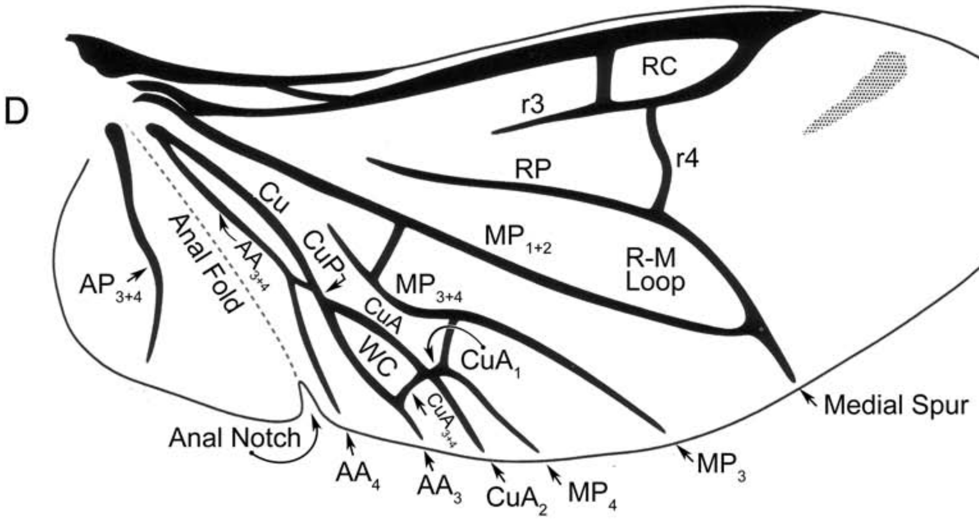


Figure 32. Adult Coleoptera. (A–C). Pterothoraces with major structures labelled. (A) *Distocupes varians* (Lea) (Cupedidae). (B) *Episcaphula australis* (Boisduval) (Erotylidae). (C) *Sclerocyphon* sp. (Psephenidae). (D) *Osslimus freyi* (Cobos) (Elateridae), hind wing.

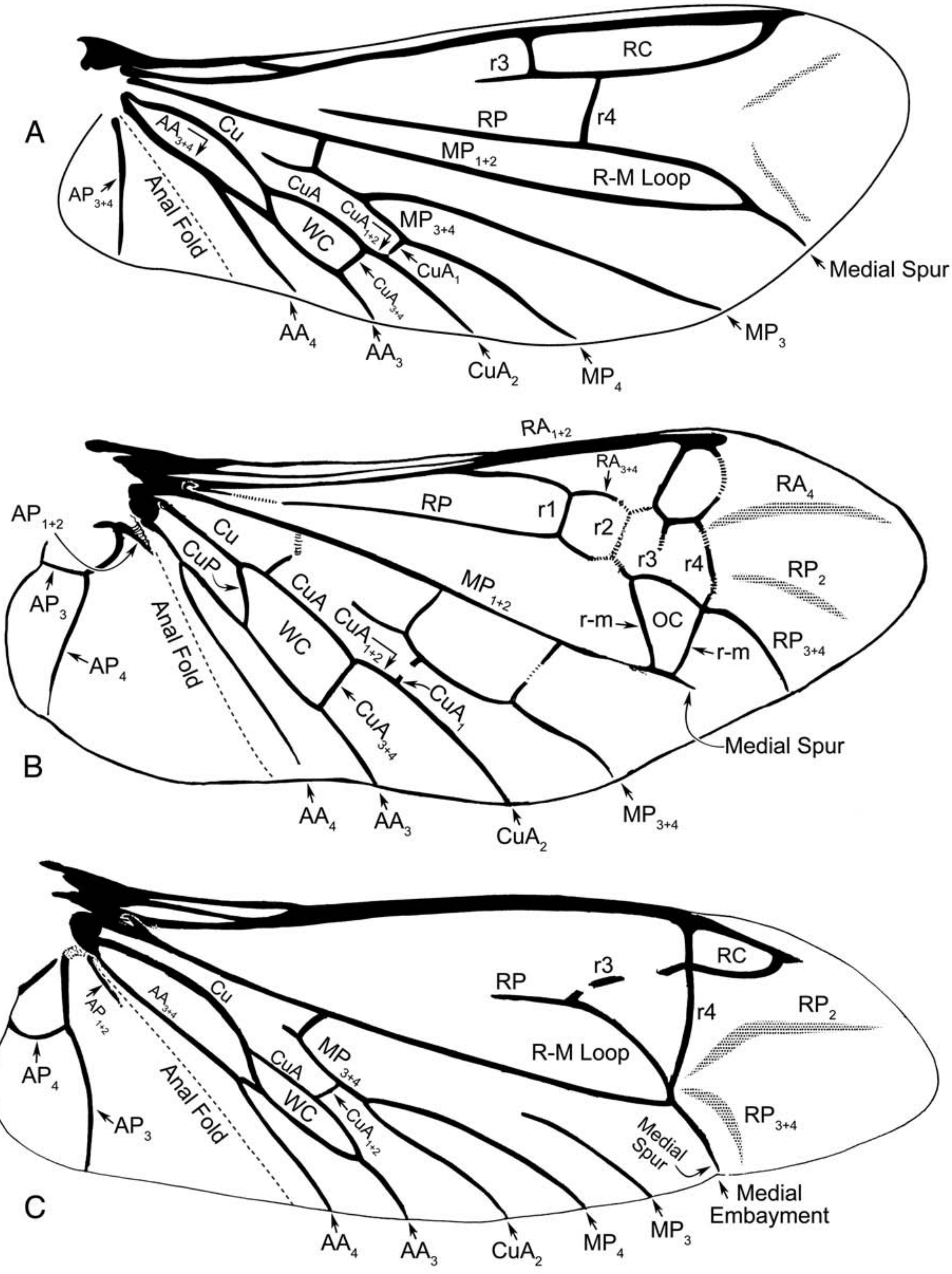


Figure 33. Adult Coleoptera. Hind wings. (A) *Stichotomus* sp. (Elateridae). (B) *Omma stanleyi* Newman (Ommatidae). (C) *Notodascillus sublineaus* Carter (Dascillidae).

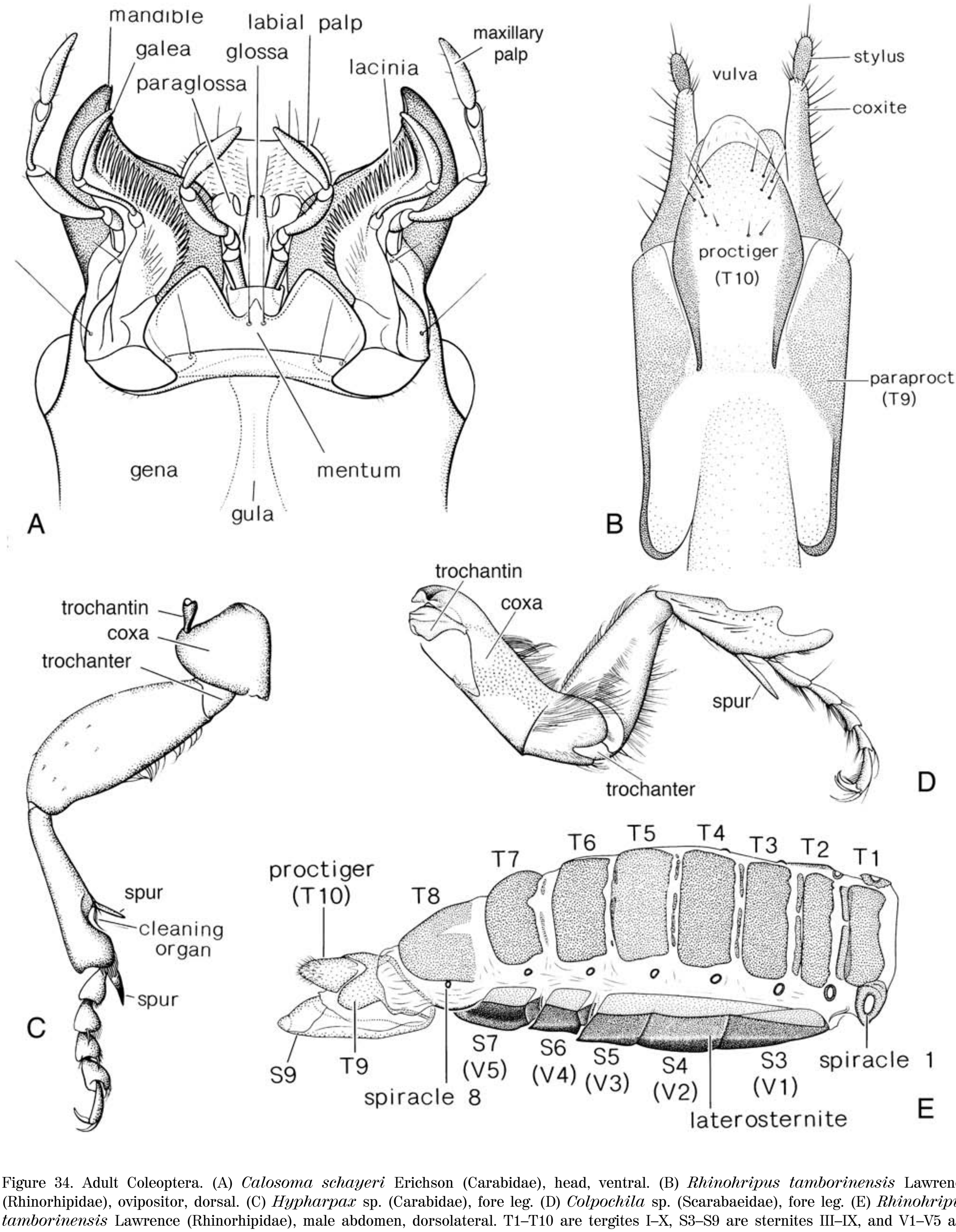


Figure 34. Adult Coleoptera. (A) *Calosoma schayeri* Erichson (Carabidae), head, ventral. (B) *Rhinohripus tamborinensis* Lawrence (Rhinorhipidae), ovipositor, dorsal. (C) *Hypharpax* sp. (Carabidae), fore leg. (D) *Colpochila* sp. (Scarabaeidae), fore leg. (E) *Rhinohripus tamborinensis* Lawrence (Rhinorhipidae), male abdomen, dorsolateral. T1–T10 are tergites I–X, S3–S9 are sternites III–IX, and V1–V5 are ventrites 1–5.

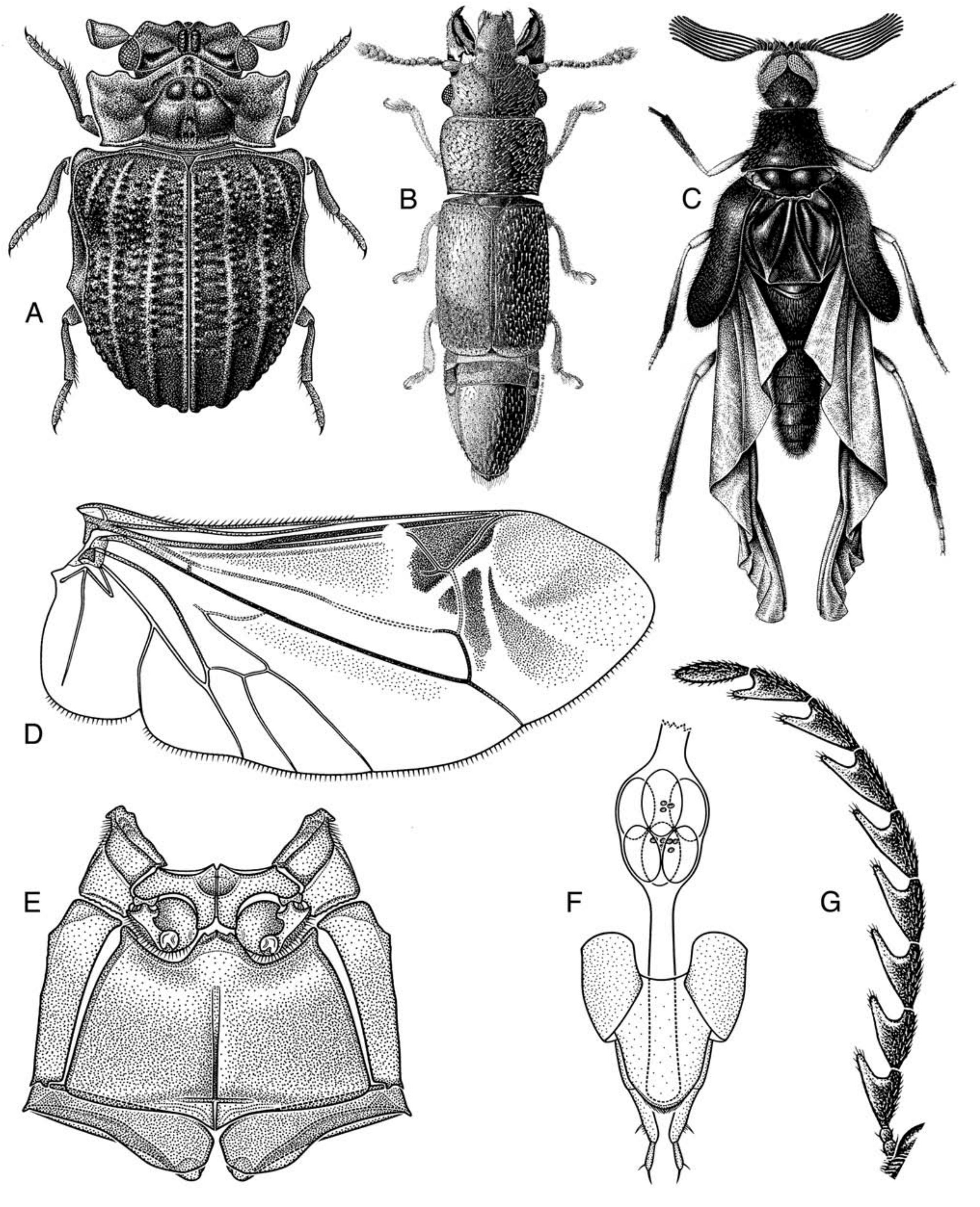


Figure 35. Adult Coleoptera. (A) *Lepicerus inaequalis* Motschulsky (Lepiceridae), habitus, dorsal. (B) *Smicrips* sp. (Smicripidae), habitus, dorsal. (C) *Rhipidioides rubricatus* Riek (Ripiphoridae), male. (D)–(F) *Declinia relicta* Lawrence *et al.* (Decliniidae). (D) hind wing. (E) pterothorax. (F) female abdominal apex, including rectum. (G) *Austrolichas monteithi* Lawrence & Stribling (Ptilodactylidae), antenna.

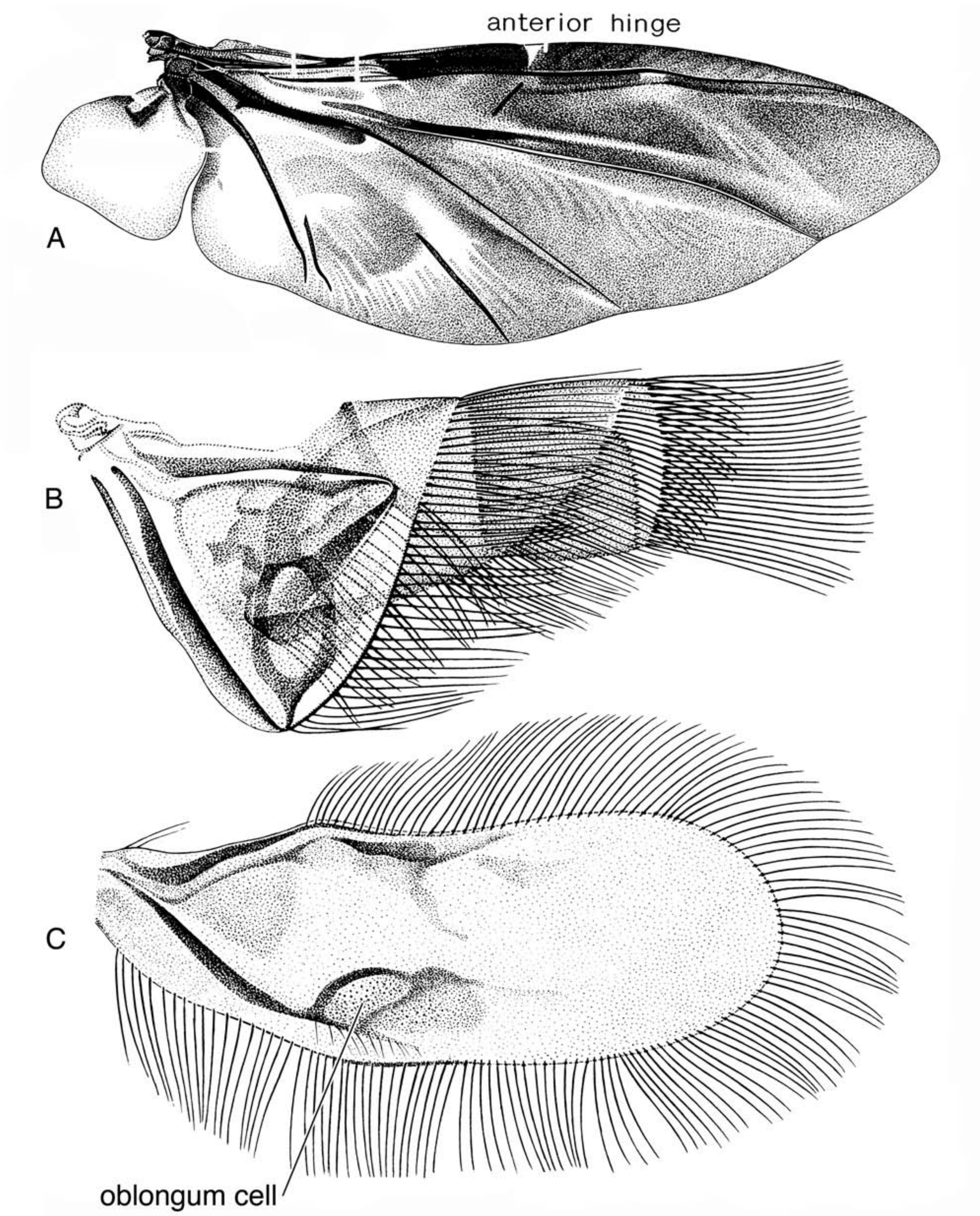


Figure 36. Adult Coleoptera hind wings. (A) *Creophilus erythrocephalus* (Fabricius) (Staphylinidae). (B) *Sphaerius ovensensis* (Oke) (Sphaeriusidae), folded wing. (C) Same, unfolded wing.

Figure 37. Adult Coleoptera heads. (A) *Cetonia* sp. (Scarabaeidae), anterodorsal. (B) *Hister abbreviatus* Fabricius (Histeridae), left side, dorsal. (C) *Nicrophorus tomentosus* Weber (Silphidae), dorsal. (D) *Lucanus capreolus* (Linnaeus) (Lucanidae), dorsal. (E) *Pleocoma linsleyi* Hovore (Pleocomidae), dorsal. (F) *Tropisternus blatchleyi* Orchymont (Hydrophilidae), left side, ventral. (G) Same, dorsal.

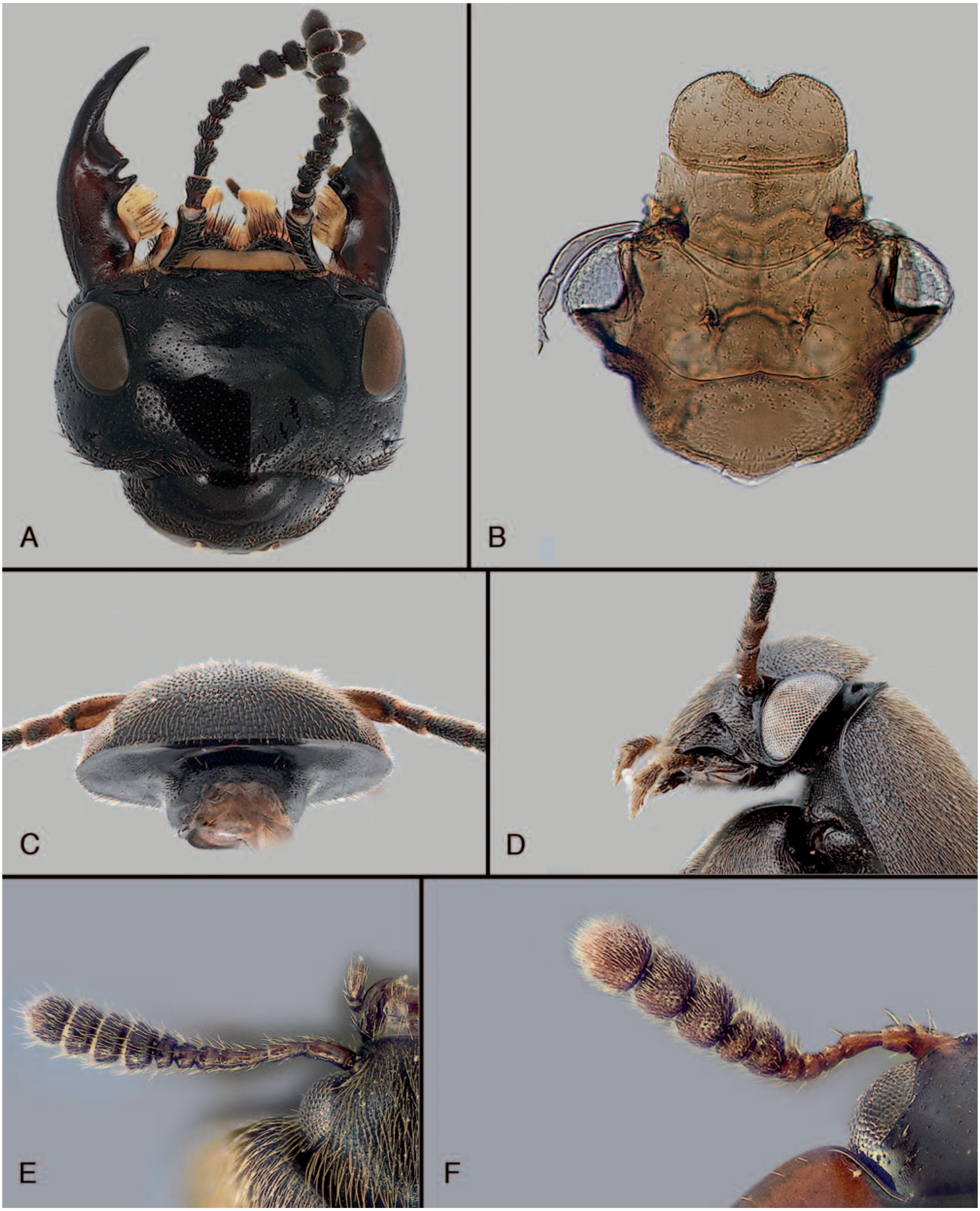


Figure 38. Adult Coleoptera. (A)–(D). Heads. (A) *Creophilus maxillosus* (Linnaeus) (Staphylinidae), dorsal. (B) *Ochthebius* sp. (Hydraenidae), dorsal. (C) *Prionochaeta opaca* (Say) (Leiodidae), dorsal. (D) Same, lateral. (E) *Colon hirtale* (Broun) (Leiodidae), antenna. (F) *Anisotoma blanchardi* Horn (Leiodidae), antenna.

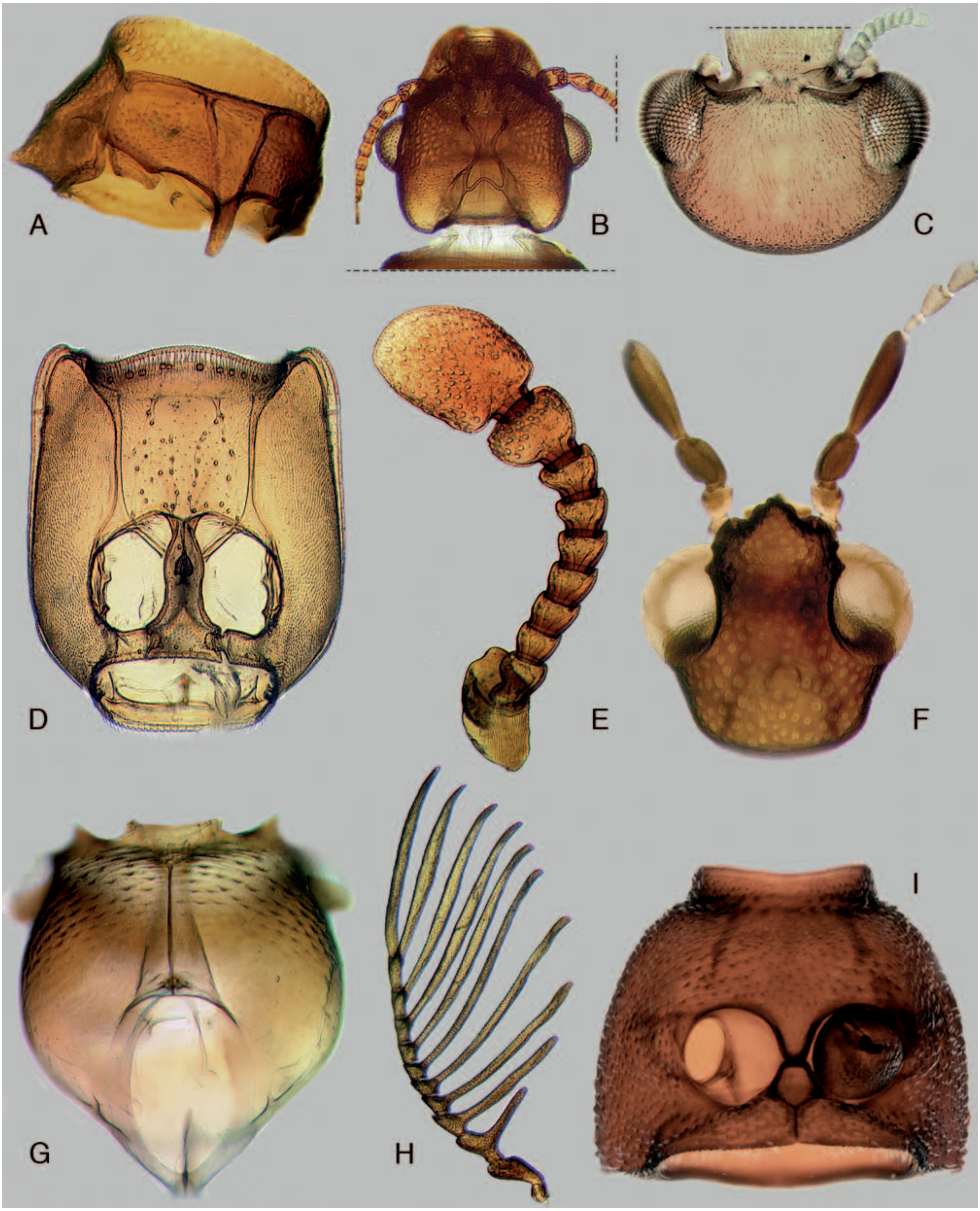


Figure 39. Adult Coleoptera. (A) *Macropogon* sp. (Artematopodidae), prothorax, posterolateroventral. (B) *Smicrips* sp. (Smicripidae), head, dorsal. (C) *Pelonomus obscurus* LeConte (Dryopidae), head, dorsal. (D) *Clivina* sp. (Carabidae), prothorax, ventral. (E) *Acalanthis* sp. (Trogossitidae), antenna. (F) *Chelonarium* sp. (Chelonariidae), head, dorsal. (G) *Dinoderus* sp. (Bostrichidae), head, posteroventral. (H) *Xenorhipis* sp. (Buprestidae), male antenna. (I) *Tranes lyterioides* (Pascoe) (Curculionidae), prothorax, ventral.

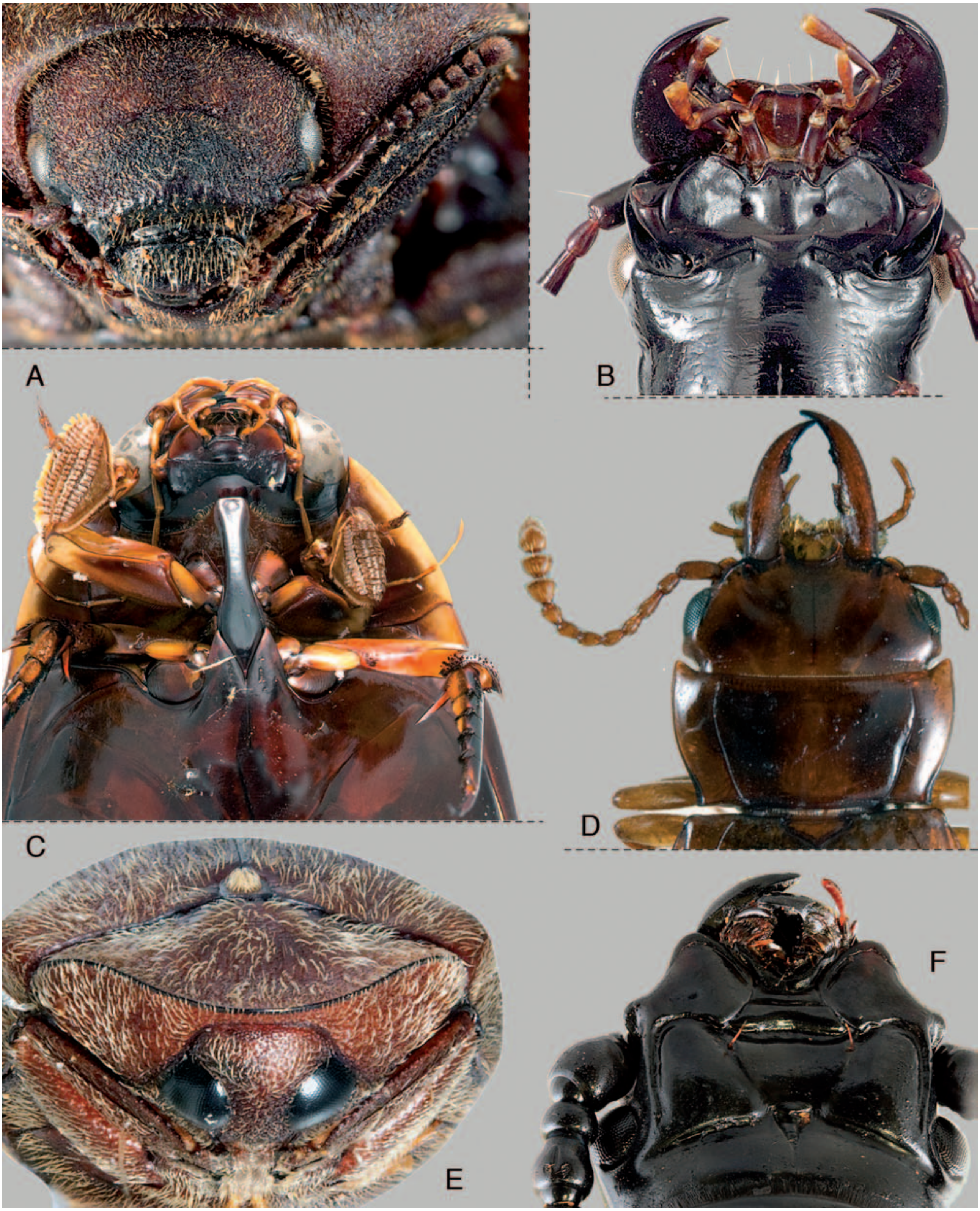


Figure 40. Adult Coleoptera. (A) *Byrrhus* sp. (Byrrhidae), head, dorsal. (B) *Lesticus* sp. (Carabidae), head, ventral. (C) *Cybister* sp. (Dytiscidae), head and thorax, ventral. (D) *Laemophloeus* sp. (Laemophloeidae), head and prothorax, dorsal. (E) *Chelonarium* sp. (Chelonariidae), head and prothorax, anterior. (F) *Passandra* sp. (Passandridae), head, ventral.

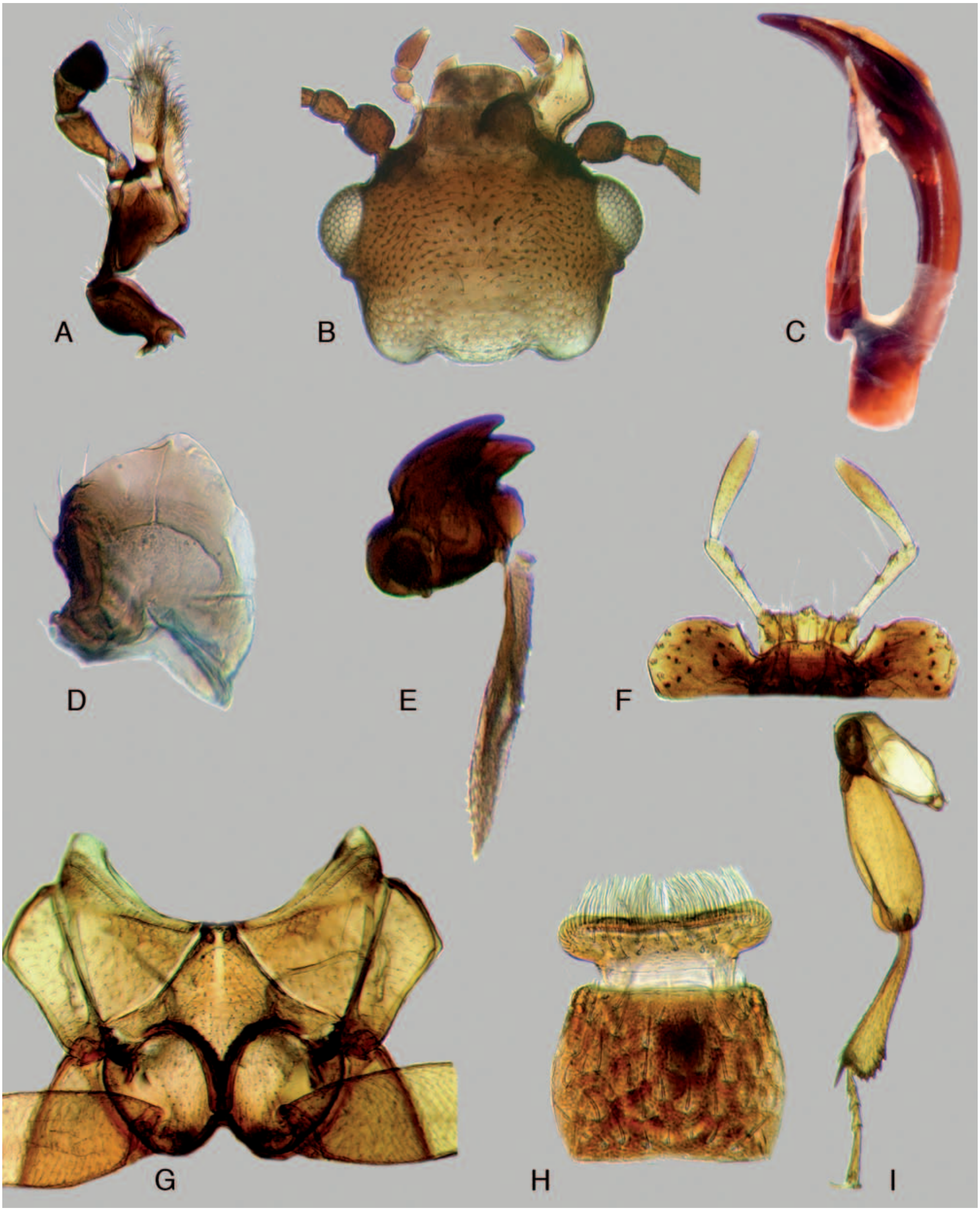


Figure 41. Adult Coleoptera. (A) *Therius* sp. (Ptilodactylidae), maxilla, ventral. (B) *Phloeostichus denticollis* Redtenbacher (Phloeostichidae), head, dorsal. (C) *Calosoma* sp. (Carabidae), aedeagus, lateral. (D) *Chelonarium* sp. (Chelonariidae), mandible. (E) *Echinocnemus* sp. (Curculionidae), mandible, dorsal. (F) *Lesticus* sp. (Carabidae), mentum and prementum, ventral. (G) *Mycetophagus* sp. (Mycetophagidae), mesothorax, ventral. (H) *Pristoderus* sp. (Zopheridae), labium, ventral. (I) *Aulonium* sp. (Zopheridae), fore leg, with long internal coxal extension.

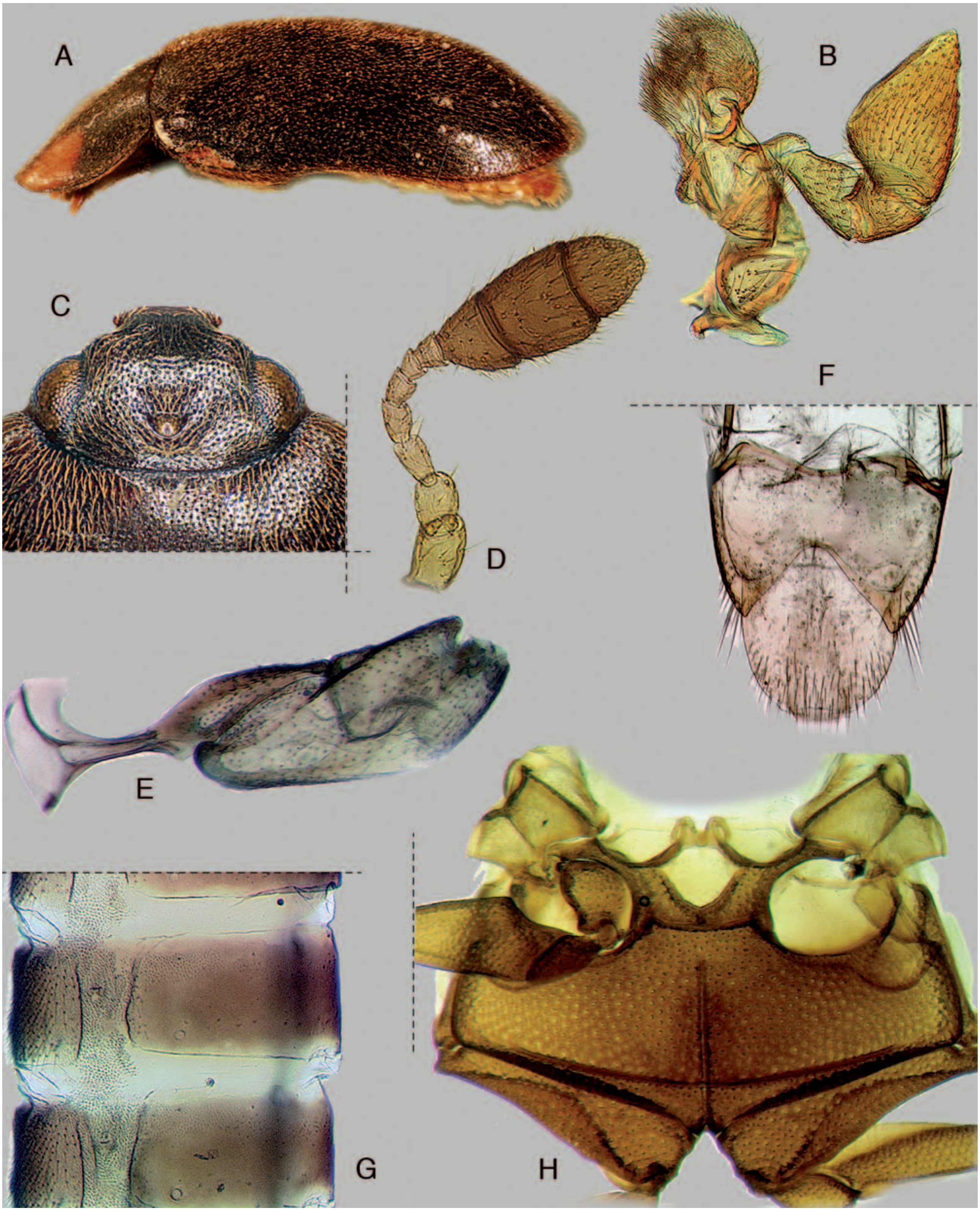


Figure 42. Adult Coleoptera. (A) *Roger boothi* Ślipiński (Coccinellidae), habitus, lateral. (B) Genus ? sp. (Coccinellidae), maxilla, ventral. (C) *Orphilodes australis* Lawrence and Ślipiński (Dermestidae), head, dorsal. (D) *Hong glorious* Ślipiński (Coccinellidae), antenna. (E) *Notodascillus* sp. (Dascillidae), procoxa and pleurotrochantin. (F) *Ampedus sanguineus* (Linnaeus) (Elateridae), male abdominal segments IX and X, dorsal. (G) Genus ? sp. (Cantharidae), abdominal segments V and VI, lateral. (H) *Byrrhinus* sp. (Limnichidae), pterothorax, ventral.

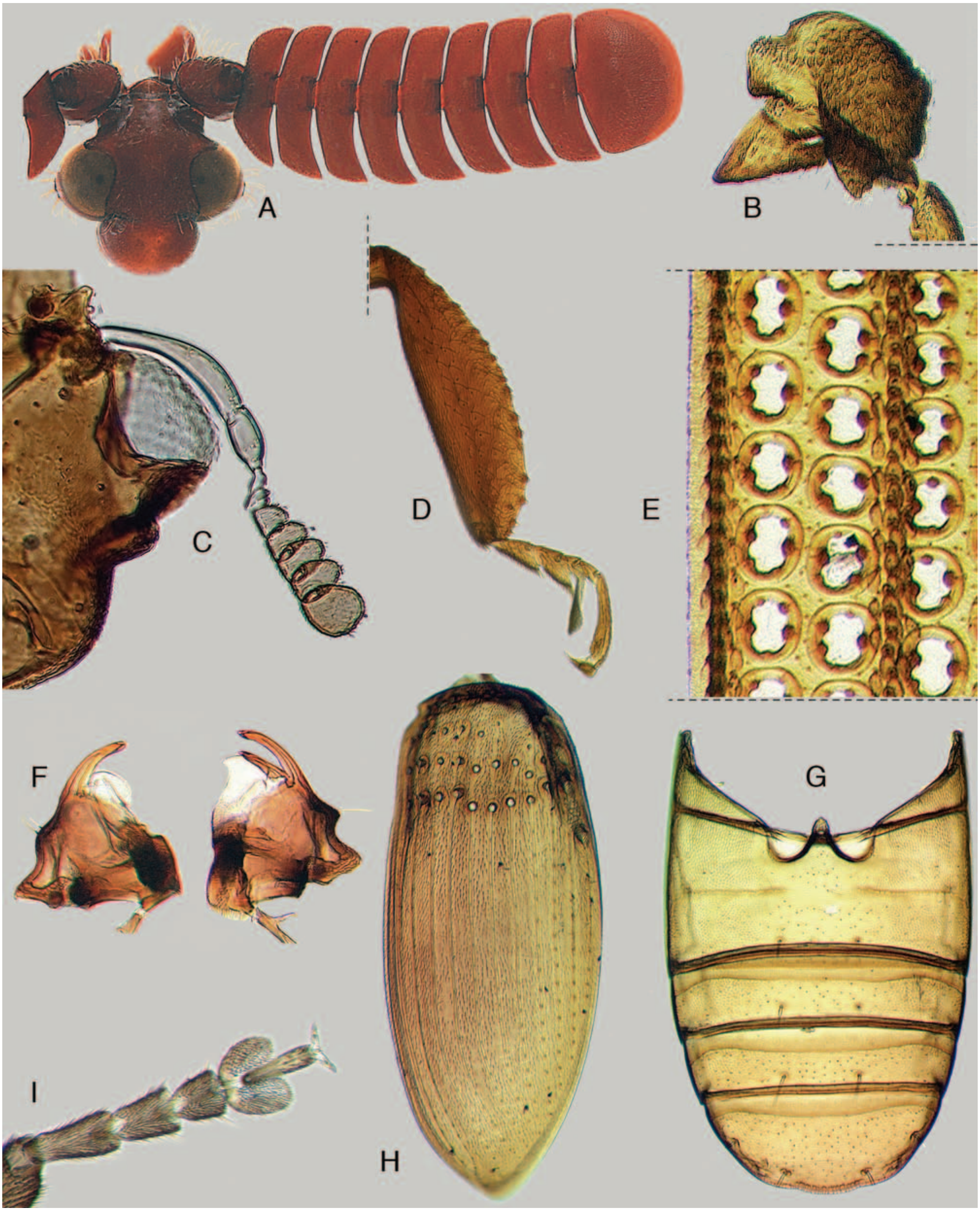


Figure 43. Adult Coleoptera. (A) *Arthropterus* sp. (Carabidae), antenna, dorsal. (B) *Adinolepis* sp. (Cupedidae), procoxa, ventral. (C) *Ochthebius* sp. (Hydraenidae), antenna, dorsal. (D) *Chelonarium* sp. (Chelonariidae), tibia and tarsus. (E) *Adinolepis* sp. (Cupedidae), section of elytron, dorsal. (F) *Lepicerus* sp. (Lepiceridae), mandibles, ventral. (G) *Clivina* sp. (Carabidae), abdomen, ventral. (H) *Nothoderodontus* sp. (Derodontidae), elytron, dorsal. (I) Genus ? sp. (Cantharidae), mesotarsus, dorsal.

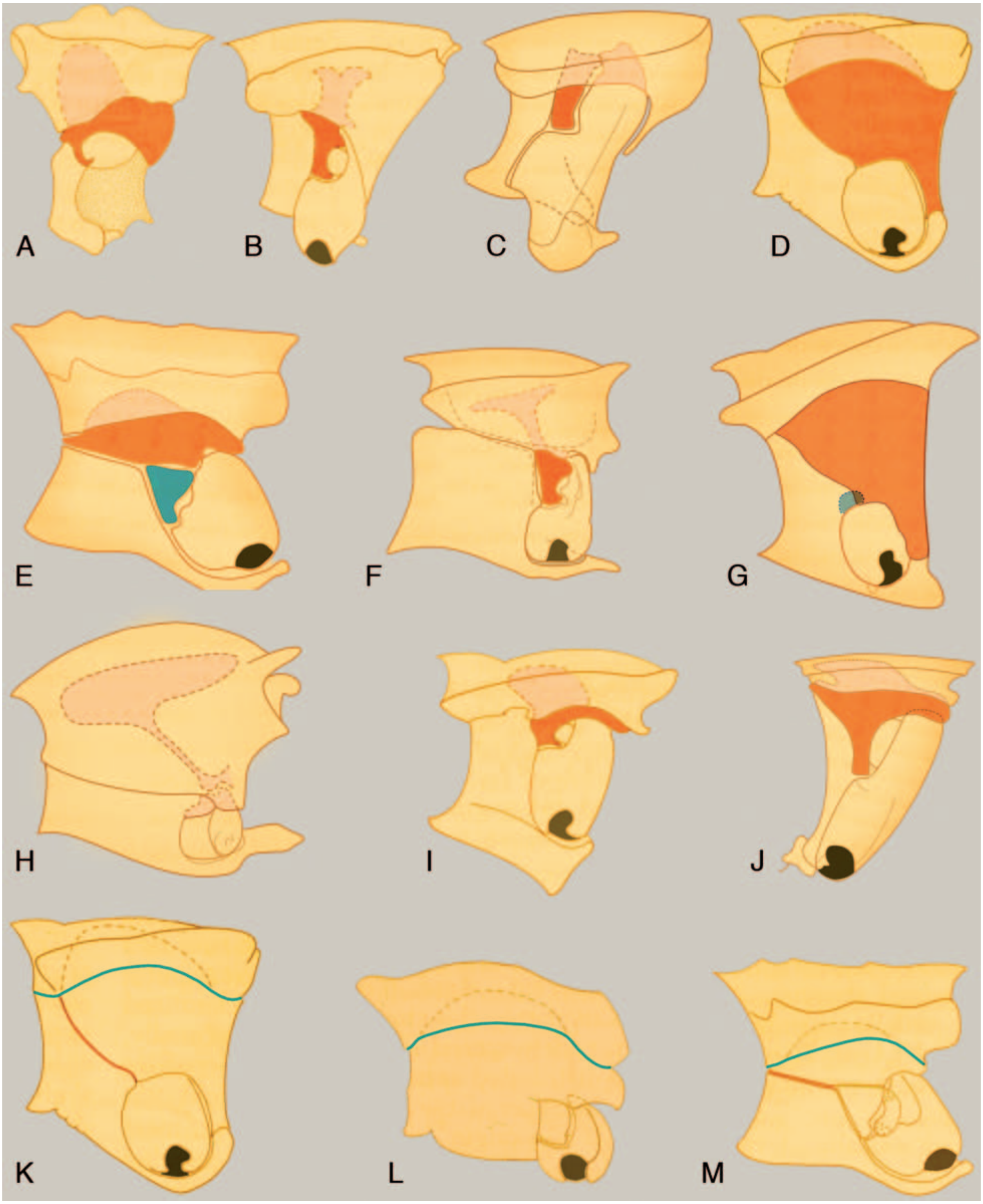


Figure 44. Adult Coleoptera. Prothoraces, lateral. (A–J) External and internal extent of propleuron or propleurotrochantin (red) and free trochantin (blue). (A) *Lepicerus inaequalis* Motschulsky (Lepiceridae). (B) *Laricobius rubidus* Leconte (Derodontidae). (C) *Pleocoma* sp. (Pleocomidae). (D) *Ozaena elevata* Bänninger (Carabidae). (E) *Priacma serrata* LeConte (Cupedidae). (F) *Pelonomus obscurus* LeConte (Dryopidae). (G) *Metrius contractus* Eschscholtz (Carabidae). (H) *Perothops muscida* (Say) (Eucnemidae). (I) *Iapir britskii (*Reichardt & Costa) (Torridincolidae). (J) *Sphaerius politus* Horn (Sphaeriusidae). (K–M) Prothoracic sutures. (K) *Ozaena elevata* Bänninger (Carabidae), notopleural, pleurosternal and notosternal sutures. (L) *Omma stanleyi* Newman (Ommatidae), notopleural suture only. (M) *Priacma serrata* LeConte (Cupedidae), notopleural and pleurosternal sutures.

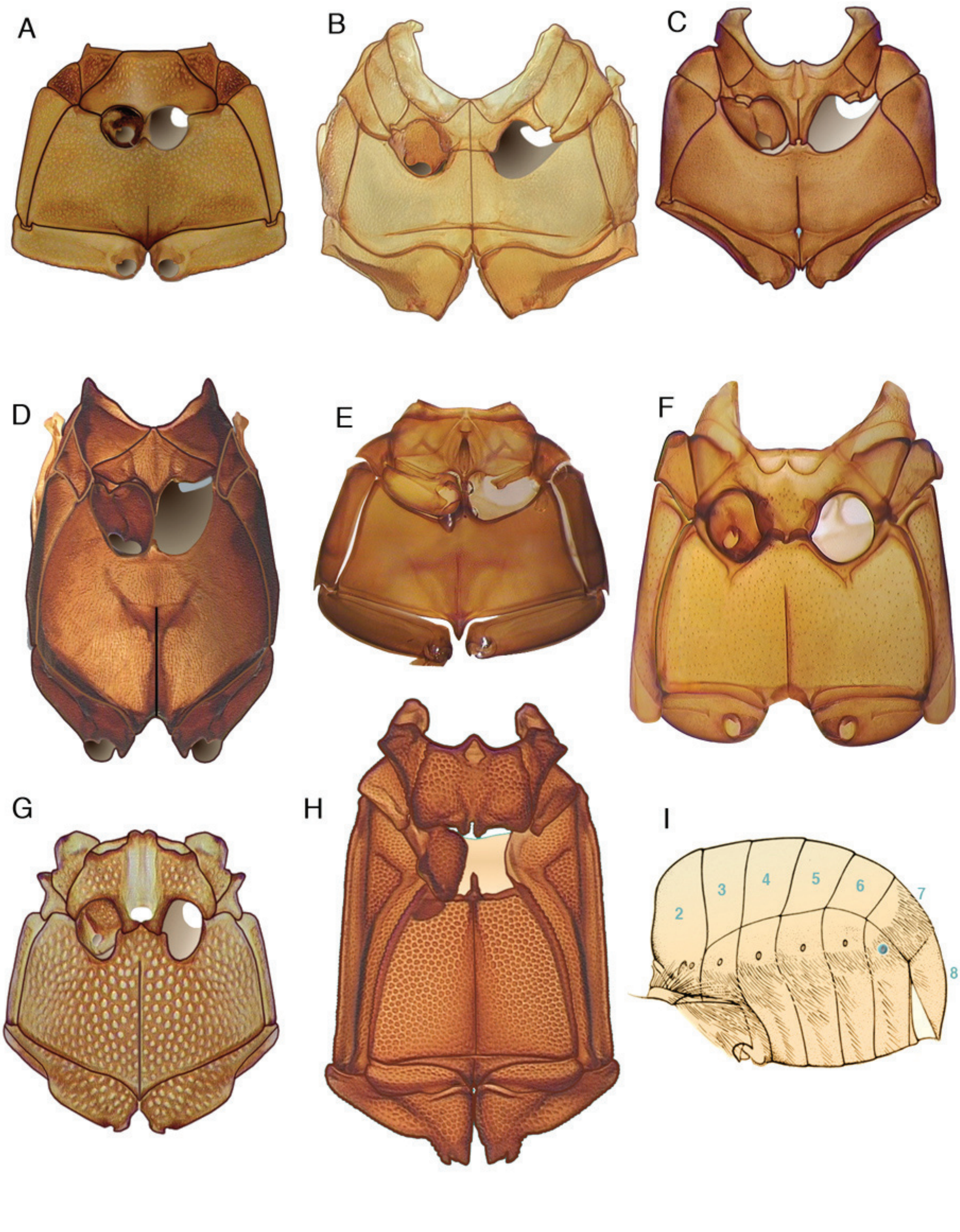


Figure 45. Adult Coleoptera. (A–H) Pterothoraces, ventral. (A) *Omorgus* sp. (Trogidae). (B) *Schizopus* sp. (Buprestidae). (C) *Sclerocyphon* sp. (Psephenidae). (D) *Pyrochroa* sp. (Pyrochroidae). (E) *Limnoxenus* sp. (Hydrophilidae). (F) *Episcaphula australis* (Boisduval) (Erotylidae). (G) *Agrypnus* sp. (Elateridae). (H) *Distocupes varians* (Lea) (Cupedidae). (I) *Colpochila* sp. (Scarabaeidae), abdomen, lateral.

Figure 46. Adult Coleoptera. (A) Genus ? sp. (Cantharidae), pterothorax, ventral. (B) *Eucinetus* sp. (Eucinetidae), mesothorax, ventral. (C) *Dinoderus* sp. (Bostrichidae), metathorax, ventral. (D) *Clivina* sp. (Carabidae), metathorax, ventral. (E) *Derodontus* sp. (Derodontidae), metendosternite, ventral.

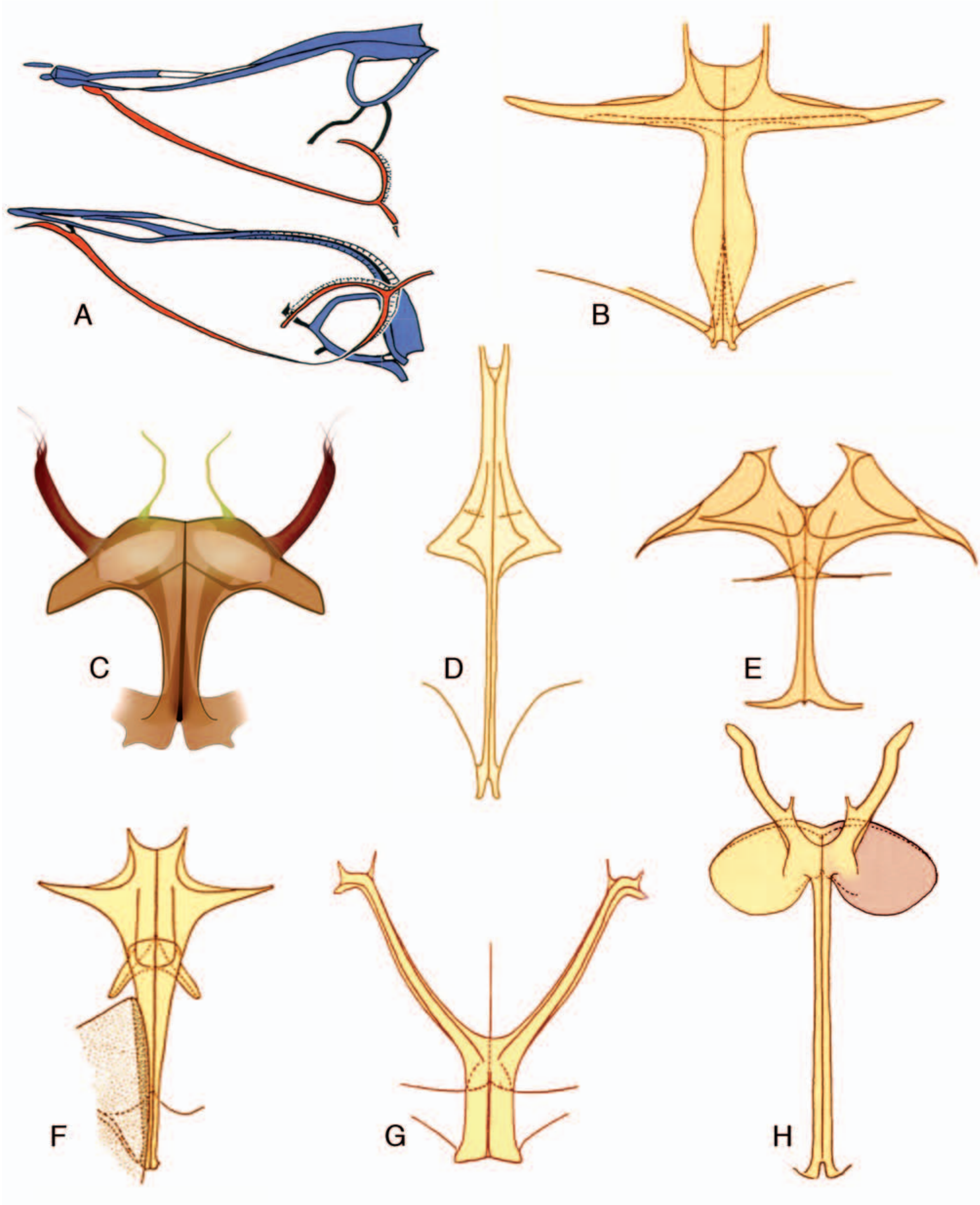


Figure 47. Adult Coleoptera. (A) *Nosodendron* sp. (Nosodendridae), anterior and posterior wing struts in unfolded and folded wing. (B–H) Metendosternites. (B) *Agyrtes castaneus* (Fabricius) (Agyrtidae). (C) *Deretaphrus* sp. (Bothrideridae). (D) *Nematodes* sp. (Eucnemidae). (E) *Hydroporus* sp. (Dytiscidae). (F) *Odeles marginata* (Fabricius) (Scirtidae). (G) *Corticeus bicolor* Olivier (Tenebrionidae). (H) *Melittomma* sp. (Lymexylidae).

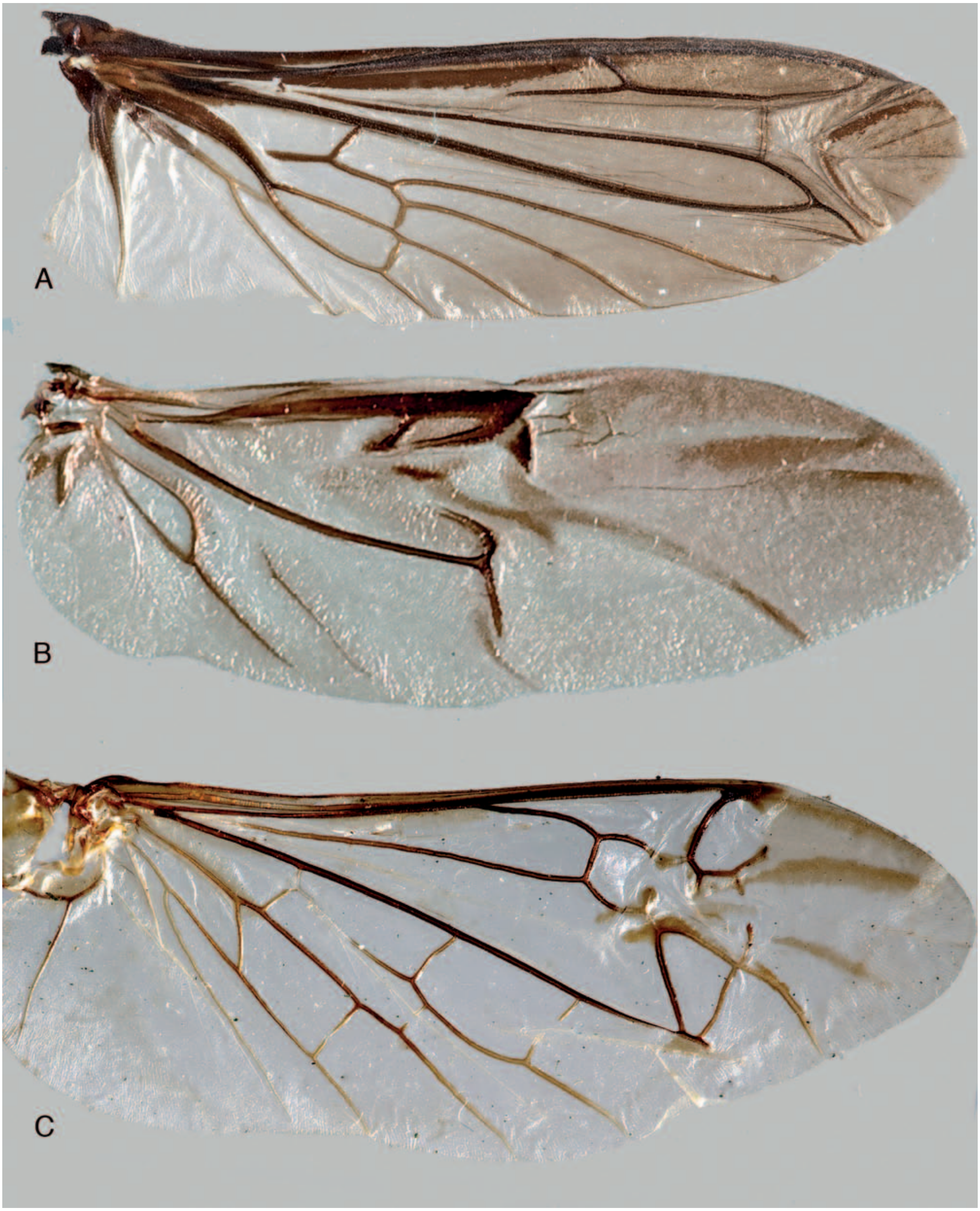


Figure 48. Adult Coleoptera hindwings. (A) *Pityobius anguinus* LeConte (Elateridae). (B) *Plagiodera* sp. (Chrysomelidae). (C) *Omma* sp. (Ommatidae).

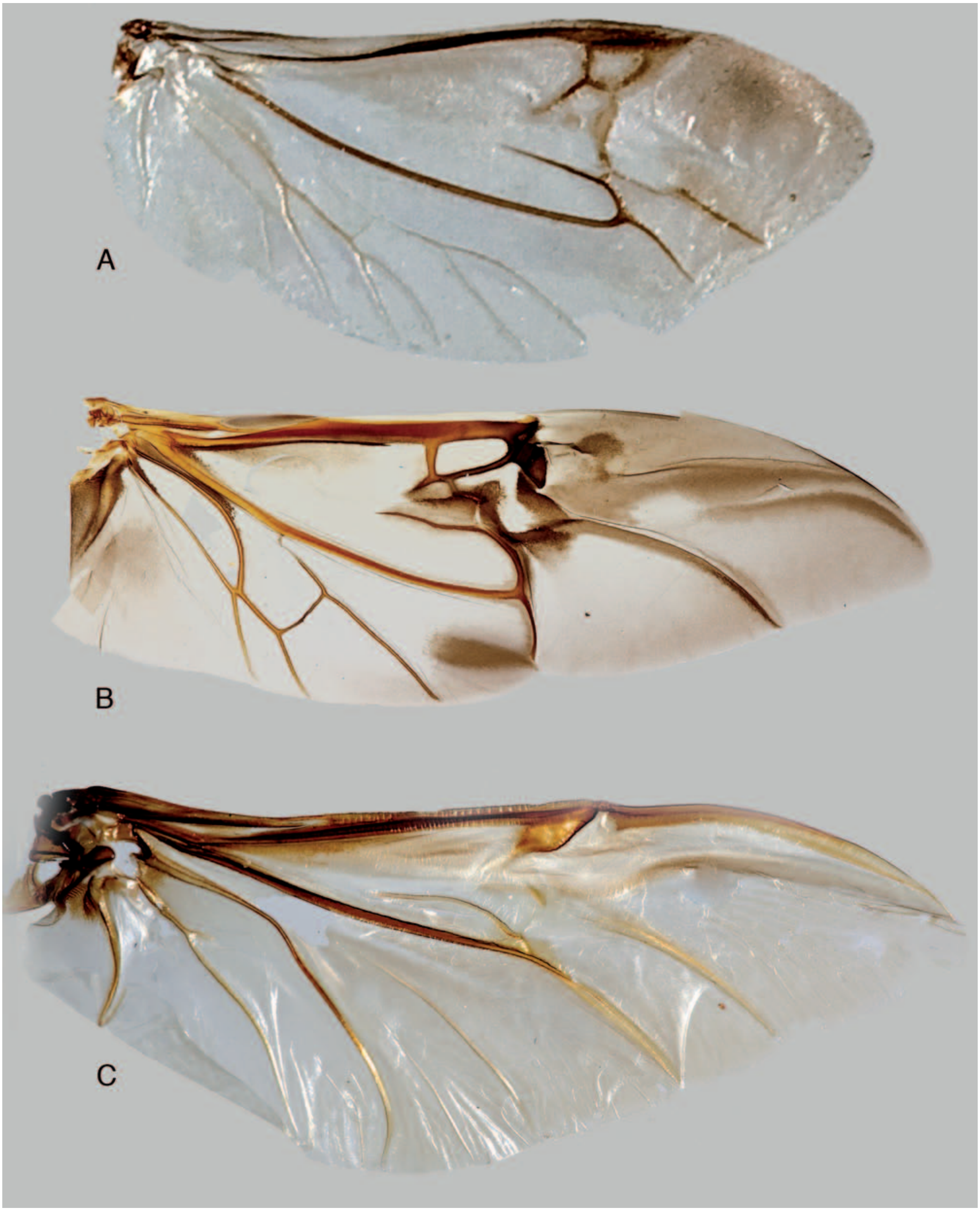


Figure 49. Adult Coleoptera hindwings. (A) *Attagenus pellio* (Linnaeus) (Dermestidae. (B) *Stenomela* sp. (Chrysomelidae). (C) *Pleocoma linsleyi* Hovore (Pleocomidae).

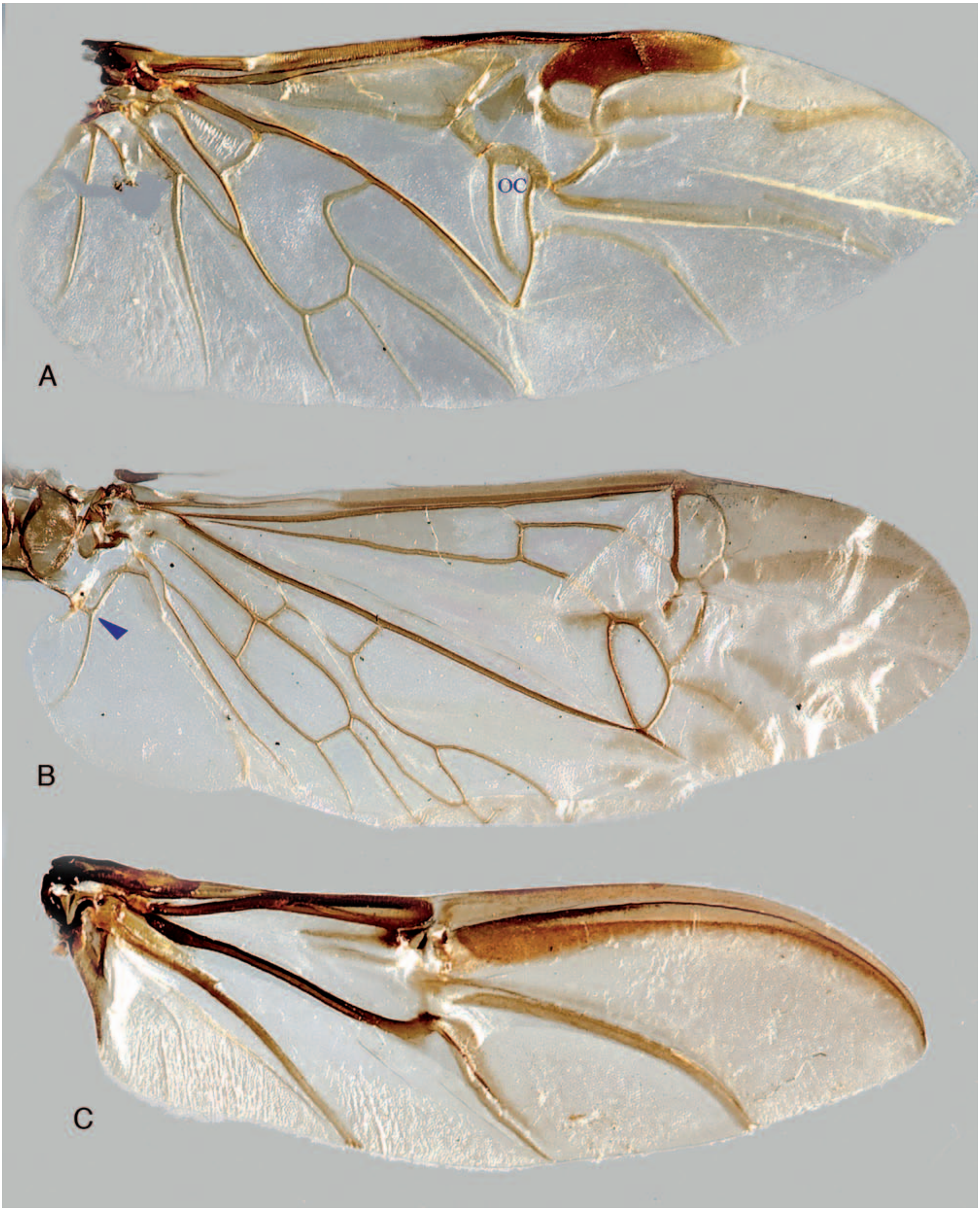


Figure 50. Adult Coleoptera hindwings. (A) *Sphallomorpha* sp. (Carabidae). (B) *Priacma serrata* (LeConte) (Cupedidae). (C). *Crossotarsus* sp. (Curculionidae).

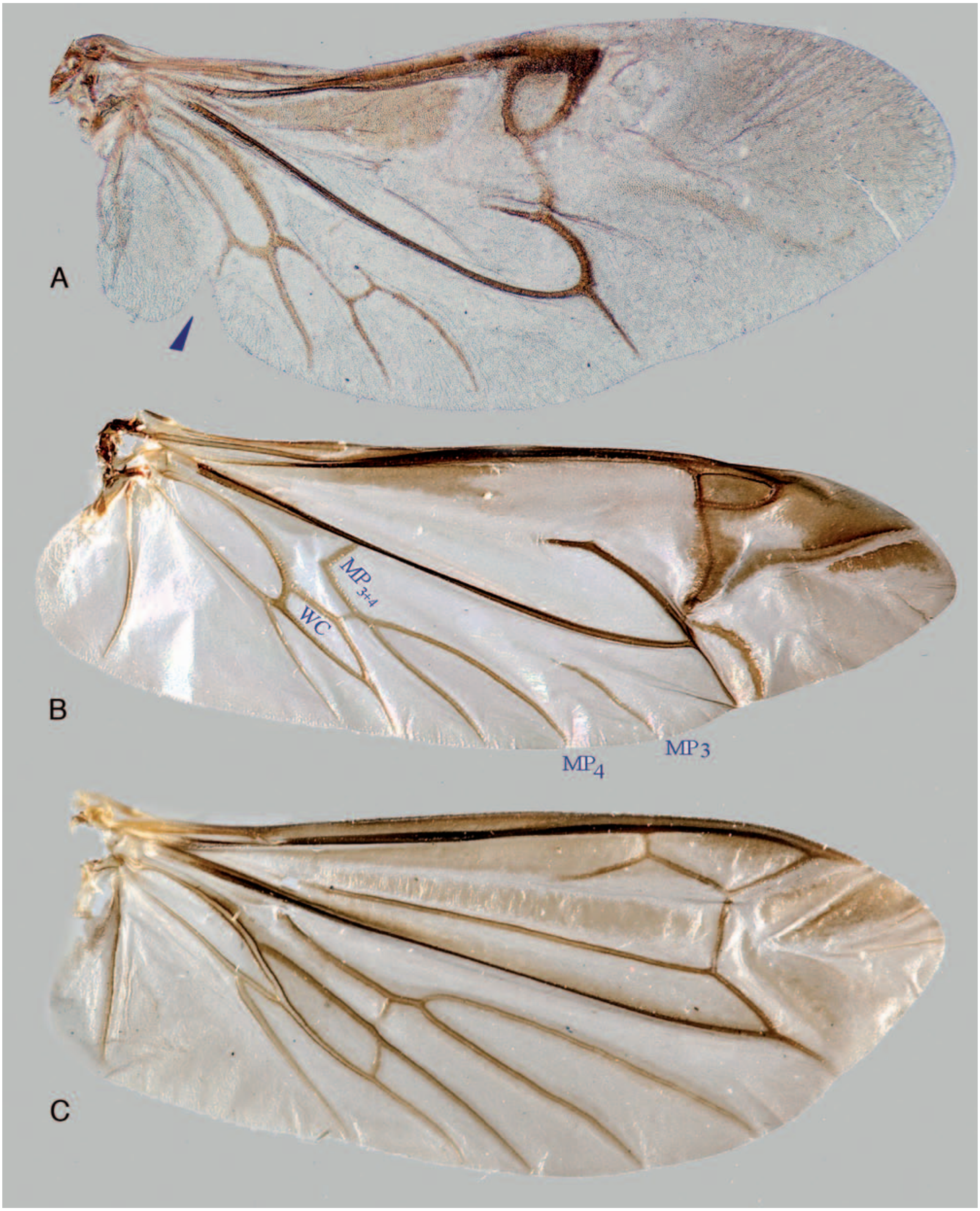


Figure 51. Adult Coleoptera hindwings. (A) *Orphilodes* sp. (Dermestidae). (B) *Notodascillus* sp. (Dascillidae). (C) *Photinus* sp. (Lampyridae).

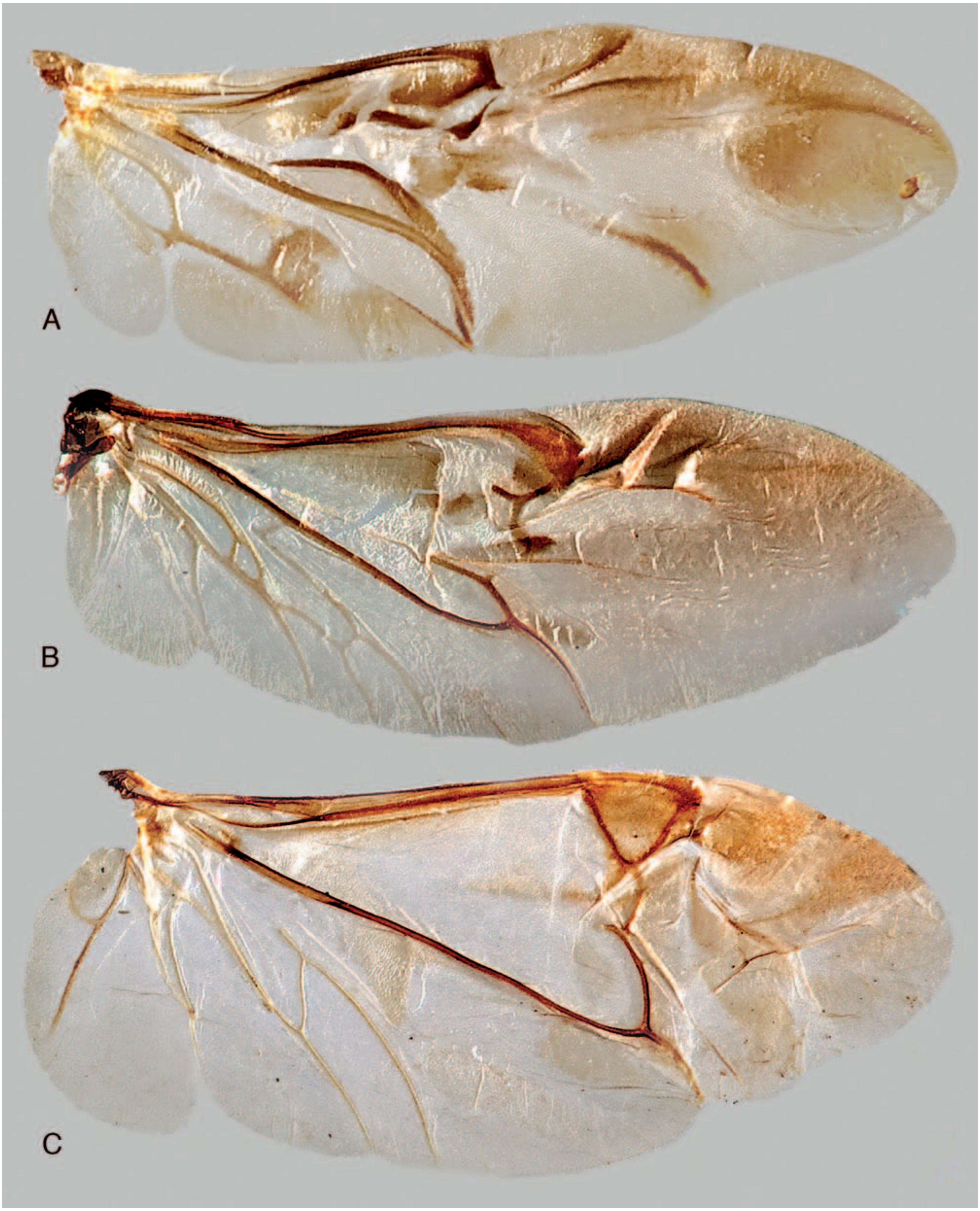


Figure 52. Adult Coleoptera hindwings. (A) *Harmonia* sp. (Coccinellidae). (B) *Trichodesma* sp. (Ptinidae). (C) *Pseudomicrocara* sp. (Scirtidae).

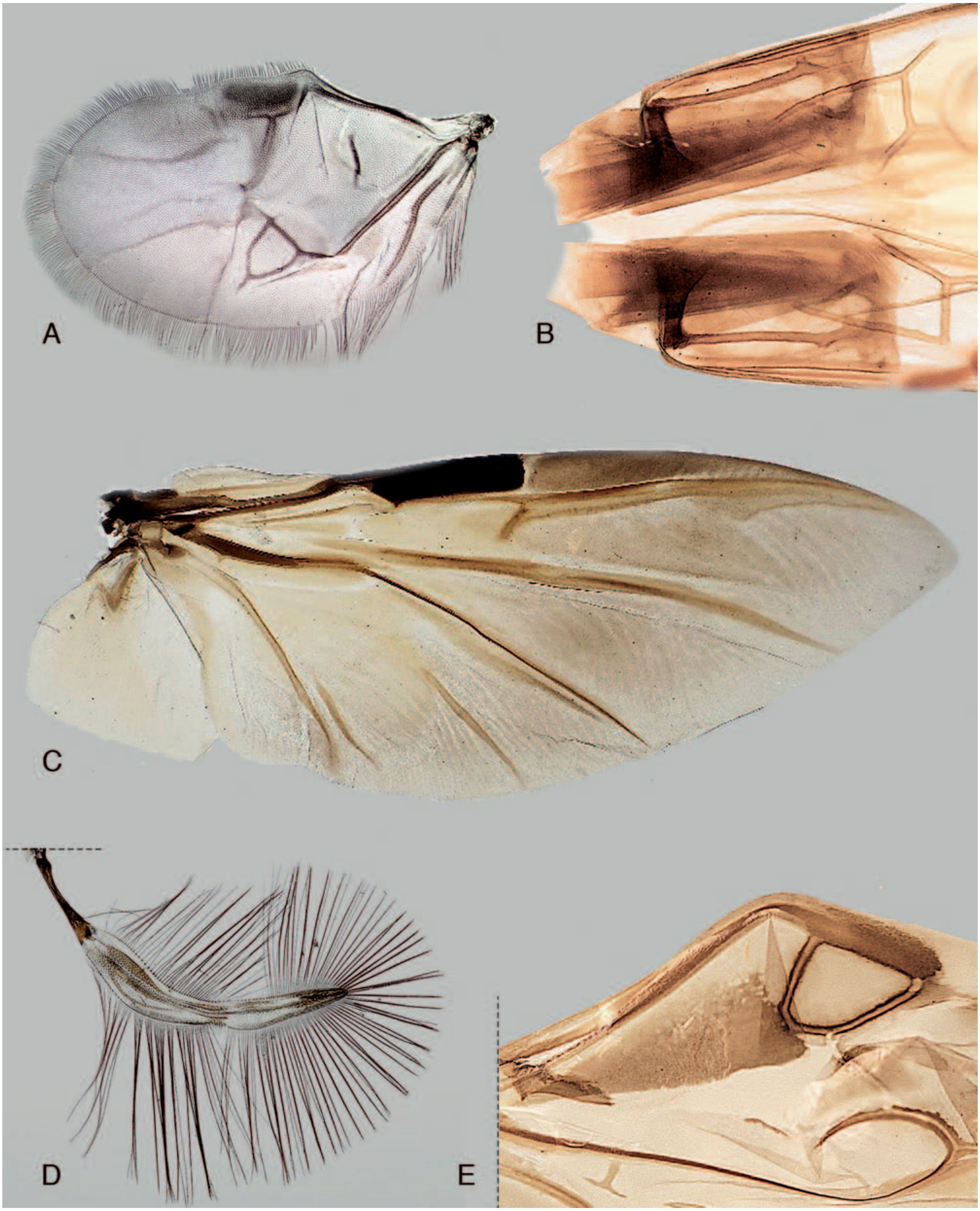


Figure 53. Adult Coleoptera hindwings. (A) *Torridincola rhodesica* Steffran (Torrodincolidae). (B) *Priacma serrata* (LeConte) (Cupedidae), folded wing apices. (C) *Creophilus maxillosus* (Linnaeus) (Staphylinidae). (D) *Acrotrichis* sp. (Ptiliidae). (E) *Nosodendron californicum* Horn (Nosodendridae), partly folded wing.

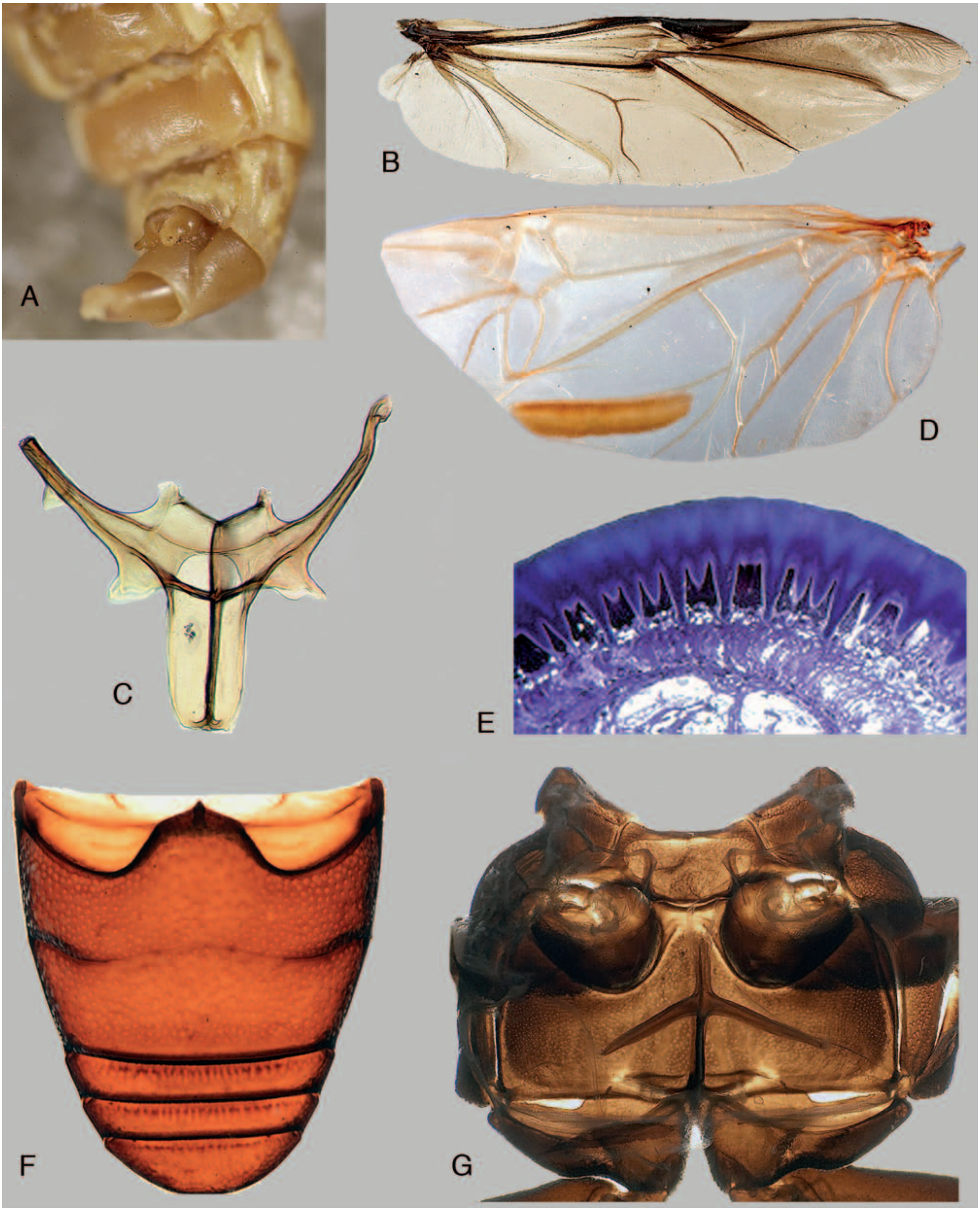


Figure 54. Adult Coleoptera. (A) *Rhagophthalmus ohbai* Wittmer (Rhagophthalmidae), female abdominal apex, posterolateral. (B) *Necrophila americana* (Linnaeus) (Silphidae), hind wing. (C) *Thymalus* sp. (Trogossitidae), metendosternite, ventral. (D) *Hyderodes* sp. (Dytiscidae), hind wing. (E) *Rhinorhipus tamborinensis* Lawrence (Rhinorhipidae)., section of compound eye, showing exocone ommatidia. (F) *Tranes lyterioides (Pascoe)* (Curculionidae), abdomen, ventral. (G) *Necrophila americana* (Linnaeus), pterothorax, dorsal.

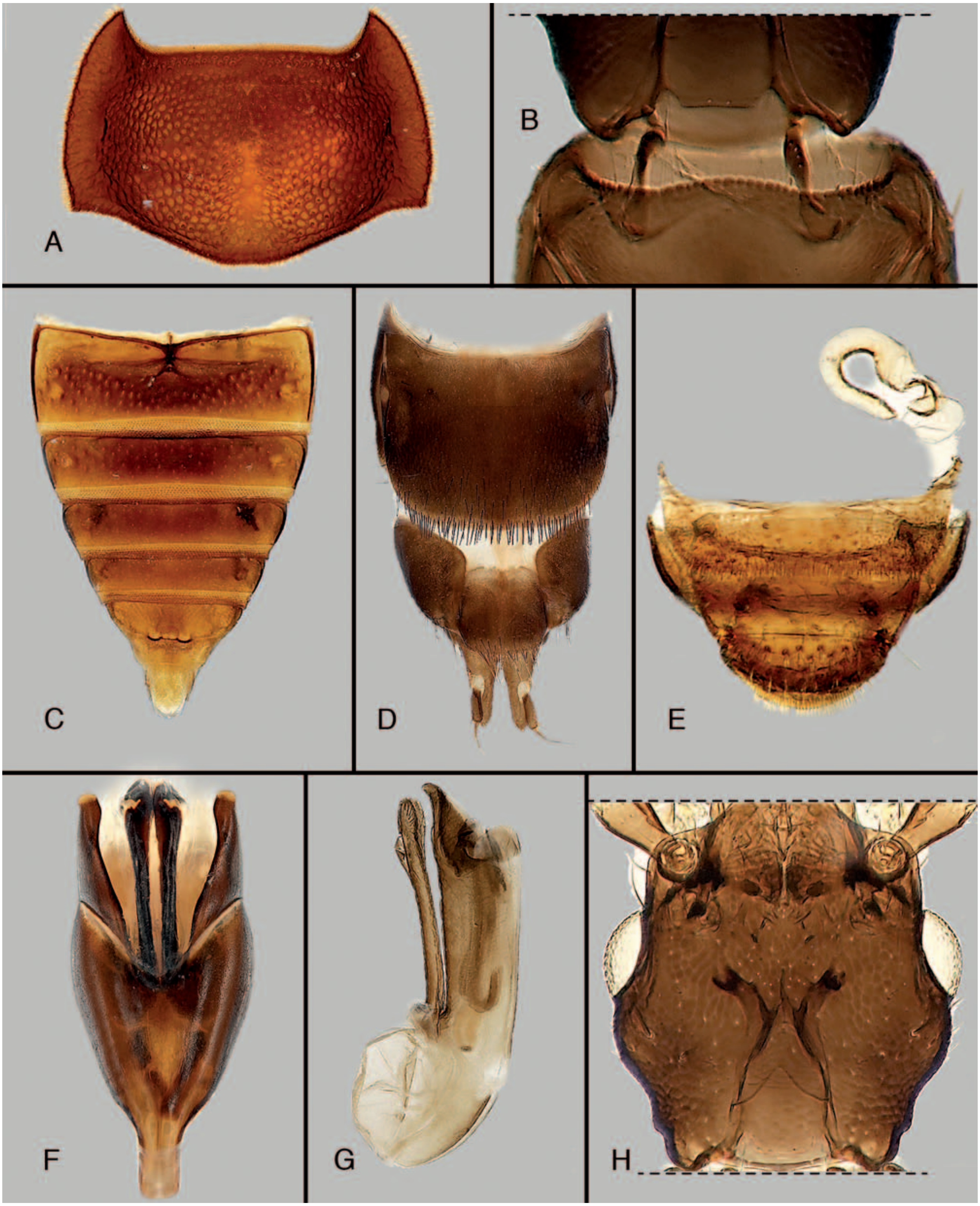


Figure 55. Adult Coleoptera. (A) *Trox aequalis* Say (Trogidae), prothorax, dorsal. (B) *Renardia* sp. (Staphylinidae), junction of head and prothorax, ventral. (C) *Glypholoma pecki* Thayer & Newton (Staphylinidae), abdomen, ventral. (D) *Necrophila americana* (Linnaeus) (Silphidae), female abdominal apex, dorsal. (E) *Hydraena californica* Perkins (Hydraenidae), female abdominal apex, dorsal [note this is mirror-image]. (F) *Pleocoma linsleyi* Hovore (Pleocomidae), aedeagus, ventral. (G) *Creophilus maxillosus* (Linnaeus) (Staphylinidae), aedeagus, lateral. (H) *Renardia* sp. (Staphylinidae), head, dorsal.

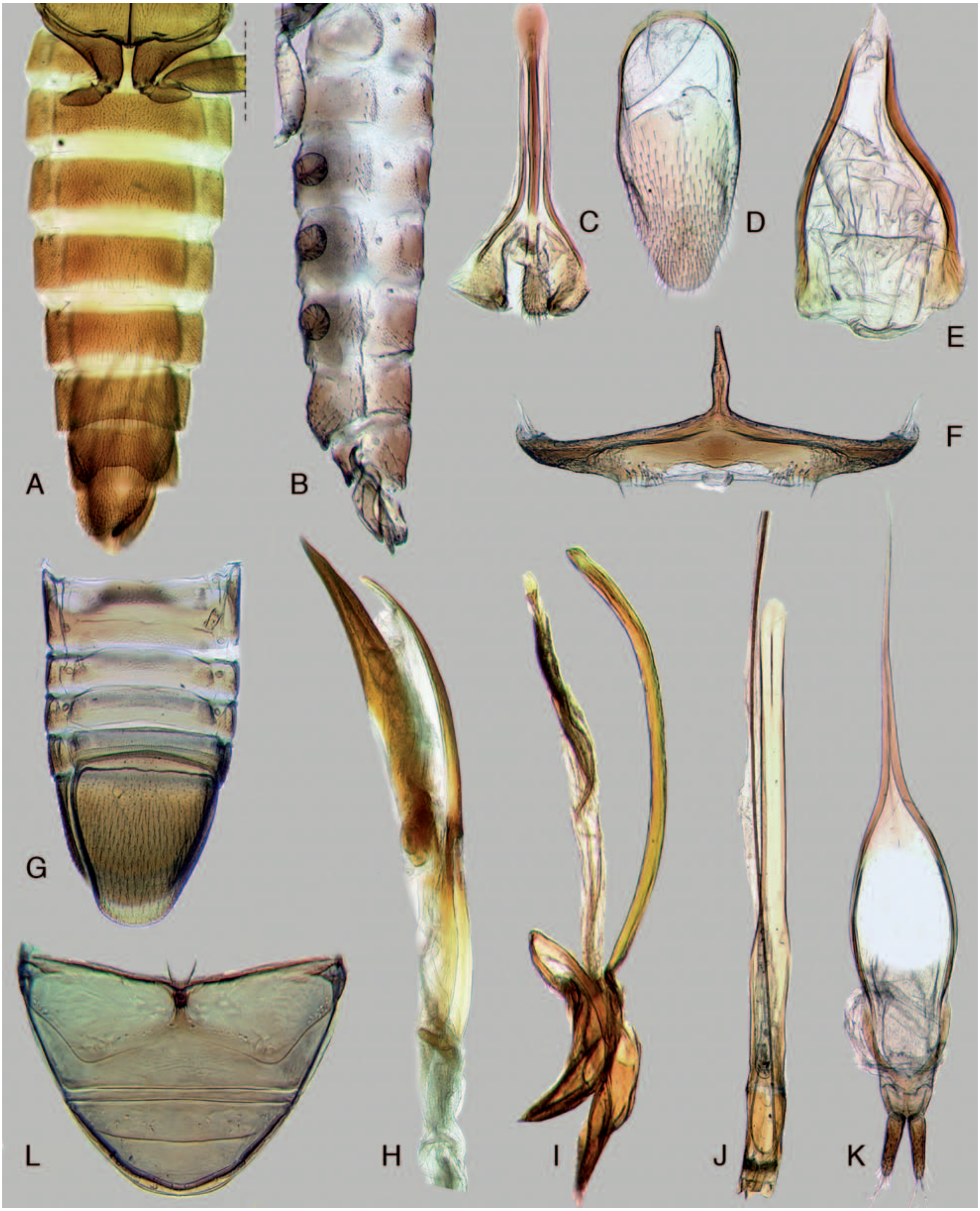


Figure 56. Adult Coleoptera. (A) Genus ? sp. (Cantharidae), metacoxae and abdomen, ventral. (B), *Micromalthus debilis* LeConte (Micromalthidae), male abdomen, lateral (left side). (C) *Cucujus clavipes* Fabricius (Cucujidae), abdominal segment IX, ventral. (D) *Ampedus sanguineus* (Linnaeus) (Elateridae), segment IX ventral. (E) *Pristocerus* sp. (Zopheridae), segment IX, dorsal. (F) *Eurhynchus laevior* (Kirby) (Brentidae), sternite VIII, ventral. (G) *Smicrips* sp. (Smicripidae), abdomen, dorsal. (H) *Eurhynchus laevior* (Kirby) (Brentidae), penis, lateral. (I) *Amartus rufipes* Leconte (Kateretidae), aedeagus, lateral. (J) *Cucujus clavipes* Fabricius (Cucujidae), penis, dorsal. (K) *Cucujus clavipes* Fabricius (Cucujidae), tegmen, dorsal. (L) *Sphaerius* sp. (Sphaeriusidae), abdomen, ventral.

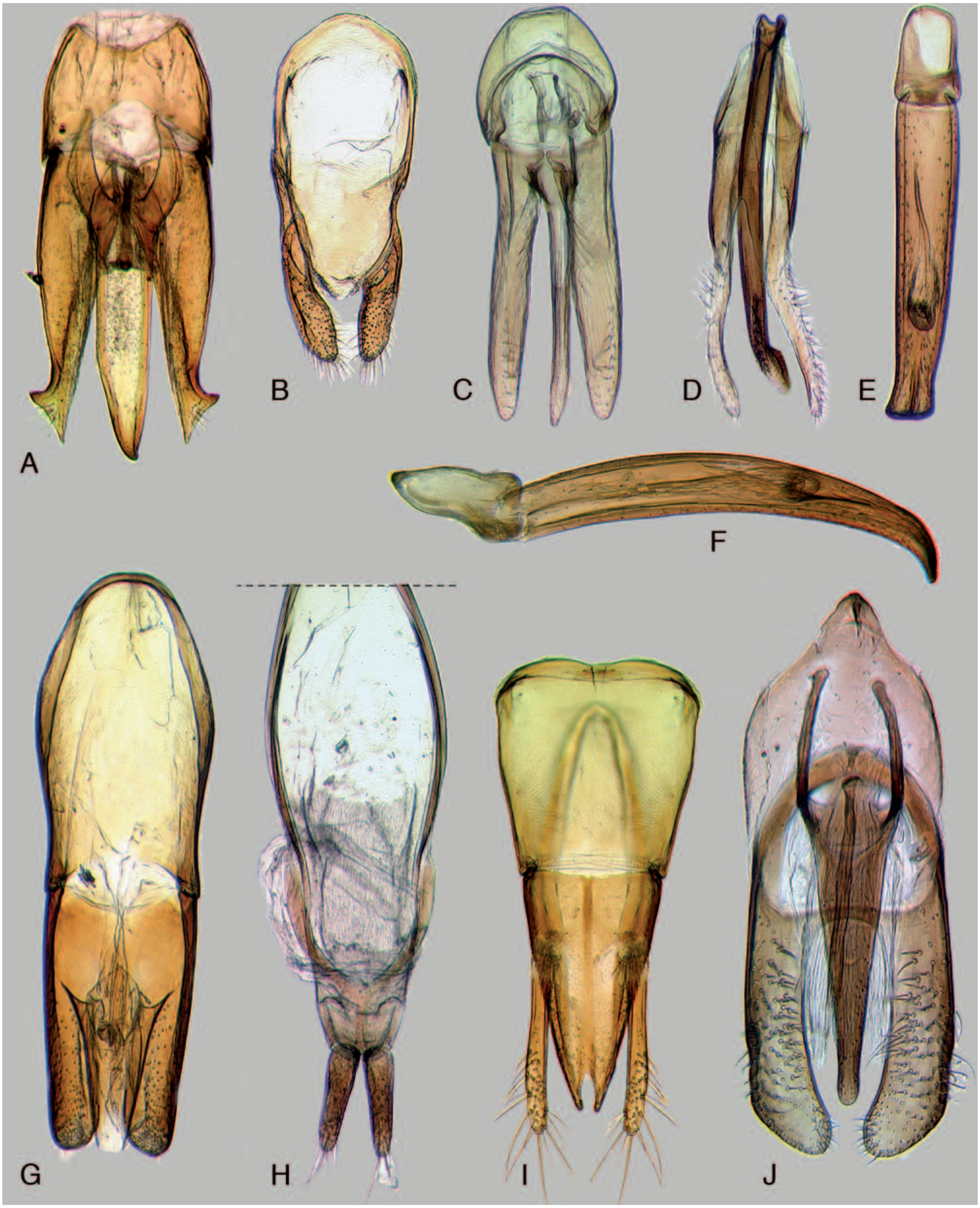


Figure 57. Adult Coleoptera male genitalia. (A) *Ampedus sanguineus* (Linnaeaus) (Elateridae), aedeagus ventral. (B) *Amartus rufipes* LeConte (Kateretidae), tegmen, ventral. (C) *Eucinetus* sp. (Eucinetidae), aedeagus, ventral. (D) *Ptinus* sp. (Ptinidae), aedeagus, ventral. (E) *Euspilotus scissus* (LeConte) (Histeridae), aedeagus, ventral. (F) *Pristoderus antarcticus* White (Zopheridae), aedeagus, ventral. (G) *Cucujus clavipes* Fabricius (Cucujidae), tegmen, dorsal. (H) *Boros schneideri* Panzer (Boridae), tegmen, dorsal. (I) *Euspilotus scissus* (LeConte) (Histeridae), aedeagus, lateral. (J) *Anthrenus scrophulariae* (Linnaeus) (Dermestidae), aedeagus, ventral.

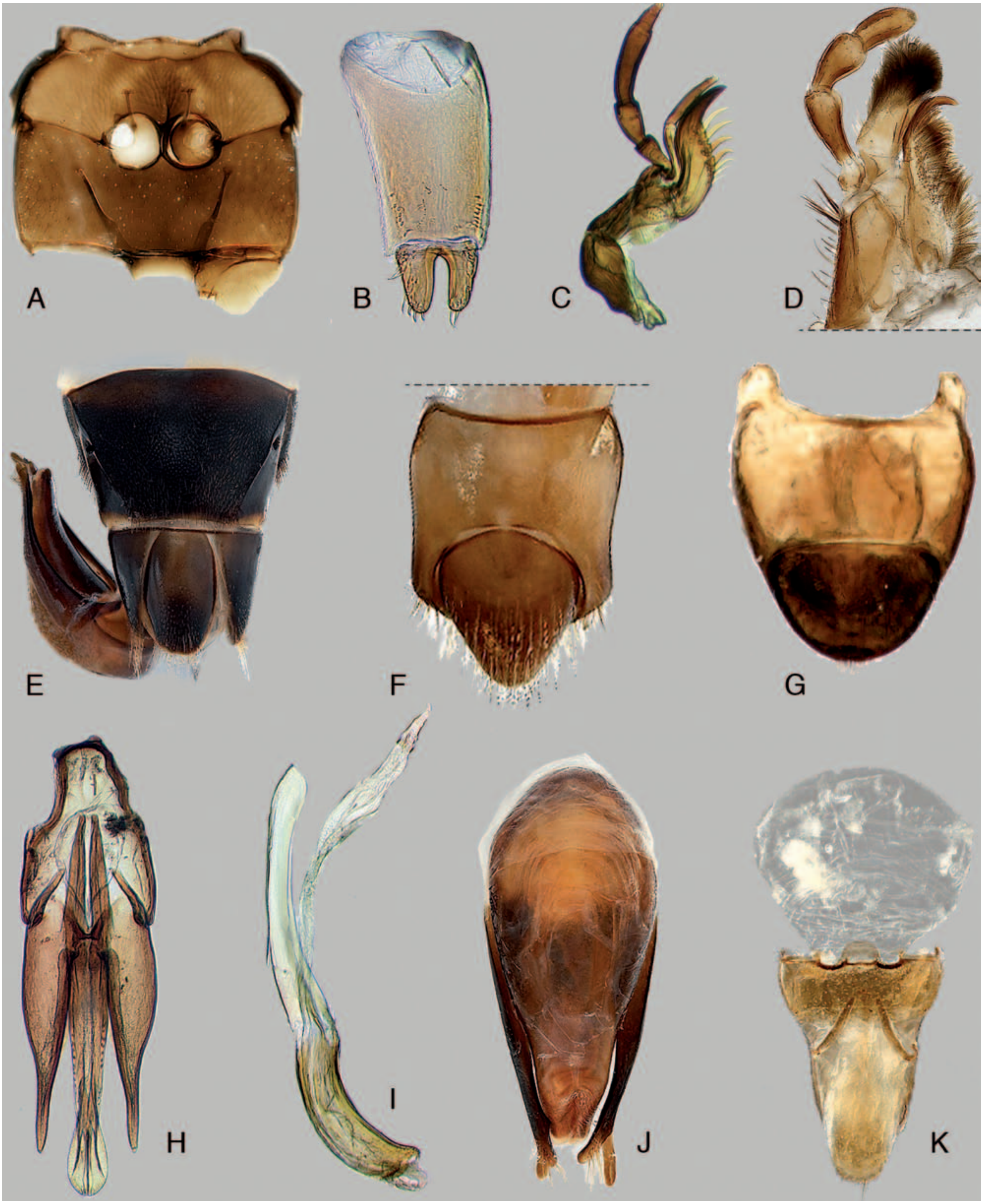


Figure 58. Adult Coleoptera. (A) *Acrotrichis* sp. (Ptiliidae), pterothorax, dorsal. (B) *Taphropiestes* sp. (Cavognathidae), tegmen, ventral. (C) *Haliplus* sp. (Haliplidae), maxilla, ventral. (D) *Necrophila americana* (Linnaeus) (Silphidae), maxilla, dorsal. (E) *Nicrophorus tomentosus* Weber (Silphidae), male abdominal tergites VIII–X, dorsal and aedeagus, lateral. (F) *Necrophilus hydrophiloides* Guérin-Méneville (Agyrtidae), male abdominal tergites IX and X, dorsal. (G) *Hydraena californica* Perkins (Hydraenidae), male abdominal tergites IX and X, dorsal. (H) *Simplocaria* sp. (Byrrhidae), aedeagus, ventral. (I) *Taphropiestes* sp. (Cavognathidae), penis, lateral. (J) *Nicrophorus tomentosus* Weber (Silphidae), aedeagus, ventral. (K) *Glypholoma pecki* Thayer & Newton (Staphylinidae), abdominal apex, ventral.

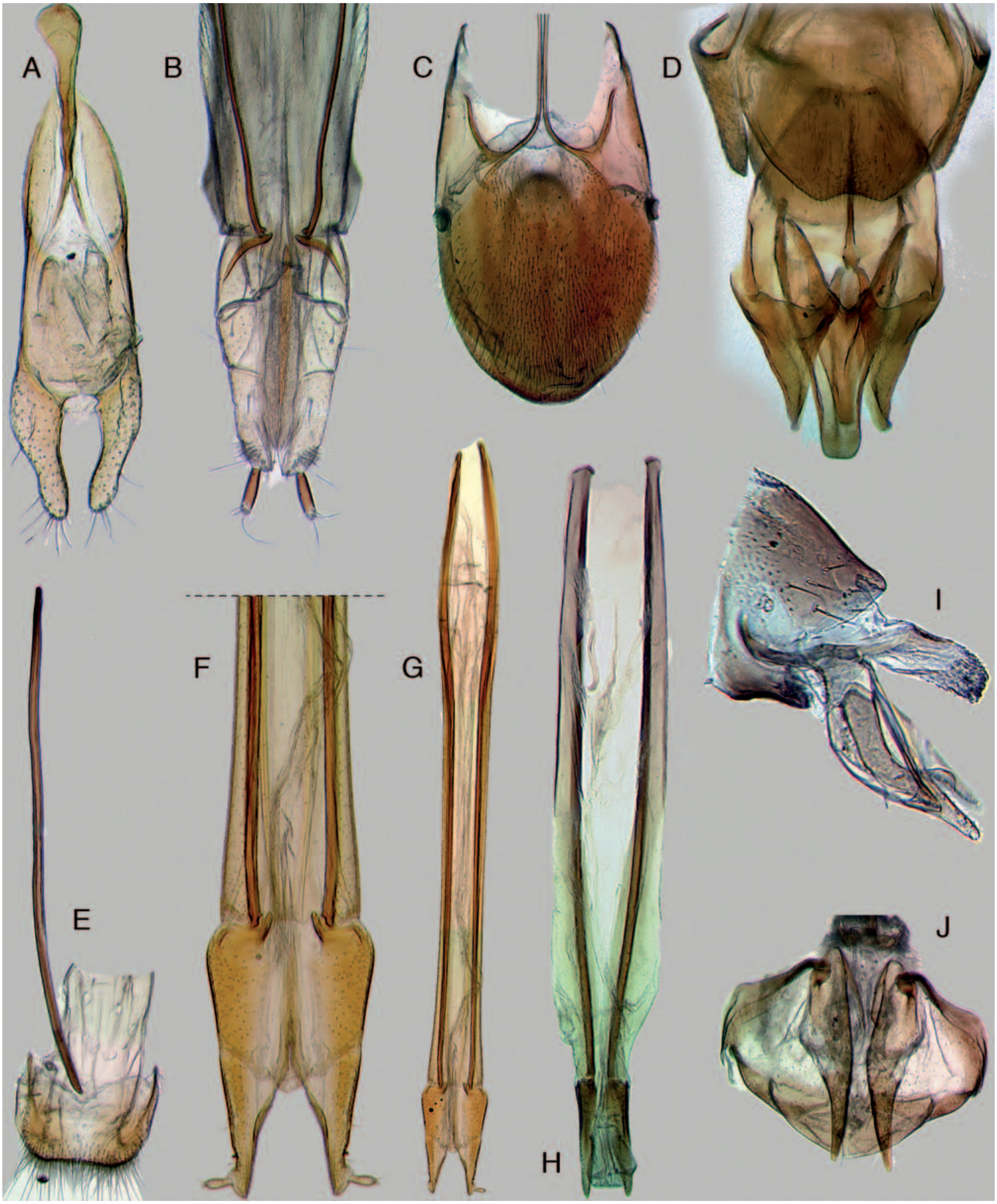


Figure 59. Adult Coleoptera. (A) *Chaetosoma scaritides* Westwood (Chaetosomatidae), tegmen, dorsal. (B) *Pristoderus antarcticus* White (Zopheridae), ovipositor, ventral. (C) *Ampedus sanguineus* (Linnaeus) (Elateridae), female abdominal segment VIII, ventral. (D) *Dascillus davidsoni* LeConte (Dascillidae), male abdominal apex, ventral. (E) *Pristoderus antarcticus* White (Zopheridae), female abdominal segment VIII, ventral. (F) *Ampedus sanguineus* (Linnaeus) (Elateridae), anterior portion of ovipositor, ventral. (G) *Ampedus sanguineus* (Linnaeus) (Elateridae), entire ovipositor, ventral. (H) *Ptilodactyla* sp. (Ptilodactylidae), ovipositor, ventral. (I) *Micromalthus debilis* Leconte (Micromalthidae), male abdominal apex, lateral. (J) *Nebria acuta* Lindroth (Carabidae), ovipositor, ventral.

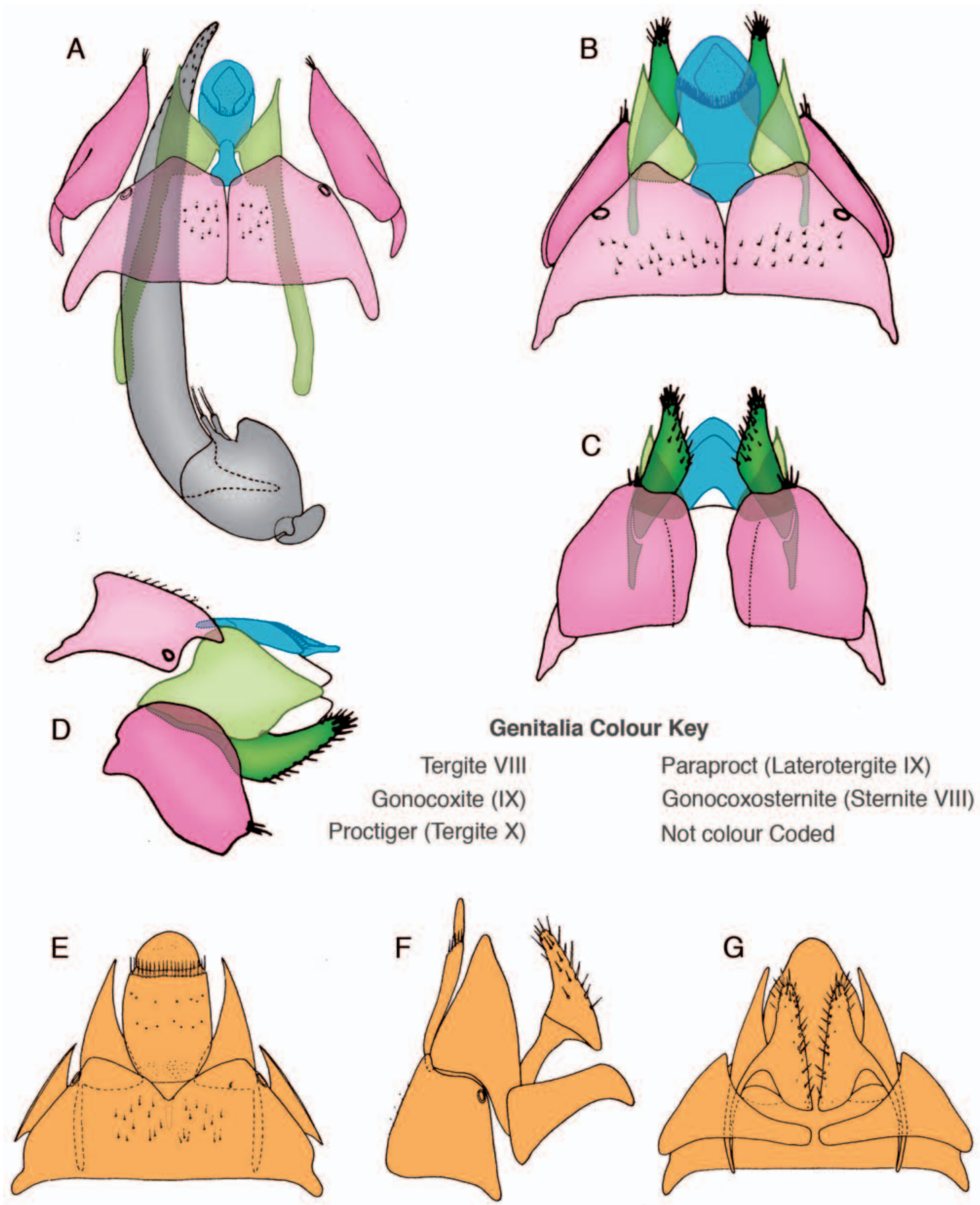


Figure 60. Adult Coleoptera. Abdominal apices. (A) *Claudiella ingens* Reichardt & Vanin (Torridincolidae), male, dorsal. (B) Same, female, dorsal. (C) Same, female, ventral. (D) Same, female, lateral. (E) *Ytu zeus* Reichardt (Torridincolidae), female, dorsal. (F) Same, lateral. (G) Same, ventral.

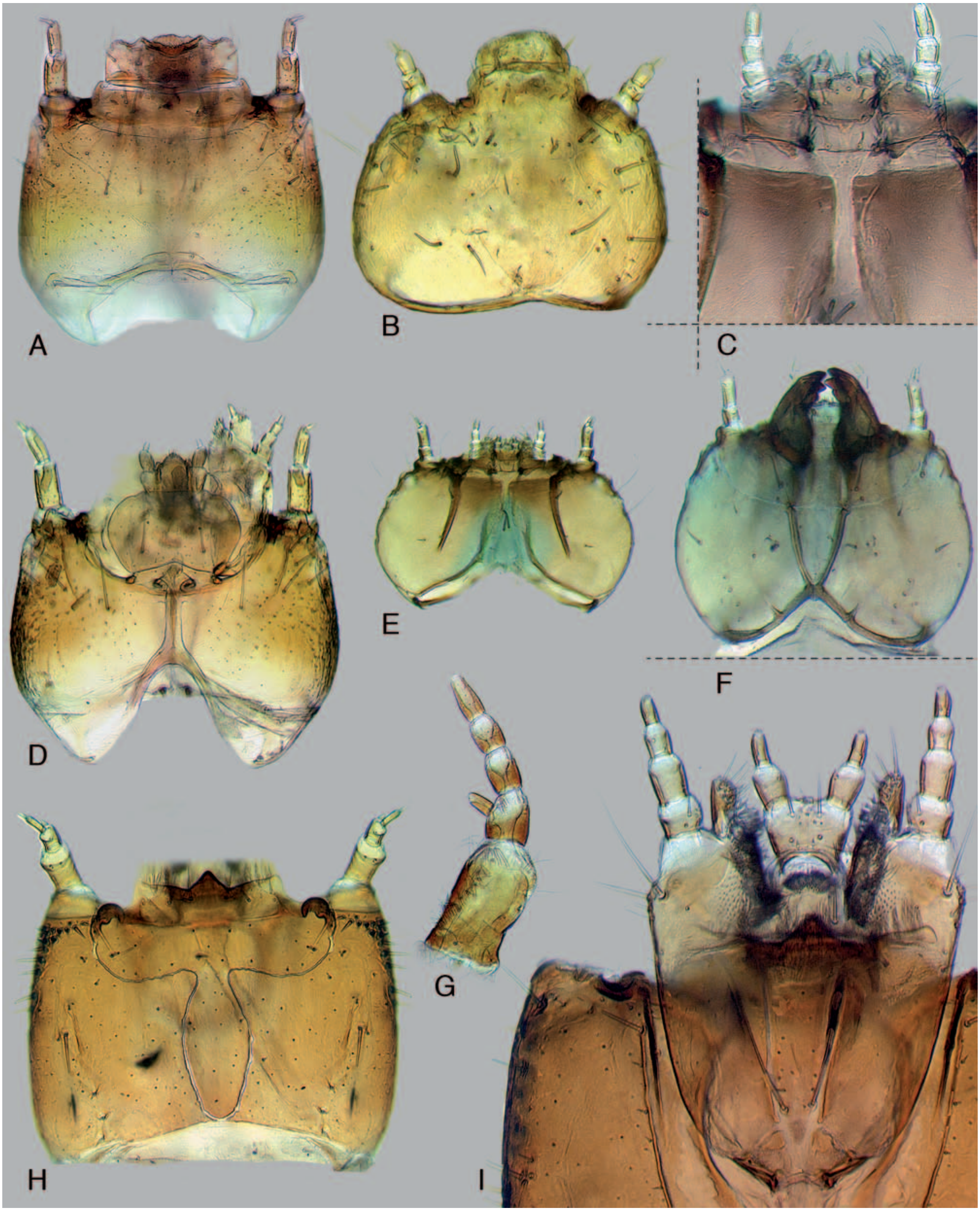


Figure 61. Larval Coleoptera. (A) *Ptilodactyla* sp. (Ptilodactylidae), head, dorsal. (B) *Byturus tomentosus* (Degeer), head, dorsal. (C) *Cyclaxyra* sp. (Cyclaxyridae), ventral mouthparts and gulamentum, ventral. (D) *Ptilodactyla* sp. (Ptilodactylidae), head ventral. (E) *Cyclaxyra* sp. (Cyclaxyridae), head, ventral. (F) Same, head, dorsal. (G) *Hister nomas* Erichson (Histeridae), maxilla, dorsal. (H) *Ampedus* sp. (Elateridae), head, dorsal. (I) Same, ventral mouthparts, ventral.

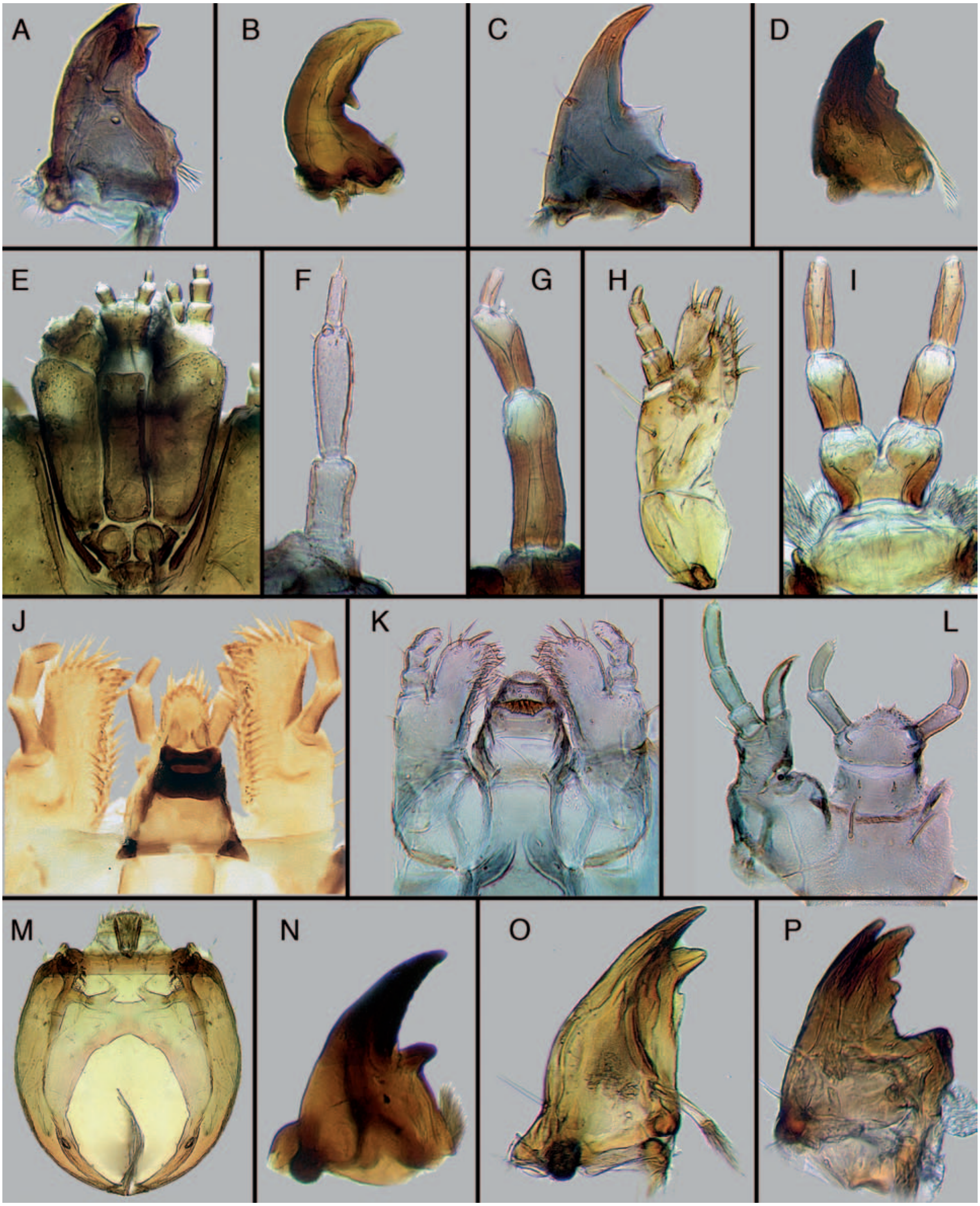


Figure 62. Larval Coleoptera. (A) *Cyclaxyra* sp. (Cyclaxyridae), mandible, ventral. (B) *Hister nomas* Erichson (Histeridae), mandible, dorsal. (C) *Paracucujus rostratus* Sen Gupta & Crowson (Boganiidae), mandible, dorsal. (D) *Grynoma* sp. (Trogossitidae), mandible, ventral. (E) *Ampedus* sp. (Elateridae), ventral mouthparts, ventral. (F) *Paracucujus rostratus* Sen Gupta & Crowson (Boganiidae), antenna, dorsal. (G) *Hister nomas* Erichson (Histeridae), antenna, dorsal. (H) *Ptilodactyla* sp. (Ptilodactylidae), maxilla, ventral. (I) *Hister nomas* Erichson (Histeridae), labium, ventral. (J) *Synchroa punctata* Newman, ventral mouthparts, dorsal. (K) *Temnopalpus* sp. (Pyrochroidae), ventral mouthparts, ventral. (L) *Paracucujus rostratus* Sen Gupta & Crowson (Boganiidae), maxilla and labium, ventral. (M) *Sphenophorus brunnipennis* Germar. (Curculionidae), head, ventral. (N) *Ampedus* sp. (Elateridae), mandible, ventral. (O) *Ptilodactyla* sp. (Ptilodactylidae), mandible, ventral. (P) *Byturus tomentosus* (Degeer) (Byturidae), mandible, dorsal.

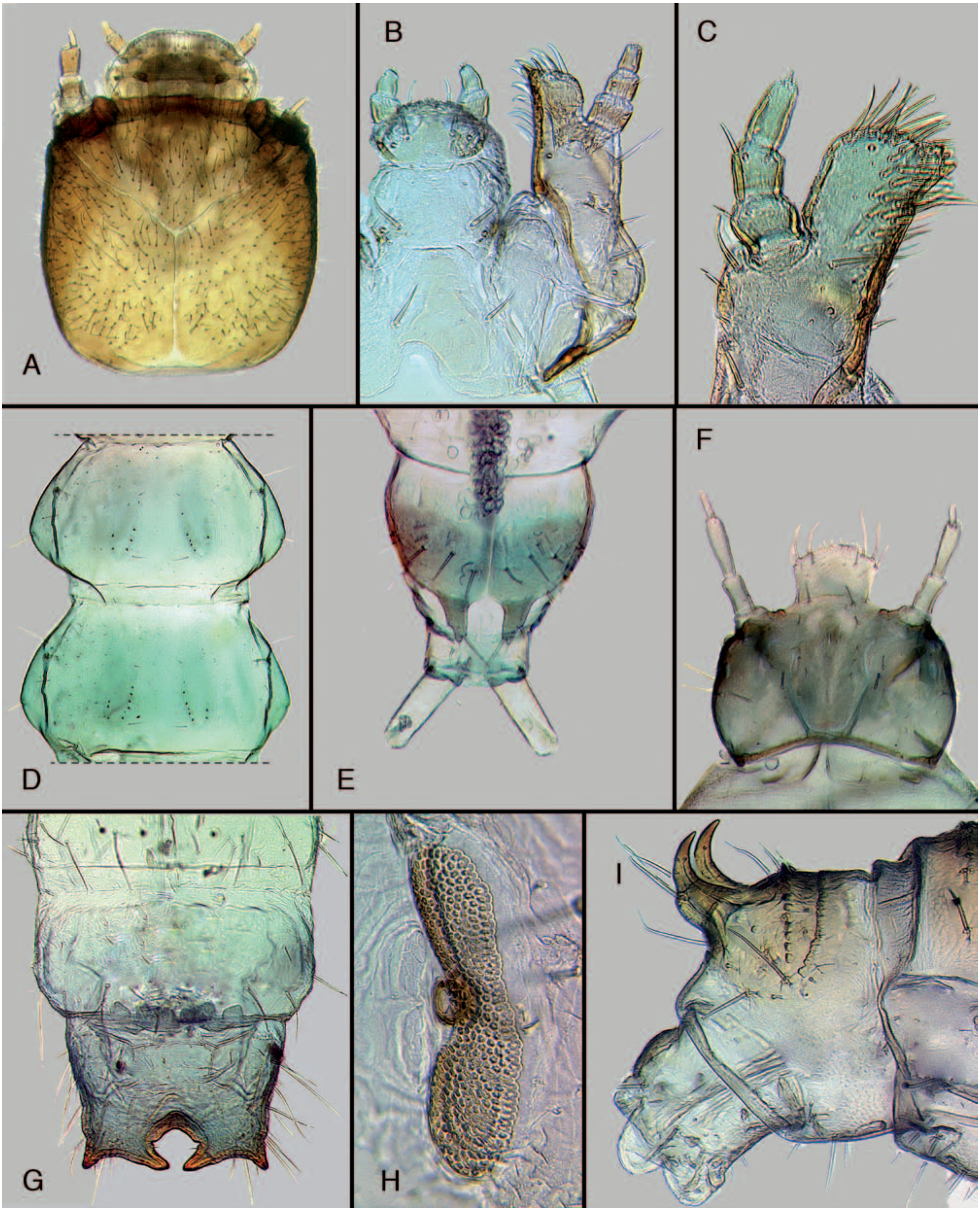


Figure 63. Larval Coleoptera. (A) *Collops* sp. (Melyridae), head, dorsal. (B) *Byturus tomentosus* (Degeer) (Byturidae), maxilla and labium, ventral. (C) *Elacatis* sp. (Salpingidae), maxilla, ventral. (D) *Lacconotus pinicola* Horn (Mycteridae), abdominal segments II and III, dorsal. (E), *Paracucujus rostratus* Sen Gupta & Crowson (Boganiidae), abdominal apex, dorsal. (F) Same, head, dorsal. (G) *Salpingus* sp. (Salpingidae), abdominal apex, dorsal. (H) *Grynoma* sp. (Trogossitidae), abdominal spiracle. (I) *Byturus* sp. (Byturidae), abdominal apex, lateral.

Figure 64. Larval Coleoptera. (A) *Buprestis viridisuturalis* Nicolay & Weise (Buprestidae), head and thorax, ventral. (B) Same, dorsal. (C) *Necrodes* sp. (Silphidae), abdominal apex, dorsal. (D) *Necrophila americana* (Linnaeus), habitus, dorsal. (E) *Tropisternus* sp. (Hydrophilidae), habitus, lateral. (F) *Passalus* sp. (Passalidae), head and thorax, ventral. (G) *Geotrupes spiniger* (Marsham) (Geotrupidae), head and thorax, ventral. (H) Genus ? sp. (Carabidae), head, dorsal. (I) *Tenomerga cinerea* (Say) (Cupedidae), head, dorsal. (J) *Ipelates* sp. (Agyrtidae), head and thorax, ventral.

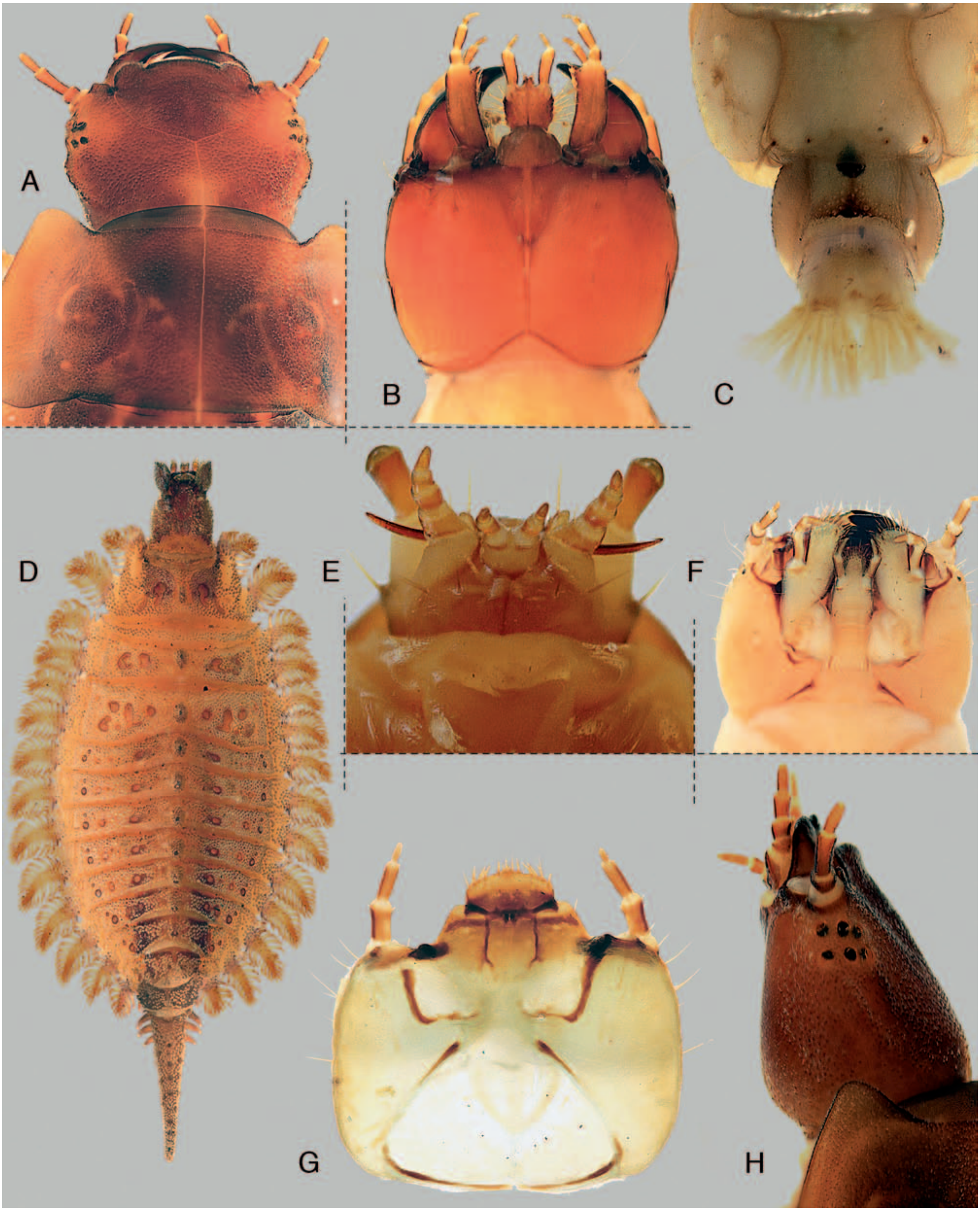


Figure 65. Larval Coleoptera. (A) *Amphizoa* sp. (Amphizoidae), head and prothorax, dorsal. (B) Genus? sp. (Carabidae), head, ventral. (C) *Ellychnia* sp. (Lampyridae), abdominal apex, ventral. (D) *Brachypsectra fulva* LeConte (Brachypsectridae), habitus, dorsal. (E) Genus ? sp. (Lycidae), head, ventral. (F) *Synchroa punctata* Newman, head, ventral. (G) Same, without mouthparts. (H) *Amphizoa* sp. (Amphizoidae), head, lateral.

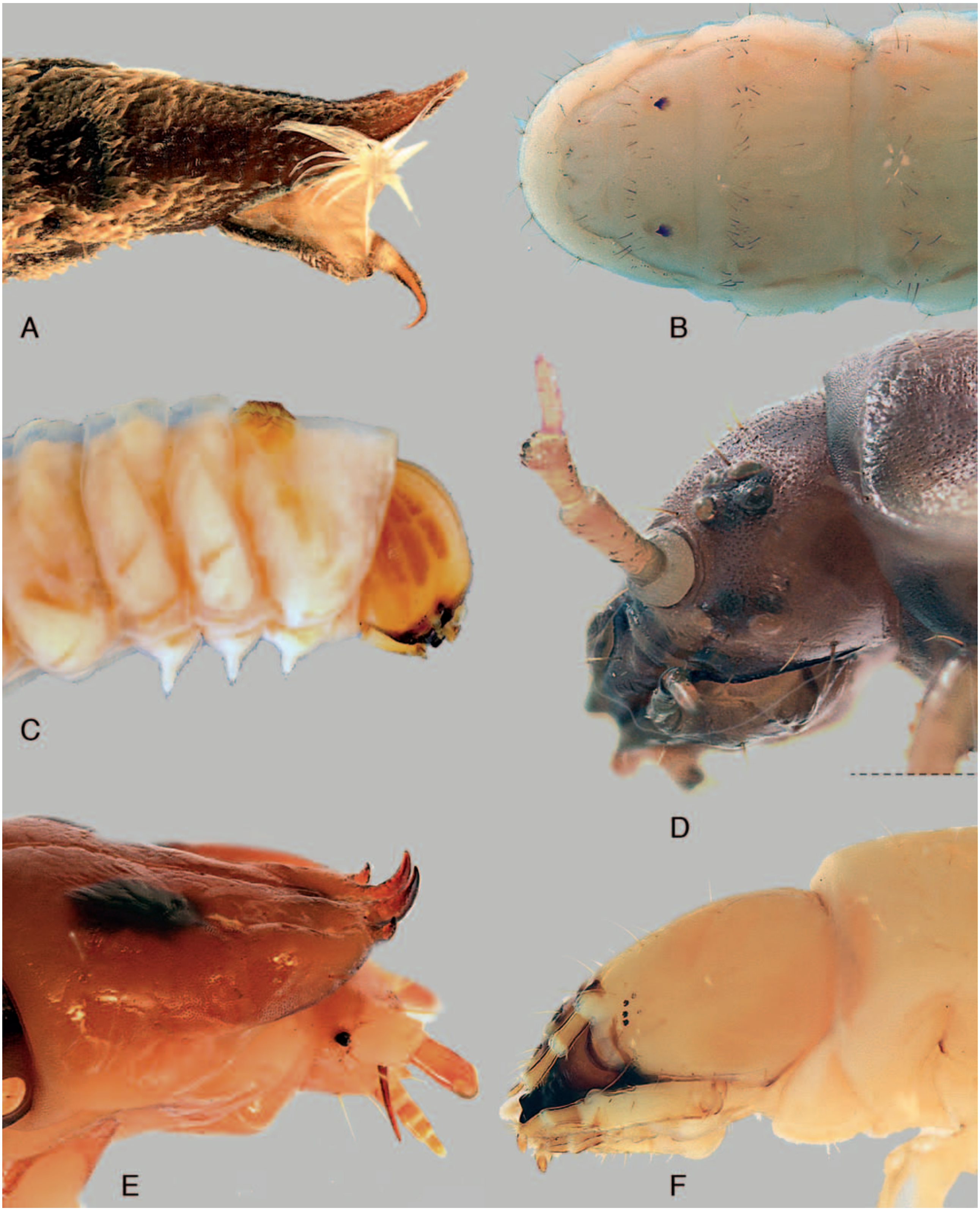


Figure 66. Larval Coleoptera. (A) *Lara avara* LeConte (Elmidae), abdominal apex, lateral. (B) *Synchroa punctata* Newman (Synchroidae), abdominal apex, ventral. (C), Genus ? sp. (Mordellidae), head and thorax, lateral. (D) *Necrodes* sp. (Silphidae), head, lateral. (E) Genus ? sp. (Lycidae), head and prothorax, lateral. (F) *Synchroa punctata* Newman (Synchroidae), head, lateral.

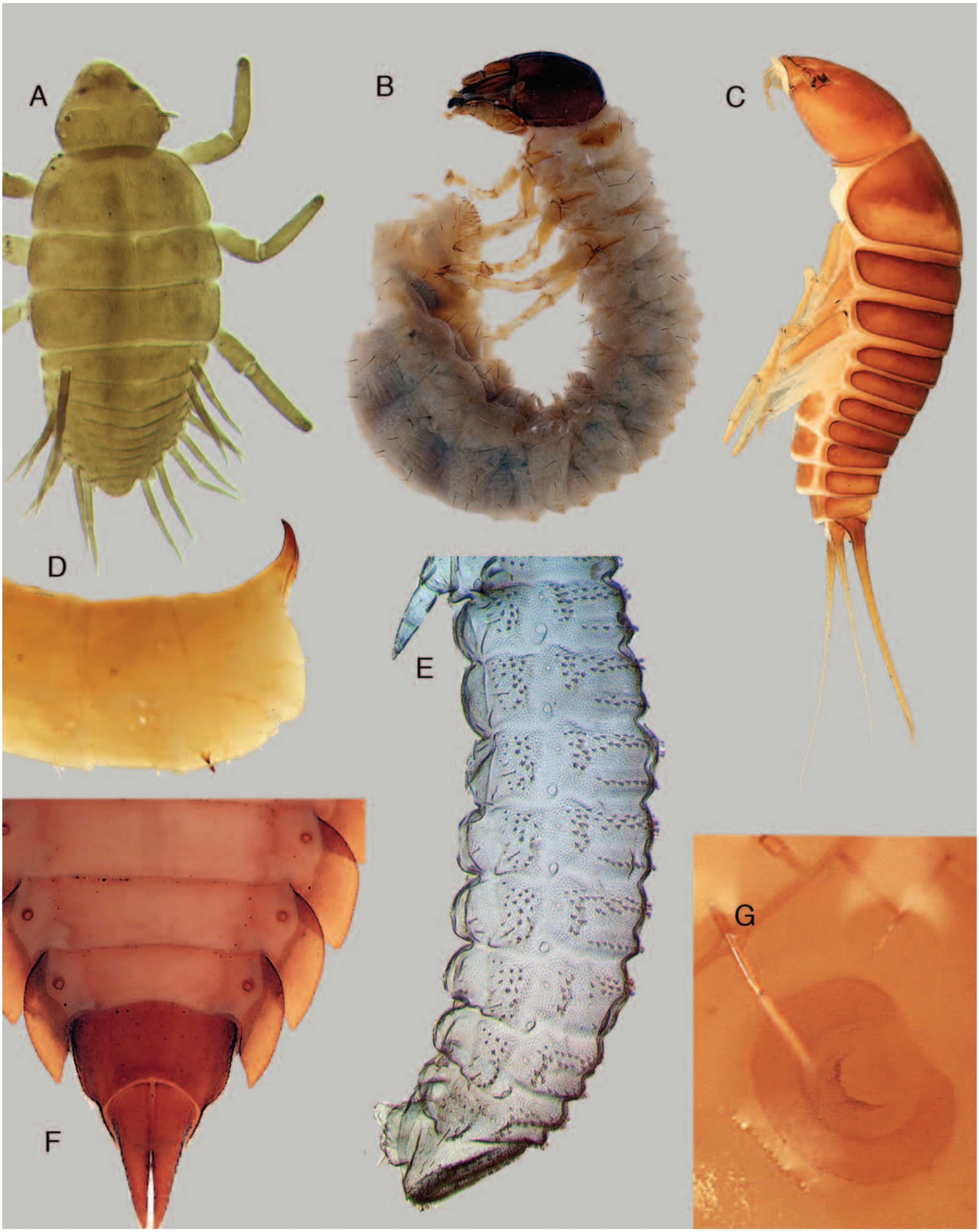


Figure 67. Larval Coleoptera. (A) *Torridincola* sp. (Torridincolidae), habitus, dorsal. (B) *Acrossidius tasmaniae* (Hope) (Scarabaeidae), habitus, lateral. (C) *Hygrobia* sp. (Hygrobiidae), habitus, lateral. (D) *Synchroa punctata* Newman, abdominal apex, lateral. (E) *Stanus* sp. (Corylophidae), abdomen, lateral. (F) *Amphizoa* sp. (Amphizoidae), abdominal apex, ventral. (G) *Liocola* sp. (Scarabaeidae), abdominal spiracle.

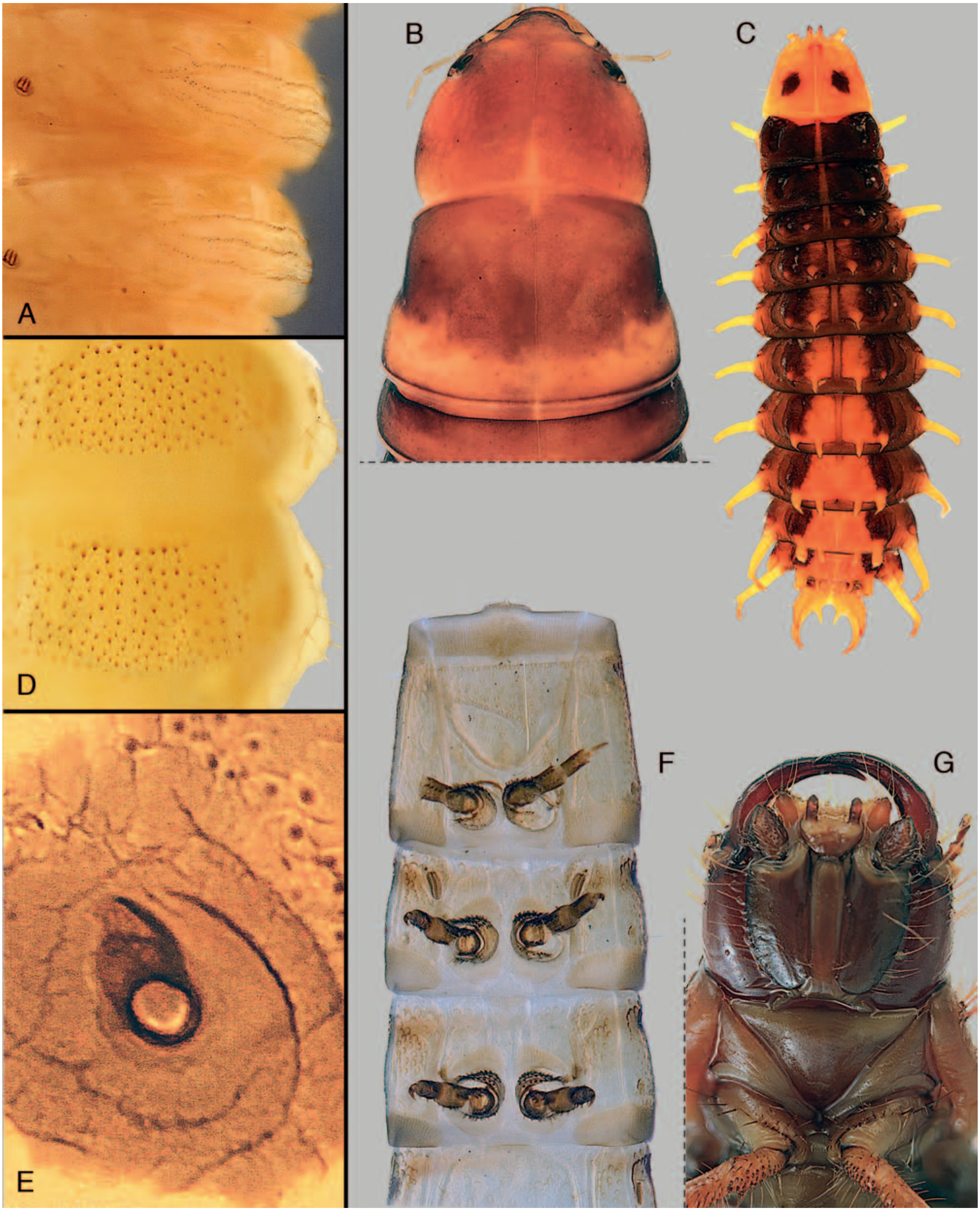


Figure 68. Larval Coleoptera. (A) *Hister nomas* Erichson (Histeridae), two abdominal terga, dorsolateral. (B) *Hygrobia* sp. (Hygrobiidae), head and prothorax, dorsal. (C) Genus ? sp. (Lycidae), habitus, dorsal. (D) *Synchroa punctata* Newman, two abdominal terga, dorsal. (E) *Chrysomela* sp. (Chrysomelidae), abdominal spiracle, lateral. (F) *Ampedus* sp. (Elateridae), thorax, ventral. (G) *Selasia* sp. (Drilidae), head and prothorax, ventral.

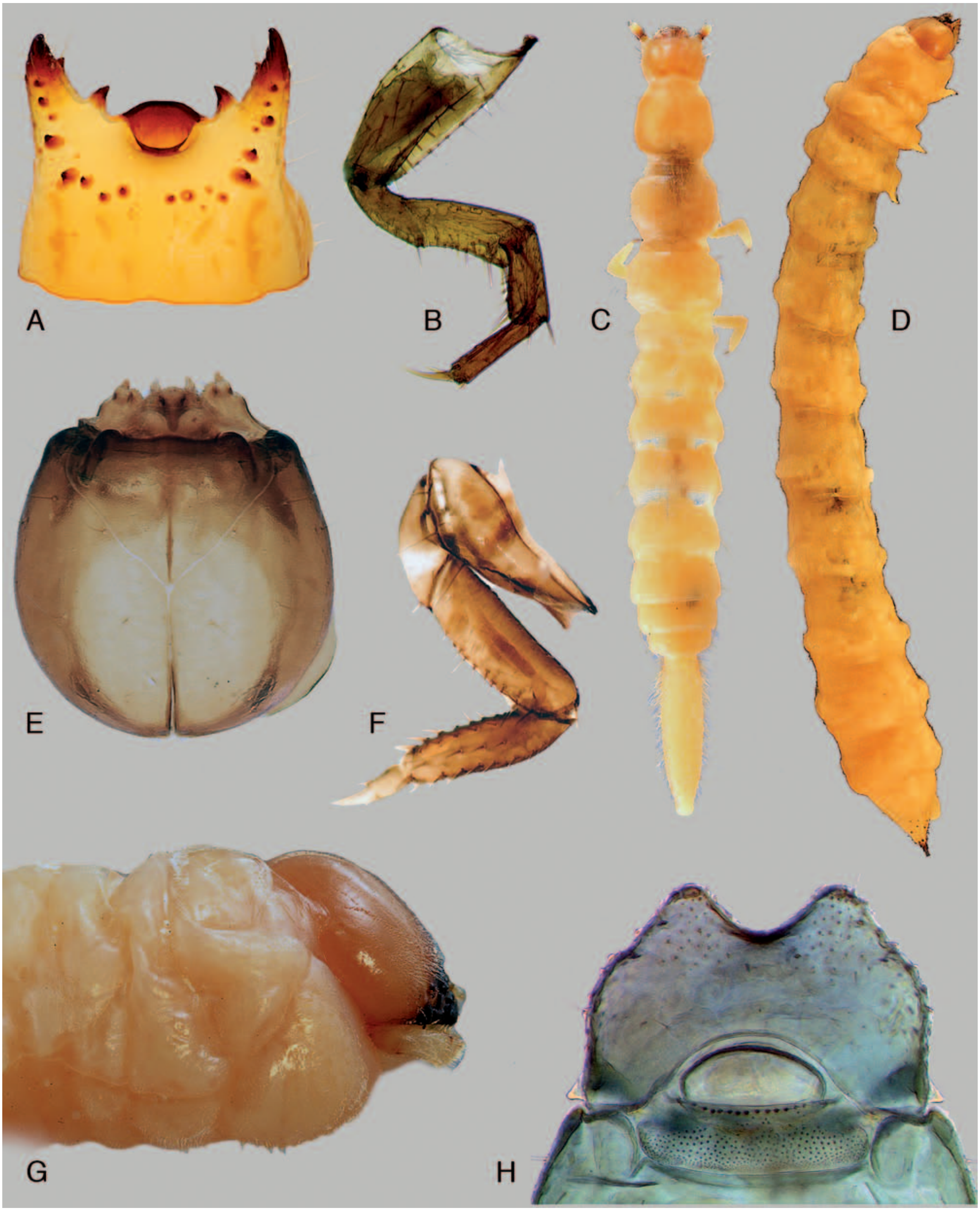


Figure 69. Larval Coleoptera. (A) *Pytho* sp. (Pythidae), abdominal apex, dorsal. (B) Genus ? sp. (Carabidae), leg. (C) *Scraptia* sp. (Scraptiidae), habitus, dorsal. (D) *Distocupes varians* (Lea), habitus, lateral. (E) *Tranes lyterioides (Pascoe)* (Curculionidae), head, dorsal. (F) *Ptomaphila* sp. (Silphidae), leg. (G) *Phloeobius* sp. (Anthribidae), head and thorax, lateral. (H) *Prostomis* sp. (Prostomidae), abdominal apex, ventral.

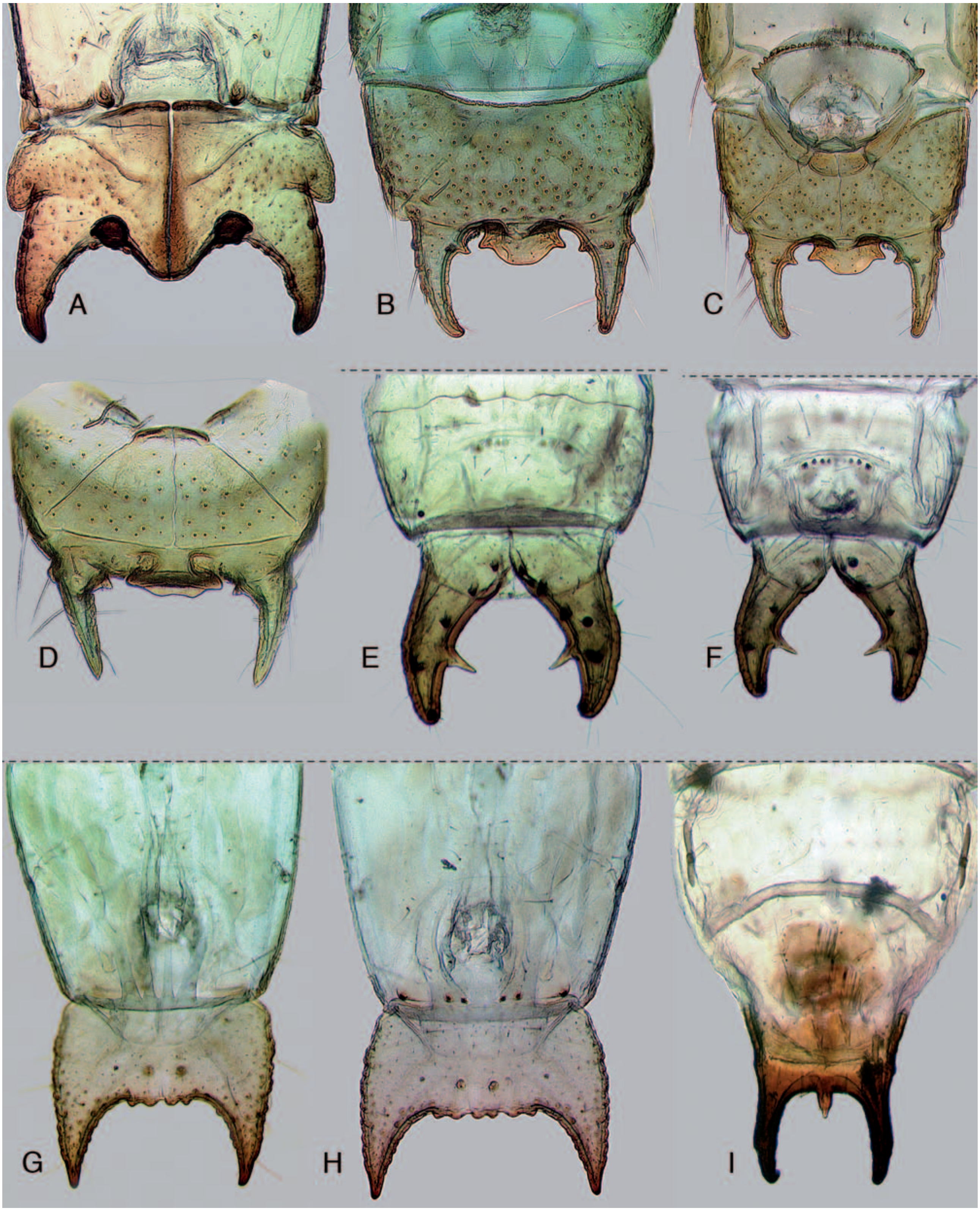


Figure 70. Larval Coleoptera. Abdominal apices. (A) *Boros unicolor* Say (Boridae), ventral. (B) *Temnopalpus* sp. (Pyrochroidae), dorsal. (C) Same, ventral. (D) Same, ventral (tergite only). (E) *Euryplatus dimidiatus* (Waterhouse) (Salpingidae), dorsal. (F) Same, ventral. (G) *Lacconotus pinicola* Horn (Mycteridae), dorsal. (H) Same, ventral. (I) *Grynoma* sp. (Trogossitidae), dorsal.

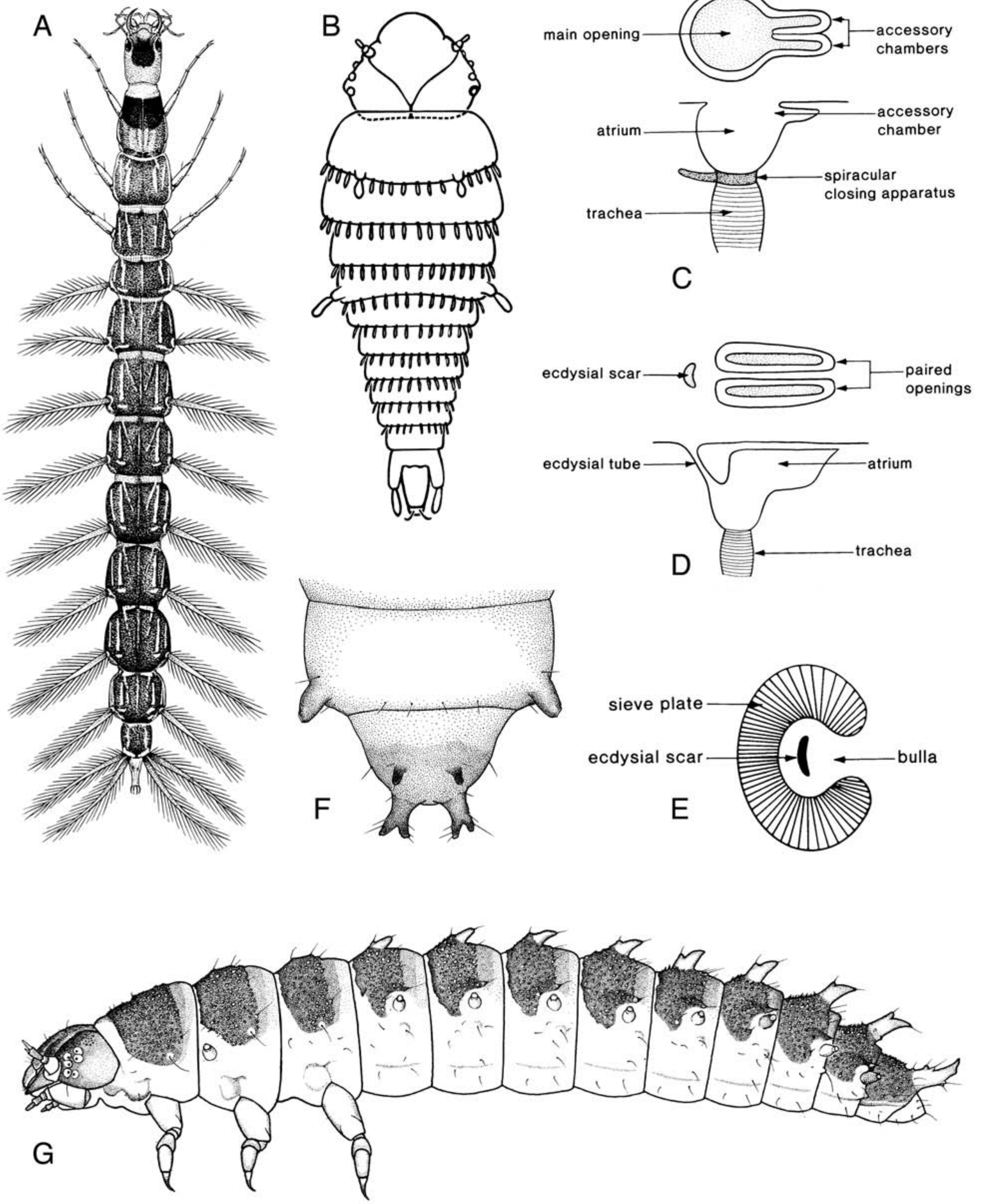


Figure 71. Larval Coleoptera. (A) *Macrogyrus* sp. (Gyrinidae), habitus, dorsal. (B) *Hydroscapha natans* LeConte (Hydroscaphidae), habitus, dorsal. (C) Annular-biforous spiracle, opening and cross-section. (D) Biforous spiracle, opening and cross-section. (E) Cribriform spiracle. (F) *Glischrochilus* sp. (Nitidulidae), abdominal apex, dorsal. (G) *Peltastica tuberculata* Mannerheim, habitus, lateral.

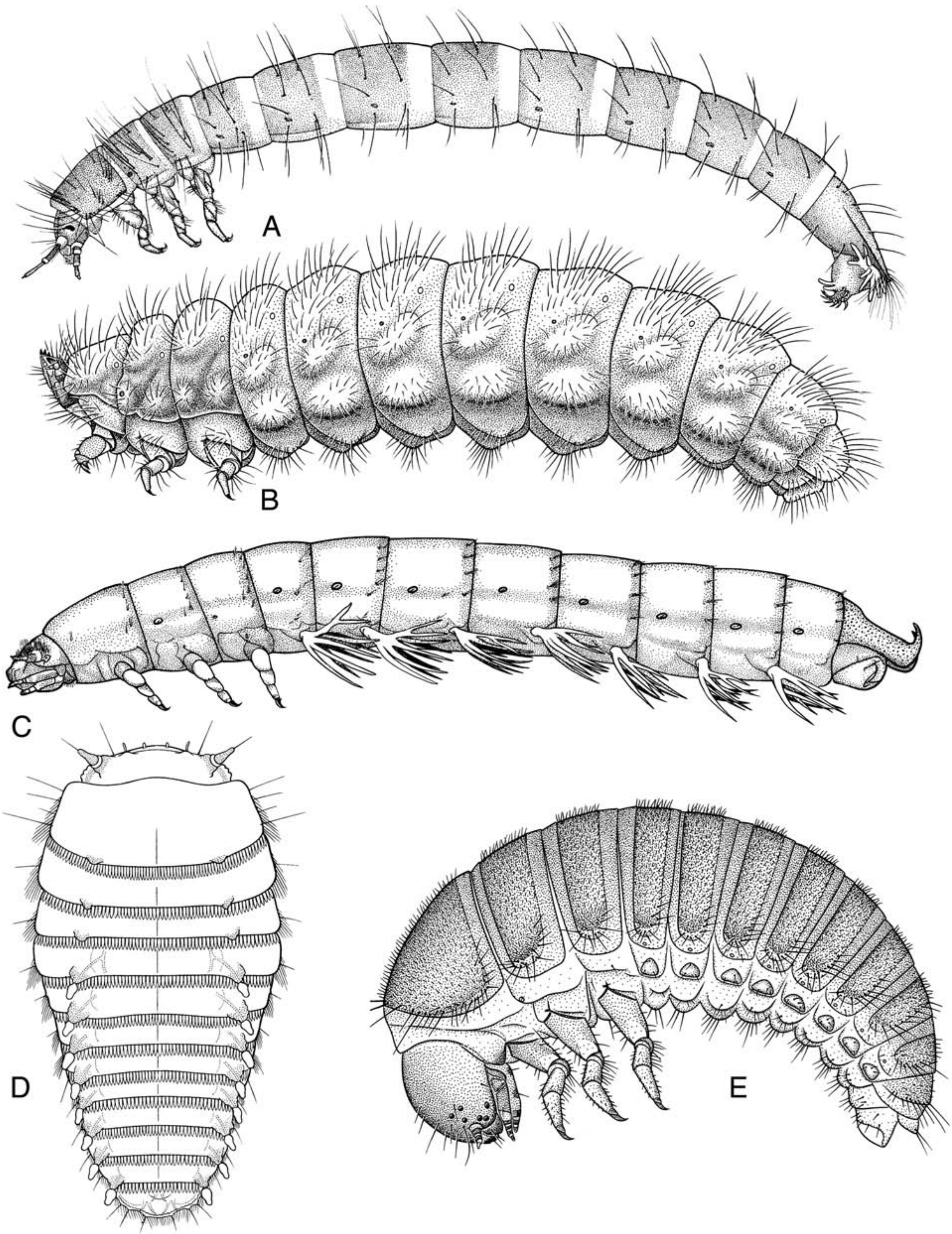


Figure 72. Larval Coleoptera. Habitus. (A) *Anchytarsus bicolor* (Melsheimer) (Ptilodactylidae), lateral. (B) *Cerophytum elateroides* Latreille (Cerophytidae), lateral. (C) *Stenocolus scutellaris* LeConte (Eulichadidae), lateral. (D) *Sphaerius ovensensis* Oke (Sphaeriusidae), dorsal. (E) *Cytilus alternatus* (Say) (Byrrhidae), lateral.

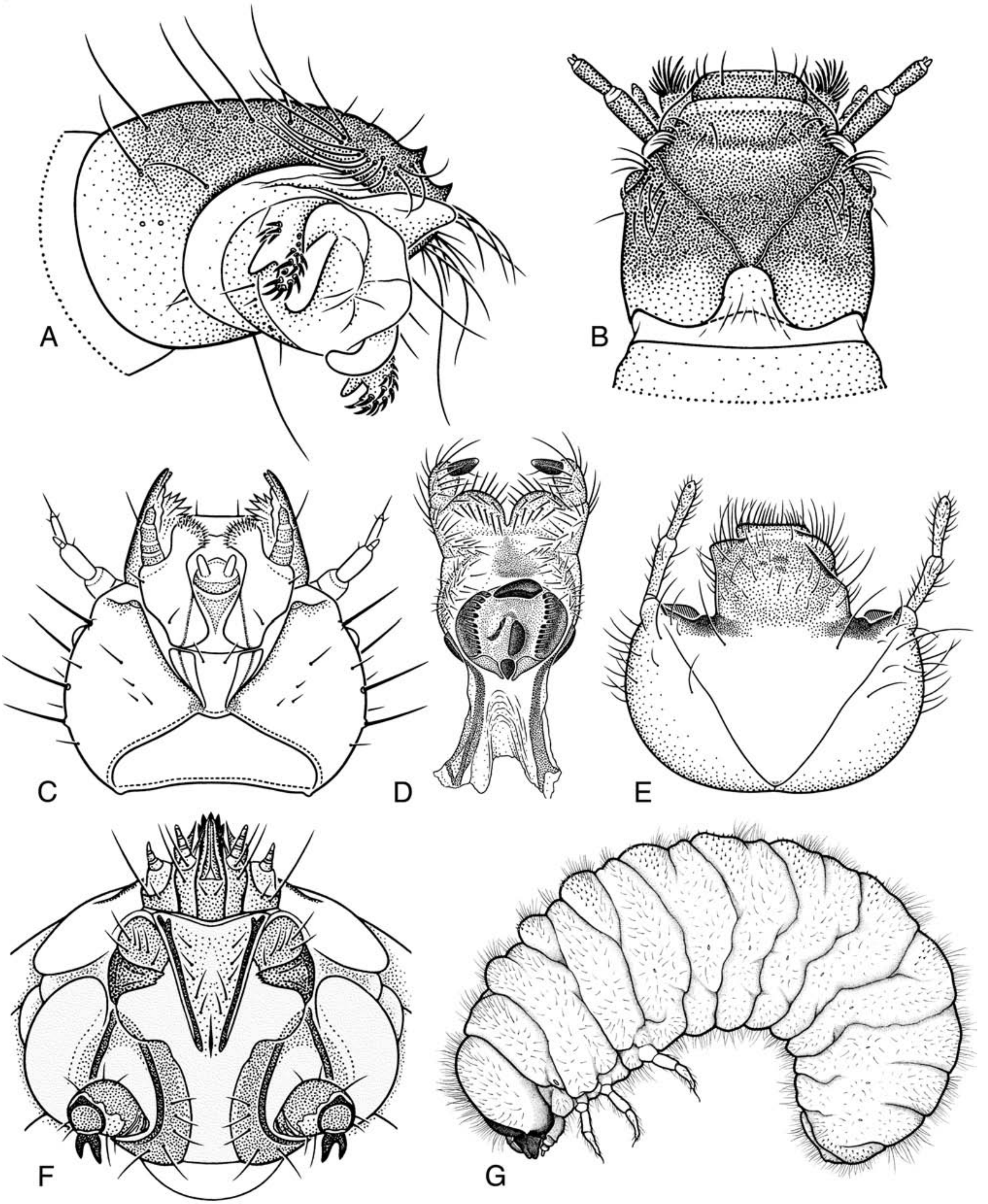


Figure 73. Larval Coleoptera. (A) *Anchycteis velutina* Horn (Ptilodactylidae), abdominal apex, posterolateral. (B) Same, head, dorsal. (C) *Epuraea* sp. (Nitidulidae), head, ventral. (D) *Dascillus davidsoni* Leconte (Dascillidae), labium and hypopharynx, dorsal. (E) Same, head, dorsal. (F) *Cerophytum elateroides* Latreille (Cerophytidae), head and prothorax, ventral. (G) *Dorcatoma* sp. (Ptinidae), habitus, lateral.

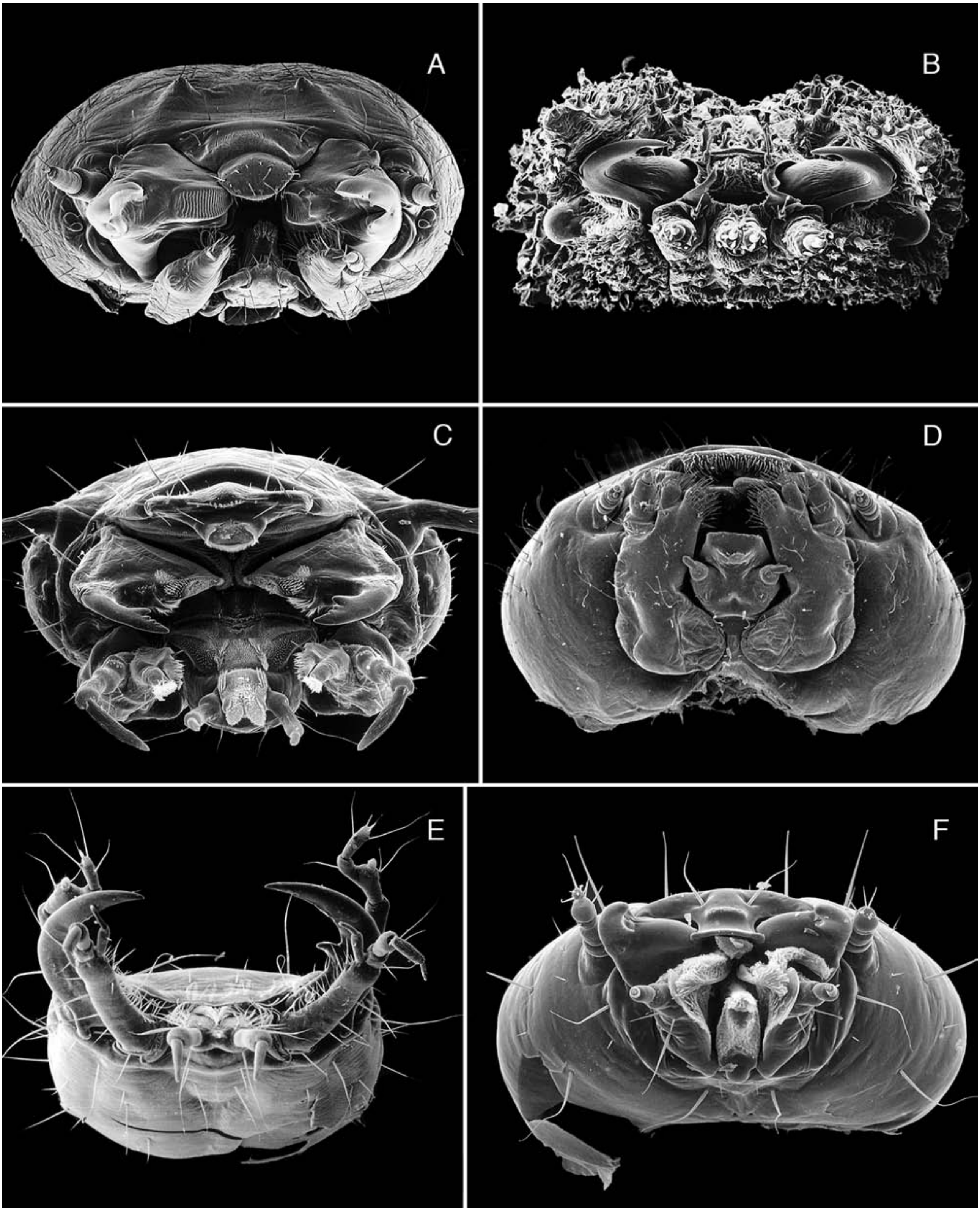


Figure 74. Larval Coleoptera. Heads. (A) *Bolitotherus cornutus* (Panzer) (Tenebrionidae), anterior. (B) *Brachypsectra fulva* LeConte (Brachypsectridae), anterior. (C) *Necrophilus pettitii* Horn (Agyrtidae), anterior. (D) *Tenomerga cinerea* (Say) (Cupedidae), anteroventral. (E) *Agonum* sp. (Carabidae), anterior. (F) *Omoglymmius hamatus* (LeConte) (Carabidae), anteroventral.

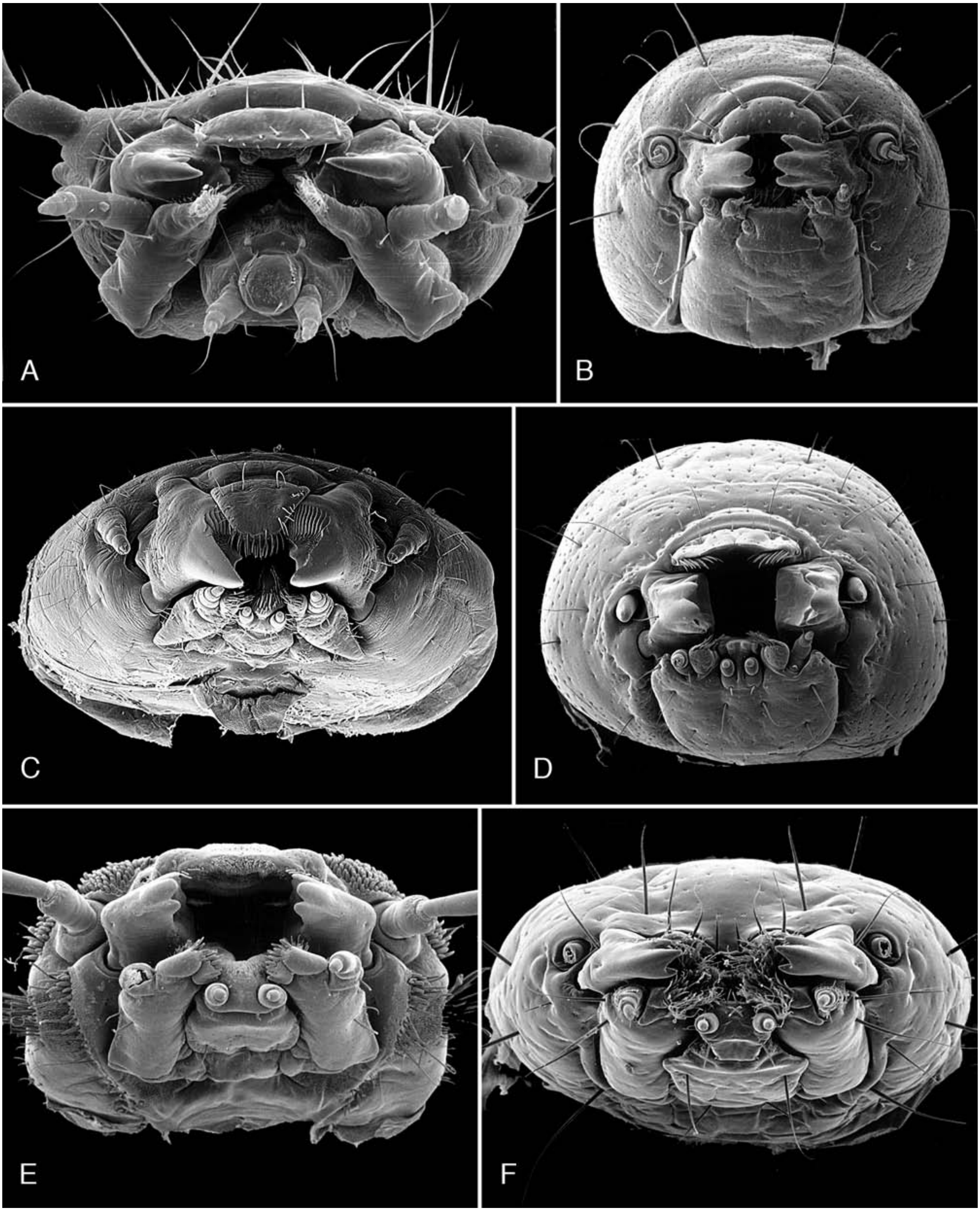


Figure 75. Larval Coleoptera. Heads. (A) *Anisotoma blanchardi* Horn (Leiodidae), anterior. (B) *Dryops* sp. (Dryopidae), anteroventral. (C) *Parandra brunnea* (Fabricius) (Cerambycidae), anteroventral. (D) *Callirhipis* sp. (Callirhipidae), anterior. (E) *Stenocolus scutellaris* LeConte (Eulichadidae), anteroventral. (F) *Eurypogon harrisi* Westwood (Artematopodidae), anterior.

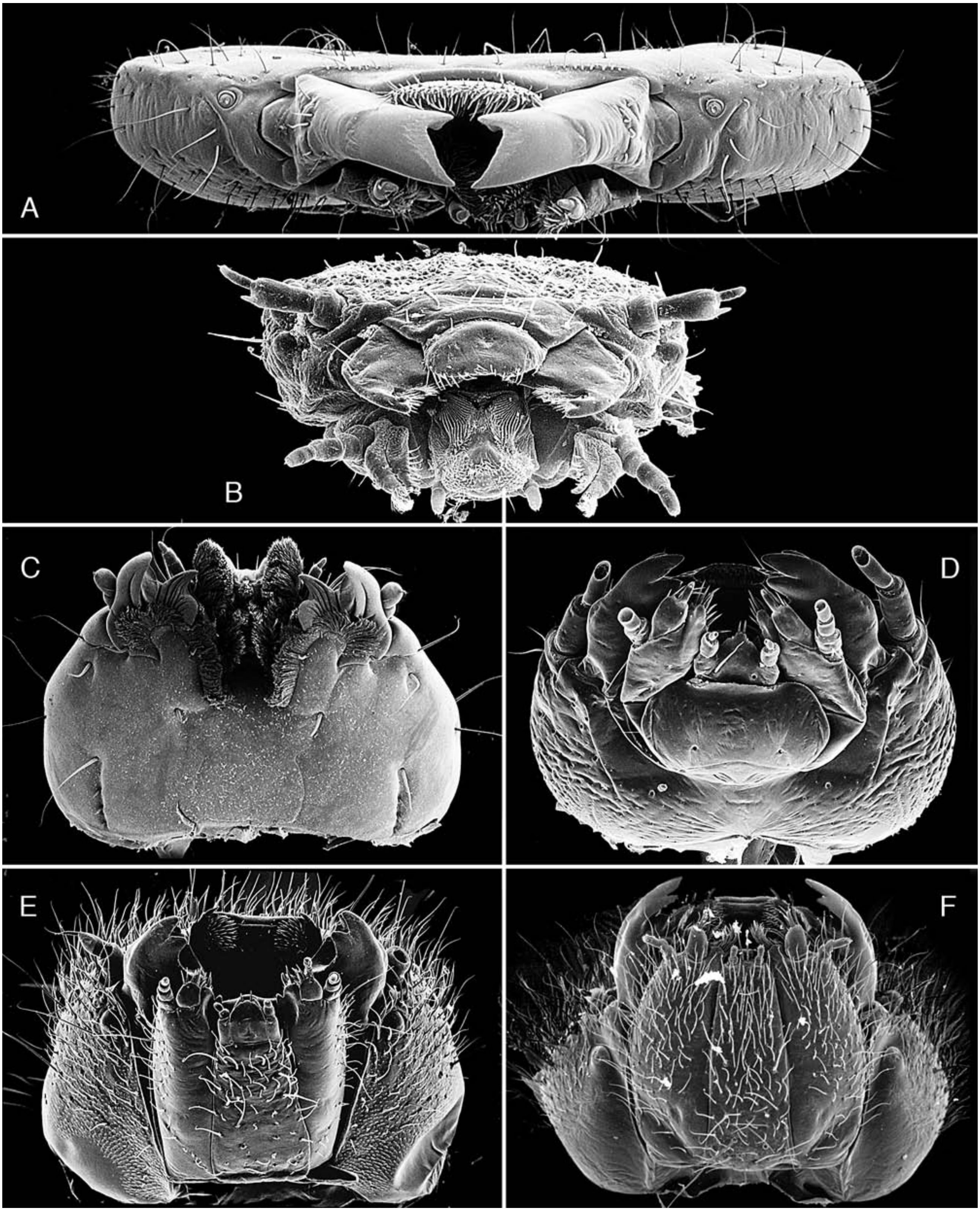


Figure 76. Larval Coleoptera. Heads. (A) *Rhagium inquisitor* (Linnaeus) (Cerambycidae), anterior. (B) *Peltastica tuberculata* Mannerheim (Derodontidae), anterior. (C) *Lissomus* sp. (Elateridae), dorsal. (D) *Ptilodactyla serricollis* Say (Ptilodactylidae), anteroventral. (E) *Byrrhinus* sp. (Limnichidae), ventral. (F) *Heterocerus gemmatus* Horn (Heteroceridae), ventral.

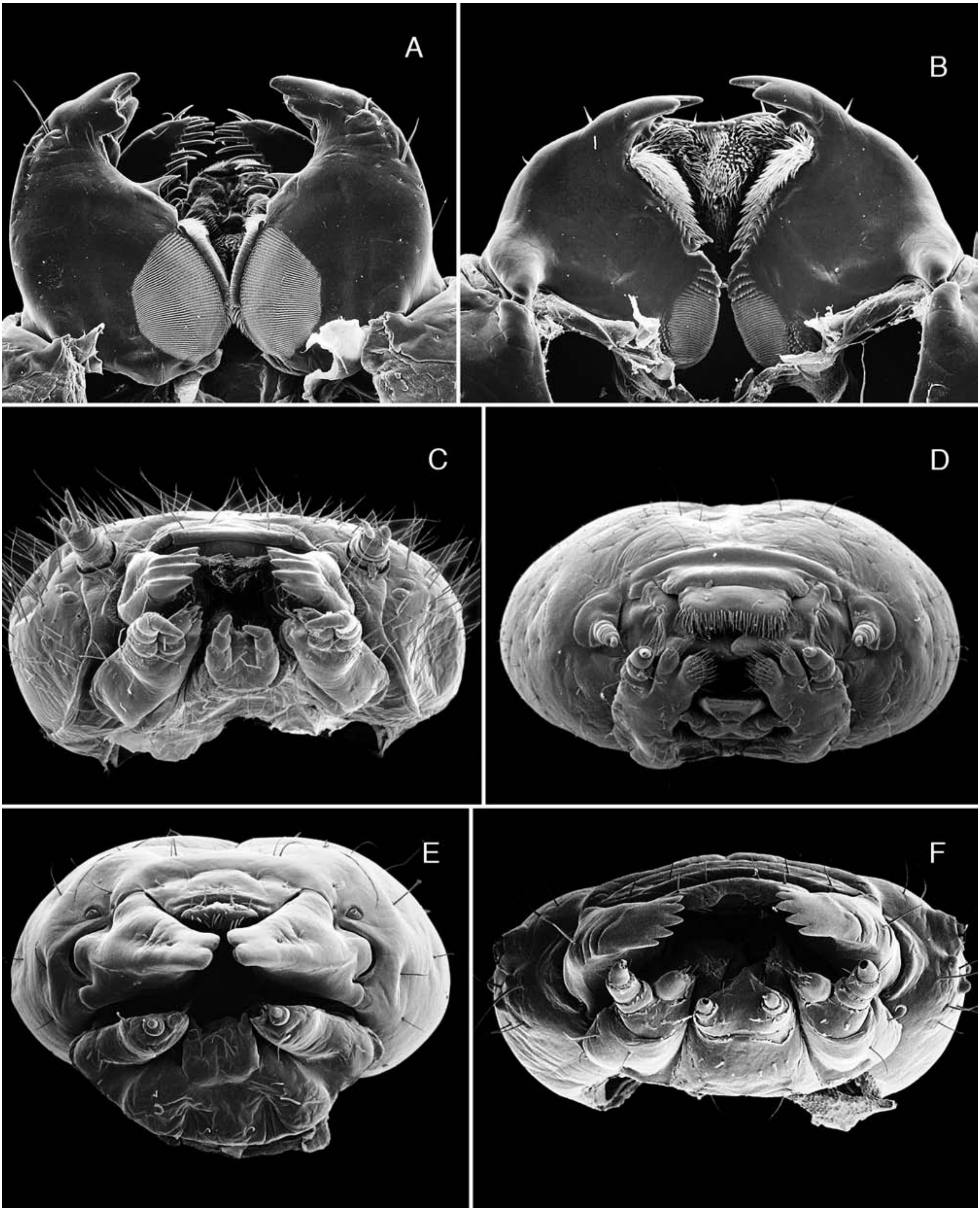


Figure 77. Larval Coleoptera. (A) *Cucujus clavipes* Fabricius (Cucujidae), left and right mandibles, dorsal. (B) *Glischrochilus* sp. (Nitidulidae), right and left mandibles, ventral. (C) *Lioon* sp. (Byrrhidae), head, anteroventral. (D) *Tenomerga cinerea* (Say) (Cupedidae), head, anterior. (E) *Curculio* sp. (Curculionidae), head, anterior. (F) *Leptinotarsa lineolata* Stål (Chrysomelidae), head, anteroventral.

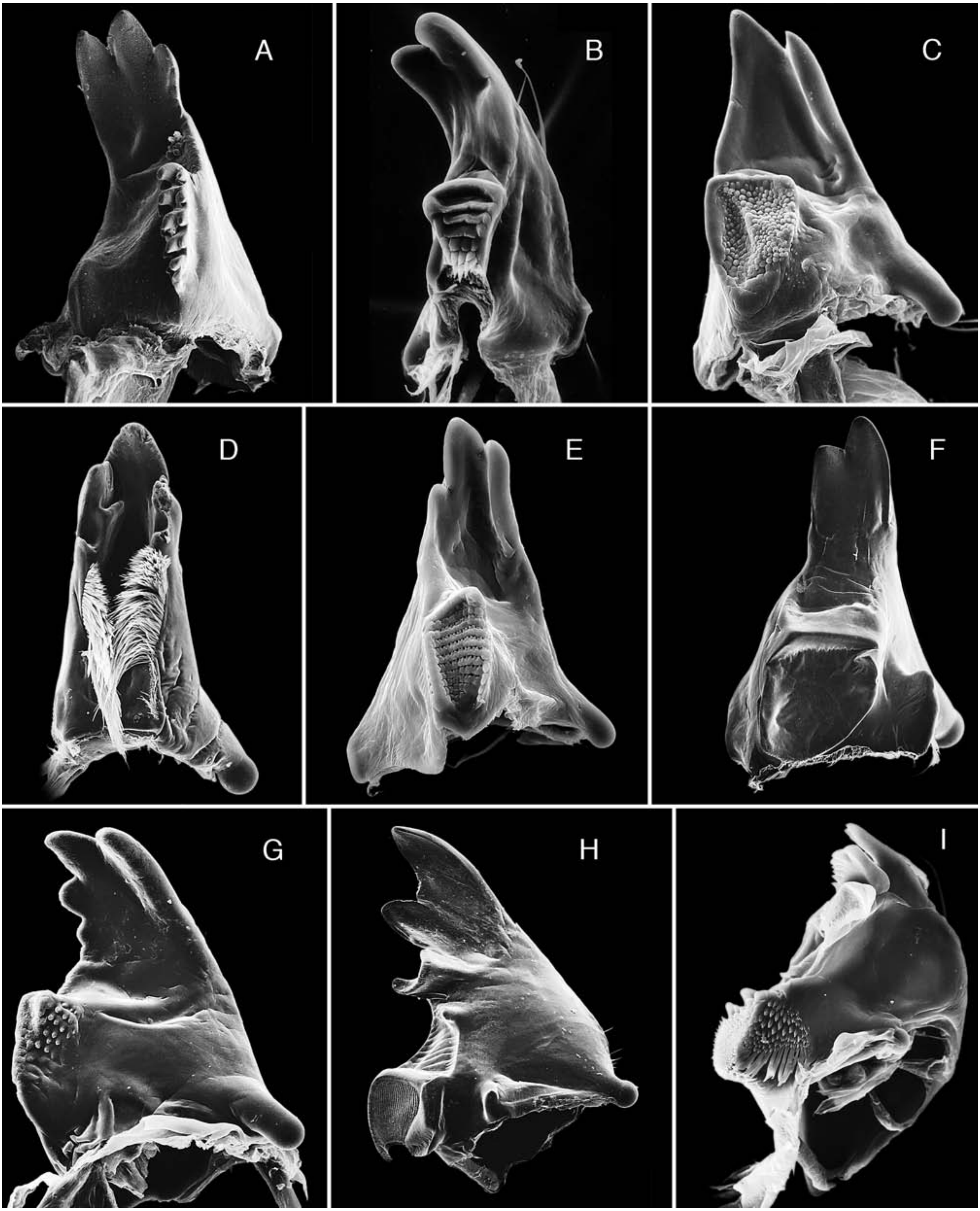


Figure 78. Larval Coleoptera. Mandibles. (A) *Phalacropsis dispar* (LeConte) (Phalacridae), mesal. (B) *Anaspis rufilabris* (Gyllenhal) (Scraptiidae), mesal. (C) *Hallomenus* sp. (Tetratomidae), mesal. (D) *Anchytarsus* sp. (Ptilodactylidae), mesal. (E) *Enneboeus barrocolorado* Merkl (Archeocrypticidae), mesal. (F) *Sinodendron rugosum* Mannerheim (Lucanidae), mesal. (G) *Namunaria pacifica* (Horn) (Zopheridae), mesoventral. (H) *Dascillus davidsoni* LeConte (Dascillidae), mesoventral. (I) *Ytu zeus* Reichardt (Torridincolidae), mesoventral.

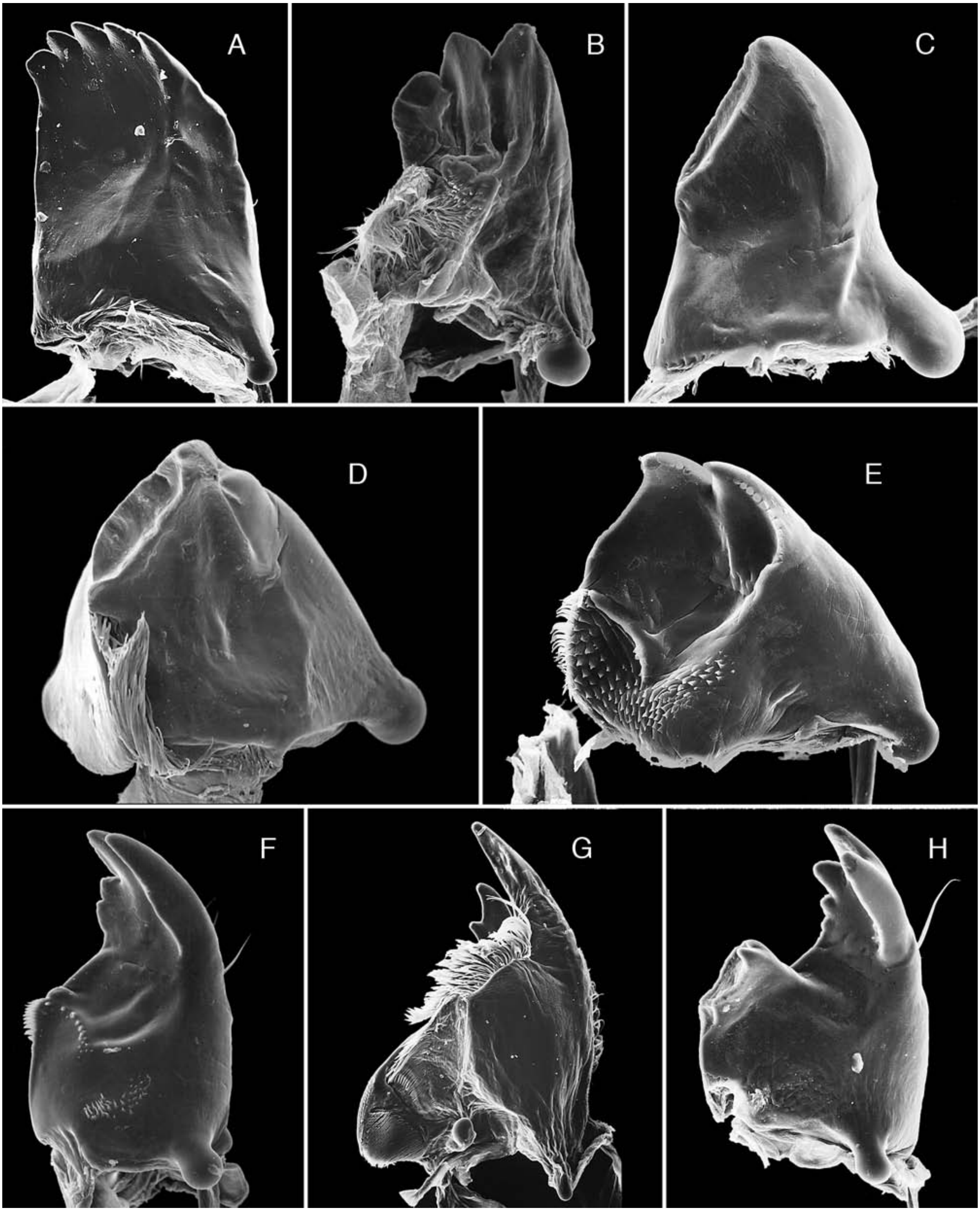


Figure 79. Larval Coleoptera. Mandibles. (A) *Leptinotarsa lineolata* Stål (Chrysomelidae), mesoventral. (B) *Megalodacne* sp. (Erotylidae), mesoventral. (C) *Mordella* sp. (Mordellidae), mesoventral. (D) *Cytilus* sp. (Byrrhidae), mesal. (E) *Eustrophopsis bicolor* (Fabricius) (Tetratomidae), mesoventral. (F) *Hyporhagus gilensis* Horn (Zopheridae), ventral. (G) *Nosodendron unicolor* Say (Nosodendridae), ventral. (H) *Lacconotus pinicola* Horn (Mycteridae), ventral.

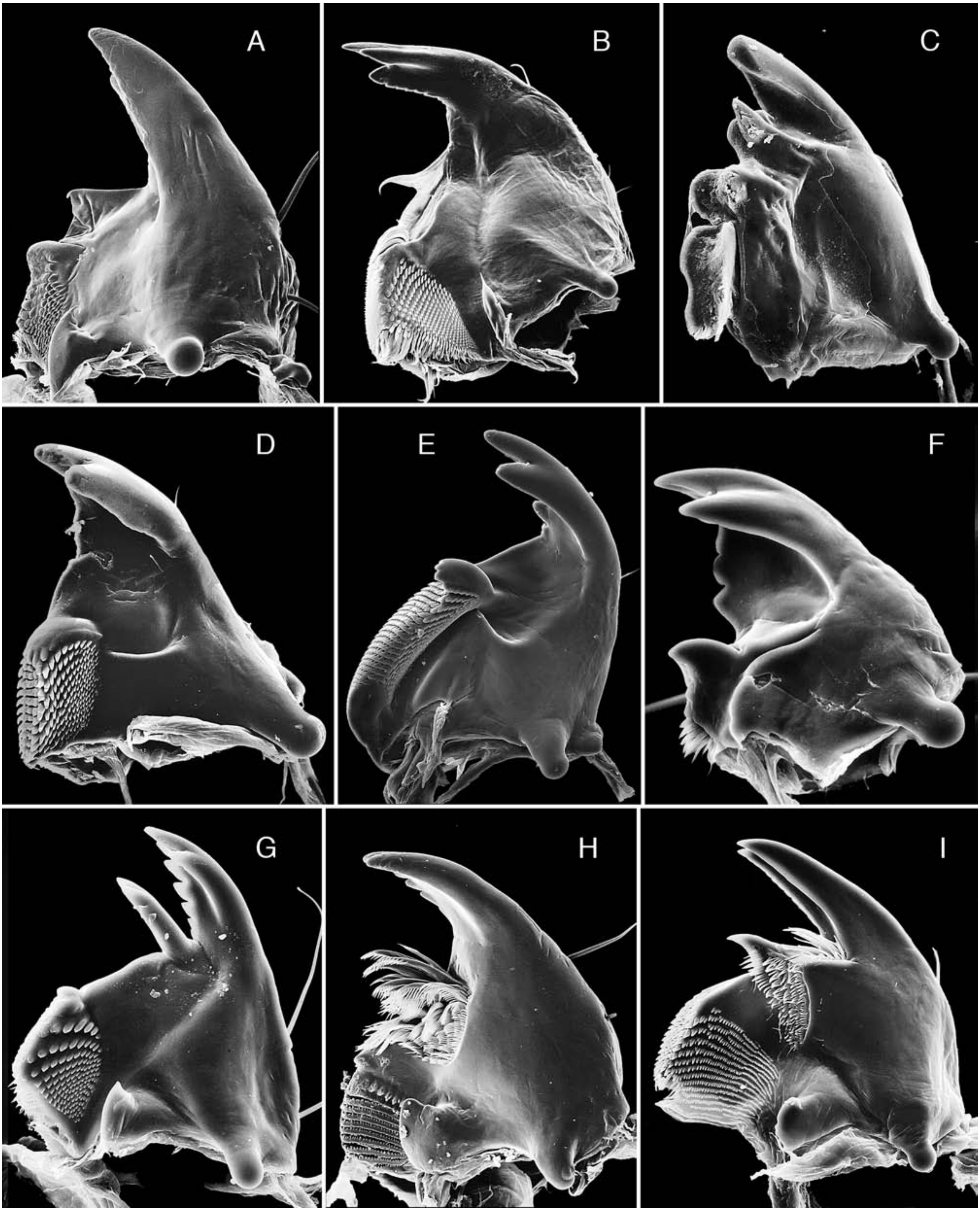


Figure 80. Larval Coleoptera. Mandibles. (A) *Hapalips* sp. (Erotylidae), ventral. (B) *Austrohyliota chilensis* (Blanchard) (Silvanidae), ventral. (C) *Heterocerus gemmatus* Horn (Heteroceridae), mesoventral. (D) *Aulonium longum* LeConte (Zopheridae), ventral. (E) *Elacatis* sp. (Salpingidae), mesoventral. (F) *Anaspis rufilabris* (Gyllenhal) (Scraptiidae), ventral. (G) *Monotoma americana* Aubé (Monotomidae), ventral. (H) *Anchorius lineatus* Casey (Biphyllidae), ventral. (I) *Derodontus* sp. (Derodontidae), ventral.

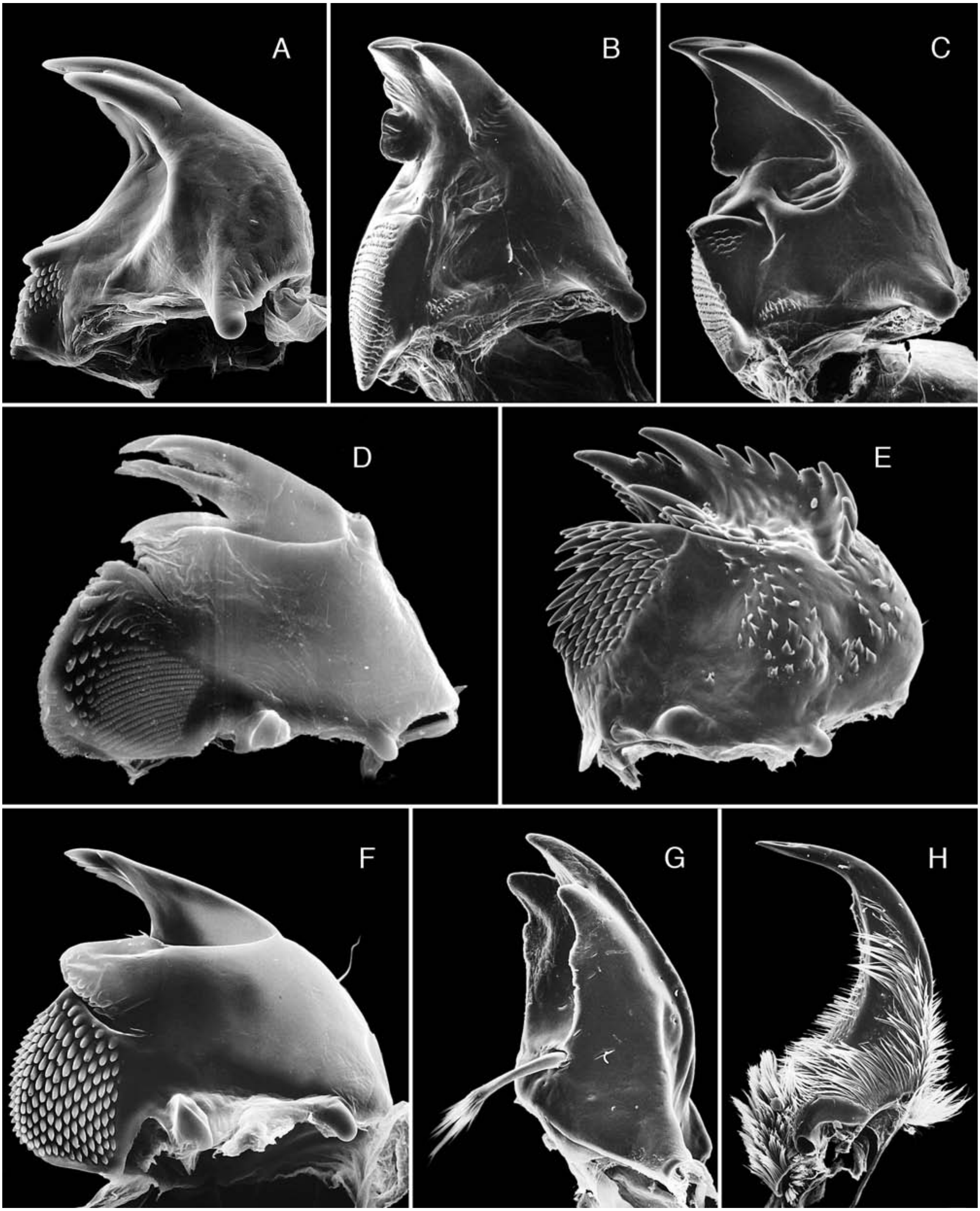


Figure 81. Larval Coleoptera. Mandibles. (A) *Enneboeus barrocolorado* Merkl (Archeocrypticidae), ventral. (B) *Pterogenius nietneri* Candèze (Pterogeniidae), left, ventral. (C) *Pterogenius nietneri* Candèze (Pterogeniidae), right, ventral. (D) *Acalyptomerus* sp. (Clambidae), ventral. (E) *Nycteus infumatus* (LeConte) (Eucinetidae), ventral. (F) *Eucinetus morio* LeConte (Eucinetidae), ventral. (G) *Ptilodactyla serricollis* (Say) (Ptilodactylidae), dorsal. (H) Genus ? sp. (Lampyridae), dorsal.

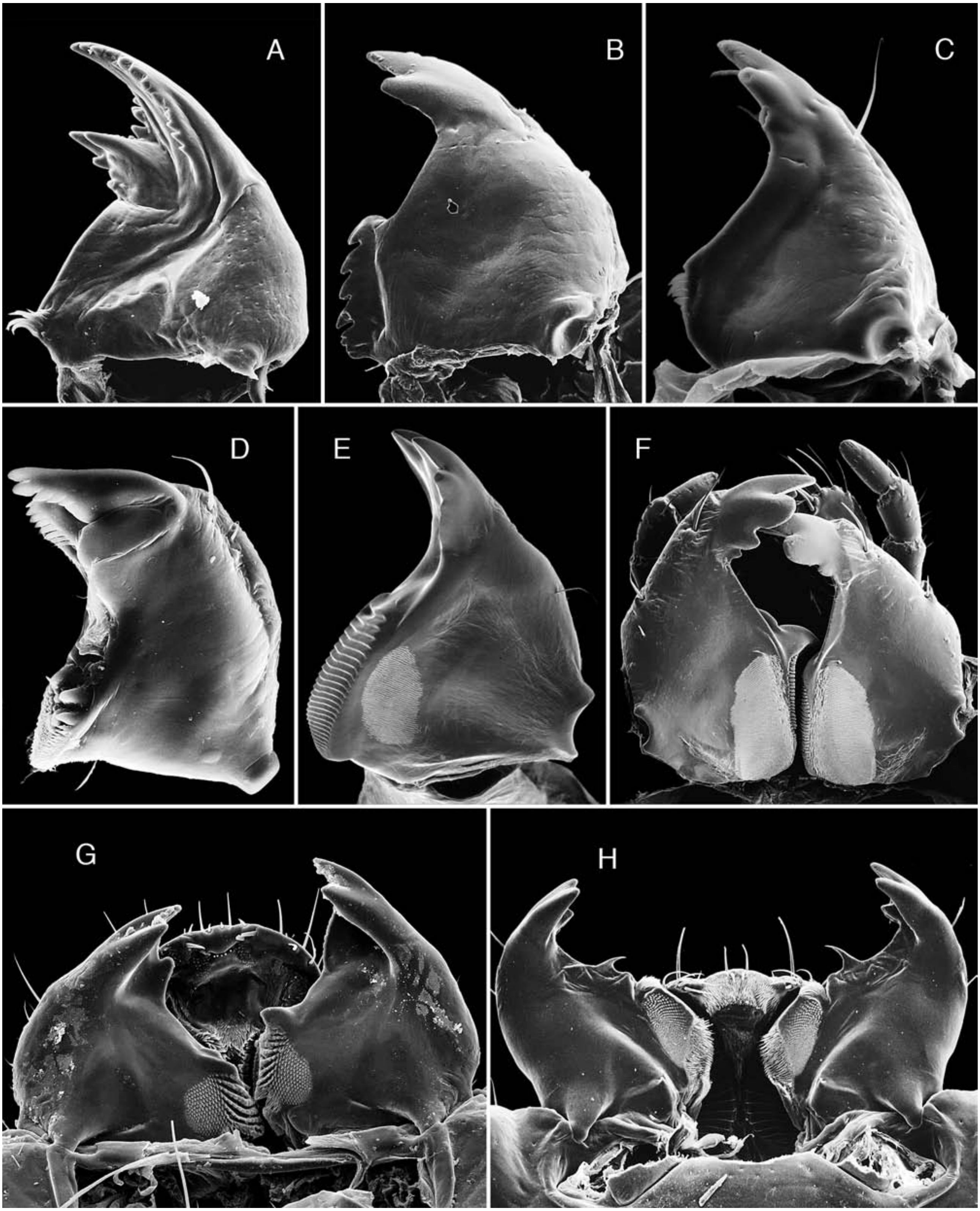


Figure 82. Larval Coleoptera. Mandibles. (A) *Epilachna argus* (Geoffroy) (Coccinellidae), dorsal. (B) *Phalacropsis dispar* (LeConte) (Phalacridae), dorsal. (C) *Salpingus* sp. (Salpingidae), dorsal. (D) *Ytu zeus* Reichardt (Torridincolidae), dorsal. (E) *Ditylus* sp. (Oedemeridae), dorsal. (F) *Dendroides* sp. (Pyrochroidae), right and left, dorsal. (G) *Mycetophagus punctatus* Say (Mycetophagidae), right and left, ventral. (H) *Cucujus clavipes* Fabricius (Cucujidae), right and left, ventral.

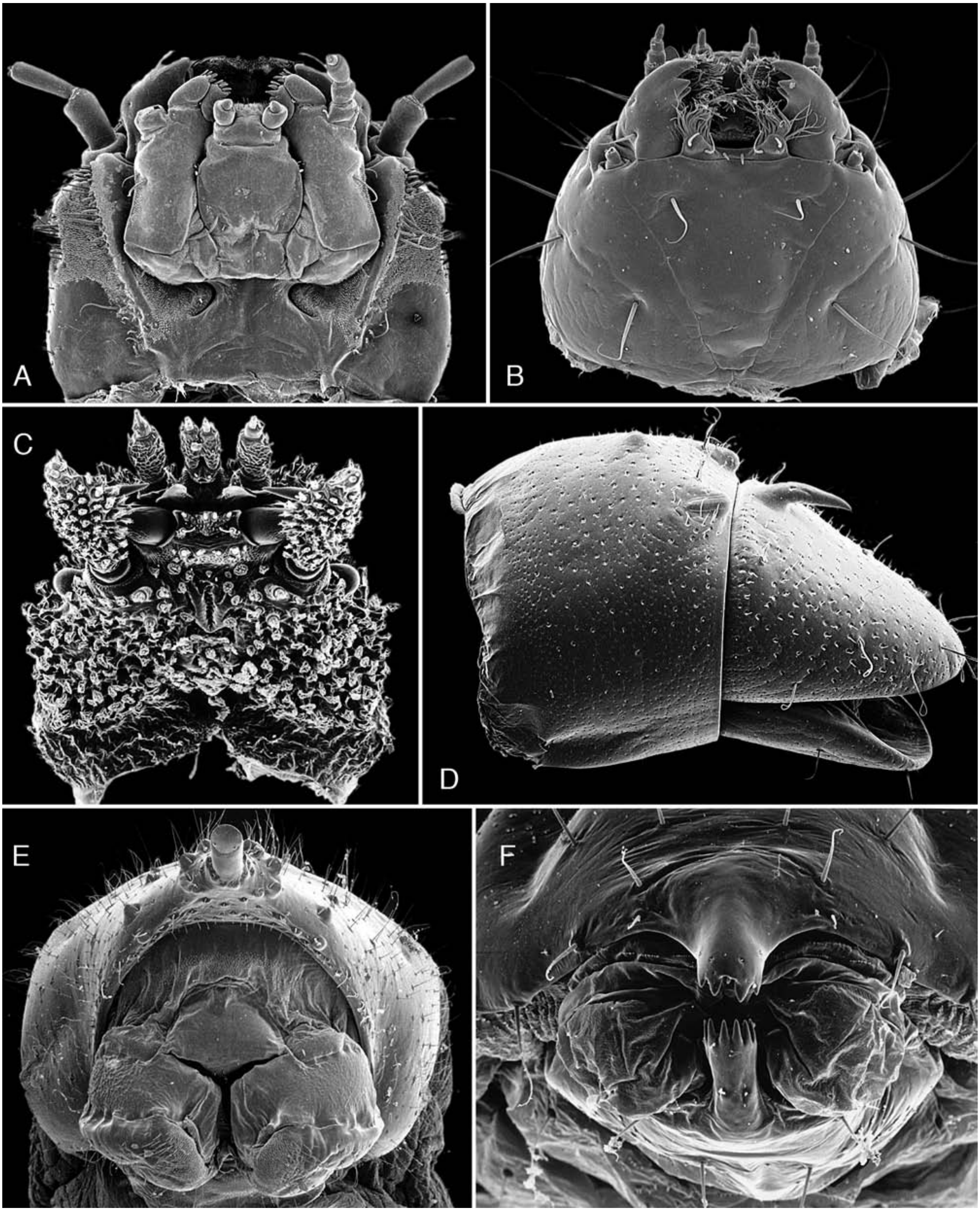


Figure 83. Larval Coleoptera. (A) *Stenocolus scutellaris* LeConte (Eulichadidae), head, ventral. (B) *Eurypogon harrisi* Westwood (Artematopodidae), head, dorsal. (C) *Brachypsectra fulva* Leconte (Brachypsectridae), head, dorsal. (D) *Dryops* sp. (Dryopidae), abdominal apex, lateral. (E) *Tenomerga cinerea* (Say) (Cupedidae), abdominal apex, posterior. (F) *Micromalthus debilis* LeConte (Micromalthidae), abdominal apex, posterior.

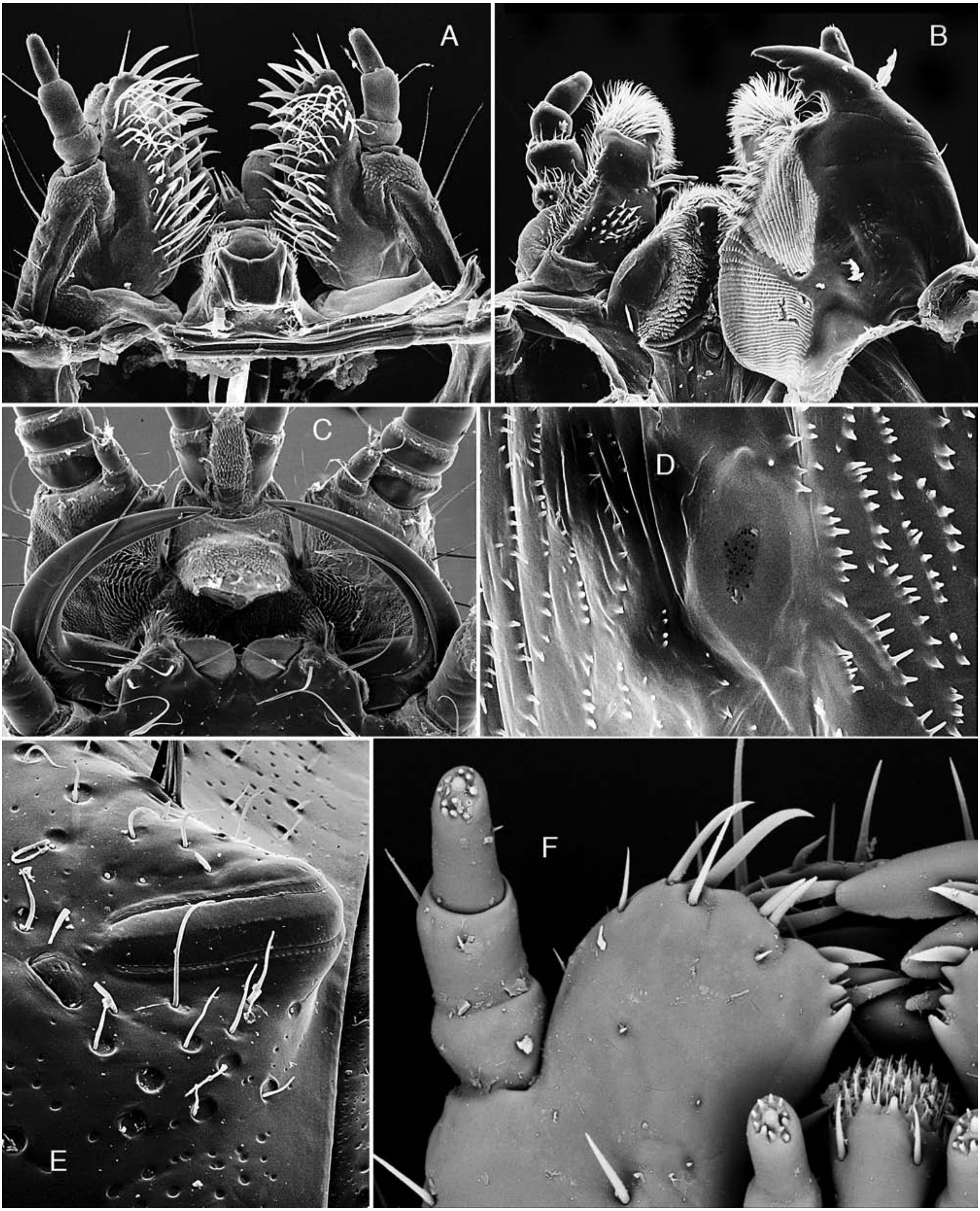


Figure 84. Larval Coleoptera. (A) *Platydema* sp. (Tenebrionidae), maxillae and hypopharynx, dorsal. (B) *Glischrochilus* sp. (Nitidulidae), mandible, hypopharynx, maxilla, dorsal. (C) *Phengodes* sp. (Phengodidae), mouthparts, dorsal. (D) *Heterocerus gemmatus* Horn (Heteroceridae), abdominal spiracle, lateral. (E) *Dryops* sp. (Dryopidae), abdominal spiracle VIII, dorsolateral. (F) Genus ? sp. (Salpingidae), maxilla ventral.

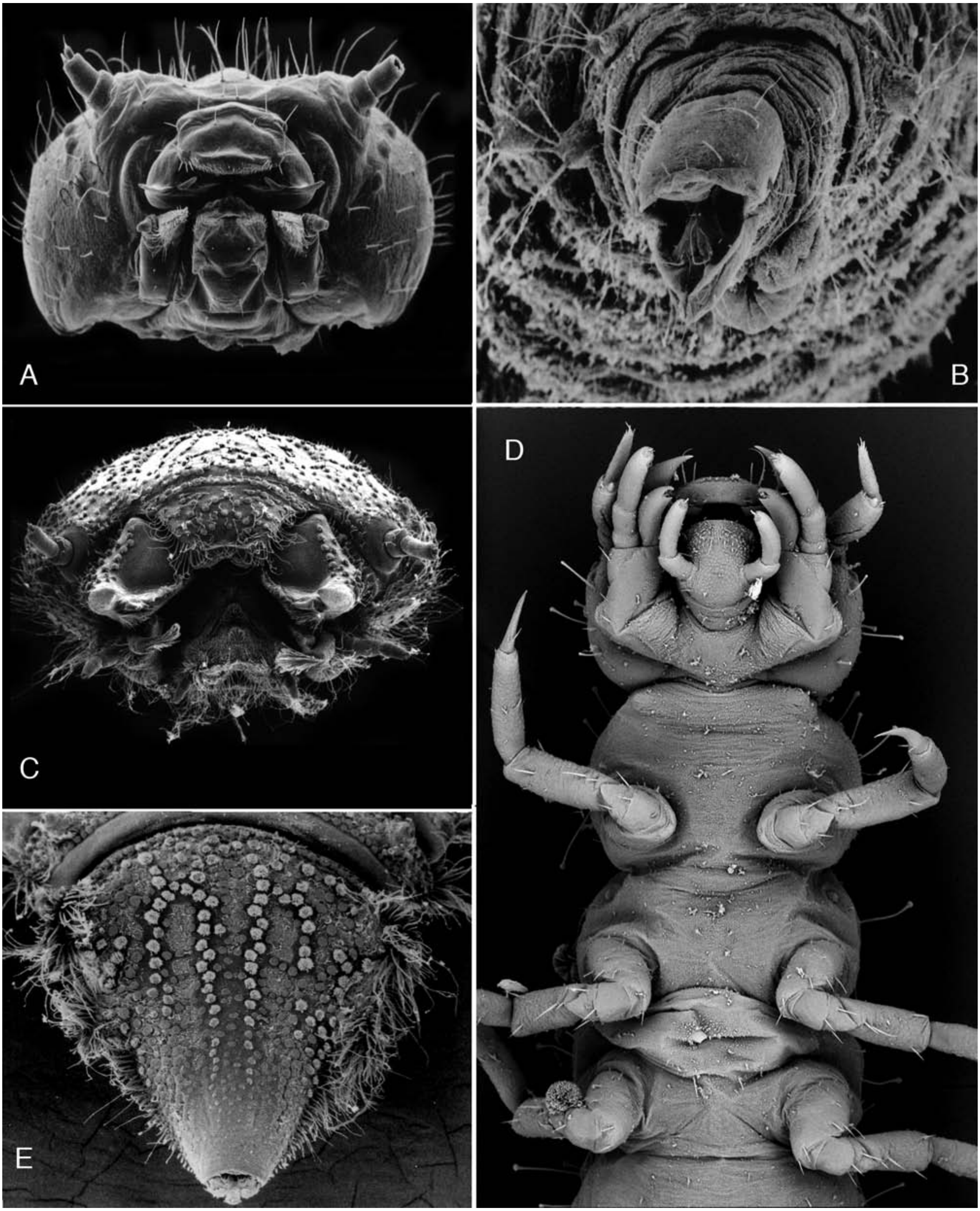


Figure 85. Larval Coleoptera. (A) *Lycoperdina* sp. (Endomychidae), head, anterior. (B) *Spercheus* sp. (Hydrophilidae), abdominal apex, posterior. (C) *Nosodendron* sp. (Nosodendridae), head, anterior. (D) *Paracucujus rostratus* Sen Gupta & Crowson (Boganiidae), head and prothorax, ventral. (E) *Nosodendron* sp. (Nosodendridae), abdominal apex, posterodorsal.

TABLES

Table 1. Morphological data matrix

	10	20	30	40	50	60
Acalanthis	111-411311	1411111111	1223111-11	11114144-1	2211141111	1111111222
Acalyptomerus	111-111231	1411111111	1223112111	11112154-1	2131141111	1111111213
Acanthocnemus	111-411311	1411111111	1121112111	11113134-1	2211131111	1111111222
Acmaeodera	111-221111	2411211111	1121111-11	1111413331	322116----	1111111321
Acrotrichis	111-111211	1421213111	1222111-11	11112134-1	2211131111	1111111323
Adelium	111-411311	2411211111	1221112111	11114132-1	221116----	1111111222
Adrastia	111-111311	1411111111	1221121-11	11113134-1	2211131111	1111111113
Aesalus	121-421211	141111111?	1222111-11	11114144-2	3321131121	11111111?2
Agabus	111-111111	142111111?	1222111-11	11114231-1	221116----	1111111221
Agapytho	1122411311	1411112111	1222111-11	11112134-1	2211131111	1111111221
Agrilus	111-121111	2411211111	1121111-11	1111213321	221116----	1111112122
Agulla	111-111311	1111111111	1121112112	11112111-1	221116----	1211111113
Agyrtodes	111-111211	1411213111	1121112221	11114134-1	2211112111	1111111111
Amartus	111-411211	1411111111	1222111-11	11114134-1	2211131111	1111111111
Ampedus	111-411211	2411111211	1222131-11	1112313321	221116----	1111111112
Amphizoa	111-111211	1411211111	1221112211	11114231-1	223116----	1111111221
Amplectopus	121-111212	1411111111	1123111-11	11112132-1	221116----	1111111111
Anaspis	1121411131	2421222111	1122112112	11112132-1	221116----	1111111211
Anchycteis	121-421211	1411111211	1121112111	1111213311	221116----	1211111111
Andotypus	111-311211	1411111111	1223112321	11213154-1	2311131211	1121112111
Anischia	111-411112	1411111111	1122121-11	11114132-1	221116----	1111111211
Anisotoma	111-411211	1411111111	1222112111	11113134-1	2211212111	1111111111
Anorus	111-311211	1411111211	2121111-11	1111413311	221116----	1211111113
Anthicus	1122421211	1411112111	1121112112	11112132-1	221116----	1111111212
Anthrenus	121-211212	2311122111	1121111-11	11112134-1	2131131112	1112111213
Apatides	121-121311	1411111211	1122122111	11112144-1	2211131111	1111112122
Apatophysis	111-411211	1411121112	2121212212	1111213331	321116----	1211111111
Aphanocephalus	111-411311	1411211111	1122112111	11113154-1	221115111-	1111111222
Aphodius	111-411112	1421221111	1222111-11	11213154-1	2211131131	1122112111
Apteroloma	111-411211	1411211111	1121112111	11114131-1	221116----	1111111113
Artematopus	111-311112	1411111211	1121111-11	11114131-1	221116----	1211111112
Arthropterus	1121111211	1411111111	1121121-11	12112145-1	311216----	1111121111
Aspidytes	111-211211	1421211111	1221111-11	11114232-1	324216----	1111111212
Atomaria	111-113211	1411112111	1111122112	11113134-1	2211131111	1111111223
Atractocerus	111-411211	1411123112	1221111-11	13114132-1	223116----	1111111321
Aulacoscelis	111-411211	1411111111	1121111-12	1111213321	223116----	1111111221
Aulonothroscus	111-411212	2411221221	1122111-11	11122134-1	2211131121	1111111111
Bacanius	111-111212	2421111111	1221112321	11112154-2	222115111-	1111111221
Bactridium	111-311211	1411111111	1222111-11	11214144-1	221115111-	1111111112
Bembidion	111-111211	1411111111	1221112111	11114131-1	221116----	1111111112
Bolboceras	111-411111	1422--1111	1223112111	11114134-1	22?1131132	1111111212
Boros	1122411311	1411112111	1221111-11	11113134-1	2211231111	1111111221
Bothrideres	111-411311	1411211111	1122112111	11113134-1	2231141112	1111111212
Brachinus	111-111312	1411111111	1221112111	11113131-1	221116----	1111111113
Brachypeplus	1121411211	1411112111	1223111-11	11113134-1	2231131111	1111111223
Brachypsectra	111-411111	1411111211	1122121-11	1111213331	223116----	1111111111
Buprestis	111-221211	2411211111	1121111-12	1111213321	231116----	1111112121
Byrrhinus	111-111112	2421211211	1221112111	11112132-1	221116----	1111111222
Bystus	111-211211	2411211111	1122112112	11112154-1	2221131111	1111111223
Byturus	111-411211	1411111111	1221111-11	11113134-1	2231131111	1111111213
Callirhipis	121-111211	1411111211	2111121-12	1111113311	321116----	1111111221
Calopus	111-111311	1411221112	2121111-12	1111313311	221116----	1111111221
Calosoma	111-411311	1411111111	1221112111	11114131-1	221116----	1211111113
Calyptomerus	121-111131	1421111111	1122112111	11112144-1	??31141112	1121111111
Car	111-411311	2411111111	1222111-11	23---134-1	2311131111	1111211213
Carpophilus	1122411211	1411111111	1223111-11	11114134-1	2231131111	1111111112
Caryobruchus	111-111311	1411111112	1121112211	2111213321	221116----	1111111111
Catogenus	111-411211	1411111111	1222111-11	11112131-1	223116----	1111111112
Cenophengus	111-111211	1411111211	1121121-11	1111412321	221116----	1211121111
Cephaloleia	111-111311	2411211111	1121211-11	11112131-1	221116----	1111111422
Cephaloon	111-411311	1411222111	1221112211	21113134-1	2211131111	1111111111
Cephus	1122111111	1111211111	1121121-11	11114111-1	221116----	1111111321

70	80	90	100	110	120	130
1111211111	3121113211	1131112111	1221111111	1121111114	1112422111	1223221131
2111111141	3121111211	2111122112	1211211112	1231211314	1322421111	3-----2112
1112122111	4121113211	1121112111	1151111121	1111111114	1112422111	1111112211
1112321111	4121111331	2111111112	1311111111	1431121114	1112423111	1411221312
1111111111	2121111211	2121112111	1123311121	1442111114	1112421111	31-1112322
1111112111	4121313211	2331112112	1123111121	1221111114	1112422111	1222211333
1111211111	3122112211	2121113131	115315----	1111111115	1112422111	31-1112222
1112211214	4121115221	1311?12112	1211111111	1421211114	2122421231	1442221122
1112221141	3121111211	1141112111	1213111121	1421111112	1112212111	1411131213
1111112111	2121111211	1131112112	1212121111	1121111214	1112422111	1223221122
1112311111	4121111221	1111111111	1351111111	1121211114	1112423121	1411131312
1112321111	3121114211	1131113121	115115----	-111111111	---1113111	31----2212
1111111111	4121112211	2121112112	1211111121	1221111114	1122421111	31-1112211
1111211131	2121112211	1131112111	1141111121	1121211114	1112422111	1223221112
1151111111	4121211212	1121122112	1221111121	1142212214	1112423131	1441121313
1111211141	3121111211	2241213212	1213111111	1221211112	1112212111	1411221322
1112321113	3121113211	2211122112	1111111111	1421111114	1122421111	12?3221111
1111111111	4121313213	2121112111	1121121111	1121211115	1122421111	31-1112223
1111111111	4121313213	2121122112	1211121111	1121221114	1112422112	1211121111
1111111131	4121113211	2321112111	1212311121	1221211114	1112422111	1112222221
1112311111	4121111211	2111121111	1211111111	1131214314	1112423231	1411121323
1111211111	3121112211	1121113112	1231311121	1221111114	1112421111	1111112212
1112321133	4121114211	1111112111	1251111121	1121211114	1112422111	1111112211
1111111111	4121311211	1121113111	122115----	-111111125	1112422111	31-1212223
1112312153	4121111211	3221112112	1211111121	1131211114	3122422111	1211121122
1111111111	4122113211	1121112111	121315----	-111111114	1112421111	22-3212313
1112222111	4121113211	1121113111	125215----	-111211114	1112422111	1212222211
1111111111	4121111211	2321112111	1153111121	1131211115	1112422111	1213321333
1111111112	4121113221	2231112111	1211111121	1321111114	1112422111	1212212112
1111111111	3121113211	1121112112	1241211121	1221111114	1112422111	31-1112211
1112321111	4121213212	1121122112	1251111121	1421211114	1112422211	1211121111
1112211224	4121111213	1341212112	1143121111	1111111112	1112212111	1412212212
1112221141	3121111211	1141112112	1243311121	1421111112	1112212111	1212231313
1111111111	4121111211	2131112111	1212111111	1121211115	1112423111	1411221121
1112311114	4121111311	3331111111	112115----	-111111114	1113422111	31----2212
1111111111	4121113211	1131112111	1211111121	1221111314	1112422111	1222211111
1152311113	4121212213	2231121112	1111121121	1142211114	1322422221	1441121321
1131111113	2121111211	1131112122	1221111121	1421111114	1322422231	1111211122
1111211111	4121111211	1311112111	1242111111	1121111114	1112423111	1412221331
1112321141	3121115211	1141112212	1223111121	1121111212	1112212111	1123211313
1111111111	1121113211	2121112112	1221111121	1421111114	1112421111	1213212112
1111111111	4121111211	2321112111	1113131121	1111111314	1112423111	1222321122
1111111112	3121111211	2321112111	1123111111	1421111215	1112423111	1212311331
1112221141	3121111211	1141112211	1233111121	1121111112	1112212111	1223211212
111111141-	-121111211	1231112111	1241111121	1221211114	1112422111	1412221111
1152321111	4121111211	1131112111	1151111111	1142212114	1112423121	1221221111
1112311111	4121111211	2221111112	1111111111	1421111114	1112423111	1411121311
2111111111	4121111211	1121111111	1221111121	1131211114	1122422121	1211121112
1111112112	4121111212	2221112111	1122111121	1211214114	1112422231	1211221132
1111112111	3121112211	2131112111	1141111111	1121211114	1112422111	1222211112
1112211111	4121111211	2211122112	1211121111	1131221214	1112422112	1212111211
1111111111	4121312212	1121112111	112215----	-111211114	1112422111	1111112222
1112121141	3121211212	1141112111	1213111121	1121211112	1112212111	1421321313
2111111151	3121111211	2111122111	1121312111	1121211115	1112421111	1211112112
1112313414	4231111211	3331213121	215315----	-111211115	1112421111	22-2112222
111111141-	-121112211	1131112111	1241111121	1121111114	1112422111	1212221111
1111112111	4121113211	1331113111	1113111121	2121211114	1112422111	1222221112
1112211113	4121113231	1132113121	1123111121	1121111114	1112423111	1213321122
1112321414	4121215311	3321212111	115115----	-111211114	1113422111	31-12?2211
1112321111	41211?1211	1121112111	1153111121	1221211114	1112422111	1412221122
1111111111	4121313213	3221113111	114115----	-131211114	1112421111	31-1212212
1112321112	4112115111	3321111111	1?1315----	-121111111	---1111111	31----2213

Table 1. Morphological data matrix. Continued.

	140	150	160	170	180	190
Acalanthis	1121214122	3122121211	1134211211	121111231-	1141112211	4335113223
Acalyptomerus	2121?22311	2122121211	2122211111	112111231-	2121111211	2325111222
Acanthocnemus	1121211111	1121131211	111-211211	111111231-	1121112211	2314111122
Acmaeodera	1121121131	1121111211	1134?11511	3121111332	1131112213	2327111123
Acrotrichis	1121211311	1121111223	111-21152-	112112231-	2121122211	7333113322
Adelium	1122-24221	3121111211	1125211111	122111231-	1141112212	2336113322
Adrastia	1122-11111	1121121211	111-211511	121111231-	1122122311	4333113323
Aesalus	1122-13121	3122121211	111-211111	122111231-	1131112232	4338113322
Agabus	1112--1221	1221121211	111-211211	3111112322	1131122212	3314213121
Agapytho	1121212122	2122121211	111-211211	2111112321	1141112212	4315113223
Agrilus	1121121131	1122111231	111-211511	2111112332	1131112213	4324112121
Agulla	1111------	111---11--	--------11	111111111-	12121121--	-1---11111
Agyrtodes	1121211311	1121111211	111-211221	211111231-	1121112211	4333113323
Amartus	1121212321	2121121222	111-211211	121111231-	1131111222	2333123122
Ampedus	1122-21131	1122121211	1125211111	2121112332	1131112212	4326113123
Amphizoa	1212--1231	1122111211	2124111211	3121112321	1141122212	3216112221
Amplectopus	2121211111	1122111211	111-211111	1121112321	1131112213	1214141222
Anaspis	1122-21311	1121111211	111-211212	111112231-	1221111231	4331111222
Anchycteis	1121211111	2122211211	1124111111	2111111321	1111111211	2326112121
Andotypus	1121211312	2122111211	1124211112	121111231-	2131112221	2232113222
Anischia	1122-21131	1122111211	1125211111	2112212332	1131122213	4335133223
Anisotoma	1121211112	2121111211	1125211211	211112231-	1331112221	2333112322
Anorus	1121211111	1122121211	1122211111	3111112322	1142111211	2315111122
Anthicus	1122-21311	1121121211	111-211212	111111231-	1131112211	4333113122
Anthrenus	2122-11121	1122111211	111-211211	3122112322	1141112213	2226143121
Apatides	1122-23311	3121131211	111-111112	122111231-	1131122212	7325111122
Apatophysis	1121213211	3121122211	111-211211	122111231-	1141111212	4335111122
Aphanocephalus	1122-24132	3122121211	111-211121	312111231-	1131122213	533711332-
Aphodius	1122-13111	3121111211	1134211211	121111231-	1121122231	4337113122
Apteroloma	1121212111	2?21121211	1125211211	211111231-	1121112231	4313113322
Artematopus	2121111131	1122111211	1122212111	3121111332	1141111213	2316143122
Arthropterus	1112--4312	3121111222	111-211521	121112231-	1322122211	4311121122
Aspidytes	1212--1321	1121111211	2125111211	3121122322	1141122212	6314212221
Atomaria	1121211132	1122121211	111-221211	2111112321	1141122213	7333113222
Atractocerus	1121211111	1121141233	111-2-1212	111111231-	14-2111431	5321113323
Aulacoscelis	1121213221	3121121211	111-211111	111111231-	1141111212	4325111122
Aulonothroscus	1122-21131	1122111211	1125211311	3122112332	1131122213	4328143323
Bacanius	1122-22111	213---1212	111-211211	312211231-	1131122213	432713332-
Bactridium	1122-14331	3121121222	1124211211	121111231-	1141122213	4335123223
Bembidion	1212--3221	2121111211	1136211211	121111231-	1141122212	2315111221
Bolboceras	1122-24111	3121111211	1121211111	121111231-	1121111231	4332113122
Boros	1121211122	2121121211	111-211211	211111231-	1121112212	4324113223
Bothrideres	1122-12131	2122121211	1124211111	111211231-	1131122213	7333113223
Brachinus	1212--3121	3121111221	111-211211	122111231-	1131122212	7315111121
Brachypeplus	1121214122	3121121223	1125211221	121111231-	1131122223	4332113222
Brachypsectra	1121211122	1122131211	1135211111	2112112322	1141111212	2325113122
Buprestis	1121121131	1122121221	2124111211	3122111332	1131112213	2327111121
Byrrhinus	2121121121	1122111211	211-211111	3122111332	1131112213	2326141122
Bystus	1122-11331	1121111211	111-211111	2111112322	1141122213	7333153222
Byturus	1121213212	3121121211	1124111111	111211231-	1121112211	4333113122
Callirhipis	1121211111	2122421211	111-211111	2111111321	1111112211	2226111122
Calopus	1121211212	1121121211	111-211212	111211231-	1141111231	4335113223
Calosoma	1212--1131	2121121211	1131111211	1112122322	213112-212	2315111121
Calyptomerus	1121211211	1122111211	111-211221	112212231-	1321112221	3311453222
Car	1122-14312	4122121211	2124211211	122111231-	1131122212	7335112222
Carpophilus	1121214321	3121121223	111-211211	111211231-	1131112223	2332113122
Caryobruchus	1121224322	3121141232	2124211211	212111231-	1131122212	2335113121
Catogenus	1122-12131	2121121211	1137221111	111211231-	1141122213	7335113223
Cenophengus	1121211111	1121141233	111-211521	111111231-	14-2111431	2331113123
Cephaloleia	1121224322	3121111211	1124111211	121111231-	1141122213	2333111122
Cephaloon	1121211211	1121121231	111-211212	111111231-	1122111331	4333113122
Cephus	1111------	111---11--	--------11	111111111-	14-21121--	-1---11112

200	210	220	230	240	250	260
1211212114	-121121612	2122132322	3113111311	22111413--	1212111111	1311111112
1211221111	2223122411	1--123---4	-3-2413311	16111533--	2133311111	1111111171
1211212114	-121123612	2122131222	3113111311	2211141112	1212111111	1211111111
2211311113	111311162?	2112133114	-2?2211311	11111333--	2112111111	1111111111
2211231111	1323134621	24--33---4	-31443134-	16111533--	2133311111	1111111171
1212132114	-223134---	----------	----------	----------	-----11111	1111111131
2211132114	-323134521	24--33---4	-3-443134-	16111533--	2133111111	1111111111
1211322114	-123121211	232233---4	-112311312	12111433--	11121112-3	2112111111
2222111224	-12312211-	1--121---4	-111113231	1221233113	1112111111	1211111111
1211322114	-322121621	231233---4	-112331331	11111413--	1212211111	1111111121
1211311111	111311162?	23?213---4	-1?3331311	11111433--	21121112-1	1111121111
1111111114	-1231226--	1--213----	---1--13--	1-111112--	21131113-1	121113-311
1211212114	-123123611	2222333113	1212111311	14111413--	2133211111	1211111111
1211322114	-222113612	24-233---4	-21441134-	15111533--	1233111112	1111111111
2211211112	1113123621	2122133113	11?2231312	1111122111	1112111111	1111111111
12?1111222	111312211-	1--121---4	-112113231	1221231113	1112111111	1111111111
1211211123	1123223321	2132131212	2113132312	24111413--	1222111111	1211111111
1221212114	-123134621	2122132114	-214231312	23121413--	1112111111	1111112131
1211312111	1123211621	2112133222	1112231311	1111121122	1112111111	1111111111
1211311114	-123123211	2232332212	1112112321	1211141112	1112111111	1211111111
2211231114	-323134621	2122131124	-213331311	13111313--	1212111111	1111111111
1211312114	-123123611	2112132214	-3?441134-	15111-33--	2132111111	1211111131
2221211113	1113111611	2112131212	2112111311	2111122113	1112111111	1111113111
1211222114	-223134621	231233---4	-21413132?	23121433--	2213411111	1111112131
2211312111	1223222311	2112131212	1112122311	12111433--	1213111111	1111111111
1211212114	-123112311	2122132212	3113122312	2211141113	1112111111	2112111112
1211312114	-122123612	2122132312	1112111312	22111333--	1112111111	1111111111
2211232114	-323134611	24-233---4	-214421321	16111533--	22331113-1	111113-371
2211211114	-123111211	2212332--4	-2?2311312	23111433--	11121112-2	2211111111
1211?22113	1123123311	2232332214	-214411312	14111433--	1232111111	1211111111
1211311113	1113111621	2112132222	1111131312	2211121122	1112111111	1111111111
2211111114	-12312211-	1--131---4	-111113212	22211313--	1122111112	1111111112
2212111222	112312211-	1--121---4	-11111324-	1221233113	1112121111	1211111111
1211222114	-322121611	24-233---4	-3-442134-	14111433--	2133211111	1111111111
1211212113	1123134621	24-233---4	-114131311	12111533--	11121113-1	111113-311
1211222114	-121123611	2122131312	1122121312	23111413--	1212111111	1111111111
2211311111	1123121621	232233---4	-3-4431322	22111433--	12121113-1	111113-311
2211132114	-323134611	24-233---4	-214311321	14111433--	2133111113	1111111111
1211232114	-323134621	231233---4	-114431321	15121533--	2133211111	1111111121
1211212112	111311211-	1--131---4	-111113231	1221131123	1222112121	1111111111
2211211114	-123111211	232233---4	-1?3211312	22111433--	11121112-2	2213111111
1211212114	-121134621	2132132214	-112231312	2211131113	1112111111	1111111131
2211132114	-323134622	24-233---4	-214331311	23111413--	1232111111	1111111161
1211112113	111312211-	1--121---4	-11211324-	12111313--	1122112121	1111111111
1211212114	-323121611	24-233---4	-114311311	14111533--	1233111111	1111111111
2211311113	1113222621	2122133112	1112231312	11111313--	11121113-1	111113-311
1211212111	1113111621	2112133112	21?3121311	1111121113	1112111111	1111111111
2211311111	112312261?	2222133224	-1?2231311	23111333--	11121113-1	111113-311
1211232114	-322134612	24-233---4	-214411312	25121533--	21331113-1	111113-361
1211312114	-121123612	2122131222	1113131312	2212141123	1212111111	1111111111
1211311112	111321162?	2122133112	11?2231312	1111121123	1112111111	1111111111
1211312114	-121122621	2122132313	2112231312	2112141123	1112111111	1111111131
2211212112	111312211-	1--131---4	-111113231	1221131123	1112112121	1211111111
2211111111	2123222411	1--123---4	-113113121	15111533--	2233311111	1111111161
2211222114	-122123611	2112132122	1112311311	13111533--	1132111111	1113221211
1211232114	-323111611	24-233---4	-114321311	15111533--	2233111112	1313111111
1211222114	-123134612	2132132222	1122111311	2211143123	1212111111	1111111311
2211211114	-222111612	2122132113	2112321311	21111313--	1212111111	1111111112
1221311114	-113111621	2122133213	1212331321	11111313--	1112111111	1111111111
2211222114	-122123622	2122132222	2112131312	2311143113	21131113-1	111113-361
12213?2114	-121123621	2122132212	1112231311	1211121112	1112111111	1111111131
1112112114	-1131346--	1--213----	---1--13--	1-111112--	12121112-1	1111112111

Table 1. Morphological data matrix. Continued.

	270	280	290	300	310	320
Acalanthis	1-11112811	1132131111	2211111122	224-311111	1111323-11	2111-14111
Acalyptomerus	1-1112-811	1122121112	2221111111	224-441111	1111311211	141--11111
Acanthocnemus	1-11112811	1133121111	2111111122	224-311111	1111311211	2111-14111
Acmaeodera	421212-821	1132141111	1111111311	1131333111	1211111111	141--12111
Acrotrichis	1-11112711	1332131111	1121111111	1131333111	1111411-31	141--11111
Adelium	6111112831	1332121111	1111111122	224-111111	1212213-13	2114111111
Adrastia	1-1112-713	1232121111	2222211111	1131333111	1111411224	142--11111
Aesalus	1-11122821	1132121111	1111111111	2231111111	1111211311	141--11111
Agabus	1-1112-631	2132122111	1111111111	2231311112	1124111-32	3311----11
Agapytho	1-11122813	1132121111	2211111112	224-311111	1111313--4	2214111112
Agrilus	421212-721	1132131111	1111111122	2231333111	1211411-31	1113-11111
Agulla	513112-111	1131221111	1111111111	1111111111	1111111111	1111-11211
Agyrtodes	1-11112711	2112121111	2222211111	1131333111	1121311311	3111-11111
Amartus	312112-811	1132121111	1122211122	224-433111	1111313--4	2111-11111
Ampedus	1-11112841	1112121111	2211111111	2211333111	1111111311	1121-11111
Amphizoa	1-1112-631	1132122111	1111111111	2211111112	1124113--4	1211-12111
Amplectopus	1-1112-831	1122131311	2222211122	224-111111	1211411-34	141--11111
Anaspis	512112-811	1332121111	1221111122	224-222111	1211313-11	241--12111
Anchycteis	4211112831	1123121111	2111111111	114-111111	1111111211	1121-11161
Andotypus	1-11112811	1132131111	2222111111	224-411111	1111111311	1111-21111
Anischia	1-1112-831	1132121212	2221111111	2231111121	2111411311	1123-21111
Anisotoma	1-11122711	1132131111	2222111111	1131333111	2111411311	3321-11111
Anorus	421112-811	2133231111	1111111111	2221222111	1111111311	1111-11141
Anthicus	611112-811	1132131111	2221111111	224-111111	1111313--4	2114111111
Anthrenus	1-1112-831	1112131211	2211111122	2231311111	1111111-31	1222-22111
Apatides	1-11113811	2122121111	1111111122	2211111111	1211411-34	1222-23211
Apatophysis	513112-811	1132121111	2221111122	224-111111	21113111-4	241--12111
Aphanocephalus	1-11112811	1232141111	2222211122	224-441111	1111513--4	241--12111
Aphodius	1-11122711	2132121111	1111111111	114-111111	1111311-34	1111-11111
Apteroloma	1-11112711	2112121111	2111111111	1131111111	1111111311	45------11
Artematopus	4211122851	1122121112	2221111111	2211111111	1111111311	1221-22111
Arthropterus	1-1112-631	2122122111	1111111111	2231311111	1224?11-34	3311----11
Aspidytes	1-1112-631	2122122111	1111111111	2232111112	1114111311	3321----11
Atomaria	1-1112-811	1132141111	2221111122	224-441111	1111113--4	241--12111
Atractocerus	1-11113311	1133221111	1111111111	114-333111	1111223-11	2121-11111
Aulacoscelis	313112-811	1132131111	2222211122	224-311111	2111313-13	2111-12121
Aulonothroscus	611112-851	1332131312	2111111111	224-111111	2111211311	1111-11211
Bacanius	1-1112-811	1132131211	1111211122	224-443112	1211211311	1113-11111
Bactridium	1-1112-811	1132141311	1222111111	224-441111	1111511--4	241--11111
Bembidion	1-1112-631	1112123111	1211111111	2231111111	1214211-34	3311----11
Bolboceras	1-11112311	1123212111	2222211111	1111111111	1111213-13	1123-11111
Boros	1-11112831	1132121111	2211111122	224-111111	1111223-13	2114211111
Bothrideres	1-1112-811	1132141111	2211111122	224-111111	1211313-13	2113-11111
Brachinus	1-1112-331	1112123111	1211111111	1131111112	1124111-31	3311----11
Brachypeplus	312112-811	1132121111	1112211122	224-433111	1111313--4	241--12111
Brachypsectra	1-11112811	1123121111	1111111122	2211111111	1111111311	1111-11111
Buprestis	421112-821	1132141111	1111111122	2231333111	1111411211	1113-21111
Byrrhinus	1-1112-831	1132131311	2222211122	2211111111	1111111-34	141--21111
Bystus	1-11112711	1132141111	2222111112	114-441111	1111213-31	241--21111
Byturus	3222112811	1332121111	2222111111	224-333111	2111313-11	241--14111
Callirhipis	1-11113831	1132121111	1111111111	2221222111	1111111311	1121-11111
Calopus	611112-721	1333121111	1111111122	124-111121	2121223-13	241--21111
Calosoma	1-1112?631	1113123111	1111111122	2211111112	1114111-34	3311----11
Calyptomerus	1-1112-711	2112131311	1221111111	114-441111	1111312211	1111-21211
Car	513112-821	1122141111	2222111122	224-433111	2111313--4	2111-12121
Carpophilus	312112-811	1132121111	1112211122	224-434111	1111313--4	2111-12111
Caryobruchus	513212-811	1132131111	1222111122	224-311111	1121313--4	241--12121
Catogenus	1-1112-811	1122131111	2111111122	224-311111	1111113--4	2111-11111
Cenophengus	1-1112-211	1133221111	1111111111	1111111111	1121211311	1121-21111
Cephaloleia	311112-821	1132131111	2111111111	224-333111	1111313--4	241--12111
Cephaloon	1-1322-711	2123121111	1111111112	224-111111	1111311211	2114111111
Cephus	1-1212-211	1131221111	1111111111	1131333111	1111111321	1211-11111

330	340	350	360	370	380	390
1211113112	3132212122	1111111111	1121121326	1111111114	2111421111	11112233-1
1211111-11	1112111111	14-1111111	11112111-8	--11111114	1131431111	1112322111
3211113112	3133212122	1121111111	1111221314	2111111114	2111411111	11112253-1
1221111-21	1131221131	1111111111	2121121329	--21111115	1122--1-11	11113213-1
1121111-11	1111111111	14-1111111	111113-1-9	--11211114	3111421211	1111115111
1221413112	3131222122	2111111211	11112211-4	1121111114	2112--3111	1111223121
1121111-12	4111121111	14-1111211	11113211-6	3113211114	2111131112	11111113-1
1221112112	4112221121	1111112112	1111221319	--21111114	2111413111	1112321121
1111321-12	4121211111	24-1111111	11113211-3	2113211213	3113----12	11311113-1
1121112112	3131212122	1111111111	11111111-4	1111111114	2111411111	1112225111
1221111-21	1131221131	1111111111	2121121329	--21111115	1132--1-11	11111213-2
4111111-11	1131211131	1211111111	11113211-2	1111111113	3113----11	11111153-1
1121211-12	1122112111	1111?11111	11112211-4	1121211114	3121111211	1111421111
1321413112	1132211131	1111111111	11111211-5	1111111114	1111421111	1111115211
1211112122	11332?2122	1121111111	11111111-8	--13211224	2211121111	11111133-2
1111121-12	31211?1111	1411211211	11112211-3	1?13211113	2111121112	11211113-1
1211111-22	4133211122	1111??????	??????????	??????????	??????????	??????????
1211113122	3133222122	1121111111	11212111-8	--11111114	2111423211	1111215211
1211112112	3133211112	1311111111	11211211-4	3121111114	2111421111	11113213-2
1211111-12	1131213121	1111111113	11111221-3	3113211124	2111221111	11111143-1
1211113112	4133212122	112112111?	111113-1-8	--13211115	1311231111	11211113-1
1121111-12	1122112111	1421111111	11111111-6	1111111114	2111111211	1111113111
1211111-12	4112211121	14-1112112	11111211-9	--22221114	2111433111	11121?5121
1211112112	3122213122	1111111111	1111221318	--11111114	2111421111	1111213212
1211112112	3132212122	1111111132	11112211-3	1121212114	2121411211	11111213-1
1211413122	4133212232	1111112111	211113-429	--21111114	3111411111	11111213-1
1221113112	3133212142	1121111111	2121121329	--21111114	1311421111	11111213-1
1211111-12	4112111111	14-1221221	12111111-6	2121111115	3122--2-11	1111321111
1221111-12	41121?1111	14-1112112	1111221319	--21111112	2111411121	1112223121
1121112212	1112222121	2111111111	11112111-3	1111111114	3111121111	1111115111
1211112112	3133122122	2111111111	11211211-8	--11211114	1211421111	11111133-2
1121121-22	11211?1111	1421111123	1121122619	--13211113	2111421111	11111133-1
1111121-22	4121121111	14-1111111	111?2211-3	2113111223	2111413111	11211133-1
1121112112	4121212122	2111111111	11111111-8	--11111114	2111421111	1112215111
1211113112	3133222122	1111111112	1111321214	1111111114	1111421111	1111113111
1221312112	3131222122	2111111111	1111221328	--11?11115	1111431111	11114113-2
1211112112	4133212122	1111111111	111113-1-9	--13211215	2111431111	12112113-1
1221411-12	4133211122	14-1111111	112113-1-9	--13221414	3111221211	11111133-2
1221112112	4121111111	1421111111	11111121-7	1111211114	2111421111	1112223111
1121321-22	11122?2121	1421111111	11112211-3	1?13211213	3111211212	11111133-1
1211111-12	31122?1111	14-1112112	1111221219	--11111114	2111111111	1112211121
1221413112	3133223122	1111121111	11112111-4	1111111114	3111213111	1111325121
1111113112	3133212122	1111111111	111113-1-9	--11211115	1121421111	11112113-1
1121321-12	2112112111	14-1111113	11211221-3	1113211213	3111211212	11111133-1
1321112112	3132212122	2221111111	11111121-5	1111211114	2111421111	1111325111
1211112112	4121222122	1111221253	11212211-8	--11111114	3111231112	11311113-1
1211111-21	1131221131	2121111111	2121121329	--21111115	1122--1-11	11113213-1
1211112112	41332?1112	14-1111111	11111211-3	1?21111114	1111423211	11113213-1
1121111-12	1121211111	14-1111212	111113-1-8	--11111114	3131431111	1111323111
1211112112	31322?2122	1121111111	11111111-3	1111211114	1111421111	1111225111
12111?2122	41332?1112	1421111112	1111221219	--21111116	1212--3-11	11113253-1
1111412112	3133222122	1121111111	1121211713	1121111114	1111411111	1111223121
1111121-22	11111?2111	2421111113	11212211-3	1?13211323	2111411111	11111143-2
1221111-11	1112111111	14-1111111	11112111-4	1121111114	2121431111	1112212111
1221112112	4122211212	1111111112	1111321315	1121212116	1122--1-11	11112153-1
1321413112	3132212122	2121111111	11111121-5	1111211114	2111421111	1111225111
1121112112	3133221212	1311112111	2111321326	1111111115	1112--1-11	11111213-1
1221413112	3133212122	1211111111	111113-1-9	--13211115	1121421111	11113213-1
1211111-11	13--------	---1111111	112113-1-8	--13211114	2111223211	11311113-1
1121112212	4111221211	14-1221212	121113-425	1121211115	2112--1-11	11114213-1
1111111-12	3131221122	14-1111111	1111211713	1111111114	2111411111	1111325121
1211111-11	1131123111	14-1111112	11113211-8	--21111113	1133----11	11113213-1

Table 1. Morphological data matrix. Continued.

	400	410	420	430	440	450
Acalanthis	2111---321	1113251112	2111121111	14---22111	111122132-	1111111122
Acalyptomerus	1111111311	111313213-	---2131121	1311133321	1113121111	1121111111
Acanthocnemus	1211---321	1113251112	2111121121	14---23211	111112132-	1111111121
Acmaeodera	1111---321	111222111-	---2131121	1111143312	-11212132-	1122111121
Acrotrichis	1111111311	111213121-	---1221121	1111123211	1123121111	1111111111
Adelium	111121-311	1112151112	1111121111	1311123131	111312122-	1111111121
Adrastia	1111---311	1121251112	1111121121	14---21211	1213123-2-	1111111121
Aesalus	111121-311	111211213-	---1111111	14---22232	-111113-12	2111121111
Agabus	1111---111	111222111-	---1111121	14---21312	-213133-11	1111111121
Agapytho	1111121311	1112151132	1211121111	1211122231	1112121211	1111111121
Agrilus	1111---121	111222111-	---2131121	1111133312	-11212132-	1122111111
Agulla	1111---121	11112?111?	???1121111	1111112112	-11313132-	1112111121
Agyrtodes	1111111311	211313123-	---1121111	1211121221	2123121111	1111111121
Amartus	111121-311	1112151112	1111121121	1311132231	111212122-	1111111122
Ampedus	1111---321	222321111-	---1111121	1311123211	121322122-	1111111111
Amphizoa	1111---111	111222111-	---1121121	14---22312	-213133-11	1111111121
Amplectopus	??????????	??????????	??????????	??????????	??????????	??????????
Anaspis	111122-311	1112151122	1311121121	1211122131	1111121311	1111111111
Anchycteis	1112---311	111211111-	---1111121	2321123212	-113221211	1111111121
Andotypus	1111---311	111322111-	---1112111	1311123112	-213132-2-	1111111121
Anischia	1111---332	--13261---	---213-221	14---33212	-213113-2-	1111111121
Anisotoma	1111111311	111313123-	---1121111	1211122221	2122121111	?111111121
Anorus	1111119211	111311213-	---1121111	1321123342	-112121212	1111111121
Anthicus	111121-311	1112151122	1111121121	1211123131	1113121211	1111111111
Anthrenus	1111---311	111213211-	---1121111	1211122211	111312112-	1111111121
Apatides	1111---221	111223211-	---1131111	1311123212	-112113-12	1112111111
Apatophysis	1111---311	1112151112	1111121111	1311122312	-111121111	1112111311
Aphanocephalus	1111112311	1112151112	1112121121	1211121221	1111121211	1112111121
Aphodius	111121-311	211211213-	---1111111	14---23242	-112113-11	2111111111
Apteroloma	1111118311	211313221-	---1121111	1321223221	2123121111	1111111121
Artematopus	1111---321	111321111-	---1111111	1311122231	121322132-	1111111121
Arthropterus	1111---111	111121111-	---1121121	14---23112	-213122-2-	1111111111
Aspidytes	1111---211	111222111-	---1121131	14---23212	-213133-2-	1111111121
Atomaria	1111115311	1112151132	1111121111	1211123221	1112121111	1111111121
Atractocerus	111121-311	1112151111	1111121111	1211122131	1113121111	1122121121
Aulacoscelis	1111---311	1113151112	1111121121	1211122112	-113121111	1111111122
Aulonothroscus	1111---322	--13251132	1111131121	1111123112	-113123-2-	1111111111
Bacanius	1111---112	--1322111-	---1112121	14---22112	-213133-2-	1111111121
Bactridium	1111111311	1112151132	1111121111	1311122221	1113221111	1111111121
Bembidion	1111---111	111322111-	---1111121	14---23112	-213132-2-	1111111121
Bolboceras	111122-211	?11211213-	---1111121	1321122242	-112113-1?	1111111111
Boros	111121-3?1	111215112?	???1121111	1111122221	1112121211	1111111121
Bothrideres	1111---312	--12151132	1111121121	1111123111	111312122-	1111111111
Brachinus	1111---111	111322111-	---1111121	14---23112	-213133-2-	1111111121
Brachypeplus	1111117321	1213251112	1311121121	1311133221	1113121111	1111111121
Brachypsectra	1111---331	113321112-	---1111121	14---23112	-213132-2-	1111211122
Buprestis	1111---221	111222111-	---2131121	1121133312	-11212132-	1122121121
Byrrhinus	1112---321	112321111-	---1111121	1211122311	1113221311	1111111121
Bystus	111121-311	1112151132	1211131121	1211123221	1112121211	1111211111
Byturus	111122-311	1113151122	1211121111	1311122221	1112121111	1111112121
Callirhipis	1111---321	1122251112	?111111121	1112123211	111322122-	1111111111
Calopus	111121-311	1112151121	1211121111	1211121231	1112121211	1111121211
Calosoma	1111---111	111221111-	---1111121	1311121212	-213132-2-	1111111121
Calyptomerus	1111111311	1113151121	1112111121	1211122331	1113121111	1111111111
Car	1111---321	1112251112	1112121122	14---33211	1111113-12	1111111121
Carpophilus	1111117321	1212251112	1311121121	1311133221	1113121111	1111111121
Caryobruchus	1111---321	1112251112	1112111121	1----43-12	-113113-11	1111111111
Catogenus	2111---221	1111251112	1111131121	14---33111	11121313??	1111111111
Cenophengus	1111---322	--1321111-	---1111121	1211122212	-213123-2-	1111111121
Cephaloleia	1111---321	1112251112	1111131121	1111133212	-113121111	1112111111
Cephaloon	111121-311	1112151111	1111121111	1311122131	1111121211	1111111111
Cephus	1111---311	111211111-	---1111121	1111121212	-111113-2-	21111?1111

460	470	480	490	500	510	
1122211121	3-11211111	1111111112	1223111112	1111111112	1111251131	311111
1122211121	2211111111	1111111112	11111-----	--11111111	1111141111	111111
1123211121	3-11211111	1111111112	1213111112	1111111112	2111251131	311111
137-------	----211111	1111111112	11111-----	--11111111	1111131161	621111
1122211122	2111211111	1111111112	1112111111	1111111111	2111112111	111111
1122211121	2111111111	1111111112	1213111122	112----113	1111321111	111111
1122211121	2111111111	1111111112	11111-----	--11111111	2111111111	111111
1123211221	2111212121	1111111112	11111-----	--11111131	1111141161	621111
1112221111	--11211111	1111111211	1212111121	1111111113	1111111111	111341
1122211121	2111211111	1111111112	1213111222	1111111112	1111251131	311121
137-------	----211111	1111111112	11111-----	--11111111	1111131161	621111
1112211112	--11211111	1111111112	11111-----	--11111111	1111221111	11111?
1122211121	2111111111	1111111112	1112121111	1111111111	2113131111	111111
1122211121	3-11211111	1111111112	11111-----	--11111111	12111?1131	311111
1121221121	2111211111	1111111112	12112-----	--11111112	21113?1151	521112
1112211111	--11121111	1111111211	1212111111	112----113	11113?1111	111331
??????????	??????????	??????????	??????????	??????????	??????????	??????
1122211121	2111211111	1111111112	1213111112	1211111112	1111251131	311111
1121211121	3-11211111	1111111112	12211-----	--11111112	1221214151	521112
1122211121	2111211131	111111112-	1212111111	1111111112	111132118-	811431
126311213-	---1211111	1111111112	12111-----	--11121112	1111331151	521111
1122211121	2111111111	1111111112	1112121121	1111111111	1111111131	311111
1122211121	1-11211111	1111111112	1213111112	1111111112	1111141161	621112
1122211121	2111211111	1111111112	1213111112	1211111112	1211241111	111111
1122211121	2111111111	1111111112	11111-----	--11111112	1111241111	111111
1122211121	4-11211131	1111111112	12111-----	--11111122	1111231111	111111
1123111121	4-11211111	1111211112	11111-----	--11111111	1111141111	111111
1122211121	3-11111111	1111111111	12111-----	--11112112	1111331111	111111
1123221121	2111211131	1111111112	11111-----	--11111111	1111121161	621112
1122221121	2111111111	1111111112	1112121121	1111111111	2113111131	311121
1122211121	4-11211111	1111111113	12211-----	--11111112	2111321151	521112
1112211121	4-11111111	1111111113	12111-----	--11111112	1111321111	111111
1111221111	--11111111	1111111111	1112121121	1111111113	1111111111	111332
1122211121	2211111111	1111111112	11111-----	--11111111	2111111111	111111
1122211121	2111112111	1111111113	12211-----	--11111112	1211224111	111111
1122211121	3-11211111	1111111113	12111-----	--11111112	?1113?1111	111111
1223111121	2111211111	1111111112	1113111111	1111111111	2111131131	311111
3122211121	2111211111	1112111112	1113121121	1111111111	2111151151	311111
1122211121	2111211111	1111111112	1213111111	1111111112	2111211132	312111
1112211121	2111211111	1111111112	1113111131	1111111111	21111?1111	111111
115?11223-	--11211121	1111111112	11111-----	--11111111	1111141161	621112
1123211121	2111211111	1111111111	2213111131	1311122112	1111321111	111111
1123111121	3-11211111	1111111111	12111-----	--11111112	1111111111	111111
1112211121	2111211111	1111111112	1113111111	1111111111	2311111111	111111
1122211121	3-11211111	1111111112	1213112211	2111111112	2111241132	312121
1123221121	2111221111	1111111113	22111-----	--11111113	1111321151	521111
137-------	----211111	1111111112	11111-----	--11111111	1111131161	621111
1122211121	3-11211111	1111111112	11111-----	--11111112	21112?2161	621112
1122211121	3-11121111	1111111112	1213111121	1111111112	1111211111	111111
1122211121	3-11211211	1111111112	1113111222	1111111111	2111151131	311111
1121111121	4-11211111	1111111111	11111-----	--2----113	11111?1151	521112
1122211121	2111212111	1212111112	1213111112	1213111112	1111221141	411111
1111221111	--11211111	1111111112	1113111222	1111111111	11111?1111	111111
1122211121	2211111111	1111111112	11111-----	--11111111	1111141111	111111
1143111121	3-11211121	1111111112	11111-----	--11111111	1111151131	311111
1123211121	2111211111	1111111112	1213111212	2111111112	2111241132	312121
112311213-	--11211121	1111111112	11111-----	--11111112	1111121111	111311
1143111121	3-11211111	1111111111	1213111112	1111111112	1111211112	112111
1122?11121	2111211111	1111111112	11111-----	--11111111	2111111151	521112
1132111121	4-11112111	1211111113	12111-----	--11111113	1111121111	111121
1122211121	2111211111	1111111112	1113111111	1111111111	2111151131	311111
1143111121	4-11211131	1111111112	11111-----	--11111111	1111121111	111111

Table 1. Morphological data matrix. Continued.

	10	20	30	40	50	60
Ceratognathus	111-411211	1411211111	1222131-11	13----44-1	3321131121	1211111321
Cerophytum	111-411211	1411111211	2111121-11	1111213311	221116----	1211121111
Cetonia	111-411211	1411121111	1222111-11	11214144-1	2221131132	1122112111
Chaetosoma	111-311211	1411112111	1221111-11	11114131-1	223116----	1111111113
Chalcodrya	111-111211	1411113111	1221112212	11113134-1	2211131111	1111111221
Chauliognathus	111-121211	1411111211	1121112111	12113131-1	221116----	1211121112
Chelonarium	221-411211	1411111211	1221131-11	1321213331	123116----	1112122111
Chiliotis	1121111212	1411113111	1121111-11	21112134-1	2231131111	1111111213
Chrysomela	111-411311	1411211111	1121112322	11114132-1	223116----	1111111211
Cicindela	111-111211	1411111111	1121112111	11112131-1	221116----	1211111112
Cis	111-411311	2411111111	1222112112	11112144-1	2231131111	3111111221
Clambus	121-411131	1422--1111	1122112211	11112144-1	2131141112	1121111213
Clinidium	1122111321	1411111111	1221111-11	11111131-1	213116----	1111111112
Clypastraea	211-411211	1411111111	1121111-11	11112134-2	2211131121	2111111421
Cneoglossa	211-411212	2411111?11	1122111-11	1111313311	321116----	1112122111
Coelus	111-411311	1411221111	1221112111	11114132-1	222116----	1111111222
Collops	111-411211	1411111111	1121111-12	1111313311	321216----	1111111221
Colon	111-411211	1411213111	1222111-12	11113134-1	2211221111	1111111212
Colydium	111-411211	1411221111	1223111-11	11113134-1	2211131111	1111111222
Copelatus	111-111111	1421111111	1223111-11	11114231-1	231116----	1111111212
Corticaria	1122111211	1411111111	1122112111	11113134-1	2231131111	1111111111
Creophilus	1123411312	1411111111	1121112111	12114134-1	2211?11111	1211111113
Crioceris	1122111211	2411121111	1121212311	11113131-1	221116----	1111111222
Cryptophagus	111-411212	1411211111	1121111-11	11113134-1	2111131111	1111111223
Cucujus	1123411212	1411211111	1221111-11	12112131-1	221116----	1111111222
Cupes	1122111221	1411111111	1121121-11	11113131-1	221116----	1111111112
Curculio	111-111311	1421111111	1222111-11	23---134-2	2311131112	1111211112
Cyclaxyra	111-311211	1421111111	1223111-11	11113134-1	1231131111	1111111321
Cylas	111-411311	1411111111	1222111-11	23---144-1	221115111-	1111211211
Cymatodera	111-411311	2411213111	1221112111	1111413331	221116----	1111111112
Cyphon	121-411212	1411111111	1122111-12	11112131-1	221116----	1211111112
Dacne	111-413211	1411112111	1223111-11	11113134-1	2231131111	1111111212
Dascillocyphon	111-411211	1411111?11	1221111-11	11113132-1	221116----	1111111121
Dascillus	111-111311	1411111211	1121111-11	1111213311	211116----	1211111112
Declinia	1121111111	2411211111	1223112111	11112134-1	2231112121	1111111111
Delphastus	111-411111	1421111111	1122111-11	11114154-1	221115111-	1111111111
Dendroctonus	111-421311	2411211111	1222111-11	13---144-2	2221121112	1111111113
Dermestes	121-411211	1411121211	1121112112	11114134-1	3231131222	1111111112
Derodontus	111-111211	1211111111	1121111-11	11112134-1	2231131111	1111111112
Derolathrus	1122111211	1411113111	1221111-11	11112134-1	1131141112	1111111212
Diabrotica	111-411211	1411111111	1111212111	11112131-1	221116----	1111111411
Diaperis	111-311211	1411222112	1221112212	11112135-1	222116----	3111111222
Dictyoptera	111-411211	1411111211	2111121-11	1111213311	222116----	1211121111
Dineutus	111-111211	1412--1121	1221112111	11113262-1	113216----	1111111222
Dioedus	111-311211	1411211111	1222112211	11112134-1	2211141111	1111111321
Diphyllostoma	1121211211	1411111111	1222132111	13112144-1	2211131121	1111111111
Diplocoelus	111-311212	1411114111	1223111-11	11213134-1	2211131111	1111111211
Dipsaconia	111-311311	1411221111	1121112311	11112134-1	2231111111	1111111222
Discoloma	111-411211	1411211111	1122112111	11212144-1	222115111-	1111111311
Distenia	111-411311	1411221111	2121222312	11113131-1	331116----	1111111121
Ditylus	111-211211	1411211111	1121111-11	11113131-1	221116----	1111111221
Drilus	111-411211	1411111?11	1121121-11	1111213311	221116----	1211111112
Dynastes	111-411211	1411221111	1221111-11	11211144-1	2111131132	1111111211
Dytiscus	111-111211	1411111111	1221112111	11114231-1	221116----	1111111221
Elacatis	111-411211	1411111111	1222111-11	11113134-1	2211131111	1111111222
Ellychnia	211-411211	1411211211	1111121-11	11112131-1	221116----	1211121111
Endecatomus	121-421311	1411111211	1221112111	11112134-1	??21131111	1111111212
Endomychus	111-311211	1411211111	1121112212	11112134-1	2211131111	1111111212
Enneboeus	111-411211	1411212111	1221112111	11113134-1	2211131111	1111111222
Eoxenos	111-111111	2411111111	1121111-11	13---18311	211116----	1211121111
Epicauta	1123121211	2411111111	1121112112	11114131-1	221116----	1111112123
Epilachna	111-411211	1411211111	1122111-12	11113134-1	2211131112	1211111223

70	80	90	100	110	120	130
1112311214	4121115211	1121113112	1111111112	1221111114	1112421111	1213222122
1112321111	4121311213	1331111111	115115----	-131211114	1112423121	1441121331
1111111113	4121112241	2351112112	1221111121	1121211114	1112421111	1213212222
1112211111	4121212212	1131113111	1121111121	1121111114	1112422111	31-1112112
1111112112	3121311212	2131212111	1123111111	1221111314	1112421111	1213311121
11123213--	4121211212	3331112121	1151112211	1111111114	1113421111	31----2211
1112321113	4121313213	2331122112	1251112211	1131221114	1122422112	1211111111
1111111111	4121111211	2131112112	1112121121	1121211115	1112422211	1411121121
1112111111	4121111211	1231112111	1353111121	1221211114	1112422111	1212221112
1112321141	3121115211	1241112111	112315----	-111111112	1112212111	1223212213
1111311111	4121115211	1121112111	1253111111	1211111114	1112422111	1221111113
2111111151	3121111211	1121122111	1211312111	1211111114	1112421111	31-1212112
1152321151	4121113221	2341212232	1153111121	1121114313	1112213111	1211221322
1112321424	-121112211	2131112111	1353112221	1121211115	2122422121	1213221331
1112321132	4121113212	2131112111	1151212211	1121211114	1112422111	1111112212
1111112111	2121212211	2321112112	1123311111	1321111214	1112422111	1221211122
1112112111	4121211211	1331112111	1151111111	1121211114	1113421111	31-1212212
1111121111	3121111211	2121112111	1233111111	1111211315	1122421111	31-1212212
1111112112	3121211211	2321112112	1123111121	1321111115	1112423111	1422211333
1112221141	3121111212	1141112112	1253311121	1431111112	1112212111	1411131313
1111111113	4121111331	1251112111	1143111112	1121111115	1112422111	1212221331
1112121111	4121113211	2121112112	1221111111	1111111114	1112422111	31-1212212
1112111111	4121111211	1131112112	115315----	-111111115	1112422111	31-2112212
1111111111	2121111211	2131112111	1211111123	3221211314	?112422111	1411221122
1111211111	4121213212	1131112111	1251111121	1121211114	1112423111	1211211131
1112321111	4121224221	2111113111	1153141111	1121211212	1122213131	1211211111
1112323414	4231115331	3321213121	235315----	-111211115	1112422111	22-3212333
1111112112	4121111211	2131112111	1122111121	1421111114	1112422111	1112221111
1112313414	4231111341	2331213121	212315----	-111111115	1112422111	22-2112222
1112211112	4121111213	1121112111	115215----	-111111115	1112422111	1222222231
1112311111	4122111211	2121122112	1211111111	1221111114	1112421111	1242221111
1111111111	3121111211	1131112111	1211111121	1221211314	1112422211	1413221121
1111112112	4121113211	2131112111	1122111121	1221111114	1112422111	1421221112
1112121131	4121114211	2111112111	1211111121	1131211114	1112422111	1111121111
1151111112	1121211222	2111121112	111111?111	1131211111	1112321221	1211211111
1112211111	4121111211	2311111111	1153111111	1321211114	1322422131	1111221122
1112312414	4232111211	1131212122	133315----	-111111115	1112421111	21-2111322
1112322111	3121112211	3131112111	1221111121	1111211214	1112421111	31-1112222
1111111111	2121111211	2121112111	1211211113	1121111114	1112322111	1313212112
1111111112	3122111211	2111112111	111315----	-111111115	1112423111	1212211323
1111111111	4122111211	2121112111	1153111121	1121211114	1112422111	1111112212
1111112112	4121211211	2321113111	1121111121	1221211115	1112421111	1222221123
1112321112	4121215212	1331111111	1151111111	1131211214	1113421111	31-1112211
11123213--	4121211211	1241112212	1113111121	1431111112	1112211111	31-1211322
1111211111	4121111211	2331113111	1223121121	1121111115	1112422111	1422221133
1112321414	4121115211	2121112111	1111111111	1111111114	1112422111	1213222112
1111112111	4121112211	2131112111	1141111122	1321211114	1112422111	1411221113
1111112112	3121112211	2321112111	1223111112	1221211114	1112422111	1213311121
1111111112	4121111211	3331112111	1153211111	2431211115	1112423111	1413221333
1111212111	4121111212	1121113111	112315----	-111111115	1112422111	31-1211321
1111111111	4121213212	1121113111	122115----	-111111114	1112422111	31-1112222
1112321113	4121111211	2221111111	1151121111	1142213214	1113422111	31-1112211
1111111113	4121111211	3111112111	1221111121	1411111114	1112421111	22-3211112
1112321141	3121111211	1141112111	1213111111	1431211112	1112211111	1221131212
1111211111	4121111211	1131112111	1223121123	1131111115	1112423111	22-2212222
1112121111	4121313213	3331211111	1251212221	1121211314	1113421111	31-1212211
1111111111	4121111211	1131112111	1213111112	1421211115	1112421111	31-1112222
1111112112	4121211211	2121112111	1211111121	1331213314	1112422111	1212221331
1111112112	2121311211	2321112111	1213111121	1221211114	1112421111	1413221313
11123215--	--4?1155--	-----11131	135315----	-111111115	1111111111	31----2213
1111112111	4121112212	2221212111	115115----	-111111115	1112422111	31-1212212
1112121112	4121311211	2121112111	1152311121	1211111114	1112422111	1111211121

Table 1. Morphological data matrix. Continued.

	140	150	160	170	180	190
Ceratognathus	1122-13111	3121121211	111-211211	122111231-	1131112221	2337113122
Cerophytum	1322-12131	1122111211	1125211211	1112222332	2131112212	4322143223
Cetonia	1122-14131	3121111222	111-211511	122111231-	1131112222	4237113121
Chaetosoma	1121211112	2121121212	111-211211	121111231-	1122112211	4334113122
Chalcodrya	1121214112	4121131231	111-211211	111111231-	1141111212	2335113222
Chauliognathus	1121211111	1121141231	111-211511	111111231-	14-2112311	2331113122
Chelonarium	1121211121	1122411211	111-211111	3121112332	1131112223	2325143122
Chiliotis	1222-11131	1122121211	111-221211	3111112322	1131122213	7326113222
Chrysomela	1121221221	1121111211	111-211111	3111112322	1141112212	2332121222
Cicindela	1212--4221	3121121221	111-211221	122111231-	1142422212	3315111121
Cis	1122-23121	3122111211	111-211221	121111231-	1121122211	4332113223
Clambus	1121211111	1121111211	211-211511	112111231-	2321112221	3311453322
Clinidium	1212--4131	3121111211	1128212121	121112231-	1141122213	4316113123
Clypastraea	1122-14311	3121121221	111-211211	121111231-	1131122213	7332113322
Cneoglossa	1121211111	1121111211	1124111111	211111231-	1222111231	2331113122
Coelus	1122-24221	3121111211	111-211111	122111231-	1141112212	2336113321
Collops	1121211111	1221121211	111-211221	111111231-	1322111331	2331112121
Colon	1121211312	2121111211	211-211211	122111231-	2141112231	2333113323
Colydium	1122-24131	3122121211	1125111211	122111231-	114112-212	7335113223
Copelatus	1112--1321	1221121211	1132211211	2111112322	1131122211	4314213121
Corticaria	1122-13311	3121121211	111-211211	121111231-	1131122212	7334113222
Creophilus	1121211111	1121111223	111-211511	111111231-	1332112311	2321113322
Crioceris	1122-14311	4121121211	1124111211	122111231-	1131122212	4335113122
Cryptophagus	1122-11132	1122121211	1124221211	2111112321	1131122213	7336113222
Cucujus	1121211122	1121121211	111-211111	1111112321	1131112213	4314113122
Cupes	2111--1121	1122131?41	1225111111	1111111321	1312111311	3211111122
Curculio	1122-23311	6122131211	2124211211	112111231-	1131122212	7333113321
Cyclaxyra	1121211131	1122121211	111-211311	311211231-	1141112213	2334143323
Cylas	1122-14311	4121121211	2124211521	121112231-	1132122211	7332113223
Cymatodera	1122-14311	3122141211	1124211211	121111231-	1122122211	7335113123
Cyphon	1121211111	1122111211	211-211211	3111111321	1111112212	4313111221
Dacne	1122-24131	3121121211	1124111111	111211231-	1141122213	7326113122
Dascillocyphon	1121214312	3121151211	211-211211	111211231-	1141111211	2333123222
Dascillus	1121211111	1122121211	111-211111	1111111322	2111111211	2226111121
Declinia	2121111121	1122111211	1124111111	3111111321	1111112212	3316112122
Delphastus	1122-11231	2122111211	111-211411	3121112321	1141122213	4334143223
Dendroctonus	1122-14311	6121131211	1124211511	122111231-	1131122213	7337113122
Dermestes	1122-11212	1121121211	111-211511	112111231-	2141312212	2336123122
Derodontus	1121213112	3122121211	1223111211	121111231-	1122112211	1313112122
Derolathrus	1122-11111	113---1211	111-21122-	111111231-	1121122212	7333111323
Diabrotica	1121212311	2121111211	111-211211	111111231-	1121111211	2335111122
Diaperis	1122-24221	3222111211	1125111211	122111231-	2141112212	4335113122
Dictyoptera	1121211111	1121141231	1224211111	111111231-	14-2111431	2331113122
Dineutus	1111--1221	2121121221	1134211211	311112131-	1111122232	4215113221
Dioedus	1122-24231	3122121211	1124211111	122111231-	1131112212	2335113222
Diphyllostoma	1121213111	3121121?11	111-211111	122111231-	1121111221	2338113322
Diplocoelus	1122-24322	3121131211	1124111111	211111231-	1131112212	2335123222
Dipsaconia	1122-24121	3122121211	1124111111	111211231-	1141111212	2336113122
Discoloma	1122-24131	3122121211	111-211121	121111231-	1131122213	533712332-
Distenia	1122-11311	2122122231	111-211211	211111231-	1141122213	4335111123
Ditylus	1121211212	1121131211	111-211511	211111231-	1322111311	2331113222
Drilus	1121211111	1121111211	111-211111	111111231-	1332111331	2331113122
Dynastes	1122-14111	3121111211	111-211211	122111231-	1121122221	4327113122
Dytiscus	1112--1121	1221111211	1133211211	3111112321	1121122212	1214213121
Elacatis	1122-23211	3121111211	111-211211	121111231-	1131122212	7335113322
Ellychnia	1121211111	1121121231	111-211121	111111231-	1332111431	3331113222
Endecatomus	1122-22211	2121121211	111-211111	211111231-	1141111232	4326123222
Endomychus	1122-11222	1121121211	111-211211	211211231-	1131112213	2324113322
Enneboeus	1121224222	3121121211	111-211111	112211231-	1141112212	2336113222
Eoxenos	113-------	111---12--	--------2-	11112-111-	14-212-1--	-1---11122
Epicauta	1121211111	1121121232	111-211512	111111231-	1322112311	3231113222
Epilachna	1122-11222	2122111211	111-211111	3?21112321	1131122212	4332141122

200	210	220	230	240	250	260
1211311114	-123111211	232233---4	-212311312	12111433--	11121112-1	2112111111
2211311114	-113123621	2112133222	1112231312	12111323--	1132111111	1111111111
1211211114	-223111211	231233---4	-212311312	23111433--	11321112-2	2112111111
1211211114	-121121612	2122132323	2113311322	23111413--	1232111111	1111111111
1211312114	-123134622	2122132314	-112231312	2212141113	1112111111	1111111131
1221111114	-11312162?	2112132114	-1?2231312	23111333--	11321113-1	111113-311
1211311111	1113211621	2112133224	-1?2231311	11111213--	11121113-3	211113-311
1211322114	-322121612	232233---4	-21232134-	13111413--	2233211111	1111111121
1211232114	-322134612	2122133223	2122111311	23111433--	11121113-1	111113-311
1211112113	111322211-	1--131---4	-111113312	1221131123	1112112111	1111111111
1211212114	-323134612	241233---4	-214211312	25121533--	21331113-1	111113-361
2212111111	2123222411	1--133---4	-3-4433321	15111533--	2133311111	1211111161
2211232114	-113122---	----------	----------	----------	-----122-1	1111111111
1211232114	-323134611	24-233---4	-3-3331311	25111533--	21332113-1	1111121261
1221212113	1113211611	2112133222	1112211311	12111313--	1112111111	1211121111
1222312114	-223134---	----------	----------	----------	-----11112	1113111131
2211121114	-123134312	2112132224	-214111311	23111413--	21131113-1	111113-311
1211212114	-123134611	24--33---4	-213311331	15111533--	2132111111	1211111111
1211212114	-12113461?	2122131214	-112211312	2212131113	1112111112	2112111161
2222111224	-12311211-	1--131---4	-111113231	1221233113	1112111111	1111111111
1211232114	-322134611	24-233---4	-213321312	25121533--	2133211111	1111111171
1211212114	-123132511	2112133214	-3?2311332	12211433--	12221112-1	1211111111
1211312114	-122134612	2122131222	2222121311	24111433--	11321113-1	1111121211
1211322114	-32212162?	2122133124	-122231312	11111413--	2212111111	1111111121
2211221114	-12112362?	2122132112	1112231311	21111313--	1112111111	1111111122
2111211111	111321141-	1--121---1	-111113211	2131112111	1111111111	1111111111
1211132114	-322134612	2122132213	2112211311	14111433--	11321113-1	111413-311
1211312114	-222123612	2132132214	-112311322	11111433--	1213111111	1111111121
2211112114	-223134611	2212131124	-213311322	14111533--	11321113-1	111113-311
1211212114	-122123612	2132132223	2113111322	2211141112	1112111111	1111111111
2211311112	112322332?	2122131322	21?3132312	22111413--	1222111111	1111111111
1211222114	-221123612	2122131312	1112131311	2212131113	1212111?2	1111111111
1211212114	-121123612	2132132222	1113111311	221?142123	1232111111	1113111112
1211311113	111312361?	2122132112	21?2212311	1111121113	1111111111	1111113111
1211311111	1123222321	2122131213	1111132312	22111213--	1222111111	1111111111
2211232114	-323134622	232233---4	-212331312	26111533--	21332113-1	111113-371
1211212114	-122134611	2112133213	1213311311	14111533--	21131113-2	211213-311
1211212112	112322361?	2122131113	2111111312	2121121113	1112111111	1111111111
2211211113	132312261?	2122132222	22?3211321	1211141112	2212111111	1111111111
2211232114	-323134621	24--33---4	-3-442134-	16111533--	2133311111	1111111171
1211322114	-123134611	2132132222	2122111322	24111413--	11321112-1	1111121311
1211312114	-123123611	2122131222	3112111311	2311131111	1132111111	1311111131
1221212114	-113111621	2112133213	1112231311	11111313--	1112111111	1111111111
2212111224	-11311211-	1--121---2	-21111324-	1221133123	11121113-2	1111111111
2211212114	-223134621	233233---4	-114131311	2511153123	2233111112	2112111131
1221212114	-123111211	232233---3	2112311312	23111433--	11121112-1	2111111111
1211212114	-122134621	2122132112	1113131312	22121413--	1212111111	1111111111
1211312114	-121134622	2132131114	-112131312	2212131113	1112111111	1111111131
2211232114	-323134611	24--33---4	-32442134-	16111533--	22331113-1	111113-371
1211222114	-123134612	2132132214	-122121312	2111131123	1112111111	1121111111
1221211114	-121134621	2112133222	3112231311	1211141113	1112111111	1111111131
1221311113	1113111621	2112133222	2112231312	14111433--	11121113-1	111113-311
1211311114	-123111211	232233---4	-2?2211312	23111433--	11321112-2	1313111111
2222111224	-12312211-	1--131---4	-11111324-	1221231113	1112111111	1211111111
1211212114	-121134611	2122132214	-114111322	1312?333--	1112111111	1111111131
1221311113	1113111621	2122133112	1111231312	1111133111	11121112-1	1111111111
1211311114	-123123311	2112132222	3113121312	1111131113	11121112-1	1111111112
1211232114	-322134612	2122132112	11123?1312	25121533--	12321113-1	111113-361
1211312114	-123134612	2112131114	-112231322	1212131113	1112111111	1211111131
1211111314	-1131346--	1--213----	---1--13--	1-111533--	21331113-1	111113-311
1221321114	-12113461?	231233---4	-113121312	23111433--	1132111111	1111111131
1211232114	-322123612	232233---4	-212311312	24111533--	1213111111	1111111161

Table 1. Morphological data matrix. Continued.

	270	280	290	300	310	320
Ceratognathus	1-11112811	2122121111	2221111111	2231111111	1111212111	1111-12111
Cerophytum	611312-841	1122121111	1111111122	2211111111	1111111311	1121-11211
Cetonia	1-11112751	1112121111	1221112111	114-222111	1111211-34	1111-11111
Chaetosoma	1-11112811	1112131111	2221111312	224-111111	1111313-11	2111-12111
Chalcodrya	1-11113841	1133121111	2211111122	224-111111	1111213-12	241--11111
Chauliognathus	6111122211	1133221111	1111121111	1131311111	1121111111	1111-22111
Chelonarium	323212-831	1132131311	2222211111	224-111111	2111211211	1121-11111
Chiliotis	1-1112-811	1132131111	2222111122	224-311111	1121313--4	2111-12111
Chrysomela	313112-811	1132131111	2211111122	224-441112	1111113--4	241--12111
Cicindela	1-1112-331	1122122111	1111111112	1211111111	1124111111	3311----11
Cis	1-1112-811	1332131111	2221111122	224-111111	1111213--4	2214111111
Clambus	1-1112-811	2122121312	2222211111	2232441111	1121311211	1114-21111
Clinidium	1--112-631	1112113111	1111111111	2231111111	1124311-21	3311----11
Clypastraea	211112-711	1232131111	1222111111	114-331111	1111113-11	2114111111
Cneoglossa	1-1212-831	1132121111	1221111111	224-111111	1111111211	1221-11131
Coelus	1-1112-831	2122121111	1111111122	224-111111	1111213-11	2114111111
Collops	1-1122-711	1133231111	1221211111	114-111111	1121413--4	241--11111
Colon	1-1112-813	1112131111	1222211211	224-411111	2111411311	1111-22111
Colydium	1-11122811	1122121111	2211111122	224-111111	1111213-12	241--11111
Copelatus	1-1112-631	2112222111	1222211111	2231311112	1124111-34	3311----11
Corticaria	1-1112-811	1132141111	1221111122	224-111111	1111413--4	241--12111
Creophilus	1-11122711	2133231121	1111111311	1131333111	1121113-11	3314111111
Crioceris	513112-811	1332141112	2211111122	224-311111	1111313--4	241--22111
Cryptophagus	1-1112-811	1332141111	2222211122	224-331111	1111313--4	2111-12112
Cucujus	1-11122811	1332121111	2111111122	224-133111	1111321--4	2111-12112
Cupes	611112-811	1113121112	2111111112	2211111111	1211111313	142--11111
Curculio	513212-822	2132131111	2222111112	224-311111	1111313--4	24---12111
Cyclaxyra	1-1112-811	1232131111	1222111122	224-311111	1121313--4	241--12111
Cylas	513112-822	1112121111	1221111122	224-111111	1121313--4	241--12121
Cymatodera	421212-711	1132121111	1111111111	114-111111	1121311-34	2411-12141
Cyphon	611212-811	213212111?	2222211122	224-311111	1211411-34	141--11111
Dacne	1-11112821	1132121111	2211111122	224-311111	1111313-13	2111-11111
Dascillocyphon	321112-711	1232121111	2211111111	114-333111	2111311111	241--14111
Dascillus	4211122811	1133121111	1111111111	2221222111	1111111311	1111-11131
Declinia	411112-831	1112121111	2221111122	224-111111	1111211211	1121-11111
Delphastus	211112-821	2132131311	1221111122	224-441111	1111311111	241--22111
Dendroctonus	513112-822	1332131111	2222111111	224-311111	1111313--4	241--12111
Dermestes	1-11122811	1122131111	1111111122	1211111111	1111211321	1221-11111
Derodontus	1-11122812	1112121211	2221111122	2211111111	2111112311	1111-11211
Derolathrus	1-1112-811	1332131111	?222211122	2211111111	2111311211	141--11111
Diabrotica	513212-811	1332131111	1222111122	224-311111	1111313--4	241--11121
Diaperis	1-11112831	1222121111	2222111122	224-111111	1113213--4	2114111111
Dictyoptera	4211122211	1133221111	1111111111	1111111111	1111211211	1111-11111
Dineutus	1-1112-331	1132222111	1111111111	1131333111	1114111-32	141--11111
Dioedus	1-11112831	1132121111	1221111122	224-111111	1111213--4	2114111111
Diphyllostoma	1-11112311	2113212111	222111111?	1?11111111	1111212211	1121-21111
Diplocoelus	322112-811	2132131211	2111111111	224-311111	2111221--4	241--14111
Dipsaconia	1-11112831	1122121111	2211111122	224-111111	2111213-12	2114111111
Discoloma	1-11112811	1232141111	2221111122	224-441111	1111513--4	241--11111
Distenia	513112-811	1132121111	2211111122	224-111111	2111313--4	241--11111
Ditylus	611112-821	1133121111	1111111122	224-111111	1121223-12	241--21111
Drilus	411112-511	1133221111	1111111111	1111111111	1111111111	1111-11111
Dynastes	1-11113351	2113112111	1111111111	114-222111	1111313-13	1111-11111
Dytiscus	1-1112-631	2132122111	1111111111	2231333112	1124113--4	1321-12111
Elacatis	1-1212-811	1132131111	1221111122	224-111121	2121213--4	2114111111
Ellychnia	611112-311	1133221111	1111111111	111?222111	1111211321	1121-11111
Endecatomus	1-11112813	1132131111	1111111122	2211111111	2111211-34	1222-12111
Endomychus	213112-711	1132141111	2221111111	114-441111	1111313-11	241--22111
Enneboeus	1-1112-821	1132131111	1221111122	224-111111	2111313--4	2114111111
Eoxenos	1-1112-111	1131221111	1111111111	114-111111	1111111111	45------11
Epicauta	1-11312711	2133221111	1111111111	114-111111	1111313-12	2114111111
Epilachna	213312-721	2132131311	2222111111	114-441111	1111311311	2111-12111

330	340	350	360	370	380	390
1221111-11	1122221111	1121112112	1111221319	--21111114	2111413111	1112321121
1311112112	4133212142	1111111111	111113-1-8	--11211114	2121431112	12111113-1
4221111-12	2112112111	14-1112112	1111221219	--21111113	2112--4-11	1112215121
1111113112	3133212122	1111111111	1121221314	1111111114	2111421111	11111133-1
3111412112	3132223122	1121111111	11112211-4	1121111114	2111411111	1111223221
1111111-22	11121?1111	1111111111	111113-418	--13211114	2111211111	11111133-2
1221112122	4133211122	14-1111121	1111221218	--21111114	1111421111	11113213-1
1121112112	4122211122	1111111211	11111121-8	--11111114	2121211111	1112215111
1121111-12	4121121211	24-1111112	1111321323	1121111114	1121411111	11114113-1
1121121-12	11321?2121	14-1112113	11212211-3	1113211223	2113----12	11111133-1
1111113112	3132212122	1111111111	111113-416	1121111115	1122--1-11	11112113-1
1111111-11	1123111132	111?111111	11112111-9	--21111114	2111421111	1111115111
1111121-22	4121212121	2421111111	11211211-9	--13211213	2111413111	11111133-1
1121111-12	3122212122	1111111151	1111122627	1111211114	2131411111	1111323111
1211112112	3132212122	1111111111	11112211-4	3111111114	2111421111	11113213-2
1211312112	3133221122	2321111111	1111321217	1121111114	2111-13111	1111223111
1121113112	3133222122	1111111111	11113211-4	2111111114	2111221111	11112253-1
1221111-12	1121112111	2111??????	??????????	??????????	??????????	??????????
1111113112	31332?3122	1121111111	1111111514	1111111114	2111411111	1111225121
1111321-12	2132111111	14-1111211	11212211-3	2113211113	2213----12	11111113-1
1321111-12	1112221111	14-1111111	11111211-5	1121111114	2121411111	1111221111
1121111-12	1112122111	1111111111	11113111-5	1113211413	2111111211	11111133-1
1121112112	4122211121	14-1111112	1111321213	1?21111114	1111121111	11114213-1
1121113112	1122212122	1111111111	11111121-7	3?12211114	2111411111	11122?5111
1121313112	31332?2112	1111121111	11112111-3	1?11211114	3121111111	1112223112
1211112112	4133211132	1111??????	??????????	??????????	??????????	??????????
1211112112	3133212112	1121112112	1111321317	??21212116	1122--1-11	11112133-1
1321112112	3132212122	1111111111	1121111514	1113211114	2111421111	11113233-1
1221112112	4121211111	1111111112	1111321317	1121212116	1112--1-11	11112153-1
1211111-12	3133222122	1111111121	1121121316	1111111114	2111411111	11111133-1
1211111-22	4133211122	1111111111	11212211-6	3121211111	3111--2-11	1112111111
1311112112	3131211112	1421111112	11112211-3	1111111114	2121421111	1112223111
1221112112	3123212132	1111??????	??????????	??????????	??????????	??????????
1211111-12	1112111111	14-1112112	11111211-9	--22121114	2111433111	1112215121
1121111-12	2122212122	1112??????	??????????	??????????	??????????	??????????
1111111-22	1112121111	14-1111111	11111211-6	1111111114	1131431111	1111111111
1221111-12	4112111111	14-1112112	1111321319	--21212116	1122--1-11	11112133-1
1211112112	31332?2112	2121111131	1111221313	1?21112114	2121111111	11113113-2
1211112112	11221?2112	1111111141	11111111-3	1?11111114	2121411111	1112215112
1111112112	1131111121	1111111111	11111121-9	--21111114	1111431111	1111215111
1121112112	4131211111	14-1111112	1121221319	--21111115	1112--1-11	11114233-1
3211112112	3133212122	24-1112111	11112211-9	--21111114	2211413111	1111223121
1111112112	4133211222	1121111111	111113-1-9	--13211115	2132--3-12	22211113-1
1111111-12	1121221121	14-1111111	11213211-3	3113211413	3113----12	11311113-1
1211112112	4111221121	14-1111111	11112211-9	--21111114	2111413211	1111321121
1121??????	??????????	??????????	??????????	??????????	??????????	??????????
1211112112	3132212122	1111111111	11111121-3	1112211114	2111421111	1112225111
1211112112	3133223122	1111111111	1111211214	1121111114	1111421111	1111213121
1111111-12	4112111111	14--221221	12111111-6	1121111115	3122--2-11	1111321111
1221413112	3133212122	1111111111	212113-428	--21111114	1121??1111	11111213-1
1111412112	3133222122	1111111111	1111221719	--11111114	2111411111	1111225121
1211111-11	1122121111	1111111213	111113-1-8	--13211114	2111421112	11311113-1
2221111-12	31121?1111	14-1112112	1111221219	--21111113	2112--4-11	1112115122
1111321-12	4132111111	14-1111111	11113211-3	1113211213	3113----12	11311113-1
1211112112	3133223122	1111111111	11112111-4	1111111114	2111421111	1111325121
1121112112	2133221112	1111111111	212113-628	--13211114	2111223112	11311113-2
1211112212	4132212122	1121112112	111113-418	--21212114	1111231111	1111213212
1121111-12	1111111111	1211211242	1111122515	1111211114	3131431111	11113233-1
1212112112	3132213122	1111111111	11112111-4	1121111114	2111411111	1111223121
1111111-11	13--------	---1221211	111113-1-4	1113211117	--------22	12111113-1
1111111-12	21121?1111	1111111111	11113111-8	--21111114	2111421111	11111153-1
1111311-12	3112111111	1311211112	11112211-6	1121211114	1131431111	11114253-1

Table 1. Morphological data matrix. Continued.

	400	410	420	430	440	450
Ceratognathus	111121-311	111211213-	---1111111	14---22232	-111113-11	2111111111
Cerophytum	1111---322	--13251142	1111111121	1111123212	-213113-2-	1211111111
Cetonia	111121-211	2212151122	1211111111	14---23232	-112113-12	2111111121
Chaetosoma	1211---321	1112251112	1111121111	1311?22211	111112132-	1111111122
Chalcodrya	111121-311	2112151112	1111121111	1311122231	1113121211	1111111111
Chauliognathus	1?11---221	12132411--	---1131111	14---23111	1213122-2-	1211111111
Chelonarium	1111---341	113321111-	---1111121	1211122212	-113232-11	1111111111
Chiliotis	1111115311	1112151132	1111121111	1111133221	1112121111	1111111121
Chrysomela	1111---321	1112251112	1111121121	14---23212	-112113-11	1211111122
Cicindela	1111---111	221222111-	---1121131	-211122112	-213132-2-	1121111121
Cis	2111---311	1112151112	1121131111	14---23111	111312122-	1111111111
Clambus	1111111311	1113151121	1111131121	1211123231	1113121111	1111111111
Clinidium	1111---321	12122611--	---1111111	1121?33112	-21312132-	1111112121
Clypastraea	1111113122	--11251112	1111121121	1111123121	111213132-	1311111131
Cneoglossa	1111---311	111211112-	---1111111	2221121312	-113221З??	1111111121
Coelus	111121-311	1112151122	1111121111	1311122131	111312132?	1111111121
Collops	3111---321	1112251122	1111121121	1311123111	1113221211	1111111111
Colon	??????????	??????????	?????-???-	??????????	??????????	??????????
Colydium	111121-311	1112151122	1211121111	1211122221	1112121111	1111111121
Copelatus	1111---311	111222113-	---1111121	14---23312	-213131311	1111111121
Corticaria	1111112311	1112151112	1111121121	1211123221	111212132-	1111111111
Creophilus	1111---311	1113251112	1111111121	1311123111	1213133-2-	111111112?
Crioceris	1111---221	111125111?	???1111111	1311133212	-111121111	1111111111
Cryptophagus	1111115311	2112151132	1111121111	1311133121	1112121111	1111111121
Cucujus	1111111311	1113151132	?11112-111	1211122221	1112131211	1111111121
Cupes	??????????	??????????	??????????	??????????	??????????	??????????
Curculio	1111---321	1112251112	1112121122	1311123311	1112113-11	1111111111
Cyclaxyra	1311---121	1111251112	1111131111	1311123212	-112131111	1111111111
Cylas	1111---321	1113251112	1112121121	14---23211	1111113-12	1111111111
Cymatodera	1111---221	1112251112	?111121121	1311122211	111113132-	1111111122
Cyphon	1111118311	111311111-	---1111121	2211121341	1113121111	2111111121
Dacne	1111112311	1112151112	1211121121	1211122231	1112121111	1111111121
Dascillocyphon	??????????	??????????	??????????	??????????	??????????	??????????
Dascillus	1111119311	111211213-	---1131111	1321123342	-112121211	1111111121
Declinia	??????????	??????????	??????????	??????????	??????????	??????????
Delphastus	111121-322	--12251112	2111121121	1311122111	111212122-	1111111111
Dendroctonus	1111---321	1113251112	1112121122	1211122211	1112113-12	1111111111
Dermestes	2111---311	111213211-	---1121111	1311122211	1113121111	1111111121
Derodontus	1111112311	211313211-	---1121111	1211122221	1113221111	1111111121
Derolathrus	1111111311	111213123-	---1121121	1311122221	1113121111	1111111121
Diabrotica	1211---321	1113251112	1111121121	1111123112	-113113-12	1111111121
Diaperis	111121-311	1112151112	1111121111	14---22131	111312122-	1111111121
Dictyoptera	1111---332	--43251132	1111111121	14---21212	-211113-2-	1111111121
Dineutus	1111---111	121221111-	---1111121	14---11112	-213132-2-	1111111121
Dioedus	111121-311	1112151122	1111121111	14---23131	111312132-	1111111121
Diphyllostoma	??????????	??????????	??????????	??????????	??????????	??????????
Diplocoelus	1111126311	1113151112	1211121111	1211123221	1113221112	1111111121
Dipsaconia	111121-311	2113151121	1111121111	14---23131	1112121211	1111121121
Discoloma	1111112311	1112151112	1112121121	1211121221	1111121211	1112111121
Distenia	1111---311	1112151112	1111121111	1211123212	-113113-13	1112111311
Ditylus	111121-311	1112151111	1211121111	1311122231	1113121211	1111121211
Drilus	1111---321	111322111-	---1111121	14---22211	1213123-2-	1111111121
Dynastes	111121-211	2112151122	1211111111	14---22232	-112113-12	2111111111
Dytiscus	1111---111	111322111-	---1111121	14---21312	-213122-11	1111111121
Elacatis	111121-311	1113151122	1211121111	1111122231	111212112-	1111111111
Ellychnia	1111---321	111322111-	---1121121	14---22112	-211113-2-	1111111121
Endecatomus	1111114221	111223211-	---1121111	1211123212	-113113-11	1111111111
Endomychus	1121---321	2112251122	1111121121	1211123111	1112121111	1111111121
Enneboeus	111121-311	1113151122	1111121111	1311121121	1111121211	1111111121
Eoxenos	1111---322	----261---	---213--31	14---23312	---3123-2-	111111?121
Epicauta	1111---121	1111251112	1111121121	14---22212	-11313132-	1111111121
Epilachna	1111---322	--12251112	1111121121	14---23111	1113121211	1111211122

460	470	480	490	500	510	
1122211221	2111212121	1111111112	11111-----	--11111131	1111141161	621111
1222211121	2111211111	1111111112	11111-----	--11111111	1111131151	521111
1123212121	1-11211131	1111111112	11111-----	--11111111	1111121161	621112
3122211121	3-11211111	1111111113	1223111112	1111111112	11112?1131	111111
1122211121	2111211211	1111111112	11111-----	--11111111	1211144111	111111
1122211121	1-11211111	1111111112	11111-----	--11111112	1111141151	521112
1123211121	3-11221111	1111111112	11111-----	--11111212	1111121152	522112
1121211121	2111211111	1111111112	1213111121	1111111111	2111251132	312111
1122211122	3-21211111	1111111112	11111-----	--11111111	1111131111	111111
1112221111	--11212111	1111111111	11111-----	--11111111	1111151111	111111
1122211121	2111211111	1111111113	1213111112	1111111112	1111251111	111111
1122211121	2211111111	1111111112	11111-----	--11111111	1111141111	1112-1
2113221121	4-11111211	1111111112	11111-----	--11111111	2111111111	111111
1122211121	3-11211111	1111111112	12111-----	--11111112	2111251111	111111
2121221121	3-11211111	1111111112	12111-----	--11111112	1221334151	521112
1121221121	2111211111	1111111112	12111-----	--11111112	1211244111	111111
1122211121	3-11211111	1111111112	1213111212	1111111113	1111221111	111111
??????????	??????????	??????????	??????????	??????????	??????????	??????
1122211121	2111212111	1111111112	1213111112	1211111112	1111251131	311111
1112211111	--11211111	1111111211	1212111111	1111111113	1111111111	111341
1122211121	3-11111111	1111111112	12111-----	--11111111	1211131111	111111
2122221121	2111211111	1111111112	1112121121	1111111111	2111111111	111111
1132211121	4-21211121	1111211112	11111-----	--11111111	1211151131	311111
1122211121	2111211111	1111111112	1213111112	1111111112	2111251131	311111
1122211121	2111211111	1111111111	2213111122	2111111112	11111?1111	111121
??????????	??????????	??????????	??????????	??????????	??????????	??????
117-------	----211131	1111111112	11111-----	--11111111	1111151131	311111
1322211121	2111212111	1211111112	12111-----	--11111112	1211251131	311111
115211213-	--11211121	1111111112	11111-----	--11111111	1111151131	311111
1122211121	3-11211111	1111111113	1213111112	1111111112	1111251111	111111
1122211121	2111211111	1111111121	11111-----	--11111113	112112118-	811431
1122211121	211121111?	1111111112	1213111212	3111111112	1111251131	311111
??????????	??????????	??????????	??????????	??????????	??????????	??????
1122221121	1-11211111	1111111112	1213111112	1111111112	1111141161	621112
??????????	??????????	??????????	??????????	??????????	??????????	?????-
1122211121	3-11111111	1111111112	11111-----	--11111111	2111111111	111111
117-------	----211131	1111111112	12111-----	--11111112	1111221131	311111
1122211121	2111211111	1111111112	1113111112	1111111111	21111?1111	111111
1122211121	2111211111	1111111112	1113111212	1111111111	11111?1132	312111
1121211121	3-11211111	1111111112	1113111112	1111111111	1111111111	111111
1122211122	3-21211131	1111111112	1213111112	1111111112	1211231111	111111
1122211121	2111211211	1111111112	12111-----	--11111112	1211231141	411111
1122211121	2111211111	1111111112	12111-----	--11111112	2111331151	521112
1112211111	--11211112	1111111112	11111-----	--11111111	211111318-	81---2
1121211121	2111211111	1111111112	12211-----	--11111113	1111321111	111111
??????????	??????????	??????????	??????????	??????????	??????????	??????
1122211121	3-11211111	1111111112	11111-----	--11111111	1111151131	311131
1122211121	2111212111	1111111112	1213111112	2111111112	1111221131	311111
1122211121	3-11111111	1111111113	12111-----	--11111112	1111331111	111111
1123111121	4-11211111	1111211113	12111-----	--11111112	1111221141	411111
1122221121	2111212111	1112111112	12111-----	--11111112	1111221141	411111
1122221121	2111221111	1111111112	1213111112	1111111112	1111221152	522122
1122211121	2111212131	1111111112	11111-----	--11111111	1111121161	621112
1112211111	--11211111	111?111211	1212111121	1111111113	1111111111	111341
1122221121	2111211111	1111111112	1213111212	3214111112	1111241131	311111
1122211121	2111211111	1111111112	12111-----	--11111112	2112331151	521112
1122211121	2111211121	1111111112	12111-----	--11111123	1111141111	111111
1122211121	3-11121111	1111111112	12111-----	--11111112	2111311111	111111
1121211121	2211111111	1111111112	1113111111	1111111111	1111121131	311111
113221213-	--11211111	1111111112	11111-----	--11111111	111121118-	8-----
1122221121	2111111111	1111111112	11111-----	--11111111	1211141111	111111
1121211122	3-11121111	1111111112	11111-----	--11111111	2111151112	112111

Table 1. Morphological data matrix. Continued.

	10	20	30	40	50	60
Epipocus	111-111211	1411211111	1121112112	11114134-1	2211131121	1111111211
Ericmodes	111-411211	1411113111	1223112211	11113134-1	2211131111	1111111222
Eronyxa	111-411211	1411211111	1222112112	11113134-1	2221131121	1111111212
Eubrianax	111-411111	1411111211	1121111-11	1111213311	223116----	1122122111
Euconnus	111-111311	2411113111	1221111-11	11113134-1	2211121111	1211111112
Euderia	121-121311	1411111?11	1221112111	11113144-1	2211131121	1111111112
Eufallia	1122111211	1411111111	1222112111	11112134-1	2231131111	1121111113
Eulichas	111-411211	1411111211	2121111-12	1111213311	221116----	1111112121
Eurhynchus	111-421311	1411111111	1222111-11	23---134-1	2211131111	1111211321
Euryplatus	111-311211	1411111111	1222112111	11112131-1	221116----	1111111223
Euspilotus	121-411212	1411211111	1222111-11	11113154-2	322115121-	1111111112
Eustrophopsis	111-411212	2411223112	1122112211	11112132-1	221116----	1211111211
Georissus	221-111212	1411111111	1221112321	11112154-1	2211131121	1111111112
Geotrupes	111-411211	1422--1111	1221112321	11113134-1	3211131131	1211111212
Glaresis	111-421212	1411121111	1222111-11	11112144-1	2221131132	1111111123
Glischrochilus	111-411211	1411111111	1223111-11	13114134-1	2211131111	1111111211
Glypholoma	111-411211	1211111111	1222112311	11113134-1	2211131111	1111111111
Grynoma	111-411211	1411213111	1222112212	11113144-1	2211131111	1111111212
Gyrinus	111-111211	1422--1121	1221112111	11112262-1	213116----	1111111222
Haliplus	111-111211	1411111111	1111112111	11112231-1	221116----	1111111112
Harmonia	111-411211	1421211111	1222111-11	11113132-1	222116----	1111111211
Helichus	121-111211	1411112111	1123111-11	1111216321	113116----	1111111223
Helophorus	111-411212	1411211111	1221112311	11112154-1	2311131221	1111111111
Helota	1121111311	1411111111	1223111-11	13113134-1	2211131112	1111111211
Hemipeplus	111-411211	1411112111	1121111-11	1111313321	321116----	1111111223
Heterocerus	111-411211	1411211211	1221112111	1111213321	221116----	1111111311
Histanocerus	111-311211	1411211111	1221112211	11113132-1	221116----	1111111222
Hister	111-411211	2421211111	1223112111	11113134-2	3321131212	1111111112
Hobartius	111-411211	1411113111	1122112212	11112134-1	2211131111	1111111212
Holoparamecus	1122411311	1411111111	1221112111	11112134-1	2211141112	1111111223
Holopsis	211-311211	1411112111	1123111-11	11113134-2	2321131121	2111112111
Hybosorus	111-411111	1421221111	1221111-11	11112144-1	2231131132	1111111111
Hydraena	111-111212	1411111111	1223112111	11114154-1	3211111221	1111111111
Hydroporus	111-111111	1421111111	1221111-11	11114231-1	221116----	1111111223
Hydroscapha	111-111211	1421111111	1222112211	11113262-1	221116----	1111111211
Hygrobia	111-411311	1411111111	1221112321	11113231-1	221116----	1111111112
Hymaea	1122411311	1411111111	1122111-11	21113134-1	2131131111	1111111221
Hypodacnella	111-411211	1411211111	1123112111	11112144-1	223115111-	1111111211
Hyporhagus	111-411212	1411221111	1221111-11	11212134-1	2221131112	1111111222
Idgia	111-411311	1411113111	1121111-12	11113131-1	221116----	1211111111
Ischalia	1122411211	2411221112	1111122211	11113132-1	223116----	1111111211
Ischyomius	111-311211	1411111111	1221111-11	11113131-1	221116----	11?1111113
Iselma	1123411311	2411211111	1121112212	11112131-1	221116----	1211112121
Isoclerus	111-411311	1411113111	1221111-11	11114134-1	2231131111	1111111112
Julodis	111-221211	2411211111	1121111-11	1111413321	221116----	1111112121
Lacconotus	111-411311	1411111111	1221111-12	1111313321	221116----	1111111221
Laccophilus	111-111111	1421111111	1223111-11	11114231-1	221116----	1111111222
Laemophloeus	111-311212	1411111111	1221212111	11112134-1	2211131111	1111111321
Lagrioida	111-111311	1411112111	1221111-11	11112134-1	2211131111	1111111213
Lamingtonium	111-411211	1411112111	1222111-11	11112134-1	2131131111	1111111322
Languria	111-411211	1411111111	1221112111	11112134-1	2231111121	1111111211
Lara	121-411211	1411211211	1122112112	11112131-1	231116----	1111111222
Laricobius	111-111211	1211113111	1122111-12	11113134-1	2231131111	1111111211
Leaus	111-311211	1411121111	1221112112	11112134-1	2211131111	1111111122
Lemodes	1122111211	1411111111	1121121-12	21112132-1	221116----	1111111211
Lepicerus	111-111112	2411111111	1222112211	11112194-1	2231151?1-	1121111221
Leucotachinus	111-411211	1411111111	1221112311	11114131-1	221116----	1111111111
Lichnanthe	111-411211	1411221111	1121121-11	11114144-1	2211131132	1111112111
Lissomus	111-411112	1411111221	1122121-11	1112313321	322116----	1111111221
Listrus	111-411211	1411112111	1122111-11	1?11213321	223116----	1111111221
Loricaster	121-111131	1422--1111	1122112111	11112164-1	2231141112	1121111211
Lucanus	111-211211	1411221111	1221111-11	13112144-2	3311121121	1211111112

70	80	90	100	110	120	130
1111112112	4121112211	2131112111	1221211121	123121?314	1112422111	1411121331
1111112111	4121112211	1121112112	1111211111	1221111114	1112422111	1222211111
1111211113	4121113211	2131112111	1121211112	1111211115	1112422111	1222221111
1112321112	4121215212	1121111111	1211212211	1111211114	1112421111	1211111111
1112221111	4122111211	2121112111	115315----	1111211114	1112421111	31-1212223
1111111111	4121111211	2131112111	121315----	-111111115	1112421111	31-1212213
1111111114	4122111311	1351112131	1133141111	1111111115	1112422111	1212212333
1111111111	4121213212	1111112112	1111111121	1431221114	1112422111	1411121111
1112313414	4231111341	2331213121	215315----	-111111115	1112421111	22-1112222
1111312111	4121111211	1221113111	1153121111	1111211115	1112422111	1412221121
1131111113	3121113211	3121112122	1251111121	1221111114	1112422231	1212211121
1111112112	4121111211	2321112111	1121112121	1131211214	1122422111	1111111313
1111111113	4121113213	2211112121	1221111111	1111111114	1122422112	31----2122
1111111112	4121113211	2231112112	122111112?	1221211114	1112421111	1213122112
1111111111	2121113212	2311112111	1211111111	1311111114	1112421111	1213212122
111111241-	-121113211	1221112111	1241111121	1321111114	1112422111	1412221111
1111111111	4121112211	2121112111	1221111121	1121111114	1112421111	31-1112111
1112322111	4121211211	2121112111	1351211111	1221211114	1112422111	1222211111
1112321151	3121215211	2241112212	1253111121	1431111112	1112211111	31-1111112
1112221141	3122111211	1141112212	1223111121	1431213112	1122212211	1411231313
1111111111	4121311211	2331112111	1153311111	1211111114	1112422111	1111211121
1111111112	4121111211	1221111111	131115----	-431211114	?112423131	1411131111
1111111111	2121113211	2111112112	1221111121	1321111114	1112422111	31-1112231
1111111111	4121113211	1131113111	1113111121	1231211114	1112422111	1413321333
1111111111	4121311211	1321113112	1253131111	1121211315	1112423111	31-1112222
1111111111	4121111211	2141112111	1231121111	1121111114	1112422121	1222221111
1111112112	4121312211	2321113121	1133111122	1211211114	1112422111	1421221113
1152111113	3121113211	2321112121	1131111121	1321114115	3122422231	1212211122
1121112112	3121111211	1131112112	1211111122	1221211114	1112422111	1211221111
1111111112	4121111211	2131112111	1251111121	1121111314	1112423111	1222321331
1111311424	-131111311	2111113111	1253312111	1121111115	1112421111	1122211111
1111211113	4121113211	2211112111	1111111111	1411111114	1112421111	1413222121
2141111111	4121113221	2111113211	1221111111	1121111114	3112422111	1213211311
1112321141	3121111211	1141111111	1253111111	1421211112	1112211111	1411131213
3111111454	-122111211	3311112111	1113311121	1431211111	1112111111	31-1112112
1111311141	3121111211	1141112112	1243111111	1221211112	1112212111	1421131122
1221111112	2121111211	1121112112	1212111113	1121111114	1112423111	1221221121
1111111112	2121111211	2131112111	1142111121	1321211115	1112423211	1413221332
1111111111	4121211211	2231112111	1133111121	1131211114	1312422211	1212221333
1111211133	4121313213	2331113111	1151111111	1111111114	1113422111	31----2212
1111111112	4121311211	3121211111	1251121111	1131211315	1112422111	31-1212221
1111111132	4121312222	1321112111	1213111121	1121111314	1112422111	1412221131
1111112113	4121111211	3221112111	112115----	-111111115	1112422111	31-1112222
1112221111	4121113213	2221112111	1112121111	1121111114	1112422111	22-3222231
1112321111	4121111331	1211111121	1151111111	1431211114	1112422111	1211221111
1111112111	4121311211	1221112111	113215----	-121111215	1112422111	31-1112223
1112221141	3121111211	1141112111	1153111111	1421211112	1112211111	1411131213
1111212112	2121111211	1131113111	1121111122	1321114115	1112423111	1213211122
1111111112	4121311211	2221113111	111115----	-111111115	1112422111	31-1112231
1112212111	4121111211	1131112111	1122111111	1221111214	1112423111	1212221121
1111111111	1121113211	2131112111	1113111121	2121111214	1112422111	1212311321
1111111111	4121211211	1121122112	1211111111	1131211214	1112421111	1211121111
1112111151	3121111211	1121112111	1221111111	2121111114	1112421111	1112212211
1111111112	4121311211	2331112111	1123111111	1121111115	1112422111	1412222331
1111112111	4121312211	2121112111	121115----	-111111125	1112422111	31-1112222
3111111454	-121111311	2331121111	1113111112	1421111111	2122111111	31-1311113
1111211111	4121213212	1121112111	1221211111	1221111114	1112421111	31-1112111
1111111113	3121113211	2331112112	1211111111	1111111114	1112421111	1213212122
1152221113	4121313213	2131121111	1221111121	1242214114	1422423131	1431121313
1112321111	4121111211	2121112111	1111111112	1121111114	1112422111	31-1112211
2111111151	3121111211	1121122111	1211312111	1211111114	1112421111	31-1212112
1112321114	4121113221	1221112112	1121111121	1321111114	1112422111	1223211122

Table 1. Morphological data matrix. Continued.

	140	150	160	170	180	190
Epipocus	1122-11221	1121121221	111-211211	211111231-	1131112213	2333121122
Ericmodes	1121214121	3121121211	111-111111	122111231-	1131111212	4335111223
Eronyxa	1121212121	2121121211	111-211211	111211231-	1121111211	2334113322
Eubrianax	1121211111	1121121211	111-211111	211111231-	1131112222	2334112121
Euconnus	1122-21311	113---1211	111-211411	111111231-	2122122311	433811332-
Euderia	1122-21311	1121121211	111-211111	111111231-	1122122211	7333113223
Eufallia	1122-24321	5122121211	1125211121	12112-231-	11-2122212	733811332-
Eulichas	1121211121	2122121211	111-211111	3121112332	1141111222	2333112122
Eurhynchus	1122-14311	4121111211	2124211511	122111231-	1132122211	7337113322
Euryplatus	1122-21231	1121131223	111-211221	121111231-	1131122212	7333113323
Euspilotus	1222-22121	2122111222	211-211211	312111231-	1131112213	4322131122
Eustrophopsis	1122-21321	1121121211	2124111111	112111231-	2121122212	2335113122
Georissus	1122-11311	1122111211	211-212211	112111231-	2131122223	6332113322
Geotrupes	1122-23111	3121111211	1121211111	1221112322	1122111221	4332113121
Glaresis	1122-14111	3121111211	1124211511	121111231-	1321111221	4331113222
Glischrochilus	1121212232	2121121232	111-211211	111211231-	1141112223	2325113223
Glypholoma	1121211111	2121121?23	1124211221	112111231-	2131112222	2325113323
Grynoma	1121211121	1121121211	111-211111	111211231-	1121111211	2334113322
Gyrinus	2112--1221	1121111221	1123211211	311112131-	1111122231	4215113222
Haliplus	1212--1231	113---1211	2124211411	3121122332	1131522213	4314311121
Harmonia	1122-11321	2122111211	111-211111	3111112321	1131122223	4332123122
Helichus	1121111131	1122121211	2125211111	3111112332	11-1112213	2328211121
Helophorus	1122-11311	2122121211	1124111212	111111231-	1121111221	4335113322
Helota	1122-24231	3121121211	1124111211	111211231-	1141122213	4326111123
Hemipeplus	1122-12311	2121121222	111-211211	121111231-	1131122211	7337113223
Heterocerus	1121211121	1122111211	211-211111	3111112322	1131112213	4333141222
Histanocerus	1122-21322	2121121211	111-211111	111211231-	1141112212	2336113122
Hister	1122-22121	2122111223	2137211211	312111231-	1131122213	4337131121
Hobartius	1121212131	2121121211	111-211211	2111112321	1141112212	4315111222
Holoparamecus	1122-22321	2121121211	111-211211	2111112321	1131122213	7333143223
Holopsis	1121212311	2121121211	111-211211	312111231-	1131122223	7332143323
Hybosorus	1122-14111	3121111211	1131211211	122111231-	1121111231	4332113122
Hydraena	1121214112	3121111211	111-111221	121111231-	1121122212	5333123323
Hydroporus	1112--1321	1221121211	111-211111	3111112322	1121122211	3314213121
Hydroscapha	1121111311	1121111223	111-211221	312111231-	1131112223	1322111222
Hygrobia	1212--1321	1221111211	211-211211	3121112322	1321122211	4311212121
Hymaea	1121212132	2122121211	1124121111	2111112321	1131122213	4315113223
Hypodacnella	1122-14131	3121121211	1136211111	121111231-	1131122213	7333143323
Hyporhagus	1122-21131	1122111211	1124111111	2121112321	1141122213	7336123223
Idgia	1121211111	1121121231	111-211211	111111231-	1322111431	2331113123
Ischalia	1121211111	1121121211	111-211111	111111231-	1322111431	2221113322
Ischyomius	1122-21122	2121131221	111-211211	111211231-	1121112211	4335113223
Iselma	1122-11111	1121131211	111-211512	111111231-	1322111331	2331113222
Isoclerus	1122-14111	3122121211	111-211211	122111231-	1131122212	7335113223
Julodis	1121121121	1121111241	211-211211	3121111332	1141111213	4337111122
Lacconotus	1122-21211	1121121211	111-211212	111111231-	1121122211	7334113222
Laccophilus	2112--1311	1221121221	111-211211	2111112332	1141122212	4315313121
Laemophloeus	1122-22231	1121121211	111-211211	121111231-	1131122213	4312113122
Lagrioida	1122-12211	2121121211	111-211212	111111231-	1131111211	4335113222
Lamingtonium	1121211122	2121121211	1124211211	2111112321	1141112213	2333113323
Languria	1122-23231	2122121211	1125111111	211111231-	1141122212	7335123222
Lara	1121211121	1122111211	2124111111	3111111322	1131111213	2336111122
Laricobius	1121212111	2122121211	1224111211	211111231-	1121112211	2312111122
Leaus	1122-24111	3121121211	1123111211	111111231-	1132122212	4333113223
Lemodes	1122-11311	1121131211	111-211212	111111231-	1222112211	4321113223
Lepicerus	1121111231	1121111211	2123211211	211111231-	1131122213	4334111123
Leucotachinus	1121212112	2121121223	111-211211	121111231-	1122112231	2323113322
Lichnanthe	1122-14111	3121121233	111-211211	121111231-	1132111222	2337113121
Lissomus	2222-21131	1122121211	111-211311	3122112332	1131122213	4325143123
Listrus	1121211111	2121131211	111-211211	211111231-	1121111212	2333111122
Loricaster	1121211111	1122111211	111-211221	112111131-	2311112221	3311113322
Lucanus	1122-14121	3121121211	111-211111	122111231-	1131112222	4338113122

200	210	220	230	240	250	260
2211132114	-322122622	233233---2	1212231312	25121413--	22331113-1	111113-361
1211322114	-222121612	2122131122	3122121322	2112131123	1212111111	1111111111
2211321114	-123213612	2122132222	1113121311	22111413--	1212111111	1111111112
1211312112	1113122621	2112133322	1112231311	12111313--	11121111?1	1111121211
2211221114	-323134521	24--33---4	-3-443134-	15111533--	2133211111	111113-311
2211311114	-123111611	2122131112	3112221312	1211143113	11121113-1	111113-311
2211132114	-323134---	----------	----------	----------	-----112-1	1111121271
1211312111	1113211611	2112133113	1112221311	2111121112	1112111111	1111111111
1211322114	-121121611	2112131122	2112311311	12111413--	11121112-1	1111111111
1221221114	-123124621	232233---4	-213131312	25111533--	2133111111	1111111131
1211132114	-323134611	24-233---4	-214311311	14111433--	12321112-3	2211111111
1211312114	-123123621	2122132314	-112231312	2211131113	1112111111	1111112131
2211132114	-323134211	241233---4	-11421134-	1311141112	22132113-1	2111111161
1211311114	-123111211	232233---4	-1?3311311	12211433--	11121112-3	2211111111
2212212114	-123111211	2122131114	-1?2321312	22111433--	12121112-2	1313111111
1211232114	-32212361?	24?213---4	-212311321	13111433--	1212111112	1213111111
1211222111	1223122511	24-233---4	-214421312	14111533--	2233211111	1211111111
1211311114	-123122622	2122131222	1113131311	22111433--	12121112-1	2111121211
2222111224	-11311211-	1--121---2	-21111324-	12211333--	11121113-2	1111111111
2212111211	311311211-	1--121---4	-111113231	12111313--	1212111111	1111112111
2211232114	-32212361?	2132132222	1112311312	23111413--	12221113-1	111113-361
2211221113	111311161?	232233---4	-1?2121312	1211132122	1112111111	1113111111
1211312114	-123122211	2232332112	1112211321	1211141112	1212111111	1212111112
2211231113	112313461?	2122133213	11?2121322	22111413--	1212111111	1111111111
12112?2114	-221123621	241233---4	-3-2231312	23121413--	2133111111	1111111131
2221311113	1113123612	2122332223	21?2131322	13111433--	1132111111	1211111161
1211312114	-223134611	231233---4	-112311322	12121313--	2113111111	1111111131
1211232114	-323134611	232233---4	-113311311	14111433--	12321112-3	1311111111
1211312114	-222121612	2122132112	3112211321	14111533--	1212111111	1111111121
1211132114	-323131621	24--33---4	-3-4431312	26121533--	2133211111	1111111171
1211232114	-322134612	24---3---4	-3-4431312	26121533--	21332113-3	111113-361
1211311114	-123123211	2122132224	-112311311	22111433--	11121112-2	2211111111
1211221114	-323134611	2112132214	-214411311	15111533--	2133111111	1111111111
2222111224	-12312211-	1--121---4	-111113231	1221233123	1112111111	1111111111
1211132111	132313441-	1--133---4	-11412334-	15111533--	22333113-1	121113-371
1212111223	111321211-	1--121---4	-11111324-	1221133123	1112111111	1111111111
1211311114	-222121611	231233---4	-112311321	11111413--	1212111111	1111111121
1211232114	-322131612	231233---4	-114111322	24121413--	1232111111	1111111161
1211232114	-321134621	2122132314	-112231312	22111213--	1112111111	1111111131
2221311114	-123214612	2132132213	1112111311	1211141113	11121113-1	1111111111
1211312114	-123134622	232233---4	-3-3131311	12111413--	11121113-1	111113-331
1211212114	-121134621	2122133214	-112231312	2212121113	1112111111	1111111131
1221312114	-121122621	232233---4	-113131311	2211131123	1112111111	1111111131
2211211114	-221122611	24-233---4	-213321311	23111533--	12121113-1	111113-351
2211211113	111311162?	2122133124	-1?4221311	11111212--	1112111111	1111111111
1211322114	-121122622	2122132223	2112231312	2212131113	1112111111	1111111131
1222111223	111312211-	1--121---4	-111113231	1221233113	1112121111	1111111111
1211232114	-322134611	24-233---4	-21422134-	15111533--	2232211111	1111111122
1211312114	-121134611	231233---4	-112231322	1212131111	1112111111	1111111131
2211312114	-322121622	2122133112	3113331322	22111413--	1212111111	1111111111
1211132114	-12112361?	2122133114	-1?2211311	2212131113	1212111111	1111111111
2211311111	1123111611	2112132222	3112231312	1111122112	1112111111	1111111111
2211311113	1223211611	231233---4	-112321311	23111413--	22332113-1	111113-311
1211312114	-123134621	2122132222	2112231311	1211131111	1112111111	1111111131
1211322114	-22113461?	2122132113	2114231312	12121313--	1112111111	1111111131
1211131112	?32313441-	1--113---4	-1?3113131	13111433--	2232211111	111111118-
1211112112	1123134511	2132133214	-214411311	13111433--	1232111111	1211111111
1211211114	-123111211	232233---4	-2?2321312	23111433--	11321112-1	1211111111
1211312111	1113123621	2122132113	1112231312	1111121121	12121113-1	111113-311
2211311114	-121134612	2122132322	3224211312	23111533--	1212111111	1111111111
2211111111	2323134---	----------	----------	----------	-----113-1	111113-361
1211212114	-123111211	232213---4	-2?2311312	12111533--	11121112-2	2112111111

Table 1. Morphological data matrix. Continued.

	270	280	290	300	310	320
Epipocus	213112-811	1132141111	2221111122	224-441111	1111111211	241--21111
Ericmodes	3121112813	1132131111	2221111122	224-111111	1111311--4	241--12111
Eronyxa	1-11112713	1132121111	2211111111	114-111121	1111323-11	2111-14111
Eubrianax	1-11212831	1123121112	2222211111	224-111111	1111111221	1211-11111
Euconnus	1-1112-713	1332121111	1222211111	1131333111	1111411234	142--11111
Euderia	1-11112822	1132121111	2211111122	2211111111	1111211234	1222-11111
Eufallia	1-1112-711	1332131111	1111111111	114-411111	1111413--4	241--12111
Eulichas	1-11113831	3112121111	1111111111	224-111111	1111111311	1221-11261
Eurhynchus	313112-822	1122121111	2222111112	224-311111	2111313--4	241--12121
Euryplatus	1-1112-811	1333231111	1112211122	224-111111	1111213--4	2114211111
Euspilotus	1-1112-811	2132121211	1111111122	224-443111	1111311111	1113-11111
Eustrophopsis	1-11112821	1112131111	2211111122	224-411111	1111313-11	2114111111
Georissus	1-1112-821	2132131111	1222111111	224-411111	1111111311	1111-11111
Geotrupes	1-11112751	2133121111	1111111111	1131111111	1111213-11	141--21111
Glaresis	1-11122811	2133221111	2221111111	2211111111	1111213-11	1111-11111
Glischrochilus	311112-811	1132131111	1222211122	224-433111	1121313--4	241--12111
Glypholoma	1-11112711	2133131121	1121111211	1131333211	1111211111	3111-11111
Grynoma	1-11112713	1113221111	2211111111	114-111111	1111213-11	2111-14111
Gyrinus	1-1112-331	1132222111	1111111111	1131311111	1114113--4	141--12111
Haliplus	1-1112-631	2212112111	2221111111	2231111112	1114111111	3311----11
Harmonia	213212-721	1332131311	2221111111	114-441111	1111311311	2111-12111
Helichus	1-1112-831	1132121111	2211111111	224-222112	1111211-34	1111-21111
Helophorus	1-11112811	1132121111	2221111122	224-411111	1111111311	1111-11141
Helota	1-11112811	1132131111	2111111122	224-333111	1111313--4	241--12111
Hemipeplus	411112-831	1332121111	1222211122	224-111111	1111113-13	2414111111
Heterocerus	1-11112831	1122131311	2222211111	2211111111	1111211-34	141--11111
Histanocerus	1-11112822	1222131111	1222111122	224-111111	2111213--4	2114111111
Hister	1-1112-811	2132121211	1111111122	224-443111	1111211321	1113-11111
Hobartius	1-11122813	1132141111	2222111112	224-311111	1111313--4	2111-12111
Holoparamecus	1-11112711	1132141111	2221111111	114-441111	1111313-31	241--12111
Holopsis	213112-711	1132141311	1222211111	114-331111	1111113-21	2114111111
Hybosorus	1-11112711	2133231111	1222111111	1131111111	1111113-22	1111-21111
Hydraena	1-1112-311	3212214112	2111111111	1111111121	1111311211	142--21111
Hydroporus	513112-631	1132122111	2221111111	2231311112	1114113--4	3311----11
Hydroscapha	1-1112-211	3113214111	1112212111	1132333111	1121413--4	141--22111
Hygrobia	1-1112-631	1132122111	1111111111	2231311112	1124113--4	1311-22111
Hymaea	1-1112-811	1132131111	2221111112	224-111111	1111323--4	2211-12111
Hypodacnella	1-11112811	1132131311	2222111122	224-111111	2111323-11	241--21111
Hyporhagus	1-1112-811	1122121111	2221111122	224-111111	2121213-21	2114111111
Idgia	1-11112711	1133121111	2111111111	114-111111	2111313--4	241--12111
Ischalia	411112-721	1233121111	2111111111	124-111111	1111113--4	2414111111
Ischyomius	411112-821	1132131111	2211111122	224-111111	1111213--4	2124211111
Iselma	1-11313711	1133121111	2211111111	114-111111	1121313-11	2114111111
Isoclerus	1-1112-811	1122131111	2221111111	114-111111	1111313--4	241--11111
Julodis	421112-821	1132121111	1111111122	2231333111	1221411211	1113-11111
Lacconotus	621212-821	1232121111	2211111122	224-111111	1111113--4	2114111111
Laccophilus	1-1112-631	2132122111	2221111111	2231333112	1124111311	3311----11
Laemophloeus	1-1112-811	1232121111	2211111122	224-311111	1121113--4	2111-11111
Lagrioida	6111122821	1132121111	2221111122	224-111111	1111313-11	2114111111
Lamingtonium	1-1112-811	1132131111	2221111122	224-111111	1111313--4	2111-12111
Languria	5131112811	1332131111	2111111122	224-311111	1111123-13	2111-11111
Lara	1-1112-831	1132121112	2222211111	2211111111	1111111311	1211-11261
Laricobius	313112-822	1112121211	2222211111	2231311111	2111212311	1111-11111
Leaus	1-1112-831	1122121111	2111111122	224-111111	1113313-11	2114111111
Lemodes	6111122811	1333131111	1111111122	224-111111	1111313--4	241--11111
Lepicerus	1--112-621	1112213111	1111111111	2232111111	1211411111	141--11111
Leucotachinus	1-1112-511	1122131121	1111111111	1131344111	1121112311	3311-11111
Lichnanthe	1-11112311	2133212111	1111111111	1131111111	1111313-11	1111-21111
Lissomus	421112-841	1122121111	1111111111	2211111111	1111111311	1121-11111
Listrus	1-1122-811	1333121111	2211111111	224-111111	1111313--4	241--11111
Loricaster	1-1112-711	1122121311	1111111111	1111111111	1111211211	1111-11111
Lucanus	1-11112811	1112121111	1111111111	2231111111	1111111311	1111-11111

330	340	350	360	370	380	390
1121111-12	1111121111	14-1211222	11111211-5	1121111114	2131421111	1112225111
1221112112	3131212122	1121111111	11112111-3	1111111114	2111431111	1112321121
1211113112	3133212122	1111121111	1111121317	1111111114	1111411111	11112253-1
1111111-12	1113112111	1111221212	12111211-4	3111111114	3111421111	11111213-2
1121111-12	1121111111	14-1211211	11113211-6	3113211115	3112--3-11	11111113-1
1211113?12	3133212132	1111112111	211113-428	--21111114	2111421111	11112133-1
1221111-12	4122221212	14-1111111	11111211-6	1111111115	1111431111	1211111111
1211111-22	3133212122	1311111111	112113-1-7	4121211114	2111421111	11113233-1
1221212112	4121211131	2111112112	1111321316	1121212116	1122--1-11	11112113-1
1121413112	3133213122	1111121111	1121111514	2111111114	2111411111	1111321211
2321411-12	2132221112	1121111113	112113-1-9	--13221414	3111211211	11111133-1
1211112112	3131222122	1111111111	11111111-4	1111212114	1111411111	11112133-1
1211111-12	1122212121	1111111113	11211211-3	1113211224	3111221211	11111153-2
2221111-12	11111?1111	14-1112112	1111221319	--11121114	2111111111	1112214122
1221111-12	31122?1121	14-1??????	??????????	??????????	??????????	??????????
1321412112	3131211122	2111111111	1111112515	1?11211114	2111411111	1111213111
1121111-12	1121212122	2311111111	11113211-3	1111211114	2111121212	11111153-1
1211113112	3133213122	1111111111	1111121317	1111111114	2111411111	11112253-1
1221111-12	4122221111	14-1111111	11112211-3	1113211223	3113----11	11311113-1
1111321-12	4121221121	14-1111111	111113-1-3	1113211113	2131421111	11311113-1
1111111-12	11111?1111	1111111111	11111111-5	1111111115	1112--1-11	1111211211
1321412112	41322?1112	14-1111111	1111221313	1121111114	1111411111	11113253-1
1211111-12	2111212121	1111111111	11211221-3	1113211224	3111211211	11111143-2
1221412112	31312?3122	2111111241	11111111-3	1?11111114	2111411111	1112225111
1211113112	3133223122	1121121111	1111211314	1111111114	3111111111	1111225111
1121411-12	42--------	---1111111	11111221-4	1121111114	1111433111	1111221211
1121112112	3131212122	2111111111	11113111-5	1111111114	2111431111	1111225121
2221411-12	1133221122	1221111113	112113-1-8	--13221324	2111214111	11111133-2
1121112112	3131212122	2111111111	11111121-4	1111111114	2111421111	1112215111
1121111-12	1112111111	14-1111111	11111211-9	--11111114	1121431111	1111223111
1121111-22	4111211121	1211221241	121113-1-7	1113211114	3121421121	11114213-1
1111111-12	2112111211	14-1112112	1111221319	--21111114	3112--1-11	1112123112
1111111-11	1112111111	1411111111	11112211-3	1111111114	3121121211	1111215111
1111321-22	411-111212	14-1111111	11112211-3	3113211213	3113----12	11311113-1
1121111-12	1132211111	14-1121?51	11122211-4	1123211115	1111421121	1112322121
1111321-22	4111221121	14-1211211	11113211-3	1113211113	3211121112	11211113-1
1221412112	3131212122	2111121111	11111221-3	1112211114	2111411111	1112325111
1111111-12	3131212122	2111111111	111113-1-7	1111111114	2121431111	1111215111
1211113112	3133213122	1111111111	1121111614	1111111114	2111411111	1111223211
1121413112	3132122122	1111111111	11113211-4	1121111114	2111421111	11112133-1
1111112112	4131212122	2121111212	11112211-8	--23211114	2132-31-11	1111215212
1111113112	3133223122	1111121111	11112111-4	2111111114	2111411111	1111325121
1111411-12	?1??22?1?2	1111111111	111133-1-9	--11111114	1111431111	1111215211
1211113112	3133212122	1111111111	11213211-4	2111111114	2111421?11	11111153-1
1211111-21	1131221131	24-1111111	211113-429	--21111114	2111232111	11111213-1
1111413112	3133213122	2221121111	11112111-4	2111111114	2111413111	1111225211
1111321-12	4121211111	14-1111111	11113211-3	1113211413	3121222112	11311113-1
1321112112	3131212122	2111121111	1121122524	1111111114	2111411111	11113233-1
1211113112	3133223122	1111111111	11211221-4	2111111114	2111413111	1111225121
1211112112	3132212122	2121111?1	1121111513	1113111114	1111421111	11113213-1
1321112112	31322?2111	1121111111	1111211719	--11111114	2111411111	1111311211
1211112112	3133212122	1111111121	11112211-4	3121111114	2111431111	11113233-2
1211111-12	1121212121	1111111111	11111121-3	1111211114	2111421111	1112113211
1111112112	3133213122	2111111111	11112211-4	2121111114	2111413111	1111223121
1211113112	31322?3122	1111111111	11112111-8	--11111114	2111213111	1111225212
1112121-22	4112111111	14-1111111	11111111-3	1?11111114	3121221111	1111425111
1121111-12	1112122221	1111111111	11113111-4	1111211114	3111121212	11111153-1
2221111-12	21111?2?11	2111112112	1111221219	--21111113	2111413111	1112214122
1211112122	4133211112	14-1121111	11111121-9	--13211224	2211414211	11111243-2
1111113112	3133212122	1111111111	1111321218	--11111114	2111421211	11112133-1
1121111-11	1122121132	1112??????	??????????	??????????	??????????	??????????
1211111-12	11112?2121	14-1112112	1111221319	--21111113	2111413111	1112225121

Table 1. Morphological data matrix. Continued.

	400	410	420	430	440	450
Epipocus	1111114311	1112151112	1111121121	1311131221	1112121111	1111211111
Ericmodes	1111121311	1112151122	1211121111	1211123231	1112121111	1111111121
Eronyxa	3111---321	1112251112	2111121111	1311122111	111113132-	1111111121
Eubrianax	1111---311	111313211-	---2131121	2111123312	-113121111	1112111121
Euconnus	1111---311	1112251122	1111121111	14---23311	1213123-2-	1111111121
Euderia	1122---?11	111213211-	---1121111	13???22212	-113113-1?	1111111111
Eufallia	111121-122	--12251122	1112131131	-4---33321	1113133-2-	1111111111
Eulichas	1112---311	111211111-	---1111111	1311122211	1113221211	1111111121
Eurhynchus	1111---321	1112251112	1112121121	1211123211	1112213-12	1111121121
Euryplatus	111121-311	1112151112	1111121111	14---23111	111212132?	1111111111
Euspilotus	1111---112	--1322111-	---1112121	14---23112	-213132-2-	1111111121
Eustrophopsis	1121---3?1	2112151112	1211121121	1211122111	1112121111	1111111121
Georissus	1111---211	211212111-	---1112111	14---21112	-213132-2-	1111111122
Geotrupes	111121-211	211211213-	---1121111	1311123242	-112113-11	1111111111
Glaresis	??????????	??????????	??????????	??????????	??????????	??????????
Glischrochilus	1111117321	1212251112	1311121111	1311133221	111312112-	1111111121
Glypholoma	1111---311	1111151131	1211121111	1211121311	1113121311	1111111121
Grynoma	3111---321	1112251112	2111121111	14---23111	111113132-	1111111121
Gyrinus	1111---111	121221111-	---1111121	14---21112	-213132-2-	1111111121
Haliplus	1111---221	111223111-	---1121121	14---23112	-213133-11	1111111121
Harmonia	111121-322	--12251112	?111111121	1311122221	111212122-	1111111122
Helichus	1111---342	--4321111-	---1111121	1111121211	1113221211	1111111121
Helophorus	1111---211	211212111-	---1112111	14---21212	-213132-2-	1111111122
Helota	1111121311	211211111-	---1121111	122?122221	1112221111	1111111121
Hemipeplus	111121-321	1111252122	1111121111	1111132221	111213132-	1111111121
Heterocerus	1111111321	112321111-	---1121121	14---23211	1113221211	1111111121
Histanocerus	111121-311	1113151122	1111121111	1311122231	111212132-	1111111121
Hister	1111---112	--1222111-	---1112121	14---23212	-21313232-	1112111321
Hobartius	1111111311	1113151132	1211121111	1311132231	1112121111	1?11111121
Holoparamecus	111121-311	1112151122	1111121121	1211123231	111112112-	1111111121
Holopsis	1111---322	--13251112	1111121121	1111133212	-111123-2-	1412111121
Hybosorus	111121-311	?11111213-	---1111111	14---22242	-112113-1?	?111111111
Hydraena	1111115311	111213123-	---1221111	1211223111	1123121111	1111111121
Hydroporus	1111---112	--12261---	---111-121	14---22212	-213133-11	1111111121
Hydroscapha	1111114311	1112151132	1212131111	1211223212	-113121211	1121111121
Hygrobia	1111---312	--13261---	---113-121	1311123212	-21313132-	1112111121
Hymaea	1111111311	1112151132	1211121111	1211122221	1112121211	1111111121
Hypodacnella	111121-311	1112151132	1211121121	1211122221	1113121211	1111211111
Hyporhagus	111121-311	1112151112	1111121111	1211123211	1111121213	1111111121
Idgia	2111---321	1112251112	1111121111	1311122111	1113123-11	1111111122
Ischalia	111121-322	--12251112	1111121121	1111122211	111212122?	1111111121
Ischyomius	111121-311	1112151112	1211121111	1111122231	1113121211	1111111111
Iselma	111121-321	1112151122	11?2121111	14---2211?	?11312122-	1111111121
Isoclerus	2111---221	1111251112	2111121111	14---22212	-11313132-	1111111122
Julodis	1111---121	111222111-	---2121121	1111133312	-111123-2-	1122111121
Lacconotus	111121-311	1112151111	1211121111	1111133221	111213122-	1111111121
Laccophilus	1111---211	111122111-	---1111121	14---22312	-213133-11	1112111121
Laemophloeus	3111---122	--11251121	1111131121	14---23212	-11113132-	1111111121
Lagrioida	121121-311	1112151121	1211121111	1211122231	1112121211	1111111111
Lamingtonium	1311---121	1111251122	1111131121	1311123212	-112121211	1111111111
Languria	1111122311	1113151132	?211121111	1211123221	1112221212	1111111111
Lara	1112---321	111221111-	---1111121	1211122312	-113221211	1111111121
Laricobius	1111112311	111213211-	---1121111	1311122221	1113121211	1111111121
Leaus	111121-311	1112151112	1111121111	1211123131	111312132?	1111111121
Lemodes	111121-311	1112?51112	1211121121	1211122221	111212112?	1111111121
Lepicerus	111121-311	1113251112	?111121121	1211?23112	-112131211	1111111121
Leucotachinus	1111---311	1112151132	1111121111	1111121211	111112122-	1111111121
Lichnanthe	111121-311	221211213-	---1111111	1311122242	-112113-12	2111111111
Lissomus	1111---321	121321111-	---1111121	1311122211	121322212-	1111111121
Listrus	3111---321	1112251112	1111121121	14---22211	1113121312	1211111111
Loricaster	??????????	??????????	??????????	??????????	??????????	??????????
Lucanus	111121-211	111211213-	---1111111	14---23242	-112113-12	2111111111

460	470	480	490	500	510	
1122211121	3-11121111	1111111112	12111-----	--11111112	1111311111	111111
1122211121	2111211111	1111111112	1213111222	3111111112	2111251132	312111
1122211121	3-11211111	1111111112	1213611132	1111111112	1111321111	111111
1122211121	3-11111111	1111121113	12111-----	--11112112	1111321151	821422
1122211121	2111111111	1111111112	11111-----	--11111111	1111111111	111111
1132211121	4-11211141	1111111112	12111-----	--11111122	1111231121	211111
1122211121	3-11111111	1111111112	11111-----	--11111111	2111211111	111111
1121221121	2111211111	1111121113	1223111122	1111111112	1111341151	521112
115311213-	---1212131	1111111112	11111-----	--11111111	1111151131	311111
1122211121	2111211111	1111111111	2213111222	1113112112	1111321132	111111
3123211121	2111211131	1111111112	1113121121	1111111111	2111151151	311111
1122211121	2111111111	1111111112	1113111122	1111111111	1111151131	311111
1133111121	4-11211111	1111111112	1112111111	1111111111	1111221131	311121
1122211221	4-12211121	1111111112	11111-----	--11111111	1111151161	621112
??????????	??????????	??????????	??????????	??????????	??????????	??????
1123211121	2111211111	1111111112	1113112112	2111111112	21111?1132	312121
1121211121	2111211111	1111111112	1112111111	1111111111	2111111111	111111
1122211121	3-11211111	1111111113	1113611132	1111111112	1111351171	711111
?112211111	--11211112	1111111112	11111-----	--11111111	211111318-	81-2-2
1112211121	2111221111	1111111112	11111-----	--11111111	1111331131	3112-2
1122211121	3-11121111	1111111112	11111-----	--11111112	11112?1111	111111
1121221121	3-11211111	1111111112	11111-----	--11111212	11111-1151	521132
1122211121	2111211111	1111111112	1213121121	1111111112	1111321131	311121
1122211121	2111221111	1111111112	1213111222	1111111112	21111?1132	312111
1122211121	2211211111	1111111111	2213111131	1111122112	1111321171	711111
1121211121	3-11111111	1111111112	11111-----	--11111311	2111111161	621112
1122211121	2111211111	1111111112	1213111112	1111111112	1111221131	311311
3123111121	4-11211141	1111211112	1212121121	1111111112	2111351151	311111
1122211121	2111111111	1111111112	1113111112	2111111111	2111151132	312111
1122211121	3-11211111	1111111112	12111-----	--11111112	21112?1111	111111
1122211121	3-11111111	111111111-	12111-----	--11111112	1111341111	111111
1123211121	2111211131	1111111112	11111-----	--11111111	1111121161	621112
1122211121	2111211111	1111111112	1112111121	1111111111	1111112111	111111
1112211111	--11111111	1111111211	1212111121	1111111113	1111111111	111341
1121211121	3-11211111	1111112112	11111-----	--11111312	1111111111	114522
1112211111	--11111111	1111121212	1212111111	112----113	1111111111	1112-1
1122211121	2111211311	1121111112	1213111112	1211111112	1111321131	311111
1122211121	3-11121111	1111111112	1213111221	1111111112	21113?1132	312111
1122211121	2111211311	1111211112	1213111112	1211111112	1111251131	311111
1122211121	3-11111111	1111111112	1213111121	1111111113	1111121111	111111
1122211121	2211111111	1111111112	11111-----	--11111111	1111131111	111111
1122221121	2111211111	1111111112	1213112212	1114111112	1111221111	111111
1122211121	2111211111	1111111112	12111-----	--11111112	12112?1111	111111
1122211121	3-11211111	1111111112	12111-----	--11111112	1111251111	111111
137-------	----211111	1111111112	11111-----	--11111111	1111131161	621111
1122211121	2111211311	1121111111	2213111112	1311122112	1111321111	111111
1112211111	--11211111	1111111211	1112111111	112----113	1111211111	111341
1122211121	3-11211311	1121111111	2213111122	1111112113	1111311131	211121
1122211121	2111211111	1111111112	1213111212	1112111112	1111251131	311111
1323211121	2111212111	1211111113	1213112212	2111111112	1111251121	213321
1122211121	2111211111	1111111112	1213111112	1111111112	1211221131	311111
1121211121	3-11211111	1111111113	1213111111	1111111312	111111128-	522112
1122211121	2111211111	1111111112	11111-----	--11111111	1111141132	312111
1122211121	2111211111	1111111112	1223111122	1111111112	1311251?71	711111
1122211121	3-11211111	1111111112	1213111111	1111111112	1111221111	111111
112221112?	3--1111111	1111111112	12112-----	--2----113	11113-1132	312111
1122211121	2111211111	1111111112	11111-----	--11111111	2111111111	111111
1122221121	1-11211131	1111111112	11111-----	--11111111	1111121161	621111
4121221121	2111212111	1111111112	1213112131	1111111112	1111331151	521112
1122211121	3-11211111	1111111112	1213111112	1111111112	1111221111	111111
??????????	??????????	??????????	??????????	??????????	??????????	??????
1122211221	1-11212121	1111111112	11111-----	--11111131	1111141161	621111

Table 1. Morphological data matrix. Continued.

	10	20	30	40	50	60
Lutrochus	111-111211	1411113111	1121111-11	1111313321	221116----	1111112121
Lyctus	111-421311	1411211211	1221112211	11114134-1	2211141111	1111112112
Lycus	111-111211	1411111211	1111111-11	2111313311	221116----	1211121111
Macrogyrus	111-111111	1422--1121	1221112111	11112232-1	113216----	1111112122
Macropogon	111-411211	1411111211	1122111-12	1111213331	221116----	1111111113
Malthodes	111-411311	1411111211	1111111-11	11212131-1	231116----	1211121111
Matheteus	111-411211	1411111211	1121111-11	1111413321	221116----	1211121112
Matus	111-111211	1421121111	1222111-11	11114231-1	231116----	1111111212
Melasis	111-111311	2411211111	1122111-11	1111413311	221116----	1111111112
Meligethes	111-411211	1411111111	1223111-11	11114134-1	2211131112	1111111112
Melittomma	111-411211	1411123112	1222112112	1111213331	2211?6----	1111111212
Melyris	111-411211	1411111111	1121112112	1111313321	221116----	1111111111
Merhynchites	111-411311	1411111111	1222111-11	23---134-1	2211131111	1111211211
Meropathus	1122411211	1211111111	1223112311	11114154-1	3321111211	1111111111
Meru	111-111211	1411211111	1222112111	11114231-1	213116----	1111111112
Meryx	111-311311	1411212111	2121111-12	11113134-1	2211131111	1111111222
Metaxina	111-411211	1411113111	1122111-12	11114134-1	2211131111	1111111113
Metrius	111-111311	1411111111	1222112111	11113131-1	221116----	1111111112
Microchaetes	111-411212	2411211211	1222132111	11122134-1	2211131?11	1111111411
Micromalthus	111-111211	1411111111	1121111-11	13---131-1	213116----	1111111321
Mordella	1221411131	2421111111	1221111-12	1111213331	221116----	1111111112
Morpholycus	111-411211	1411111111	1121121-12	1111213311	223116----	1111111221
Murmidius	111-111212	2411213111	1123112111	11213144-1	223115111-	1111111222
Mycetophagus	111-411211	1411211111	1222112112	11112134-1	?211111111	1111111212
Myrabolia	111-412211	1411111111	1222111-11	11112134-1	2131131111	1111111222
Nebria	111-111212	1411111111	1121112111	11113131-1	221116----	1111111112
Necrobia	111-411211	1411113111	1221111-12	11114134-1	2211131111	1111111113
Necrophila	111-411211	1411211111	1121111-11	11114134-1	2211131211	1111111212
Necrophilus	111-411211	1411111111	1221112211	11114134-1	2211211111	1111111111
Nemonyx	111-421311	1411111111	1222111-12	21112134-1	2211131111	1111111111
Neochlamisus	111-421211	2411221111	1122111-11	11113132-1	221116----	1111111321
Nesolathrus	1122411311	1411111111	1221112211	11112134-1	2211131111	1111111222
Nicagus	111-411211	1411111111	1222131-11	111114??1	221113?121	1111111221
Nicrophorus	1121411211	1411211111	1121112322	11114134-1	3211131231	1111111112
Nosodendron	111-311211	1411211211	1223111-11	11112134-1	2221131212	1111111111
Nossidium	111-111211	1411213111	1222111-11	11112134-1	2211141111	2111111212
Noterus	111-111212	1421111111	1222112111	11113231-1	114116----	1111111212
Nothoderodontus	111-111211	1211112111	1121112112	11112134-1	2131131111	1111111112
Notomicrus	111-111111	1421111111	1221111-11	11112232-1	124116----	1111111222
Nycteus	121-411212	1411111111	1122111-11	11113131-1	231116----	1111111113
Ocholissa	1121411211	1411111111	1222111-11	11112134-1	2211131111	1111111223
Ochthebius	1121411212	1211112111	1222122211	11114154-1	3321111221	1111111221
Olibrus	111-411211	1421211111	1222111-11	11112134-1	2231131111	1111111222
Omalisus	111-411211	1411211211	2111121-11	11112131-1	221116----	1211121111
Omma	1122121211	1411211111	1122111-11	13---131-1	221116----	1111111321
Omoglymmius	1123111321	1411111111	1121111-11	11111131-1	221116----	1111111112
Onichodon	111-411212	2411111111	1122111-11	1121413311	331116----	1111111112
Optioservus	111-211211	2411211211	1121112112	11113232-1	113116----	1111111211
Orchesia	111-411212	2411223112	1122111-12	11112132-1	221116----	1111111212
Orphilus	121-311211	1311111111	1122111-11	11112134-1	2231131112	2111111112
Orthoperus	111-211211	1411111111	1121111-11	11112154-1	2211131111	2111111211
Oryzaephilus	1122411211	1411113111	1222111-11	21113134-1	2211131111	1112111221
Ostomopsis	111-111211	1411111111	1123112111	11112144-1	223115111-	1111111321
Ototretadrilus	111-411211	1411111211	1111121-11	1111213311	221116----	1211121111
Oxycraspedus	111-411311	1411111111	1222211-11	23---134-1	2211131111	1111211212
Oxypeltus	1121421311	1411221112	2121222311	1111213311	221116----	1111111221
Palaeostigus	1123111311	1411111111	1121121-11	11114131-2	231116----	1211121213
Palophagus	111-411211	1411221111	1221112112	11112131-1	221116----	1111111112
Panorpa	121-111111	1111111111	1111111-11	23111111-1	211116----	1221121112
Paracardiophorus	121-211211	1411111211	1221131-11	1112213321	221116----	1111111112
Paracucujus	111-111211	1411111111	1221112111	21214134--	2211131111	1111111113
Parahelops	111-111311	1411?12111	1121111-12	11113134-1	2231131111	1111111212

70	80	90	100	110	120	130
1111111112	4121311213	1121111111	1211111111	1421214114	1122422121	1241121111
1111211113	4121111211	1121112111	1123121112	1121111115	1112422111	1212211332
1112321131	4121215211	-111212112	1151211121	1131211114	1113421111	31-1112211
11123213--	4-21211213	1241112212	1243111111	1431111112	1112211111	31-1211112
1112211111	4121213212	1111122112	1151121121	1131211114	1112422211	1211211111
1112321113	4121111211	3321212131	1351131111	3121111114	1113421111	3-----2211
1112321111	4121213212	2211112111	1251211121	1111211214	1113421111	31-1212211
1112321141	3121111211	1141112112	1253311121	1431111112	1112212111	1411131313
111232141-	-121111211	1131111111	1151121111	1131211114	1112423111	1441121313
111121141-	-121112211	2231112111	1141111121	1221211114	1112422111	1213221112
1112311111	4121113211	2121112111	1121111111	1121111115	1112422111	31-1212212
1112211113	4121113211	2231112111	1151111112	1221114115	1112422111	31-1112212
1112313111	4221111211	3331213121	222315----	-111111115	1112421111	22-3112212
2111111151	3122111221	3121112111	1241111111	1121111114	1112422111	1112112212
1112321141	3121111211	3141112111	1243111122	1131211312	1112212111	1212221323
1111112112	4121311211	2311112111	1233111112	1121211114	1112422111	1213321122
1112211111	4121211212	2131112111	1111111111	1111111114	1112422111	31-1112212
1111211141	3121211212	1141112212	1223111111	1331211212	1112212111	1443221113
1111112111	4121111211	1131112111	1111111121	1431211114	1322422211	1211221111
11123215--	-121135211	?----1?131	135315----	-111111115	11135--111	31----2213
1111111111	4121213211	2111112111	1111311121	1121211114	1122422111	1211112212
1111111111	4121313213	2121112111	113315----	-121211214	1112422111	1111112221
1111112112	4121111211	2111112111	1143111111	1121211114	3122423231	1111311332
1111111111	4121112211	2331112111	1131111121	1131211314	1112422111	1121211122
1111112112	2121111211	1221112112	1121111112	1121111115	1112423111	1213221331
1112311141	3121111211	1141112111	1213111121	1321111112	1112212111	1211121312
1112121111	4121111211	2221112111	1123111111	1111111114	1112422111	1111112111
1111112111	3121112211	1121112112	1221211121	1221211114	1112422111	31-1112211
1111111111	4121113211	1121112112	1211211121	1211111114	1112422111	31-1112111
1111312111	4121113211	1331212111	135115----	-111111115	1112422111	31-1112222
1112321111	4121111211	2131111111	1153111111	2421211115	1122421221	1412231112
1111111113	4121111211	2121113111	1132111112	1131111315	1112423111	1122211323
1111111113	4121115212	3111112112	1211111112	1421111114	1112422111	1213212112
1112111111	4121113211	2121112121	1221111121	1111111114	1112421111	31-1112212
1111111111	2121113221	3211112111	1241311121	1421111114	1122421111	1111111112
1111111111	2121111211	3321112111	1113111111	1321111115	1112422111	1111111122
1112221141	3121111211	1141112211	1243111121	1421111112	1122212131	1212231213
1111111111	2121111211	2121112111	1211111112	1121111114	1112422111	1212212222
1112221141	3121111211	1141212111	1153111121	1431111112	1122212131	1412231313
1111112111	2121111211	2121122111	1111111111	1211111114	1112421111	1111222112
1111112112	4121112211	1321112111	1253111123	1121111115	1112423111	1213221332
2111111111	3122113221	2331112212	1231111112	1121111114	3112422111	1111112112
1111112112	3121112211	1311112111	1323311121	1421211114	1112422111	1122211322
1112121111	4121213211	2321112111	1251111111	1131214114	1113422111	31-1212212
1312321111	4121335223	2121113112	13?315----	-121111113	1112213111	31-1112311
1152311141	4121113221	2341212112	1153111121	1121211113	1112213111	1213211312
1112321111	4121115211	2111111111	1151111121	1142211114	1222423121	1441121313
1111111141	4121111211	2121111111	1111111121	1421213114	1112422221	1111221112
1111112112	4121311212	2131112111	1111121111	1121211114	1122421111	1111121113
1131211112	2121113211	3211112111	1211111111	1431211115	2122422111	1113211112
1111111424	-121111211	2311112131	1353311121	1221111114	1112421231	1221111122
1211112111	4121111211	2231112111	1242141113	1111111115	1112423111	1412221332
1111111111	4121111211	2121112111	1143211112	1221211114	1112423111	1212221333
111232141-	-121113211	3211111111	1151111111	1121211114	1113421111	31-1212211
1112313121	4221115211	3211213111	2112111112	1321111115	1112422111	24-2-21121
1111211111	4121113211	1121112111	111115----	-131211114	1112422111	1241111112
1112111111	4122112211	2131113132	115315----	1111111115	1112422111	31-1212222
1311111111	4121113211	1131112111	1111111111	1121111114	1112422111	1212212212
1112321111	4111115311	3321111111	111115----	-111111111	---1111111	31----2212
1152211112	4121213212	2121121111	1151141111	1142213114	1112423131	1441231323
1321211113	2121113211	2121112111	1123111121	1121111114	1112422111	1112311112
1111112112	4121211211	2121112111	1121111111	1121111114	1112422111	1213221222

Table 1. Morphological data matrix. Continued.

	140	150	160	170	180	190
Lutrochus	1121211131	1122111211	211-211111	3111111332	1131111213	3337141122
Lyctus	1122-24321	3122131231	111-111211	121111231-	1131122212	7323113323
Lycus	1121211111	1121151231	111-211211	?11111231-	1132111413	3233113122
Macrogyrus	1111--1211	2121111221	111-211221	311112121-	1111122232	4216113122
Macropogon	2121111121	1121121211	1123212211	2111112321	1141112212	2316113122
Malthodes	1121211111	1121121232	111-211221	111111231-	14-2111431	2331113222
Matheteus	1121211111	1121131211	111-211111	111111231-	14-2111431	2331113222
Matus	1112--1331	1221121211	111-211211	3121112332	1131622212	3315313121
Melasis	1122-21231	1121121211	1125211411	1111212332	1121122212	4233113222
Meligethes	1121213321	3121121221	111-211211	111211231-	2141111223	2332123322
Melittomma	1121211111	1121131232	111-211212	111111231-	1332111431	2221113323
Melyris	1121211111	1121131211	111-211111	111111231-	1121111321	2233113121
Merhynchites	1122-13312	3121141231	1124111211	122111231-	1121122232	4335113121
Meropathus	1121211111	2121121211	111-211121	121111231-	1121122211	7332113323
Meru	2212--1221	113---1211	2124211411	31212-2332	1131122212	433211322-
Meryx	1122-14121	3121121211	111-111111	121111231-	1141111212	2325113222
Metaxina	1121211112	2121131211	111-211221	121111231-	1122112211	4335113222
Metrius	1212--4131	3121121211	1135111111	111212231-	1141122212	4315112121
Microchaetes	2221221131	1122111211	2134212211	311111?322	1131112213	3326142122
Micromalthus	113---1111	1121131233	111-211211	111111231-	14-212-421	1311113222
Mordella	1121211211	1121121232	111-211222	112112231-	1131112212	4333111121
Morpholycus	1121211112	1121121211	111-211112	111111231-	1221112211	2331113222
Murmidius	1122-11131	1122111211	111-211211	312111231-	1131122213	7337143123
Mycetophagus	1121221222	1121121211	1123211211	111211231-	1121112211	4335113122
Myrabolia	1121222132	2121121211	1124211111	211111231-	1141122213	7325113223
Nebria	1212--1121	2121111211	1125111211	3122112322	1141122213	4215111121
Necrobia	1121212111	2121121211	1124211212	111111231-	1121112211	3324113122
Necrophila	1121211111	1121111221	111-211211	111111231-	1131111222	4322113321
Necrophilus	1121211111	2121121211	1125211211	211111231-	1121112221	4213111322
Nemonyx	1122-12311	2121131211	111-211211	122111231-	1121112312	2333111122
Neochlamisus	1121213 1?2	3122331212	111-211511	111211231-	2141122213	4336211121
Nesolathrus	1122-22121	2121121211	111-211221	211111231-	1121112211	4335113223
Nicagus	1121213111	3121121211	111-211111	122111231-	1131111231	4337113122
Nicrophorus	1121211111	1121121223	111-211211	111111231-	1141111233	2337113322
Nosodendron	1121211121	1122111211	111-211211	3111112321	1141112213	2314141222
Nossidium	1122-12111	2121111211	111-21122-	121112231-	2131122212	5333123323
Noterus	2212--1221	2122121211	2125111211	3121122322	1141122212	4314113121
Nothoderodontus	1121223112	3122121211	1133211211	121111231-	1131112211	3313112222
Notomicrus	1212--1221	1121111211	211-211211	3121122322	1141122213	4314213122
Nycteus	1121111121	1122111211	2124211211	2111111321	1111112232	3225112221
Ocholissa	1122-23221	3121121211	1124111111	121111231-	1141122212	7336113323
Ochthebius	1121211111	2121111211	1124211221	211111231-	1121122211	7325113323
Olibrus	1121221322	1121121211	1125211111	112111231-	2141122212	7337113222
Omalisus	1121211111	1121121211	1224211111	111111231-	1342112311	2331113123
Omma	2111--1111	1122121211	1224111111	311111111-	1312111311	1111111222
Omoglymmius	1212--4131	3121111211	1126212121	121112231-	1141122213	4315113223
Onichodon	1122-21131	1122121211	1124211111	1112212332	1141122212	4333113323
Optioservus	1122-21131	1122111211	2124211211	3111112322	1141112213	4336111123
Orchesia	1122-21321	1121121231	111-211221	112211231-	2121112231	2333113222
Orphilus	2321211221	1122111211	111-211311	112211231-	2141512213	2335111122
Orthoperus	1122-13321	3121121223	111-211311	312111231-	1141112223	7332143322
Oryzaephilus	1122-14331	3122121211	1125211121	121111231-	1131122212	4332113223
Ostomopsis	1122-22131	2122131211	1124211221	111211231-	1131122213	7332113223
Ototretadrilus	1121211111	1121131233	111-211211	111111231-	1332111431	2331113222
Oxycraspedus	1122-14321	6121121211	111-211111	121111231-	1131112212	2335111123
Oxypeltus	1122-24321	3121111231	111-211211	122111231-	1141122212	4225111121
Palaeostigus	1122-11111	1121111231	111-21152-	121111231-	1132122312	7335113323
Palophagus	1121214211	4121122211	111-211211	211111231-	114111121?	4335111222
Panorpa	1111------	111---11--	--------2-	111111111-	12121121--	-1---11112
Paracardiophorus	1122-22131	2122111211	1125211111	2122112332	1131122213	7327113122
Paracucujuss	1121222121	2121121211	1124111211	2111112321	1131112212	2315111122
Parahelops	1122-14121	3121121211	1124111211	122111231-	1141112212	2335113222

200	210	220	230	240	250	260
2211312111	111312361?	2122131122	21?2111312	2211131112	11121113-1	111113-311
2211231114	-32311161?	2112131122	31?2121322	25111533--	12331112-1	1111121211
1212211113	1113123621	2112133112	1111231312	12111323--	1132111111	1111111111
1222211223	111311211-	1--131---2	-211113221	12211333--	11121113-2	1111111111
1211311113	112312162?	2122132112	11?2231311	1111121122	1112111111	1111111111
1221211114	-113111621	231233---3	2112331312	13111433--	1132111111	1111111111
1221311113	1113211621	2112132222	1111231312	1111132112	1112111111	?111111111
2222111224	-11312211-	1--121---4	-111113231	1221233113	1112111111	1211111111
2221311112	1113111621	2122133314	-112231312	1111131122	11121112-1	1111121211
1211232114	-323122611	24-233---4	-214421321	14111533--	1213211113	1111111111
1211211113	1121123621	2132132214	-112131311	1211141112	11121113-1	1111111111
1211311114	-123134611	2132133224	-114111312	1211141112	12121113-1	111113-311
1211322114	-121123612	2122131112	1112111312	12111313--	1112111111	1111111111
1211212114	-323134---	----------	----------	----------	-----11111	1111111111
22---1-323	112313441-	1--121---4	-21111334-	15111533--	2233311111	1111113111
1211312114	-123134612	2122131214	-112131322	2212131113	1112111111	1111111161
1211211114	-221123612	2122132223	3113331322	13111433--	1132111111	1111111111
1222112112	1123122---	----------	----------	----------	-----12111	1111111111
2211311111	112311361?	2112132224	-1?3211311	21111333--	1112111113	1211111111
1211222114	-12312141-	1--121---4	-111113221	14111413--	21331112-1	1111121211
2222111224	-123134611	2132132212	3112111312	12111333--	1112111111	1111111131
1211322114	-121134621	2122132214	-112231312	1211131113	1112111111	1111111131
2211232114	-323134621	24-233---4	-3-4431322	26121533--	21332113-3	111113-361
1211312114	-12113461?	2112131114	-112121312	2212131113	1112111111	1211113161
1211322114	-322123622	231233---4	-212231322	22111433--	1212211111	1111111121
1211112112	111312211-	1--121---4	-11111324-	1221131113	1112112121	1211111111
1211311114	-12112361?	2122131222	1112111312	2211141111	1212111111	1111111111
1211212114	-123111511	2122133214	-114411311	22111333--	1112111111	1211111111
1211212112	1123123311	2232333214	-213311312	12211433--	1212111111	1211111111
1211212114	-121123612	2122131312	1112111321	22111333--	1112111111	1111111111
1211222114	-22311361?	2112132212	32?3121311	23111533--	12121113-1	111113-311
1211212114	-323134621	24--33---4	-3-4431312	26121533--	2133211111	1111111171
2211311114	-123121211	2122132224	-1?2311312	12111433--	11121112-2	2112111111
1211212113	1123111511	24-233---4	-3-2311312	13111433--	1112111112	1213111111
1211211111	1123122311	2112131312	1112122322	2111121122	1212111112	1313111111
2211312112	1323134611	24-233---4	-3-441134-	15111533--	2133311111	1111111171
2212111222	112312211-	1--121---4	-11111324-	12112333--	11121212-1	1211111111
2211211111	1223122611	24-233---4	-3-3311321	12111413--	2213211111	1111111111
2212211322	111312211-	1--121---4	-111113231	13211333--	1232111111	1211113111
2222211111	112312131?	2112131212	2113112312	2211133122	1212111112	1211112111
1211312114	-223134611	2122133114	-114311312	24121313--	2233211111	1111111161
1211312114	-123122621	2132132214	-21443134-	15111533--	2133211111	1211111111
1211212114	-322123612	231233---4	-212131322	13111413--	1213111112	1111111121
1221311113	111311362?	2122133213	1112231312	1111141123	11121113-1	111113-311
1111111113	111322241-	1--121---1	-111113231	1231111111	1111111111	1111111111
2211132112	121311211-	1--131---4	-111113311	13111313--	11321123-2	111213-311
2221211112	1113111621	2122133212	1111231312	11111313--	11121112-1	1111111111
1211231112	1223134621	24-233---4	-3-443134-	16111533--	2133111111	1111111111
2211111224	-123134622	232233---4	-114231311	1212131123	1112111111	1111112131
1211311111	1123223311	2122131222	2113121312	22111213--	1212111111	1311111111
2211132114	-323134621	24-233---4	-3-4431322	16111533--	21333112-1	1111121261
2211132114	-323134611	24-233---4	-114411322	21111313--	12121113-1	111113-311
2211232114	-323134621	24-233---4	-3-4431311	26111533--	21332113-1	111113-371
1221311113	1113111621	2122133114	-112231311	22111433--	1132111111	1111111111
1211212114	-222121612	2122132312	1112131311	12111433--	1212111111	1112111112
1211212114	-123111611	2132133213	1113111311	21111313--	1112111111	1111111111
2211132114	-323134---	----------	----------	----------	-----11111	1111111111
1211311114	-121123612	2122132122	1112111321	11121311--	1112111111	1111111111
1112111114	-1?????6--	1--213----	---1--13--	1-111122--	2132111111	1211112111
2211311112	1113123621	2122132213	1112231312	11111333--	1212111111	1111111111
1211212114	-22212161?	2122132222	12?2211322	22111413--	1212111111	1111111111
1211232114	-323134---	----------	----------	----------	-----11111	1111111131

Table 1. Morphological data matrix. Continued.

	270	280	290	300	310	320
Lutrochus	1-1112-821	2132131111	1111111111	2211111111	2111311-34	141--21111
Lyctus	1-11112811	1332131111	2111111122	224-111111	1211211111	1222-11111
Lycus	4111122311	1133221111	1111111111	111?111111	1111111211	1121-21111
Macrogyrus	1-1112-331	2132122111	1111111111	1131333111	1114113--4	141--12111
Macropogon	4211122851	1332121112	2221111111	2211111111	1111111311	1121-11111
Malthodes	611212-211	1133221111	1111121111	1111111111	1121111111	1111-11111
Matheteus	421112-211	2233221111	1111111111	1111111111	1111111311	1111-11111
Matus	1-1112-631	2132222111	1111111111	2231111112	1124113--4	1311-22111
Melasis	1-1112-851	1132121111	2111111122	224-111111	1111111111	1121-11161
Meligethes	313112-811	2232131111	1222211122	224-433111	1111313--4	2111-11111
Melittomma	1-11112611	1133221111	1111111122	224-111111	1111223-11	212--11111
Melyris	1-1212-711	2123121111	1111111111	114-111111	111131--31	241--12111
Merhynchites	513212-841	1122121111	1221111122	224-433111	1111313--4	241--12121
Meropathus	1-1112-511	1112114111	1111111111	1111111111	1111311211	142--21111
Meru	1-13121631	2112222111	2221111111	224-444111	1114113--4	3311----11
Meryx	1-1112-831	1132121111	2211111122	224-111111	1121313--4	2114111111
Metaxina	1-11112711	1112131112	1111111111	114-111111	1111213-11	2211-12111
Metrius	1-1112-631	2112123111	1111111122	2211111111	1124111214	3321--1111
Microchaetes	1-1112-821	1332141311	2222111111	2231333111	1221111311	1113-21111
Micromalthus	1-1112-311	1133221111	1222211111	2231111111	1111211-31	141--11111
Mordella	1-1322-811	1332121111	1222211122	224-111111	1121213-21	2114122111
Morpholycus	611212-711	1132121111	2211111112	124-111111	1111313-12	2114211111
Murmidius	1-1112-811	1132141311	2222111111	224-441111	2111213--4	241--12111
Mycetophagus	1-11112811	1332121111	1211111122	224-111111	2111313--4	2114111111
Myrabolia	1-11122813	1132141111	2211111122	224-311111	1111213--4	2111-11111
Nebria	1-1112-631	2112123111	1111111111	2231111111	1124111-3-	3311----11
Necrobia	3131112711	1333131111	2222211311	114-311111	1111313--4	241--12111
Necrophila	1-11122311	1113113111	1122211311	1131331111	1111211211	1111-11111
Necrophilus	1-11112711	2112121111	2211111111	1131111111	2211311311	3321-21111
Nemonyx	513212-813	1233121111	1211111122	224-311111	2111313--4	2411-12121
Neochlamisus	513212-811	1332141111	2222111122	224-333111	1111313--4	241--12112
Nesolathrus	1-1212-811	1332131111	1211111122	224-111111	2111313--4	2114111111
Nicagus	1-11112811	2122121111	1111111111	2211111111	1111113-11	1111-11111
Nicrophorus	1-11112311	2123212111	1112211311	1131333111	1111211321	3111-11111
Nosodendron	1-1112-811	1132131311	2211111111	224-311111	2121211311	1111-11111
Nossidium	1-11112511	1112121111	2222211111	1111111121	1111111111	141--21111
Noterus	1-1112-631	2132122111	2221111111	2231111111	1124111311	3321-21111
Nothoderodontus	1-1112-813	1122131211	2222211111	2231111111	2111212311	1111-11111
Notomicrus	1-1112-631	2132122111	2222111111	2231111111	1124111314	3321-21111
Nycteus	1-11122721	1332131111	1111111111	1131111111	2121211211	1111-11111
Ocholissa	1-1212-821	1232131111	2222111122	224-211111	1111313--4	2114111211
Ochthebius	1-1112-211	2112114112	2221111111	1111111111	1111311211	142--11111
Olibrus	513212-813	1132121112	2222211122	224-111111	1111313--4	2114125211
Omalisus	6?11122211	2133221111	1111111111	1111111111	1111111311	1111-11111
Omma	1-11122811	1113131111	2111111122	2211111111	1111111111	141--11111
Omoglymmius	1-1112-631	1112213111	1221111111	2231111111	1224311-24	3311----11
Onichodon	611212-851	1132121111	1111111111	2211111111	1111111121	1121-11111
Optioservus	1-1112-831	1132121111	1122211111	224-331111	2211311-31	1111-21111
Orchesia	612112-821	1122131111	2211111122	224-111111	1121213-11	2114311111
Orphilus	1-1112-811	1112131111	1111111111	2211111111	2111111211	1122-12111
Orthoperus	1-1112-711	1132131111	1222211111	114-441111	1111113--4	24---12111
Oryzaephilus	512112-821	1132131312	2111111111	224-311111	1111313--4	2111-12112
Ostomopsis	1-11112811	1132131111	1221111122	224-441111	1111313--4	241--12111
Ototretadrilus	621112-211	1133221111	111111111?	1?11111111	1111111211	1121-11111
Oxycraspedus	313112-811	2132131111	2211111122	224-111111	1121313--4	241--12121
Oxypeltus	313112-811	1122141111	1211111122	224-111111	1111514--4	241--12111
Palaeostigus	1-1112-513	1333231111	1111111111	1131311111	1111411311	141--21111
Palophagus	513112-811	1332121111	2211111122	224-311111	1121313-11	2111-22121
Panorpa	1-1312-211	1131221111	1111112111	1111111121	1111111111	1111-11111
Paracardiophorus	1-12122841	1122121112	2211111111	2231333111	1111111311	1121-11111
Paracucujus	3131122811	1132131111	2211111111	224-311111	2111123--4	241--21111
Parahelops	1-11112831	1132121111	1111111122	224-111111	1111313--4	2114111111

330	340	350	360	370	380	390
1211112112	41332?1112	14-1111111	11111211-4	1121111114	2211431111	11113233-2
11111?3122	41332?2122	1121112111	211113-419	--21111114	2111421111	1111421211
1111111-12	1132211212	1121111211	211113-1-8	--13211115	2122--3-12	22211113-1
1121111-12	4133221111	14-1111111	11112211-3	3?13221413	3113----12	11311113-1
1211112122	4133222122	1111111111	11111221-8	--11211114	1211421111	11112253-1
1111111-11	1?22121111	14-1111111	111113-??8	--13211224	2111231211	11211153-1
1211112112	3133222122	1111111211	11112211-7	1113211224	2111213?11	11211113-1
1211321-12	1121221111	1411111111	11113211-3	1113211113	3211111112	11311113-1
1211113112	4133212112	14-1111111	111113-619	--13211115	1311131111	12111113-1
1321413112	3132211122	1121111111	11111221-6	1113211114	1121421111	1111111111
1311112112	3133222122	1111111112	1111321219	--21211114	1111421111	1111111111
1111113112	3133213122	1111111111	11112211-5	1111111114	2111211111	11111233-1
1211112112	4121111212	1311112111	211113-423	1121212115	1112--1-11	11112133-1
1121111-11	1112111111	14-1111111	11112211-4	1111111114	2111422111	1111215111
1121111-12	4111111111	14-1111111	11111121-3	2113221213	3121311111	11211133-1
1211112112	3132223122	1121111111	11112111-4	1111111114	2111411111	1111223221
1211113112	3133212122	2111111111	11212211-4	1111111114	2111421111	11111133-1
1121121-22	1112211111	2421111143	1121221618	--13211413	2111211111	11111133-1
1111211-22	1111121111	14-1111112	1111211213	1121?11114	1111421111	11112153-2
1211111-12	4122211212	14-1111111	112113-429	--21211114	1111421111	1111321121
1111212112	3132223122	1121111112	111113-419	--11111114	1112--1111	11111133-1
1211113112	3133222122	1111121111	11212111-7	1111111114	2111413111	1111323121
1111111-12	4111121121	14-1221231	121113-419	--11111114	2111131111	1111213111
1211112112	3132213122	1111111111	11112111-4	1?11111114	2111113111	1111213121
1221112112	3132212122	2111121111	11211111-7	1111111114	2111421111	11113213-1
1121121-22	1111221121	14-1111111	11112211-3	2113211413	3111211112	11111133-1
1211113122	31332???22	1111111111	1121122324	2111111114	2111411111	11111153-1
1211111-12	1122212121	1121111211	11112211-4	1112211114	3121124211	11111133-1
1111112212	1131212122	2111111141	11112111-3	1111111114	3121111211	1111115111
1221112112	3132211221	2421112112	1111221319	--11111116	1212--1-11	1111213111
1121111-12	2112111111	14-1112112	11113211-3	1111211114	1111133111	11112233-1
1211112112	3122211122	1111111111	11112211-9	--11111114	2111431111	1111223121
1221111-11	11222?1111	1111112112	1111221319	--21111114	2111413111	1112221121
1121111-12	1122122111	1111111111	11112211-9	--13211114	2111111111	11111113-1
1121112112	3132212122	2111111111	11111121-4	1113211214	2111411111	1112114111
1121111-11	1121111111	14-1111111	111113-1-8	--11211114	2111421211	1111115111
1111121-22	4122211111	1421111111	11112111-3	3113211223	2113----11	11111133-1
1211112112	1121112112	1111111111	11111111-4	1111111114	2111421111	1112225111
1111121-22	4123211111	14-1??????	??????????	??????????	??????????	??????????
1211111-11	11211?2121	1112111112	11112111-3	1112111114	2131432111	1112215111
1121113112	3133212122	1111111111	11212111-4	2111111114	2111421111	1111323121
1111111-11	1112111111	1411111111	11112211-4	1121211114	3121422211	1111115112
1221112?12	3132212122	1221111111	1121111813	2112211114	1121122111	11113213-1
1211111-12	?1332?1122	1111111111	111113-1-8	--23211214	3111431112	11211133-1
1211113112	?133211122	1111111111	112113-A15	1111111113	1111411111	1111223121
1111121-22	4121212121	2421111111	11112211-9	--13211213	2111413211	11111113-1
1221113112	4133212122	1111121111	111113-1-9	--13211115	1331131111	12112113-1
1211112112	4133212122	1111111111	11112211-4	3111?11114	2111432111	11113213-1
3211112112	3132223122	1121111111	1111221714	1121111114	1111431111	11112233-1
1211111-12	1121211121	2121111132	11112211-9	--21111114	2111421111	1112211212
1121111-12	1122211111	1111211141	11111221-7	1111211114	1131431111	1111323111
1321113112	3131212122	2111111111	11111111-3	1111211115	3112--1-11	1112311111
1211113112	4121212122	1111??????	??????????	??????????	??????????	??????????
1211??????	??????????	??????????	??????????	??????????	??????????	??????????
1221112112	3122221131	2121112111	212113-928	--21111116	1122--1-11	11112213-1
1221112112	42--------	---1111111	2121121323	1113211214	1311??1111	11111133-1
1121111-12	1111121111	24-1111111	11113211-8	--13211412	3121131111	11111133-1
1211113112	4131111112	14-1111111	1121121323	1123211214	1111121111	1111213211
4111111-11	13--------	---1111112	11113211-1	3121111114	2111414211	1111113121
1211112112	3133212122	1321121111	11111221-8	--13211314	2111213111	12112153-2
1221112112	31312?2122	1121111141	11111111-3	1?23211114	3111411111	1112111111
1111112112	3133223122	1121111111	11112111-4	1121111114	1111421111	11113213-1

Table 1. Morphological data matrix. Continued.

	400	410	420	430	440	450
Lutrochus	1111---322	--1321111-	---1111121	111112?312	-113221311	1111111121
Lyctus	1111124211	111213211-	---1121111	1311133112	-113113112	1121111111
Lycus	1111---342	--13251112	???1111121	14---23112	-213113-2-	1111111121
Macrogyrus	1111---111	121221111-	---1111121	14---21112	-213132-2-	1111111121
Macropogon	1111---321	111321111-	---1111121	14---23231	121322132-	1111111121
Malthodes	1111---321	121321111-	---1111111	14---23211	1213123-2-	1211111111
Matheteus	11?1---321	111222111-	---1111121	14---2121?	?21313????	1111111111
Matus	1111---111	111222111-	---1111121	1311121212	-213131311	1111111121
Melasis	1111---332	--4-26----	---113-231	14---33112	-213123-2-	1121121111
Meligethes	1111112321	1212251112	1111121111	1311133221	111312112-	1111111122
Melittomma	111121-311	2112151112	1111111111	1111121131	1113121111	1121121111
Melyris	3111---311	1112251112	1111131121	1311123211	1111121311	1411111122
Merhynchites	1111---321	1112251122	1111121121	1311123211	1113113-12	1111121111
Meropathus	1111115311	211213113-	---1221111	1211221211	1123121211	1111111121
Meru	1111---211	111122111-	---1111121	14---21112	-21313112-	1111111121
Meryx	111121-311	1112151121	1211121111	1211122131	111212122-	1111111121
Metaxina	1211---321	1111251112	2111121111	1311123112	-11313132-	1111111122
Metrius	1111---311	111321113-	---1121121	1211122212	-213132-11	1111111111
Microchaetes	1111---311	111211111-	---1111111	1????22211	1113213-12	1111111111
Micromalthus	111121-311	211211111-	---1121121	1112132231	111112122-	1111111111
Mordella	1111---311	1112151112	1112121121	1211123111	1112113-11	1111111111
Morpholycus	111121-311	1112151121	1211121111	1111122231	1112121211	1111111121
Murmidius	1111111311	2212151112	1111131121	1211123321	11111?1???	1112111121
Mycetophagus	111121-311	1113151122	?111121111	1211122221	111112122-	1111111121
Myrabolia	4111---311	1112151122	1111121111	131112?211	11121?????	1111111121
Nebria	1111---211	111321113-	---1111121	1311122212	-213132-2-	1111111121
Necrobia	1111---221	1111251121	2111121111	14---23211	?11313132-	1111111121
Necrophila	1111---311	211213121-	---1111111	1321122311	111112112-	1111111121
Necrophilus	1111118311	211313221-	---1121111	1221222221	2122121111	1111111121
Nemonyx	111121-311	1112151122	1211121121	1311123231	1111113-11	1111111111
Neochlamisus	1111---321	1113251112	1111111121	1311122312	-113213-12	1111111121
Nesolathrus	111121-311	1113151122	1111121111	1311122121	111112122-	1111111121
Nicagus	111121-311	111211213-	---1111111	14---22232	-112113-12	2111111111
Nicrophorus	1111---311	211213211-	---1111111	1321122211	1113121111	1111111121
Nosodendron	1111116311	111213213-	---1111111	1121122321	1112221111	1111111121
Nossidium	1111111311	111213121-	---1221111	1211123211	1123121211	1111111111
Noterus	1111---311	211222111-	---1111121	14---22212	-21313112-	1111111121
Nothoderodontus	1111112311	111213211-	---1121111	1211122221	?113121211	1111111121
Notomicrus	??????????	??????????	??????????	??????????	??????????	??????????
Nycteus	1111118311	111213112-	---1121111	1311123121	1113113-11	1111111111
Ocholissa	111121-311	1113151122	1111131111	1211123131	111212122?	1111111121
Ochthebius	1111115311	111213113-	---1221111	1211223211	1123121211	1111111121
Olibrus	1211---221	1111251112	1111121121	1211123212	-112121211	1111111111
Omalisus	1111---321	121322111-	---1111121	1111122212	-21312112-	1111111121
Omma	111?21-311	111211111-	---1111121	1112122231	111212122-	1111111211
Omoglymmius	1111---321	121223111-	---1111111	1121133112	-21312132-	1111112121
Onichodon	1111---332	--4-26----	---213-221	1311133112	-213113-2-	1111111121
Optioservus	1112---321	111221111-	---1111111	1111122212	-113221211	1111111111
Orchesia	1111---311	1122151112	1111121121	1111123111	111212122-	1111111121
Orphilus	1111114321	111223211-	---1121111	1211122221	1113113-11	1111111121
Orthoperus	111121-122	--11251112	1112131121	1311133?21	111113132-	1311111131
Oryzaephilus	1111111311	1112151132	1111121111	1211123221	1112121111	1111111121
Ostomopsis	??????????	??????????	??????????	??????????	??????????	??????????
Ototretadrilus	??????????	??????????	??????????	??????????	??????????	??????????
Oxycraspedus	1111---321	1112251111	1111121121	1211122211	1113113-12	1111111111
Oxypeltus	1111---311	1112151112	1111111121	1211122112	-113113-13	1111111321
Palaeostigus	1111---311	1112151111	1111111121	14---23211	1213121111	1111111121
Palophagus	111121-311	1112151112	1111121111	1311123212	-112121111	1111111321
Panorpa	1111111121	111121111-	---1111121	14---21112	-113121112	2111111121
Paracardiophorus	1111---321	122321111-	---1111121	14---22111	1213232-2-	1111111121
Paracucujus	1111111311	111215113?	???1131111	1211123331	111112112-	1111111121
Parahelops	1111---311	1112151112	1111121111	14---22111	111212112-	1111111121

460	470	480	490	500	510	
1121211121	3-11111111	1111111113	11111-----	--11111312	1111121251	521112
1122211121	4-11211121	1111111111	11111-----	--11111122	1111131111	111311
1121211121	2111121111	1111111112	12111-----	--11111112	2111331151	521112
2112211111	--11211112	1111111112	11111-----	--11111111	211111318-	81-2-2
1121221121	2111211111	1111111113	12211-----	--11111112	21112?1151	521112
1122211121	1-11211111	1111111112	11111-----	--11111111	1111141151	521112
1122211121	??11211111	1111111112	12111-----	--11111112	11113?11??	??1???
1112211111	--11211111	1111111211	1212111121	1111111113	1111111111	111341
127-------	----212111	1211111112	12111-----	--11111112	1111331151	521111
1122211121	3-11211111	1111111112	11111-----	--11111111	1111141131	311111
1122211121	2111211111	1111111112	12211-----	--11111112	1211221111	111111
1122211121	3-11211111	1111111112	1213111122	1111111112	1111121112	112111
117-------	----212121	1111111112	11111-----	--11111111	1111151131	311111
1121211121	2111111111	1111111112	1112121121	1111111111	2111112111	111111
1112221111	--11211111	1111111112	1112111111	1111111112	111111118-	811532
1121211121	2111211111	1111111112	1213111112	1111111112	1111221131	311111
1122211121	3-11211111	1111111112	1213111122	1111111112	1111251131	311111
1112211111	--11111111	1111111113	12111-----	--11111112	1111321112	112111
1122211121	2111211111	1111111113	12211-----	--11111112	1111241151	521112
1112211111	--11111111	1111111112	11113-----	--11111113	1411131111	111111
115311213-	---1211111	1111111113	12113-----	--11111112	1111351111	111111
3122211121	2111211111	1111111112	2213111212	1314112112	1111321111	111111
1122211121	3-11111211	1111111113	12111-----	--11111112	11113?1111	111111
1122211121	2111211111	1111111112	1213111112	1111111112	1111121131	311111
1122111121	2?11211111	1111111112	1213111111	1111111112	21112?1111	111111
1112211111	--11211111	1111111112	1112111121	1111111111	2111111111	111111
1122211121	3-11211111	1111111112	1213111112	1111111112	1111221131	311111
3122221121	3-11221111	1111111112	1112121111	1111111111	1111121111	111111
1122221121	2111211111	1111111112	1112121121	1111111111	2113111131	311111
1123111121	4-11211121	1111111112	12111-----	--11111112	1111341131	311111
1123211122	3-11211121	1111111112	11111-----	--11111111	1111151111	111111
1122211121	2111211111	1111111112	1213111112	1111111112	1111121131	311111
1122211221	2211211121	1111111112	11111-----	--11111131	1111141161	621111
1123211121	2111211121	1111111112	1112121111	1111111111	2111111111	111111
1122211121	2111211111	1111111211	12111-----	--11112113	1111331132	312141
1121211121	2111111111	1111111112	1112111121	1111111111	2111112111	111111
1111211111	--11211111	1111111211	1213111111	1111111113	1111111111	111342
1122211121	2111211111	1111111112	1113111112	1111111111	1111141132	312121
??????????	??????????	??????????	??????????	??????????	??????????	??????
1122211121	2211111111	1111111112	11111-----	--11111111	1111151112	112111
1122211121	2111211111	1111111112	1213112112	1113111112	1111221131	311111
1122211121	2111211111	1111111112	1112111121	1111111111	1111112111	111111
1122211121	3-11211111	1111111111	1113111222	112----113	11112-1131	311121
1122211121	2111211111	1111111112	11111-----	--11111111	2111111151	521112
1113111111	--11211111	1111211112	11111-----	--11111113	1111141111	111111
2113221121	4-11211211	1111111112	11111-----	--11111111	2111111111	111111
117-------	----211111	1111111112	12111-----	--11111112	1111331151	521111
1121211121	3-11211111	1111111113	11111-----	--11111312	1111111251	521112
1122211121	3-11211111	1111111112	12111-----	--11111112	1111251131	311111
1121211121	2111211111	1111111112	1213111111	1111111113	1111221111	111111
1122211121	3-11111111	1111111112	12111-----	--11111112	11112?1111	111111
1122211121	3-11211111	1111111111	11111-----	--2----111	2111141111	111111
??????????	??????????	??????????	??????????	??????????	??????????	??????
??????????	??????????	??????????	??????????	??????????	??????????	??????
117-------	----211121	1111111112	12111-----	--11111112	1111341121	211111
1123111121	4-11211111	1111211112	11111-----	--11111111	1111141111	111111
1122211121	2111211111	1111111112	11111-----	--11111111	2111111111	111111
114311213-	---1211111	1111111112	11111-----	--11111111	1111111131	311111
1132211121	4-11211111	1112111112	1113111121	1111111111	2112151161	631112
1121221121	2111211111	1111111112	12111-----	--11111112	23113?1151	521112
1122211121	2111211111	1111111112	1113111111	1111111111	13111?1131	311111
1122211121	2111211111	1111111112	1213111122	1111111112	1111221171	711111

Table 1. Morphological data matrix. Continued.

	10	20	30	40	50	60
Parandra	111-411311	1411221111	1221111-11	1211113311	213116----	1111111123
Paraphloeostiba	111-411211	1211111111	1221111-12	11114132-1	221116----	1111111112
Passalus	111-111211	1411121111	1222111-11	1111414341	322116----	1211111323
Passandra	111-411111	1411211111	1222111-11	11113232-1	221116----	1111111113
Pedilus	1122411311	1411221111	1121112112	1111513321	221116----	1111111122
Pelecotoma	1122411221	2411211111	1221111-12	1111313321	221116----	1112111112
Peltodytes	111-111211	1411111111	1211112111	11112231-1	221116----	1111111112
Penthe	111-421311	1411211112	1221111-12	11112131-1	221116----	1111111211
Periptyctus	111-411212	1411111111	1122121-11	11112134-1	1211131121	2121121211
Phalacrinus	111-211311	1411111111	1222111-11	11112134-1	2211131121	1211111111
Pharaxonotha	111-313211	1411112111	1221111-11	11113134-1	2111131111	1111111212
Phellopsis	111-411311	1421211111	1222111-11	11113134-1	2221131111	1111111222
Phengodes	111-411211	1411111211	1121111-11	1111412321	321116----	1211111111
Philothermus	111-411311	1411211111	1122111-12	11113134-1	2231141112	1111111213
Phloiotrya	121-411311	1411212111	1222111-12	11113131-1	221116----	1111111212
Phoracantha	111-411211	1411122112	2121212112	11114131-1	321116----	1111111111
Phycosecis	211-311211	1411114111	1222111-11	11113144-1	223115111-	1111111222
Platynaspis	111-411111	2421123111	1221111-11	11113152-1	221116----	1111111221
Platypus	111-421211	2411111111	1222111-11	13---184-2	321115111-	1111111112
Pleocoma	111-411211	1411111211	1221131-11	13112134-1	3211111121	1111111111
Podabrocephalus	111--11311	1411111?11	1221121-11	11113131-1	221116----	1211121111
Polypria	111-411211	1411223111	1221111-12	1111213321	221116----	1111111121
Priacma	1122111311	1411111111	1221111-11	11114131-1	221116----	1111111113
Priasilpha	111-111311	1411211112	1121111-11	11112134-1	2211131111	1111111221
Prionochaeta	1121411131	2411213111	1121112111	11114134-1	2311212111	1111111111
Prionus	111-411211	1411221111	2121212212	1111412311	321116----	1111111112
Pristoderus	111-411311	1411111111	2222111-11	11112134-1	2211131111	1111111212
Propalticus	111-111112	2411211111	1121111-11	11112134-1	2211131111	1111111222
Prostomis	111-111211	1411111111	1221112111	11111134-1	2211131111	1111111223
Protosphindus	111-111211	1411111111	1223112211	11113134-1	2231131111	1111111321
Pselaphacus	111-411211	1411211111	1223111-11	11113134-1	2211131111	1111111212
Psephenus	111-411211	1411111211	1121121-11	1111413321	221116----	1122121111
Pterostichus	111-111312	1411111111	1222112111	11113131-1	221116----	1111111113
Pterotus	111-411111	1411111211	2111121-11	1111213311	221116----	1211121111
Ptilodactyla	121-411111	1411111211	1221132211	1111313321	221116----	1111111221
Ptinus	111-121311	2411111211	1121111-11	11113131-1	221116----	1111111112
Pycnomerus	111-411311	1411211111	1222111-11	11113134-1	2131141111	1111111221
Pyrochroa	1122411311	1411211111	1121111-12	1111213311	221116----	1111111222
Pyrocoelia	211-411111	1411111211	1111121-11	1111213311	221116----	1211121111
Pytho	111-411311	1411211111	1221111-12	11113131-1	221116----	1111111223
Renardia	1122411211	1411111111	1222111-11	11114131-1	221116----	1111111211
Rentonellum	121-411311	1411111111	1123111-12	11113134-1	2131131111	1111111213
Rhagophthalmus	111-311111	1411111211	1111121-11	1111412311	221116----	1111111111
Rhinorhipus	121-111311	1411111211	2121121-11	21211131-1	221116----	1211111111
Rhinotia	111-411311	1411211111	1222111-11	23---134-1	2311121111	1111211321
Rhipidioides	111-311311	1411113112	2211121-11	13---13321	213116----	1---------
Rhizonium	111-311211	1411112111	1221111-11	11112134-1	2131131111	1111111311
Rhizophagus	111-411211	1411111111	1223111-11	11213134-1	2231141112	1111111212
Rhopaea	111-211211	1411121111	1221132111	11114144-1	3211111131	1111111112
Rhopalotria	111-411311	1?11111111	1222211-11	23---134-1	2211131111	1111211222
Rhynchitomacerinus	111-411311	1411111111	1222111-11	21112134-1	2211131111	1211211113
Rhyzobius	111-411211	1411213111	1223111-11	11112134-1	2221131122	1111111222
Rhyzopertha	121-121311	1411111211	1221112111	11112144-1	2211131121	1111111112
Rodolia	111-311211	2411213111	1222111-11	11114164-1	2231131111	1111111211
Rutpela	1121411321	1411221112	2121212112	11114131-1	321116----	1111111111
Sabatinca	111-111111	2211111111	1121112111	11112111-1	221116----	1121111421
Salpingus	111-411311	1411111111	1121111-11	21112134-1	2211111111	1111111222
Sandalus	121-411311	1411111221	2221121-11	1311313311	221116----	1211111111
Saphophagus	111-411211	1411211111	1221111-11	11112134-1	2211131111	1111111211
Satonius	111-111211	1421211111	1122112111	11112232-1	213216----	1111111223
Scaphidium	111-111211	2411121112	1121112111	11113134-1	2311111111	1111111221
Scarabaeus	111-411211	1412--1111	1221111-11	11213154-2	3311131131	1121112111

70	80	90	100	110	120	130
1111211114	4121111211	1322113111	1253111121	11211?1114	1112422111	1223211111
1111111111	1121111211	1121112111	1221111121	1121111114	1112422111	31-1112211
1111311121	2121111211	1241113112	1221111121	1411111114	1112422131	1413211112
1112221113	4121113231	1132113122	1153111121	1331114115	1112422111	12?2221331
1111112111	4121313212	1121112111	121115----	-111211114	1112422111	31-1112222
1112321113	4121113211	2221112111	1121121111	1121211314	1113422112	1211112212
1112111141	3121111211	1141112211	1223111121	1431211112	1112212211	1411231313
1111112112	3121212211	2331112111	1121121111	?131211214	1112422111	1112211122
1111111424	-121111311	3121112111	1153111111	1331214214	1112423231	1213221131
1111112111	4121112211	1321112111	1353311121	1231211114	1112422111	1112211122
1111112111	4121111211	2131112111	1211111121	1221211314	1112422111	1212221122
1111112112	2121111211	2331112112	1213111111	1321111114	1112422111	1212321331
1112321143	4122213212	2321113121	1151211121	1131211114	1113421111	31----2211
1111111151	4122111211	3131112111	1141111121	1221211114	1112423111	1211221333
1111112111	4121311211	2131112112	1153111111	1121111114	1112421111	31-1112222
1112221111	4121213212	1221112111	121115----	-111111114	1112423111	1122311331
1112221111	4121112211	2131113111	1112111111	1411111114	1112422111	1223221121
1111111111	4121311211	2331112111	1153111121	1321111114	1112422111	1112211121
1112311414	-231315211	2131211122	115315----	-111111115	1122422111	22-2212222
1112321111	3121115211	2111112112	1111111121	1221211114	1112421111	1213212122
1112311414	412?311211	?????23111	1111111111	1141211114	1112423111	31-1112212
1111111111	4121311212	2221112112	1123111111	1121111314	1112422111	1111112222
1112311111	4121223212	3311113112	135312-111	1131111211	?112113111	1221111111
1111111112	2121112211	1131112111	1213111121	1221211214	1112422111	1211211122
1111112111	3121112211	1121112111	1241111121	1121111114	1122421111	31-1212212
1112311214	4121212212	1121112111	1221111124	1231211114	1112422111	1411121111
1111112112	31212155--	3221112111	1113211114	1321111114	1112422111	1111211331
1111111112	2121111211	1221112111	1333111111	1421111115	1112423111	1412221331
1111111111	4121111211	1131113111	132315----	-121111114	?112423111	1413221331
1321112111	4121112221	2111112111	1121111113	1121111114	1112422111	1223211112
1111112111	4121311212	2331112111	1111111121	2321211214	1112422211	1212321131
1112121111	3121315211	1131112112	1221111111	1131211114	1112421111	1211121111
1112321141	3121111211	1141112211	1223111121	1221111212	1112212111	1243211313
1112321213	4121111211	3321112111	1151212111	1131211314	1113422111	31-1212211
1111211111	4121213212	1121122111	1251121121	1131221114	1112422111	1111212131
1112221111	4121111211	2111112111	125315----	-111111115	1112421111	1222121213
1111111112	4121111211	2121112111	1112111121	1421111114	1112423111	1212221333
1111112113	4121313212	1111113111	122115----	-111111114	1112422111	31-1112221
111212143-	-121313213	3331211111	1151212221	1121211114	1113421111	31-1212211
1111211111	4121211211	2121113111	121315----	-121111114	1112422111	31-1112222
1111111111	2121113211	1111113111	122115----	1111111115	1112423111	31-1112333
1111111112	4121111211	1131113112	1231311111	1211111114	1112421111	31-1112113
1112321113	4121111211	3321112121	1151111111	1131211114	1113421111	3-----2211
1332211111	4121113211	2131112111	121215----	-121111314	1112422111	1211122221
1112313111	4221111211	3311213111	215315----	-121111115	1112421111	22-2112322
-------5--	--4-1155--	-----13121	1151121111	1131211115	1113421111	31----2213
1111111111	4121111211	2221112111	1213121112	1111111324	1112423111	1111111333
1111111111	4121111211	2131112112	1252111111	1111111114	1112423111	1413221112
1111111121	3121111211	3321112112	1111111121	1221211115	1112421111	1213212112
1112323414	4231111331	3231213121	213315----	-111111114	1112421111	22-2211121
1111212113	2121113211	1331213111	135215----	-111111115	1112422111	22-2211321
1111111111	4121211212	2331112111	1121111121	1121111314	1112422211	1212221131
1111111111	3121111211	1321112121	1213121111	1111111115	1112421111	31-1112122
1111112111	4121311311	2331112111	1152111121	1211111114	1112421211	1142211111
1111111111	4121113211	1111112111	112115----	-131211114	1112422111	1223312212
1111311113	4112115211	2121211111	111115----	-111111111	---1111111	31----2212
1112211111	4121111211	1331113111	111315----	-111111115	1112422111	31-1112233
1112321114	1121111211	2321211112	1151121111	1121221114	1112421111	31-1212211
1111111112	2121113221	1111112111	1253111121	1131111114	1112423111	1413221123
311111141-	-122111321	3331112111	1123111121	1421111112	1112212211	1111211111
1121111111	4121112211	3321112121	1211111121	1142211114	1112422111	1111212222
1111111111	4121113211	2211112112	1211111112	1111111114	2112421111	1213212122

Table 1. Morphological data matrix. Continued.

	140	150	160	170	180	190
Parandra	1121212121	2121111211	111-211111	112211231-	1141112212	3335113223
Paraphloeostiba	1121211111	2121111223	111-211221	211111231-	1121112211	3313113322
Passalus	1122-14111	3121111211	1134211111	121111231-	1131121212	7237113323
Passandra	1122-22131	2122121211	111-221111	121111231-	1141122213	7334113122
Pedilus	1121211112	1121111211	111-211212	11111?231-	1222111211	2331113222
Pelecotoma	1121221211	1121131231	111-211211	111111231-	2322111231	2331113322
Peltodytes	1212--1231	1121111221	2124211211	3121122332	1131522213	4214311122
Penthe	1121211122	1121111211	2121211112	112211231-	1141111212	2336113122
Periptyctus	1122-13331	3122121211	111-211211	111211231-	1131122213	7322113322
Phalacrinus	1121221222	1121121211	1125211111	212111231-	1131122212	7332113122
Pharaxonotha	1122-12221	2122121211	1124111111	2111112321	1131122212	7315113222
Phellopsis	1122-12131	2122121211	111-211111	222111231-	1141122213	7236113123
Phengodes	1121211111	1121131?33	111-211511	111111231-	14-21114-1	2331113222
Philothermus	1122-22131	2122121211	1126211111	211211231-	1131122212	7335113223
Phloiotrya	1122-11211	1121121231	111-211221	111111231-	2121122232	4333113223
Phoracantha	1122-12321	2121112221	1124111211	212111231-	1141422213	7325111123
Phycosecis	1122-13122	3121121211	111-211221	122111231-	1121122212	7334111221
Platynaspis	1122-11322	2122111211	111-211411	3121112321	1131122213	4332143122
Platypus	1122-23311	6121111211	112621122-	121112231-	1131122212	7333113222
Pleocoma	1121212111	2121121211	111-211111	111111231-	1121122331	4337113122
Podabrocephalus	1121211112	1122121231	111-211122	111111231-	11?2112211	???6113222
Polypria	1121212212	2121131211	111-211212	111111231-	1131111211	4334113222
Priacma	2111--1111	1122151231	1224111111	111111121-	1312111211	1311111122
Priasilpha	1121212131	2122121211	111-221211	211111231-	1131112213	4326113222
Prionochaeta	1121211312	1121111211	111-211211	121111231-	1322112231	4311113322
Prionus	1221211121	1121121211	111-211211	111211231-	1141111212	2235111122
Pristoderus	1122-12131	2122121211	1135111111	211111231-	1131122212	7325113123
Propalticus	1122-22131	1121121211	111-211211	121111231-	1131122213	7337113122
Prostomis	1122-24231	3121121211	1124211111	121111231-	1131122213	7333113223
Protosphindus	1121214121	3121121211	111-211111	211111231-	1141112213	2326113123
Pselaphacus	1122-14131	3121121211	1124211111	111211231-	1141122212	7336123122
Psephenus	1121211111	1121111211	111-211111	2111111322	1111111211	2333112122
Pterostichus	1212--3131	3121111211	1135111211	122112231-	1141122212	4315111121
Pterotus	1121211111	1121131231	111-211211	111111231-	1322112331	2331113222
Ptilodactyla	1122-11122	1122211211	111-211111	2111111321	1111112222	4326?13222
Ptinus	1122-21211	1121111211	1124111511	1121112322	2121122212	7335113222
Pycnomerus	1122-24131	3122121211	1124212211	121111231-	1141122212	7336113223
Pyrochroa	1121211111	1121121231	111-211212	111111231-	1222111311	4331113222
Pyrocoelia	1121211111	1121111231	111-211221	111111231-	1322111411	2331113221
Pytho	1121211112	1121121211	1124211212	111111231-	1321112211	2331113322
Renardia	1122-21311	1121121223	111-211221	111111231-	1321112311	4331113322
Rentonellum	1121211311	1121121211	111-211211	112112231-	2321122221	2331153323
Rhagophthalmus	1121211111	1121131231	111-211211	111111231-	1332111431	2331113222
Rhinorhipus	1121111111	1122121211	1222221211	1111112322	2142111211	2316113222
Rhinotia	1122-14312	4122121211	211-111511	122111231-	1131111212	2335111122
Rhipidioides	1121221211	1121141233	111-21152-	111111231-	14-2112431	2?31113222
Rhizonium	1122-21122	1121131211	111-211211	211111231-	1141122212	7335113223
Rhizophagus	1121214132	3121121222	1124211211	121111231-	1131112212	2335111223
Rhopaea	1122-14111	3121121222	111-211211	121111231-	1121111231	4233113122
Rhopalotria	1122-14311	6121131231	111-211211	121111231-	1131122212	7337113222
Rhynchitomacerinus	1122-14312	3121122211	1124111211	121111231-	1131122212	7335111222
Rhyzobius	1122-11331	1122111211	211-211211	3121112321	1131122213	4337141123
Rhyzopertha	1122-21211	2122131211	1123111211	121111231-	1321122211	7331113322
Rodolia	1121211232	2122111211	111-211211	312111231-	1131111212	2334141122
Rutpela	1121213312	3121112231	111-211211	121111231-	1141112212	2325111122
Sabatinca	1111------	111---11--	--------11	111111111-	12121111--	-1---11112
Salpingus	1122-12211	2121121211	111-211212	111111231-	1121122212	7335113322
Sandalus	1121221111	1122111211	111-211211	311111231-	1142111322	4226111121
Saphophagus	1122-14121	3121121211	111-211221	121111231-	1121122212	7333121323
Satonius	2121111311	1122111211	211-211411	1121112321	1131112213	1324141222
Scaphidium	1122-21111	1121121222	111-211211	311112231-	1131122213	7326143123
Scarabaeus	1122-14111	3121111222	1137211211	121111231-	1131122233	4238113121

200	210	220	230	240	250	260
1211212114	-123121612	2222332112	1122111311	23111233--	1112111112	1112111111
1211112113	1123122521	232233---4	-3?3331311	15111533--	2133111111	1311111111
1211312114	-113111211	221233---4	-2?4411311	13111433--	11121112-1	2112111111
1211211114	-121111612	232233---3	2112121312	21111313--	1212111111	1112111112
1211312114	-121134621	2122132214	-112131311	1211131113	1112111111	1111111131
1221212114	-123121621	2122132113	2112231312	12111333--	11121112-1	1111121231
2212111211	311311211-	1--121---4	-111113131	12111313--	1212111111	1111111111
1211312114	-121134612	2122132113	1112121312	2212131113	1112111111	1111111131
1211232114	-3221346-1	24--33---4	-3-443134-	16?21533--	21331113-1	111113-361
2211312114	-222134612	24-233---4	-3-2111322	12111533--	12121113-1	1111121261
1211212114	-222123621	2122132312	1112231312	22121413--	1212111111	1111111111
1211232114	-323134---	----------	----------	----------	-----11111	1111111131
1221211114	-113121621	2112133113	1112131311	2111142111	11121113-1	111113-311
1211232114	-323122611	24-233---4	-3-4431312	25111533--	21331112-1	1111121261
1221212114	-121122621	232233---4	-3-4231312	1312131112	1132111111	1111113131
2211211114	-12212261?	2122132214	-123111311	22111333--	1112111111	1111111111
2211312114	-223124---	----------	----------	----------	-----11111	1111111161
1211232114	-322122612	232233---4	-3-2131312	14111433--	12131113-3	111113-361
2211212114	-223134612	242213---4	-114111311	15111533--	11331113-2	111123-311
1211312114	-123111211	2122132224	-2?2311312	12111433--	11121112-2	2111111111
1221312113	1113121621	211213322?	?112231311	?2111?33--	1112111111	1211112111
1211312114	-121122622	2122132222	3112131312	2211131113	1112111111	1111111131
1111311112	111321141-	1--121---1	-1?1113221	2131112111	1111111111	1111111111
1211332114	-32212161?	2112132113	1112311322	11111413--	1212111111	1111111121
1211212113	1123121611	233233---4	-214411311	14111533--	1132111111	1211113111
1211312114	-123134611	2112133212	1112111311	2211133113	1112111111	2112111111
1211212114	-12112362?	2122131124	-112131312	2212131111	11121113-1	111113-361
2211332114	-323134621	24-233---4	-3-443134-	16111533--	21332112-1	111113-311
1211232114	-32313462?	2112133114	-114231312	23121413--	1112111112	1112111161
1211212114	-223121612	2112132122	2122121322	2112131123	1212111111	1111111121
1211222114	-121123611	2122132222	1112121311	2212131112	1112111112	1111111111
1211212113	1123113611	2132132113	1112111312	22111333--	1112111111	1111111111
1212112112	112312211-	1--121---4	-111113131	1221131123	1112112121	1211111111
1221311113	1113121621	2112133113	1112231311	11111223--	1112111111	1111111111
1221312112	1113123621	2112133222	11?2231321	22111333--	1112111111	1211112111
1211322114	-123123611	232233---4	-113231312	12111533--	1212111111	1111111111
2211132114	-323134621	2122132114	-113131312	22111413--	1212111111	1112111161
1221221114	-121124621	232233---3	2112131311	1211131123	1112111111	1111111131
1221211113	1113111621	2112133112	1111231311	1111131112	11121113-1	111113-311
1211312114	-12113462?	2122132214	-112131312	1211131112	1112111111	1111111131
1211212113	1113122511	233233---4	-3-4411311	14111433--	2113211111	1111111111
1211222114	-322134621	2122132214	-214131312	15111533--	2133111112	1211111111
1221312113	1113121621	2122133213	1112231321	2111132112	1112111111	1111111111
1211211113	1123211621	2112133112	3112131312	1111121113	1112111111	1111111111
1211222114	-121123612	2122133112	1112111311	21111213--	11121112-1	1111211111
1221312114	-123121621	24--33---4	-3-4431311	14111533--	11321113-1	111113-341
1211322114	-323134611	24-233---4	-21331134-	25121533--	2133211111	1111111161
1211222114	-222121622	231233---4	-112331321	13121413--	1232111111	1311111121
1211311114	-123111211	231233---4	-112211312	13?11433--	11121112-1	2212111111
1211222114	-121121612	2112133322	2113211311	13111433--	1212111112	1111111111
1211212114	-122122612	2122131112	1122211321	11111233--	1212111111	1111111111
1211232114	-322134622	233233---4	-212331322	15111533--	22331113-1	1111111161
1211212114	-123121611	2112132224	-113121312	25111533--	12331112-1	2112111112
1211232114	-322122612	231233---4	-212211312	24111533--	12221113-3	111113-371
1211112114	-121121612	2122133112	1122211312	11111313--	1112111111	1111111111
1122111114	-1231116--	1--213----	------13--	1-111112--	213?1113-1	111113-111
1211312114	-321124621	2132133114	-114211322	1312141121	1212111111	1111111131
1211311113	1123111611	2112132212	1112211311	1111121113	1111111112	2112111111
1211222114	-323134611	24-233---4	-214411321	15111533--	2133211111	1211111111
1211312111	132313441-	1--122---4	-111113131	13111213--	2112311111	1111111161
1211232114	-223134511	2112132114	-2?2111312	14111533--	2133111111	1111111111
2221311114	-123121211	2222331--4	-1?2311311	23111533--	11121112-1	1111121211

Table 1. Morphological data matrix. Continued.

	270	280	290	300	310	320
Parandra	1-1112-811	1332121111	2211111122	224-111111	2111313--4	241--11111
Paraphloeostiba	1-11112711	1122131111	1111111211	1131333211	1111111111	3311-11111
Passalus	1-11112651	2112112111	1111111122	2211111111	111111-34	1111-11111
Passandra	1-1112-811	1132131111	2211111122	224-111111	1111113--4	2111-11111
Pedilus	611212-711	1132121111	221?11111?	1?4-222111	1111313-12	2114111111
Pelecotoma	1-1312-711	1123131111	1111111111	114-111111	1121213-11	2114121111
Peltodytes	1-1112-631	1112212111	2221111111	2231333112	1114113--4	3311----11
Penthe	1-1111-821	1132121111	1111111122	224-111111	2111213-12	2114111111
Periptyctus	213112-811	1132141111	1111111111	224-333111	1111111311	2114121111
Phalacrinus	311212-811	1132131111	2222211122	224-111111	1111213--4	2114115111
Pharaxonotha	1-2112-811	1132131111	2111111111	224-311111	1111223-13	2111-11111
Phellopsis	1-1112-841	1132121111	1111111122	224-111111	1111213-13	2114111111
Phengodes	612112-211	1133221111	1111111111	1111111111	1111211311	1121-211?1
Philothermus	1-11112811	1132131111	2211111122	224-441111	1111313--4	241--21211
Phloiotrya	6112122811	3122131111	211?111122	224-111111	1111213-11	2114111111
Phoracantha	5131122811	1332131111	2211111122	224-111111	2111313--4	241--12111
Phycosecis	1-11122813	1132131111	1111111111	224-311111	1111113--4	241--11111
Platynaspis	213212-721	2132131311	2221111111	114-441111	1111311211	2111-12111
Platypus	1-2112-811	1132121111	1222211122	224-333111	1111513--4	241--12111
Pleocoma	1-11112611	1133221111	1111111111	1111111111	1111111311	1111-12151
Podabrocephalus	323212-831	??3?22111?	?????11122	224-111111	2?11211111	112??11111
Polypria	611212-821	1132131111	2221111122	224-111111	1121223-11	241--11141
Priacma	1-11122811	1113121111	1111111112	2211111121	111111-31	142--11111
Priasilpha	1-11112821	1332121111	2221111122	224-311111	1121323-13	2111-11112
Prionochaeta	1-11112711	2112121111	1221111111	1131333111	1111211221	1111-11111
Prionus	513112-811	1332121111	1111111112	224-111111	2111313--4	241--12121
Pristoderus	1-11122851	1122131111	2211111122	224-111111	1111213-11	2114111111
Propalticus	1-1112-811	1132131111	1222211122	224-111111	1121313--4	2114113211
Prostomis	1-1112-821	1132121111	2222211122	224-111111	1111213--4	2114111111
Protosphindus	1-11112813	1132131111	2111111122	224-311111	1111211--4	241--11111
Pselaphacus	513112-821	1132131111	2111111122	224-111111	1111223-12	2111-11111
Psephenus	1-1112-531	1123131111	1222211111	114-111111	1111111121	1111-11131
Pterostichus	1-1112-631	2112123111	2211111111	2231111111	1114211-34	3311----11
Pterotus	612112-211	1133221111	1111111111	1111111111	1111111311	1121-11141
Ptilodactyla	3232122831	1332121111	2222211122	224-111111	2211311311	1121-11111
Ptinus	611112-831	1212121112	2221111122	2211111111	1111311-31	1222-11111
Pycnomerus	1-1112-831	1132121111	1221111122	224-111111	1111213--4	2114111111
Pyrochroa	6111122811	1133221111	2111111122	224-211111	1111313-12	2114111111
Pyrocoelia	611112-311	1133221111	1111111111	1131333111	1111211111	1121-21111
Pytho	1-11122811	1132121111	2111111122	224-333111	1121213-13	2124211111
Renardia	1-1112-711	1133231111	1111111211	1131333111	1111113-21	3311-11111
Rentonellum	1-11112811	3132141311	1111111111	224-111111	2111213--4	241--12111
Rhagophthalmus	611112-211	1133221111	1111111111	1111111111	1111211111	1221-11111
Rhinorhipus	1-13113831	1122121111	1111111122	2211111111	2111111211	1111-11111
Rhinotia	513112-811	1122131111	2111111112	224-111111	2111313--4	241--12121
Rhipidioides	1-1112-311	1133221111	1111111111	114-411111	1111313-34	241--11111
Rhizonium	1-1112-811	1332131111	1211111122	224-111111	2111113-12	2114111111
Rhizophagus	1-1112-811	1232141111	1222211112	224-333111	1111313--4	241--11112
Rhopaea	1-12112751	2123221111	1111112111	114-222111	1111111-34	1111-11111
Rhopalotria	513112-811	1332121111	1221111122	224-111111	1111313--4	241--12121
Rhynchitomacerinus	513212-811	1132131111	1221111112	224-333111	2111313--4	241--11121
Rhyzobius	213212-821	1332141311	1122111122	224-441111	1211311111	2111-12111
Rhyzopertha	1-11112811	1132121111	1111111122	2211111111	1111212214	1222-11111
Rodolia	211212-722	1132131311	1222111111	114-441111	1121413-11	2111-12111
Rutpela	5131122811	1332121111	2111111122	224-333111	2111313--4	241--12121
Sabatinca	1-11112311	1131221111	1111?11111	114-111111	1111113211	4111-11111
Salpingus	1-1112-811	1132131111	2221111122	224-111111	1111313--4	2114211111
Sandalus	4211113821	1133221111	1111111122	2231111112	1111111221	1111-11141
Saphophagus	1-1112-822	1112131211	2222211122	2231311111	2111311111	141--11111
Satonius	1-1112-621	1222122311	2111111111	2232111111	1221411311	1111-11111
Scaphidium	1-1112-711	1132141311	1122211222	2231444111	1111113-11	341--11111
Scarabaeus	1-1112-751	1112141111	1111111111	114-111111	1111411-31	1113-11111

330	340	350	360	370	380	390
1211113112	31332?1122	1421111111	212113-329	--21111114	1111413111	11111113-1
1121111-12	4121212112	1111111111	11112111-4	1111211114	2111131211	11111153-1
4221111-12	4111111211	14-1111112	11112211-9	--21111115	1112--3-11	1111321111
1321413112	3133212122	1211111111	111113-1-9	--13211115	1111421111	11113213-1
1211113?12	3133223122	1111111111	1121211719	--11111114	2111423111	1111223121
1111111-12	4131222141	1221111111	111113-919	--21111114	1111421111	11113213-1
1111321-12	41122?1111	14-1111111	111113-1-3	1113211113	2131421111	11311113-1
3111412112	3132222122	1111111111	11112111-4	1111111114	1121411111	1111213221
1121111-12	1122112112	1111121251	11111211-7	1113211114	3131221121	1111211111
1221111-12	4112212111	1111111142	111113-413	1121111114	3131412111	12113253-1
1221113112	3131212122	1111111111	1111112314	1111211114	2111411111	1112221111
1211112112	3133223122	1111111111	1121211719	--11111114	1111411111	1111221111
1221111-11	13--------	---1111111	111113-418	--13211114	3111213212	11311113-1
1121113112	3131212122	1111111242	121113-1-9	--11211114	3131432112	12111113-1
3211413112	3133213122	1111111111	1121221714	1121111114	1111421111	11112133-1
1221112112	3133212142	1111111111	212113-418	--21111114	1121411111	11111213-1
1111112112	4111212121	1311111111	11112211-3	1111111114	1111421111	11112233-1
1111111-12	3111121131	1211221252	111113-1-6	1111211114	1131131111	1111111211
1111111-12	42--------	---1111112	1111321219	--21212116	1132--1-11	1111111211
1221111-12	4112121111	1121112112	1111321219	--21111114	3111421111	1112121122
11?1??????	??????????	??????????	??????????	??????????	??????????	??????????
1121113112	3133223122	1111??????	??????????	??????????	??????????	??????????
1211112212	31332?1132	1111111111	1121211328	--13211115	1111231111	1111215121
1121112112	31322?2122	2111221241	11111121-3	3211111114	2131421111	1112321121
1221111-12	1132212112	2111111111	11112211-6	1111111113	3121221211	1111211111
1221312112	3133211112	24-1111111	212113-429	--21111114	1121413111	11111133-1
1211113112	31332?3122	1111111111	11211111-4	1?11111114	2111411111	1111225211
1321112112	3121212122	2111111111	11211225?7	1111111114	1111421111	11112133-1
1111111-12	41112?1111	14-1121111	11211111-6	3?11121114	2111111111	1111321121
1221112112	3131212122	1121111111	11112111-3	1111111114	2111421111	1112321111
1321112112	3121222121	21111111?1	11111111-3	1111111114	2111411111	11112133-1
1211112212	1122112112	1111221211	12112211-3	3121111114	3111431111	11111213-2
1121121-22	3112212121	2421111113	11212211-3	2113211113	3111211212	11111133-1
1211111-12	1121112131	1311111111	11112211-8	--13211214	3111421111	11311133-2
1211112122	41332?1112	14-1111111	11111211-3	3?21211114	2111421111	11113233-1
1111112112	3133222122	1111112112	111113-419	--21111116	1112--1-11	11111133-1
1211113112	3131212122	1221111111	1111221719	--11111114	1111421111	1111225111
1111413112	3133222122	1121121111	1121211515	1111111114	3111421111	1111323121
1111112112	4133221112	1121121211	2221311218	--13211114	3111423212	11311113-2
1211113112	31332?2122	1111111111	11112111-4	1?11111114	2111411111	1111225121
1122111-12	4122111111	14-1111111	11112211-9	--11211114	3111121211	11113253-1
1211113112	3132212122	2111111111	1121121323	1121111114	2111421111	11112153-1
1111111-11	1113111111	1111111111	111113-1-8	--13211124	3111423112	113?1113-1
1211?122?2	3133212122	1111??????	??????????	??????????	??????????	??????????
1211112112	3132221131	2111112111	211113-913	3121211115	1111431111	11111213-1
1111111-12	4131111111	1311111112	111113-1-5	1113211115	11-3------	----------
1211112112	4132212122	1111111111	111113-419	--11111114	2111421111	11112253-1
1221112112	3131212122	1221111111	11111121-5	2111211114	2111421111	1112225111
2221111-12	3112111111	14-1112112	1111221219	--21111113	3111411111	1112113121
1221112112	4122111111	1121112111	212113-928	--21111116	1112--1-11	11112253-1
1221112112	3132211122	2121111112	1111221315	1111111116	1212--1-11	1111213111
1111111-22	3122111112	1311211211	11111111-6	1111111114	1121431111	1111221211
1211113122	4133212122	1111112111	211113-419	--21111114	1111421111	1111115212
1111111-12	1111221111	1311211111	11111211-6	1111211115	1121112111	1111111211
1221412112	3133211142	1111111111	1121121326	3121111114	1121421111	11111133-1
1111111-11	4122121112	14-1211141	22212211-4	3121111114	3123----11	11113243-1
1211113112	3133213122	2111111111	1121111514	2111111114	2111421111	11113233-1
1211113112	41332?2122	1111111111	11112211-9	--13211116	1113----11	11111113-1
1111112212	3121111121	1211111111	11111121-9	--21111114	2111421111	1111225111
1211121-21	1112121111	14-1221211	11122111-5	1221211115	2132--1-11	1111222111
1121111-12	1112122121	14-1111111	11112211-3	1111211114	3131111211	11112253-1
2221111-12	4111211111	14-1112112	1111221319	--21111114	2111411121	1112115121

Table 1. Morphological data matrix. Continued.

	400	410	420	430	440	450
Parandra	1111---311	1112151112	?111121111	1211121112	-111123-12	1112121211
Paraphloeostiba	1112---311	1112151131	1111121111	1211123211	1111121211	1111111121
Passalus	111121-311	211211113-	---2121111	1211122212	-112113-11	2111111121
Passandra	1111---212	--12151112	1113131121	14---33311	111213????	1111111111
Pedilus	111121-311	1112151121	1211121111	1111123231	1113121211	1111111111
Pelecotoma	1111---311	1112151112	1111121121	1111133311	111312112-	1111111111
Peltodytes	1111---121	111221111-	---1131121	14---23112	-213133-11	1111111121
Penthe	111122-311	2112151112	1111121111	1111122121	1113121111	1111111121
Periptyctus	111121-322	--13251122	1111121121	1111223111	1111121211	1121111121
Phalacrinus	1111---131	1151251112	1111121121	1311123112	-113113-11	1121111111
Pharaxonotha	1111122311	1112151132	1111121111	1211123231	1112121111	1111121121
Phellopsis	111121-311	2112151121	1211121111	1211122221	1112121111	1111122111
Phengodes	1111---321	121222111-	---1111121	1311122112	-213123-2-	1111111121
Philothermus	1111---112	--12251142	1111131131	1211123112	-113113-11	1111111121
Phloiotrya	1111---311	1112151112	1111131121	14---23111	11121212??	1111111111
Phoracantha	1111---211	1112151112	1111121111	1211122212	-111121311	1112111121
Phycosecis	1112---321	1112251112	2111121111	1211123211	1111121211	1111111121
Platynaspis	111121-322	--12251112	2112121121	1211123211	11131?????	1211111111
Platypus	111121-321	1112251112	1113121122	1311133111	1113113-11	1111111111
Pleocoma	111121-211	211211213-	---1121111	14---23212	-111113-12	2111111111
Podabrocephalus	??????????	??????????	??????????	??????????	??????????	??????????
Polypria	??????????	??????????	?????????-	??????????	??????????	??????????
Priacma	111121-311	111211111-	---1121121	1112133131	111212122-	1111111111
Priasilpha	1111111311	1112151132	?111121111	1311122221	1112131211	1111211111
Prionochaeta	1111111311	221213223-	---1121111	1221121211	2122121211	1111111121
Prionus	1111---211	1112151112	1111121111	1111122312	-111121112	1112111311
Pristoderus	111122-311	1113151112	?111121111	1111132311	1112121211	1111112111
Propalticus	1111---12?	??11251122	11111?1121	1????2??1?	?11213??2?	1111111111
Prostomis	111121-311	1111151112	?111121111	1311122221	1112121211	1111111111
Protosphindus	1111111311	2112151122	1111121111	14---23221	1112121111	1111111122
Pselaphacus	1121---311	1112151121	1211121121	1311122111	1113121111	1111111121
Psephenus	1111---311	121211111-	---1111121	1311122312	-113121111	1111111121
Pterostichus	1111---111	111321111-	---1111121	1311123212	-213132-2-	1111111121
Pterotus	1111---321	111321111-	---1111121	14---21212	-21112122-	1111111121
Ptilodactyla	1112---311	111111111-	---1111111	2211122212	-113222-2-	1111111121
Ptinus	1111---311	111213211-	---1121111	14---33212	-113113-11	1111111111
Pycnomerus	111121-311	1113151112	1111121111	1211123211	1111121211	1111121121
Pyrochroa	111121-311	1112151121	1211121111	1111122231	1112121211	1111111111
Pyrocoelia	1111---321	121222111-	---1111121	14---21212	-21112122-	1111111121
Pytho	111121-311	1113151121	?211121111	1211122231	1113221111	1111111121
Renardia	1111---311	2112151132	1111121121	1211121211	111312122-	1111111121
Rentonellum	2111---?21	1112251122	11121?11?1	1????3??11	11111?1?1?	1111111121
Rhagophthalmus	1111---321	111322111-	---1111121	1211122112	-21112122-	1111111121
Rhinorhipus	??????????	??????????	??????????	??????????	??????????	??????????
Rhinotia	1111---321	1112251111	1111121121	1211122211	1113113-13	1112112111
Rhipidioides	----------	-----6----	---211-1--	-----4--12	--1311--2-	1111111111
Rhizonium	2111---311	1112151122	1111121121	1211123111	111312122-	1111111111
Rhizophagus	1111111311	1112151132	1111121111	1211123221	1112221111	1111111121
Rhopaea	111122-211	2212151111	1211111111	1311122332	-112113-12	2111111111
Rhopalotria	111121-311	1112151122	1211131121	1311123131	1112113-11	1111111321
Rhynchitomacerinus	111121-311	1112151122	1211131121	1311123131	1112113-11	1111111321
Rhyzobius	111121-322	--13251112	2111121121	14---23221	1112121211	1111111111
Rhyzopertha	1111114311	111213211-	---1131121	1311133212	-113113-13	1112111111
Rodolia	111121-322	--12251112	2112121121	14---23221	111312112-	1211111132
Rutpela	1111---311	1111151112	1111121111	1111122212	-111121111	1112111?21
Sabatinca	1111---321	1112251112	1211121111	1111123212	-113123-2-	1111111121
Salpingus	1211---311	1112151122	1111121111	14---23111	111112132?	1111111111
Sandalus	1111---322	--1323113-	---2131131	-311133211	11131212??	1111111111
Saphophagus	1111111311	111213123-	---1121111	1121122221	1113221211	1111111121
Satonius	1111114311	1112151122	1111131111	1211222212	-113121111	1111111121
Scaphidium	1111---311	2112151132	1111121111	1211123211	1111122-2-	1111111121
Scarabaeus	111121-311	221213113-	---1121111	1311122232	-111113-11	1111111111

460	470	480	490	500	510	
1123111121	4-11211111	1111211112	11111-----	--11111113	1111141141	411111
1122211121	2111211111	1111111112	1113111111	1111111111	2111111112	112121
1122211221	2112212111	1111111112	11111-----	--11111111	1111141161	621111
1143111121	3-11211111	1111111111	1213111112	1111111112	11112?1111	111111
1122211121	2111211111	1111111112	1213112112	1312111112	1111221141	411111
112221213-	--11211111	1111111111	1113111112	1111111111	1111141111	111111
1112221121	2111211111	1111111112	12131?1121	1111111112	11113?1131	3112-2
3122211121	2111212111	1111111112	1213111112	1111111112	1111251131	311111
1122211121	3-11121111	1111111113	12111-----	--11111112	2111311111	111111
1122211121	3-11111111	1111111112	1213111121	1111111113	1111221112	112121
1122211121	2111212111	1111111112	1213111112	2111111112	2111241131	311111
1122221121	2111212211	1211111112	1213111122	1111111112	1111251131	311111
1122?21121	2111211111	1111111112	11111-----	--11111111	2111111151	521112
1122211121	3-11121111	1111111112	1213111111	1111111112	2111311111	111111
1123111121	??11211111	1111111111	11111-----	--1111111?	11112?1131	311111
1133111121	4-11211121	1111111112	11111-----	--11111?11	1111141111	111111
1122211121	3-11211111	1111111112	1213111111	1111111112	1211241111	111111
112???1122	3-11211111	1111111113	12111-----	--11111112	11113?1111	111111
117-------	----211131	1111111112	12111-----	--11111112	1111321121	211111
1122221221	2111212131	1111111112	11111-----	--11111111	1111121161	621112
??????????	??????????	??????????	??????????	??????????	??????????	??????
??????????	??????????	??????????	??????????	??????????	??????????	??????
111221112?	21?1111111	1111111113	12113-----	--11111113	11113?1111	111111
1122211121	2111121111	1111111112	1213111121	1111111113	1111221132	312121
1122211121	2111111111	1111111112	1112121111	1111111111	2111111111	111111
1133111121	4-11211131	1111211112	11111-----	--11111111	1111121111	111111
1122221121	2111211211	1111111112	1213111112	1211111112	11112?1131	311111
1122211121	2?11?11111	1111111111	22111-----	--11111113	11113?1111	111111
1122221121	2111211111	1111111112	2213111112	1111211112	1111321132	311111
1122211121	2111111111	1111111112	1113111212	1111111111	1111241131	311111
1122211121	2111111111	1111111112	1113111121	1111111111	1211131131	311111
1122211121	3-11111111	1111121112	12111-----	--11111113	111132118-	811422
1112221111	--11211111	1111111112	1113111111	1111111111	2111131111	111111
1122211121	2111111111	1111111112	12111-----	--11111112	1112231151	521112
2122221121	3-11211111	1111111112	11111-----	--11111112	1211334151	521112
1123211121	3-11211121	1111111112	12111-----	--11111122	1111231121	211111
1122211121	2111212111	1111111112	1213111112	1211111112	1111251131	311111
3122211121	2111211111	1111111111	2213111111	1314112112	1111321111	111111
3122221121	2111111111	1111111112	12111-----	--11111112	21123?1151	521112
3122221121	2111211111	1111111112	1213111212	3214111112	11112?1111	111111
1122211121	2111211111	1111111112	1112111121	1111111111	2112111111	111111
112??11121	3-11?11111	1111111112	12113-----	--11111112	1111241131	311111
1122?21121	2111211111	1111111112	11111-----	--11111111	2111111151	521112
??????????	??????????	??????????	??????????	??????????	??????????	??????
117-------	----211131	1111111112	11111-----	--11111112	1111141111	111111
1121211121	4-11111111	1111111111	11111-----	--11111113	11111?1111	1112-1
1122211121	2111211111	1111111112	1213111112	1111111112	1111251131	311111
1122211121	2111211111	1111111112	1213111212	2111111112	2111251131	311111
1123221121	2111212131	1111111113	11111-----	--11111111	1111121161	621112
116311213-	---1211121	1111111112	11111-----	--11111111	1111141131	311111
116311213-	---1211121	1111111112	11111-----	--11111111	1111141131	311111
1122211122	3-11211111	1111111112	12111-----	--11111112	1111251111	111111
1123211121	4-11211121	1111111111	11111-----	--11111122	1111131111	111111
1122211122	3-11121111	1111111112	12111-----	--11111112	1111251111	111111
3123111121	3-11211111	111121111?	11111-----	--11111111	1111141141	411111
1132111122	3-11211111	1111111112	11111-----	--11111112	1111221111	111111
1122211121	2111211111	1111111112	1213112112	1112111112	1111251131	311111
1143111121	3-11211111	1111111111	1213111112	1111111112	1111211131	31111?
1122211121	2111211111	1111111112	1213111111	1111111111	2111231111	111111
1122211122	3-11121111	2111111112	1113111111	1111111113	111112118-	112121
1122211121	2111111111	1111111111	1112121111	1111111111	2112111111	111111
115321213-	--11211111	1111111112	11111-----	--11111111	1111151161	621112

Table 1. Morphological data matrix. Continued.

	10	20	30	40	50	60
Schizopus	111-121211	1411211111	1121111-12	1111313321	221116----	1111111222
Scraptia	1121211121	2411223112	1121112211	11112131-1	221116----	1111111223
Selonodon	111-311111	1411111?11	1121111-11	1111313311	221116----	1211111111
Sialis	111-111211	1411111111	1121112121	11112111-1	221116----	1211111113
Silis	111-111211	1411111211	1121111-11	11112131-1	221116----	1211111111
Simplocaria	121-211211	1411211211	1221112112	11122134-1	2211111111	1111111411
Sirrhas	111-311211	1411212111	11?1111-12	11113134-1	1211131111	1111111222
Smicrips	111-411211	1411111111	1222112211	11112134-1	2211131111	1111111322
Spaminta	111-411111	1411111111	1111111-11	11112111-1	221116----	1111111112
Spanglerogyrus	111-111111	1422--1?21	1122112211	11113232-1	223116----	1111111221
Spercheus	1222111212	1411112111	1222112111	11114174-1	2311131311	1111111212
Sphaerites	111-411311	1411111111	1121112211	11114134-1	2221131212	1211111113
Sphaerius	111-111211	1421211111	1123112111	11112134-1	3231131112	1111111211
Sphaerosoma	111-411211	1411111111	1122112111	11112144-1	2211131111	1111111221
Sphenophorus	111-411311	1411211111	1222111-11	23---164-2	331115111-	1121221321
Sphindocis	111-111311	1411211111	1222112112	11113134-1	2211131111	1111111221
Sphindus	111-111211	1411213111	1123112211	11113144-1	2211141112	1111111112
Statira	1121311221	1411111111	1221111-11	11113134-1	221115111-	1111111211
Stegobium	121-121311	1411213211	1221111-12	11112134-1	2211131121	1111111113
Stelidota	1122411212	1411112111	1223111-11	11114134-1	2221131111	1111111112
Stethorus	111-411111	1421113111	1122111-11	11112132-1	121116----	1111111112
Sympiezoscelus	111-411312	2411111111	1222111-11	23---134-2	2211131112	1111221113
Synchroa	111-111211	1411213112	1221111-12	1111213331	221116----	1111111222
Syntelia	111-411311	1411211111	1223111-11	12114134-2	3321131212	1211111113
Sypilus	111-411211	1411211111	2121111-11	13---13321	321116----	1211111112
Systolosoma	111-111212	1411111111	1222112111	11114131-1	221116----	1111111112
Syzeton	1121411221	1411123112	1121112111	11114131-1	221116----	1111111213
Tanylypa	111-311311	1411222111	1221111-12	11113132-1	221116----	1111111211
Taphropiestes	111-411211	1411111111	1221111-11	11113134-1	2231131111	1111111212
Taurocerastes	111-411311	1421221111	1222111-11	11114144-1	2211131131	1111112122
Telegeusis	111-411311	1411111211	1221121-11	11115131-1	221116----	1211111111
Temnoscheila	111-411311	1411211111	1223211-11	11114134-1	2211131121	1111111113
Tenomerga	1121111221	1411111111	1121211-11	11113131-1	223116----	1111111112
Teredolaemus	111-411211	1411113111	1121112111	11113134-1	2231141112	1111111212
Tetraopes	111-411211	2412--1111	2121211-12	11112131-1	221116----	1111111121
Tetraphalerus	1123111311	1411111111	1223111-11	21112231-1	221116----	1211112121
Tetratoma	111-411211	1411122111	1221112212	11114134-1	2211121111	1111111211
Thymalus	111-411211	1411211111	1223111-12	11112134-1	2321131111	1111111211
Toramus	111-111212	1411111111	1223111-11	11112134-1	2211131111	1111111211
Torridincola	111-111211	2421221111	1222112111	21112252-1	213116----	1111111211
Toxonotus	111-121311	1411111111	1222211-11	11112134-1	1311131111	1111211113
Trachelostenus	111-311311	1411221111	1221112212	11112131-1	223116----	1111111222
Trachypachus	111-111212	1411111111	1222112211	11114131-1	221116----	1111111112
Tranes	111-411311	2421111111	1222111-11	23---134-2	3311131112	1111211222
Tribolium	111-411211	1421221111	1221111-11	11113132-1	221116----	1111111212
Trichodes	111-411211	1411221111	1121111-12	11114134-1	2211131111	1111111113
Trictenotoma	111-411211	1411221112	1221112112	11114134-1	3311131121	1211111113
Tropisternus	111-411111	1411211111	1222112321	11113154-1	2311131211	1111111222
Trox	111-411212	1411111111	1222111-11	11111144-1	2231131131	1111111112
Uleiota	1122211212	1411111111	1221111-11	11112131-2	331116----	1111111222
Urodontus	111-411311	2411112111	1222111-11	12112144-1	2231131111	1111111111
Veronatus	121-111211	1411111111	1123122111	11114131-1	221116----	1211111113
Vesperus	1123411311	1411111111	2121121-11	11112131-1	321116----	1111111111
Xerasia	111-411211	1411112111	1221111-12	11113134-1	2211131111	1111111213
Xylariophilus	111-411211	1411111111	1121112211	11113134-1	2231141112	1111111212
Ytu	111-111211	2421211111	1222112111	21112252-1	213116----	1111111211

70	80	90	100	110	120	130
1112311111	41211?1211	2121111111	1111121111	1421211214	1112422111	1212221111
1111112112	4121311213	1231112112	1151121111	1131211115	1112422111	31-1112212
1112322111	4122215212	2111122111	1221121111	1142211114	1112422121	1421121322
1112321111	4122111211	1331112111	111115----	-111111111	---1111111	31----2212
1112321111	4121313213	3221211111	1151212111	1131111314	1113421111	31----2211
1151111111	4121111211	2221111111	1211111111	1431111114	1312422111	1111211111
1111112112	3121311211	2311113111	1133111111	1111211114	1112422111	1213212222
111121141-	-121111311	2131112111	1231111111	1121111114	1112423111	1211221122
1112321131	4121111211	3121111111	121115----	-111111111	---1111111	31----2212
1112221141	3121111211	1241212211	1223111121	1432211112	1112211111	31-1111312
1111111151	4121112211	1321112112	1211211113	1321211114	2112421111	1211212111
1111211111	2121113211	1111113112	1211211121	1221211114	1112421111	1111312111
3111111454	-122111231	2121112111	1113311121	1421111111	1112111111	1111111111
1111111113	4121211212	1331112111	1111111121	1421111114	1112422111	1211221112
1112323414	4231112433	3321213121	212315----	-111111115	1112422111	21-2212331
1111311111	4121111211	2131112111	1133111113	1221111114	1112422111	1211111122
1321211111	2121112212	2121112111	1113111122	1111111114	1112422111	1213311113
1111111111	4121312211	2221113111	113315----	-131111115	1112422111	1422221333
1112211113	3121313213	2131111111	1223111?2	1111111115	1112422111	1111222223
111111241-	-121111211	2131112111	1231211121	1221211114	1112422111	1412221111
1111111112	4121111211	2331112111	1153111121	1221211114	1112422131	1212221122
1112323414	4231115211	3321212121	215315----	-122211115	1112422212	22-3221332
1111111112	4121311211	2121112112	1111121121	1121211314	1112422111	1221221122
1112221113	4121113211	1131112111	1221111121	1321111114	1112422111	1212221121
1112311111	4121115211	1121112111	1253111111	1121111114	1112421111	1221211112
1111311141	3121111211	1141112212	1233111111	1221211212	1112212111	1211221313
1111111112	4121311213	2131112112	112115----	-111211115	1112421111	1211122222
1111111111	3121211211	2321112112	1123111121	1121211114	1112423111	1222221321
1111112112	3121111211	1121112112	1222121111	1111111114	1112422111	1212221122
1111111112	4121111211	2311113111	1211111121	1421111114	1112421111	22-3212122
1112321111	4121111311	2221112111	1353111111	1121111114	1113421111	31-1112212
1112211111	4121113211	1131112121	1151111121	1421111114	1112422111	1212221111
1112321111	4121224222	2111113111	1123141111	1121211112	1112213131	1211211111
1111111112	3121112211	2121112111	1222111111	1121111114	1112423111	1111111332
1112321111	4121112211	1121111111	135315----	-121111115	1112422111	1213222212
1112321111	4121135221	3121113131	1323111112	1131111112	1112213111	31-1112211
1111111112	4121111211	2321112111	1211111111	1121211314	1112422111	1121311122
1111311111	2121112211	2321113111	1111211121	1211111114	1112422111	1112221112
1111111111	4121111212	2131112111	1113111121	1121211314	1112422111	1222221123
311111145-	-122111221	3331112111	1113111121	1321211112	1112212211	1212221112
1111312111	4121113211	2231212131	1353121121	1121111115	1112422111	22-2211331
1111112112	4121311211	2331112111	122315----	-111111114	1112422111	1212212222
1111311141	3121111211	1141112212	1233111111	1421111212	1112212111	1212221312
1112323414	4232115311	3121213121	235315----	-121111115	1112422111	21-2211321
1111112112	2121112211	2311112111	1123111121	1221211114	1112422111	1212211133
1112111113	4121213213	2131112111	112215----	-121111114	1112421111	1111112212
1111211113	4121211212	1231113112	1323111124	1421211114	1112422111	1412331111
1111111112	3121111211	2131112111	1211111121	1331111114	1122421111	31-1312211
1111112121	1121111221	2231112111	1211211111	1431211114	1112421111	22-3212122
1211112112	2121112211	1131112111	1213111113	1121111315	1112423111	1212211331
1112312141	4121111211	1221212131	1352121111	1111111115	1112422111	31-1111331
1112321133	4121112211	2121122112	1211111111	1121211114	1112421111	1221122212
1112311111	4121212211	1121113112	111115----	-121111115	1112422112	31-1112211
1111112111	3121111211	1131112111	1141111111	1111211114	1112421111	1222211112
1111111112	3121111211	2111112111	1142111111	1221111114	1112423111	1111111332
311111145-	-122111211	3321212111	1113111111	1321211112	1112212211	1212221112

Table 1. Morphological data matrix. Continued.

	140	150	160	170	180	190
Schizopus	1121111121	1122111211	111-211211	3111111322	1131111213	3332111121
Scraptia	1121211212	1121111231	111-211222	111111231-	2222111331	4331113322
Selonodon	1122-21132	1121121211	1125211111	1112112332	1122122311	2233113122
Sialis	1111------	111---11--	--------11	111111111-	13121111--	-1---11111
Silis	1121211111	1121111231	111-211221	111111231-	1332111431	4331113122
Simplocaria	1121221131	1122111211	2124211211	3111112322	1131112213	3316111222
Sirrhas	1122-14111	3121121211	111-211112	122111231-	1141112211	2336113222
Smicrips	1121211131	2121121222	111-211211	111211231-	1141112223	4333111222
Spaminta	1111------	111---11--	--------11	111111111-	13121111--	-1---11111
Spanglerogyrus	1212--1221	1121111221	111-211221	311112121-	1111122231	3215111222
Spercheus	1121214322	3122111211	111-211112	121111231-	1342112221	2331113322
Sphaerites	1121212111	2122121223	1124211211	122111231-	1131111222	4333113222
Sphaerius	1121111221	1121111211	211-211211	312111231-	1131112223	1337113323
Sphaerosoma	1121221121	1121121211	111-211211	2111112321	113?112213	4333123323
Sphenophorus	1122-14311	4121111222	2134211211	121111231-	1141122212	7336113222
Sphindocis	1122-22121	2121121211	111-211211	211111231-	1121112211	2335113223
Sphindus	1122-23132	3121121211	1124111211	211111231-	1141112213	2333111122
Statira	1122-24321	3121131211	1124111111	122111231-	1141112212	2336113122
Stegobium	1222-21221	1121121211	1124111211	1111112321	2121122212	7335113222
Stelidota	1121214232	3121121211	?125111211	111211231-	1141112223	2335?23122
Stethorus	1121211332	1122111211	111-211211	3121112321	1131122213	4337141123
Sympiezoscelus	1122-14311	6121121211	2124211111	122111231-	1131122212	7333112222
Synchroa	1121211222	1121121211	111-211211	1111112321	2131111212	4325113222
Syntelia	1122-14111	3121111222	1124211111	121111231-	1131122212	4327113122
Sypilus	1122-23221	3121121211	111-211211	121111231-	1141111212	4335112122
Systolosoma	1212--1221	1121121211	111-211211	2111112322	1141122212	4215111221
Syzeton	1122-11121	1121131211	111-211221	111111231-	1132112212	4335113322
Tanylypa	1222-22121	2121121211	1124111111	111211231-	1131112212	2325113223
Taphropiestes	1122-22131	2121121211	111-221111	211111231-	1141112213	4316113223
Taurocerastes	1122-13111	3121111211	111-211111	121111231-	1122112231	4233112122
Telegeusis	1121211111	1121131233	111-211221	111111231-	14-2111431	2331113123
Temnoscheila	1121214121	3121111211	111-211211	121111231-	1141112212	4335113222
Tenomerga	2111--1121	1122131231	1224111111	1111111321	1312111311	3311111122
Teredolaemus	1122-121?1	2122121211	1124212111	211111231-	1131122212	7335113223
Tetraopes	1121212311	2121132231	111-211211	121111231-	1221111212	4332111222
Tetraphalerus	2111--1111	1121131211	1224112111	211111121-	1312111311	1211111222
Tetratoma	1121211122	2121121211	111-211111	211111231-	1131112211	2332113222
Thymalus	112121112?	1122121211	111-211111	3111112321	1141112222	4336121122
Toramus	1122-21231	1122121211	111-211111	3112112321	1131122213	7326113122
Torridincola	1121111131	1122121211	211-211411	311211231-	1131112213	1332133122
Toxonotus	1122-14321	6122131211	2124111211	122111231-	1131222212	7333111122
Trachelostenus	1122-13211	3121121231	1124111211	111211231-	1141112212	4335113223
Trachypachus	1212--1221	1121121211	1121111211	2111112322	1141122212	2315112221
Tranes	1122-14321	4122121211	2124211511	122111231-	1131122212	7333113222
Tribolium	1122-24121	3221111211	1125111211	121111231-	1121112212	4335113222
Trichodes	1121211111	1121141211	111-211211	211111231-	114?111211	4335113222
Trictenotoma	1122-21132	2121111211	111-211111	112211231-	1141122223	4235213221
Tropisternus	1121211222	1122111211	1125111212	112111231-	2131112222	2235113222
Trox	1122-14121	3121111211	1124211111	121111231-	1321122211	7331113322
Uleiota	1122-11131	1122121211	1125211211	111211231-	1131122213	4332113223
Urodontus	1122-14311	5121111222	111-211521	122111231-	1131122212	7335113122
Veronatus	1121211111	1122111211	211-211111	3111111322	1111112231	1316111122
Vesperus	1121221211	2121121231	111--11211	111111231-	1142111332	2335111222
Xerasia	1121213312	3121121211	111-211211	211111231-	1121112211	4333113222
Xylariophilus	1122-121?1	2122121211	1124211111	211111231-	1131122212	4335113223
Ytu	1121111131	1122121211	2135211411	311211231-	1131112213	1332133122

200	210	220	230	240	250	260
1211211112	1113122621	2112132112	1112211311	1111121113	1112111111	1111111111
1221212114	-123134612	2132132114	-214111311	23111313--	11121112-1	1111112131
1211111112	1113111621	2122132112	3111131311	1111122112	1112111111	1211111111
1112111114	-1221346--	1--213----	---1--13--	2-111122--	2111111111	1111111131
1221311114	-113111621	2112132123	2111231312	23111313--	1132111111	1111111112
1211311111	121312261?	231233---3	21?3221321	13111333--	2113111113	1111111111
1211312114	-121134612	2132131113	3112231322	2212141113	1112111111	1111122211
1211232114	-323111621	24--33---4	-3-443134-	16111533--	2133211111	111113-312
1112111114	-1131226--	1--213----	---1--13--	1-211122--	21121113-1	1111111111
1212111223	112312211-	1--121---4	-111113131	12211333--	12121112-3	1111121271
1211211114	-123122211	233233---4	-113112331	2211131112	21131113-1	221113-311
1211212114	-122123211	2132133112	3112321311	23111313--	1212111111	1211111111
2211111111	132313441-	1--133---4	-11411314-	14111533--	21333112-1	1111121271
1211132114	-323134622	24--33---4	-3-443134-	16121533--	2133211111	1111111161
1211132114	-12313461?	2122133213	21?2311311	14111533--	11121113-1	111413-311
1211212114	-123134611	232233---4	-113221312	1312141113	1132111111	1111111161
1211222114	-32212161?	24-213---4	-212121321	15111533--	22331113-1	111113-321
1211222114	-123134621	2122132114	-112231312	2211131113	1122111111	1111111131
1211322111	1123123611	24-233---2	3212131312	14111533--	12321112-1	1111111111
1211132114	-323122611	233233---4	-114311321	14111533--	2213111112	1111111111
1211232114	-322134622	24-233---4	-3-2331312	15111533--	21332113-1	111113-361
1211132114	-322123612	2132132213	3114211311	14111533--	11131113-2	111413-311
1221212114	-121134621	2122133113	1112231312	1212121112	1112111111	1111112131
1211212114	-223111211	2122132114	-112111311	23111433--	1212111111	2312111111
1211212114	-123134612	2112132212	1112121312	22111213--	1112111112	1113111211
2212111222	112312211-	1--121---4	-111113231	1221231123	1111112111	1111111111
1211322114	-123121612	231233---4	-113111321	13121313--	12325113-1	111113-331
1211212114	-123124621	2122132112	3112231312	1212131113	1112111111	1111111131
1211222114	-322121622	231233---4	-212231331	11111433--	12122112-1	1111121211
2222211114	-123121211	232233---4	-112311311	23111433--	11121112-2	2113111111
1211111113	1113111621	231233---4	-213331311	15111533--	1132111111	1111112111
1211211114	-123111612	2122131222	3112121312	1211141112	1112111111	1111111112
2111111111	111321141-	1--121---1	-111113211	1131112111	1111111111	1111111111
1211212114	-222123612	232233---4	-113321312	2312141122	1232111112	1112111161
1211312114	-121122612	2122133222	1113111311	11111413--	1112111111	1121111111
1111111113	111321241-	1--121---1	-111113221	2231111111	1111111111	1111111111
1211312114	-221134612	2132132224	-113231312	2212141123	1112111111	1111111131
1211311114	-22112361?	2122131222	2113111312	2211141112	1212111111	1111111111
1211222114	-323134621	231233---4	-214331331	13121413--	22132113-1	111113-311
1211322111	132313441-	1--132---4	-113113131	13111433--	2132311111	1111111161
1211212114	-122121612	2122131222	3122111322	13111333--	11321113-1	111113-311
1211222114	-123134621	2122132222	3112231311	1211131113	1112111111	1111111131
1212211222	112312211-	1--121---4	-111113231	1221231123	1111112111	1211111111
1211132114	-322134612	2112133213	2114211321	12111433--	11321113-1	121413-311
1211222114	-22213462?	2122131113	1112131311	2211131112	1112111111	1111111131
2211111114	-122113612	2122132113	1113121312	22111413--	1112111111	1111111112
1211312114	-123134611	2122132214	-112111311	2211121113	1112111111	1111111131
1211211114	-123122212	2132131122	1112112321	1211123113	1112111111	1211111112
2211211114	-123123211	2122131224	-1?2311311	22111533--	12121112-2	2312111111
1211322114	-322123621	231233---3	2112231322	11111313--	1212111111	1111111161
2211212114	-122121612	2112132224	-113331322	25111533--	12321113-1	111113-311
1211211113	112322332?	2112131222	2113132312	23111413--	1222111111	1211111111
1211212114	-323134612	2112133222	1112121312	11111433--	1112111111	1111111111
1211312114	-222122612	2122132322	2113111312	221?141123	1212111111	1111111111
1211222114	-322123612	231233---4	-213311312	25121433--	2233211111	1111111161
1211312111	132313441-	1--132---4	-113113131	13111433--	2132311111	1111111161

Table 1. Morphological data matrix. Continued.

	270	280	290	300	310	320
Schizopus	421212-721	1112131111	2211111111	1231111111	1121111111	141--21111
Scraptia	611112-811	1222121111	1221111122	224-111111	1121313--4	2114111111
Selonodon	1-11112441	2133212111	1111111111	2111111111	1111111311	1121-11211
Sialis	611112-111	1131221111	1111111111	1111111111	1111111111	45--------
Silis	6111112211	1133221111	1111121111	1131311111	1121111214	1111-11111
Simplocaria	5131112821	1132131111	2222211122	2211111111	2111111211	1111-21111
Sirrhas	1-1112-831	1122121111	2211111122	224-111111	1211313--4	2114111111
Smicrips	1-1112-811	1232131111	1222211122	224-431111	1111313--4	2111-11111
Spaminta	1-1122-111	1131131111	1111111111	1131111111	1111111111	1111-11111
Spanglerogyrus	1-1112-331	2222122111	2221111111	1131311111	1124113-13	1111-22111
Spercheus	1-11113813	1132121111	2221111122	224-411111	1111113-13	1111-11111
Sphaerites	1-11112623	1112221111	1122111122	224-433112	1121211211	1113-21111
Sphaerius	1-1112-911	1332141111	2222111111	2232333111	1211413-11	141--21111
Sphaerosoma	212112-811	1132131311	1111111111	224-311111	1111313-11	2111-22111
Sphenophorus	513112-821	2132121111	1222211122	224-411111	1111313--4	241--12121
Sphindocis	1-1112-821	1332131111	2221111122	224-111111	2121313--4	2114111111
Sphindus	1-1112-811	133213111?	2221111122	224-443111	1111111--4	241--11111
Statira	6111112831	1132121111	2211111122	224-111111	1113313-11	2114111211
Stegobium	611212-821	1132121111	2211111111	2211111111	1111111-34	1222-21111
Stelidota	312112-811	1232131311	1222211122	224-431111	1111313--4	241--12111
Stethorus	213212-721	1132141311	1221111111	114-441111	1121411111	2111-11111
Sympiezoscelus	513112-822	1132121111	2221111112	224-111111	1111313--4	241--12111
Synchroa	1-11112821	1122121111	2111111122	224-111111	1111223-11	2114111111
Syntelia	1-11112811	2112131111	1222111122	224-433111	1121211311	1113-11111
Sypilus	1-2112-811	1132131111	1111111122	224-411111	2111313--4	2111-12111
Systolosoma	1-1112-631	2112123112	2211111111	2231111111	1114113-11	3311-11111
Syzeton	513112-822	1132131111	1221111122	224-411121	1121113-13	2114111111
Tanylypa	1-1112-831	1122121111	2111111122	224-111111	1121213--4	2114111111
Taphropiestes	1-1112-813	1132131111	2211111122	224-311111	1111313--4	2111-12112
Taurocerastes	1-11112711	1123221111	1111111111	113?111111	1111113-11	1113-11111
Telegeusis	611312-211	1133222111	111111111?	1?11111111	1111111111	1221-11111
Temnoscheila	1-11112811	1112121111	2211111122	224-111111	1111313-11	2111-14111
Tenomerga	411112-811	1113121112	2111111112	2211111111	1211111313	142--11141
Teredolaemus	1-11112811	1222131111	2221111112	224-333111	2111413-13	2111-12111
Tetraopes	513212-811	1133131111	2221111122	224-311111	2121313--4	241--12121
Tetraphalerus	1-1112-811	1113131111	2111111122	2211111111	1111211111	1111-11111
Tetratoma	1-11112811	1332131111	2211111122	224-111111	2111213-11	2114111111
Thymalus	1-11112821	1332121111	2221111122	224-111111	1111313-11	2111-14111
Toramus	313312-811	1132131211	2222111122	224-441111	1111213--4	2111-11111
Torridincola	1-1112-811	1232131311	2222111111	2232111111	1211413-11	141--21111
Toxonotus	513212-841	1132121111	1222111122	224-333111	2121313--4	2114112121
Trachelostenus	1-11112731	2123121111	2211111111	114-111111	1121313-12	2114111111
Trachypachus	1-1112-631	2112123112	2211111111	2211111111	1114113-11	3311-11111
Tranes	513112-822	1132121111	2222211112	224-311111	1111313--4	241--12111
Tribolium	1-1112-831	1332121111	2211111122	224-111111	1113213--4	2114111111
Trichodes	4211112711	2133131111	2111111111	114-111111	1111313--4	241--12111
Trictenotoma	1-1112-821	1122131111	1111111111	224-111111	1121211313	2124211111
Tropisternus	1-11112711	2122121111	1111111111	114-411111	1111111313	1111-11111
Trox	1-1112-811	1122121111	1221111111	2211111111	1111213-11	1111-11111
Uleiota	1-11122821	1332121111	2111111122	224-311111	1111113--4	2111-11111
Urodontus	513212-811	1132121111	1222212112	224-311111	1211313--4	241--12111
Veronatus	611112-821	1222121111	2111111122	224-111111	1111411-31	141--11131
Vesperus	513112-811	1333131111	2211111122	224-111111	2111313-23	241--12121
Xerasia	3222112811	1332121111	2211111111	224-311111	2111313-11	241--14111
Xylariophilus	1-1112-811	1132131111	2221111112	224-333111	2111413-14	2111-12111
Ytu	1-1112-811	1232131311	2222111111	2232111111	1211413-11	141--11111

330	340	350	360	370	380	390
4121111-11	1111121131	24-1111111	2111321316	1121111115	2112--1-11	11113213-1
1111113112	3133223122	1111111111	11112211-9	--11111114	2111413111	1111325121
1111112122	4133211112	1421111112	11112111-9	--13211224	1211411111	11111133-2
----111-11	2112121111	1321111111	11113211-3	2121111113	3113----12	11111153-1
1?21111-12	4112122111	1321111111	111113-??8	--13211224	2111221111	11211133-1
1211112212	1111122121	2111111112	1111211213	1121211114	2111411111	11112153-2
1221112112	3132223122	1121111111	11112111-4	1121111114	2121411111	11113253-1
1311112112	4131212122	2111111111	11211221-8	--11111114	2111411111	1111323211
1111111-11	1112111111	14-1211111	1111???1-7	3?13211214	2123----11	12211113-1
1211121-12	4122221??1	14-1??????	??????????	??????????	??????????	??????????
1221111-12	3121212121	1111111111	11111211-4	1113211114	3113----11	11112133-1
1111411-12	4123211112	2221111111	11211221-9	--13211224	2111214211	11111133-2
1121111-22	4122211131	1211111152	11111111-4	1111111114	1111131111	111?213111
1111112112	1121111111	1111111111	11111111-4	1111111114	1111131111	111?213111
1221112112	4122121211	1221112112	1111321318	--21212116	1112--1-11	11111113-1
3211112112	3132213122	1111111112	11113211-5	1121111114	1121431111	11112233-1
1221112112	41322?1122	1121111111	11112111-3	1?12211114	2121421111	1112115111
1111113112	3131223122	2111111111	11112211-4	3121111115	2112--3-11	1111323121
1111112112	4133212122	1111112112	111113-419	--21111116	1112--1-11	11111133-1
1321412112	3131211122	1121111111	11111121-6	1111111114	2111421111	1111215111
1111111-12	1113211111	1111111111	11111211-6	1111111116	1122--2-11	1111111211
1221112112	4121111111	1111112112	1111321319	--21212116	1112--1-11	11112113-1
1211313112	3133223122	1111111111	1111211714	1111111114	2111411111	1111223121
1211111-12	1132222122	2121111111	11112211-8	--13211224	3111214212	11111133-2
1221112112	3133221122	24-1111111	212113-1-9	--21111114	2311421111	11111213-1
1121121-22	1121211121	14-1111111	11112211-3	1113211423	2111213211	11111133-1
1321112112	3131223122	1211111111	1111121519	--11111114	2111421111	1111323211
3211112112	3133213122	2121111111	11112211-9	--21111114	2111413111	1111225121
1121112112	3132212122	2111111111	11111121-3	1111111114	2111411111	11113213-1
1221111-12	2111211111	14-1112112	1111221319	--21111114	2111121111	1112113121
1211-?????	??????????	???1??????	??????????	??????????	??????????	??????????
1211113112	3133213122	1111111111	1121221315	2111111114	2111411111	11112133-2
3211112112	4133211132	1111111111	112113-329	--21111113	1111421111	1111321111
1211113112	3131212122	1111111211	11112111-3	1111111114	1111431111	1112225111
1221413112	4131111112	2121111111	2121121329	--21111115	1321421111	11111213-1
1211??????	??????????	??????????	??????????	??????????	??????????	??????????
1211112112	3132223122	1111111111	11112111-4	1111111114	1111421111	11112133-1
1211113112	31332?2122	2111111111	11211211-4	1?21111114	1111421111	11112133-1
1221112212	4112211112	1311111111	11111111-4	1111111114	2121231111	1112215111
1221121-22	1122121111	1311221211	11122111-6	1211211115	1132--1-11	1111112111
1221112112	3131212132	2121112112	111113-417	1111111116	1212--1-11	1111123211
1221413112	3131223122	1121111111	11112211-4	2121111114	2111413111	1111223221
1121121-22	1121211121	1421111111	11112211-3	1113211423	3111213211	11111133-1
1221112112	4122111111	1121112112	1111321317	1121212116	1112--1-11	11112233-1
1111112112	41212?3122	2121111111	11112211-4	3?21111114	2111413111	1111213211
1211112112	31332?3122	1111111111	1121121314	1111111114	2111411111	11111133-1
1211412112	3133223122	1111111111	11112111-9	--11111114	211????11	1111311211
1211111-12	3121212111	1111111113	11112211-3	1113211114	3123----12	11111133-1
1211111-12	11111?1111	1111112112	1111221218	--11111114	2111411111	1112213122
1321113112	3132222122	2111121111	11111111-3	3112211114	3111421111	1112225112
1211111-12	4131212132	2111112111	2111321318	--11111116	1212--1-11	1111213121
1111111-22	4133211122	1111111211	11111221-9	--21211111	3111--2-11	1112115111
1221113112	3133211122	2111111111	2121121316	1111111114	2111413111	11111213-1
1221112112	3122212122	1221111111	11111111-3	1113211114	1111421111	1112215111
1211113112	3121212122	1111111141	111113-1-3	1111111114	1111431111	1112225112
1221121-22	1122121111	14-1221211	11122111-6	1211211115	2132--1-11	1111112111

Table 1. Morphological data matrix. Continued.

	400	410	420	430	440	450
Schizopus	1111---121	111222111-	---2121131	-111133312	-113123-2-	1111111111
Scraptia	111121-311	1113151122	1111121111	1111122221	111312122?	1111111121
Selonodon	1111---321	212321111-	---1111121	1311123211	1212122-2-	1112111121
Sialis	1111---321	121221111-	---1112111	1311121312	-113221211	2111111121
Silis	1111---321	121321111-	---1111111	14---23211	1213123-2-	1211111111
Simplocaria	1111---311	111211111-	---1111111	1311122211	1113213-11	1111111121
Sirrhas	1111---311	2112151121	1211121111	1211122121	111312122-	1111111121
Smicrips	111121-122	--12251112	1112131121	14---33131	111113132-	1111111121
Spaminta	1111---112	--1-2411--	---4---131	14---13112	--11121111	1111111111
Spanglerogyrus	??????????	??????????	??????????	??????????	??????????	??????????
Spercheus	1111---311	111211111-	---1112121	1311133212	-213121211	1111111121
Sphaerites	1111---112	--1222111-	---1112111	14---22112	-21313132-	1111111132
Sphaerosoma	111121-311	1112151112	1111121111	1211122221	11121?????	1111111121
Sphaerius	111121-311	1112151112	1111121111	1211122221	11121?????	1111111121
Sphenophorus	1111---321	1113251112	1112121122	1211123211	1111113-12	1111111111
Sphindocis	1111---311	1112151112	1121121111	1311123121	111322122-	1111111121
Sphindus	1111111311	1112151112	?111121111	14---23221	1112121111	1111111121
Statira	111121-311	1112151112	1111121111	1311122131	1113121211	1111111121
Stegobium	1211---311	111213111-	---1121111	1311122212	-113113-11	1111111111
Stelidota	1111117321	1212251112	1311111121	1311133121	111312112-	1111111121
Stethorus	111121-322	--12251112	1111121131	-211122211	111112112-	1111111111
Sympiezoscelus	1111---321	1112251112	1112121122	1211123211	1112113-12	1111111111
Synchroa	111121-311	2112151122	1211121111	1211122231	1113121211	1111121111
Syntelia	1111---211	111322111-	---1112121	14---23112	-213133-2-	1111111121
Sypilus	1111---311	1112151112	1111121111	1121123212	-113113-13	1112111311
Systolosoma	1111---111	111222111-	---1112121	14---21212	-213132-2-	1111111121
Syzeton	111122-311	1113151122	1211121111	1211123221	111312122-	1111111121
Tanylypa	111121-311	1112151121	1211121111	1211122231	111312122?	1111111121
Taphropiestes	4111---311	1112151132	1211121111	1211122211	1112121211	1111111121
Taurocerastes	111121-211	111211213-	---1111111	1321122242	-112113-12	1111111111
Telegeusis	??????????	??????????	??????????	??????????	??????????	??????????
Temnoscheila	1111---321	1123251112	2111121121	14---22111	111122122-	1111111322
Tenomerga	111121-311	111211111-	---1121121	1112122231	111212122-	1111111211
Teredolaemus	111121-311	1112151132	1111121111	1211123121	1112121211	1111111121
Tetraopes	1111---231	1152251112	1112121121	1211123212	-111123-11	1112111311
Tetraphalerus	??????????	??????????	??????????	??????????	??????????	??????????
Tetratoma	1211---311	1113151112	1211121111	1211123111	1112121111	1111111121
Thymalus	1211---321	1112251122	1211121121	14---21111	1111121211	1111111121
Toramus	1111112311	1212151132	1111121111	1311132231	1112131111	1111111121
Torridincola	1111114311	1112151122	1113131111	1211222212	-113121211	1111111121
Toxonotus	111121-311	1112152112	1111131121	14---23131	1111113-11	1122111111
Trachelostenus	111121-311	1112151112	1111121111	1211123131	111312122-	1111111121
Trachypachus	1111---111	111222111-	---1112121	14---21212	-213132-2-	1111111121
Tranes	1111---321	11122511121	112121122	1311122211	1112113-11	1111111121
Tribolium	111121-311	1112151112?	111121111	1311123111	111312132?	1111111121
Trichodes	1111---321	11122511222	111121121	1311122211	111113132-	1111111121
Trictenotoma	111121-311	11121511211	311121111	1211122121	1113121 1??	1111112111
Tropisternus	1111---112	--1322111--	--1112121	1211123112	-213132311	1111111122
Trox	111121-311	111211213--	--1121111	1311122222	-113113-11	1111111121
Uleiota	1111111311	11121511321	111121111	1211122221	1112121111	1111111111
Urodontus	111121-311	11121521121	112131121	1----43-31	1111113-11	1111111211
Veronatus	1111118311	111213111--	--1111121	2311121341	1113121211	2111111111
Vesperus	1111---311	11121511121	111121111	1211122112	-113113-13	1111111111
Xerasia	1111126311	11131511221	211121111	1311122331	1112121111	1111111121
Xylariophilus	1111111311	11121511221	111121111	1211123121	1112121211	1111111111
Ytu	1111114311	11121511321	113131111	1211222212	-113121111	1111111121

460	470	480	490	500	510	
117-------	----211141	1111111112	11111-----	--11111111	11111?1151	521111
1122211121	2211111111	1111111111	11114-----	--11111113	1111121111	111111
1121221121	2111211111	1111111112	12111-----	--11111112	1111331151	521112
1112211111	--11111111	2111111112	11111-----	--11111111	1111??1111	1112--
1122211121	1-11211111	1111111112	11111-----	--11111111	1111141151	521112
1122211121	2111211111	1111111112	12111-----	--11111112	1111241151	521112
1122211121	2111111111	1111111113	1223111212	1111111112	1111221171	711111
1122211121	3-1121111?	1111111112	1213111132	1111111112	1111241131	311111
1133111111	--11211111	1111111111	11111-----	--11111111	1111111111	111111
??????????	??????????	??????????	??????????	??????????	??????????	??????
1122211121	2211111111	111111112-	1212111111	1111111112	11113?118-	81143?
?12??11121	??11?11211	112111111?	1?12121121	11?????11?	?111??1151	31111?
112??11121	3-11111111	1111111112	1213111132	1111111112	21113?1131	312121
112??11121	3-11111111	1111111112	1213111132	1111111112	21113?1131	312121
117-------	----211131	1111111112	12111-----	--11111112	1111251131	311131
1121211121	2111211111	1111111113	12211-----	--11211112	1111251131	311111
1122211121	2211111111	1111111112	11111-----	--11111111	11111?1111	111111
1122211121	2111111111	1111111112	1213111111	112----113	1111251111	111111
1123211121	2111212221	1111111112	11111-----	--11111122	1111231121	211111
1122211121	2111211111	1111111112	1213111112	2111111112	2111241132	312121
1122211122	3-11111111	1111111112	12111-----	--11111112	1111211111	111111
117-------	----211131	1111111112	11111-----	--11111111	1111141131	311111
1122221121	2111212111	1111111112	1213111122	1212111112	1111251131	311111
3123211121	2111211411	1121111112	1212121121	1111111112	1111231151	311111
1123121121	2211211111	1111211112	11111-----	--11111111	1111141111	111111
1112211111	--11211111	1111111112	11111-----	--11111111	21111?1111	111111
1122211121	2211211111	1111111112	1213111112	1111111112	1111121111	111111
1122211121	2111211111	1111111111	1213111122	1111111112	1311321111	111111
1122211121	2211211111	1111111112	1113111111	1111111111	2111151131	311111
1122211221	1-12211121	1111111112	11111-----	--11111111	1111151151	521112
??????????	??????????	??????????	??????????	??????????	??????????	??????
3122211121	3-11211111	1111111112	1213111112	1111111112	1111251131	311111
1113111111	--11211111	1111211112	12113-----	--11111112	1411231111	111111
1122211121	3-11121111	1111111112	1213111232	2111111112	1111221131	311121
117-------	----211111	1111211112	11111-----	--11111111	1111141111	111111
??????????	??????????	??????????	??????????	??????????	??????????	??????
1122211121	2211211111	1111111112	1213111212	2111111112	1111251131	311111
1123211121	3-11211111	1111111113	1113111222	1111111112	11111?1131	311111
1122211121	2211121111	1111111112	1213111111	1111111112	2111211112	112111
1122211121	3-11111111	2111111113	1112111111	1111111113	111111118-	112121
115311213-	---1211121	1111111112	12111-----	--11111112	1111241111	111111
3121211121	2111211111	1111111112	1223111122	1111111112	1211251111	111111
1112211111	--11211111	1111111112	1113111111	1111111111	21111?1111	111111
117-------	----211131	1111111112	11111-----	--11111111	1111151131	311111
1122211121	2111211111	1111111112	1213111112	1111111113	13112?1111	111111
1122211121	3-11211111	111?111112	1213111112	1111111112	1111251111	111111
1122211121	??11211411	1211111112	1213111112	1114111113	1111221111	11111?
1122211121	2211111141	111111112-	1212111111	1111111112	111132118-	811431
1122221121	2111211121	1111111112	11111-----	--11111111	111112?151	521111
1122211121	2111211111	1111111111	2113111121	112----111	2111111111	111111
117-------	----211111	1111111111	11111-----	--11111113	1111151131	211111
1121211121	4-11211111	1111111122	11111-----	--11111111	111112118-	811431
1123111121	3-11211111	1111111112	11111-----	--11111113	1111121111	111111
1122211121	3-11211111	1111111112	11111-----	--11111111	2111151131	311111
1122211121	3-11111111	1111111112	1213511232	1111111112	1111221132	312121
1122211121	3-11111111	2111111111	1112111111	1111111113	131114118-	112121

Table 2. List of character state changes supporting each numbered node discussed in text.

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4	117:2, 129:2, 134:2, 184:3, 197:2, 211:2, 214:2, 227:1, 465:2
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7	4:1, 173:4, 215:1, 333:3, 340:2, 419:1, 490:2
8	242:2, 397:2
9	126:2, 139:3, 181:7, 204:1, 218:1, 307:3, 311:2, 331:3, 406:5, 434:2
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