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## Arthropoda: Insecta

Editors Niels P. Kristensen & Rolf G. Beutel

**DE GRUYTER**

Richard A. B. Leschen  
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(Volume Editors)

# **Coleoptera, Beetles**

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*Scientific Editors*

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## 2.4 Cerambycidae Latreille, 1802

Petr Svacha and John F. Lawrence

**Distribution.** A worldwide family with approximately 35,000 described species (database Titan). The family is presently divided into eight subfamilies: Prioninae (over 1000 species), Parandrinae (119), Dorcasominae (over 300), Cerambycinae (ca. 11,000), Spondylidinae (ca. 100), Necydalinae (ca. 70), Lepturinae (ca. 1500), and Lamiinae (over 20,000). Species richness is highest in the tropics, where the fauna comprises mainly taxa belonging to the subfamilies Prioninae, Cerambycinae and Lamiinae. Some higher taxa (at the level of subfamilies, the primarily Northern Hemisphere Necydalinae, Lepturinae and Spondylidinae) are absent or scarce in the tropics and often limited to higher elevations. Dorcasominae is very diverse (second largest following Lamiinae) in Madagascar. Only four subfamilies (Prioninae, Parandrinae, Cerambycinae, and Lamiinae) occur in Australia, New Zealand and the Pacific islands, and Australia belongs to the very few major regions where species of Lamiinae are outnumbered by Cerambycinae (McKeown 1947; Forchhammer & Wang 1987).

**Biology and Ecology. Adult defense and mimicry.** Ancestral cerambycids were probably dull, somber-colored, crepuscular or nocturnal beetles. Such species still prevail in Prioninae, Parandrinae, Spondylidinae, and in the two related families Disteniidae and Vesperidae. Some nocturnal adults are hidden during the day (they may even return to their exit galleries), and their adaptations are generally “mechanical”, such as antipredatory spines or pilosity, burrowing modifications, etc. However, the perplexing diversity of color and form and the clear mimetism of many forms active or exposed during the day suggest that visually orienting vertebrate predators are high on the list of their enemies. Many cerambycids (particularly Lamiinae) are cryptic, resembling bark, lichens or even bird droppings. Although crypsis is useful to both diurnal and nocturnal species, mimicry occurs more in day-active forms. Lycid, cantharid or meloid beetles (Fig. 2.4.4 F) or aculeate Hymenoptera (Fig. 2.4.4 U, 2.4.5 J, N, 2.4.6 K, L, 2.4.8 G) are models for Necydalinae and some members of the remaining subfamilies, except Parandrinae. Hymenopteran mimicry may involve body shape, color pattern, reduced elytra and exposed hind wings (sometimes without apical folding) and characteristic movements. Ant mimics may occur among their models on the host trees (Vives *et al.* 2011; Vives 2012) but inquillines are unknown. Cerambycid mimicry has been mostly assumed to be Batesian, although palatability of mimics was seldom rigorously tested. In a very unusual case of a

Batesian mimic (*Elytroleptus* Dugés, Cerambycinae) feeding upon its lycid model (Eisner *et al.* 1962), the wounds inflicted by the cerambycids are often non-lethal, and *Elytroleptus* apparently is not unpalatable or distasteful even if much of the lycid prey is consumed (Eisner *et al.* 2008). In some cases, for instance the East Asian lamiine genus *Doliops* Waterhouse mimicking various species of the curculionid genus *Pachyrhynchus* Germar, the model is not known to be noxious. However, unlike *Doliops*, the weevils are extremely heavily sclerotized and may be mechanically protected. In some species possessing very different discrete color forms and/or remarkable sexual dimorphism/dichroism (e.g., some anacoline Prioninae), either one form or sex may be mimetic, or each possibly mimics a different model; in extreme cases, the male and female beetles are difficult to reconcile as conspecifics (Fig. 2.4.2 L, M).

Bright coloration of some cerambycids is considered true aposematism. The lamiine genus *Tetraopes* Dalman in Schoenherr, with predominantly red adults, sequesters cardenolides from its host-plant *Asclepias*, although the effectiveness of the chemical protection has been questioned (references in Allison *et al.* 2004), and Linsley (1959) cites examples of birds feeding on *Tetraopes* beetles. Other antipredatory modes, such as iridescent colors that abruptly change with viewing angle or brightly colored abdomens visible only in flight, are common in cerambycids. The lamiine *Onychocerus albitarsis* Pascoe has spine-like terminal antennomeres (present also in other species) modified as scorpion-like stingers that are used in defense (Berkov *et al.* 2008).

Both sexes in subfamilies other than Prioninae and Parandrinae usually possess a stridulatory device consisting of a striated plate on the mesoscutum (Fig. 2.4.14 D–G) and ridge(s) on the ventral face of the posterior pronotal margin. Because both sexes usually stridulate when disturbed or handled, the sound is assumed to be defensive, though some adults also produce sounds during courtship and copulation. Certain Prioninae developed a different sound-producing mechanism as a defense (rubbing ridged hind femora against finely striate lateral elytral margin).

**Adult feeding.** Butovitsch (1939) attempted to classify the types of adult feeding in Cerambycidae. In many presumably basal groups (Parandrinae, most Prioninae, many Cerambycinae, Spondylidinae), the adults do not feed and the midgut may be rudimentary and thread-like, or they may imbibe fluids, such as fermenting sap, or feed on ripe or fermenting fruits. Samuelson (1994) proposed pollinophagy as the ancestral type of chrysomeloid adult feeding, but this proposal does not fit cerambycids, in which presumed basal forms are often large and/or lack a suitable type of mouthparts. Widespread florivory in the Lepturinae, Dorcasominae and Cerambycinae does not extend to some of

their possible basal groups; however, feeding on anemophilous pollen, spores or similar material might be ancestral and precede modified mouthparts with a prominent galea and lacinia bearing long, often apically curved, setae. Crepuscular florivory has been recorded by Danilevsky & Miroshnikov (1981) for the lepturine *Enoploderes sanguineum* Faldermann that visits flowers of *Swida sanguinea* at sunset. The universal obligatory adult feeding of Lamiinae on living plants (typically leaves or fresh bark, usually but not always of the same plant taxon that serves as larval host) or on dead bark and fungi is undoubtedly apomorphic. Fungal fruiting bodies are a poorly known but possibly overlooked and relatively widespread adult food source for certain lamiine taxa (review and references in Adlbauer 2004), and records of other Lamiinae feeding on bark of dead branches (e.g., some *Mesosa* Latreille or *Pogonocherus* Dejean in Cherepanov 1983, 1984) may in part concern unrecognized fungivory. Pollen- or nectar-feeding is very rare in Lamiinae and probably just a supplementary food source. Adults of an undescribed Chinese lamiine species of *Falsomesosella* Pic that developed in fallen rotting branches of a broadleaved tree produced dark feces while in pupal chambers and are thought to have fed on the (possibly fungal) material on the walls of the pupal cells (C. Holzschuh, personal communication).

Whereas the life span of emerged adults is usually measured in weeks or even days for many species, certain larger Lamiinae may be active for several months under laboratory conditions when provided with food. Little is known about some temperate Lamiinae in which emerged adults overwinter and may show activity both before and after winter.

**Chemical ecology** of cerambycid adults was summarized by Allison *et al.* (2004). A variety of chemical cues is used for host location, such as host kairomones, pheromones of other herbivores (e.g., bark beetles) or smoke volatiles. Mating usually occurs on or near the host plants, florivorous species typically mate on flowers. Volatile male-produced sex (attracting females) or aggregation (attracting both sexes) pheromones are known in several Cerambycinae, Lamiinae and *Tetropium* Kirby of Spondylidinae (Silk *et al.* 2007 for the latter). They usually contain short-chain alpha-hydroxyketones or diols, fuscumol (= geranyl acetol) in *Tetropium* and some Lamiinae and possibly Cerambycinae (Mitchell *et al.* 2011), but occasionally different compounds and/or more complex blends (e.g., Lacey *et al.* 2008; Ray *et al.* 2009 b); they may also work in synergy with host volatiles (Ginzel & Hanks 2005; Silk *et al.* 2007, 2010). Although this type of pheromone was termed long-range in Allison *et al.* (2004), in *Hylotrupes* Audinet-Serville the effect was in fact limited to a few meters (Reddy *et al.* 2005). In Cerambycinae, the glands were found on the male prothorax in many species of several tribes (Hesperophanini

and relatives, Callidiini, Clytini or Curiini: Nearn & Ray 2006; Ray *et al.* 2006). The larger, more complex prothorax in many males of various tribes (particularly in Cerambycinae and Prioninae) may be associated with production of such pheromones (Fig. 2.4.14 A–C). Male-produced volatile pheromones cannot be expected (and associated modified male prothoraces do not occur) in some Prioninae in which females are flightless, at least until a portion of the eggs are laid (virtually no Cerambycinae have flying males and flightless females). A short-range, female-produced volatile sex pheromone was implied in *Semanotus japonicus* (Lacordaire) by Fauziah *et al.* (1992). True long-range female sex pheromones were presumed or behaviorally demonstrated in some Prioninae (*Prionoplus reticularis* White: Edwards 1961 b; *Prionus californicus* Motschulsky: Cervantes *et al.* 2006; Barbour *et al.* 2006) and Cerambycinae (*Callisphyris* Newman: Kraemer 1990). The pheromone of *P. californicus* is produced in glands associated with the ovipositor and was identified as (3R,5S)-3,5-dimethyldodecanoic acid (Rodstein *et al.* 2009, 2011). In Lepturinae, (Z)-11-octadecen-1-yl acetate was identified as a probable female long-range pheromone in *Ortholeptura* Casey (Ray *et al.* 2011), and (4R,9Z)-hexadec-9-en-4-olide in *Desmocerus* Dejean (Ray *et al.* 2012). Because long-range pheromones require high sensitivity by the receiver, males often have flattened, serrate or pectinate/flabellate antennae with large sensory surfaces (Fig. 2.4.1 B, E, 2.4.2 H, 2.4.3 R, 2.4.4 R, etc.), which occur in several subfamilies but are nearly unknown in Lamiinae.

Long-range female pheromones may be plesiomorphic because of their presence in Vespertidae (*Migdolus* Westwood and *Vesperus* Dejean) and Oxypeltidae; however, the identified compounds in *Migdolus* and *Vesperus* differ chemically and may be produced by glands at different locations. Cross-attraction of different related species was observed for aggregation pheromones (e.g., Lacey *et al.* 2009; Teale *et al.* 2011) and long-range female pheromones (Kraemer 1990; Barbour *et al.* 2011), and the same compounds may be used by unrelated taxa from different subfamilies (e.g., fuscumol or its acetate; Mitchell *et al.* 2011).

Many species probably lack long-range volatile pheromones and aggregate on suitable host plants or on flowers; mate location depends on antennal and in some species also palpal contact (in some Lamiinae, visual or perhaps vibrational stimuli may have supplementary roles: Wang *et al.* 1996; Fukaya *et al.* 2005; Lu *et al.* 2007). Males of many flower-visiting Lepturinae ignore proximate females until antennal contact, and Heintze (1925, *vide* Butovitsch 1939) showed that males of some Lepturinae became “frigid” after complete (but not partial) amputation of antennae, although they could live for a week and were capable of food location.

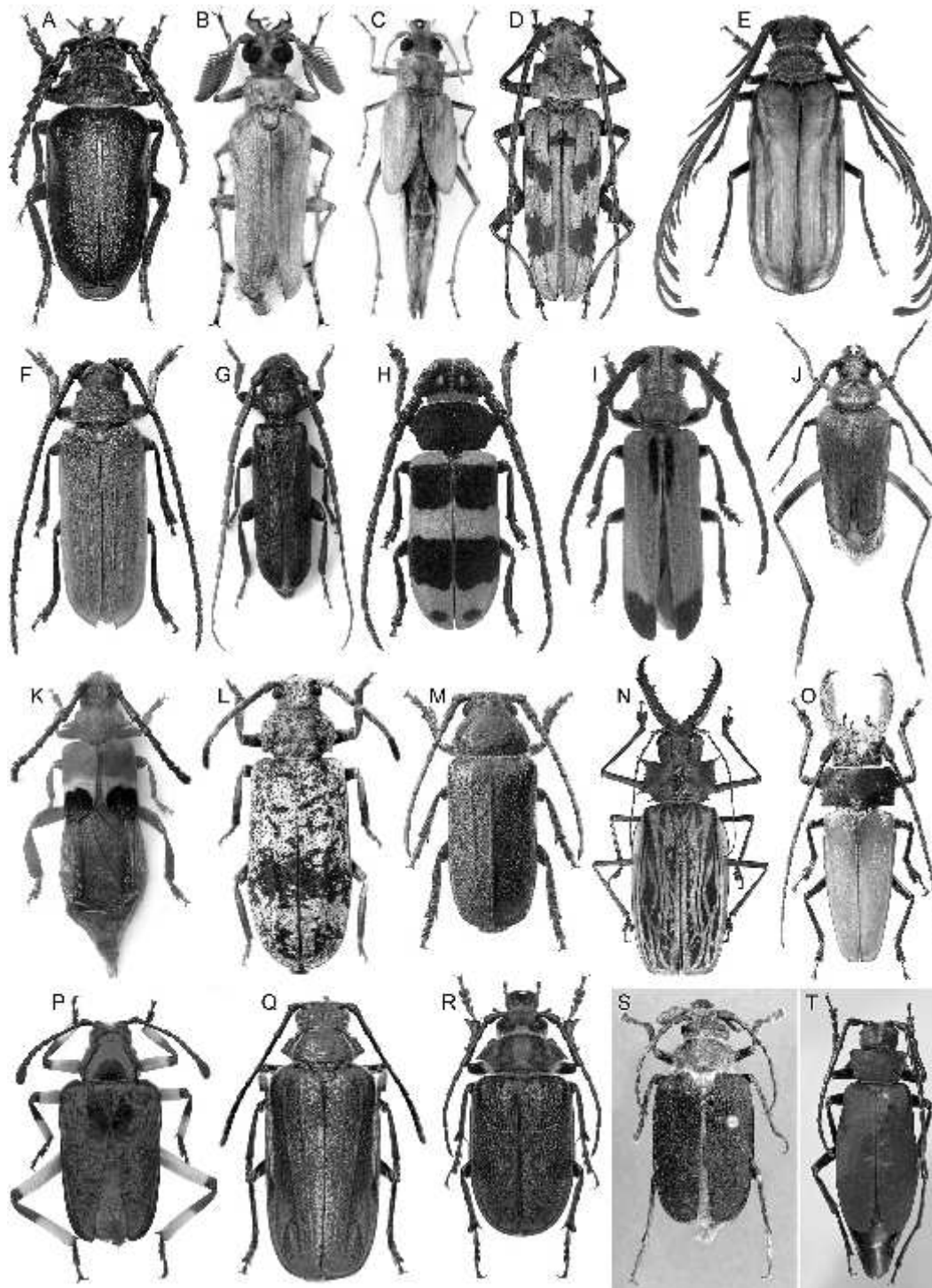


Fig. 2.4.1 Adults of Prioninae, dorsal view (data about size or sex not available for some specimens in plates 2.4.1 to 2.4.9). A, *Prionus coriarius* (Linnaeus), male, size unknown; B, *Microarthron komaroffi* (Dohrn), male, 22 mm; C, *M. komaroffi*, female, 32 mm; D, *Baraliphton maculosum* J. Thomson, male, size unknown; E, *Eboraphyllus middletoni* McKeown, male, 36 mm; F, *Delocheilus prionoides* J. Thomson, male, 26 mm; G, *Anoeme nigrita* (Chevrolat), male, 25 mm; H, *Sobarus poggei* Harold, male, 22 mm; I, *Stolidodere dequaei* Basilewsky (possibly a junior synonym of *S. aurivillii* Hintz), male, 20.5 mm; J, *Drumontiana amplipennis* (Gressitt), male, size unknown; K, *Erythraenus borneensis* Bates, female, 19 mm; L, *Lulua squamosa* Burgeon, female, 11 mm; M, *Elaptus brevicornis* Pascoe, male, 18 mm; N, *Macrodonia cervicornis* (Linnaeus), male, size unknown; O, *Callipogon barbatum* (Fabricius), male, 89 mm; P, *Casiphia vietnamica* Drumont & Komiya, female, 24.5 mm; Q, *Phaolus metallicus* (Newman), female, 16 mm; R, *Sceleocantha* sp., male, 26 mm; S, *Sceleocantha gigas* Carter, male, 24 mm (holotype of *Tillyardia mirabilis* Carter); T, *Meroscelis opacus* Buquet, female, size unknown. (A © M. Hoskovec; B, C © M. L. Danilevsky; D © S. Ziarko; E, Q, R © CSIRO, Canberra; F–H, K–M, O © I. Jeniš; J © W. Bi; N © V. Seichert; S © Museum Victoria, Melbourne; T © N. P. Lord & E. H. Nearn.)

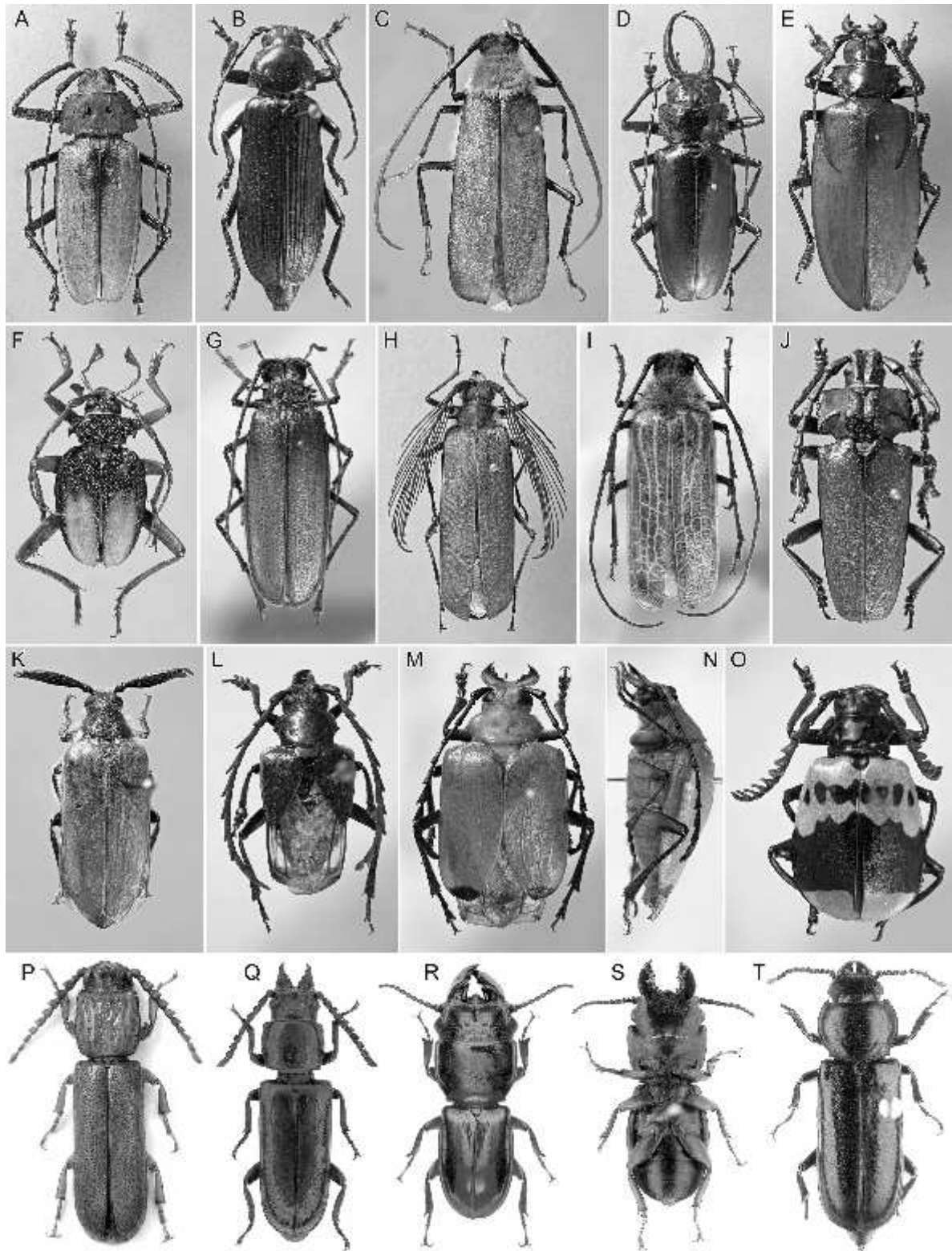


Fig. 2.4.2 Adults of Prioninae (A–N), Parandrinae (P–T) and uncertain subfamily position (O), dorsal view except for N and S; size unknown for A–O. A, *Xixuthrus domingoensis* Fisher, male; B, *Apocaulus foveiceps* (Harold), female; C, *Erioderus pallens* (Fabricius), male; D, *Stenodontes exsertus* (Olivier), male; E, *Titanus giganteus* (Linnaeus), male; F, *Apterocaulus heterogama* (Burmeister), male; G, *Trichoderes rugosus* Bates, male; H, *Sarifer seabrai* Fragoso & Monné, male; I, *Prionoplus reticularis* White, male; J, *Solenoptera dominicensis* (Gahan), male; K, *Tereticus pectinicornis* Waterhouse, male; L, *Anacolus sanguineus* (Le Peletier & Audinet-Serville in Latreille), male; M, *A. sanguineus*, female; N, *A. sanguineus*, female, lateral view; O, *Cycloprionus flavus* Tippmann, male; P, *Erichsonia dentifrons* Westwood, male, 8 mm; Q, *Stenandra kolbei* (Lameere), female, 21 mm; R, *Storeyandra frenchi* (Blackburn), male, 18 mm; S, *S. frenchi*, male, 25 mm, ventral view; T, *S. frenchi*, female, 22 mm. (A–O © N. P. Lord & E. H. Nearn; P © I. Jeniš; R © CSIRO, Canberra; S, T © A. Santos-Silva.)

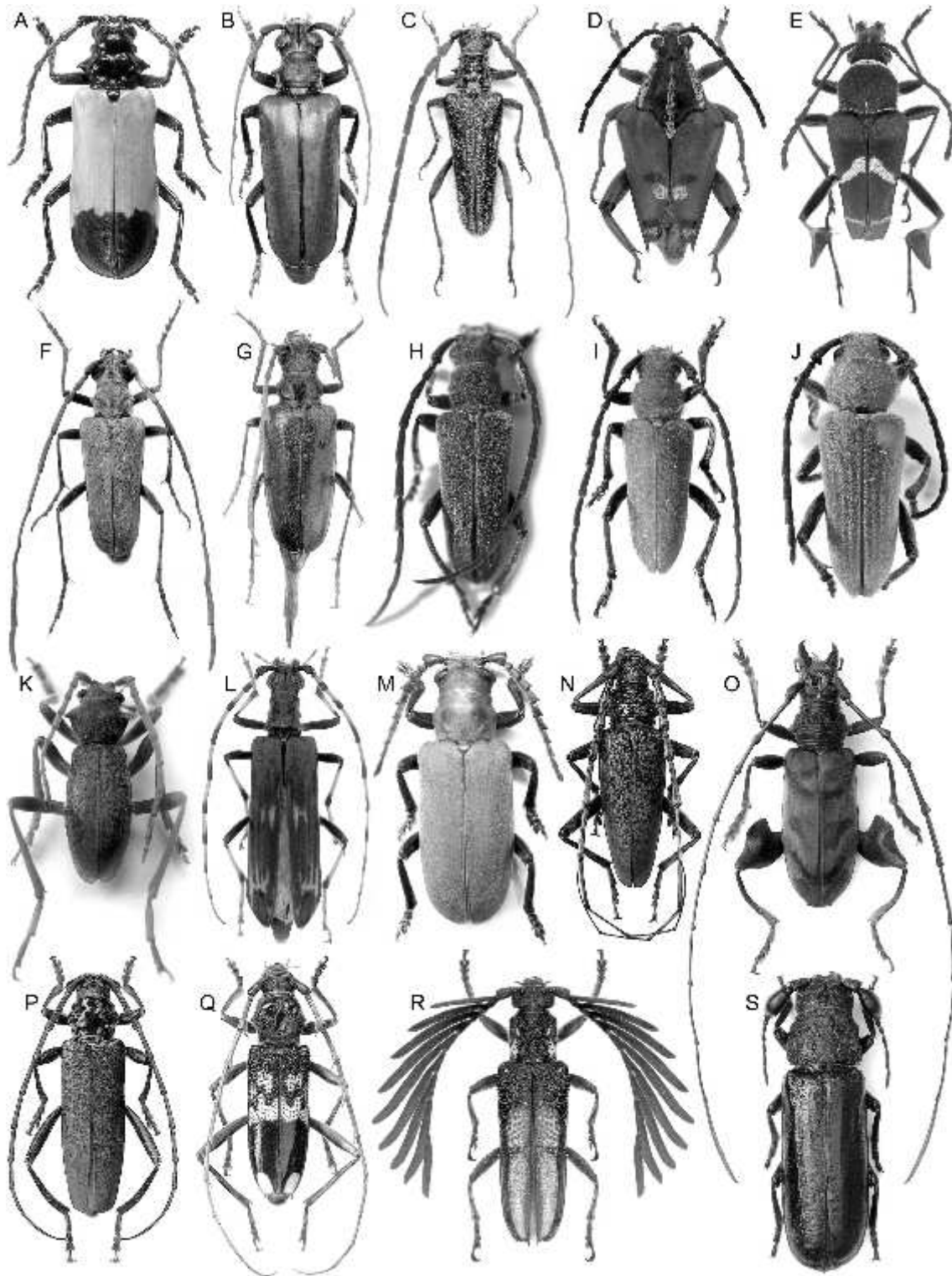


Fig. 2.4.3 Adults of Dorcasominae (A–L and possibly M) and Cerambycinae (N–S), dorsal view. A, *Dorcasomus delegorguei* Guérin-Méneville, male, 26 mm; B, *Xanthopiodus* sp., male, 28 mm; C, *Capetoxotus rugosus* Tippmann [possibly a junior synonym of *Aristogitus cylindricus* (J. Thomson)], male, 18 mm; D, *Trichroa oberthuri* Fairmaire, female, 21 mm; E, *Phyllotodes obliquefasciatus* Adlbauer, female, 12 mm; F, *Apatophysis barbara* (Lucas), male, 11 mm; G, *A. serricornis* (Gebler), female, size unknown; H, *Epitophysis substriata* (Gressitt & Rondon), holotype male, 10.2 mm; I, *Protaxis bicoloripes* Pic, male, 12 mm; J, *P. fulvescens* Gahan, male syntype, 13.5 mm; K, *Apterotoxitiades vivesi* Adlbauer, male holotype, 10.5 mm; L, *Zulphis subfasciata* Fairmaire, female, 20 mm; M, *Trigonarthron cinnabarinum* Boppe, male, 16 mm; N, *Cerambyx cerdo* Linnaeus, male, size unknown; O, *Utopia castelnaudi* J. Thomson, male, 35 mm; P, *Aromia moschata* (Linnaeus), male, size unknown; Q, *Phoracantha semipunctata* (Fabricius), male, size unknown; R, *Piesarthrius marginellus* Hope, male, 19 mm; S, *Bolbotritus bainesi* Bates, male, 55 mm. (A–C, F, I, M, O, S © I. Jeniš; G © M. L. Danilevsky; H © E. Vives; J © Natural History Museum, London; K © Lynette Clennell; N, P, Q © S. Ziarko; R © CSIRO, Canberra.)



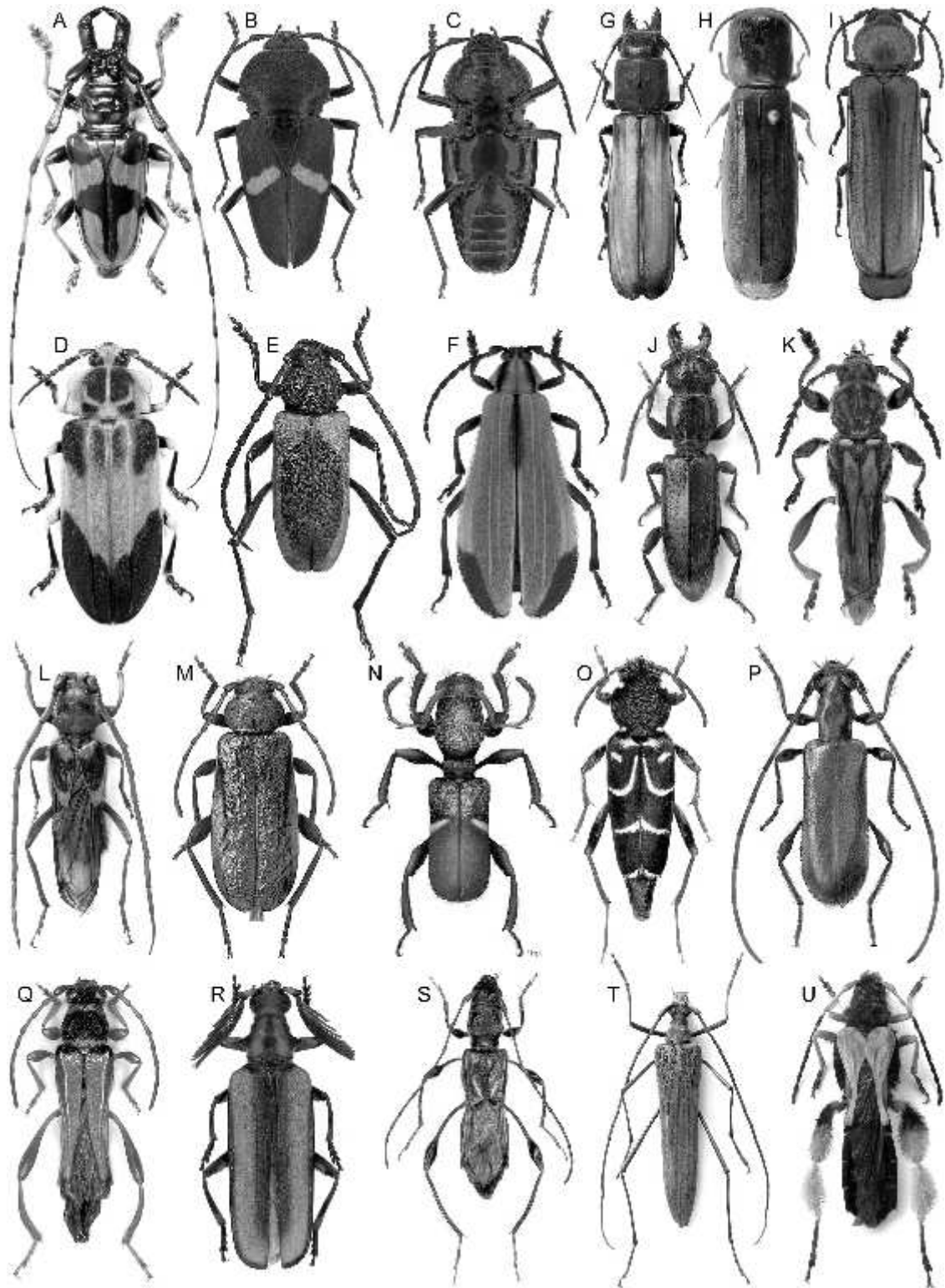


Fig. 2.4.4 Adults of Cerambycinae, dorsal view except for C. A, *Trachyderes mandibularis* (Dupont), male, 34 mm; B, *Megaderus stigma* (Linnaeus), female, 20 mm; C, same, ventral view; D, *Allocerus spencei* (Kirby), male, 27 mm; E, *Purpuricenus kaehleri* (Linnaeus), female, size unknown; F, *Amphidesmus theorini* Aurivillius, female, 20 mm; G, *Torneutes pallidipennis* Reich, male, 66 mm; H, *Thaumasus gigas* (Olivier), male, 45 mm; I, *Xenambyx lansbergei* (J. Thomson), female, 37 mm; J, *Erlandia inopinata* Aurivillius, male, 14 mm; K, *Acypoderes abdominalis* (Olivier), female, 18 mm; L, *Macropsebium cotterilli* Bates, male, 42 mm; M, *Callidium aeneum* (De Geer), female, size unknown; N, *Licracantha formicaria* Lingafelter, holotype male, 4.9 mm (modified from color painting by Taina Litwak in Lingafelter 2011); O, *Xylotrechus antilope* (Schoenherr), female, size unknown; P, *Obrium cantharinum* (Linnaeus), male, size unknown; Q, *Stenopterus flavicornis* Küster, female, size unknown; R, *Plectogaster noellae* Bouyer, male, 43 mm; S, *Molorchus minor* (Linnaeus), female, size unknown; T, *Holopterus chilensis* Blanchard in Gay, male, 38 mm; U, *Callisphyrus macropus* Newman, female, 24 mm. (A, D, G, H, J, L, T, U © I. Jeniš; E, M, O, P, S © S. Ziarko; Q © M. Hoskovec.)

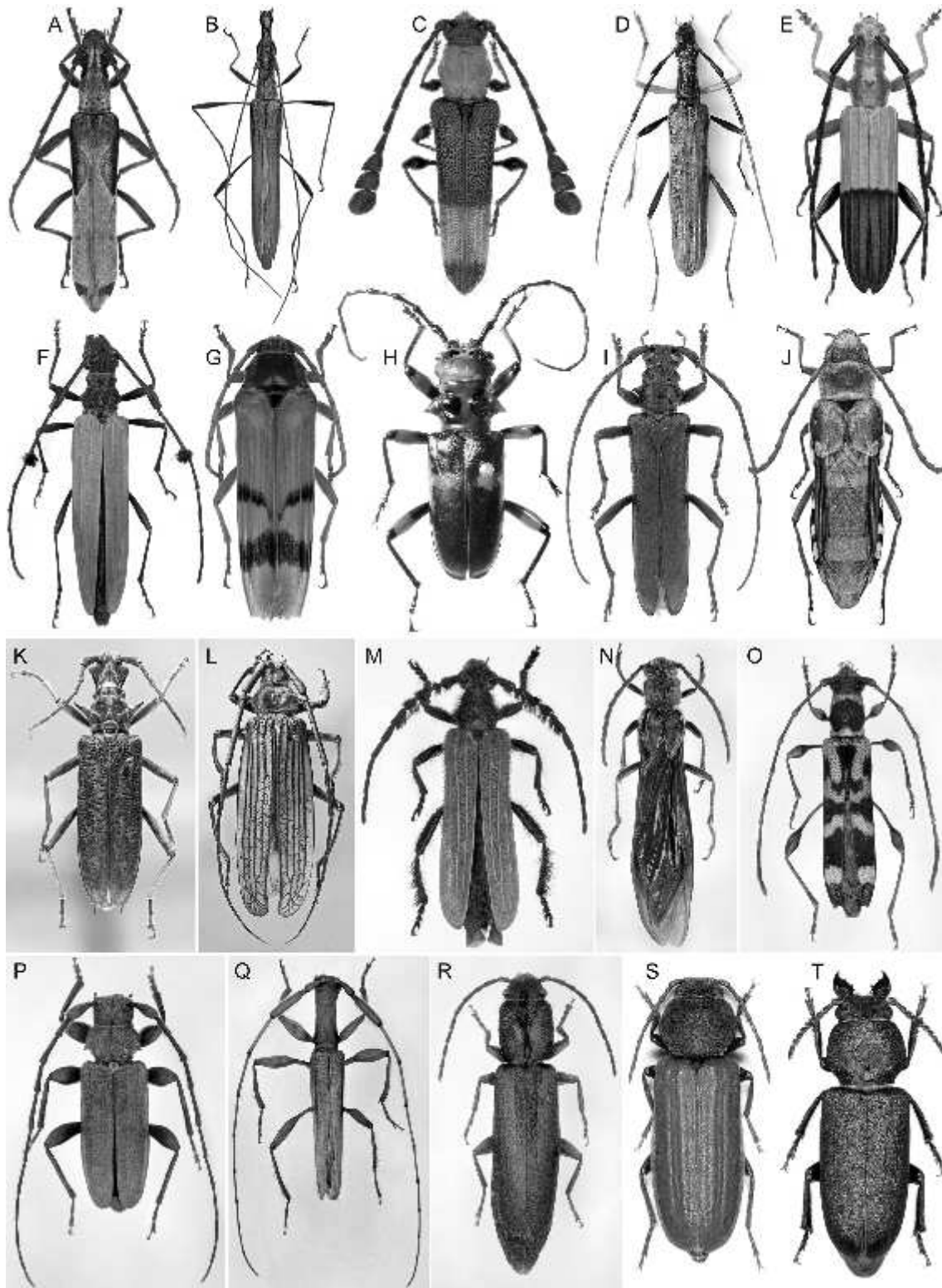


Fig. 2.4.5 Adults of Cerambycinae (A–Q) and Spondylidinae (R–T), dorsal view. A, *Uracanthus triangularis* Hope, female, 23 mm; B, *Rhinophthalmus* sp., sex unknown, 17 mm; C, *Telocera wollastoni* White, male, 7 mm; D, *Stenopotes pallidus* Pascoe, female, 19 mm; E, *Stenoderus ostricilla* Newman, sex uncertain, 12 mm; F, *Tritocosmia* sp., female, 19.5 mm; G, *Tragocerus spencii* Hope, female, 27 mm; H, *Australodon nearnsi* Escalona & Šlipiński, male, 21 mm; I, *Phlyctaenodes pustulosus* Newman, male, 23 mm; J, *Hesthesis* sp., female, 24 mm; K, *Blosyropus spinosus* Redtenbacher, female, size unknown; L, *Acideres ricaudii* Guérin-Ménéville, male, size unknown; M, *Eroschema poweri* Pascoe, male, 12.5 mm; N, *Cauarana iheringi* (Gounelle), male, 20 mm (including wings); O, *Cleomenes takiguchii* K. Ohbayashi, female, 11.5 mm; P, *Opsimus quadrilineatus* Mannerheim, male, 11 mm; Q, *Sydax stramineus* Lacordaire, male, 11 mm; R, *Nothorhina punctata* (Fabricius), female, 10.5 mm; S, *Asemum striatum* (Linnaeus), female, size unknown; T, *Spondylis buprestoides* (Linnaeus), female, 17 mm. (A–C, E, G, H, J © CSIRO, Canberra; D © I. Jeniš; K, L © N. P. Lord & E. H. Nearn; S © M. Hoskovec.)

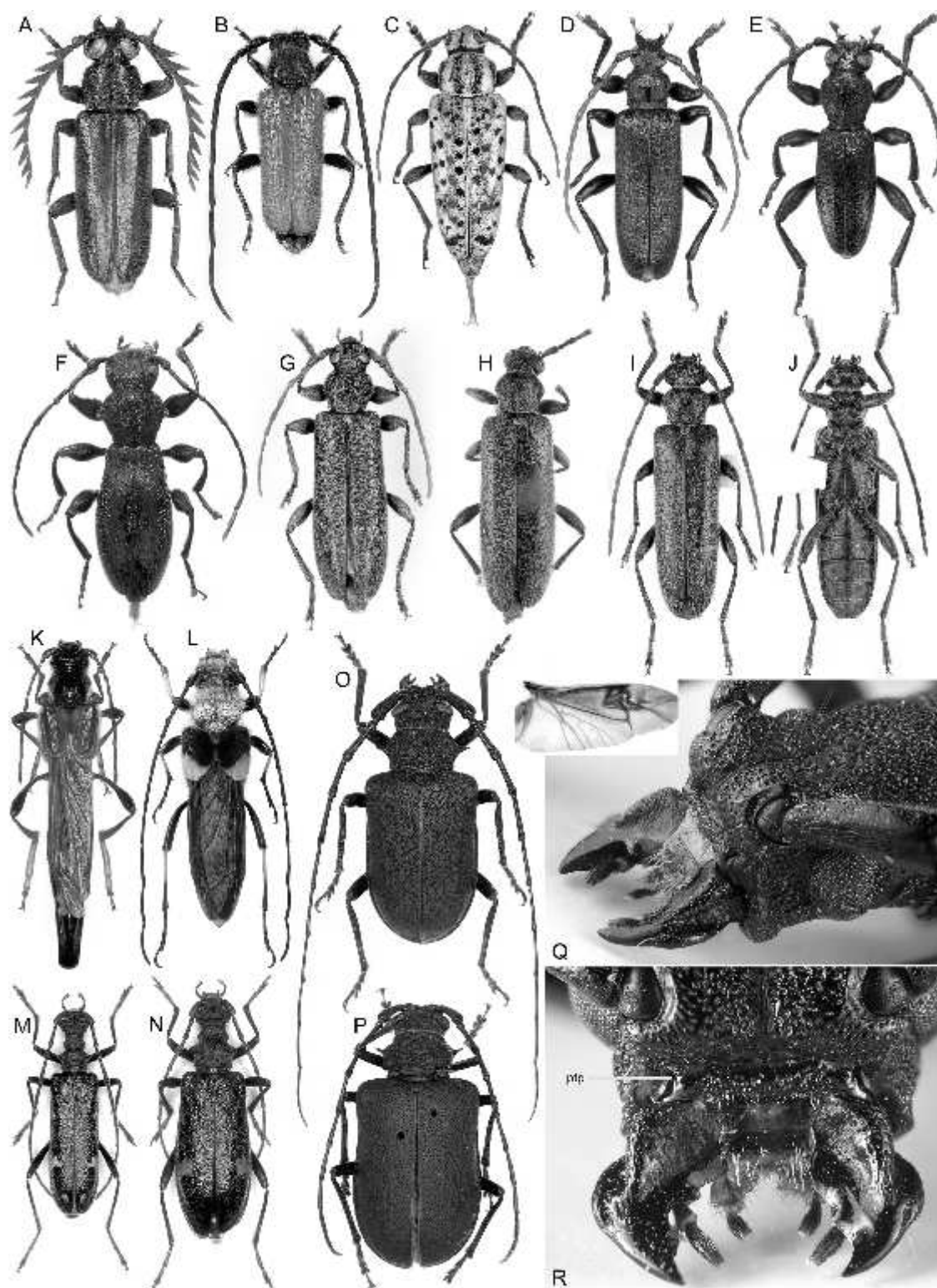


Fig. 2.4.6 Adults of Spondylidinae (A–J), Necydalinae (K, L), and Lepturinae (M–R), dorsal view except for J, Q, and R. A, *Pectoctenus scalabrii* Fairmaire, male, 9 mm; B, *Anisarthron barbipes* (Schrank), male, 8 mm; C, *Atimia huachucae* Champlain & Knull, female, 15 mm (excluding ovipositor); D, *Saphanus piceus* (Laicharting) (specimen from Czech Republic), male, 17 mm; E, *Drymochares starcki* Ganglbauer, male, 12 mm; F, *Michthisoma heterodoxum* LeConte, female, 10 mm (excluding ovipositor); G, *Oxypleurus nodieri* Mulsant, female, 13 mm; H, *Proatimia pinivora* Gressitt, holotype female, 13 mm; I, *P. pinivora*, male, 12.5 mm; J, same, ventral view; K, *Necydalis major* Linnaeus, female, size unknown; L, *Ulochaetes leoninus* LeConte, male, 22 mm; M, *Xylosteus spinolae* Frivaldszky von Frivald, male, size unknown; N, *X. spinolae*, female, size unknown; O, *Peithona prionoides* Gahan, male, 22 mm; P, *P. prionoides*, holotype female, 23 mm; Q, *P. prionoides*, male, head, lateral view (inset, right wing of the female holotype); R, *P. prionoides*, male, anterior part of head, anterodorsal view (ptp, pretentorial pit). (H © W. Bi and Sun Yat-sen University, Guangzhou; I, J © W. Bi; K, M, N © M. Hoskovec; L © I. Jeniš.)

Deantennation of males strongly impaired copulation efficiency in *Semanotus japonicus* (Fauziah *et al.* 1992). Final mate recognition depends on antennal contact even in *Prionus californicus*, which has a long-range sex pheromone (Barbour *et al.* 2007). The contact or tracing pheromones are cuticular organic compounds (hydrocarbons and derivatives; e.g., Yasui *et al.* 2007; Ginzl 2010; Spikes *et al.* 2010; Silk *et al.* 2011), usually in specific blends. In males of species depending primarily on antennal contact, particularly those searching tree stems, the antennae are sometimes very long to enable screening of larger surface areas (up to approximately 5 times the body length in males of some Acanthocini of Lamiinae), but without distinct surface enlargements or remarkable olfactory sensory areas (Hanks *et al.* 1996). According to Wang *et al.* (1996), males of the lamiine *Phytoecia rufiventris* Gautier attempt to copulate with conspecifics of both sexes and do not recognize females until the terminal part of their abdomen touches the female's last abdominal sternum. Some cerambycids possess glands producing human-perceptible scents, the role of which apparently remains unclear; in some cases, they may repel potential enemies.

**Mating systems.** Males are generally the (more) active sex in mate location and courtship and, at least in temperate species, are often protandrous (emerge earlier than females). The Australian *Storeyandra frenchi* (Blackburn) (Parandrinae) has brachypterous flightless males and winged females (Fig. 2.4.2 R–T), but its mating system is unknown. In some Neotropical Torneutini (Cerambycinae), the females are the more active sex; females of *Torneutes* Reich are attracted to light and males, although winged, remain in their galleries with their heads protruding (Fragoso *et al.* 1987: 198). If the torneutines *Thaumasus gigas* (Olivier) (Fig. 2.4.4 H; only brachypterous males known) and *Xenambyx lansbergei* (J. Thomson) (Fig. 2.4.4 I; only winged females known) are the same species (Fragoso *et al.* 1987; Monné & Napp 2005), they probably exemplify the extreme dimorphism associated with such a mating system. Enlarged male prothoraces and adjacent body regions bear probable glandular areas (Fig. 2.4.14 B, C) that may produce attractants, as known in some other Cerambycinae.

Sexual dimorphism ranges from virtually none to extreme (Fig. 2.4.1 B, C, 2.4.2 L, M) and males may be distinctly smaller (Fig. 2.4.7 N) or distinctly larger than females. Size-associated male dimorphism is known in some taxa and is assumed to be a non-Mendelian polyphenism “characterized by a relatively abrupt switch between morphs that corresponds with a critical, or threshold, body size” (Hartfelder & Emlen 2005). It may also apply to behavior, as in the cerambycine *Trachyderes mandibularis* Dupont, in which the male morphs use different mating strategies (Goldsmith 1985, 1987). Males may compete for mates or displace copulating or mate-guarding males (e.g., Ray *et al.* 2009 a), whereas females are often “choosy”, indi-

cating female sexual selection (Butovitsch 1939; Michelsen 1963, 1966; Funke 1957 for Lamiinae; Lingafelter 1998 for Parandrinae).

Copulation lasts from several seconds to several hours, and repeated copulations with the same or a different partner are common, although females may gradually become less receptive. Multiple copulations impaired reproductive success in *Phoracantha* Newman (Bybee *et al.* 2005) and may damage the female genital tract. Copulation mechanisms are poorly understood and may differ between higher taxa (Hubweber & Schmitt 2010). Details of sperm transfer and storage by females are virtually unknown; according to Edwards (1961 a), the prionine *Prionoplus* White does not form a spermatophore. Precopulatory isolation mechanisms may not be very strong in many taxa and intergeneric, intertribal and even intersubfamilial matings have been recorded, e.g., *Dinoptera collaris* (Linnaeus) (Lepturinae) and *Glaphyra umbellatarum* (Schreber) (Cerambycinae) (K. Adlbauer, personal communication).

In Lamiinae, adult food appears necessary for producing offspring, and some feeding usually precedes first copulation in both sexes; for instance, adults of *Monochamus galloprovincialis* (Olivier) become sexually mature in 5 to 12 days after emergence, immature males do not release attractants for mature females, and immature females are not attracted to mature males (Ibeas *et al.* 2008). Adults of other subfamilies sometimes do not feed at all; those that do feed are often capable of producing at least some offspring without adult feeding, and copulation may occur shortly after emergence.

**Host location, oviposition.** At longer distances, hosts are located by volatile chemical cues (host kairomones, volatiles of other xylophagous taxa such as bark beetles, probably fungal volatiles in species depending on specific types of fungal decay, pheromones in species that mate on suitable hosts). On a finer scale, other strategies may be added, such as visual selection (Campbell & Borden 2009) or random landing and probing (Saint-Germain *et al.* 2007). The selection of appropriate host and within-host oviposition site is important and, except in species with mobile terricolous larvae, determines the quality of larval food, although considerable within-host variability exists in dead decaying wood, enabling considerable substrate selection by the larvae and apparently lowering the oviposition selectivity of the females in the lepturine *Anthophylax attenuatus* (Haldeman) (Saint-Germain *et al.* 2010). Larger females may lay more numerous and larger eggs (e.g., Kato *et al.* 2000; Togashi 2007; Walczyńska 2008 a), and larger first instars may be better at overcoming host defense or other adverse effects.

Butovitsch (1939) classified the types of cerambycid oviposition. Eggs of most species are laid in or on the host substrate (in wood crevices, under bark or bark scales, etc.), either singly or in batches; some terricoles or root feeders oviposit in soil. Numerous species lay eggs on freshly dead or living hosts and

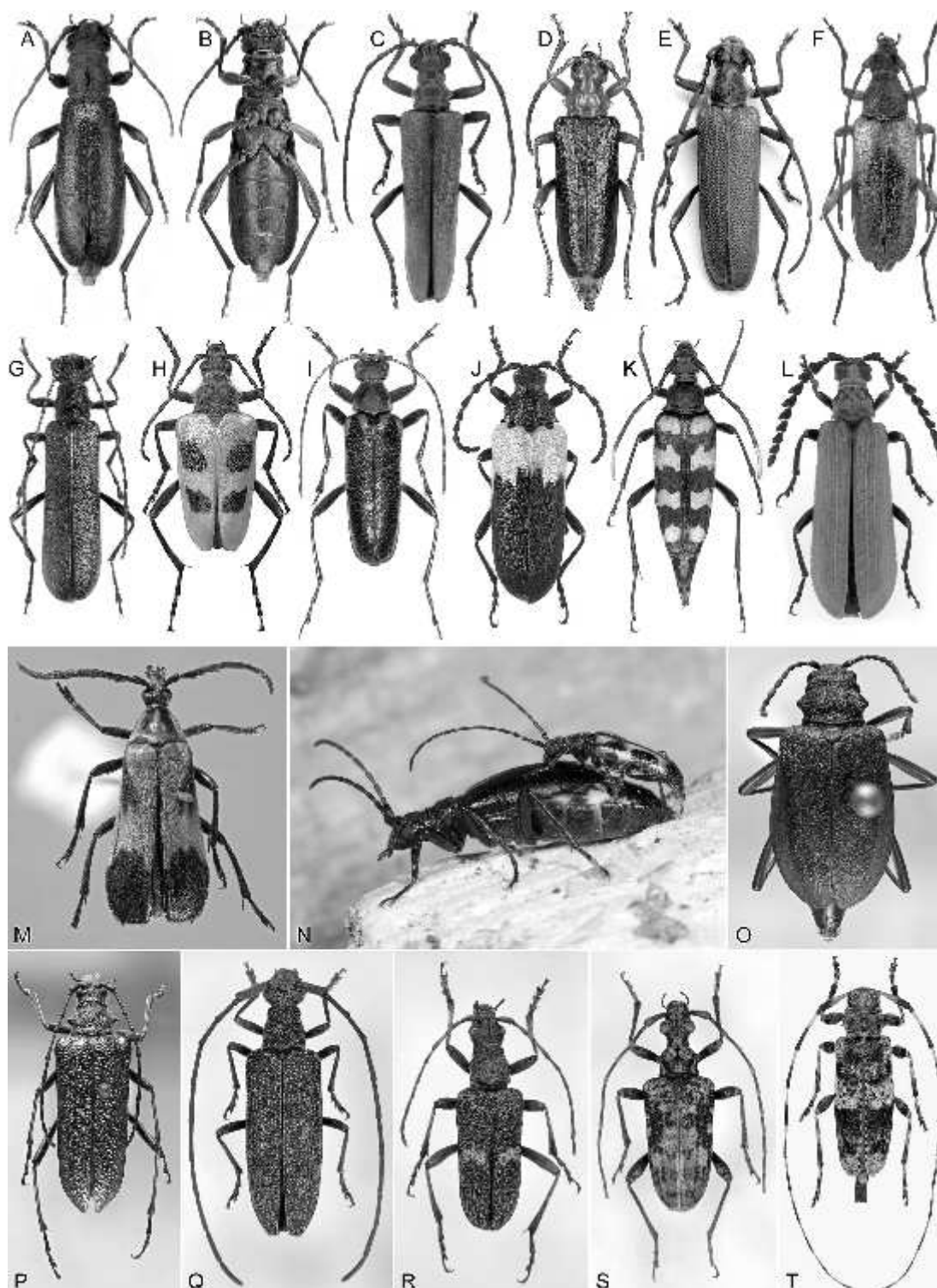


Fig. 2.4.7 Adults of Lepturinae (A–S) and Lamiinae (T), dorsal view except for B and N. A, *Teledapus celsicola* Holzschuh, female, 18 mm; B, same, ventral view; C, *Centrodera decolorata* (Harris), male, 21 mm; D, *Rhamnusium bicolor* (Schrank), female, 21 mm; E, *Enoploides sanguineum* Faldermann, male, size unknown; F, *Xenoleptura hecate* (Reitter), female, 10 mm; G, *Encyclops macilentus* (Kraatz), female, 7.5 mm; H, *Pachyta quadrimaculata* (Linnaeus), female, size unknown; I, *Cortodera humeralis* (Schaller), male, size unknown; J, *Desmocerus palliatus* (Forster), female, size unknown; K, *Leptura quadrifasciata* Linnaeus, female, 24 mm; L, *Pyrocalymma pyrochroides* Thomson, female, 22 mm; M, *Euryptera* sp., sex and size unknown; N, *Katarinia teledapoides* Holzschuh, copulating pair; O, *Piodes coriacea* LeConte, female, size unknown; P, *Anthophylax hoffmanni* Beutenmüller, male, size unknown; Q, *Caraphia lepturoides* (Matsushita), female, 12 mm; R, *Sachalinobia koltzei* (Heyden), male, 13 mm; S, *Apioccephalus punctipennis* Gahan, female, 12.5 mm; T, *Acanthocinus griseus* (Fabricius), female, 10.5 mm. (E © J. Kurzawa; F, G © M. L. Danilevsky; H © S. Ziarko; I © M. Hoskovec; J © S. W. Lingafelter; M, O, P © N. P. Lord & E. H. Nearn; N © W. Bi.)



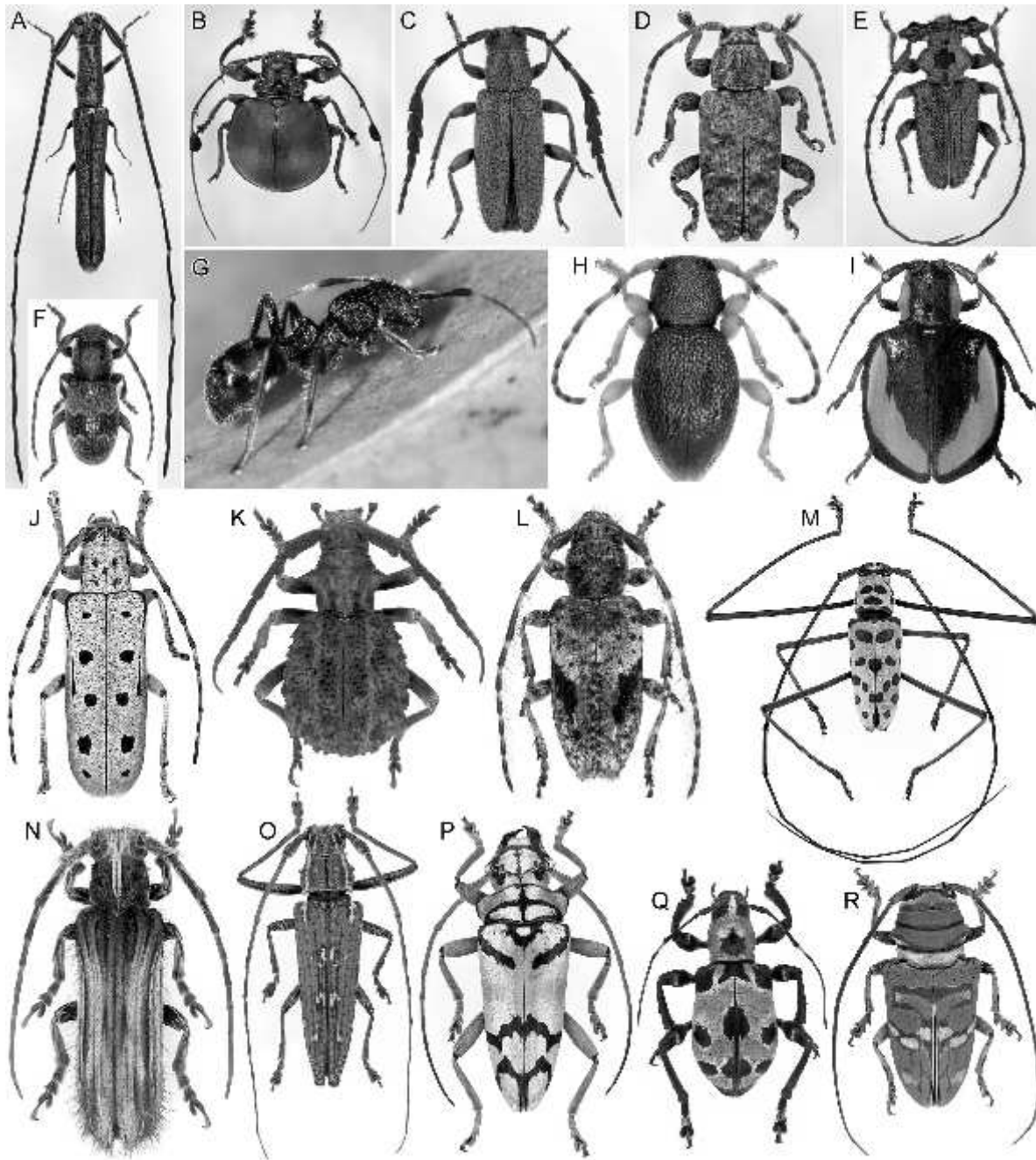


Fig. 2.4.8 Adults of Lamiinae, dorsal view except for G. A, *Anauxesis* sp., male, 12 mm; B, *Cyclopeplus batesi* J. Thomson, male, 10 mm; C, *Hemiladus dejeani* Buquet, female, 7 mm; D, *Enaretta* sp., male, 10 mm; E, *Tapeina* ?*melzeri* Zajciw, male, 9.5 mm; F, *Parmena balteus* (Linnaeus), ?female, size unknown; G, *Falsohomaemota novaecaledonica* Hayashi, a species mimicking ants of the genus *Rhytidoponera* (pers. comm., G. Monteith), sex and size unknown; H, *Somatidia aranea* Olliff, sex unknown, 4 mm; I, *Lycodesmus* sp. or *Ites* sp. (Hemilophini), sex unknown, 14 mm; J, *Saperda perforata* (Pallas), female, 16 mm; K, *Phantasis avernica* J. Thomson, male, 23 mm; L, *Pogonocherus decoratus* Fairmaire, female, 6 mm; M, *Gerania bosci* (Fabricius), male, 15 mm; N, *Xylorhiza adusta* (Wiedemann), male, 36 mm; O, *Homonoeca albosignata* Breuning, male, 28 mm; P, *Tmesisternus rafaellae* Lansberge, male, 29 mm; Q, *Doliops magnificus* (Heller), female, 13 mm; R, *Sternotomis pulchra* (Drury), female, 19 mm. (F © M. Hoskovec; G © Queensland Museum, Brisbane, photograph by J. Wright; H © CSIRO, Canberra; I © I. Jeniš.)

many trees have smooth bark, presumably to minimize oviposition opportunities. Most non-lamiine taxa use only the ovipositor for egg-laying (exceptionally, a circular oviposition incision is made by females of *Torneutes* of Cerambycinae; Fiorentino *et al.* 1997). When suitable oviposition sites are scarce, eggs may be attached by secretion to the host

surface and covered by debris, which is a strategy generally associated with a short, reduced ovipositor and brushes or combs on the female abdomen for collecting and applying cloaking material (e.g., trachyderine or obriine complexes in Cerambycinae). Females of some root-feeding Lepturinae (*Stenocorus* Geoffroy, *Pachyta* Dejean, *Akimerus*

Audinet-Serville) lay eggs at ground level, usually in the surface soil and often in large batches, and the active first instar larvae search for suitable roots. Larval feeding in those taxa typically commences far from the stem and proceeds proximally so that the larva enters thicker roots as it grows. In Spondylidini (*Spondylis* Fabricius and *Neospondylis* Sama), the feeding larvae behave similarly (Cherepanov 1979; Gardiner 1970), but the burrowing females of *Spondylis* oviposit directly on the roots (Cherepanov 1979) and first instars do not have to search for food.

Females of Lamiinae primarily use their mandibles to make often inconspicuous slits in the bark or in stems of herbs, through which they insert their slender ovipositor; lamiines are not known to oviposit on wood lacking bark (e.g., Kojima 1960). Usually only one or very few eggs are inserted through each slit. Eggs are on average larger than in other subfamilies, in extreme cases only a few mature eggs can be accommodated in the abdominal cavity. Even species of Dorcadiini, whose late instar larvae are terricolous, often oviposit in incisions on stem bases of their host monocots, usually grasses, and the young larva may feed internally for a short period (Fabbri & Hernández 1996). However, females of some *Acanthocinus* Dejean prefer to oviposit through bark beetle holes (Schroeder 1997; Dodds *et al.* 2002), as observed in laboratory colonies of *Morimonella bednariki* Podaný (personal observation, P. Svacha). Some Lamiinae (such as certain Saperdini) ovipositing in living trees make larger and more complex incisions that also serve to modify sap flow. Females of some Onciderini completely girdle living branches or stems in which they subsequently oviposit, which is the maximum parental investment known in cerambycids.

**Eggs and eclosion.** Cerambycids are oviparous. Eggs are elongate oval or fusiform to broadly elliptical and often have thin flexible chorion, and their shape can adapt to the tight spaces in which they are usually laid. Egg numbers range from dozens to hundreds; references to over 1000 are cited by Butovitsch (1939) and Duffy (1953), but the latter author cautions that eggs found in the ovaries at dissection may not be a realistic estimate of the species' oviposition capability. In fact, they may be either overestimations if females have eggs formed at emergence and die without laying all of them (e.g., Wang *et al.* 1998) or heavy underestimations in lamiines in which the eggs continuously form in the ovaries during most of the female's life. Among Palaearctic species, high numbers of eggs (up to over 400: Cherepanov 1979; P. Svacha, personal observation) have been recorded, for instance, in the lepturine *Aredolpona rubra* (Linnaeus) feeding in dead wood, and numerous eggs occur also in the soil-ovipositing root feeders. Eggs of such species are rather small: 1–1.5 × 0.3–0.5 mm in *Aredolpona rubra* (Duffy 1953; Cherepanov 1979), in which females measure up to 20 mm. However, even higher cumulative numbers of laid eggs (up to approximately 600–700) were reported for fed

females of some Lamiinae that survived and continuously oviposited for up to several months in the laboratory (Zhang & Linit 1998; Togashi 2007). Lamiine eggs (and thus first instars) are on average larger compared with other subfamilies, a feature facilitating faster development (see below).

Hatching usually occurs within 1 to 4 weeks from oviposition, sometimes less in warm regions (Butovitsch 1939), but in some Lamiinae the larvae may overwinter within the chorion, particularly if the eggs were laid late in the season [*Saperda carcharias* (Linnaeus): Ritchie 1920; some populations of *Psacotha hilaris* (Pascoe): Shintani & Ishikawa 1999 a; rarely in *Anoplophora* Hope: Lingafelter & Hoebeke 2002]. At hatching, the larva opens the chorion using egg bursters and/or mandibles; first instars of *Saphanus* Audinet-Serville (Spondylidinae) have been observed to use also the sharp urogomphal blades (Svacha & Danilevsky 1987) and urogomphal egg bursters are also present in the lamiine *Pterolophia* Newman (Kurakawa 1978). Although the function of the lateral thoraco-abdominal egg bursters has been questioned (Duffy 1953: 6–7), they laterally slit the egg chorion as a result of peristaltic movements of the larva. Because egg bursters are close to spiracles, the primary role of the lateral slits may be to enable breathing while the larva is still within the chorion, even if in many species (such as most Cerambycinae) the slits are entirely sufficient for the larva to escape from the eggshell (Gardiner 1966; Oka 1977; Kurakawa 1978; Kurakawa & Hukuhara 1979). The chorion is usually partly devoured by the hatching larva. First instars are fully functional and actively feeding.

**Larval biology.** Larvae are endophytic or live in soil, no free-living larval stages are known except for mature larvae of some subcortical Lepturinae and most Dorcasominae, which leave the hosts (usually at night) to pupate in soil. Some derived larvae of Lepturinae are capable of caterpillar-like locomotion when placed outside their galleries.

The cerambycid ancestor was probably a dead wood feeder and some cerambycid subfamilies still contain predominantly or exclusively species developing in dead wood (Parandrinae, Prioninae, Spondylidinae, Necydalinae, Dorcasominae). Some taxa of several subfamilies develop in dead wood in direct contact with living tree tissue, such as inner wood of tree hollows, wound scars or moist bases of dead branches surrounded by a living callus. Such habits are shared by some Spondylidinae (Anisarthrini) and Lepturinae (*Rhamnusium* Latreille, *Enoploderes* Faldermann, *Pedostrangalia* Sokolov, *Neopiciella* Sama, *Pachypidonia* Gressitt, etc.), and some Prioninae and Necydalinae also prefer this habitat. Development in fresh or living woody plants or in herbs is apomorphic and occurs predominantly in some groups of the remaining subfamilies; some species may induce galls. Larval feeding in dry, hard, seasoned wood is likewise apomorphic and virtually restricted to some Cerambycinae, the larvae of which possess specialized round “gouge-shaped” mandibles (Fig. 2.4.21 J,

2.4.25 E, F), a long cryptonephridial part of the gut (Fig. 2.4.19 J, K), and possibly other adaptations that make them suitable for such extreme conditions. The largely or completely subcortical feeding of many species may also be derived; in Lepturinae, for instance, the strongly flattened subcortical larval forms occur mainly among Rhaigiini, and, very rarely, in Lepturini. Some specialized groups develop in deep roots, in thick bark of living trees (some Dorcasominae, Lepturinae or *Nothorhina* Redtenbacher and *Tetropium aquilonium* Plavilstshikov of Spondylidinae), and a few species of Lamiinae and Cerambycinae feed as larvae in lianas but enter the supporting tree for pupation (Bee-son & Bhatia 1939; Duffy 1953: 43; Martins 2005 a: 31). Feeding in generative plant organs, such as cones or seed pods, is infrequent; development entirely within the seeds is exceptional. There is apparently only one confirmed leaf miner, the New Zealand *Microlamia pygmaea* Bates (Lamiinae) (Martin 2000). The transition to herbs was undoubtedly via thin branches and twigs of trees and shrubs in many Lamiinae, and some species (such as some *Parmena* Dejean or *Deroplia* Dejean) are capable of developing in both. The lamiine tribe Dorcadiini or some Lepturinae and Prioninae, however, probably became herb root feeders via transitional forms feeding in woody plants at or below ground level, and both types can occur among species of the same genus (such as *Cortodera* Mulsant). Some of the root feeders of woody plants and herbs sooner or later enter soil and feed on the roots externally, and a few groups spend almost their entire larval life in the soil (e.g., the entire lamiine tribe Dorcadiini and some derived Prioninae and Lepturinae). The biology of the lepturine *Pseudovadonia livida* (Fabricius), the larvae of which live in decomposing plant litter containing mycelium of the basidiomycete fungus *Marasmius oreades* (Agaricales) (Burakowski 1979), appears unique; the supposed closest relatives live in very strongly rotten wood or in fungus-infested outer bark.

**Larval hosts.** Host selection, host use and related issues have been extensively reviewed (Linsley 1959, 1961; Hanks 1999). There is no evidence that conifer feeding, considered plesiomorphic in the Phytophaga assemblage (Farrell 1998; Farrell & Sequeira 2004), is plesiomorphic for *extant* cerambycids (or other cerambycoids, see biology of Disteniidae, Vesperidae, and Oxypeltidae), though xylophagy or xylomycophagy is almost certainly a groundplan character and the *ancestral* cerambycids (if the taxon is indeed older than angiosperms, an assumption not universally agreed upon, see, e.g., Gomez-Zurita *et al.* 2007 b) could develop in gymnosperms. However, numerous and repeated switching between gymnosperms and angiosperms must have occurred since broad polyphagy (sympatric or allopatric) or sharp differences in host preferences between closely related species are not uncommon. Duffy (1953: 35) concludes that “the wide range of hosts selected by certain primitive groups of cerambycids seems to suggest that

polyphagy is phylogenetically a primitive habit”, and in a molecular phylogenetic study of a subgroup of Lamiinae, both monophagy and conifer feeding appeared to be derived (Toki & Kubota 2010). Of the two major extant gymnosperm families, the far more abundant Pinaceae is much more widely utilized, whereas species feeding on Cupressaceae are fewer and occasionally remarkable specialists (e.g., the spondylidine genus *Atimia* Haldeman). Monocots are used by very few possibly derived and often polyphagous xylophagous taxa (but palms are preferred by the Neotropical prionine genus *Macrodontia* Lacordaire; Monné 2002 b). However, some advanced herb feeders or root-feeding terricoles are monocot specialists (e.g., some *Typocerus* LeConte of Lepturinae, some Prionini of Prioninae, all Dorcadiini and some Agapanthiini of Lamiinae).

The reasons for and mechanisms of maintaining plant-host specificity are as poorly understood as in other groups. Species feeding in fresh or living plants are typically more host-specific, and it is no coincidence that the lamiine *Tetraopes*, feeding on living *Asclepias* plants (protected by cardenolides) and thought to receive from them chemical defense, has been investigated for possible coevolution with its host taxon (Farrell & Mitter 1998). However, the *Asclepias* cardenolides do suppress the root-feeding larvae and the advantage of *Tetraopes* may in fact be its ability to escape competition in a plant inaccessible to other herbivores rather than the acquired protection of adults, which is doubtful (see above). In addition to the partly induced cardenolides, attacked roots emit increased amount of volatiles attracting entomopathogenic nematodes (Rasmann *et al.* 2010). More studies, such as that by Michaud & Grant (2005) (who found individuals of *Dectes texanus* LeConte developing in soybean and sunflower biologically compatible although strongly differing in average mass), are needed to clarify whether, and at what rate, we may encounter host races or sympatric cryptic host-specific species. The supposedly conspecific allopatric populations of widely distributed species often have more or less different (though usually overlapping) regional host associations; those differences can only be partly explained by the lack of potential hosts in certain regions (e.g., Logarzo *et al.* 2011). A seasonal switch in host-plant preference was even proposed for some tropical Acanthocinini (Lamiinae) (Berkov & Tavakilian 1999), but subsequent DNA analyses suggested that complexes of cryptic species were involved differing in both seasonality and host range (Berkov 2002). Linsley (1961) summarized some experience in cerambycids concerning the “Hopkins’ host selection principle” (Hopkins 1916; Craighead 1921), which states that “a species which breeds in two or more hosts will prefer to continue to breed in the host to which it has become adapted”. Some subsequent authors (but not Hopkins himself) implied involvement of a “larva-to-adult” transmetamorphic memory; such memory (“preimaginal conditioning”) has been very rarely demonstrated in



holometabolans and the observed “host selection principle” phenomenon rather depends on environmental effects “transferred” from the larva and on early imaginal experience (Barron 2001).

Species developing in dead rotting woody plants are often more sensitive to the type and degree of fungal or microbial decay than to the taxonomic relatedness of the “host plant” and are xylomycophagous rather than xylophagous or “herbivorous” in the strict sense. Some species are restricted to specific fungal taxa (e.g., *Necydalis ulmi* Chevrolat to the polypore genus *Inonotus*: Rejzek & Vlasák 2000); such species would falsely appear “host-plant-specific” if such was the fungal taxon. The importance of fungi is clearly demonstrated by the biology of *Pseudovadonia livida* mentioned above.

**Digestion, symbiosis.** Of the two main types of fungal wood decay (e.g., Webster & Weber 2007), cerambycids are often found in various stages of white rot caused by fungi simultaneously degrading all major wood components and using a complex of cellulolytic enzymes for digesting cellulose while avoiding dark rots that leave the wood lignin intact. Existence of cellulolytic enzymes in the cerambycid gut has long been known, but the opinion on their origin gradually evolved (reviewed in Martin 1987). When the intracellular symbiotic yeasts (see below and larval gut morphology) were found to lack cellulolytic activity in culture, there was a tendency to accept self-production of all cellulases as the only alternative. However, in several cerambycids the gut cellulolytic activity, requiring concerted action of at least two groups of enzymes (the endo- and exo- $\beta$ -1,4-glucanases; see Watanabe & Tokuda 2010), depended on enzymes acquired from ingested non-symbiotic white-rot fungi and disappeared with their removal (Kukor & Martin 1986 a, b; Kukor *et al.* 1988). Gut fungi and bacteria capable of digesting cellulose or the lignocellulose complex have also been found in some species (see Delalibera *et al.* 2005 and Scully *et al.* 2012). Self-production of the exo- $\beta$ -1,4-glucanases (necessary for digestion of intact very resistant microcrystalline cellulose) has never been convincingly demonstrated in cerambycids (recently Zverlov *et al.* 2003; Pavlovič *et al.* 2012), whereas genes of presumably endogenous endo- $\beta$ -1,4-glucanases have been cloned from larvae of several Lamiinae (Sugimura *et al.* 2003; Wei *et al.* 2006; Calderón-Cortés *et al.* 2010). The claim of Wei *et al.* (2006) that all three genes were strongly expressed in both foregut and midgut of the larvae of *Apriona* Chevrolat is incorrect, because what was identified as “foregut” included a large anterior portion of the midgut.

In addition to cellulolytic gut activity, cerambycid larvae have been reported to possess a variety of other more commonly encountered digestive enzymes (see references in Linsley 1959, 1961). Chitinases may require special mention as they might seem unnecessary in xylophagous species; some cerambycids (larvae and/or adults) ingest fungi in which cell walls contain chitin and, more importantly, perhaps all cerambycid larvae devour the

shed cuticle to improve the nitrogen budget (see below). Indeed a midgut-specific endogenous chitinase was cloned from the lamiine *Apriona germari* (Hope) (Choo *et al.* 2007; again the claim of strong expression in the foregut was due to misidentified anterior midgut).

Digestive efficiency is moderately high; between 20% and 50% of ingested food, depending on host suitability, was reported for *Stromatium barbatum* (Fabricius) (Mishra & Singh 1978). Studies that report very low food to body mass conversion rates of several percent may be underestimations as they are based on the premise that the volume of excavated galleries equals the volume of actually consumed food (Ikeda 1979; Cannon & Robinson 1981; Banno & Yamagami 1989). This premise is particularly difficult to accept in *Eupromus ruber* (Dalman) studied by Banno & Yamagami (1989), even if the volume of the pupal chamber was excluded, as the larvae of Monochamini are known for their considerable building activities and the ejection of large amounts of obviously undigested material out of their galleries. Thus, the estimated 1%–4% (dry weight) food conversion efficiency for larvae is undoubtedly too low (body mass further decreases during metamorphosis, see Cherepanov 1979–1985). In the more precise experiments of Walczyńska (2007, 2008 b) for *Aredolpona rubra*, a lepturine feeding in dead wood, in which the mass of undigested “pinedust” was subtracted from the consumption values, the assimilation (production + respiration to consumption), gross growth (P to C) and net growth (P to P + R) efficiencies were 29.1%, 12.5% and 43%, respectively.

Although digestion of basically energetic compounds such as sugars is undoubtedly important, available nitrogen (or possibly also phosphorus), very low particularly in dead wood, may be much more limiting than energy. Development of larval *Hylotrupes bajulus* (Linnaeus) was considerably accelerated in wood treated with peptones (Becker 1938). Benham (1971) lists microorganisms cultivated from larval guts of *Prionus laticollis* (Drury); some bacteria were capable of using inorganic nitrogen. Fungi can concentrate nitrogen from extensive substrate volumes and may also improve cerambycid nitrogen budget. Ikeda (1979) and Mishra *et al.* (1985) discovered “efficiency” of nitrogen utilization so high that it might indicate fixing of atmospheric nitrogen by some gut prokaryotes, and such activity was detected in the gut of *Prionoplus* (Prioninae) (Reid *et al.* 2011). Girdling of living branches by ovipositing females of *Oncideres* Lacordaire (Lamiinae) was shown to trap nitrogen-rich compounds transported from the leaves (Forcella 1982), and a number of other species (not only cerambycids) may use those girdled branches (e.g., Hovore & Penrose 1982; Di Iorio 1995 a; Calderón-Cortés *et al.* 2011). Possibly all cerambycid larvae devour the shed cuticle after larval/larval moults; even so, the strongly sclerotized exocuticular parts may not be recyclable, which may explain why species developing in particularly nitrogen-poor

substrates (like some Cerambycinae feeding in long-dead, dry and fungus-free wood) often convergently minimize cranial exocuticular sclerotization, presumably to maximize reuse of cuticular nitrogen from dissolved endocuticle and devoured shed exocuticle at ecdyses.

Finally, many larvae will readily devour other xylophagous insects including their own species (Victorsson & Wikars 1996; Anbutsu & Togashi 1997; Akbulut *et al.* 2004; Ware & Stephen 2006); lamiine larvae, in particular, are aggressive. The long-known negative effect of lamiine larvae on bark beetles has been recently interpreted as predation rather than competition (e.g., Dodds *et al.* 2001). The results of Schroeder & Weslien (1994) might be interpreted as showing *Acanthocinus aedilis* (Linnaeus) (Lamiinae) and *Thanasimus formicarius* (Linnaeus) (Cleridae) as competing predators; however, whereas the former is inferior and less effective, it is also much more versatile than the latter because it can thrive equally well on the phloem alone without its partial “predigestion” by bark beetles (Schroeder 1997).

The intracellular “yeast-like” symbionts residing in mycetomes on the anterior midgut (see larval gut morphology and Fig. 2.4.19 L, M), in addition to other possible roles such as synthesis of vitamins or steroids, may be involved in nitrogen waste recycling as in Ptinidae (Jurzitza 1972). The few cerambycid symbionts studied in detail belong to Saccharomycetales (Jones *et al.* 1999), but the great diversity shown by Schomann (1937) indicates possible involvement of other Ascomycota (as is the case in ptinids) and thus multiple origins of the endosymbiosis (not necessarily of the mycetomes). The mycetome cells periodically discharge content, including the symbionts, into the midgut lumen. The midgut mycetomes disappear during metamorphosis, but in females some symbiont-containing material remains in the gut and within several days after the adult hatches, it is transferred to the glandular invaginations at the ovipositor base (Heitz 1927; “Intersegmentalschläuche” of Schomann 1937; Fig. 2.4.18 I, J, 2.4.19 O), which are not homologous to the chrysomelid “vaginal pouches” as presumed by Mann & Crowson (1983 b). In ovipositing females, the symbiont-containing secretion is transported via flap-covered canals on the ovipositor surface (“Vaginaltaschen” of Schomann 1937) to the ovipositor tip, and is pressed out by and smeared on the chorion of the egg being laid; the symbionts are ingested with the chorion by the hatching larva. Screening dry collection female adults of numerous species, Schomann (1937) found symbionts in the ovipositor-associated pockets also in some Cerambycinae and Dorcasominae (the Madagascan *Toxitiades* Fairmaire and *Mastododera* J. Thomson classified by him in Lepturinae), whereas morphologically distinct mycetomes on the larval midgut have not been found in those subfamilies (presently they are known in Spondylidinae, Necydalinae, and most but not all Lepturinae), and the symbionts

in those cases may be luminal. Grinbergs (1962) found yeast-like microorganisms morphologically, biochemically and serologically very similar to some intracellular symbionts of European lepturines both in gut lumens and external environment of some Prioninae and Cerambycinae in Chile (where the subfamilies with larval midgut mycetomes do not occur), and the evolution of the intracellular symbiosis and specific transmission mechanism was probably via luminal gut commensals. In many species studied by Schomann (1937), the glandular pockets and at least the ventral canal on the ovipositor were present but did not contain symbionts, and their original function might thus be different. Both structures were almost always absent in Lamiinae and Semenova & Danilevsky (1977) proposed secondary loss of endosymbiotic yeast associations in that subfamily, yet luminal gut yeasts apparently related to some cerambycid endosymbionts were found also in lamiines (Berkov *et al.* 2007; Calderon & Berkov 2012). Scully *et al.* (2012) indicate that a filamentous ascomycete fungus of the genus *Fusarium* occurring in the gut of the lamiine *Anoplophora* may likewise improve the nitrogen budget. Schomann’s conclusion (often cited by later authors) that the intracellular midgut yeast-like symbionts are always absent from species developing in fresh angiosperms (Schomann 1937) was imprecise and an artifact of species selection and the poor biological knowledge then available.

The cerambycid larval gut contains a more or less rich community of bacteria (e.g., Benham 1971; Schloss *et al.* 2006; Reid *et al.* 2011), and recent research (Grünwald *et al.* 2010; Calderon & Berkov 2012) discovered bacterial endosymbionts in gut and fat body cells of several species, including one lamiine. The role and maintenance of those bacterial communities have been poorly investigated. Although the results of Geib *et al.* (2009) are difficult to interpret and the original data are unfortunately not provided, the authors suggest that some of the bacteria associated with *Anoplophora* may be vertically transmitted.

**Larval growth and polymorphism.** The number of instars is rarely known and was usually individually variable in species studied in sufficient detail. Adachi (1994) found that under simulated natural temperature conditions, some individuals of *Anoplophora malasiaca* (J. Thomson) (Lamiinae) underwent a 1-year life cycle (through seven to nine instars, with the final instar almost always attained before overwintering), whereas other individuals went through a 2-year life cycle (with 11–15 instars), and a proportion of those individuals increased with a simulated later oviposition date. A strong dependence on temperature for development and number of instars of *Anoplophora glabripennis* (Motschulsky) was demonstrated by Keena & Moore (2010). In laboratory-reared *Psacotheta hilaris*, the number varies between four and eight (rarely three or nine) and is likewise higher in specimens undergoing diapause (Shintani *et al.* 1996 b). In lab-

oratory-reared *Morimus funereus* Mulsant, five to 12 instars were observed (Dojnov *et al.* 2011). Variable numbers of instars were also firmly established for the cerambycine *Semanotus japonicus* (Togashi 1985, and references therein). Starzyk (1977) described five larval instars for laboratory-bred lepturine *Carilia virginea* (Linnaeus). On the low side, four instars are common in some quickly developing Lamiinae in laboratory rearing and three are possible, albeit in a minor portion of the population (Pershing & Linit 1989; Shintani *et al.* 1996 b). Quick development and low numbers of instars are in part made possible by the usually large lamiine eggs produced by the extensively feeding females. The developmental strategy of most cerambycids allows considerable to extreme variability of adult size (Andersen & Nilssen 1983; Walczyńska *et al.* 2010), primarily dependent on food quality and availability (e.g., Munyiri *et al.* 2003; Shintani *et al.* 2003). Because of the potential variability in instar number and adult size, plus the often remarkable sexual size differences, biometrical analysis is generally unusable to estimate the number of instars, and direct observation is necessary (Togashi 1985; Pershing & Linit 1989), which is difficult under natural conditions. Laboratory counts may not provide realistic numbers if larvae are fed soft artificial diets because personal rearing experience suggests that moults may occur as a reaction to wear-and-tear, particularly to strongly worn mandibles, and data from soft artificial diets may thus represent the lowest possible instar numbers. Unsuitable conditions (particularly the lack of some necessary prerequisite for metamorphosis) may increase the number of instars; in the Adachi's (1994) study, some larvae reared at a constant temperature of 30°C reached 16–20 instars (all individuals in that experiment died as larvae). Unsuitable hosts may cause much longer development (Hanks *et al.* 1995), and desiccation of the food material may lead to cases of longevity (up to dozens of years, see Duffy 1953).

Although a similar study is lacking in cerambycids, in lepidopteran phytophagous larvae the physical properties of larval food had a strong effect on the head morphology of later instars (Bernays 1986); thus, different natural or artificial diets may also affect larval morphological traits such as head size or cranial proportions in cerambycids (and larvae reared on soft artificial diets may not be fully adequate for morphological descriptions).

Larval growth is not entirely isomorphic, and first instars in particular always differ in proportions. Certain species (at least some Callichromatini of Cerambycinae, first described by Duffy 1949 in *Aromia* Audinet-Serville; some herb-feeding Phytoeciini of Lamiinae: Svacha 2001) have developed a shorter, stouter, remarkably desclerotized and non-feeding final larval instar (Fig. 2.4.20 S). Under normal conditions, there is very probably always only one such instar (confined to the pupal chamber), not more as Duffy (1953: 202) presumed. In *Aromia*, prothetely is easily induced in that instar by suboptimal conditions (Duffy 1953; P. Svacha,

personal observation). The lamiine *Musaria argus* (Frölich) has a morphologically “bimodal” last larval instar requiring investigation (P. Svacha, personal observation); rearing experiments suggest that the darker and paler forms do not coincide with males and females or the annual and biannual development (see below).

**Larval competition, defense, communal feeding.** Competition and aggression (including intraspecific: Anbutsu & Togashi 1997; Akbulut *et al.* 2004) brings about territoriality in some species. As previously mentioned, Lamiinae females usually oviposit singly or in small groups, and dispersion at oviposition may be enhanced by marking oviposition-detering substances (Allison *et al.* 2004). Larval sound production, believed to be territorial because it was usually observed in densely colonized hosts, has been described in Lamiinae (*Pogonocherus*: Svacha & Danilevsky 1987: 71; *Monochamus* Dejean: Victorsson & Wikars 1996) and Cerambycinae (*Icosium* Lucas: Kočárek 2009), and sounds resulting from larval feeding may be employed for maintaining distance between galleries of individual larvae (Saliba 1972). Chorusing by several larvae has been observed in *Icosium* and *Pogonocherus*. The abdominal chordotonal organs (Hess 1917) may be the vibration receptors.

Strategies differ within the group, and whereas in *Monochamus* (having very aggressive larvae and living in conifer logs of temporally limited breeding suitability) the semiochemicals from conspecific larval frass are oviposition deterrents, in *Hylotrupes* (having non-aggressive larvae and developing often for many years in the same material) they are attractants (Allison *et al.* 2004). Nevertheless, although some larvae may feed gregariously, there are very few known cases of truly communal larval feeding with a common gallery system. Johki & Hidaka (1987) described such larval feeding in the cerambycine *Xystrocera festiva* J. Thomson. The larval “nests” originated from the same egg batch and thus undoubtedly involved siblings. The first author observed a number of larvae of the Madagascan lamiine *Protorhopala sexnotata* (Klug) in an extensive interconnected system of hollow subcortical galleries; each larva apparently had its own retreat gallery leading deep into the wood, and fragmentary observation indicated that their defensive behavior (such as cessation of movement or retreat into the wood galleries) was coordinated, possibly using vibrational signals. It is not known whether the larvae were siblings. Advantages of such communal feeding in cerambycids are unknown; active collective defense by the larvae has never been observed, and the possible coordination of defensive behavior in *Protorhopala sexnotata* may in fact minimize disadvantages of communal feeding rather than being a goal by itself.

**Pupation** typically occurs in the food material. Some species feeding in decomposing wood enter regions of better quality. Many subcortical larvae enter wood for pupation and some make a

retreat wood gallery long before finishing feeding; such species, although removing large volumes of wood, often do not ingest it and return for feeding under bark. Larvae feeding in thin twigs and herbaceous plants usually girdle them above the pupal chamber so that the distal part breaks off, which prevents damage in the weakened region of the pupal cell by wind. Some species feeding in twigs and branches also girdle them below the pupal chamber so that the part with the mature larva falls to the ground. Larvae of *Deltosoma* J. Thomson (Cerambycinae) completely separate a piece of wood containing the pupal chamber from the surrounding wood so that it remains attached only to the overlying bark, a behavior interpreted as an evolutionary continuation of the conspicuous false entrance tunnels built by some other cerambycines next to the true plugged entrances to their pupal chambers (Di Iorio 1995 b). Some species developing in lianas enter the supporting tree for pupation. Whereas most species separate the pupal cell only by frass or coarse wood fibers, the larvae of most Cerambycini (exceptions include *Sphallo-trichus* Frago or *Criodion* Audinet-Serville; Martins 2005 a) and a few other Cerambycinae (*Xystrocera* Audinet-Serville and some Callichromatini) additionally secure it with calcareous opercula or build complete calcareous cocoons from material produced by a subset of Malpighian tubules and regurgitated through the mouth (Beeson 1919; Duffy 1953).

Some cerambycids pupate in soil. This presumably derived habit occurs in species with terricolous larvae, in many root feeders, and in some Lepturinae in which larvae feed in or under loose bark, but also in some non-subterranean wood-feeding species (e.g., Oxymirini of Lepturinae and most Dorcasominae), where its advantages are less obvious. The soil pupal cells are usually broadly ovoid to subspherical, which is reflected in the pupae being strongly curved and usually setose dorsally to maintain distance from the cell walls (Fig. 2.4.32 C, D). *Pseudovadonia livida* (developing in plant litter with mycelium) pupates in “parchment-like” cocoons made of non-calcareous material of unknown origin.

Mobility of cerambycid pupae is limited to a simple abdominal wriggling motion in most species. However, in *Agapanthia* Audinet-Serville (Lamiinae) and some relatives having long hollow pupal cells in upright stems of herbs or thin twigs, the long flexible spinose abdomen enables the pupa to move fast along that pupal cell (Fig. 2.4.32 M, N). Some large pupae possess so-called “gin traps” (sharp sclerotized opposed margins of neighboring abdominal terga that can be brought together by muscular action, Fig. 2.4.31 P), which are believed to be “a means of defense against animals much smaller than the pupae” (Hinton 1955).

Spatial restrictions in some special habitats strongly affect pupal morphology and may cause far-reaching (and potentially taxonomically confusing) parallelisms across all stages; slender elon-

gate larvae, pupae and adults of species developing in thin twigs may be an example.

**Life cycle.** The development period and details of the life cycle are usually variable, enhanced by geographic differences and, in some Lamiinae, also by the long adult life and oviposition period. Differences that include the overwintering stage and presence or absence of photoperiodically induced larval diapause may occur even between allopatric populations of the same species that interbreed along the contact zone (Shintani & Ishikawa 1999 b), and Logarzo & Gandolfo (2005) reported a change of voltinism and diapausing properties along a latitudinal gradient. The simultaneous occurrence of larvae of different sizes does not always indicate a biannual or longer life cycle because larval development may be synchronized at a later, often quiescent, stage. Shintani (2011) experimented with day length and temperature that optimize the timing of pupation and adult hatching in the temperate lamiine *Phytoecia rufiventris*, which overwinters as adults in their herbaceous hosts; too early or too late pupation lowered survival of adults and pupae, respectively. Some univoltine herb feeders that pupate only after overwintering (such as some *Agapanthia* of Lamiinae) undergo a period of summer inactivity because larvae are still very small in late summer (although oviposition occurs in spring) and quickly grow afterwards. Diapause has been very poorly studied; in a population of *Psacotheta hilaris* (Lamiinae), it is induced by a short-day photoperiod (Shintani *et al.* 1996 a), involves about two extra instars, and larvae entering diapause have high juvenile hormone and low ecdysteroid titers (Munyiri & Ishikawa 2004). The removal of larval stemmata had no pronounced effect on larval photoperiodic response (Shintani & Numata 2010). However, day length cannot be the inducing factor in some species because larvae develop in constant darkness, such as in deep roots, and yet their adult emergence is well synchronized. Very little is known about diapause termination of taxa from seasonal tropics; increased humidity may be a factor inducing continuation of development in the lamiine *Obereopsis brevis* (Gahan) in West Bengal (Dutt & Pal 1988). In temperate species, the winter diapause before the year of adult emergence is usually obligatory, and to continue development, the diapausing stages require at least several weeks of cold treatment; subzero temperatures are not generally needed, though tolerated, but fluctuating temperature may be more effective than constant cold in a freezer. Usually the last overwintering stage is the mature larva or prepupa in a pupal chamber, but some species overwinter as pupae or unemerged adults. Overwintering of “eggs” (unclosed first-instar larvae) in some Lamiinae has been mentioned above. Seldom, particularly in some Lamiinae such as *Pogonocherus*, *Plectrura* Mannerheim, some *Mesosa* and *Deroplia genei* (Aragona), the adults emerge before winter and hibernate in forest litter, under bark and elsewhere. Autumn emergence of such species has occasionally

been mistaken for a second generation, whereas bivoltinism in temperate species is undoubtedly rare although not impossible (Duffy 1953). Overwintering larvae or adults usually avoid freezing by having low supercooling points (below  $-10$  and down to almost  $-30^{\circ}\text{C}$ ; Ma *et al.* 2006; Zachariassen *et al.* 2008), but both freeze-avoiding and freeze-tolerant populations or individuals may occur within a species (e.g., *Acanthocinus aedilis* is freeze-avoiding in Europe and partly freeze-tolerant in Siberia; Li & Osakovskii 2008; Kristiansen *et al.* 2009). Seasonality in the tropics is usually determined by alternating dry and humid seasons and may disappear in regions without pronounced dry periods, such as in the Andaman Islands (see Khan & Maiti 1983), even if some peaks of adult occurrence remain. Tropical species can have two or more generations per year; in rearing experiments in Central and South America, adults usually began emergence 4–5 months after bait branches were cut and exposed, with the shortest recorded time during a hot dry period in Panama being about 2 months (A. Berkov, personal communication).

Being strictly and synchronously univoltine may be risky because all individuals of the same ontogenetic stage may be sensitive to environmentally “bad” years. At least some herb-feeding Phytoeciini employ the tactics of prolonged diapause to stagger emergence (Tauber *et al.* 1986: 198; Hanski 1988; type C of polymodal emergence as defined in Waldbauer 1978): all larvae complete feeding by the end of summer, but whereas some individuals pupate, overwinter in the host plant as adults and emerge next spring, other larvae delay metamorphosis by a full year.

**Genetics, sex ratio, parthenogenesis.** Karyologically, cerambycids appear relatively conservative. The prevalent chromosome number is  $2n = 20$  (the presumed ancestral number of Polyphaga) or close to that value, although numbers from 10 to 36 have been recorded (Smith & Virkki 1978; Petitpierre 1987; Rožek *et al.* 2004). Males typically show the  $Xy_p$  type of sex chromosomes (a small y chromosome forming a “parachute” pattern with chromosome X at meiotic metaphase I) or slight modifications (such as duplicate X or one or two supplementary chromosomes). In American species of the genus *Monochamus*, several such modifications are known but with constant  $2n = 20$  chromosomes (Smith & Virkki 1978); in contrast, European species lack modifications but some have 22 or 24 chromosomes (Cesari *et al.* 2005). Parthenogenesis is rare (Cox 1996); thelytoky has been documented in *Kurarua rhopalophoroides* Hayashi (Cerambycinae) in Japan (Goh 1977) and undoubtedly occurs in female-only populations of *Cortodera* (Lepturinae) from the Caucasus and one species of Neotropical Acanthocinini (Lamiinae) reared by the hundreds (A. Berkov, personal communication). At least in *Cortodera*, parthenogenesis is probably of a recent origin because very similar populations may be either bisexual or female-only, and a distinct spermatheca with spermathecal gland was found

in a dissected female of a parthenogenetic population. Although infections by the widespread *Wolbachia* (an intracellular bacterial parasite transmitted through the host eggs which, among other reproductive irregularities, may cause parthenogenesis or manipulate sex ratio by male-killing) have not been apparently reported from cerambycids, a large *Wolbachia* genomic region was found inbuilt in an autosome of *Monochamus alternatus* Hope (Aikawa *et al.* 2009). The sex ratio in bisexual populations is usually close to parity and occasional collection bias may reflect sex-related behavioral differences rather than actually skewed sex ratios. Estimations of true sex ratios require rearing and extracting beetles from their pupal cells or mark-release-recapture studies (e.g., Drag *et al.* 2011). The dependence of the sex ratio on the host size was reported by Starzyk & Witkowski (1986) for two lamiine species; of the two suggested possible explanations (sex manipulation by ovipositing female and differential survival of sexes), the former is unlikely because no genetic system enabling such manipulation is known in cerambycids.

**Cerambycid enemies** (pathogens, parasitoids and predators) are very numerous and will not be treated in detail. Common entomopathogenic fungi include *Beauveria* spp., *Isaria farinosa* (often included in *Paecilomyces*) and *Metarhizium* (e.g., Dubois *et al.* 2008; Meyers *et al.* 2009); see also Benham (1971) for a survey of fungi, bacteria and viruses attacking cerambycids. Compiled lists of cerambycid predators and parasitoids are included in regional monographs (e.g., Picard 1929; Heyrovský 1955; Linsley 1961; Heliövaara *et al.* 2004); however, identification or taxonomic interpretation of older records may be problematic (Kenis & Hilszczanski 2004).

Predators of larvae are usually not specific, attacking other wood borers. They include many larval Coleoptera (Histeridae, Elateridae, Melyridae, Cleridae, Trogossitidae, some Tenebrionidea), but also Raphidioptera and Diptera (some Asilidae, *Xylophagus* Meigen and other dipterans). Ants often invade galleries and prey on larvae. Vertebrates feeding on larvae include woodpeckers, but more accessible larvae (under thin bark and in thin twigs) may be preyed on by other birds and occasionally other vertebrates. New Caledonian crows use tools for extracting larvae of the prionine *Agrianome fairmairei* (Montrouzier) from decaying wood (Bluff *et al.* 2010). Predation of armadillos on subterranean root-feeding larvae of *Apterocaulus* Fairmaire (Prioninae) was described by Di Iorio (1996, as *Psalidognathus*), and roots of herbs infested by the larvae of Phytoeciini (Lamiinae) were often found destroyed by burrowing mammals (P. Svacha, personal observation).

Egg and larval parasitoids are mostly hymenopterans. This includes Braconidae and Ichneumonidae of Ichneumonoidea, Bethyloidea of Bethyloidea, some Chalcidoidea (including egg parasitoids), some Platygastroidea (egg parasitoids), Aulacidae of Evanioidea, Stephanidae and

Megalyridae. Diptera is represented by a few Tachinidae. Coleopteran parasitoids are uncommon and include Bothrideridae and some Ripiphoridae. The ectoparasitoid female mites of the genus *Pyemotes* Amerling have been found on immatures (e.g., Hanks *et al.* 1992; Cakmak *et al.* 2006; P. Svacha, personal observation).

Entomogenous nematodes are listed in Poinar (1975). A number of laboratory and field tests have evaluated the potential of entomopathogenic nematodes of the families Steinernematidae and Heterorhabditidae against wood-boring cerambycid larvae (e.g., Fallon *et al.* 2004, 2006). Those nematodes may be of particular importance for subterranean cerambycid immatures, the enemies of which remain very poorly known. Mermithidae may be another nematode family of similar importance; the herb-root-feeding larvae of the lepturine *Cortodera villosa* Heyden were found heavily infested by an unidentified species of that family (Svacha & Danilevsky 1989), whereas mermithids have not been recovered from typical wood-boring larvae during many years of rearing by the first author (although some are cited for wood-boring cerambycids by Poinar 1975).

Termites have been proposed as a possible reason of absence of some dead-wood-feeding taxa, such as Lepturinae, in humid tropics (Forchhammer 1981); ecologically this may be a valid idea even if at that time Lepturinae were lumped with Dorcasominae and the bipolar distribution (to be explained by the competition with termites in the tropics) was in reality an artifact of the dorcasomine radiation in Madagascar where many of them are lepturine “ecological vicariants”.

Predators of adults are basically similar to those of other insects; known parasitoids include Sarcophagidae (see Linsley 1961). Adults frequently carry mites or nematodes, both externally and in the subelytral space; this is usually just a phoretic association, but flight may become difficult or spiracles blocked in heavy infestations. Some mites (Podapolipidae; Husband 2008) are ectoparasites presumed to feed on hemolymph; the infestations are not deadly in this case but will reduce vigor (whereas infestations of larvae by the hemolymph-sucking *Pyemotes* are fatal).

**Economic importance.** Together with other xylophages, cerambycids are a major force in recycling dead wood and an important component of healthy forest ecosystems. Certain taxa may be important pollinators (Gutowski 1990), particularly in the forest canopies, but studies are lacking. A majority of serious cerambycid pests are harmful in the larval stage and contained in the Cerambycinae and Lamiinae. Although species that injure hard, dry, seasoned wood belong exclusively to Cerambycinae, both subfamilies contribute species that harm living or freshly dead plants. Some species have considerable invasive potential, as demonstrated recently by some *Anoplophora* (Lamiinae) (Lingafelter & Hoebeker 2002; Carter *et al.* 2009, 2010; Hu *et al.* 2009; Haack *et al.* 2010), but outbreaks of native spe-

cies may also occur for reasons not well understood, such as that of the cerambycine *Enaphalodes rufulus* (Haldeman) in oak forests of Arkansas (Riggins *et al.* 2009; Haavik & Stephen 2010). The hidden larval mode of life generally makes both timely detection of and protection from damage difficult. Larvae feed on synthetically less active tissues and new genetic mechanisms of plant protection may not be effective; larvae of *Anoplophora* fed without apparent problems in fresh branches of transgenic poplars containing genes for a chitinase and scorpion insect neurotoxin, whereas leaves suppressed a lepidopteran defoliator (Yang *et al.* 2008). Adult feeding by lamines on living plants is seldom of economic concern by itself, but some are suspected vectors of fungal plant pathogens, and certain species are confirmed vectors of xylophilous nematodes; some *Monochamus* are principal vectors of the infamous *Bursaphelenchus xylophilus*, which causes pine wilt disease (Mota & Vieira 2004; Togashi & Shigesada 2006; Togashi & Jikumaru 2007; Akbulut & Stamps 2012).

**Some major sources on cerambycid biology.** [Reviews: Butovitsch 1939; Hanks 1999; Linsley 1959. Comprehensive regional works, systematic volumes and catalogues with substantial biological data (ordered primarily geographically): Allenspach 1973; Bílý & Mehl 1989; Ehnström & Holmer 2007; Heliövaara *et al.* 2004; Klausnitzer & Sander 1978; Sama 1988, 2002; Sláma 1998; Tatari-nova *et al.* 2007; Teppner 1969; Villiers 1946, 1978; Vives 1984, 2000; Danilevsky & Miroshnikov 1985; Cherepanov 1979–1985; Ohbayashi & Niisato 2007; Beeson & Bhatia 1939; Veiga Ferreira 1964, 1966; Santos Ferreira 1980; Hawkeswood 1992, 1993; Hudson 1934; Linsley 1961–1964; Linsley & Chemsak 1972–1997; Martins 1997–2010; Monné 2001–2004; Machado *et al.* 2012. Works on immatures: Craighead 1915, 1923; Demelt 1966; Duffy 1953–1980; Dumbleton 1957; Mamaev & Danilevsky 1975; Nakamura 1981; Svacha 2001; Svacha & Danilevsky 1987–1989. Forest pests: Baker 1972; Dominik & Starzyk 1989; Furniss & Carolin 1977; Hellrigl 1974; Plavilstshikov 1932. Atlases of larval and adult work: Csóka & Kovács 1999; Ehnström & Axelsson 2002.]

**Morphology, General Remark.** Internal structures of larvae and adults requiring dissection have been studied in a very limited number of species, and much greater variability should be expected. In particular, the very small species have been rarely studied and assessing the presence or absence of very fine structures (such as the rudimentary tentorial bridge in both larvae and adults of the Lamiinae) would often require serial sectioning (the heads of lamiine larvae are usually drawn as if having no tentorial bridge, which is incorrect). Particularly in the very small forms can we expect significant simplifications due to miniaturization.

**Morphology, Adults** (Fig. 2.4.1–9). Length 2.4–175 mm. Body cylindrical to strongly dorsoventrally flattened, usually elongate (up to about



8 times as long as wide) and more or less parallel-sided, rarely (some Anisocerini of Lamiinae; Fig. 2.4.8 B) nearly circular. Surfaces glabrous or clothed with hairs or scales.

Head (Fig. 2.4.10, 2.4.11, 2.4.12 A–C) prognathous to strongly declined in the anterior half, sometimes abruptly constricted posteriorly to form a neck (e.g., many Lepturinae); produced anteriorly to form a short to moderately long muzzle in some Lepturinae, Dorcasominae and Cerambycinae (head prolongation in such cases involves mainly peristomal cranial parts, and antennae remain close to eyes); transverse occipital ridge usually absent. Frontal region not or only slightly deflexed in most subfamilies, but strongly deflexed from vertex (between eyes) and more or less vertical in most Lamiinae and a few Cerambycinae and Prioninae; often with median longitudinal groove marking a more or less deep internal endocarina that may continue posteriorly and approach or reach occipital region (many Prioninae, all Lamiinae; in the latter it forms a deep internal crest, almost reaching posterior cranial margin). Frontoclypeal boundary distinctly impressed (often with two deeper paramedian impressions) to externally indistinguishable, almost straight to sharply angulate; pretentorial pits lateral to dorsal/frontal and

occasionally very far from mandibular condyles (Fig. 2.4.11 K, 2.4.12 C), in some cases rather indistinct (some Dorcasominae and Cerambycinae). Postclypeus and anteclypeus sometimes not sharply separated; postclypeus of variable shape (elongate triangular in some rostrate forms, Fig. 2.4.11 E; always very short and strongly transverse in Lamiinae, Fig. 2.4.11 I), sclerotized and more or less setose, never with median endocarina; usually simple or slightly transversely carinate, seldom strongly projecting (Fig. 2.4.10 G) or bearing a pair of distinct horns (males of some Mauesiini of Lamiinae); anteclypeus usually glabrous, flat to moderately convex, quadrangular or trapezoidal; in some cases membranous and allowing partial retraction of labrum; front margin usually straight to shallowly emarginate. Labrum free and movable to fused with anteclypeus and both parts sclerotized (Parandrinae and some Prioninae, rarely elsewhere), strongly transverse to distinctly longer than wide. Eyes very large to strongly reduced but never absent; not to strongly protuberant, oval to vertically elongate, rarely trilobate (Fig. 2.4.10 H); not to deeply emarginate at antennal articulations, occasionally completely divided into upper and lower parts; ommatidia (Gokan & Hosobuchi 1979 a, b; Wachmann 1979; Schmitt *et al.* 1982;

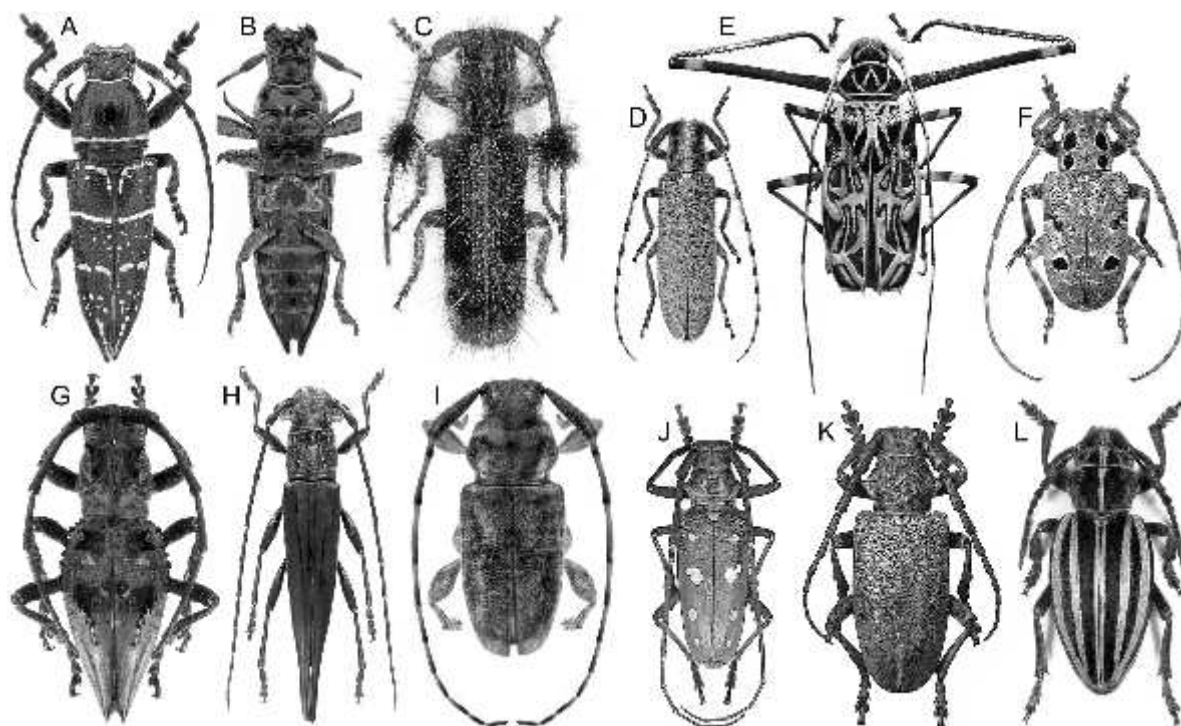


Fig. 2.4.9 Adults of Lamiinae, dorsal view except for B. A, *Xiphotheata saundersii* Pascoe, male, 25.5 mm; B, same, ventral view; C, *Apodasya pilosa* Pascoe, male, 9.5 mm; D, *Agapanthia villosoviridescens* (De Geer), female, size unknown; E, *Acrocinus longimanus* (Linnaeus), male (complete antennae are about twice as long as body), size unknown; F, *Mesosa curculionoides* (Linnaeus), male, size unknown; G, *Ceraegidion horrens* Boisduval, female, 17 mm; H, *Enicodes fichtelii* (Schreibers), male, 26 mm; I, *Microlamia viridis* Ślipiński & Escalona, male, 3 mm; J, *Batocera rubus* (Linnaeus), male, size unknown; K, *Lamia textor* (Linnaeus), male, size unknown; L, *Dorcadion scopoli* (Herbst), female, size unknown. (D, F, J, K © S. Ziarko; E © V. Seichert; G–I © CSIRO, Canberra; L © M. Hoskovec.)

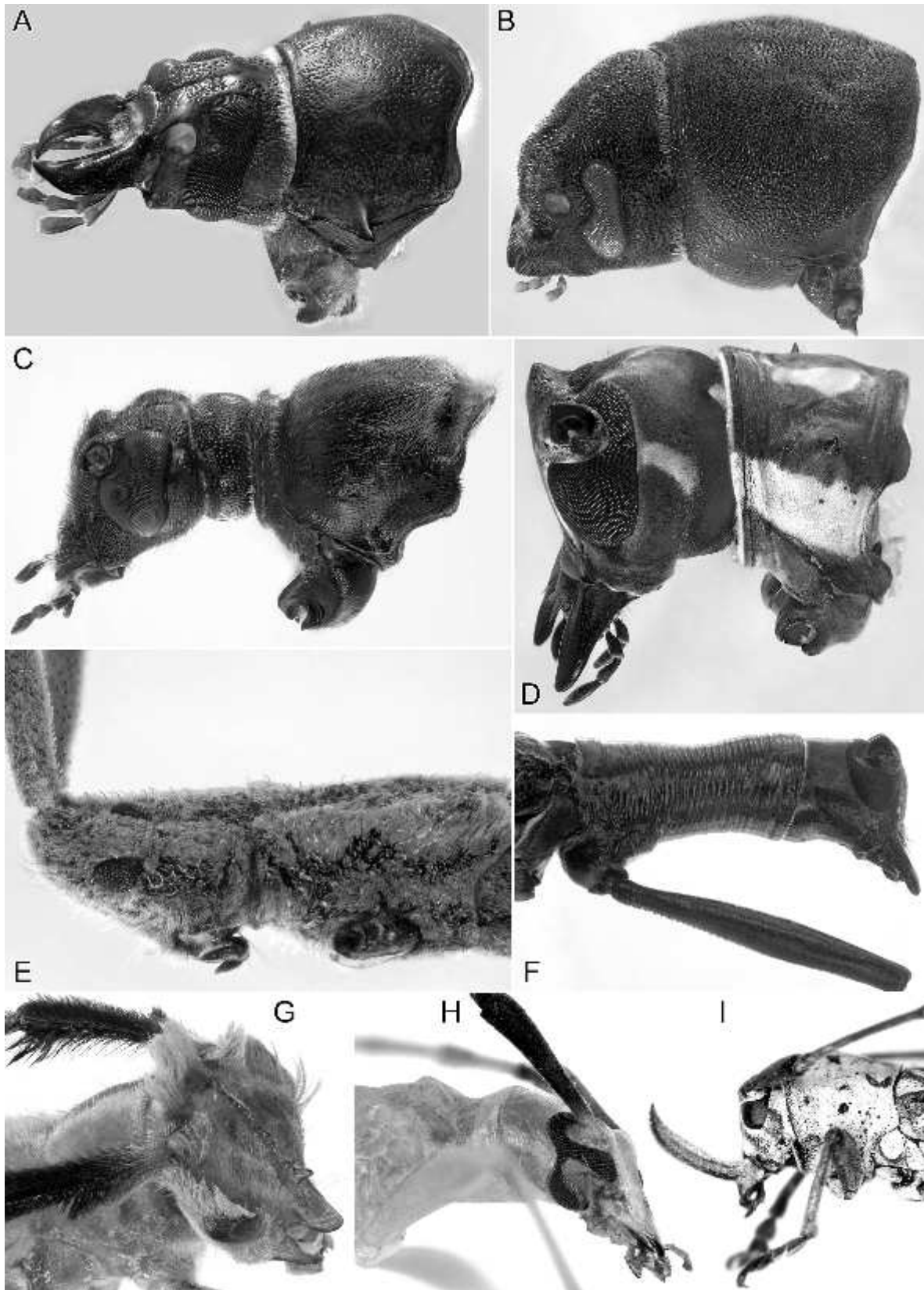


Fig. 2.4.10 Adults, head and prothorax lateral or laterodorsal. A, *Prionus coriarius* (Prioninae), female; B, *Aseum striatum* (Spondylidinae), female; C, *Leptura quadrifasciata* (Lepturinae), male; D, *Batocera victoriana* J. Thomson (Lamiinae), female; E, *Tetraglenes hirticornis* (Fabricius) (Lamiinae), male; F, *Gnoma luzonica* Erichson (Lamiinae), male; G, *Momisis melanura* Gahan (Lamiinae), male (dentate median frontal line and strongly projecting postclypeus); H, *Tricheops ephippiger* Newman (Cerambycinae), male; I, *Chemsakiellus taurus* Villiers (Lamiinae), male. (G, H © CSIRO, Canberra; I © K. Adlbauer.)



Caveney 1986; Meyer-Rochow & Mishra 2009) acone with biconvex corneal lens and with open rhabdoms formed by two central (occasionally distally shortened) and six peripheral reticular cells; peripheral and central rhabdoms may be separate or partly fused; former lost in *Tetrops* Kirby, latter in *Phytoecia* Dejean (both Lamiinae); ommatidia fewer, larger and more convex, and rhabdom more voluminous in crepuscular and nocturnal species. Antennal insertions exposed, of variable position (but always far from mandibular condyles in Lamiinae), dorsal and approaching each other to sublateral and widely separate; articulations mostly supported medially by raised tubercles that are rarely produced into distinct horns (males of some Onciderini of Lamiinae); subantennal groove absent; antennal sockets sometimes connected with mandibular condyle by a ridge or sulcus (Fig. 2.4.12 C). Antennae usually 11-segmented, very rarely with fewer antennomeres as in some Prioninae (eight in female *Allaiocerus* Galileo; eight in female *Casiphia* Fairmaire with four terminal flagellomeres more or less perfectly fused into a club, Fig. 2.4.1 P; nine in both sexes of *Drumontiana* Danilevsky, Fig. 2.4.1 J) or in some Lamiinae where flagellomeres 1 and 2 are long, whereas the remaining flagellum is reduced and sometimes with annulation partly lost; 12 segments in a number of unrelated groups by subdivision of terminal flagellomere; more than 12 in a few Cerambycinae and Prioninae (up to over 30 in the latter); antennae never distinctly geniculate between scape and pedicel, although scape may be very long (occasionally surpassing pronotal base) in a Gondwanan cerambycine subgroup including Rhagiomorphini, Macronini and several other groups (Fig. 2.4.5 F), and the antenna of some ant mimics with long scape and first flagellomere resembles the geniculate antennae of ants (Fig. 2.4.4 N, 2.4.8 G); usually filiform or serrate and moderately to very long (up to about 5 times as long as body in males of some Acanthocinini of Lamiinae); occasionally moniliform, pectinate, bipectinate or flabellate (Fig. 2.4.1 E, 2.4.2 H, 2.4.3 R, 2.4.4 R), rarely clavate or capitate (e.g., both sexes of the Australian cerambycine *Telocera* White, Fig. 2.4.5 C, or female *Casiphia*); scape variable, may be swollen (Fig. 2.4.8 B), rarely with large spines or other projections or a subapical spiculate field; occasionally with a small apical area more or less completely separated by a ridge and/or with a different sculpture (Fig. 2.4.12 J; this structure is called a cicatrix, particularly in Lamiinae); pedicel almost always simple, usually very short, not or slightly longer than broad (without its basal condyle), and thus contrasting with the usually long antennae; rarely distinctly elongated (2.5–3 times as long as broad in Opsimini of Cerambycinae and in some Spondylidinae); some flagellomeres may be strongly swollen, either only in males (e.g., first flagellomere in *Rhodopina* Gressitt of Lamiinae, or *Bolbotritus* Bates of Cerambycinae, Fig. 2.4.3 S) or in both sexes (some Lamiinae), and/or provided with brushes of hairs (Fig. 2.4.9 C); some

of these structures may be associated with glands. Mandible short and broad to moderately elongate, seldom (mainly in males of some Prioninae) strongly enlarged and modified; apex in unmodified mandibles usually unidentate, seldom bidentate (Fig. 2.4.11 D) or scalpriform; incisor edge simple or with one or more teeth and in some cases bearing a row of longer setae; distinct prostheca absent; inner basal margin in some cases with more or less extensive field or row of microtrichia of various sizes arising from desclerotized cuticle; desclerotized region usually more or less completely enclosing a flat plate-like often variously sculptured molar sclerite in Lepturinae and Necydalinae (Fig. 2.4.12 K), other subfamilies without such sclerite although sometimes with molar protuberances of various shape. Maxilla (Fig. 2.4.13 A–C) almost always with distinct setose galea and lacinia; the latter always without uncus and strongly reduced in Parandrinae and most Prioninae; palp four-segmented; apical palpomere fusiform and pointed (most Lamiinae) to triangular or securiform; maxilla in some cases strongly modified in relation to particular feeding habits (such as florivory; Fig. 2.4.13 C). Submentum more or less completely fused with gula to form a gulamentum; often more or less projecting between maxillary bases (“intermaxillary process”, Fig. 2.4.11 F, J; always reduced or absent in Prioninae and Parandrinae); mentum very rarely expanded laterally and partly covering maxillary base; ligula membranous to sclerotized, usually emarginate or bilobed, sometimes undivided or strongly reduced; palps three-segmented; apical palpomere fusiform to expanded apically; both maxillary and labial terminal palpomeres enlarged and palmate (bearing multiple digitiform branches) in males of the Australian prionine *Scelocantha gigas* Carter (Fig. 2.4.1 S), but not in males of remaining congeners (Fig. 2.4.1 R); maxillolabial complex may be partly hidden behind anterior gulamentum particularly in some fossorial forms. Metatentorial slits (Fig. 2.4.11 B, F, J) at posterior cranial margin (on “neck” in taxa with posteriorly constricted head), converging anteriorly (almost transverse in some Lamiinae with very short heads), separate from each other; gulamentum often not or poorly defined laterally anterior to metatentorial slits. Tentorial bridge (Fig. 2.4.12 E–H) from broad and often roof-like (with a median ridge) to narrow or rudimentary (particularly in Lamiinae); median process fine or absent; pre- and metatentorial arms usually connected (Fig. 2.4.12 E–G), but disconnected in Dorcasominae and most Cerambycinae (Fig. 2.4.12 H); dorsal arms distinct and sclerotized in some groups (some Prioninae or Lepturinae; Fig. 2.4.12 F); pretentorial arms never connected by a bridge. Cervical sclerites (Fig. 2.4.11 J) present to absent.

Prothorax (Fig. 2.4.10 A–F, 2.4.13 D–J) strongly transverse to approximately 4 times as long as broad (in some cases longer than elytra); base not to distinctly narrower than basal width of combined elytra. Lateral pronotal carinae present in

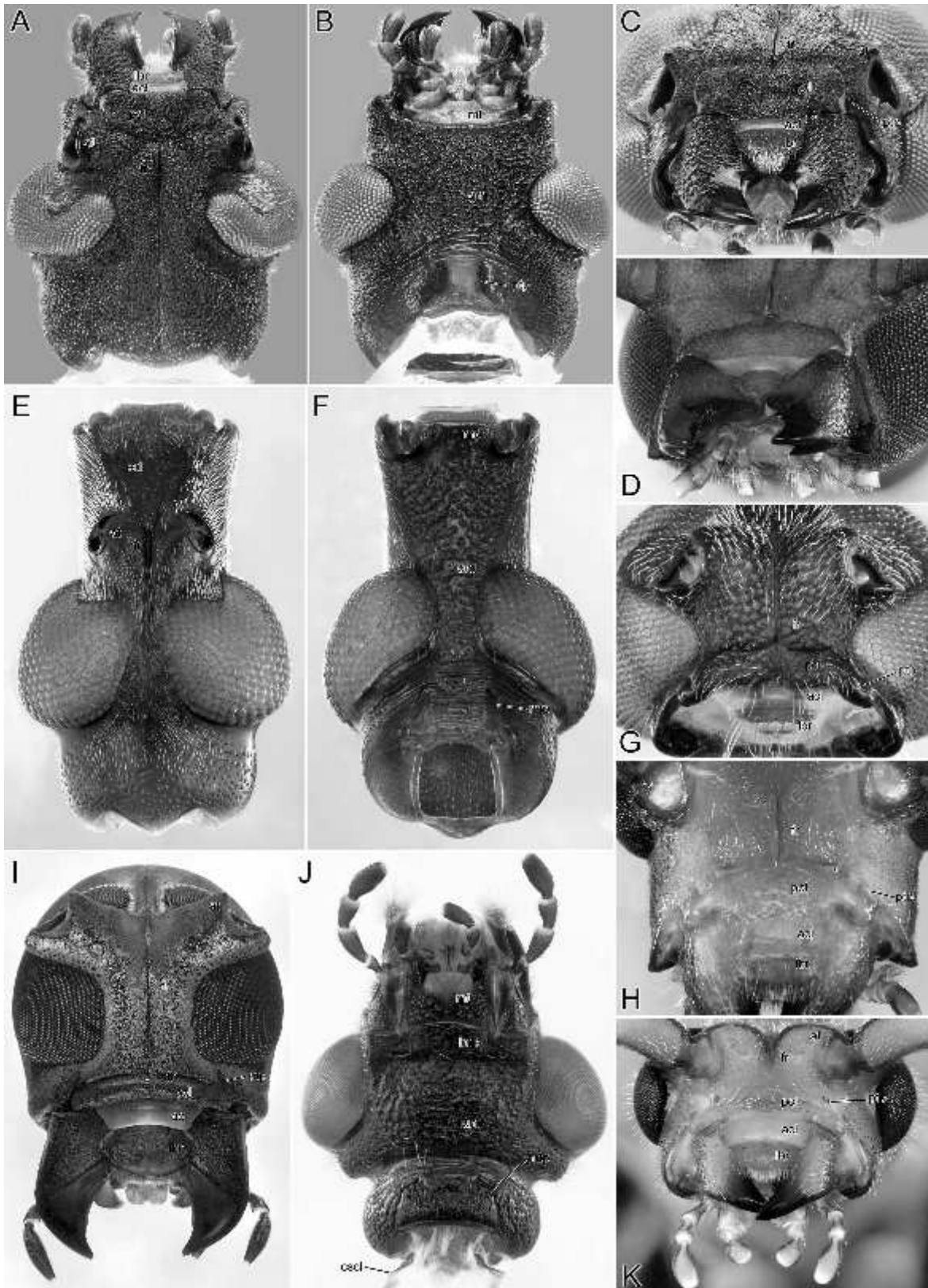


Fig. 2.4.11 Adult head structures, Prioninae (A–D), Dorcasominae (E, F), Cerambycinae (G, H), Lamiinae (I), and Lepturinae (J, K). A, *Aegosoma scabricorne* (Scopoli), female, head, dorsal view; B, same, ventral view; C, same, anterior view; D, *Delocheilus prionoides* J. Thomson, female, head, anterolateral view; E, *Logisticus* sp. female, head without mouthparts, dorsal view; F, same, ventral view; G, *Achryson surinamum* (Linnaeus), female, head without mouthparts, anterior view; H, *Compsocerus violaceus* (White), female, head, anterodorsal view; I, *Batocera victoriana*, female, head, anterior view; J, *Stictoleptura cordigera* (Fuessly), male, head, ventral view; K, *Rhamnusium bicolor*, female, head, anterior view. acl, anteclypeus; at, antennal tubercle; cscl, cervical sclerite; fr, frons; gm, gulamentum; imp, intermaxillary process (anterior gulamentum projecting between maxillary bases); lbr, labrum; mt, mentum; mtp, metatentorial pit; pcl, postclypeus; ptp, pretentorial pit; \* in H, deep paramedian impression on frontoclypeal sulcus.

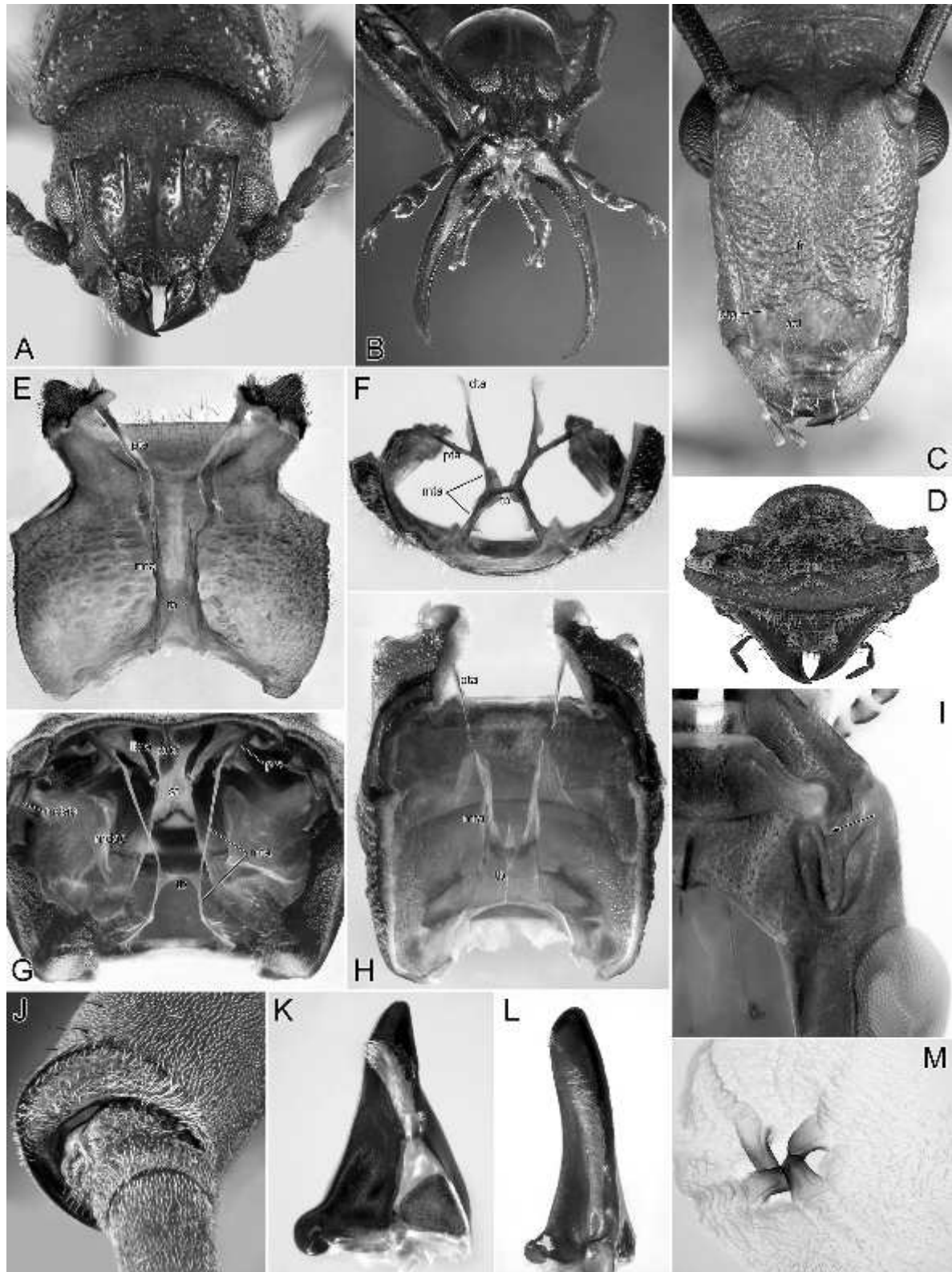


Fig. 2.4.12 Adult structures of Parandrinae (A), Prioninae (B), Cerambycinae (C, E, H, I), Lamiinae (D, G, J, M), Lepturinae (F, K), and Dorcasominae (L). A, *Erichsonia dentifrons* Westwood, female, head, anterodorsal view; B, *Dorysthenes walkeri* (Waterhouse), head, anterior view; C, *Macrones rufus* Saunders, male, head, anterodorsal view; D, *Enicodes fichteli*, male, head, anterior view; E, *Oplatocera siamensis* Hüdepohl, male, dissected tentorium, dorsal view; F, *Sachalinobia rugipennis* (Newman), male, dissected tentorium, posterior view; G, *Paranaleptes reticulatus* (J. Thomson), male, cleared head opened at the level of lower eye margin, dorsal view; H, *Schmidtiana evertsi* (Ritsema), male, dissected tentorium, dorsal view; I, *Stenoderus suturalis* (Olivier), male, right postmandibular impression with linguiform projection and outlet of internal glandular reservoir (arrow), dorsal view; J, *Pebblephaeus decoloratus* (Schwarzer), female, apex of left scape with completely delimited cicatrix; K, *Aredolpona rubra* (Linnaeus), female, right mandible, mesal view; L, *Mastododera lateralis* (Guérin-Méneville), male, right mandible, mesal view; M, *Phosphorus virescens* (Olivier), male, four sclerotized teeth in stomodeal valve, anterior view. (A © N. P. Lord & E. H. Nearns; D © CSIRO, Canberra.) dta, dorsal tentorial arm (of metatentorial origin); enc, median frontal endocarina; fr, frons; lbra, labral apodeme; mdab, slender apodeme for mandibular abductors; mdad, large apodeme for mandibular adductors; mta, metatentorial arm; pcl, postclypeus; pta, pretentorial arm; ptp, pretentorial pit; st, stomodaeum (cut); tb, tentorial bridge.

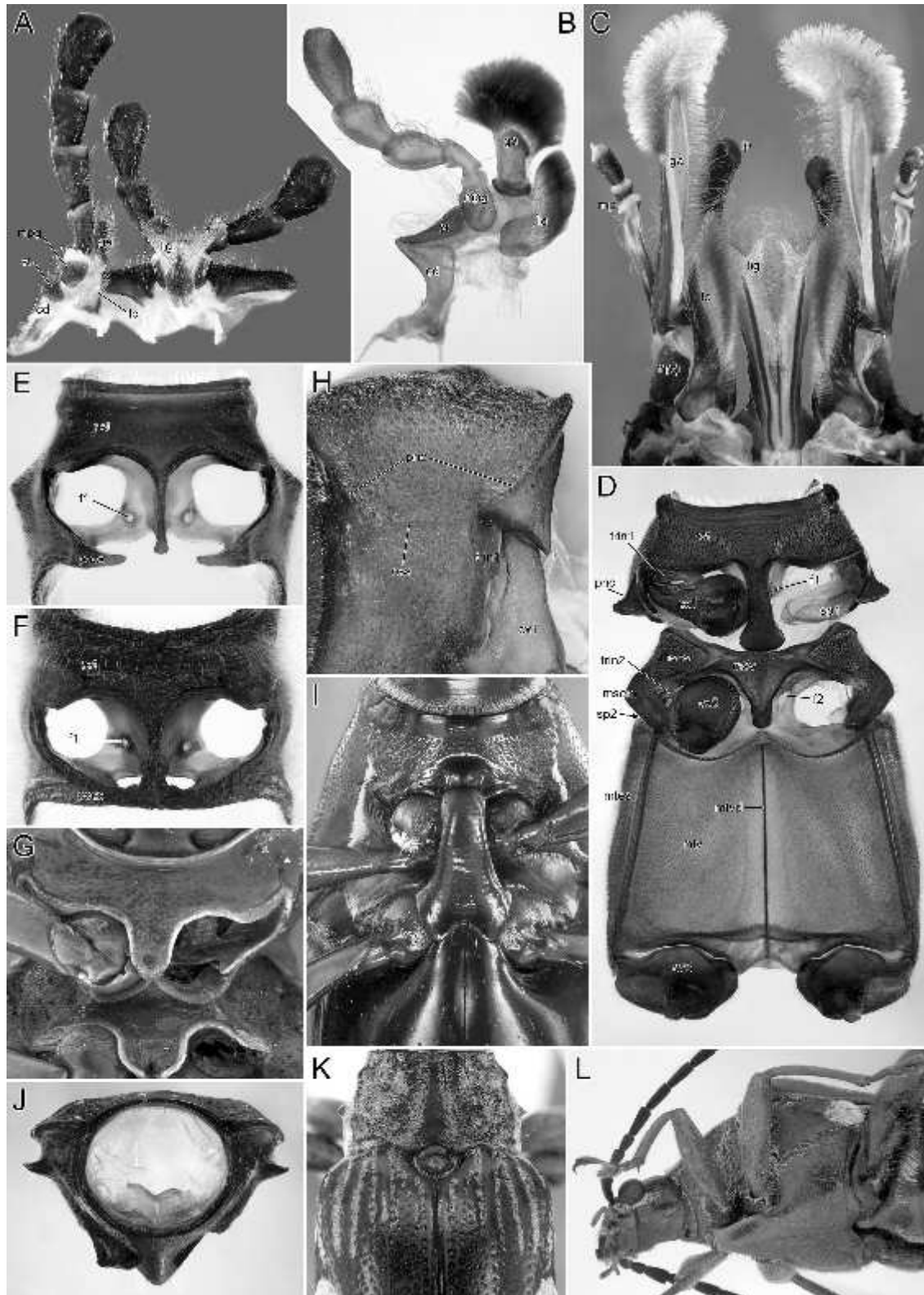


Fig. 2.4.13 Adult structures of Prioninae (A, B, D, H), Cerambycinae (C, I), Dorcasominae (E, L), Necydalinae (F), Lamiinae (J, K), and of uncertain subfamily (G). A, *Mallodon* sp., female, left maxilla and labium, dorsal view; B, *Hoplideres aquilus* Coquerel, female, left maxilla, dorsal view; C, *Pachyteria dimidiata* Westwood, male, specialized maxillo-labial complex of a floricolous species, dorsal view; D, *Aegosoma scabricorne*, female, thoracic venter, ventral view; E, *Logisticus* sp., female, prothorax, ventral view (membranes and mesothoracic spiracles removed); F, *Necydalis major*, male, same; G, *Cycloprionus flavus*, pro- and meso-venter, ventral view (© G. Biffi); H, *Aegosoma scabricorne*, male, prothorax, left lateral view; I, *Spintheria gratiosa* (Pascoe), male, thorax, ventral view; J, *Sphingnotus insignis* Perroud, male, prothorax with false "lateral pronotal margin" above lateral spine, anterior view; K, *Tmesisternus* sp., pronotum and base of elytra, dorsal view; L, *Trichroa oberthuri*, female, head and thorax, ventrolateral view. cd, cardo; cx1, 2, 3, pro-, meso- and metacoxa; f1, 2, invagination of pro- and metasternal furca; ga, galea; lc, lacinia; lig, ligula; lp, labial palp; mp, maxillary palp; mpg, maxillary palpiger (palpifer); msem, mesepimeron; mses, mesanepisternum; msv, mesoventrite with mesoventral process; mtes, metanepisternum; mtv, metaventricle; mtvd, metaventral discrimen; nss, prothoracic notosternal suture; pnc, lateral pronotal carina; pocx, postcoxal process (of protregal origin); pst, prosternum with prosternal process; sp1, 2, meso- and metathoracic spiracle (latter not visible); st, stipes; trin1, 2, pro- and mesothoracic trochantin.

Parandrinae and most Prioninae (often serrate to coarsely dentate in the latter), usually absent or incomplete in remaining subfamilies; anterior pronotal angles usually not produced; posterior angles broadly rounded to obtuse or right; acute in some Lepturinae and rarely elsewhere; posterior edge usually more or less straight or evenly rounded, sometimes distinctly sinuate or variously lobed; disc occasionally with paired basal impressions, median longitudinal groove, or paired and/or unpaired tubercles. Prosternum in front of coxae shorter to much longer than shortest diameter of coxal cavity; prosternal process usually complete; incomplete in some Cerambycinae and Lepturinae and in *Trichroa* Fairmaire of Dorcasominae, where the mesoventrite and prosternal process are covered by a hypertrophied anterior metaventral process (Fig. 2.4.13 L); from tapering to strongly and abruptly expanded apically; apex usually rounded or truncate, sometimes bearing spines, articulating with a mesoventral tubercle or fitting into a pit of the mesoventrite; rarely mesoventrite projecting anteriorly above prosternal process (*Spintheria* J. Thomson of Cerambycinae, Fig. 2.4.13 I). Notosternal sutures complete (often in Prioninae), incomplete or absent. Procoxae sometimes projecting well below prosternum (especially in Lepturinae); trochantin and lateral coxal projections concealed by prosternal flap (many Cerambycinae and Lamiinae) or exposed. Procoxal cavities strongly transverse to circular, contiguous to widely separated (Fig. 2.4.4 C); externally usually broadly open to narrowly closed (broadly closed in some Lamiinae); internally more or less closed (a complete sclerotized bridge separating procoxal articulation membrane from intersegmental membrane and mesothoracic spiracle, Fig. 2.4.13 E, F) except in Parandrinae and Prioninae where internally open (the bridge is desclerotized, Fig. 2.4.13 D) with rare exceptions (narrow sclerotized bridge present in *Anoeme* Gahan). Accessory medial articulation of procoxa with prosternal process present in some cases (the condyle may be on either of the involved parts, indicating multiple origin). Scutellar shield visible, usually moderately elevated; anteriorly flat, step-like or separated from mesoscutum by impression, rarely (some Tmesisternini of Lamiinae) slightly projecting above pronotal base (Fig. 2.4.13 K); posteriorly acute to rounded or truncate or occasionally emarginate or spinose; mesoscutum often with glabrous transversely striate stridulatory plate (Fig. 2.4.14 D–G); punctate and/or setose and lacking a plate in Parandrinae and Prioninae; internal mesoscutal median carina complete to strongly reduced; if complete, striation of stridulatory plate usually “divided” (Fig. 2.4.14 D) or at least less distinct/regular medially; in species with well developed plate, internal carina often reduced to rudiments on anterior vertical mesonotal phragma (Fig. 2.4.14 E; e.g., most Cerambycinae or some Dorcasominae), or displaced to one side (usually left) so that

one half of the originally divided striated plate is reduced or lost (Fig. 2.4.14 F, G; some “southern” Cerambycinae, a few Lepturinae, and the ground-plan situation in Lamiinae). Elytra in slender species up to approximately 5.5 times as long as combined width, rarely shorter than wide (Fig. 2.4.8 B); punctation, if distinct, rarely forming regular rows; elytra occasionally with longitudinal “veins”, ridges or costae that are rarely connected by cross elements and partly reticulate in posterior half (Fig. 2.4.2 I, 2.4.5 L); elytral apices meeting at suture or independently rounded or acute, occasionally with one or two pairs of spines; epipleura complete, incomplete or absent; elytra shortened and/or narrowed and exposing several abdominal terga in Necydalinae (Fig. 2.4.6 K, L), some Cerambycinae (Fig. 2.4.4 L, S, U, 2.4.5 J, N), some Prioninae (flightless females of some Prionini, Fig. 2.4.1 C; males or both sexes of some genera of Anacolini and Meroscelisini, Fig. 2.4.2 L), and some Lepturinae and Dorcasominae. Mesoventrite almost always separated by complete sutures from mesanepisterna, which are distinctly separated at midline; anterior edge occasionally on different plane than metaventrite, with or without paired procoxal rests. Mesocoxal cavities circular to strongly transverse, not or slightly oblique, laterally open or closed in Spondylidinae, Cerambycinae and Lamiinae, open in remaining subfamilies. Mesocoxae rarely slightly conical and projecting (e.g., Methiini of Cerambycinae), narrowly to widely separated, contiguous in *Thaumasus gigas* and *Xenambyx lansbergei* (Cerambycinae: Torneutini); trochantins exposed or concealed. Mesometaventral junction simple or complex, rarely concealed by metaventral process (huge in *Trichroa*); accessory articulation of mesocoxae with posterior mesoventral projection occasionally present (some Cerambycinae or Lamiinae). Metaventrite with discrimen very long to absent; postcoxal lines absent; exposed portion of metanepisternum short and broad to very long and narrow. Metacoxae contiguous to widely separated (mainly some flightless forms), horizontal or oblique, extending laterally to meet elytra or not; plates absent. Metendosternite (Fig. 2.4.15 A–C) with lateral furcal arms moderately to very long; laminae large to absent; anterior process short or absent and anterior tendons close together to widely separated; in flightless forms metathorax shortened and meso- and metafurcal tendons become thicker, in extreme cases one or both firmly attached to the opposite furca and/or to each other, forming sclerotized interfurcal bridges (Fig. 2.4.14 H). Hind wing (terminology of Kukalová-Peck & Lawrence 1993, 2004; Fig. 2.4.15 D–H, 2.4.16, 2.4.17 A–E) of variable shape and color, very dark in some diurnal forms; apical field moderately to very long (short in some very large forms; Fig. 2.4.15 D) and with up to three more or less complete remnant veins; anterior two veins diffuse or indistinct proximally, often only the third one complete; second and third veins (if distinctly developed)



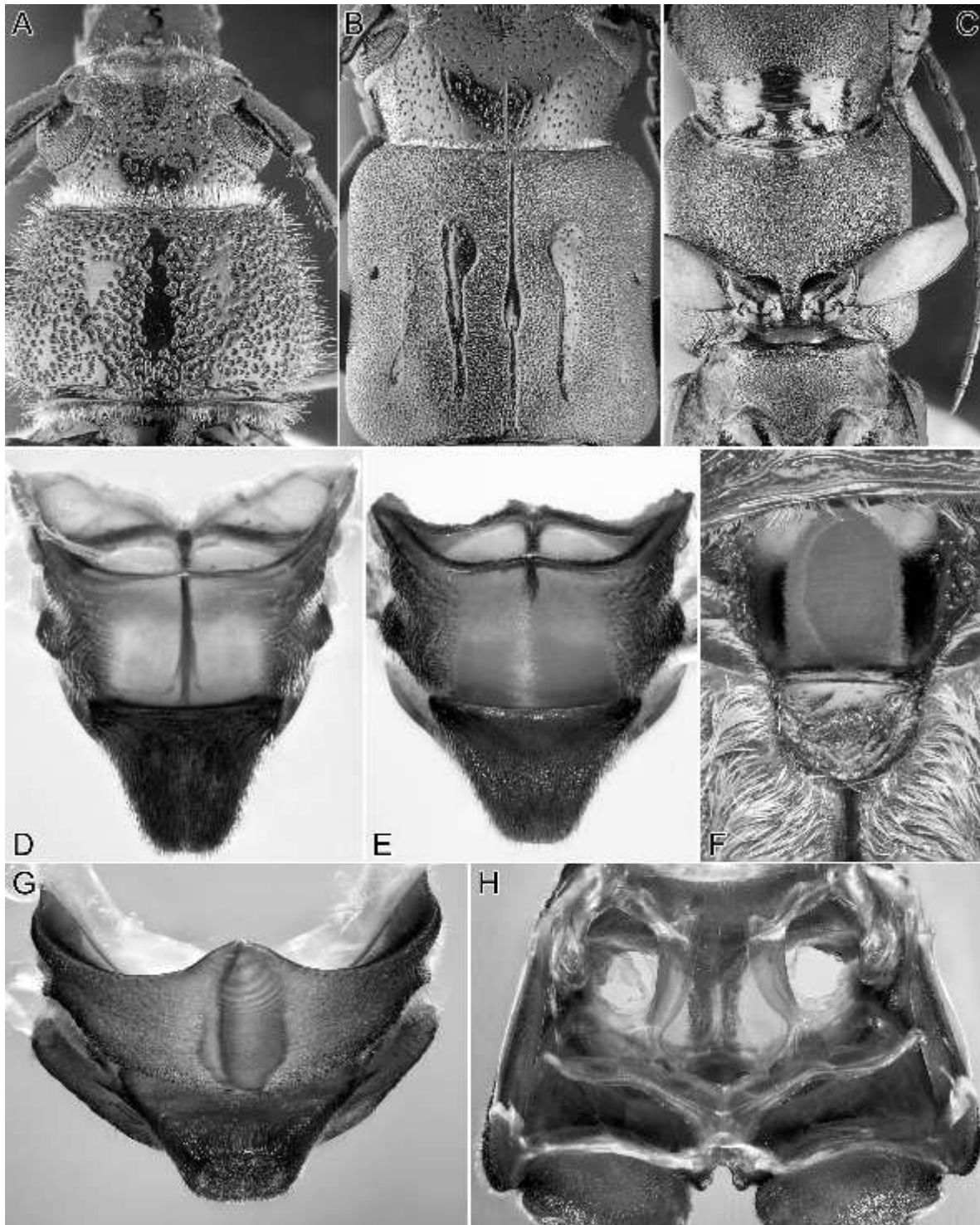


Fig. 2.4.14 Adults of Cerambycinae (A–C, F), Dorcasominae (D, E), and Lamiinae (G, H). A, *Torneutes pallidipennis* Reich, female, head and prothorax, dorsal view; B, *T. pallidipennis*, male, head and prothorax, dorsal view; C, same, head, pro- and mesothorax, ventral view (probably glandular fields on anterior head, prothorax and mesoventrite); D, *Tsivoka simplicicollis* (Gahan), female, mesoscutum and mesoscutellum, anterodorsal view (internal carina completely dividing stridulatory file); E, *Mastododera lateralis*, male, same (internal carina restricted to anterior phragma, stridulatory file undivided); F, *Rhagiomorpha lepturoides* (Boisduval), male, mesoscutum and scutellar shield, dorsal view (asymmetrically divided stridulatory plate); G, *Phosphorus virescens*, male, mesoscutum and mesoscutellum, anterodorsal view (strongly asymmetrically divided stridulatory plate); H, *Phantasis avernica* J. Thomson, female, pterothoracic venter with endoskeleton, dorsal view (flightless species with short metathorax and closely associated meso- and metathoracic furca).

typically converge and then diverge to form a scissor-like figure. Dark sclerite apicad of radial cell usually present and also a subtriangular sclerite crossing r4; latter crossvein usually attached on radial cell, seldom on r3, with spur long to absent; radial cell often well-developed and more or less elongate, but sometimes short and broad or lacking basal limit. Crossvein r3 usually slightly to strongly oblique, sometimes absent; basal portion of RP long to very short and not or hardly surpassing r4 (most Cerambycinae and Lamiinae). Medial field usually with four or five free veins (sometimes with three or rarely fewer) and without medial fleck; wedge cell well-developed in almost all Prioninae and some Lepturinae and Spondylidinae (with transitional states in latter two), or absent. Hind wings exposed in macropterous forms with shortened elytra (often giving beetles a hymenopteran appearance), and their apex is then sometimes not folded (e.g., all Necydalinae); wings shortened or completely reduced in numerous Lamiinae (usually both sexes) and Prioninae (usually only females), seldom in Cerambycinae (both sexes in *Blosyropus* Redtenbacher; completely missing in *Hybometopia* Ganglbauer, M. L. Danilevsky, personal communication), Lepturinae (e.g., females in *Xylosteus* Frivaldsky, both sexes in *Teledapus* Pascoe and relatives) and Spondylidinae (both sexes of *Drymochares* Mulsant and *Michthi-soma* LeConte of Saphanini); very rarely only males are brachypterous (*Storeyandra* Santos-Silva, Hefern & Matsuda of Parandrinae; *Thaumasus* of Cerambycinae: Torneutini if the macropterous *Xenambyx* is its female). Legs mostly cursorial (in some taxa with strong fossorial modifications, in some Lamiinae adapted for clinging to twigs), usually moderately to very long and slender; all legs particularly long in males of *Gerania* Audinet-Serville (Lamiinae) (Fig. 2.4.8 M); forelegs enlarged in some (particularly male) Prioninae and Lamiinae, extremely long in lamiine *Acrocinus* Illiger (Fig. 2.4.9 E; fore femur in large males as long as body); hind legs never adapted for jumping, and femora seldom enlarged (males of the cerambycine *Utopia* J. Thomson, Fig. 2.4.3 O, or some Dorcasominae, distal hind tibia broad and plate-like in some Cerambycinae and Dorcasominae (Fig. 2.4.3 E); trochanterofemoral joint transverse to strongly oblique, occasionally with base of femur abutting coxa; inner side of male femora may be flat or longitudinally excavated and bearing dense brush of hairs, for instance, the mid and hind femora in *Anisarthron* Dejean (Spondylidinae) (Fig. 2.4.17 F), *Georgiana* Aurivillius (Cerambycinae), *Cycloprionus* Tippmann (subfamily uncertain), or the fore and mid femora in *Ulochaetes* LeConte (Necydalinae); a similar brush occurs on the inner side of all tibiae in males of *Apatophysis* sg. *Angustephysis* Pic (Dorcasominae; Danilevsky 2008); base of tibial flexor apodeme in Lamiinae with a prominent bilobed sclerite (Marinoni 1979; Fig. 2.4.17 G), elsewhere sclerite flat to indistinct; femora and/or tibiae strongly spinose in some

Prioninae, tibiae are widened and often toothed at apex and sometimes dentate along outer margin in Parandrinae, some Prioninae and Spondylidini; tibial spurs usually 2-2-2, reductions to 1 or 0 uncommon and usually occur only on some leg pairs; in Lamiinae protibia usually with oblique pubescent groove (antennal cleaner) on inner face and mesotibia (seldom also metatibia) sometimes with similar groove on outer face; rarely protibia with similar structure in some Cerambycinae (e.g., some Methiini); tarsi 5-5-5 in both sexes (4-4-4 in some Lamiinae by fusion of tarsomeres 4 and 5, Fig. 2.4.17 I), usually pseudotetramerous (Fig. 2.4.17 H) with highly reduced tarsomere 4 partly concealed by the (bi)lobed tarsomere 3; tarsal lobes absent in *Thaumasus* and almost so in some other Cerambycinae, in Parandrinae and more or less so in some Prioninae (Fig. 2.4.17 J, K); tarsomeres 1-3 or at least 2 and 3 usually with dense primarily adhesive pilosity beneath; mid and hind tarsomeres 1 and 2 inflated in males of some Eburiini of Cerambycinae; pretarsal claws without long inner seta(e) (usually devoid of setae altogether, seldom short setae present on basal outer face); simple or seldom toothed to bifid (mainly some Lamiinae: Calliini, Tetraopini-Astathini complex, Phytoeciini, some Saperdini), very strongly divaricate to approximate and subparallel (e.g., many Lamiinae, the epipedocerine subgroup of Tillomorphini of Cerambycinae where claws fuse into one in *Clytellus mononychus*: Holzschuh 2003); empodium exposed and protruding (then often with one to several setae, Fig. 2.4.17 K) to absent.

Abdomen usually with five visible sterna (III-VII); first usually not much longer than second, seldom almost as long as the remaining combined (e.g., female Oabriini of Cerambycinae), without postcoxal lines. Intercostal process acute to broadly rounded or angulate, or absent and medial part of reduced sternum II visible between hind coxae (e.g., Necydalinae and some slender wasp-mimicking Cerambycinae, exceptionally segment II completely visible and III forming a petiolus-like basal piece; Fig. 2.4.17 L). In most lamiine females, tergum VII forms anteriorly a flat, usually bilobed apodeme (Fig. 2.4.17 N), increasing space for attachment of strong muscles manipulating modified tergum VIII. Functional spiracles present on segments I-VII (first very large particularly in flying forms), located in lateral membrane; spiracle VIII vestigial and closed but (where looked for) with rudimentary trachea attached internally. Male terminalia (Sharp & Muir 1912; Ehara 1954; Iuga & Rosca 1962; Li 1986; Fig. 2.4.18 A-F) with tergum VIII well sclerotized and anterior edge of sternum VIII mostly bearing median strut (rudimentary or absent in some taxa); anterior edge of sternum IX with spiculum gastrale; terga IX and X fused together and more or less membranous. Aedeagus cucujiform, symmetrical (but usually rotated to one side within abdominal cavity when at rest); tegmen forming complete sclerotized ring, anteriorly with single

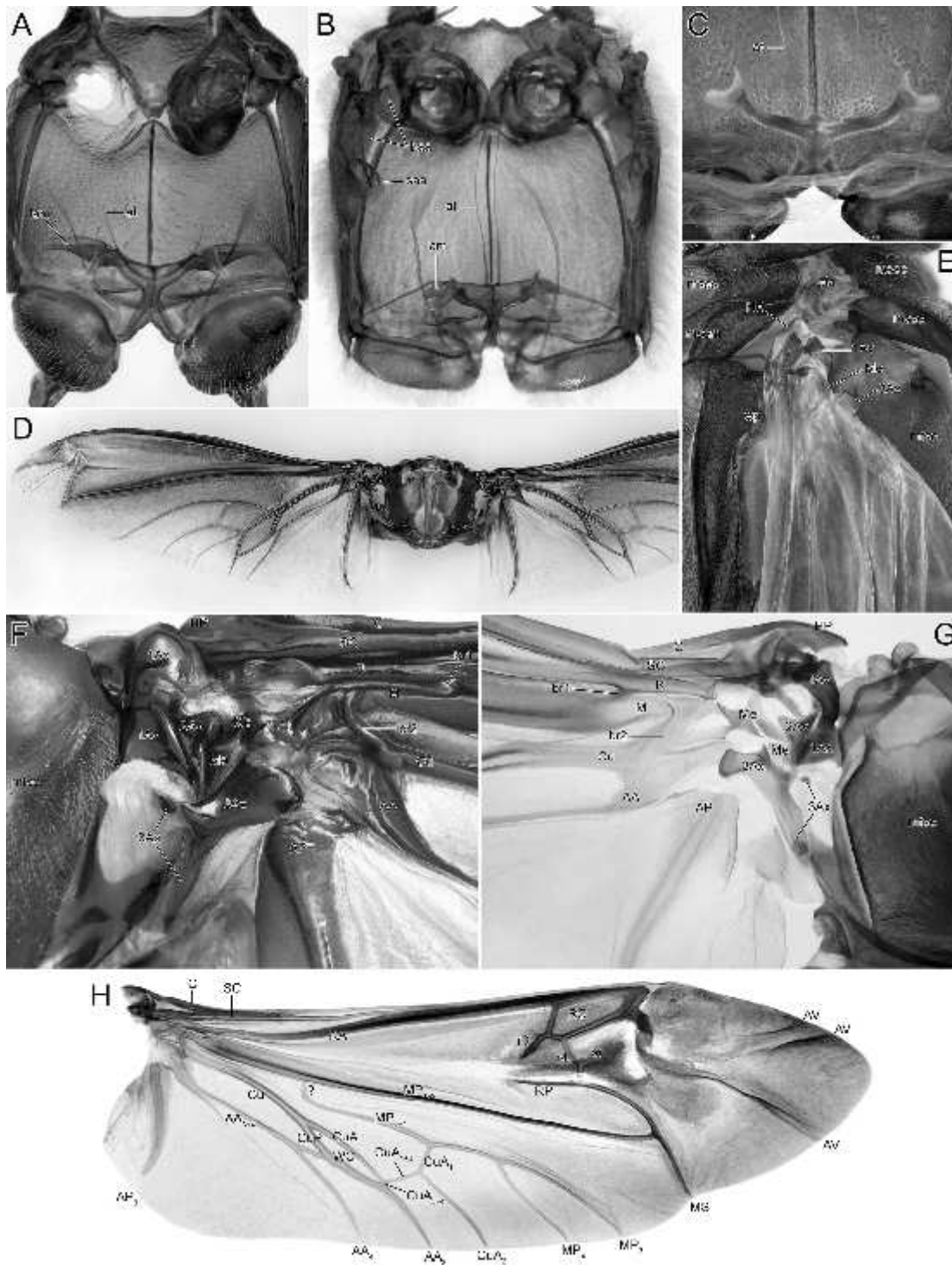


Fig. 2.4.15 Adults of Cerambycinae (A), Prioninae (B–D, F), and Lepturinae (E, G, H). A, *Callidium violaceum* (Linnaeus), male, pterothoracic venter with endoskeleton, dorsal view (metendosternite with large laminae and broadly separate anterior tendons); B, *Closterus grandidieri* Lameere, male, same (metendosternite with moderately sized laminae and very narrowly separate anterior tendons); C, *Rhaphipodus* sp., female, metendosternite without laminae and with moderately broadly separate tendons, dorsal view; D, *Titanus giganteus* (Linnaeus), male, wings and metanotum, dorsal view; E, *Aredolpona rubra*, female, folded left wing base, laterodorsal view; F, *Titanus giganteus*, male, extended right wing base, incident light, dorsal view; G, *Aredolpona rubra*, female, extended and slightly deformed (flattened) left wing base, combined illumination, dorsal view; H, *Oxymirus cursor* (Linnaeus), male, right wing (see also Fig. 2.1.5 A). 1Ax, 2Ax, 3Ax, first, second and third axillary sclerites (2Ax anteriorly connected by a sclerotized bridge with base of R, 3Ax with rotator muscle attached on a small separate sclerite); at, anterior tendon of metendosternite; AV, veins in apical wing region; baa, apodeme of basalare; br1, medial bridge (presumed vestige of MA) of Kukulová-Peck & Lawrence 1993, (anterior) arculus of some authors; br2, bridge between bases of M and Cu (not to be confused with the mp-cu crossvein, or arculus of some authors, which is placed distad of medial bridge and is absent in all cerambycoids); ela, elytral articulation; HP, humeral plate; lam, metendosternal lamina; Me, partly fragmented medial plate; MS, medial spur; mses, mesanepisternum; msem, mesepimeron; mssc, mesoscutum; msscl, mesoscutellum; mtsc, metascutum; RC, radial cell; saa, apodeme of subalare; sr, spur on crossvein r3; WC, wedge cell; wp, metapleural wing process (formed by metanepisternum and metepimeron); ?, a vein of uncertain homology (either a crossvein or base of  $MP_{3+4}$ ).



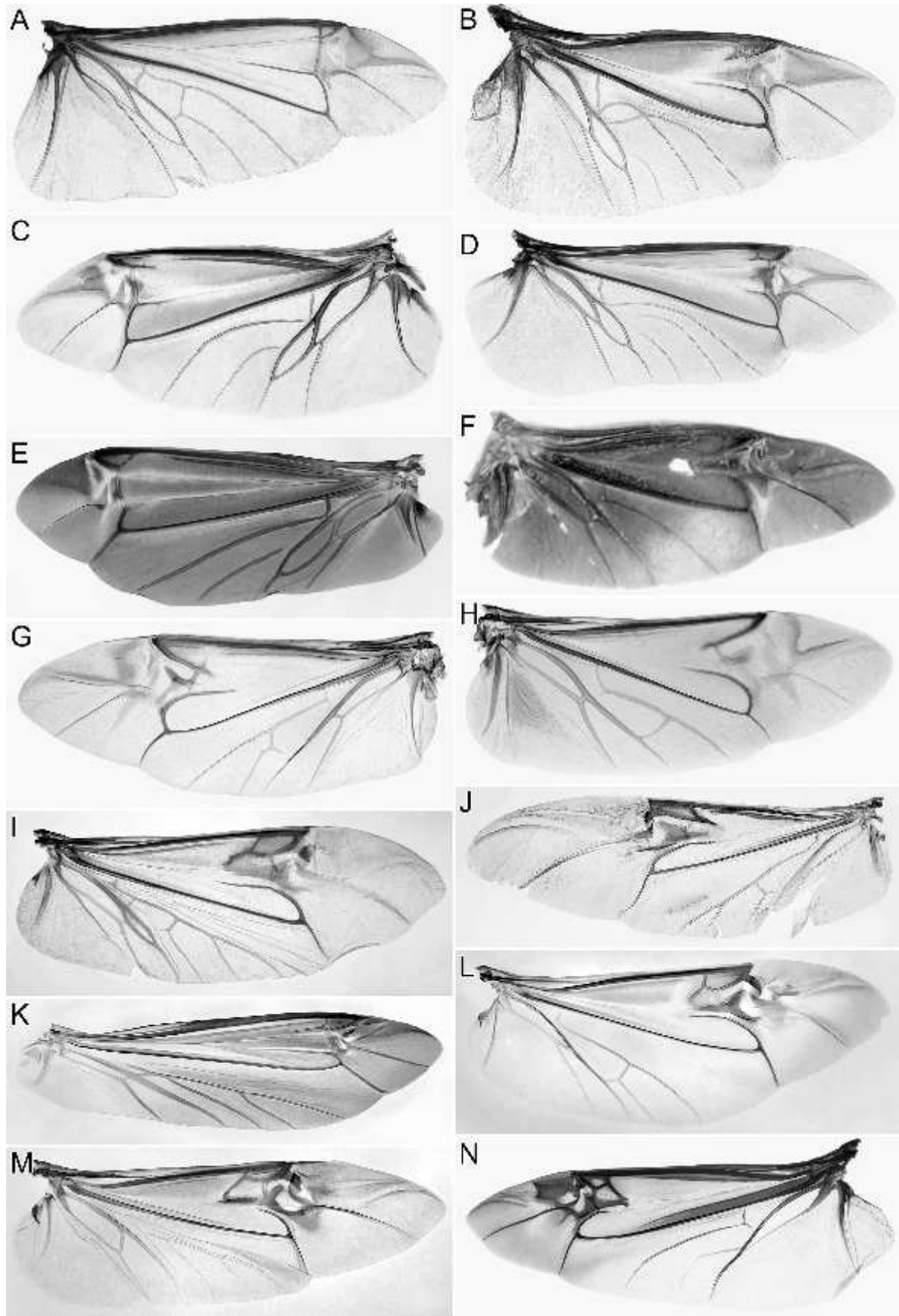


Fig. 2.4.16 Hind wings of Prioninae (A–E), Parandrinae (G, H), Spondylidinae (I, J), Necydalinae (K), Lepturinae (L), Lamiinae (M, N), and of uncertain subfamily (F). A, *Tithoes maculatus* (Fabricius), male; B, *Sceleocantha* sp., male; C, *Prionus coriarius*, male; D, *Hoplioderes aquilus*, female; E, *Stolidodere dequaei*, male; F, *Cycloprionus flavus*, male (© A. Santos-Silva); G, *Acutandra gabonica* (J. Thomson), male; H, *Stenandra kolbei*, female; I, *Saphanus piceus*, male (specimen from Czech Republic); J, *Proatimia pinivora*, male (© W. Bi); K, *Necydalis major*, male; L, *Centrodera sublineata* LeConte, female; M, *Acanthocinus aedilis* (Linnaeus), female; N, *Zographus aulicus* Bertoloni, female.

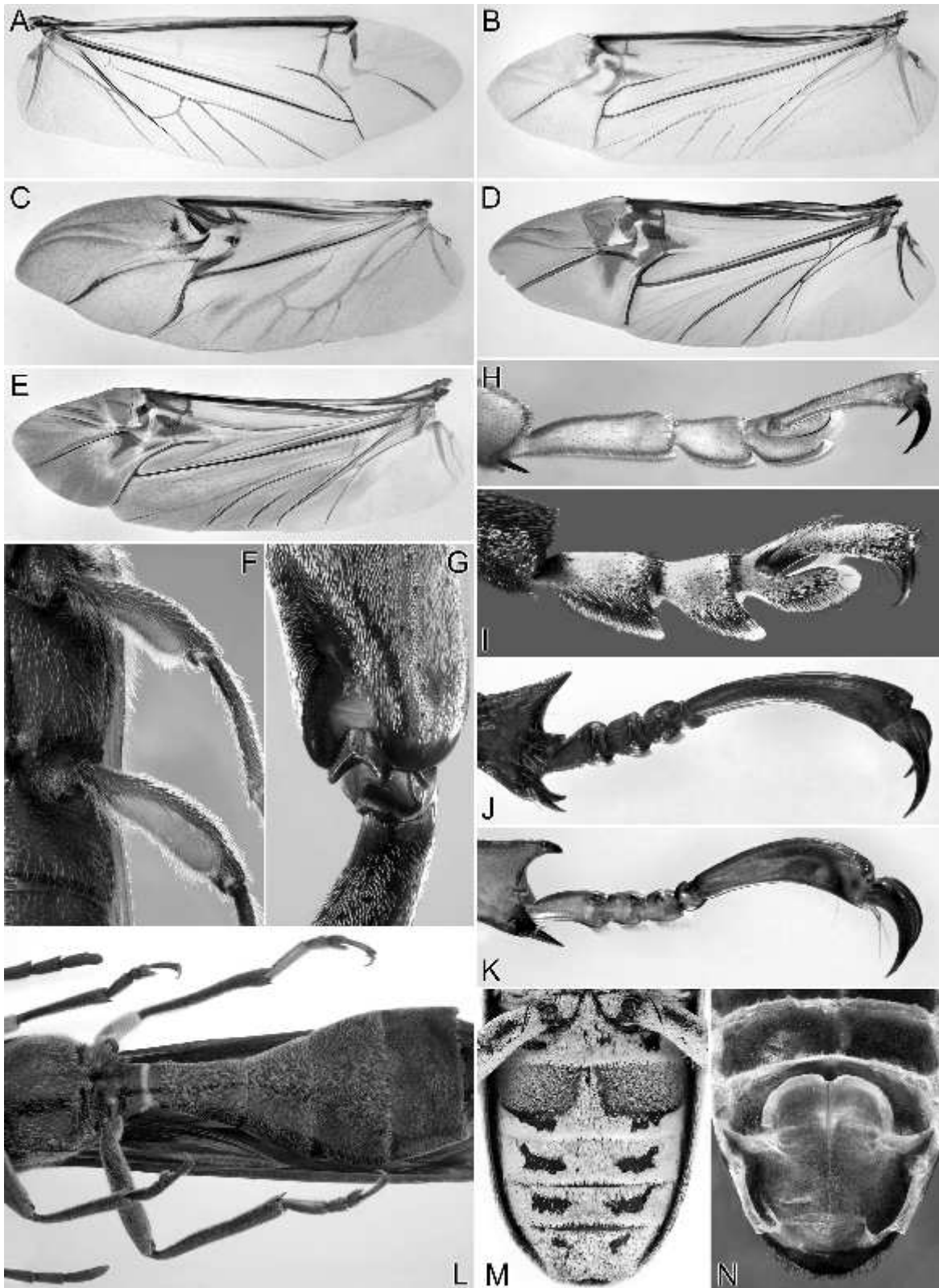


Fig. 2.4.17 Adults. A–E, hind wings of Cerambycinae (A–D) and Dorcasominae (E): A, *Stenopotes pallidus*, male; B, *Phlyctaenodes pustulosus*, male; C, *Opsimus quadrilineatus*, male; D, *Sphinteria gratiosa*, male; E, *Tsivoka simplicicollis*, male; F, *Anisarthron barbipes* (Spondylidinae), male, left middle and hind femur with dense pubescent pads, ventral view; G, *Phosphorus virescens* (Lamiinae), male, left hind femorotibial articulation, bidentate sclerite at invagination of tibial flexor apodeme, ventral view; H–K, right middle tarsus, posterior view: H, *Schmidtiana evertsi* (Cerambycinae), male, pseudotetramerous; I, *Anoplophora malasiaca* (J. Thomson) (Lamiinae), male, tetramerous (tarsomeres 4 and 5 fused); J, *Cantharocnemis plicipennis* Fairmaire, female, pentamerous; K, *Parandra glabra* (De Geer) (Parandrinae), female, pentamerous with long empodium bearing two groups of closely adjacent setae; L, *Cauarana iheringii* (Cerambycinae), male, metathorax and abdomen, lateroventral view (abdominal segment II visible behind coxae, III forming narrow petiolus of the posterior extensively movable abdomen); M, *Rhytiphora saundersi* Pascoe (Lamiinae), male, paired pubescent areas (gland evaporatoria?) on abdominal sternum IV (© CSIRO, Canberra); N, *Tragocephala jucunda* (Gory) (Lamiinae), female, terminal abdominal terga, ventral view (tergum VII with broad bilobed apodeme on anterior margin). 5/8/14 6:21 PM

strut (occasionally abbreviated or with a bifurcate tip); parameres usually fused to tegmen and free from one another, but more or less completely fused in *Pectoctenus* Fairmaire (Spondylidinae) and in some Cerambycinae (e.g., Molorchini-Obriini complex where nearly absent in *Certallum* Dejean, some Plectogastrini, or Neotropical Ectenessini); anterior edge of penis almost always with paired struts; sclerotized parts of male copulatory organs are relatively simple and uniform within major taxa with relatively few partial exceptions (e.g., rather robust aedeagus in at least some Oxymirini compared with other Lepturinae, Fig. 2.4.18 B, or some Madagascan Dorcasominae having the aedeagus extremely long and slender, Fig. 2.4.18 C and Villiers *et al.* 2011); internal sac (endophallus) (Fig. 2.4.18 D, E) entirely inverted at rest, length correlated with length of female ovipositor (Danilevsky *et al.* 2005; Kasatkin 2006); structure variable, in some cases with distinctive sclerotized structures such as asperities, paired or unpaired sclerites, sclerotized ridges or rods or a spine or flagellum at the gonopore (Fig. 2.4.18 A). Ejaculatory duct unpaired or only shortly forked proximally, but more or less completely paired (often up to the gonopore on the internal sac) in Lamiinae of the Batocerini-Lamiini-Dorcadiini complex (Fig. 2.4.18 F); without internal sclerotized tube or rod except for some Lamiinae such as *Acanthocinus* (Ehara 1954; referred to as a flagellum) or some Astatini (personal communication, M. Lin). Female terminalia (Iuga & Rosca 1962; Li 1986; Saito 1989–1993; Fig. 2.4.18 G–O, 2.4.19 O–Q) with sternum VIII bearing anterior apodeme (spiculum ventrale) that may reach deep into the thorax; sternum and tergum VIII are usually partly desclerotized and tend to form tubes or capsules enclosing the “anus-ovipositor” complex and sometimes protruding from the abdomen, either “naked” (e.g., some Aegosomatini of Prioninae) or (partly) protected by posterior sternal and tergal projections of segment VII (e.g., some *Acanthocinini* of Lamiinae); ovipositor usually long and flexible with styli (sub)apical and usually well-developed (paraprocts are short and without baculi and styli are small in Lamiinae, Fig. 2.4.19 Q); major deviations include reduced ovipositors in some groups (mainly Cerambycinae) ovipositing on host surface (Fig. 2.4.19 P; usually combined with abdominal brushes or combs used for covering eggs with debris), or ovipositors with apex sclerotized and styli lateral or laterodorsal and often reduced and sunken in coxites (Fig. 2.4.18 L, M; Parandrinae, some Prioninae, rarely elsewhere). One or two pairs of glandular integumental invaginations are often present at the ovipositor base; in species with larval fungal symbiosis, they serve as mycangia (Schomann 1937). Spermatheca present and more or less sclerotized (adjacent part of the spermathecal duct may be also sclerotized and variously coiled), simple (often elongate curved capsule bridged by spermathecal compressor), and usually with distinct and

sometimes very large (Fig. 2.4.18 O) spermathecal gland arising on spermathecal capsule or on distal duct. Bursa copulatrix usually present, spermathecal duct arising near to its base.

Nerve cord (Mann & Crowson 1983 a; Penteadodias 1984) with fused ganglia T(thoracic)3–A(abdominal)II and AVII–AVIII, often also AVI and in many Lamiinae AV fuse with the terminal mass (in a few studied species the fusions were present also in pupae); terminal ganglionic mass does not reach beyond abdominal segment VI and in some cases is as far anterior as segment III; connectives paired. Midgut (Edwards 1961 b; Benham 1970; Yin 1986, 1987) reduced and threadlike in prionines and some cerambycines (less reduced in floricolous species), long and well-developed in Lamiinae. Six cryptonephridial Malpighian tubules. Male internal reproductive organs (Ehara 1951, 1956; Iuga & Rosca 1962; Li 1986) with testes forming one to several pairs of testicular lobes; up to 12 pairs in Lamiinae (Li 1986), 12–15 pairs in *Prionoplus* (Prioninae), and 22–24 pairs in *Ochrocydus* Pascoe (Cerambycinae) (Edwards 1961 a); each lobe with radially arranged testicular follicles. Basal parts of vasa deferentia may be broadened into seminal vesicles (tightly coiled and enclosed in a muscular capsule in some Lepturinae); testicular lobes may degenerate in short-lived adults whereas spermatogenesis continues during much of adult life in Lamiinae (Edwards 1961 a; Ehara 1951, 1956). One to two pairs of accessory glands present at or before fusion of vasa deferentia; secondary glands may be also present on ejaculatory duct. Ovaries (Iuga & Rosca 1962; Li 1986) paired, with variable number (up to several tens) of ovarioles.

[Color photographs of adults from various regions: Adlbauer 2001; Chalumeau & Touroult 2005; Chemsak 1996; Chou 2004; Di Iorio 2005; Ehnström & Holmer 2007; Galileo *et al.* 2008; Hequet & Tavakilian 1996; Hua *et al.* 2009; Japanese Society of Coleopterology 1984; Jeniš 2001, 2008, 2010; Martins & Galileo 2004; Ohbayashi & Niisato 2007; Sama 2002; Sláma 2006; Šlipiński & Escalona 2013; Vives 2001; most recent keys to larger regions: Bense 1995; Breuning 1957; Chemsak 1996; Cherepanov 1979–1985, 1996; Danilevsky & Miroshnikov 1985; Gahan 1906; Gressitt 1951, 1956, 1959; Gressitt *et al.* 1970; Hüdepohl 1987, 1990, 1992; Kostin 1973; Lawrence *et al.* 1999 b; Lingafelter 2007; Linsley 1962–1964; Linsley & Chemsak 1972–1995; Plavilstshikov 1936–1958; Turnbow & Thomas 2002; Martins 1997–2010; Ohbayashi & Niisato 2007 (pictorial key); Quentin & Villiers 1975; Santos Ferreira 1980; Veiga Ferreira 1964, 1966; Villiers 1946, 1978; Villiers *et al.* 2011; Vives 2000.]

**Morphology, Larvae** (later instars, Fig. 2.4.20, 2.4.21 A–D, G–M; for differences of first instars, see end of larval description). Oligopodous to apodous, prognathous, more or less elongate, subcylindrical to extremely dorsoventrally depressed, soft-bodied larvae in which body shape and

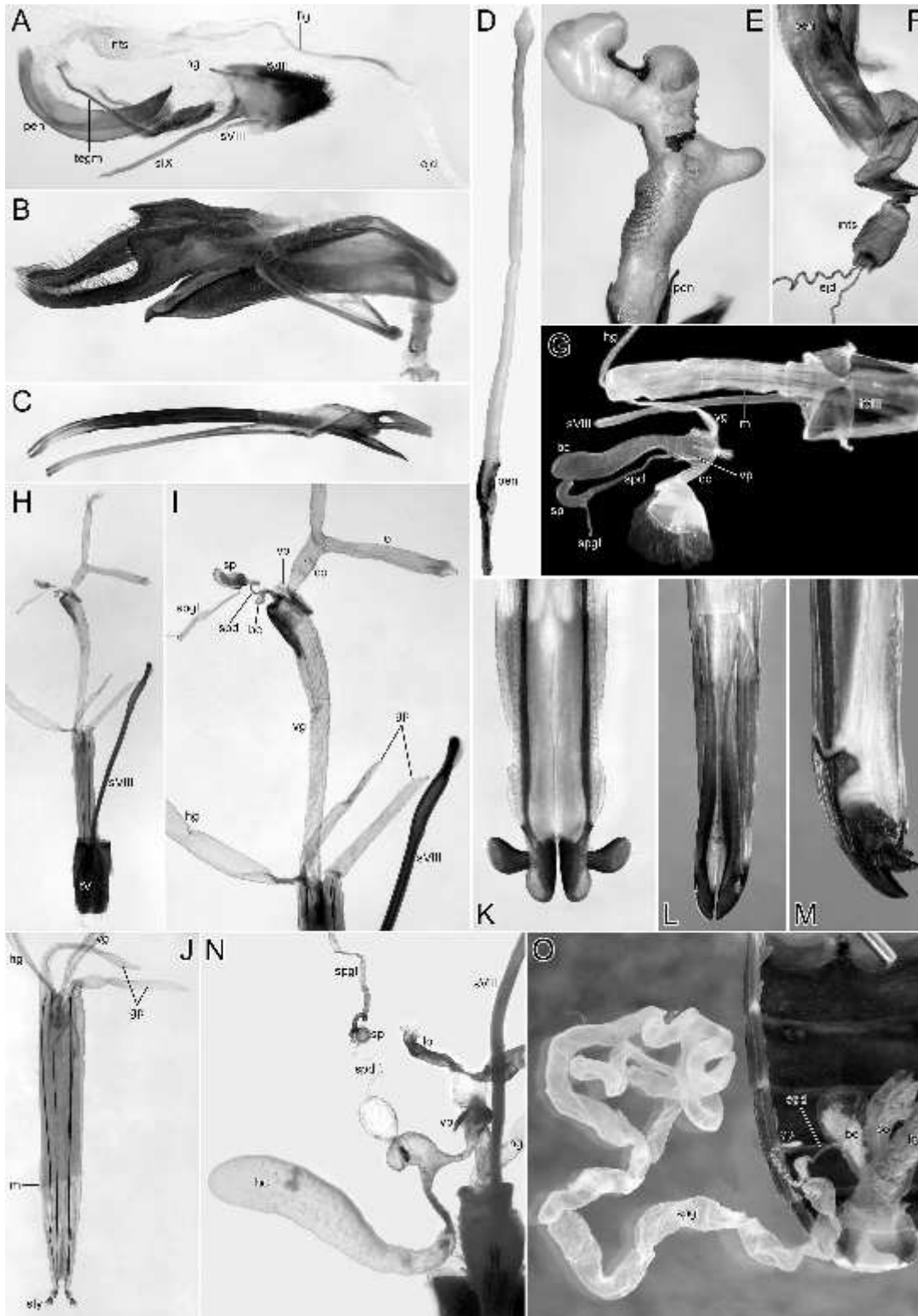


Fig. 2.4.18 Adult terminalia and internal genital structures, Lepturinae (A, B, H–J), Dorcasominae (C), Prioninae (D, G, K, L), Cerambycinae (E), Lamiinae (F, N, O), and Parandrinae (M). A, *Leptura aurulenta* Fabricius, male, terminal abdominal sclerites and genitalia, ventral view; B, *Oxymirus cursor*, male, penis and tegmen, right laterodorsal view; C, *Sagrifida maculosa* (Guérin-Ménéville), male, penis and tegmen, left lateral view (the complex is longer than abdomen and its base protrudes into metathoracic cavity at rest); D, *Aegosoma scabricorne*, male, everted internal sac, lateral view (© D. Kasatkin); E, *Pavieia superba* Brongniart, same (© D. Kasatkin); F, *Morimus funereus* Mulsant, male, paired ejaculatory ducts reaching internal sac; G, *Rhaphipodus* sp., female, abdominal segment VIII and internal genitalia, dorsal view; H, *Aredolpona rubra*, same; I, same, detail of H; J, same, exposed anus-ovipositor complex with part of ensheathing membrane intact, dorsal view; (cf. Fig. 2.4.19 O); K, *Mallodon* sp., female, apical part of ovipositor, dorsal view; L, *Notophysis forcipata* (Harold), same, laterodorsal view; M, *Parandra glabra*, same, lateral view; N, *Zographus aulicus*, female, internal genitalia, dorsal view; O, *Phantasia avernica*, female, abdominal venter and internal genitalia, dorsal view. ejd, ejaculatory duct(s); flg, flagellum; ints, internal sac; pen, penis; sVIII, apodeme of sternum VIII (spiculum ventrale in females); sIX, apodeme of sternum IX in male (spiculum gastrale); tVIII, tergum VIII; tegm, tegmen with parameres; for other abbreviations see Fig. 2.4.19 O.

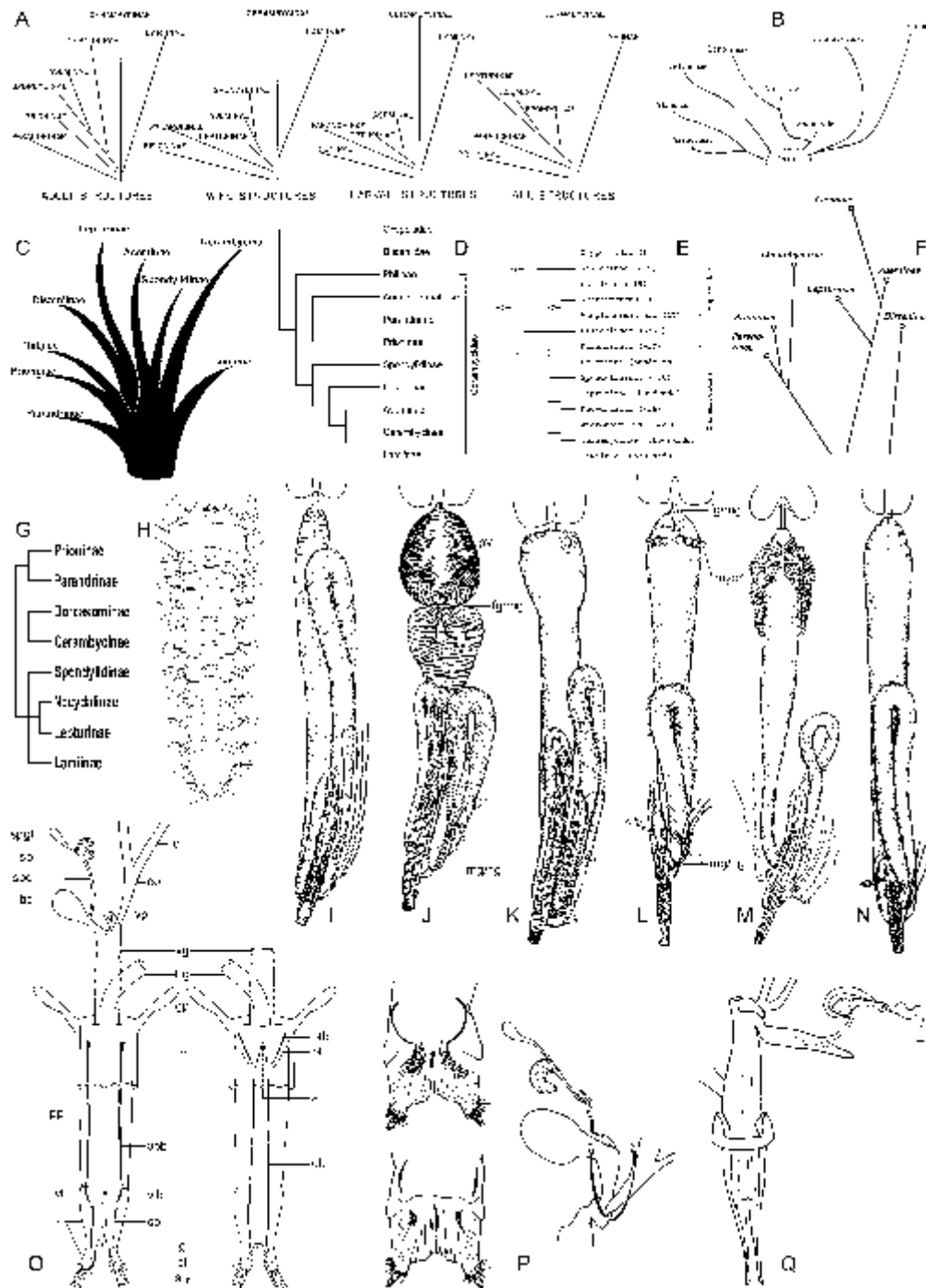


Fig. 2.4.19 A–F, cerambycoide relationships proposed by various authors: A, Linsley (1961) (based on various structures); B, Nakamura (1981); C, Villiers (1978); D, Napp (1994) (reconstructed from text and approved by the author); E, Svacha *et al.* (1997); F, Danilevsky (1979 a); G, preliminary incompletely resolved relationships of the subfamilies of Cerambycidae as proposed in the present chapter; H, *Apiocephalus punctipennis* (Lepturinae), larva, semidiagrammatic, dorsal view (from Svacha & Danilevsky 1987); I–N, larval gut of Cerambycidae, dorsal view (modified from Danilevsky 1976): I, *Aegosoma scabricorne* (Prioninae); J, *Stromatium barbatum* (Fabricius) (Cerambycinae) with foregut forming large proventriculus; K, *Hylotrupes bajulus* (Linnaeus) (Cerambycinae); L, *Drymochares starcki* (Spondylidinae) with small round mycetomes on anterior midgut; M, *Necydalis major* (Necydalinae) with large complex mycetomes; N, *Saperda scalaris* (Linnaeus) (Lamiinae); O, diagrammatic drawing of female ovipositor, internal reproductive organs and associated structures of Lepturinae, ventral (left) and dorsal (right) views (modified from Saito 1989 a); P, *Purpuricenus spectabilis* Motschulsky (Cerambycinae), female, very short ovipositor in ventral (upper left) and dorsal (lower left) view and internal reproductive organs (right) (from Saito 1993 a); Q, *Cagosima sanguinolenta* J. Thomson (Lamiinae), ovipositor and internal reproductive organs, ventral view (from Saito 1993 b). a, anus; bc, bursa copulatrix; c, coxite; cb, coxital baculum; cl, coxite lobe; co, common oviduct; db, dorsal baculum; fg/mg, border between foregut and midgut; g, gonopore; gp, glandular pocket; hg, hindgut; lo, lateral oviduct; m, membrane anatomically following segment VIII, ensheathing the entire proctiger-anus-ovipositor complex and forming the glandular pockets if present; mg/hg, border between midgut and hindgut; myc, mycetomes; pp, paraproct; ppb, paraproctal baculum; pt, proctiger (epiproct); ptb, proctigeral baculum; pv, proventriculus; sp, spermatheca; spd, spermathecal duct; spgl, spermathecal gland; sty, stylus; vg, vagina; vl, valvifer; vlb, valvifer baculum; vp, vaginal plate.

mechanics depend upon hemolymph pressure. Cranium well-developed, often strongly sclerotized and pigmented (particularly the anterior “mouth frame”); biting mouthparts with powerful strongly sclerotized mandibles; body white to yellow, rarely grayish or reddish, generally soft, with at most some prothoracic regions and very rarely also abdominal end (Fig. 2.4.21 B) or some other abdominal regions (Fig. 2.4.21 C) extensively sclerotized; exceptionally, body cuticle entirely brown, leathery and “velured” in *Macrodontia cervicornis* (Linnaeus) (Prioninae) (Fig. 2.4.20 D). Spiracular system peripneustic (mesothoracic plus eight abdominal functional spiracles, metathoracic spiracle rudimentary and closed but usually visible), in later-instar larvae spiracles annular to annular multiforous (Fig. 2.4.30 I–M) with spiracular atrium broadly open, rarely partly closed by thin cuticular flaps extended inward from spiracular margin (some Phytoeciini of Lamiinae). Invaginated wing imaginal discs absent, studied cerambycids belong to the “simple type” of development (Tower 1903). Abdomen at least dorsally with more or less retractile and differently sculptured ambulatory ampullae (Fig. 2.4.28, 2.4.29 H–M, 2.4.30 A); similar less prominent structures may be present on pterothoracic terga and sterna. Setae usually abundant (sparse in some Lepturinae) and, except for a limited number of primary setae (often difficult to distinguish in later instar larvae), relatively inconsistent. Trichobothria (specialized thin loosely articulated setae registering airborne vibrations or currents) absent except for tips of lateral abdominal processes of aberrant larvae of *Apiocephalus* Gahan and *Capnolymma* Pascoe (Lepturinae) (Fig. 2.4.31 A–C). Large body regions may be covered with microscopic spine-like microtrichia; asperities may become larger on some regions (particularly on pronotum), up to very coarse sclerotized and often carinate granules (Fig. 2.4.21 M, 2.4.27 L, M) that rarely fuse into sclerotized ridges (Fig. 2.4.27 J).

Head (terminology in Fig. 2.4.22) usually more or less deeply retracted, but largely exposed in some Lepturinae and Lamiinae (Fig. 2.4.20 M, Q, T). Head capsule well-sclerotized, bilaterally symmetrical, of rather variable shape (Fig. 2.4.23–25) but always without exposed coronal suture (epicranial stem); medial dorsal head retractors attached immediately at or on posterior frontal angle; however, frons may narrowly reach to posterior cranial edge in ventral layer of dorsomedian cranial duplication (Fig. 2.4.27 G); this firmly fused bilayered region is long in all subfamilies except for Necydalinae and most Lepturinae, where short or absent (see Fig. 2.4.22, 2.4.27 A–D); in some Lamiinae the entire retracted part of cranium is firmly cemented to the prothoracic membranous pocket ensheathing it. Frontal arms (if distinct) broadly V-shaped, seldom subparallel posteriorly (Fig. 2.4.25 C); anteriorly passing laterad of pretentorial pits and dorsal mandibular articulations and reaching cranial

margin through or immediately below lower parts of antennal openings (Fig. 2.4.22 E, F, 2.4.23 H, 2.4.25 G), ending in or vanishing before antennal sockets (Fig. 2.4.24 L, 2.4.25 E), or absent (Fig. 2.4.31 E); they sometimes do not function as cleavage lines even if present; middle section of frontal lines formed as secondary shortcut bridging original incurved portions of the presumed lyriform frontal arms of chrysomeloid or phytophagan ancestor; consequently, dorsal arms of metatentorium (if distinct), pretentorial arms and antennal muscles are all attached in or point to an apparently “frontal” instead of epicranial region (compare Fig. 2.4.27 E–I); diffuse rudiments of original incurved middle parts of frontal arms may be rarely visible, and in some Lepturinae their transverse anterior sections are secondarily distinct and more or less completely connected medially in later instar larvae, forming a transfrontal line (Fig. 2.4.20 Q, 2.4.22 B; sometimes with blind posterior branches). Median unforked frontal endocarina usually present, but absent in *Apiocephalus* and *Capnolymma* (Lepturinae) (Fig. 2.4.31 D, E) and indistinct in some Cerambycinae; may or may not reach epistomal margin, usually visible externally as a darker median frontal line. In some Lepturinae, its pigmentation interrupted by transfrontal line. Anterior margin of frontal plate is named epistomal because of its origin; it always forms a strengthened and more or less infolded transverse bar incorporating postclypeus (= epistoma of some authors) and bears three pairs of epistomal (originally postclypeal) setae, occasionally with supplementary setae; epistomal margin projects more or less strongly above anteclypeal base in most Prioninae and Dorcasominae and a few Cerambycinae (Fig. 2.4.22 E, 2.4.23 D, F, J, 2.4.25 G; projection referred to as the epistoma or epistomal carina); in Prioninae typically associated with additional carinae above epistoma and behind dorsal mandibular articulations (frontal and postcondylar carinae, respectively, in Fig. 2.4.22 E); in Cerambycinae and less so in Dorcasominae, medial pair of epistomal setae is shifted posteriorly (at least placed behind massive epistomal projection in the latter subfamily) and appears to be frontal (arrowheads in Fig. 2.4.23 F, H–K, 2.4.25 E, I). Cerambycinae has been therefore usually incorrectly described as having only two pairs of epistomal setae. Clypeus (= anteclypeus) broad, trapezoidal, soft or at most moderately sclerotized basally and laterally, filling space between dorsal mandibular articulations except for Cerambycinae, where abruptly constricted and reaching those articulations only by narrow often indistinct basal arms (Fig. 2.4.21 J, 2.4.24 A, C, D, G, 2.4.25 E, I); setae usually lacking, seldom regular lateral setae present (e.g., most Saperdini of Lamiinae). Labrum free, from subcircular or cordate (particularly long in Parandrinae; Fig. 2.4.23 C) to strongly transverse; long labrum usually correlated with the presence of mandibular pseudomola; the small labrum in Cerambycinae is associated with narrow anterior clypeus and specialized



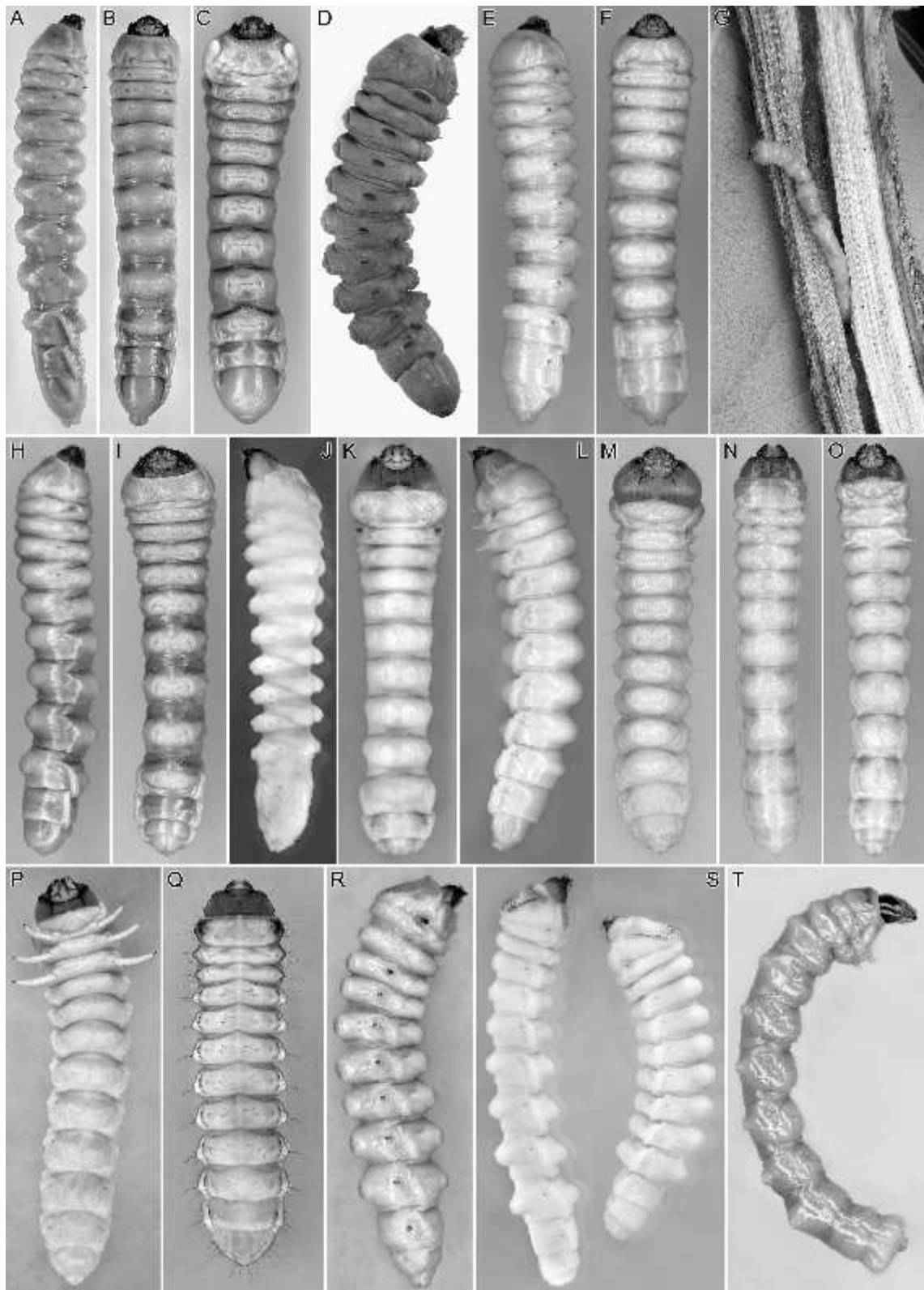


Fig. 2.4.20 Later-instar larvae of Prioninae (A–D), Dorcasominae (E, F), Cerambycinae (G–I), Spondylidinae (J, K), Lepturinae (L–Q), and Lamiinae (R–T). A, *Prionus coriarius*, lateral view; B, same, ventral view; C, *Neoprion batesi* (Gahan), ventral view; D, *Macrodonia cervicornis* (Linnaeus), lateral view; E, *Tsivoka simplicicollis*, laterodorsal view; F, same, ventral view; G, *Macropsebium cotterilli* Bates, live larva in its gallery (© G. Sama); H, *Cerambyx cerdo*, lateral view; I, same, ventral view; J, *Atimia okayamensis* Hayashi, laterodorsal view; K, *Arhopalus rusticus* (Linnaeus), ventral view; L, *Aredolpona rubra*, laterodorsal view; M, *Etorofus pubescens* (Fabricius), ventral view; N, *Pachyta quadrimaculata*, dorsal view; O, same, ventral view; P, *Judolia sexmaculata* (Linnaeus), ventral view; Q, *Dinoptera collaris* (Linnaeus), dorsal view; R, *Saperda carcharias* (Linnaeus), lateral view; S, *Phytoecia caerulea* Scopoli, lateral view of active feeding larva (left) and last larval instar from pupal chamber (right); T, *Agapanthia dahli* (Richter), lateral view.

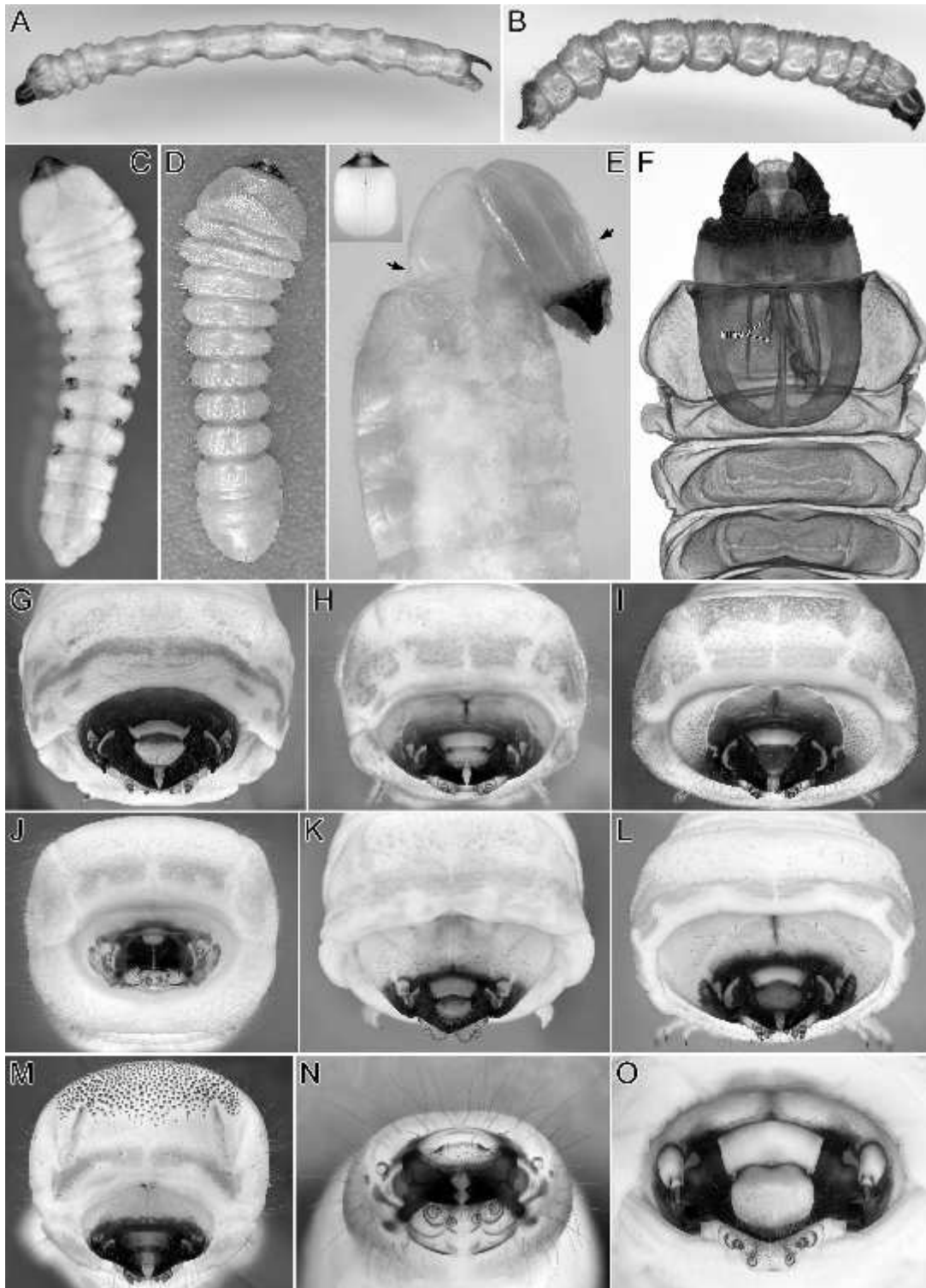


Fig. 2.4.21 Larvae. A–F, later-instar larvae of Lamiinae: A, *Aerenicopsis mendosa* Martins & Galileo, lateral view; B, unidentified larva from Barro Colorado (Panama) labelled as “*Parysatis* or *Esthlogena*” (former genus is now a synonym of *Ataxia* Haldeman), lateral view; C, *Pseudhoplomelas elegans* (Fairmaire), dorsal view; D, *Exocentrus adspersus* Mulsant, dorsal view; E, *E. testudineus* Matsushita, head and thorax, lateral view (both layers of dorsomedian duplicate region separated and the membranous pocket became everted during preservation, cf. Fig. 2.4.21 F, points superimposed when the head is in normal position are marked by arrows), and head of *E. adspersus* in dorsal view (inset); F, *Saperda perforata* (Pallas), cleared head, thorax and abdominal segment I, dorsal view (dorsal body cuticle removed; rma, apodemes of dorsomedian head retractor muscles labelled RM in Fig. 2.4.27 B, D); G–M, head and prothorax in anterior or anterodorsal view: G, *Prionus coriarius* (Prioninae); H, *Saphanus piceus* (Spondylidinae); I, *Arhopalus rusticus* (Spondylidinae); J, *Anaglyptus mysticus* (Linnaeus) (Cerambycinae); K, *Necydalis major* (Necydalinae); L, *Aredolpona rubra* (Lepturinae); M, *Phytoecia nigricornis* (Fabricius) (Lamiinae); N, *Agapanthiola leucaspis* (Steven) (Lamiinae), head, anterior view; O, *Cantharocnemis strandi* Plavilstshikov (Prioninae), same.



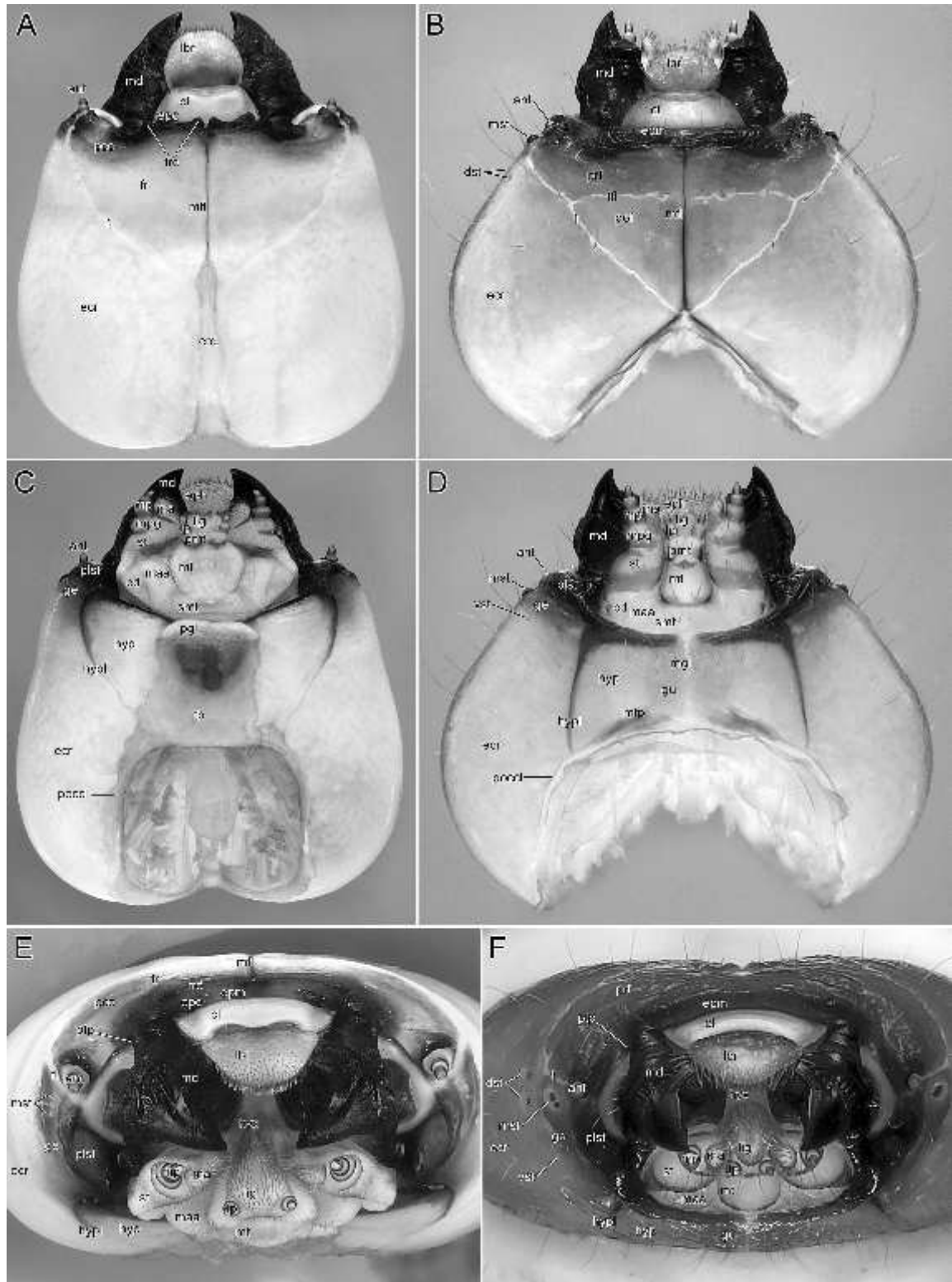


Fig. 2.4.22 Larval head, terminology, *Aegosoma scabricorne* (Prioninae; A, C, E) and *Oxymirus cursor* (Lepturinae; B, D, F) in dorsal (A, B), ventral (C, D), and anterior (E, F) view. ant, antenna; cd, cardo; cl, clypeus (in cerambycids actually anteclypeus); crd, dorsomedian cranial duplicature; dst, dorsal stemmata; ecr, epicranium; epc, epistomal carina; eph, epipharynx; epm, epistomal margin (of postclypeal origin); fl, frontal lines (frontal arms); fr, frons; frc, frontal carina; ge, gena; gu, gula; hyp, hypostoma; hyp1, hypostomal line; hyx, hypopharyngeal region; lbr, labrum; lig, ligula; lp, labial palp; maa, maxillary articulating area; md, mandible; mfl, median frontal line; mgl, median gular line; mp, maxillary palp; mpg, maxillary palpiger; mst, main stemmata; mt, mentum; mtp, metatentorial pits; pcc, postcondylar carina; pgl, postgular lobe (hiding the short gula in *Aegosoma*); plst, pleurostoma; pmt, prementum; poccl, postoccipital line; pof, postfrontal region; prf, prefrontal region; ptp, pretentorial pits; smt, submentum; st, stipes; tb, tentorial bridge; tf1, transfrontal line; vst, ventral stemma.

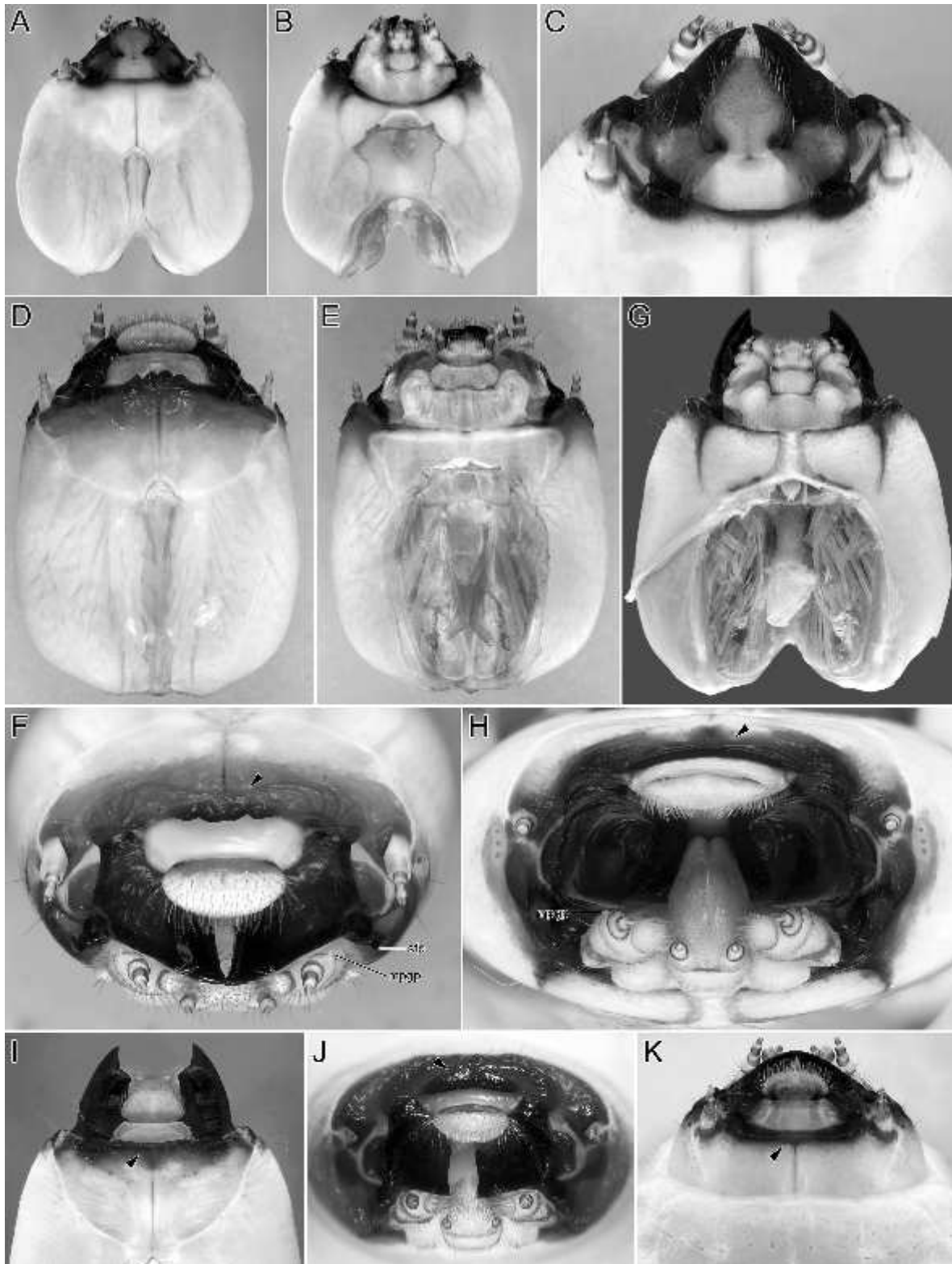


Fig. 2.4.23 Larval head of Parandrinae (A–C) and Dorcasominae (D–K). A, *Neandra brunnea* (Fabricius), head, dorsal view; B, same, ventral view; C, same, anterior head, anterodorsal view; D, *Artelida crinipes* J. Thomson, head, dorsal view; E, same, ventral view; F, same, anterior head, anterodorsal view; G, *Dorcasomus gigas* Aurivillius, head, ventral view; H, same, anterior view; I, same, anterior head, dorsal view; J, *Apatophysis barbara*, head, anterior view; K, *Zulphis subfasciatus*, anterior head, dorsal view. mjpg, dorsolateral process of maxillary palpiger; sfp, subfossal process; arrowheads in F and H–K mark medial epistomal seta (in Dorcasominae distant from basal clypeal margin).

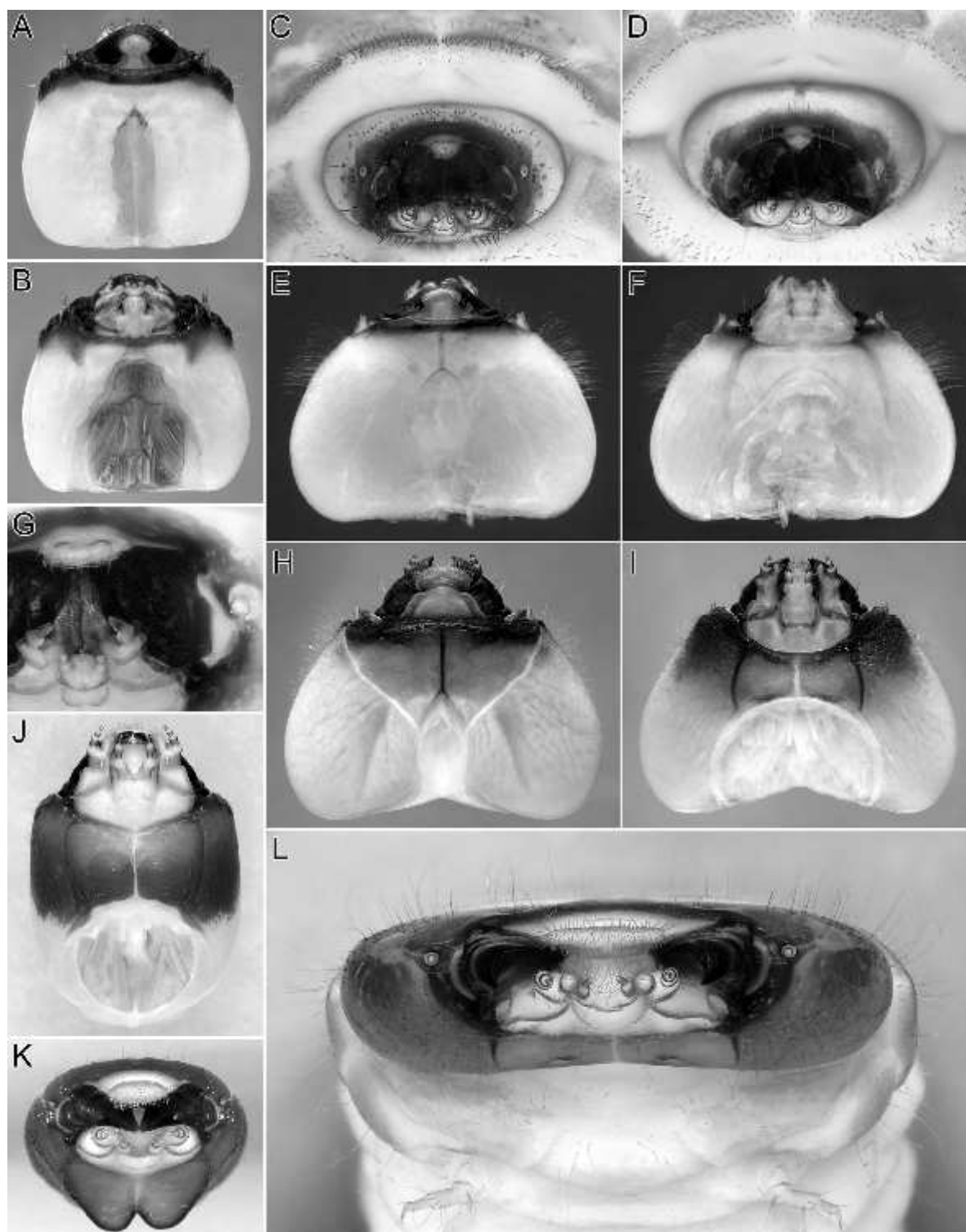


Fig. 2.4.24 Larval head of Cerambycinae (A–G), Spondylidinae (H, I), Lamiinae (J, K), and Lepturinae (L). A, *Xylotrechus antilope* (Schoenherr), head, dorsal view; B, same, ventral view; C, *Holopterus chilensis*, head, anterior view; D, *Callisphyris macropus*, same; E, *Opsimus quadrilineatus*, head, dorsal view; F, same, ventral view; G, same, mouth parts and left antenna, anterior view; H, *Spondylis buprestoides*, head, dorsal view; I, same, ventral view; J, *Deroplia albida* (Brullé), head, ventral view; K, same, anterior view; L, *Rhagium inquisitor* (Linnaeus), head and prothorax, anterior view.

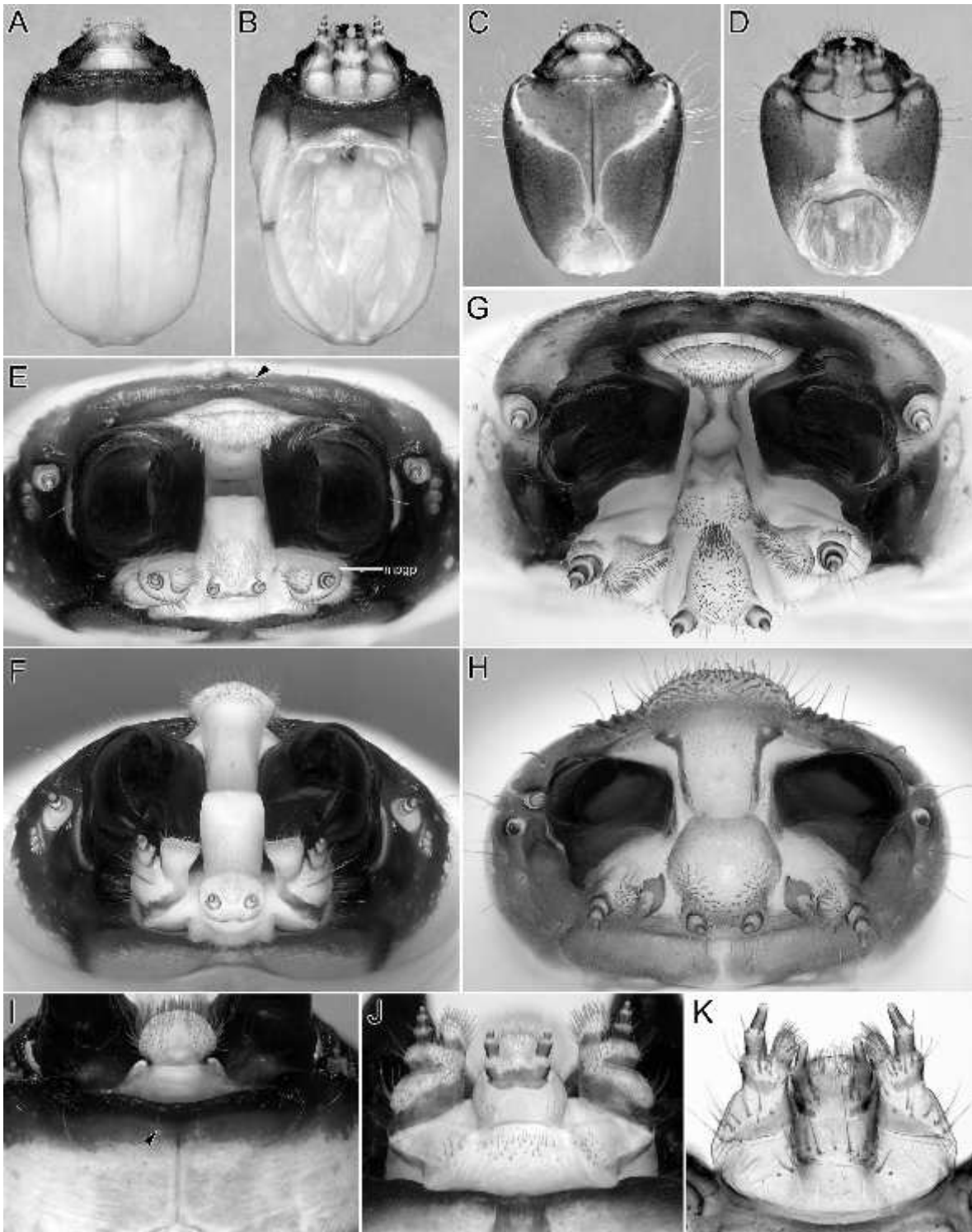


Fig. 2.4.25 Larval head and mouth parts of Lamiinae (A–D, H, K), Cerambycinae (E, F, I, J), and Prioninae (G). A, *Epiglenea comes* Bates, head, dorsal view; B, same, ventral view; C, *Agapanthia villosoviridescens*, head, dorsal view; D, same, ventral view; E, *Cerambyx cerdo*, head, anterior view; F, *Plagionotus* sp., head with unnaturally broadly open mouth parts, anterior view (left mandible split by heat used in preservation); G, *Tragosoma depsarium* (Linnaeus), broadly open mouth parts, anterior view; H, *Oplasia cinerea* (Mulsant), head with unnaturally broadly open mouth parts, anterior view; I, *Cerambyx cerdo*, frons, clypeus and labrum, anterodorsal view; J, same, maxillolabial complex, ventral view; K, *Pogonocherus hispidus* (Linnaeus), same. mppg, dorsolateral process of maxillary palpiger; arrowheads in E and I mark medial epistomal seta (in Cerambycinae moved far from basal clypeal margin).

mandibular type; labrum setose anteriorly and usually more or less sclerotized in basal half; epipharynx (Fig. 2.4.26 C, D) with setae variable, often with extensive fields of microtrichia, and with two groups of sensilla: anterior usually including three pairs of sunken sensilla and some minute setae or pegs and posterior usually composed of at least 5+5 often scattered sunken sensilla, occasionally multiplied but rarely reduced (e.g., 2+2 in *Exocentrus* Dejean of Lamiinae, Fig. 2.4.26 D) and placed on a raised posteromedial region facing the hypopharyngeal part of the maxillolabial complex; that raised region often with median sclerite and usually lined laterally with longitudinal sclerotized bands that may (Fig. 2.4.25 H) or may not (Fig. 2.4.26 C) be fused with tormae. Pleurostoma (lateral portion of mouth frame between antennal socket and ventral mandibular articulation) usually strongly sclerotized and more or less raised, mostly asetose; rim of mandibular pit may bear subfossal process (Fig. 2.4.23 F). Genal region may be distinguished from epicranium by different sculpture and/or darker pigmentation and bears up to six pairs of regular stemmata distributed in three groups (Fig. 2.4.22 F): three (often fusing, e.g., all Lamiinae) main stemmata in a vertical row just behind pleurostoma and near to antennal socket, two dorsal stemmata slightly behind and above the main group, and one ventral stemma below and slightly behind that group; seventh stemma (fourth main stemma) was rarely found in some specimens of certain Prioninae and Cerambycinae; stemmata absent in some later instars (e.g., in many subterranean larvae). Epicranial region (delimited dorsally by frontal arms, anteriorly by genal region and ventrally by hypostomal lines) dorsomedially fused very shortly or at one point (i.e., having no or very short dorsomedian cranial duplicature) in Necydalinae and most Lepturinae (Fig. 2.4.22 B, 2.4.27 C, D), fused along its entire dorsal length (resulting in an entirely ventral placement of the occipital foramen) in Lamiinae (Fig. 2.4.25 A–D), and usually intermediate between these extremes in remaining subfamilies (Fig. 2.4.22 A, 2.4.23 A, D, 2.4.24 A, E, H). If present, dorsomedian cranial duplicature ventrally flat or bearing low median endocarina except for Lamiinae, where the ventral layer forms an infolded median crest reaching deep into cranial cavity, thus increasing space for attachment of strong mandibular adductors (Fig. 2.4.21 F, 2.4.25 B); the dorsal layer does not participate in forming that crest (Fig. 2.4.21 E). Frontal lines enter separately the ventral layer and, where they can be followed, appear to run separately along both sides of median endocarina and fuse near posterior cranial margin (Fig. 2.4.27 G); we therefore prefer interpreting the cerambycid larval head as not having a concealed epicranial stem because the fine dorsal layer may be of postcranial origin (Fig. 2.4.21 E). Strengthened margin of occipital foramen in some Lamiinae bears paired lateral structures (Fig. 2.4.25 B) that appear to be “hinges” (very short sections of flexible cuticle delimited on

both sides by stronger sclerotization) allowing slight flexion of the posterior portion of the very long lamiine head capsule. Antennae moderately long (and then with extensive connecting membrane) to minute, primarily trimerous (Fig. 2.4.26 A), never with secondary subdivisions, but various reductions and/or fusions may occur leading to monomeric antennae (Fig. 2.4.26 B); antennal sensorium in apical membrane of antennomere 2, flat or at most roundly convex in later instars of Prioninae, Parandrinae and *Icosium* (Cerambycinae), conical in remaining taxa. Mandibles symmetrical, strongly sclerotized, separate at base (Fig. 2.4.25 E–H); basal portion relatively simple, without medial molar armature or articulated appendages, and with two or more lateral setae; apical part always asetose; it is strongly specialized, rounded and “gouge-like” in Cerambycinae (Fig. 2.4.21 J, 2.4.25 E, F); in remaining subfamilies pointed (rarely apex bidentate, Fig. 2.4.21 N, 2.4.26 K) and with a more or less distinct dorsal angle not separated by a distinct notch and connected with apex by a straight, emarginate or angulate cutting edge; a subapical often striated keel at dorsal angle (pseudomola of Lawrence 1991) may be present (Fig. 2.4.26 F–H) to vestigial or absent (Fig. 2.4.26 I, J, L) (mandibular types II and I, respectively, of Svacha & Danilevsky 1987), species with at least small pseudomola occur in all subfamilies with pointed mandibles except for Lamiinae; mesal apical surface usually with three keels or ledges converging toward apex (Fig. 2.4.26 E–K), only two in most Lamiinae and Lepturinae and some Parandrinae (Fig. 2.4.26 L); mandibular base laterally bearing a thin elongate apodeme for mandibular abductor, and medially a large apodeme (usually consisting of two perpendicular plates) for strong adductor. Maxillolabial complex not retracted; basal margin in ventral view placed shortly behind level of mandibular pits; basal part formed by submentum, maxillary articulating areas (connecting lobes of Svacha & Danilevsky 1987) and cardines; articulating area in some taxa divided into smaller anterior and larger posterior lobe; base of submentum and maxillary articulating areas fused to anterior gular margin; in Lamiinae, cardo extremely reduced, fixed and displaced laterally so that virtually entire maxillolabial base is fused to cranium (Fig. 2.4.25 K); in other subfamilies, cardo free and more or less movable (small in Spondylidinae, Fig. 2.4.24 I, very large in some Cerambycinae, Fig. 2.4.24 B), its sclerotization never forming two separate sclerites; distal maxilla composed of stipes, maxillary palpiger (palpifer), mala, and maxillary palp; mala from broadly triangular to slender and finger-like, often apparently inserted onto palpiger in ventral view (Fig. 2.4.22 D, 2.4.24 I, J, L, 2.4.25 K); two sensilla homologous to those on malar organ of Vesperidae (see Fig. 2.1.10 E–H) present but usually not arising from a common tubercle; palp trimerous, rarely (some Lamiinae and Cerambycinae) dimerous (by fusion of palpomeres 1 and 2, not 2 and 3 as erroneously stated by Svacha

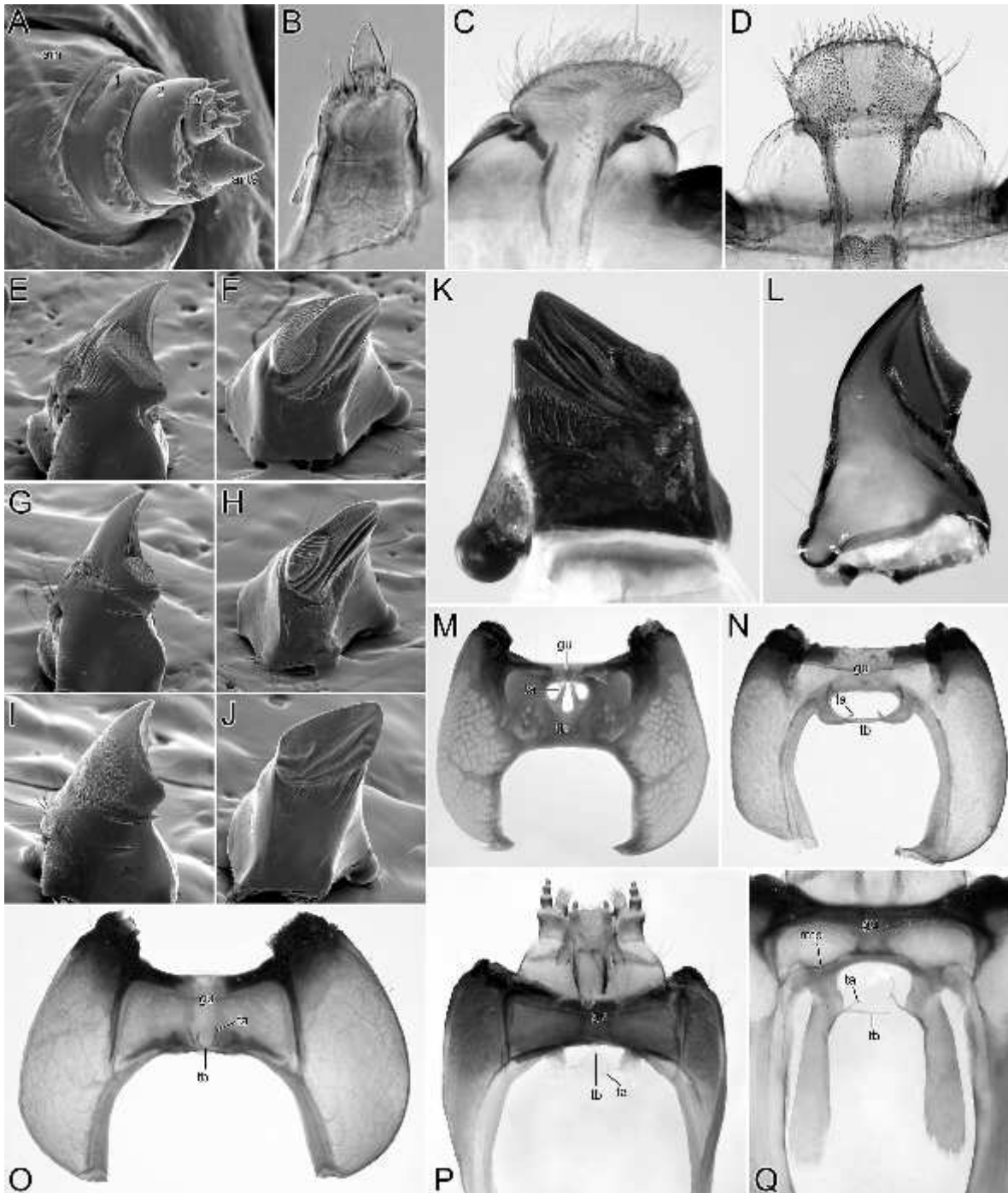


Fig. 2.4.26 Larval structures of Lamiinae (A–D, L, P, Q), Prioninae (E, F, K, M), Lepturinae (G, H, O), Spondylidinae (I, J) and Dorcasominae (N). A, *Monochamus sutor* (Linnaeus), right antenna, dorsolateral view (SEM, modified from Svacha 2001); B, *Pogonocherus hispidus*, right antenna, lateral view; C, *Niphona picticornis* Mulsant, epipharynx, lateroventral view; D, *Exocentrus lusitanus* (Linnaeus), epipharynx, ventral view; E–J, left mandible in dorsal and mesal view (SEM, from Svacha *et al.* 1997): E, F, *Ergates faber* (Linnaeus); G, H, *Oxymirus cursor*; I, J, *Saphanus piceus*; K, unidentified South African prionine larva, possibly *Delocheilus* sp., right mandible, mesal view; L, *Aegomorphus clavipes* (Schrank), right mandible, ventral view; M, *Aegosoma scabricorne*, ventral cranium, dorsal view; N, *Apatophysis barbara*, same; O, *Aredolpona rubra*, same; P, *Monochamus galloprovincialis* (Olivier), ventral cranium and maxillolabial complex, dorsal view; Q, *Dorcadion ?pedestre* (Poda), ventral cranium, ventral view (thin tentorial bridge damaged). am, antennal articulating membrane; ants, antennal sensorium (a compound probably olfactory sensillum); gu, gula; mtp, metatentorial pit; ta, thin to rudimentary intracranial arms arising from metatentorium, may or may not reach frontal region; tb, tentorial bridge.



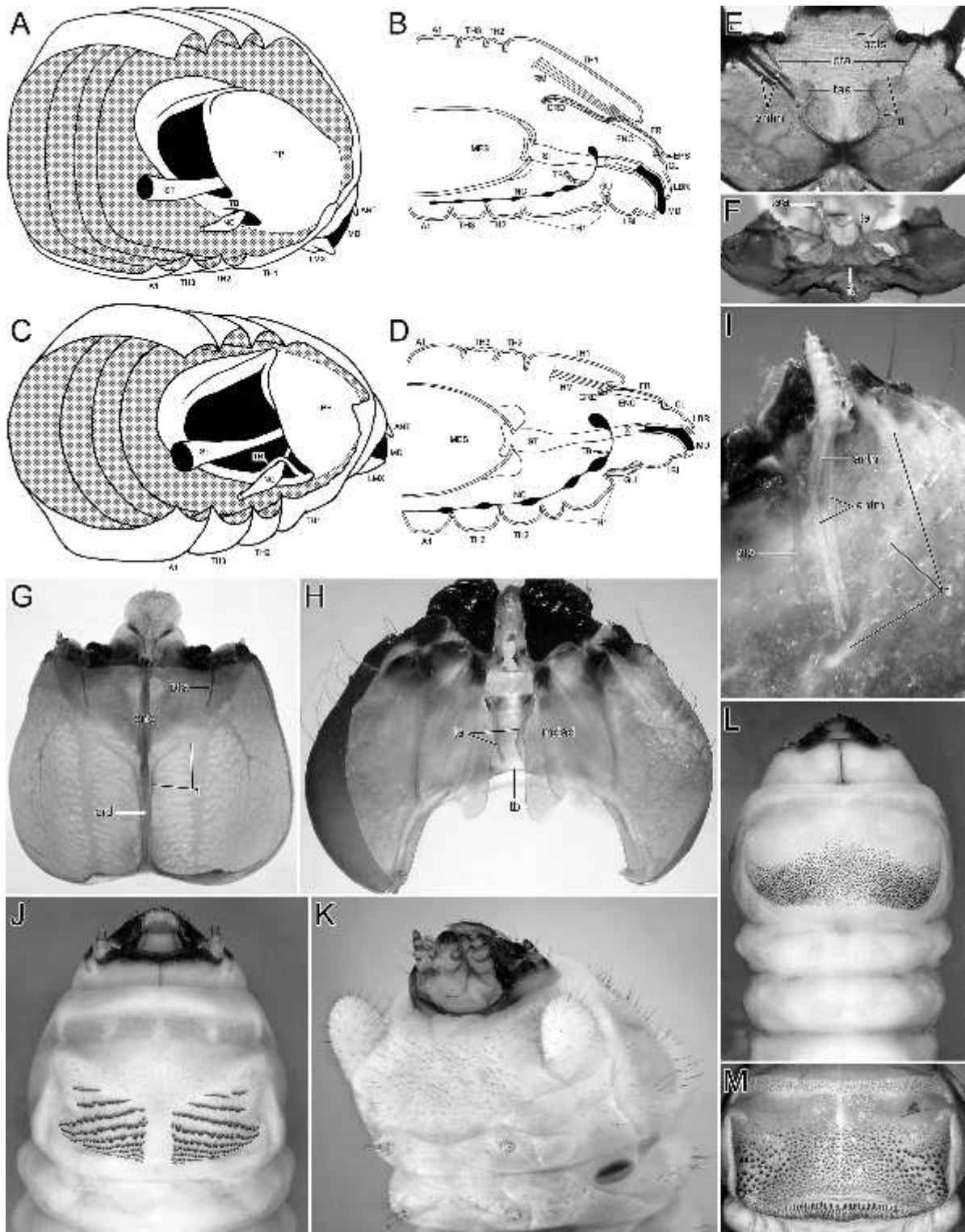


Fig. 2.4.27 Larval structures. A, C, Prioninae and Lepturinae, respectively, head, thorax and first abdominal segment, posterolateral view, diagrammatic (right lateral part of body wall removed to show relative position of some internal structures, more or less deeply retracted head inserted in membranous prothoracic pocket, and conformation of tentorial bridge); B, D, Prioninae and Lepturinae, respectively, semidiagrammatic submedial section through head, thorax and first abdominal segment (A–D from Svacha *et al.* 1997); E, *Pyrochroa coccinea* (Linnaeus) (Pyrochroidae), dorsal cranium with incurved lyriform frontal lines (antennal muscles, pretentorial and dorsal metatentorial arms attach on epicranium within that incurvation), dorsal view; F, *P. coccinea*, ventral cranium in posterior view showing a pair of arms of metatentorial origin whose dorsal attachments lie within the incurvation of frontal lines; G, *Aegosoma scabricorne* (Prioninae), dorsal cranium in ventral view, showing frontal lines (running on both sides of median endocarina through the ventral layer of dorsomedian cranial duplicature, not fusing into a coronal stem) and pretentorial arms ending within frontal region; H, *Oxymirus cursor* (Lepturinae), cleared head with dorsal cranial cuticle and clypeolabral region removed, dorsal view (thin metatentorial arms run dorsad toward frontal region

in Svacha & Danilevsky 1987); terminal palpomere usually with one digitiform sensillum, but with several in some Prioninae (character poorly studied); palpiger in nearly all Cerambycinae and some Prioninae, Dorcasominae and Spondylidinae with a laterodorsal process bearing sensilla (Fig. 2.4.23 F, H, 2.4.25 E), in some Cerambycinae first maxillary palpomere with similar process. Mentum may fuse with maxillary articulating area and/or submentum; prelabium well-separated and more or less retractile; very long and protractile (though deeply retracted at rest) in *Pseudobottegia* Duffy (Duffy 1957) and *Macropsebium* Bates (Cerambycinae: Psebiini); labial palpigers seldom with distinct lateral sensory process (some Cerambycinae and some Saphanini of Spondylidinae); palps dimerous; ligula usually well-developed (rudimentary in some Cerambycinae with subcontiguous palps), membranous, covered with setae and/or microtrichia. Hypopharyngeal region usually not distinct from dorsal ligula, rarely separated by a notch (Fig. 2.4.25 G), distinctly step-like in Cerambycinae (Fig. 2.4.25 E, F); at most with fine sclerotization, never with well-developed hypopharyngeal sclerome; hypopharyngeal bracon absent. Paired tubular glands opening on membrane at base of hypopharyngeal region, usually passing below tentorial bridge (through anterior portion of “divided” occipital foramen) and reaching more or less deeply into thorax (see Schmidt 1972). Hypostomal rods usually distinct, reaching postoccipital lines or not, rudimentary or rarely absent in some Lamiinae (Fig. 2.4.21 N). Hypostomal plates always bridged by sclerotized material of non-cranial (and in cerambycid larvae apparently also postlabial) origin, the gula. Gular bridge is very narrow (and occasionally covered by a membranous prosternal postgular lobe and not externally visible) in Parandrinae and Prioninae (Fig. 2.4.22 C, 2.4.23 B, 2.4.27 B, 2.4.29 E), longer and exposed/exposable in remaining subfamilies; lateral borders of gula (gular lines) posteriorly reach metatentorial slits when present (e.g., Fig. 2.4.23 G), anteriorly (if complete) abruptly diverge and approach lateral ends of basal maxillo-labial attachment; gular lines may be obliterated and gula fused with hypostomal plates to form a single ventral cranial sclerite (e.g., Fig. 2.4.25 B), which may be transversely raised or bear various projections (Fig. 2.4.24 J, K); pale median gular

zone or line present or absent. Pre- and metatentoria (anterior and posterior tentorial arms) disconnected; antennal muscles attached on lateral frontal region (originally epicranial, see above and Fig. 2.4.27 E–I); pretentorial arms invaginate laterad of dorsal mandibular articulations (but pretentorial pits usually not distinct externally), forming slender rods directed toward attachment area of antennal muscles; tentorial bridge (Fig. 2.4.26 M–P) of variable position and width, broad and rigid (Prioninae, Parandrinae) to rudimentary (e.g., Lamiinae); dorsal metatentorial arms arising from bridge, in some taxa relatively distinct and running upward between strong mandibular adductors and almost reaching the frontal region on both sides of the frontal endocarina (Fig. 2.4.27 H), in others rudimentary (Fig. 2.4.26 P, Q); metatentorium invaginates on occipital margin without forming distinct cranial metatentorial pits in Prioninae, Parandrinae, Cerambycinae and Dorcasominae except *Dorcasomus* (Fig. 2.4.22 C, 2.4.23 B, E, 2.4.24 B, 2.4.26 M, N), where the occipital foramen appears to be “divided” in ventral view by the tentorial bridge; in other groups cuticular region behind metatentorial invaginations sclerotized and metatentorial pits more or less distinct and “cranial” (e.g., Fig. 2.4.22 D, 2.4.23 G, 2.3.24 I, 2.4.26 Q); metatentorium may then become more oblique and partly to entirely hidden behind the gula in ventral view (“undivided” occipital foramen of most Lepturinae and some Spondylidinae, Fig. 2.4.26 O); metatentorial invaginations with very long posterior apodemes in some Dorcadiini of Lamiinae (Fig. 2.4.26 Q).

Thorax and abdomen, general remarks. Due to usually deep head retraction, the prothorax is enlarged and modified. The pterothoracic segments, representing a less derived situation, are therefore described first. Thoracic and abdominal terminology is shown in Fig. 2.4.28; these figures depict species with completely defined body regions, many derived forms become considerably simplified or modified and difficult to homologize without careful comparative study (examples in Fig. 2.4.29 B, C). We use the terminology of Craighead (1916, 1923) as modified in Svacha & Danilevsky (1987). The terms “pleural tubercle” and “pleural disc” are here modified to “epipleural” as both structures lie entirely within the abdominal

close together between large apodemes of mandibular adductors); I, *Aredolpona rubra* (Lepturinae), left antenna and adjacent dorsal cranium, ventral view (the area with attachments of antennal muscles and pretentorial arms being part of frons); J, unidentified South African prionine larva, possibly *Delocheilus* sp., head, pro- and metathorax, dorsal view; K, *Neoprion batesi* (Prioninae), head, pro- and mesothorax, lateroventral view; L, *Archandra caspia* (Ménétriés) (Parandrinae), head and thorax, dorsal view; M, *Batocera rufomaculata* (De Geer) (Lamiinae), pronotum, dorsal view. A1, first abdominal segment; ANT, antenna; antm, antennal muscles; antn, antennal nerve; CL, clypeus; CRD, crd, concealed dorsomedian cranial duplicature; ENC, enc, median frontal endocarina (continues also on crd); fl, frontal line; FR, frons; GU, gula; LBI, labium; LBR, labrum; MD, mandible; mdad, large apodeme of mandibular adductor muscles; MES, mesenteron; NC, nerve cord; pcls, postclypeal setae of *Pyrochroa* (homologous to cerambycid epistomal setae); PP, prothoracic membranous pocket embracing deeply retracted head; RM, dorsomedian head retractor muscles (diagrammatic); ST, stomodaeum; ta, dorsal arms of metatentorial origin; taa, attachment of ta; pta, pretentorial arms; TB, tb, tentorial bridge; TH1–3, pro-, meso- and metathorax.

epipleuron (the membranous connection between tergal and sternopleural regions) and have no relation to the pleuron.

Meso- and metathorax short, often shortest of body segments except for abdominal segment X. Tergum consisting of lateral alar lobes and median notum that is divided by two curved more or less distinct lines into anterior prescutum, posterior scutellum and intermediate medially constricted scutum; small separate anterolateral lobes were termed scutum-I by Craighead (1916); prescuto-scutal and scuto-scutellar lines may be fused into an X-shaped pattern on both segments, metanotum in some cases divided by a single transverse line, or all dividing lines may be absent; "postnotum" (Fig. 2.4.28 A, B, 2.4.29 A, B) present in Dorcasominae, most

Cerambycinae and some Prioninae; postnotal fold (mesonotal in origin and formed by the prescutum and anteromedian portion of both lobes of scutum-I) may appear intersegmental or proximate to the posterior pronotal margin; its origin is associated with a posterior shift of a pair of muscles originally attached to the pro/mesothoracic border at medial extremities of both halves of scutum-I. Epipleuron is deeply invaded dorsally by wedge-shaped alar lobes; anterodorsal epipleural angle bears thoracic spiracles (large in mesothorax, rudimentary and closed in metathorax); spiracle-bearing mesoepipleural area in some cases more or less protruding into prothoracic region (Fig. 2.4.29 C, E), or spiracle tends to integrate into alar lobe (Fig. 2.4.28 D). Coxae connected by simple trans-sternal line separating

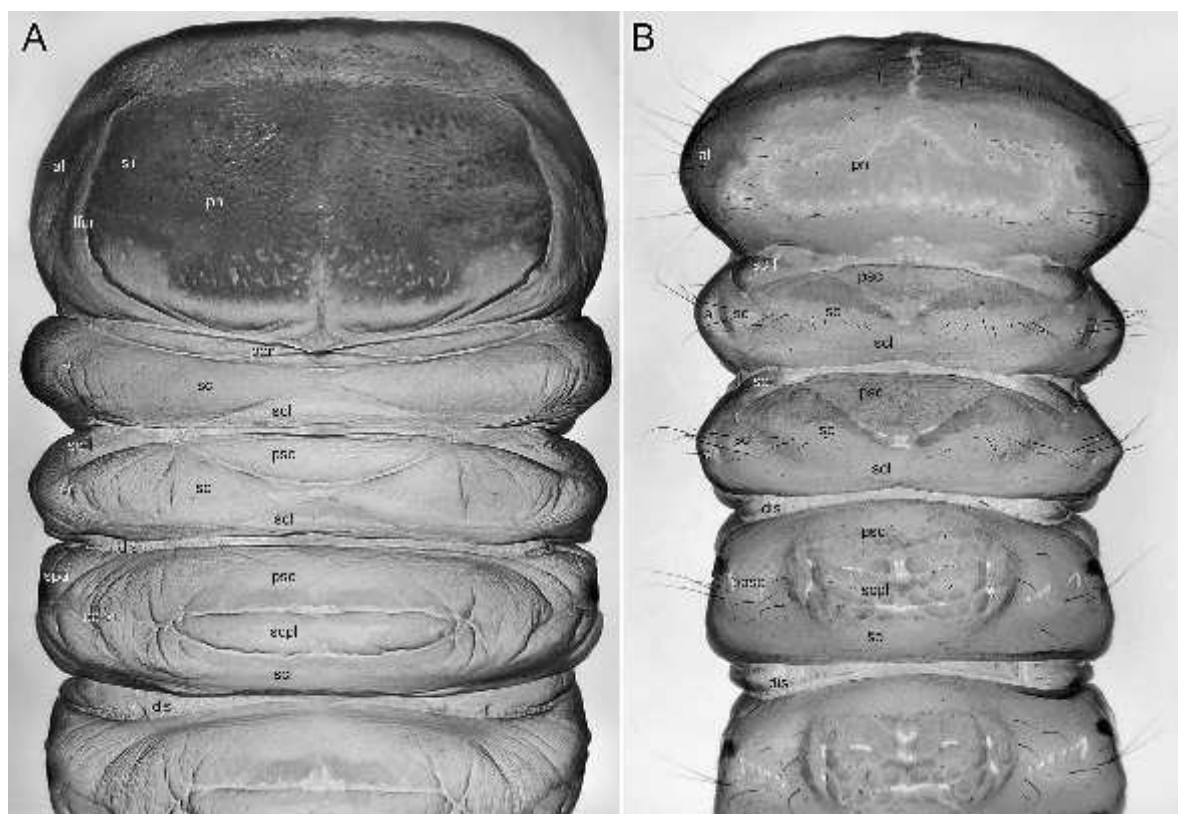
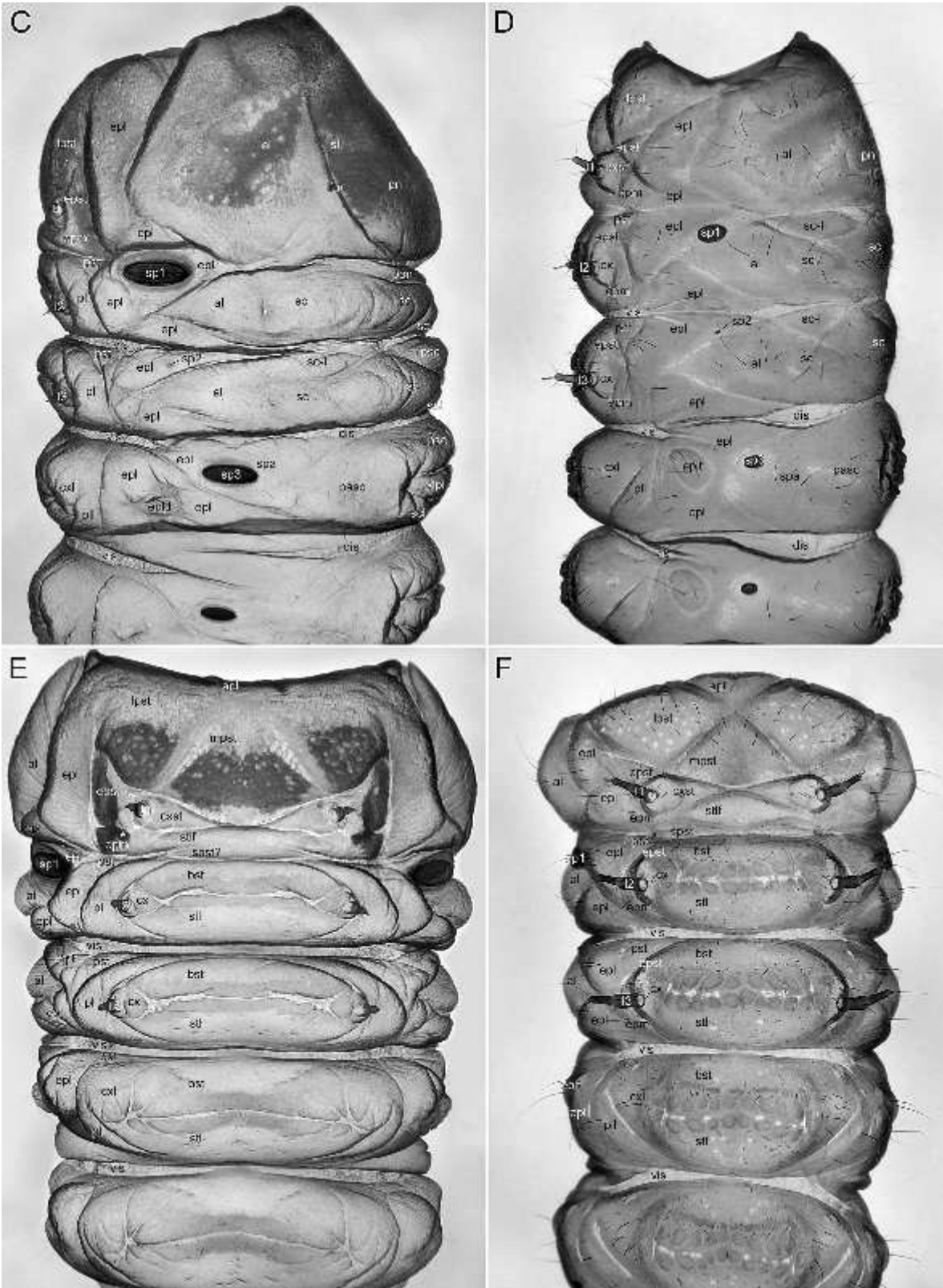


Fig. 2.4.28 (continued on opposite page) Larval thorax and abdomen, terminology, *Aegosoma scabricorne* (Prioninae; A, C, E) and *Oxymirus cursor* (Lepturinae; B, D, F) in dorsal (A, B), lateral (C, D), and ventral (E, F) views. al, alar lobe; apl, anterior presternal lobe; bst, basisternum; cx, coxa; cxst, coxosternum (fused prothoracic coxa and anterolateral part of basisternum); dis, dorsal intersegmental zone; epl, epipleuron; epld, epipleural disc; eplt, epipleural tubercle; epm, epimeron; epst, episternum; l1, l2, l3, pro-, meso- and metathoracic distal legs (without coxa); lfur, lateral pronotal furrow (rudimentary in *Oxymirus*); lpst, lateropresternum (in prothorax); mpst, mediopresternum (in prothorax); pasc, parascutum (in abdomen); pl, pleuron (fused episternum and epimeron); pll, pleural lobe (in abdomen); pn, pronotum; pon, postnotum (fused mesothoracic prescutum and anteromedial portion of scutum-I); psc, prescutum; pst, presternum; sc, scutum (in mesothorax of *Aegosoma* incorporating posterolateral portion of scutum-I); sc-I, scutum-I; scl, scutellum; scpl, scutal plate (of dorsal abdominal ampulla); sli, sublateral pronotal impression; sp1, sp2, sp3, mesothoracic, metathoracic (rudimentary and closed) and first abdominal spiracle; spa, spiracular area; spst, supposed spinasternum (may be distinct only between pro- and mesothorax), sometimes with rudimentary spina; stl, sternellum; stlf, sternellar fold (fused prothoracic sternellum and posteromedial part of basisternum); vis, ventral intersegmental zone; \* (in prothorax of *Aegosoma*), short internal pleural apodeme visible through the cuticle.



anterior basisternum and posterior sternellum; often with cuticular modifications similar to those on abdominal ventral ambulatory ampullae (Fig. 2.4.28 F); basisternum sometimes divided by one or two pairs of oblique impressions. Pleuron broad and undivided (i.e., lacking pleural sulcus; Fig. 2.4.28 C, E) or divided into episternum and epimeron (Lep-

turinae and Necydalinae, Fig. 2.4.28 D, F); usually not distinctly delimited from basisternum and sternellum. Pterothoracic presternum reduced to two broadly separate lateral triangles, often fused with anterior epipleuron. Protergum usually more or less completely divided by pair of lateral furrows marking attachments of head muscles (reduced or absent

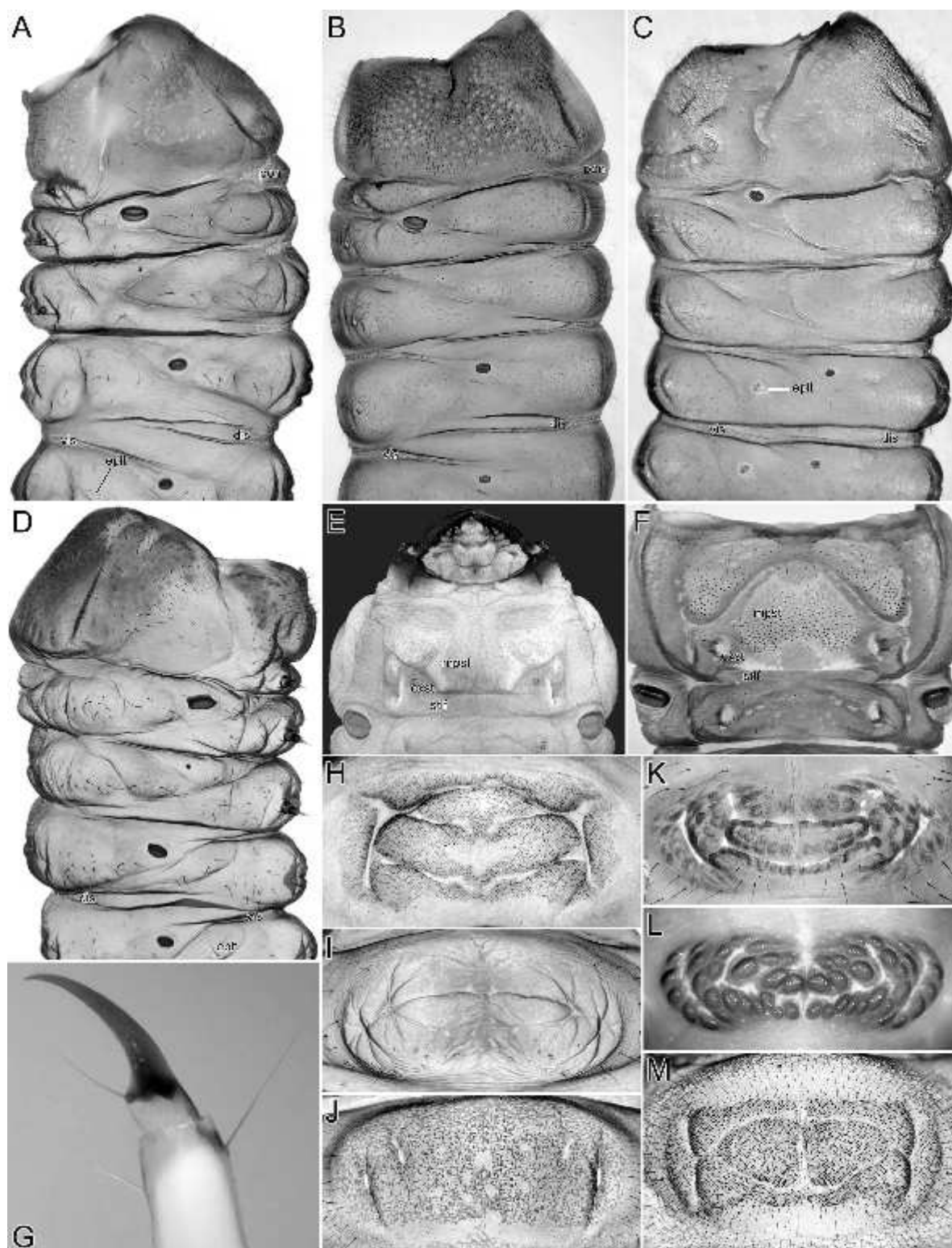


Fig. 2.4.29 Larvae. A–D, thorax and abdominal segments I and II, cleared cuticle stained with Chlorazol Black E, lateral view: A, *Artelida crinipes* (Dorcasominae); B, *Plagionotus* sp. (Cerambycinae); C, *Exocentrus adspersus* (Lamiinae); D, *Saphanus piceus* (Spondylidinae); E, *Rhaesus serricollis* (Motschulsky) (Prioninae), head and prothorax, ventral view; F, *Neandra brunnea* (Parandrinae), pro- and mesothoracic venter, cleared stained cuticle; G, *Judolia sexmaculata* (Lepturinae), right hind pretarsus and apex of tibiotarsus, anterior view; H–M, dorsal abdominal ampullae of Lepturinae (H), Spondylidinae (I, J), and Lamiinae (K–M), dorsal view: H, *Akimerus schaefferi* (Laicharting), ampulla V; I, *Saphanus piceus*, ampulla III; J, *Arhopalus rusticus*, ampulla II; K, *Monochamus galloprovincialis*, ampulla VII; L, *Mesosa curculionoides* (Linnaeus), ampulla V; M, *Saperda perforata*, ampulla IV. Abbreviations as in Fig. 2.4.28.



in taxa with less retracted head, e.g., Lepturinae, Fig. 2.4.28 B, or Agapanthiini of Lamiinae) defining medial and paired lateral regions (named pronotum and alar lobes, although the latter are probably homologous to alar lobes plus lateral parts of scutum of pterothoracic segments); paired transverse or oblique sublateral pronotal impressions often present, in Phytoeciini (Lamiinae) forming long oblique sclerotized and usually pigmented sublateral furrows (Fig. 2.4.21 M); pronotal base may be raised and/or bear sculpturing (striation, micro- or macro-asperities, rarely sclerotized ridges; Fig. 2.4.27 J, L, M); anterior protergal margin usually more or less distinctly pigmented, pigmentation always interrupted by median cleavage line and in some cases also by lateral furrows (always in Cerambycinae and Spondylidinae; Fig. 2.4.21 H–J). Epipleuron anteriorly tapering and completely defined in Necydalinae, Lepturinae and Cerambycini (Cerambycinae) (Fig. 2.4.28 D, F), incompletely defined anterovertrally in remaining groups (Fig. 2.4.28 C, E, 2.4.29 A, D, F) except for some Prioninae, where it is closed anteriorly by a transverse furrow (Fig. 2.4.29 E); the region immediately posterad bears a pseudopod-like process in *Eudianodes* Pascoe and *Neoprion* Lacordaire (Eurypodini) (Fig. 2.4.20 C, 2.4.27 K). Prothoracic episternum and epimeron (even if one of them fuses with other regions) usually separated by distinct pleural sulcus where the upper (lateral) end may form a small pleural apodeme (relatively distinct in some Prioninae; Fig. 2.4.28 E, asterisk). Prothoracic coxal and sternal region strongly modified, with coxae more or less completely fused with paired anterolateral portion of basisternum, whereas the posteromedian portion of the basisternum is fused with sternellum; former region is termed the coxosternum (procoxae of authors), latter the sternellar fold (sternellum of authors); coxosternal halves usually medially approximate (Fig. 2.4.28 E, F), but reduced and broadly separate in Parandrinae and some Prioninae (Fig. 2.4.29 E, F); prothoracic presternum enlarged and divided into triangular to half-oval mediobasal mediopresternum (eusternum of authors) and anterolateral lateropresternum, both of which may be partly to completely fused, and the presternal region may be divided by secondary impressions. Legs short in groundplan, very long legs in some later-instar Lepturinae (Fig. 2.4.20 P) are exceptional and derived; coxa, trochanter, femur, tibiotarsus and pretarsus present except for some Cerambycinae (showing various degrees of leg reduction up to complete absence) and all Lamiinae (legs rudimentary or absent); trochanter indistinct also in some Prioninae; coxa lacking sclerotized condyle articulating with lower end of pleural sulcus and paired sclerotized rods supporting trochanteral articulation; trochanter lacking distinct condyles, but a basal sclerotized ring may be present; coxae flat, integrated into body wall, often poorly defined; in some long-legged Lepturinae coxae (or coxal parts of prothoracic coxosternal halves) secondarily prominent (Fig. 2.4.20 P); pretarsus never with membranous appendix; pointed, sometimes sclerotized or

apically claw-shaped; distinct medial seta present in Necydalinae and Lepturinae (Fig. 2.4.29 G) except for *Pyrocalymma* J. Thomson; in other subfamilies setae absent or (some Prioninae) minute and unstable in presence (occasionally more than one) and position.

Abdomen with ten distinct segments, or segment X fused with IX. Segments I to VII usually bearing dorsal and ventral more or less protuberant and retractile ambulatory ampullae with cuticular modifications (reticulations, protuberant granules, asperities; Fig. 2.4.29 H–M, 2.4.30 A); number may be reduced or ampullae may be absent ventrally (Fig. 2.4.20 T), but some dorsal always remain; ampullae on segment VIII present only in *Capnolymma* and *Apioccephalus* (Lepturinae) (Fig. 2.4.19 H). Intersegmental regions behind segments I–VIII (and sometimes less distinctly between metathorax and abdominal segment I) with dorsal and ventral intersegmental folds or stripes not meeting laterally but overlapping (thus improving body flexibility), with dorsal one more anterior (Fig. 2.4.28 C, D, 2.4.29 A, B, D), but secondarily fused between anterior segments in some Lamiinae (e.g., Pogonocherini; Fig. 2.4.29 C, 2.4.30 G), and broadly sclerotized in the pogonocherine *Pseudhoplomelas elegans* (Fairmaire) (Fig. 2.4.21 C). Dorsal ampullae (Fig. 2.4.28 A, B, 2.4.29 H–M) in plesiomorphic situations divided by two transverse furrows (presumably homologous to prescuto-scutal and scuto-scutellar lines of pterothorax) laterally delimited by a pair of short oblique or longitudinal impressions dividing scutum into medial scutal plate and lateral parascuta; Necydalinae, Spondylidinae (except *Pectoctenus*) and the lamiine groundplan have two more or less distinctly separate pairs of lateral impressions (Fig. 2.4.29 I–L) corresponding with split retractor muscles; pattern may be further modified and simplified. Areas laterad of parascuta (the spiracular areas) are presumably serially homologous with pterothoracic alar lobes, but in abdominal segments, they bear spiracles (first usually largest). Epipleuron forms a protuberant fold at least on abdominal segments VII–IX (e.g., Fig. 2.4.20 B, C, F, I, K, 2.4.21 D), rarely only on VIII and IX in some Cerambycinae; in Lepturinae, some Necydalinae and some Lamiinae it is protuberant on all nine segments (Fig. 2.4.20 L–S); when non-protuberant, it is often poorly defined dorsally and ventrally, in particular its anterodorsal angle often fuses with spiracular area (e.g., Fig. 2.4.29 D); epipleuron of first seven or eight segments, or of their posterior subset, often bears a more or less sharply defined protuberant epipleural tubercle (Fig. 2.4.28 D) along the long axis of which a chordotonal organ is stretched internally (Hess 1917); one or both points of its attachment may be modified, e.g., forming sclerotized pits (Fig. 2.4.30 C); tubercles I–VII are strongly modified (much smaller and less protuberant than VIII and having a broad pocket-like internal apodeme at the ventral extremity; Fig. 2.4.29 C, 2.4.30 G, H) in Pogonocherini of Lamiinae (many are currently misclassified in other tribes); epipleural



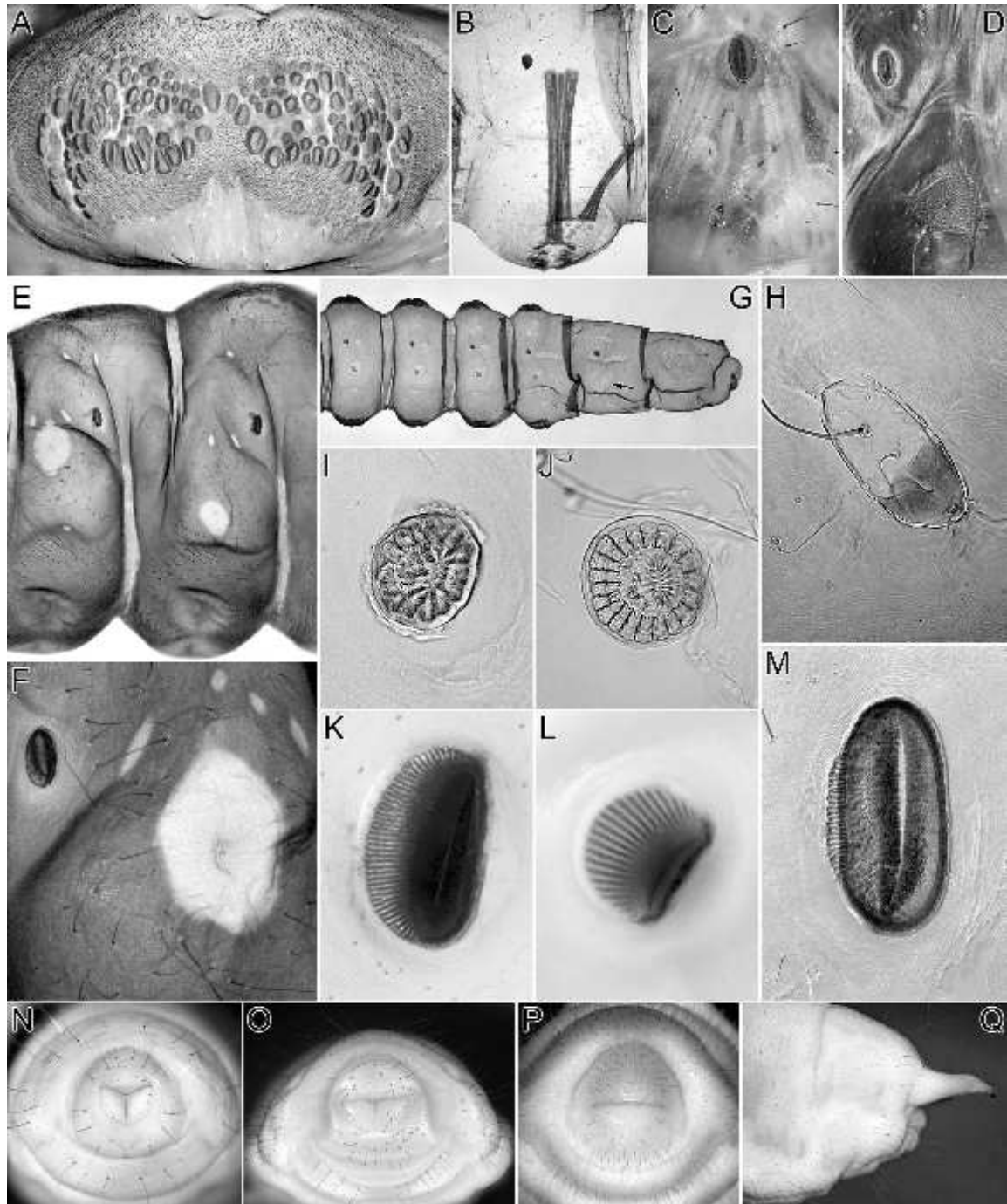


Fig. 2.4.30 Larval structures of Necydalinae (A, B), Lamiinae (C, G–J, N–P), Prioninae (D), Cerambycinae (E, F, K, L), Parandrinae (M), and Lepturinae (Q); A, D, E–H, cleared cuticular preparations stained with Chlorazol Black E. A, *Necydalis major*, ventral ambulatory ampulla 4 (showing two pairs of lateral impressions), ventral view; B, *N. major*, lower right half of abdominal segment IV in mesal view showing single origin (on upper epipleural margin) but split insertions of main retractor muscle of ventral ampulla (other soft tissues manually removed); C, *Acalolepta luxuriosa* (Bates), left abdominal spiracle IV and epipleural tubercle with sclerotized pits at both ends, lateral view; D, *Prionus coriarius*, left abdominal spiracle III and epipleural disc, lateral view; E, *Callidium violaceum*, right half of abdominal segments II and III, lateroventral view (thin cuticle of epipleural discs does not uptake stain; discs I, not shown, and II in this species placed very low on epipleuron); F, *C. violaceum*, detail of left abdominal spiracle III and epipleural disc, lateral view; G, *Pogonocherus hispidus*, left halves of abdominal segments IV–X, lateral view (simple continuous intersegmental stripes between anterior segments, normal epipleural tubercle on VIII marked by arrow, those on preceding segments modified); H, *P. hispidus*, right epipleural tubercle VII; I, *P. hispidus*, right abdominal spiracle VII; J, *Miccolamia glabricula* Bates, right abdominal spiracle I; K, *Holopterus chilensis*, right abdominal spiracle V; L, *Callisphyrus macropus*, same; M, *Neandra brunnea*, right abdominal spiracle I; N, *Oplosia cinerea*, end of abdomen, caudal view (triradiate anus); O, *Monochamus galloprovincialis*, same (anus with ventral radius very short); P, *Dorcadion decipiens* Germar, same (transverse anus); Q, *Rhamnusium bicolor*, end of abdomen, left lateral view.

tubercles form long processes in *Apioccephalus* and *Capnolymma* (see Fig. 2.4.31 A–C and Lepturinae); in some Prioninae and Cerambycinae, which always lack distinct epipleural tubercles on abdominal segments I–VI, the cuticular area surrounding the posterodorsal chordotonal attachment differs in sculpture, forming an epipleural disc (Fig. 2.4.30 D–F). Subdivision of abdominal venter is similar to that of pterothoracic segments; trans-sternal line separates basisternum and sternellum, laterally terminated within ventral ambulatory ampulla by a pair of lateral impressions partially separating coxal lobes; curved line partially separates posterolateral pleural lobe (which may be poorly defined and fused with surrounding areas); main retractor muscles of ventral ampullae (originating on dorsal epipleural border and inserted on lateral impressions) occasionally divided into two strands, one of which moves slightly medially along trans-sternal line; in Necydalinae, this results in a second pair of lateral impressions (Fig. 2.4.30 A, B). Presternum of abdominal segments usually poorly defined. Division of tergum and/or venter on segments lacking dorsal and/or ventral ampullae mostly obscured. Segment IX usually large in Prioninae and Parandrinae (Fig. 2.4.20 A–D). Anal segment usually small, terminal or posteroventral; occasionally fused with segment IX and anus then in some cases slightly posterodorsal (Parandrinae and some Prioninae). Anal slit usually triradiate, in some Lamiinae transverse or transitional (Fig. 2.4.30 N–P); two lateroventral anal papillae may be more protuberant in larvae with the posteroventral anal segment used as a pseudopod (some Lepturinae). Posterior margin of tergum IX may bear urogomphi, unpaired spine or more rarely other types of caudal armature (Fig. 2.4.21 A, 2.4.30 Q); sclerotizations on other abdominal segments uncommon, extensive sclerotization of abdominal end (Fig. 2.4.21 B) entirely exceptional. Form of caudal armature may undergo strong ontogenetic changes.

Ventral nerve cord (Beier 1927; Pentead-Dias 1984) with three thoracic and a full complement of eight abdominal ganglia (VIII rarely tends to fuse with VII but remains distinguishable); anterior shifts between segments none or minimal except for ganglion VIII always placed in segment VII; in some small species having relatively large ganglia, suboesophageal ganglion may more or less displace first thoracic to mesothorax. Connectives approximate but distinctly paired. Digestive tube (Edwards 1961 b; Danilevsky 1976; Semenova & Danilevsky 1977; Yin 1987; Fonseca-Gessner 1990; Fig. 2.4.19 I–N) with foregut mostly short, sometimes scarcely protruding from cranium and at most moderately broadened posteriorly; distinct muscular proventriculus (but without internal armature) present in some Cerambycinae (Fig. 2.4.19 J); Mansour & Mansour-Bek (1934) described a nearly identical proventriculus in *Macrotoma palmata* (Fabricius) (Prioninae), but their larvae may have been misidentified Cerambycinae (Danilevsky 1976); available larvae of a South American species of *Malloodon*

Lacordaire without a proventriculus with subquadrate internal sclerite which was described by Duffy (1957) in *M. downesi* Hope. Some laboratory studies misinterpreted anterior midgut as foregut or crop (Wei *et al.* 2006; Choo *et al.* 2007; Watanabe & Tokuda 2010; Reid *et al.* 2011). Midgut and hindgut each form a recurrent anterior loop; midgut loop in some Prioninae reaches the metathorax; anterior midgut in some taxa (Necydalinae, Spondylidinae, most Lepturinae) with distinct mycetomes in form of gut wall diverticula (very large and complex in Necydalinae) containing intracellular yeast-like symbionts (Heitz 1927; Schomann 1937; Fig. 2.4.19 L, M); posterior midgut often with numerous small scattered evaginated crypts; those of *Hylotrupes* were described as nests of regenerative cells peripherally differentiating merocrine secretory cells (Schmidt & Ahlborn 1970), but this conclusion was refuted by Semenova & Danilevsky (1977) who assume that the crypts may be refuges of extracellular luminal microorganisms. Six cryptonephridial Malpighian tubules enter the gut separately, often in two clusters of three.

Differences of first instars. Setae usually distinctly longer. Proportional changes at first moult generally much more abrupt compared with following moults. Mouth frame without carinae or subfossal process (except for some Lamiinae using similar structures as cranial egg bursters; Fig. 2.4.31 F). Stemmata usually more distinct and may be more numerous, including presence in species with “blind” later instars. Prominent setose hypostomal tubercles (Fig. 2.4.31 M) occur in first instars of some (mainly herb-feeding) Lamiinae (usually more or less abruptly disappearing in later instars). Antennal sensorium more prominent in Parandrinae and some Prioninae (even more or less conical in *Aegossoma* Audinet-Serville) where it is flat in later instars. Legs usually slightly more developed compared with later instars, long to very long in Necydalinae and Lepturinae (Fig. 2.4.31 J); in Asemmini and Spondylidini (Spondylidinae) with very long flagelliform pretarsus (Fig. 2.4.31 L). Spiracles (Fig. 2.4.31 K) without broadly open atrium (appears after the first moult) and with two large occasionally unequal marginal chambers; latter indistinct and spiracle basically narrowly annular in first instars of *Agapanthia* (Lamiinae; Duffy 1952). Egg bursters (Gardiner 1966; Oka 1977; Kurakawa 1978; Kurakawa & Hukuhara 1979; Cox 1988; Fig. 2.4.31 F, H–K) in the form of sclerotized and often flat and blade-like spines may occur on sides of pterothoracic and first eight abdominal segments (the spiracle-bearing segments) or on a continuous subset of those (pterothoracic spines absent in Cerambycinae, Dorcasominae, Parandrinae, and Prioninae), in some Lamiinae also on sclerotized cranial mouth frame and on lateral mandibular surface. Dorsal ambulatory ampullae divided into two strongly protractile opposable lobes (functioning as dorsal prolegs) in some *Agapanthia* of Lamiinae (Duffy 1952; Carrière 2001; Fig. 2.4.31 N); at least in *A. villosoviridescens* (De Geer), this modification remains

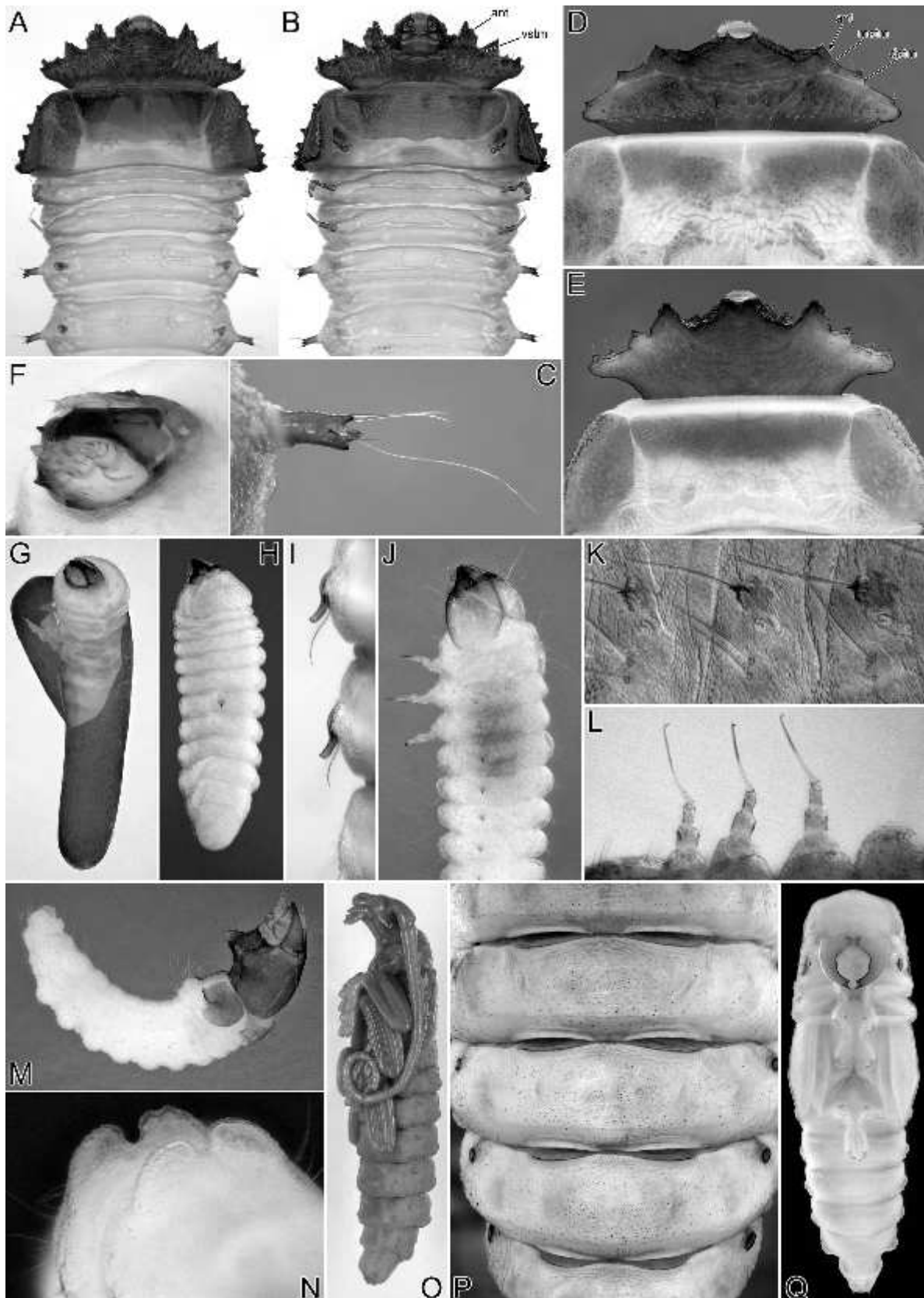


Fig. 2.4.31 A–E, aberrant larvae of the *Capnolymma-Apiocephalus* group of Lepturinae: A, *Capnolymma* sp. (Chiang Mai, Thailand), head, thorax and abdominal segments I and II of a cleared larva, dorsal view; B, same, ventral view; C, same larva, right epipleural process on abdominal segment VII bearing long trichobothrium, dorsal view; D, *Capnolymma* sp. (“Siam”, collection of Natural History Museum London), head and prothorax, dorsal view (a secondary cleavage line runs from frontal lines towards middle cranial process bearing dorsal stemmata); E, genus uncertain (“Siam”, NHML), a specimen lacking all cranial and medial pronotal cleavage lines, indicating a modified type of moulting; F–N, first instars of Lamiinae (F, G, M, N), Prioninae (H, I), Lepturinae (J, K), and

Spondylidinae (L): F, *Dorcadion fulvum* (Scopoli), head with four pairs of cephalic egg bursters (frontal, subfossal near to mandibular pit, hypostomal, and lateral mandibular), anterolateral view; G, same larva within the egg shell; H, *Aegosoma scabricorne*, lateral view (large lateral egg burster present on abdominal segment IV); I, *Mallosodon* sp., left egg bursters on abdominal segments III and IV (small spine visible also on V), dorsal view; J, *Rhamnusium bicolor*, laterodorsal view (lateral egg bursters present on pterothorax and abdominal segments); K, *Leptura quadrifasciata*, right abdominal egg bursters (with a seta at base), spiracles, and bisetose epipleural tubercles I–III, lateral view; L, *Spondylis buprestoides*, left legs with long flagelliform pretarsi, mesal view; M, *Agapanthia villosoviridescens*, lateroventral view; N, *A. villosoviridescens*, bilobed dorsal ambulatory ampullae (functioning as dorsal pseudopods) of segments VI and VII, anterior view; O, *Aegosoma scabricorne* (Prioninae), male pupa, 49 mm, lateral view; P, *Nothopleurus arabicus* (Buquet) (Prioninae), female pupa, abdominal dorsum showing gin traps following terga II–V; Q, *Archandra caspia* (Parandrinae), male pharate adult, 24 mm, ventral view (note that the pupal cuticle has large subtriangular labrum and broad subcontiguous mandibles and the reductions occur during pupal/adult transformation). ant, antenna (minute and placed ventroapically on first cranial process); dstm, dorsal stemma (lateral on second cranial process); mstm, main stemma (lateral to antennal socket); vstm, ventral stemma (ventrally at base of second cranial process).

functional also in the second instar. Prioninae and Parandrinae do not have ninth abdominal segment enlarged. Caudal armature usually reduced or absent; distinct urogomphi present in *Pterolophia* and *Parmena* (Lamiinae; Kurakawa 1978; P. Svacha, personal observation) or *Saphanus* (Spondylidinae; Svacha & Danilevsky 1987), and at least in *Saphanus* they are used as supplementary egg bursters. [Craighead 1915, 1923; Duffy 1953–1980; Kojima 1959; Teppner 1969; Mamaev & Danilevsky 1975; Cherepanov 1979–1985; Svacha & Danilevsky 1987–1989, last volume under preparation; Ohbayashi *et al.* 1992; Lawrence *et al.* 1999 a; Svacha 2001.]

**Morphology, Pupae.** Exarate, generally soft and pale except for some special structures such as spines or gin traps. Usually with head strongly bent ventrally and mouthparts pointing caudally (Fig. 2.4.31 Q, 2.4.32), except for some Prioninae having more or less prognathous pupae (Fig. 2.4.31 O). Body regions facing pupal cell walls, particularly body dorsum, usually bear spines or strong setae maintaining distance, large dorsal abdominal spines of some mobile lamiine pupae (Fig. 2.4.32 M, N) also perform locomotory function. Many dorcasomine and some lepturine pupae from sub-spherical soil pupal chambers have strongly curved dorsum often bearing particularly numerous setae (Fig. 2.4.32 C, D). Dense fields of microspines lacking. Antennae, when long, usually separately looped back between mid and hind legs, rarely (some Cerambycinae and Lamiinae) forming a joint oval, in a subgroup of Lamiinae coiled; at least basal antennal segment(s) usually spinose in Spondylidinae (Fig. 2.4.32 G–J) except for *Megasemum* Kraatz of Asemmini (Cherepanov 1979; Nakamura 1981). Usually 5–7 pairs of functional abdominal spiracles (number variable within most subfamilies or even within tribes), the following more or less rudimentary and obviously non-functional; rarely spiracle VIII well-developed, sclerotized and apparently functional (*Pyrrhidium* Fairmaire of Cerambycinae: Callidiini; Fig. 2.4.32 E, F). Paired abdominal gin traps (Fig. 2.4.31 P) present between some abdominal terga in certain Prioninae and Phrynetini of

Lamiinae (Duffy 1953, 1957). Abdominal tergum IX may bear a pair of urogomphi (Spondylidinae and Nelydalinae, many Lepturinae, less frequently elsewhere) or a single spine (Fig. 2.4.32 K, L; upturned in most Lamiinae); both absent in Cerambycinae where segment IX is typically reduced and non-prominent. Male genital lobe unpaired, female lobes paired, very large in Atimiini of Spondylidinae (Fig. 2.4.32 J), usually small in Lamiinae. Some adult reductions (such as shortened elytra) occur already in pupae whereas others (e.g., sickle-shaped male mandibles and reduced clypeolabrum in Parandrinae) develop only during adult morphogenesis (Fig. 2.4.31 Q). [Duffy 1953–1980; Cherepanov 1979–1985; Nakamura 1981; Ohbayashi *et al.* 1992.]

**Phylogeny and Taxonomy.** The families Oxypeltidae, Vesperidae (including Philinae, Anoplodermatinae and *Vesperoctenus* Bates), Disteniidae and Cerambycidae as defined in this book represent the Cerambycidae *sensu lato*, “Longicornia”, or Cerambycoidea *sensu stricto* of most earlier authors (e.g., Lawrence & Newton 1995). These four families are here informally called the cerambycoid assemblage or cerambycoids, as opposed to the chrysomelid assemblage (the present families Megalopodidae, Orsodacnidae and Chrysomelidae).

The superfamilies Chrysomeloidea and Curculionoidea have often been placed in an informal subgroup of the Cucujiformia called Phytophaga (some authors used this name as a synonym of the present Chrysomeloidea), which is often resolved as a monophyletic group (e.g., Lawrence *et al.* 2011 based on morphology; Marvaldi *et al.* 2009 based on 18S and 28S rDNA; non-monophyletic in Hunt *et al.* 2007). Morphologically, the group is mainly defined by the “pseudotetramerous” (also called “cryptopentamerous”) tarsus – tarsomere 3 is (bi) lobed, 4 is reduced, hidden in the emargination or cavity of tarsomere 3; tarsomeres 1–3 are typically provided with dense ventral pads of modified setae. Some fusions may occur (such as tarsomere 4 fusing with 5), but all tarsi have the same number of segments in both sexes. The scattered occurrences of pentamerous tarsi in some groups (in

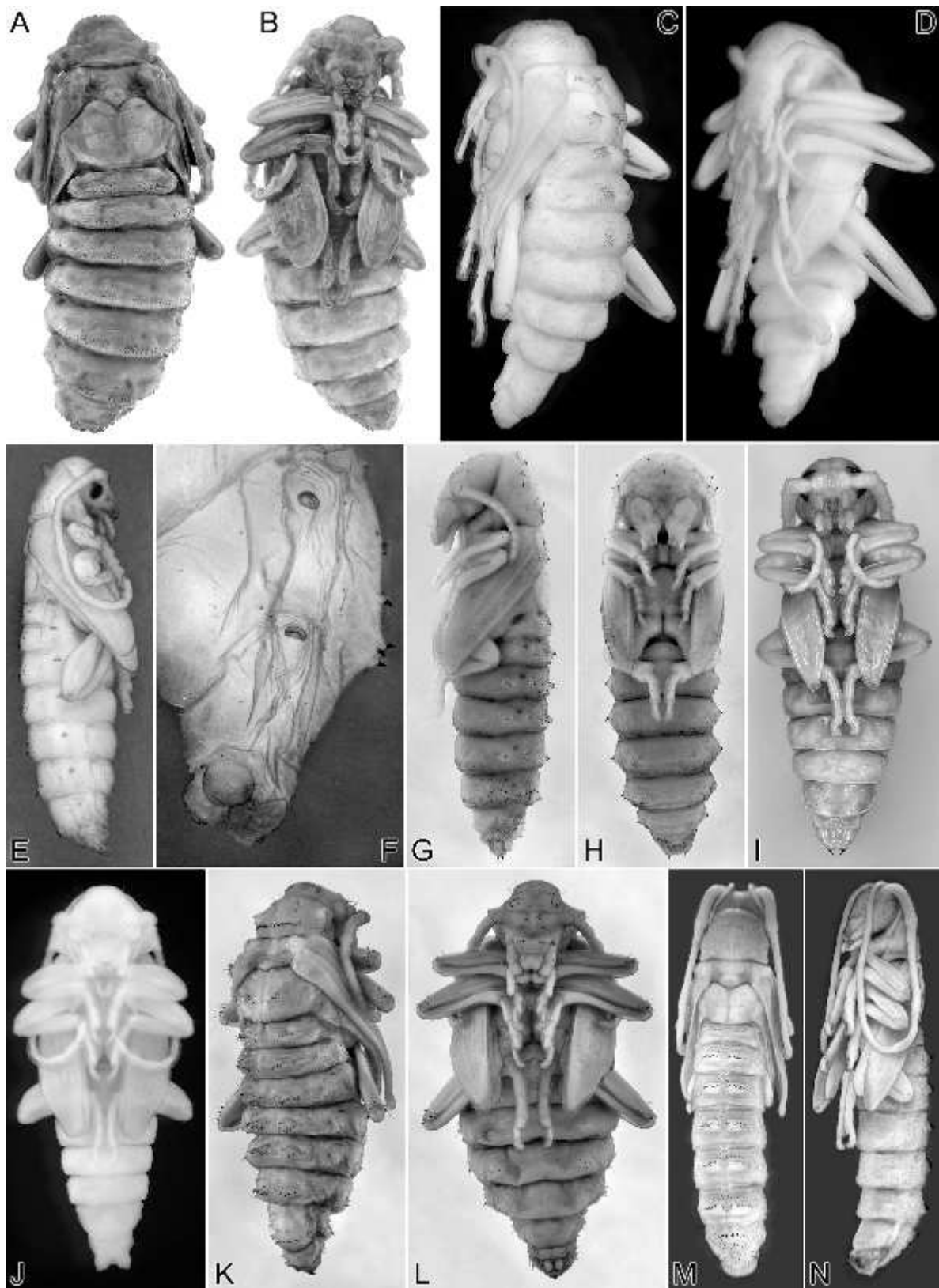


Fig. 2.4.32 Pupae of Dorcasominae (A–D), Cerambycinae (E, F); Spondylidinae (G–J), Lepturinae (K, L), and Lamiinae (M, N). A, *Dorcasomus gigas*, female, 38 mm, dorsal view; B, same, ventral view; C, *Tsivoka simplicicollis*, female, 19.5 mm, laterodorsal view; D, same, lateroventral view; E, *Pyrrhidium sanguineum* (Linnaeus), male, 13 mm, lateral view; F, *P. sanguineum*, female, end of abdomen, left lateral view (note the very unusual presence of distinct and apparently functional spiracle on abdominal segment VIII); G, *Spondylis buprestoides*, male, 28 mm, lateral view; H, same, ventral view; I, *Arhopalus rusticus*, female, 24 mm, ventral view; J, *Atimia okayamensis*, female, 7 mm, ventral view; K, *Rhagium bifasciatum*, female, 20 mm, laterodorsal view; L, same, ventral view; M, *Agapanthia dahli*, female, 21 mm, dorsal view; N, same, lateroventral view (note dorsal abdominal crochets and antennal tips looped around bases of scape in this mobile pupa).

cerambycoids mainly Cerambycidae: Parandrinae, Fig. 2.4.17 K, and some Vesperidae: Anoplodermatinae) are probably reversals associated with modified adult habits; typical pseudotetramerous padded tarsus appears to be adapted for walking on smooth surfaces such as leaves, smooth bark, etc. However, similar “pseudotetramerous” tarsi occur in some Cucujoidea (some cucujoids are probably a sister- or stem-group of the Phytophaga, see the three phylogenetic studies cited above). Also the other characters defining Phytophaga in Lawrence *et al.* (2011) occur elsewhere in the Cucujoidea or Cucujiformia. Larvae of Phytophaga never possess the strongly incurved or lyriform frontal arms widespread in less derived larvae of other Cucujiformia including Cucujoidea. Such frontal arms likely did occur in the phytophagan ancestry as at least in the cerambycoids the incurved portion of each arm was probably bridged by a secondary shortcut and then reduced or modified (see cerambycid larval morphology). The frontal arms are thus partly non-homologous to typical cucujoids. The chrysomelid assemblage and curculionoids may share this modification, but further study is required. Soft-bodied larvae with limited or no pterothoracic and abdominal sclerotization are characteristic for most Phytophaga and may indicate ancestrally concealed larval feeding. Free exposed larvae are probably derived and occur in some Chrysomelidae and very few Curculionidae, but none are known in the cerambycoids.

Whether Phytophaga is monophyletic or not, both included superfamilies appear to be. The curculionoid adult groundplan probably includes a rostrate head with antennal sockets placed laterally on the “snout” (rostrate forms do exist in Chrysomeloidea but are not considered basal and the antennal sockets usually remain close to eyes and even if slightly removed, they are of a more dorsal position compared with curculionoids) and the wing lacks a wedge cell (occurs in some chrysomeloids). Curculionoid larvae generally lack urogomphi (present in some chrysomeloids). Chrysomeloid adults very rarely possess clubbed antennae (nearly universal in curculionoids and widespread in Cucujoidea), and larvae always lack the hypopharyngeal sclerome and bracon (at least the latter belongs to a curculionoid groundplan and is plesiomorphic as it also occurs in many other Cucujiformia). The spur on crossvein r4, sometimes considered unique (although not universal) to the chrysomeloids (e.g., Crowson 1955), does occur in some curculionoids (Zherikhin & Gratshev 1995). Differentiated larval mandibular molae, present in some curculionoids, also occur in Megalopodidae (Palophaginae).

Traditionally, the Chrysomeloidea in the present broad sense (Cerambycoidea *sensu* Monrós 1955) were divided into the chrysomelid and cerambycid branches, accepted by many earlier authors as families Chrysomelidae and Cerambycidae *sensu lato* (Bruchidae is now universally placed within the Chrysomelidae *sensu stricto*). Certain authors treated cerambycoids as a suprafamilial

taxon “Longicornia” (Pascoe 1864–1869; Bates 1874, 1879–1886; Gahan 1906; etc.) or as a superfamily Cerambycoidea (more recently, e.g., Svacha & Danilevsky 1987–1989), but placing the cerambycoids in a broad Chrysomeloidea is more widely accepted and there is some evidence that both the cerambycid and chrysomelid assemblages in the traditional extent may not be monophyletic (particularly the Oxypeltidae may be closer to some megalopodids than to any cerambycoids).

The cerambycid assemblage was usually defined by characters (none of which is unique) connected with the long antennae of the adults: presence of “antennal tubercles” (i.e., raised medial margins of the antennal socket which provide better support and enable flexing the long antennae back over the body; Fig. 2.4.11 A, C, E, G, I, K); the antennal pedicel does not enlarge proportionally with antennal elongation (and thus appears conspicuously short), and its connection with the first flagellomere is rather inflexible (however, short ring-like “inflexible” pedicels do occur in the chrysomelid group). Cases of short antennae (e.g., Spondylidini, Parandrinae, some female Vesperidae and both sexes of *Hypoccephalus* Desmarest) are probably secondary and often result in reduced tubercles. Similar long cerambycid-like antennae with antennal tubercles also occur in some unrelated beetle families (e.g., some Oedemeridae), but seldom if ever in the Cucujoidea. However, neither this nor the other adult characters mentioned in Crowson’s (1955) key (tibiae usually with two spurs, complete ring-like tegmen with paired parameres and penis with paired struts, usually long ovipositor, frequent presence of mesoscutal stridulatory file) are entirely reliable and work only in combination. Moreover, with possible exceptions of the long antennae, their associated characters and the mesoscutal stridulatory plate, cerambycoids may typically bear the plesiomorphic states of those characters. Also wing venations of certain Vesperidae, Disteniidae and Cerambycidae are the most complete and, presumably, plesiomorphic among Chrysomeloidea and Phytophaga (Fig. 2.4.15 H, 2.3.4 C, 2.1.5 A, B).

In larvae, one potential cerambycid synapomorphy could be the very broad tentorial bridge. However, this implies a secondary loss in most Cerambycidae (present only in the Prioninae and Parandrinae), whereas some chrysomelid taxa also have relatively broad bridges. The abdominal locomotory protuberances (ambulatory ampullae) are also more or less well developed in Megalopodidae. Cerambycid larvae (with the possibly secondary exception of *Vesperus*) lack an exposed coronal stem, which is present in some taxa of the chrysomelid assemblage.

Cerambycid higher classification has been unstable (see Crowson 1955; Linsley 1961; Napp 1994; classifications before 1860 in Thomson 1860: x–xiii). The group’s size and popularity has unfortunately often led to typological, non-phylogenetic and regional approaches and contemporaneous use of different classifications, a



problem that to a considerable extent survives to the present day. Whereas we may be gradually arriving at monophyletic chrysomeloid families and cerambycid subfamilies, we often have very dim ideas about their interrelationships, and the situation becomes much worse in tribal and lower classification, particularly within the large subfamilies. Comments on taxonomic history of the Disteniidae (Chapter 2.3), Vesperidae (2.1) and Oxypeltidae (2.2) can be found under those chapters, comments on Cerambycidae in the present sense are below.

Although a classification with four to six primary subtaxa was proposed by some early authors (such as Schiødte 1864), most 19<sup>th</sup>-century authors divided cerambycoids (whether classified as a family or superfamily) into two or three primary subdivisions. When two, they were usually the Lamiinae vs. the remainder (Thomson 1864; Ganglbauer 1881; Gahan 1906; Lamiinae are large and have always been easy to define), but the “remainder” was basically defined as not being lamiine, and some authors therefore preferred a basal trichotomy (Prioninae, Cerambycinae, Lamiinae) used, e.g., by Lacordaire (1868) or in the Junk-Schenkling world catalogue (Aurivillius 1912, 1922, 1923; Lameere 1913) and popular during much of the first half of 20th century. Systems with more than three primary subtaxa became more widespread after Craighead (1915, 1923) confirmed the previous opinion of Schiødte (1876) that the larvae of Lepturinae and “Aseminae” (current Spondylidinae) cannot be easily accommodated in any of the previous three major subdivisions and described the very different larvae of the Disteniinae (a group raised to subfamily level by Gahan 1906); he also pointed out the differences between the Necydalini (considered by him transitional to the Aseminae) and the remaining Lepturinae. Crowson (1955) integrated adult and larval data and recognized Prioninae, Parandrinae, Anoploderminae (misspelling), Philinae, Disteniinae, Lepturinae (with *Vesperus*, Oxypeltini and *Mantitheus* Fairmaire mentioned as doubtful or transitional), Aseminae (including *Spondylis*), Cerambycinae and Lamiinae. He considered Prioninae, Parandrinae and Anoplodermatinae to form a “prionine” branch, as opposed to the “cerambycine” branch, but pointed out problems with “too many intermediate forms (e.g., *Anoeme*, Philinae, Oxypeltini)”. Disteniidae was ranked as a family by Linsley (1961, 1962 a), based partly on larvae. Duffy (1960) described larvae of the Oxypeltini and raised the group to subfamily, and though he (Duffy 1957) did not propose taxonomic changes when redescribing larval *Vesperus*, Crowson (1967) did and later (1981) placed all present non-cerambycid cerambycoids (except for Anoplodermatinae) in Disteniidae, presumably defined by the lack of a gula in larvae (larval Anoplodermatinae were then poorly known). Svacha in Svacha & Danilevsky (1987) redescribed larvae of *Migdolus*

(the only known anoplodermatine) and classified the groups lacking a larval gula as independent families (Disteniidae, Vesperidae, Anoplodermatidae and Oxypeltidae). Saito (1990) pointed out similarities between female genitalia of *Vesperus* and *Philus* Saunders, which lack a sclerotized spermatheca. Svacha in Svacha *et al.* (1997) redescribed the larvae of the Philinae (the last missing major group) described shortly before by Yin (1994) and proposed the classification used also in the present book by joining Vesperinae, Philinae, and Anoplodermatinae under Vesperidae.

**Relationships of the families** are largely uncertain. Svacha in Svacha *et al.* (1997) did not provide a formal phylogenetic analysis, but proposed possible relationships (Fig. 2.4.19 E) and some potential synapomorphies. Cerambycidae *sensu stricto* was defined primarily by the presence of a larval gula (absent in all other Chrysomeloidea and all Curculionoidea except for similar structures in some strongly flattened leaf miners); additional doubtful synapomorphies might be the long dorsomedian cranial duplicature (if secondarily reduced in Necydalinae and Lepturinae), the mandibular pseudomola (occurring in some or all species of six of the eight subfamilies, always absent in Cerambycinae and Lamiinae), and the uniform gut conformation (Fig. 2.4.19 I–N; cf. Fig. 2.3.10 A; 2.1.13; 2.2.6 D). Very few potential adult apomorphies are known. Svacha *et al.* (1997) proposed a simple unidentate mandibular apex (paralleled in Vesperidae), but although the bidentate mandibular apices in some Lamiinae may be apomorphic and associated with their extensive feeding, those in some Prioninae (Fig. 2.4.11 D) make this proposition questionable. Oxypeltidae, Disteniidae, some Vesperidae, and a considerable proportion of randomly selected taxa of the chrysomelid assemblage have an internalized sclerotized tube or rod in much of the ejaculatory duct’s length (e.g., Fig. 2.1.5 I; 2.2.3 A, B); this condition is rare in Cerambycidae (occurs only in a few Lamiinae), and the absence might be another cerambycid apomorphy.

A sister group relationship between Disteniidae and Cerambycidae is suggested by the identical construction of the “epistomal margin” and annular multiforous larval spiracles (spiracles annular in Vesperidae and annular-biforous in Oxypeltidae). Of the alternative possible apomorphies shared by Disteniidae and *Vesperus* (Svacha *et al.* 1997: 363), the transverse larval anus is no longer valid, as a short yet distinct ventral radius (making the anus triradiate) has been found in *Noemia* Pascoe of Disteniidae. Flightless (even if often winged) females were proposed as a possible synapomorphy of Oxypeltidae and Vesperidae, but females of some Philinae can fly (see Phylogeny and Taxonomy of Vesperidae). Relationships of the Oxypeltidae and Vesperidae are unclear.

Phylogenetic studies of the Phytophaga or Chrysomeloidea (Reid 1995 on morphological data; molecular data or combined data sets in

Farrell & Sequeira 2004; Gomez-Zurita *et al.* 2007 a, b; Marvaldi *et al.* 2009; see also Hunt *et al.* 2007; Lawrence *et al.* 2011) were often biased toward the chrysomelid assemblage or curculionoids, and the cerambycoids were poorly sampled or imprecisely scored; combined with their frequent molecular long-branch problems, the results are usually difficult to interpret. The monophyletic cerambycoids in Reid (1995: 604, Fig. 42), in addition to the antennal tubercles, were supported by the absence of the so-called vaginal pouches (Mann & Crowson 1983 b), very problematic structures with uncertain homologies among the chrysomelid groups possessing them.

Napp (1994) is the only special phylogenetic study of the cerambycoid complex. Although she used example species as terminal taxa, a hypothetical ancestor was employed for polarization of characters in some analyses. The results are occasionally affected by poor sampling (only Cerambycinae were well represented). Analyses of adult characters rather consistently yielded two groups: Prioninae + *Parandra* + *Anoplocleroma* Guérin-Méneville (with the latter two usually placed as sister groups) and the non-prionine cerambycid branch (occasionally invaded by *Oxypeltus* Blanchard in Gay and/or *Distenia* Le Peletier & Audinet-Serville) with monophyletic Lamiinae and Cerambycinae, often as sister groups, and usually with monophyletic Lepturinae (including *Necydalis* Linnaeus). Spondylidinae was not resolved as monophyletic, mostly because *Spondylis* appeared more basally than the (often monophyletic) *Saphanus* + *Atimia* + *Asemum* Eschscholtz. Positions of *Philus*, *Distenia* and *Oxypeltus* (when included in the analyses) were variable. *Anoplocleroma* + *Parandra* + Prioninae (represented by *Mallodon* and *Praemallaspis* Galileo & Martins) were held together primarily by the reduced and/or sclerotized labrum, the metendosternite without laminae, the more or less reduced galea and lacinia, and the absence of the mesonotal stridulatory plate if the respective analysis treated it as apomorphic. The first three characters are artifacts of poor sampling of Prioninae. *Anoplocleroma* + *Parandra* were characterized by the similar wing venation lacking the wedge cell, the male falciform mandibles (not in all Anoplocleratinae and Parandrinae and present in numerous Prioninae), and by the pentamerous tarsi (pseudotetramerous in males of some Anoplocleratinae). Cerambycinae + Lamiinae, when resolved as sister groups, were characterized by deeply emarginated eyes surrounding the antennal socket (the presence in certain other forms was not acknowledged, for an unknown reason the character was coded as “missing data” in *Saphanus* and *Atimia*, both having deeply emarginate eyes), the absence of prothoracic notosternal suture (scattered also in other taxa, the suture may be at least partly distinct in some Cerambycinae), or the vein RP absent or very short proximally of crossvein r4 (Fig. 2.4.16 M, N, 2.4.17 C, D; it is very long in some Cerambycinae, Fig. 2.4.17 A, B). As a whole, some characters defin-

ing the above groups are reductions likely to occur parallelly and/or are influenced by insufficient sampling. Larval and combined analyses will not be discussed because of some problems with coding of larval characters (which were compiled from literature). A formal phylogenetic tree was not provided, but we summarized the conclusions in Fig. 2.4.19 D (approved by D. S. Napp).

**Relationships within Cerambycidae.** Division of and relationships within the Cerambycidae of various authors were rather variable (Fig. 2.4.19 A–F). For potential characters defining the Cerambycidae in the present narrow sense see above; only the larval gula is clearly apomorphic and uniformly present. We include the following subfamilies: Prioninae, Parandrinae, Dorcasominae (previously Apatophyseinae: Özdikmen 2008), Cerambycinae, Spondylidinae (synonymous to or including Aseminae of some authors), Necydalinae, Lepturinae, and Lamiinae (for possible apomorphies, if known, see under individual subfamilies).

Of those subfamilies, most authors considered the prionine branch (including Parandrinae, the relationship of which to Prioninae is now almost universally accepted) as the most basal group. Some taxonomists proposed relationships between Cerambycinae and Lamiinae, but we see no convincing morphological support for that in adults (see the above discussion of the paper by Napp 1994) and particularly in larvae. Some unpublished molecular data (Sýkorová 2008; D. McKenna *et al.*, in preparation) show a tendency to group the prionine branch with Dorcasominae and Cerambycinae, whereas the remaining four subfamilies form another cluster (data are not yet sufficient to elucidate monophyly of and relationships within those clusters). Such division has been rarely proposed on classical data (e.g., Danilevsky 1979 a based on “divided” vs. “undivided” larval occipital foramen, respectively; Fig. 2.4.19 F). Until further phylogenetic studies, we therefore provide a reference tree with an unresolved basal trichotomy (Fig. 2.4.19 G) and discuss below possible synapomorphies for the major groups.

Branch 1 (Prioninae + Parandrinae, the former possibly paraphyletic, see below) is widely accepted. Possible synapomorphies of adults include the absence of the mesoscutal stridulatory plate (its presence is undoubtedly a groundplan character of the other subfamilies, of the Disteniidae, and a more or less distinct plate is present in some Vesperidae) and internally open procoxal cavities (*Anoeme* being an exception; procoxal cavities are at least narrowly closed internally in all other cerambycoids); in larvae, the flat or at most roundly convex antennal sensorium in later-instar larvae (the occurrence of flat sensorium in Vesperidae may be due to parallel evolution). Adults differ from most other cerambycids by the usual presence of a lateral pronotal margin, but this character is shared with many vesperids, and the polarity is uncertain. Considering the extremely broad tentorial bridge

and lack of gula in larval Oxypeltidae, Vesperidae and Disteniidae, the very short transverse gula and relatively broad tentorial bridge in the same plane with the hypostomal plates (the classical “divided” occipital foramen; Fig. 2.4.22 C, 2.4.23 B, 2.4.26 M) of the prionine branch may be regarded as the most plesiomorphic situation in Cerambycidae (but it will readily identify members of that branch). Despite some external adult similarities to Vesperidae (particularly the Neotropical Anoplodermatinae), the larval and some internal adult characters of these groups differ (Penteado-Dias 1984; Svacha & Danilevsky 1987; Svacha *et al.* 1997; Fonseca-Gessner 1990).

Branch 2 (Dorcasominae + Cerambycinae). Most dorcasomines were long classified in Lepturinae; relationships with Cerambycinae were proposed by Danilevsky (1979 b) when raising the subfamily “Apatophysinae” (present Dorcasominae) on larval characters. Larvae possess a well-developed postnotum (Fig. 2.4.29 A, B; probably secondarily lost in some cerambycine tribes and a similar, less well-separated structure is present in many Prioninae, Fig. 2.4.28 A, C), and the medial pair of epistomal setae are placed dorsally at the base of an epistomal projection (Fig. 2.4.23 F, J) or, if that projection is integrated into frons, are broadly removed from the basal clypeal level (Fig. 2.4.23 H, I, K, 2.4.25 E, I); due to this shift, the medial pair of epistomal setae was usually regarded as frontal and Cerambycinae were erroneously described as having only two pairs of epistomal setae (as opposed to three main pairs in other subfamilies and in Disteniidae). Two included dorcasomines (*Tsivoka* Villiers and *Apatophysis*) clustered away from Lepturinae and with the (poorly represented and often non-monophyletic) prionine-parandrine-cerambycine cluster in Šýkorová (2008). Dorcasomine adults do not have the mandibular molar plate usually present in Lepturinae (Fig. 2.4.12 K, L). The branch has no obvious adult synapomorphies. Wings are always without a wedge cell, usually with four veins in the medial field or less and  $CuA_{1+2}$  is incomplete basally or missing (also lost in all Lamiinae); however, some Gondwanan Cerambycinae have five regular veins in the medial area (Fig. 2.4.17 A, B) and  $CuA_{1+2}$  may be complete (Fig. 2.4.17 A, C). At least some larval characters (abruptly constricted clypeus and round mandibles, Fig. 2.4.21 J; 2.4.24 A, C–E, G, 2.4.25 E, F, I) support the monophyly of Cerambycinae, whereas no convincing apomorphies are available for Dorcasominae.

The monophyly of branch 3 (Spondylidinae + Necydalinae + Lepturinae) + Lamiinae) is uncertain, and the potential apomorphies are problematic. Adults of all four subfamilies have a narrow tentorial bridge (Fig. 2.4.12 F, G), whereas it is broad in branch 1, in some taxa of both subfamilies of branch 2, and in Vesperidae and Disteniidae (an intermediate state occurs in Oxypeltidae). In larvae, moderately to strongly oblique bases of the metatentorial arms and more or less distinct

metatentorial pits (Fig. 2.4.22 D, 2.4.24 H, 2.4.25 B) may be synapomorphic if we accept the broad tentorial bridge without distinct pits as plesiomorphic. Midgut mycetomes are known in all subfamilies except Lamiinae (where they were considered secondarily lost by Semenova & Danilevsky 1977), but absent in the remaining cerambycoids. Pterothoracic egg bursters (Fig. 2.4.31 J) occur in first instars of at least some species of all four subfamilies (but rare in Lamiinae), whereas they are absent in other cerambycoids (first instars unknown in Vesperidae: Anoplodermatinae and Oxypeltidae).

Within that branch, Necydalinae and Lepturinae appear related on most types of data, and the former has often been classified as a tribe of the latter. Adult synapomorphies may include the prominent temples followed by a constricted “neck” (but absent in many Lepturinae and occurring in some other groups) and possibly the mandibular molar plate, which is not known in other cerambycid subfamilies (but occurs in many Disteniidae, in Oxypeltidae and some other chrysomeloids); it is best developed in typical floricolous Lepturinae and less distinct in some presumed basal forms and in Necydalinae. Possible larval synapomorphies include the broadly separate dorsal epicranium (Fig. 2.4.22 B, 2.4.27 D; exceptions rare), the tendency for reduction of pronotal lateral furrows (rudimentary or absent in Lepturinae, Fig. 2.4.28 B, intermediate in Necydalinae, Fig. 2.4.21 K), the long legs (very long in first instars, Fig. 2.4.31 J, even if moderately long in later instars), and the distinct pretarsal seta. As in the case of the adult mola, virtually all those larval characters could be interpreted as plesiomorphies (relatively long legs occur in some Vesperidae, pretarsal seta in all Vesperidae, lateral pronotal furrows are absent or short in Oxypeltidae and Vesperidae, broadly separate epicranium with dorsomedian duplicature short or absent is universal in all non-cerambycid cerambycoids, and all four characters occur in some groups of the chrysomelid assemblage), but such interpretation, placing the lepturine-necydaline lineage at a very basal position in the Cerambycidae, would contradict other characters. Interrelationships among the Lepturinae-Necydalinae clade and Lamiinae and Spondylidinae are uncertain.

Relationships among the three major branches are tenuous at best (and the monophyly of branch 3 is questionable). The relationship of 1 to 3 (or any of its subgroups) is not supported by any characters and has not been proposed in the literature, with the partial exception of some authors placing together Parandrinae and Spondylidini (e.g., in a separate family Spondylidae by LeConte & Horn 1883). Branches 1 and 2 are held together mainly by the (admittedly still rather limited, inconclusive and unpublished) molecular data; wings usually have four or fewer veins in the medial field, but five veins occur in some Cerambycinae and Prioninae of the Southern Hemisphere; the larval postnotum (present in Dorcasominae, most

Cerambycinae and many Prioninae) has usually been regarded as a homoplasy; for tentorial morphology see below. Possible synapomorphies of branches 2 and 3 include the longer well-exposed larval gula and narrow tentorial bridge. The distinct metatentorial pits and slightly oblique arms of *Dorcasomus* may be either plesiomorphic if branch 2 is related to 3, or an apomorphic parallelism if related to branch 1 (in that case also the narrow tentorial bridge of Dorcasominae and Cerambycinae would be a parallel development with branch 3 if we accept the tentorial morphology of Parandrinae and Prioninae as the most plesiomorphic in cerambycids). The “undivided” occipital foramen (i.e., the metatentorium strongly oblique and almost invisible in ventral view) is not a universal feature in branch 3 (as sometimes incorrectly assumed) as the metatentorium is almost completely visible ventrally in many Lamiinae (Fig. 2.4.26 P, Q) and some Spondylidinae.

Considering the tendencies in molecular studies to cluster branches 1 and 2, combined with some distributional patterns and the obvious concentration of plesiomorphic characters of the worldwide Prioninae and Cerambycinae in the southern Gondwanan regions (see under those subfamilies), we should test a hypothesis that those two branches may be of “southern” origin, whereas branch 3 might be “northern”, although Lamiinae is today the most successful and widely distributed subfamily, and a few taxa of the possibly plesiomorphic spondylidine tribe Anisarthrini are Afrotropical. Lamiinae is outnumbered by the Cerambycinae in Australia and southern South America (McKeown 1947; Forchhammer & Wang 1987; Cerda 1986, 1988 for Chile, all Lepturinae and Aseminae of that list should be added to the Cerambycinae count, making the Chilean Cerambycinae to Lamiinae score at that time a surprising 121 to 37 after exclusion of the undoubtedly introduced cerambycine genera *Nathrius* Bréthes, *Phoracantha* and *Hylotrupes*). The close affinities of many Australian and New Zealand Cerambycinae to those of the southern Andean-Patagonian region (but not of southern Africa) – a typical pattern of numerous Gondwanan taxa – apparently do not recur in the Lamiinae, suggesting possible secondary independent lamiine immigration in both regions. Gressitt (1959: 61), arguing that the insect fauna of New Guinea is closer to the Oriental rather than Australian Region, writes: “However, the subfamily Lamiinae indicates for New Guinea a closer relationship with the Oriental Region than do the Prioninae and Cerambycinae. The subfamily Cerambycinae, particularly, shows more relationship with the Australian fauna than do many other groups of insects in New Guinea. This appears to be in part related to the fact that the subfamily Cerambycinae is dominant in Australia”.

**Catalogues and monographs** for major regions (the most recent selected; many with full bibliographies): Aurivillius 1912–1923 (world,

exclusive of Parandrinae and Prioninae); Lameere 1913, 1919 (world, Parandrinae and Prioninae); Boppe 1921 (world, Lepturinae *sensu lato*); Breuning 1958–1969, Gilmour 1965 (world, Lamiinae); Löbl & Smetana 2010 (Palearctic, including China); Plavilstshikov 1936–1958 (former Soviet Union, Lamiinae incomplete); Cherepanov 1979–1985 (northern Asia); Bezark & Monné 2013 (New World); Linsley 1962–1964, Linsley & Chemsak 1972–1995, Chemsak 1996 (North America); Zayas 1975 (Cuba); Monné 2005–2006, 2012 (Neotropical); Martins 1997–2010 (South America, Parandrinae, Cerambycinae); McKeown 1947 (Australia, excluding Parandrinae); Ślipiński & Escalona 2013 (Australia, Lamiinae); Gilmour 1956 (Afrotropical, Prioninae); Breuning 1957 (Madagascar, Lamiinae); Ferreira & Veiga-Ferreira 1959 a, b (Afrotropical, excluding Lamiinae); Veiga Ferreira 1964, 1966 (mainly Mozambique, but covering a wider area); Quentin & Villiers 1975 (Madagascar, Parandrinae and Prioninae); Santos Ferreira 1980 (southern part of continental Africa, Parandrinae and Prioninae); Vives 2009 b (Seychelles); Villiers *et al.* 2011 (Madagascar, Dorcasominae); Gahan 1906 (India, Sri Lanka, Burma, excluding Lamiinae); Makihara *et al.* 2008 (Sri Lanka, excluding Lamiinae), Gressitt *et al.* 1970 (Laos); Hüdepohl 1987, 1990, 1992 (Philippines, Prioninae, Parandrinae, Cerambycinae *partim*); Heffern 2005 (Borneo); Bentanachs *et al.* 2012 (Borneo, Cerambycinae *partim*); Gressitt 1959 (New Guinea, excluding Lamiinae), 1956 (Micronesia), 1978 (Hawaii); Hayashi 1961 (New Caledonia, Lamiinae incomplete); Sudre *et al.* 2010, Vives *et al.* 2011 (New Caledonia); Dillon & Dillon 1952 (Fiji); Heffern 2011 (Hawaii). Several online databases currently cover Cerambycidae or Lamiinae worldwide: Biological Library, Titan, or Lamiaires du Monde.

## Prioninae Latreille, 1802

**Distribution.** Approximately 300 genera and over 1000 species; worldwide, predominantly in warmer regions, including dry habitats; temperate species are few.

**Biology and Ecology.** Larvae usually develop in dead wood, but not infrequently in dead parts of living trees, with some species able to penetrate recently dead or living tissue. No subcortical forms are known. Some groups (e.g., many Prionini, Cantharocnemini) develop more or less exclusively underground, and larvae of some species of those groups can move temporally through the soil or feed externally on roots of trees or herbs; females of such species usually oviposit in the soil along the roots, whereas most prionines lay eggs directly on or in the food material. Development may be long, several years are not exceptional in temperate regions. A pupal chamber is usually constructed in the food material; terricoles and some root

feeders pupate in the soil. Adults are typically crepuscular or nocturnal and of sombre colors; brightly colored (sometimes mimetic) or metallic diurnal species are few and mostly tropical. Adults appear to be relatively short-lived and most apparently do not feed or, at most, imbibe fluids. Flightlessness or brachyptery is relatively common, particularly in dry regions, but is usually restricted to females that may be also brachelytrous and physogastric (Fig. 2.4.1 C); some winged females cannot fly until they lay a portion of the eggs (Edwards 1961 a for *Prionoplus*). Some long-legged species are flightless in both sexes (the peculiar New Hebridean *Psalidocoptus* White, the Neotropical *Apteroacaulus* and *Prionacalus* White), but even then, related genera may have winged males (*Psalidognathus* Gray). In species with males capable of flight, the male antennae are often serrate, pectinate, bipectinate or flabellate and may have more than nine flagellomeres (Fig. 2.4.1 B, E, 2.4.2 H); some species use long-range female-produced sex pheromones (Barbour *et al.* 2006; Cervantes *et al.* 2006; Rodstein *et al.* 2009).

**Morphology, Adults** (Fig. 2.4.1, 2.4.2 A–N). Length rarely below 10 mm (males of the Neotropical *Chariea* Audinet-Serville may be as small as 6 mm; Galileo 1987 b); specimens of *Titanus* Audinet-Serville, *Xixuthrus* J. Thomson and *Macrodonia* reaching 150–175 mm. Sexual dimorphism may be strong and may concern size, general form (including brachelytry and exposed wings in males; Fig. 2.4.2 L), antennal morphology, enlarged male mandibles (Fig. 2.4.12 B), color, flightless females and winged males (Fig. 2.4.1 B, C), etc. Both sexes are flightless and have long legs and palps in some *Psalidognathini* (Fig. 2.4.2 F). Compact digging forms with strong spined fossorial legs and very short antennae occur particularly in *Cantharocnemini*.

Head without a distinctly constricted neck, never rostrate, usually prognathous or moderately oblique; rarely anterior head with mouthparts distinctly directed ventrally. Median frontal groove and associated low endocarina often continue posteriorly and approach or reach hind cranial margin. Frontoclypeal sulcus usually distinct, straight to strongly angulate; postclypeus narrow and transverse to long and triangular; pretentorial pits lateral or (particularly in some flattened heads) laterodorsal with rare exceptions (almost frontal and relatively far from mandibular articulations in *Erythraenus*). Labrum of limited mobility, occasionally short and tending to fuse with (usually small) anteclypeus; in extreme cases, labrum and anteclypeus are fused and completely sclerotized. Antennal insertions usually close to mandibular condyles, but both relatively broadly separated (and often connected by a distinct carina) in some forms with mouthparts strongly pointing ventrad and antennae inserted higher on head (e.g., *Anoeme*, *Delocheilus* J. Thomson, *Sobarus* Harold, *Stolidodere* Aurivillius, *Erythraenus*, *Rhipidocerus*

Westwood, a few Neotropical forms classified in *Anacolini* but not *Anacolus* Latreille); antennal sockets oriented mostly laterally. Eyes variable, in some cases very large and approaching or nearly meeting dorsally and/or ventrally, but never projecting between antennal sockets and dorsal mandibular articulations. Antennae of variable lengths (but distinctly surpassing base of pronotum except for some *Cantharocnemini*) and structure; in some cases strongly sexually dimorphic; in some *Prionini* with up to more than 30 flagellomeres in males; rarely with less than 11 antennomeres: three terminal flagellomeres fused in both sexes of *Drumontiana* (Komiya & Niisato 2007; Fig. 2.4.1 J), four in females of *Allaiocerus* and *Casiphia*, forming a distinct club in the latter (Galileo 1987 b; Drumont & Komiya 2002; Fig. 2.4.1 P); flagellomere 1 often distinctly longer than the following. Mandibles extremely variable, without distinct molar plate (but a conspicuous molar protuberance may be present); inner edge without fringe of long hairs, at most with short pilosity mainly in molar region (but other mandibular parts may be extensively hairy; Fig. 2.4.1 O); apex in unmodified mandibles usually simple, but bidentate (Fig. 2.4.11 D) in *Tragosoma* Audinet-Serville, *Microplophorus* Blanchard in Gay, *Rhipidocerus*, *Enneaphyllus* Waterhouse, *Prionoplus*, *Toxentes* Newman, *Delocheilus* or *Schizodontus* Quentin & Villiers (Quentin & Villiers 1974); mandibles in some groups (especially in males) strongly enlarged and modified and may be either curved ventrad (males of some *Dorysthenes* Vigors of *Prionini*; Fig. 2.4.12 B) or directed anteriorly (Fig. 2.4.1 N); males of some species are dimorphic. Maxillae and labium relatively reduced (except for palps, which are often long, extremely so in some Neotropical *Psalidognathini*; Fig. 2.4.2 F); lacinia typically very small to rudimentary (Fig. 2.4.13 A), but relatively distinct for instance in *Callipogonini sensu stricto* or *Hoplideres* Audinet-Serville (Fig. 2.4.13 B). Gulamentum not forming a distinct intermaxillary process; ligula typically short and transverse, often more or less sclerotized. Terminal segments of maxillary and labial palps ovoid (but not pointed) to extremely broadly securiform. Metatentorium with a broad arched or roof-like bridge and connected (even if sometimes very thinly) with pretentorial arms; dorsal arms often present. Cervical sclerites usually rudimentary or absent, but large in some taxa (*Tragosoma*, *Microplophorus*, *Closterus* Audinet-Serville, *Hoplideres*, *Prionoplus* and *Aesa* Lameere).

Pronotum usually with complete or incomplete lateral carina, which is often dentate or spinose, rarely sides of pronotum with an isolated spine when carina incomplete in middle (*Rhipidocerus*); carina either running from posterior angles toward lateral extremity of procoxal cavities (ending there or closely following the usually distinct notosternal suture laterally; Fig. 2.4.13 H), or more or less distant from procoxal cavities and suture

(Fig. 2.4.10 A; all transitions exist); procoxal cavities transverse, almost always open internally (closed in *Anoeme*) and also externally (posteriorly). Prosternal process usually well-developed, often expanded apically and resting/sliding on anterior margin of mesoventrite. Procoxae transverse, relatively free, may or may not have auxiliary medial articulation with prosternal process, not or at most slightly projecting below that process, trochantin visible. Mesoscutum short and usually broadly emarginate anteriorly; lacking stridulatory plate, usually punctate and/or setose and with distinct simple or rarely posteriorly bifurcated median endocarina. Mesocoxal cavities open laterally. Metendosternite usually without laminae, but distinct laminae present for instance in *Tragosoma*, *Microplophorus*, *Anoeme*, *Closterus*, *Priopoplus*, *Aesa* and *Enneaphyllus*. Wing in macropterous specimens (Fig. 2.4.15 D, F, 2.4.16 A–E) with radial cell usually closed proximally; RP usually extends far basally beyond crossvein r<sub>4</sub>, the latter with spur short to absent; wedge cell almost always present (absent in *Myzomorphus* Dejean; Galileo 1987 b). Medial field typically with only four free veins (Fig. 2.4.16 C, E; distal two here considered MP<sub>3+4</sub> and CuA<sub>2</sub>) and no CuA<sub>1</sub>, or sometimes also CuA<sub>2</sub> missing; however, some taxa have CuA<sub>1</sub> (*Elaptus* Pascoe; *Tithoes* J. Thomson, Fig. 2.4.16 A) and/or five free veins in the medial field (Fig. 2.4.15 D, 2.4.16 B, D). Tarsi usually pseudo-tetramerous and padded beneath, but tarsomere 4 distinct and in some taxa with cryptic habits (such as some *Cantharocnemini*) the lobes of tarsomere 3 are strongly reduced and the tarsi become distinctly pentamerous (Fig. 2.4.17 J); claws usually divaricate, always freely movable, never closely associated or even fusing basally; empodium from prominent and multisetose to indistinct.

Ovipositor usually with styli more or less lateral and coxites often sclerotized (e.g., Wu & Chen 2012), very strongly so, for instance, in cases of a “digging” ovipositor of some taxa with known or presumed subterranean larval development (Fig. 2.4.18 L); fully terminal styli are rare (e.g., *Anoeme* and nearly terminal in some *Aegosomes*); female abdominal segment VIII may be long and tubular and projecting from abdomen (some *Aegosomes*). Midgut short and thread-like.

**Morphology, Larvae** (Fig. 2.4.20 A–D). Subcylindrical. Head deeply retracted, pale posteriorly, cranium slightly transverse to subquadrate, notched to subtruncate posteriorly, epicranial halves broadly fused. Frontal arms (if distinct) enter separately duplicated cranial region, the latter without a deep intracranial carina. Frons without transfrontal line. Epistomal, frontal and postcondylar carinae usually present, but absent or rudimentary in some groups such as *Anoeme*, an unidentified South African larva presumed to be *Delocheilus* (Fig. 2.4.27 J), *Sarmydyus* Pascoe, *Psephactus* Harold, *Drumontiana* (W. Bi, personal

communication), *Macrotomini sensu stricto* and the very similar *Cantharocnemis* Audinet-Serville (Fig. 2.4.21 O). Clypeus trapezoidal, filling space between mandibular articulations. Labrum variable, but never as elongate as in *Parandrinae*. Stemmata variable (six pairs to absent). Antennae short to moderately long, never rudimentary, trimerous or antennomere 3 reduced; sensorium in later instars flat or roundly protuberant (but may have a raised sclerotized basal rim), never conical. Mandibles short, robust, pseudomola present (although sometimes its dorsal striation is reduced or lost and mandibles resemble the type without a pseudomola); apex usually unidentate (Fig. 2.4.26 E, F), rarely bidentate (Fig. 2.4.26 K), usually with three inner keels. Maxillolabial complex with large movable cardo and the maxillary articulating area often distinctly divided (anterior part always small); mala cylindrical to expanded medially but never very slender, finger-like and appearing to arise exclusively from palpiger; the latter rarely with distinct laterodorsal sensory process; maxillary palps trimerous. Mentum often trapezoidal and broadest anteriorly; ligula broad, bearing numerous setae. Hypostomal lines strongly converging posteriorly. Gula always present but short, strongly transverse, in some taxa covered by membranous postgular lobe and not visible in ventral view (Fig. 2.4.22 C). Tentorial bridge broad, rigid, entirely in the same plane as the large hypostomal plates (“divided” occipital foramen); no distinct metatentorial pits.

Pronotum delimited by distinct lateral furrows that do not interrupt the anterior pigmentation (Fig. 2.4.21 G) except for some unusual forms (Fig. 2.4.27 J); pronotal base with asperities in *Spinimegopsis cingalensis* (White) (Gardner 1931 a, as *Megopsis*) or *Chorenta reticulata* (Dalman) (Duffy 1960, as *Stictosomus*); asperities rarely arranged in transverse rows (presumed *Delocheilus*; Fig. 2.4.27 J) or completely fused into transverse ridges (*Anoeme*). Proepipleuron anteriorly broadening and incompletely delimited ventrally, but occasionally closed anteriorly by a transverse impressed line, and with large pseudopod-like process just posterad of that line in *Eudianodes swanzyi* Pascoe (Duffy 1957) and *Neoprion batesi* (Gahan) (Fig. 2.4.20 C, 2.4.27 K) (both *Eurypodini*, but the process is absent in *Eury-poda antennata* Saunders). Propleuron large; episternum usually with thick cuticle and separated from epimeron by S-shaped furrow projecting internally as small pleural apodeme. Coxosternal halves approximate (Fig. 2.4.28 E) to reduced and broadly separated (Fig. 2.4.29 E); mediopresternum from distinct to fused with lateropresternum. Postnotum present (Fig. 2.4.28 A, C; always less well-defined compared with typical *Cerambycinae*) to absent. Mesothoracic spiracle usually slightly protruding into prothorax (Fig. 2.4.28 C, 2.4.29 E). Meso- and metathoracic pleuron entire and broadly separating coxae from epipleuron. Legs short (at most slightly longer than maxillary palps), with a



full number of segments (trochanter may be rather indistinct); pretarsus usually without setae, or they are minute and inconstant.

Abdomen with dorsal and ventral ampullae on segments I–VII; both with one pair of lateral impressions (Fig. 2.4.28 A, E). Epipleuron protuberant on segments VII–IX, non-protuberant on I–VI and often bearing epipleural discs (usually distinctly radially striate) on some or all of them (Fig. 2.4.30 D). Segment IX very often enlarged (Fig. 2.4.20 A–D), always without caudal armature. Segment X short, often fused with the enlarged segment IX; anus triradiate, terminal or (if segments IX and X are fused) often slightly shifted dorsally. Anterior midgut lacking mycetomes (Fig. 2.4.19 I).

The very few known first instars are short and robust, with short legs, without cephalic and pterothoracic egg bursters; abdominal egg bursters may be absent or microscopic as in *Prionus* Geofroy (Duffy 1953), *Psephactus* (Oka 1977) or *Prinobius* Mulsant, but very large on segments III and IV in *Maliodon* (Duffy 1957; Fig. 2.4.31 I), and on IV in *Aegosoma* (Fig. 2.4.31 H); distinct egg bursters present on segments I–VI in *Prionoplus* (Duffy 1963). Antennal sensorium may be prominent and more or less conical (*Aegosoma*). Abdominal segment IX not enlarged.

**Phylogeny and Taxonomy.** Prioninae have no larval apomorphies and may be paraphyletic with respect to Parandrinae. The only potential prionine apomorphy (the lack of vein  $CuA_1$ , which is retained in many Parandrinae) has been rendered invalid by the discovery of a distinct and complete  $CuA_1$  in some prionine genera from the Southern Hemisphere, and the wing characters now known to occur in prionines (Fig. 2.4.15 D, 2.4.16 A–E), if combined in a single taxon, would make for a wing as plesiomorphic as any known in the cerambycid complex. The pentamerous adult tarsus and “tenebrionid” habitus of Parandrinae may be secondary and similar characters occur in some Prioninae (Fig. 2.4.17 J, K). Prionine tribal classification is unsatisfactory and will not be discussed. Some characters considered “typical” for the subfamily reflect a “northern taxonomic bias” and the important variability and some potentially plesiomorphic characters (such as short unmodified mandibles with bidentate apex, presence of distinct cervical sclerites, metendosternite with laminae, or more complete wing venations) have been found almost exclusively in certain “southern” genera (*Tragosoma* being the only northern taxon bearing some of those characters but its closest relatives probably occur in the Southern Hemisphere).

The subfamilial placement of *Cycloprionus flavus* Tippmann (Fig. 2.4.2 O), known only by males, is uncertain (A. Santos-Silva, personal communication). It is currently classified in Prioninae: Anacolini, but it displays several non-prionine characters

such as reduced wing venation (without wedge cell and with only three free veins in the medial field;  $MP_{3+4}$  is unbranched and the  $CuA_{1+2}$  complex completely lost; Fig. 2.4.16 F), procoxal cavities apparently closed internally (Fig. 2.4.13 G), or mesoscutum with a glabrous matt (even if not striated) central area and separated from scutellar shield by a distinct impression. All the above characters are compatible with Cerambycinae, and the species bears some resemblance to certain Trachyderini.

### Parandrinae Blanchard, 1845

**Distribution.** Two tribes (Parandrini and Erichsoniini) with 16 genera and 119 species (see Phylogeny and Taxonomy for a list of genera and their distributions). *Erichsonia dentifrons* Westwood, the single species of Erichsoniini, occurs in Central America (southern Mexico to El Salvador). Parandrini are distributed worldwide, but mainly in warmer regions; truly temperate species are few. Neotropical Region currently has 43 species in three genera with some subgenera (Bezark & Monné 2013; one species of *Parandra* reaching the USA), 42 species in six genera were listed from SE Asian islands and Australasia by Santos-Silva *et al.* 2010 (not including *Stenandra*, see below), and a revision of Afrotropical Parandrinae listed 25 species in four genera (Bouyer *et al.* 2012). *Stenandra* was Afrotropical (one species in continental Africa, one in Madagascar) until, somewhat unexpectedly, two additional species were recently described from Vietnam and Sulawesi (Komiya & Santos-Silva 2011). The subfamily is poorly represented in America North of Mexico (two species of the Nearctic *Neandra* and one *Parandra*), continental Eurasia (the remarkably geographically isolated *Archandra* and the Vietnamese species of *Stenandra*), and continental Australia (the endemic monospecific eastern Australian *Storeyandra* and one species of the predominantly New Guinean *Papuandra* occurring in Queensland). At the same time species of Parandrini are known from numerous islands including isolated Pacific islands (Norfolk Is., New Caledonia, Fiji, Solomon Is., Hawaii, Galapagos Is.); at least some of those occurrences cannot be relic and indicate a relatively strong ability to spread, possibly in floating tree trunks (see Biology and Ecology).

**Biology and Ecology.** Unknown in Erichsoniini. Larvae of Parandrini develop in dead moist logs of moderate to large diameter, or in dead wood of living trees, sometimes even in closed and healed over hollows in which the adults may reproduce without leaving the tree (Linsley 1962 a). Many species are polyphagous (Linsley 1962 a; Monné 2002 b); angiosperms are usually preferred, but some southern species are associated with the gymnosperm tree genus *Araucaria* (e.g., Webb 1994). Pupal cells are constructed inside the wood. Adults are found in tree hollows, wood cracks and under loose bark,

and are mostly nocturnal. Oviposition occurs in the wood with several generations often developing within the same material. Sexual and associated behavior of *Parandra glabra* (De Geer) was described by Lingafelter (1998). Nothing is known about the mating system of the Australian *Storeyandra frenchi* with flightless males and winged females.

**Morphology, Adults** (Fig. 2.4.2 P–T). Moderately large (9–40 mm), parallel-sided, unicolored (yellow-brown to almost black) or with head darker; *Erichsonia* Westwood less depressed and bearing moderately long pilosity; Parandrini are flat, of a somewhat “tenebrionid” appearance and nearly glabrous or with sparse very short pitted, often spatulate, setae, rarely some ventral regions with long pilosity.

Head prognathous or slightly oblique, without constricted neck. Frontal and occipital regions without endocarina or median groove in Parandrini; in *Erichsonia* with rudiments of frontal endocarina and two pairs of external longitudinal carinae or elongate tubercles (Fig. 2.4.12 A). Clypeus short, transverse and entirely sclerotized; medial portion of frontoclypeal suture may be externally indistinct; pretentorial pits lateral to mandibular articulations. Labrum short and transverse, sclerotized, connate with clypeus, anterior margin often with median projection. Antennal insertions very close to mandibular condyles, lateral and widely separated, without distinct antennal tubercles. Eyes moderately sized, lateral and placed behind antennal sockets, not approaching dorsally or ventrally; vertically extended and at most shallowly emarginate in Parandrini, distinctly emarginate in *Erichsonia*. Antennae very short, not or slightly surpassing base of pronotum, slightly serrate (mainly some males, including *Erichsonia*) to moniliform; flagellomeres anteriorly either more or less carinate with a sensory area on each side of the carina, or (in many Parandrini) carina reduced to a longitudinal dividing bar or absent on some or all flagellomeres (and both sensory areas then fused). Mandibles without distinct molar plate or basal membranous pilose area (but molar region may bear hairs); apex in some cases with small supplementary ventral tooth; males of some Parandrini may have prominent sickle-shaped mandibles (males of different sizes often show non-proportional variability or dimorphism); mandible of females may bear dorsal basal setose cavity. Lacinia nearly absent. Gulamentum not forming intermaxillary process; mentum broad and partly covering maxillary bases; all parts of distal labium short and strongly transverse; ligula sclerotized; terminal segments of both palps not truncate, usually slightly tapering apically, with moderately large apical sensory areas. Tentorium with broad bridge and narrowly connected thin pre- and metatentorial arms; dorsal arms virtually absent. Cervical sclerites absent.

Pronotum usually with distinct and complete simple lateral carinae (incomplete anteriorly in

males of some *Parandra*). Notosternal suture fine, in some cases incomplete. Procoxal cavities transverse, open internally, open or (some Parandrini) narrowly closed posteriorly; prosternal process well-developed. Procoxae transverse, lacking auxiliary articulation with prosternal process, trochantin visible. Mesoscutum without stridulatory plate, divided by median endocarina. Mesocoxal cavities open. Metaventral discrimen usually reduced to absent. Metendosternite without laminae. Wings (Fig. 2.4.16 G, H) developed except for brachypterous males of the monospecific Australian *Storeyandra* (Fig. 2.4.2 R, S); radial cell proximally open or closed; RP extends far basally beyond crossvein r<sub>4</sub>, the latter with spur present to absent; wedge cell absent; medial field usually with four (more rarely three) free veins, but as in the other groups, the venation of this region individually variable; MP<sub>3+4</sub> always unbranched; CuA<sub>2</sub> (if present) always connected basally with MP<sub>3+4</sub> (i.e., CuA<sub>1</sub> present), in *Erichsonia* and more or less completely in some Parandrini also connected with the region of former wedge cell (i.e., CuA<sub>1+2</sub> present); in some Parandrini, CuA<sub>2</sub> or the entire CuA<sub>1+2</sub> complex is absent and only three free veins remain in the medial field; wing in females of *Stenandra kolbei* (Lameere) (males and other species not studied) with a sclerotized rugose fleck between AA<sub>4</sub> and AP<sub>3</sub> (Fig. 2.4.16 H). Legs short, coxae at most moderately prominent; all tibiae compressed and bearing two often strongly unequal apical spurs, outer side more or less carinate and in Parandrini with apical tooth; tarsi distinctly pentamerous (Fig. 2.4.17 K); tarsomeres 1–3 short, with very small ventral pads, third with lobes small to absent, fourth therefore well visible; tarsomere 5 long; claws free, particularly in Parandrini long and sickle-shaped; empodium distinct (then bearing one or two setae, or two tight clusters of setae; Fig. 2.4.17 K) to absent.

Apex of ovipositor very strongly sclerotized; styli partly reduced, sclerotized, dorsolaterally placed (Fig. 2.4.18 M).

**Morphology, Larvae** (unknown in Erichsoniini). Basically similar to Prioninae, differences or restrictions as follows:

Head (Fig. 2.4.23 A, B) always notched posterodorsally. Anterior frons and epistomal margin without carinae. Labrum cordate and very long, covering dorsal face of large striate mandibular pseudomola (Fig. 2.4.23 C). Stemmata usually absent or small non-fused pigment spots of three main stemmata visible, rarely with very indistinct dorsal stemmata. Antennae trimerous. Mandibles with large striated pseudomola, apical part with two or three inner keels reaching simple apex. Maxillolabial complex relatively gracile in comparison with typical Prioninae; maxillary palpiger without process; mala narrow, subcylindrical. Submentum medially longitudinally raised. Gula exposed (not covered by postgular lobe).

Pronotum posteriorly with a field of sclerotized asperities of a characteristic shape (Fig. 2.4.27 L); asperities also present on other prothoracic regions (Fig. 2.4.29 F), pterothoracic terga and sterna, ambulatory ampullae and occasionally some other abdominal regions. Prothoracic epipleuron without transverse furrow or pseudopod-like processes. Coxosternal halves broadly separated by large mediopresternum (whose lateral boundaries may be secondary); sternellar fold very short and poorly separated from, or medially fused with mesosternum (Fig. 2.4.29 F). Postnotum non-developed. Mesothoracic spiracle almost not protruding into prothorax.

Abdomen without distinct epipleural discs. Anal segment fused with large somewhat “inflated” segment IX. Anus often slightly posterodorsal.

First-instar larvae (available for *Neandra brunnea*) similar to later instars including long labrum, body asperities, and fusing and slightly dorsally shifted abdominal segment X. Antennal sensorium prominent, rounded apically. Legs short. Cephalic and pterothoracic egg bursters absent, small lateral abdominal egg-bursting spines present on segments I–VI and minute spine usually also on VII.

**Phylogeny and Taxonomy.** Although retained here as a separate subfamily, Parandrinae may render Prioninae paraphyletic (see above) and many of the “archaic” adult characters, such as the pentamerous tarsus with small remains of ventral pads (Fig. 2.4.17 K), short antennae and peculiar adult habitus (Fig. 2.4.2 P–T) are very probably derived characters reflecting the concealed adult habits. Larval workers mostly either placed Parandrinae in Prioninae (Craighead 1915, 1923), or pointed out that parandrine larvae are basically of a modified prionine type (Danilevsky 1979 a; Svacha & Danilevsky 1987). All larval characters used in Duffy’s (1953–1980) keys to subfamilies for distinguishing Parandrinae from Prioninae have exceptions. The lack of wing wedge cell (paralleled in the undoubtedly unrelated *Myzomorphus* of Prioninae: Anacolini) is likewise apomorphic, and the  $CuA_1$ , apparently belonging to parandrine groundplan, has been found in a few Prioninae. Penteado-Dias (1984) considered the adult nerve cord of Parandrinae (an unidentified species of Parandrini) as the most primitive cerambycid, but her own figures show that all proposed plesiomorphies occur also in some other species and that the studied parandrine has at least one apomorphy (the third abdominal ganglion moved to posterior metathorax) not shared by some species of other subfamilies having that ganglion in anterior abdomen; moreover, only few prionines were studied. Based on female reproductive organs of *Komiyandra formosana* (Miwa & Mitono) (as *Parandra*), Saito (1990) concluded that “*Parandra* seems to be most primitive in all the cerambycids in a strict sense, because the paraproct, which is heavily sclerotized, is not perfectly

tubular, being separated into clearly defined sternite and tergite in the anterior part, and completely embraces the vagina and its plates, and the styli are articulated to the dorsal side of the coxite lobes. These features are not found in any other cerambycids that I have examined”. However, the heavily sclerotized “thrusting” ovipositor as a whole and the reduced displaced styli (both occurring also in some prionines not studied by Saito) can hardly be considered plesiomorphic as they do not occur in any potentially related group except for the Vesperidae: Anoplodermatinae with specialized terricolous habits, and the unmodified ovipositors of most cerambycids would have to be regarded as reversals; thus the other characters may also be open to reinterpretation. Larvae apparently share some apomorphies (reduced broadly separate prothoracic coxosternal halves, Fig. 2.4.29 F; enlarged abdominal segment IX fused with X) with certain prionine subtaxa.

Parandrinae is usually divided into two tribes, Parandrini and Erichsoniini. The former had been long treated as containing single genus *Parandra*, but some former subgenera were elevated to generic status and a number of new genera have been recently described (Quentin & Villiers 1972, 1975; Santos-Silva 2002; Santos-Silva & Shute 2009; Santos-Silva *et al.* 2010, the latter paper contains detailed taxonomic history and a key to 13 world genera of the Parandrini; two additional Afrotropical genera and 18 new species were described by Bouyer *et al.* 2012). The currently recognized genus-group taxa of Parandrini are *Acutandra* Santos-Silva (five Neotropical and 22 Afrotropical species), *Adlbauerandra* Bouyer, Drumont & Santos-Silva [*A. morettoii* (Adlbauer), Central Africa], *Archandra* Lameere [*A. caspia* (Ménétriés), southern Caspian region], *Birandra* Santos-Silva (five, Neotropical), *Caledonandra* Santos-Silva, Heffern & Matsuda (two, New Caledonia), *Hawaiiandra* Santos-Silva, Heffern & Matsuda [*H. puncticeps* (Sharp), Hawaii], *Hesperandra* Arigony (four, Neotropical; subgenus of *Parandra*), *Komiyandra* Santos-Silva, Heffern & Matsuda (25, SE Asian islands from Ryukyus and Taiwan, reaching New Guinea), *Malukandra* Santos-Silva, Heffern & Matsuda (three, Sulawesi?, Halmahera, New Guinea), *Melanesiandra* Santos-Silva, Heffern & Matsuda (five, Fiji, Solomon Is., Bouganville Is., New Guinea), *Meridiandra* Bouyer, Drumont & Santos-Silva [*M. capicola* (J. Thomson), South Africa], *Neandra* Lameere (two, Nearctic), *Papuanandra* Santos-Silva, Heffern & Matsuda (seven, New Guinea, Normamby Island, Queensland, Norfolk Island), *Parandra* Latreille (11, Neotropical), *Stenandra* Lameere (two Afrotropical and two Oriental), *Storeyandra* Santos-Silva, Heffern & Matsuda [*S. frenchi* (Blackburn), eastern Australia], *Tavandra* Santos-Silva (10, Neotropical, one species reaching USA; subgenus of *Parandra*), *Yvesandra* Santos-Silva & Shute (eight, Neotropical; subgenus of *Birandra*). The Erichsoniini contains the single poorly

known Central American species *Erichsonia dentifrons* Westwood. It was originally separated from the remaining parandriines among other on the absence of a distinct pretarsal empodium, but it is indistinct also in some Parandriini.

### Dorcasominae Lacordaire, 1868

**Distribution.** More than 300 species occurring in the Oriental, southern Palaearctic (including northern Africa) and Afrotropical Regions. The group is extremely diversified in the Madagascan subregion (78 genera with 257 species, all are endemic; Villiers *et al.* 2011). Apatophyseini occur in all regions whereas Dorcasomini (containing only *Dorcasomus* with eight species) are restricted to continental sub-Saharan Africa. This is the most recently established subfamily and has not yet been generally accepted; some dorcasomines may be still misclassified (particularly in Cerambycinae and Lepturinae) and the range may therefore expand.

**Biology and Ecology.** *Dorcasomus* (Dorcasomini) is known to develop in *Bersama* (Melianthaceae) (Duffy 1957, 1980). Larvae of *D. gigas* excavate wide galleries along the center of stems and branches of living trees and pupate in the host plant. Larvae of *Apatophysis* (Apatophyseini) lack stemmata and develop in dead or moribund underground parts of trees and shrubs and in dry often treeless habitats also larger perennial herbs. Mature larvae usually leave the host and pupate in soil. Undescribed larvae of many Madagascan and one South African (*Otteissa* Pascoe) genera were found in dead, often rotting wood, mostly above ground, but some species are subterranean (and larvae also tend to lose stemmata); less frequently in relatively freshly dead branches where larvae usually feed subcortically; unidentified dorcasomine larvae were also found in the outer bark layer of large living broad-leaved trees. Although the hosts usually could not be identified, some species feeding in rotting wood are undoubtedly polyphagous as larvae of several species were found in the introduced *Eucalyptus* and *Pinus*. No pupae of Madagascan Apatophyseini were found in any type of wood, and nearly all mature larvae in breedings abandoned the host material and pupated in soil. *Zulphis* Fairmaire (Fig. 2.4.3 L) and *Zulphisoma* Villiers, Quentin & Vives are possible exceptions; larvae were found in relatively solid dead wood and pupated in vials filled with host material without “wandering” attempts typical for last instars of species pupating in the soil; the pupa of *Zulphis* differs from the “soil” type (shown in Fig. 2.4.32 C, D) in being less curved, more elongate and thoracic and abdominal terga bearing fine setae and strong spines. Adults are nocturnal or diurnal, some (particularly Madagascan) Apatophyseini are floricolous and habitually resemble Lepturinae.

**Morphology, Adults** (Fig. 2.4.3 A–L and possibly M, see Phylogeny and Taxonomy). Small to moderately large (6–42 mm), usually elongate with tapering or subparallel elytra and often long cursorial legs.

Head prognathous (rarely mouthparts oblique and anterior frons therefore moderately declivous, e.g., *Dorcasomus* or *Capetoxotus* Tippmann), sometimes distinctly rostrate (Fig. 2.4.11 E, F), may be constricted immediately behind eyes, but never with prominent temples followed by a constricted neck. Median frontal groove and associated endocarina often distinct, disappearing behind eyes and not reaching posterior cranial margin. Frontoclypeal suture usually distinct and often with paramedian impressions; in rostrate heads strongly V-shaped. Pretentorial pits lateral or laterodorsal (often on lateral side of an elevation connecting mandibular condyles with antennal sockets); in elongate heads at the end of a blind line branching off the frontoclypeal suture; occasionally indistinct. Intracranial postmandibular pocket (glandular reservoir?) present in *Dorcasomus*. Anteclypeus short to moderately long, usually flat. Labrum free. Antennal insertions of variable position, but at least slightly removed from mandibular condyle (relatively close in *Protaxis* Gahan and *Epitophysis* Gressitt & Rondon); antennal sockets usually facing laterally or laterodorsally, but anterolaterally in some specialized floricolous species with approximate antennal sockets, such as *Sagridola* J. Thomson. Eyes moderately sized to very large; emarginate to entire (in some specialized floricolous Apatophyseini), strongly constricted in *Dorcasomus*, in some cases approximated dorsally and ventrally (almost touching in some *Logisticus* Waterhouse); not projecting between antennal socket and mandibular condyle. Antennae of variable length but always distinctly surpassing pronotal base, 11-segmented (rarely last flagellomere partly subdivided); flagellum may be flattened to strongly serrate. Mandibles never enlarged, with unidentate apex; inner margin usually with distinct fringe of hairs; molar plate absent, molar region (if desclerotized) only with narrow crossbar (Fig. 2.4.12 L). Maxillae and labium well-developed; lacinia distinct; gulamentum with very short to long intermaxillary process; ligula usually large, membranous and emarginate or bilobed; terminal segments of both palps usually more or less truncate. Tentorial bridge broad to narrow; pretentorial arms fine and in cleared specimens disconnected from metatentorium. Cervical sclerites present.

Pronotum without lateral carinae (or at most with short oblique rudiments at posterior angles); often with a pair of lateral tubercles or spines. Procoxal cavities closed internally and at least narrowly open posteriorly. Notosternal suture may be relatively distinct and complete. Prosternal process usually narrow but complete (reduced in *Trichroa*). Procoxae transverse to subglobular, prominent, projecting at least slightly below

prosternal process. Mesoscutum with median endocarina complete (Fig. 2.4.14 D; often in forms lacking stridulatory plate), abbreviated posteriorly, or restricted to rudiments on anterior mesonotal phragma (Fig. 2.4.14 E); stridulatory plate (if present) divided (either physically by interrupted striation or at least by a median dark line) or undivided. Mesocoxal cavities open laterally. Metendosternite with laminae present and usually large. Elytra in some macropterous taxa strongly narrowed and separated or also shortened posteriorly, partly exposing hind wings, yet almost always distinctly surpassing posterior pterothoracic margin (only slightly so in the Madagascan *Molorchineus* Villiers, Quentin & Vives). Usually macropterous in both sexes; *Apterotoxittades* Adlbauer (Fig. 2.4.3 K) apterous; the presumed female of *Urasomus* Adlbauer very strongly brachelytrous (elytra only slightly surpassing pterothorax), apterous and somewhat physogastric; females of *Apatophysis* are more or less brachypterous and slightly physogastric (Fig. 2.4.3 G). Hind wing (Fig. 2.4.17 E) in macropterous taxa with radial cell closed proximally; RP extends beyond crossvein r4, the latter with spur long to rudimentary; wedge cell absent; medial field usually with three or four free veins (MP<sub>3+4</sub> unbranched, CuA<sub>2</sub> present to absent; higher number of veins may occur as individual variation); CuA<sub>2</sub>, if present, mostly disconnected from CuA base (i.e., CuA<sub>1+2</sub> absent or basally broadly interrupted) and sometimes also from MP<sub>3+4</sub> (CuA<sub>1</sub> absent). Tarsi pseudotetramerous and padded beneath; tarsomere 5 in males of some taxa strongly broadened distally; claws free, divaricate to moderately divergent, in some taxa very long and sickle-shaped; empodium indistinct.

Ovipositor usually with styli apical, but at least in *Apatophysis* (with subterranean larval development) the apex sclerotized and styli small and lateral (Fig. 2.4.3 G). Ovipositor very short in *Dorcasmus* (developing in living branches), indicating oviposition on bark surface. Aedeagus in some taxa extremely long and slender (Fig. 2.4.18 C).

**Morphology, Larvae** (Fig. 2.4.20 E, F). Subcylindrical. Head (Fig. 2.4.23 D–K) deeply retracted, cranium very slightly elongate to slightly transverse, hind margin dorsally deeply notched to truncate; coloration variable, at least posterior half pale. Epicranial halves broadly fused. Frontal arms enter separately duplicated cranial region, which lacks a deep intracranial carina; transfrontal line absent. Frontal and postcondylar carinae absent; epistomal region in later instars often projecting above clypeus (Fig. 2.4.23 D, F, J; the projection does not consist of two more or less separate lateral lobes as in many Prioninae); medial pair of epistomal setae positioned dorsally behind the epistomal projection, or considerably distant from clypeal border if that projection is absent (arrowheads in

Fig. 2.4.23 F, H–K). Clypeus trapezoidal, filling space between mandibular articulations. Labrum more or less transverse. Stemmata from six pairs to absent (in some subterranean forms); main three pairs separate (*Dorcasmus*, Fig. 2.4.23 H; *Criocerinus* Fairmaire) or mostly at various stages of fusion. Antennae short, always trimerous; sensorium conical. Mandible short, robust; apical part short and broad but with distinct apex and three inner keels; pseudomola small (*Dorcasmus*, Fig. 2.4.23 H, I) or vestigial and invisible dorsally. Maxillolabial complex (Fig. 2.4.23 E, G) with large movable cardo (but smaller than in most Cerambycinae) and divided maxillary articulating area (small anterior part usually not visible in specimens with retracted mouthparts); mala cylindrical but not arising exclusively from palpiger; latter with distinct laterodorsal sensory process (Fig. 2.4.23 F); palps trimerous; ligula broad, bearing numerous setae. Hypostomal lines converging posteriorly, subparallel in *Dorcasmus*; hypostoma and gula moderately long, usually glabrous. Metatentorial arms in *Apatophysis* slightly oblique, tentorial bridge narrow and somewhat countersunk in cranial cavity (Fig. 2.4.26 N) and pits rather indistinct (Fig. 2.4.23 E); arms more oblique and pits distinct in *Dorcasmus* (Fig. 2.4.23 G).

Pronotum delimited by distinct lateral furrows that do not interrupt the anterior pigmentation; pronotal base without asperities. Proepipleuron anteriorly broadening and incompletely delimited ventrally. Propleuron moderately large, episternum usually poorly separated from epipleuron, its cuticle not distinctly thickened. Coxosternal halves approximate; mediopresternum distinct. Postnotum present, similar to that of Cerambycinae (Fig. 2.4.29 A). Mesothoracic spiracle not protruding into prothorax. Pterothoracic pleuron entire and broadly separating coxa from epipleuron. Legs short (at most slightly longer than maxillary palps), but with all segments distinct; pretarsus without setae.

Abdomen with dorsal and ventral ampullae on segments I–VII, both with one pair of lateral impressions and devoid of asperities (Fig. 2.4.20 E, F). Epipleuron protuberant on segments VII–IX; segments I–VI without epipleural discs or they are poorly developed and with irregular sculpture; epipleural tubercles present but less distinct on anterior segments, particularly I. Segment IX small, without caudal armature. Segment X short but separate, subterminal, without sclerotizations. Anus triradiate. Midgut lacking crypts with symbionts.

First instars (available of Madagascan *Artelida* J. Thomson, *Tsivoka*, and *Logisticus*) with short legs, without cephalic egg bursters, and with distinct somewhat flattened lateral egg-bursting spines on first two abdominal segments.

[Description based on Palaearctic *Apatophysis* (Mamaev & Danilevsky 1975; misidentified as "*Prionus komarovi*"; Danilevsky 1979 b; Svacha & Danilevsky 1988), Afrotropical *Dorcasmus* (Duffy 1957,

1980; Svacha & Danilevsky 1987), and undescribed larvae of South African *Otteissa* and numerous Madagascan genera. An unidentified Afrotropical larva of Apatophyseini collected in Malawi (Zomba) is in the collection of the Natural History Museum in London and may belong to *Afroartelida quentini* described from Malawi by Vives (2011).]

**Phylogeny and Taxonomy.** The group was elevated to subfamily rank by Danilevsky (1979 b, as Apatophysinae Lacordaire, 1869; the correct spelling Apatophyseinae was used by most later authors) based on correct identification of the larvae of *Apatophysis*. The larva of *A. caspica* Semenov had been previously erroneously described as an aberrant prionine and tentatively associated with *Microarthron komaroffi* (Dohrn) (as *Prionus komarovi*) (Mamaev & Danilevsky 1975; Danilevsky 1976; true larvae of *M. komaroffi* were later described by Danilevsky 1984) because dorcasomines were then almost universally included in Lepturinae whereas their larval morphology is very different from lepturines. The subfamily should have been renamed to Dorcasominae Lacordaire, 1868 (having both volume and year priority; for nomenclatoric details see Bousquet *et al.* 2009) after the inclusion of *Dorcasomus* by Svacha (in Svacha & Danilevsky 1987). The renaming was formally published by Özdikmen (2008). Based on Danilevsky (in Löbl & Smetana 2010: 48), who refused to place *Apatophysis* in Dorcasominae because of some larval and adult differences between *Apatophysis* and *Dorcasomus* and retained the subfamily name Apatophyseinae, Bouchard *et al.* (2011) formally accepted separate subfamilies Apatophyseinae and Dorcasominae, which is not followed here. The only adult difference listed by Danilevsky (1979 b), the divided mesoscutum (without a stridulatory plate) in *Dorcasomus* and the undivided stridulatory plate in *Apatophysis*, is variable and connected by a complete chain of transitional situations in various Apatophyseini (Fig. 2.4.14 D, E), and the only other genus (*Formosotoxotus* Hayashi) included in the Apatophyseinae in Löbl & Smetana (2010) has no stridulatory file and mesoscutum divided by a median endocarina just like *Dorcasomus* (Ohbayashi 2007).

Lacordaire (1869) placed in his Apatophysides also the South African *Pachyticon* J. Thomson and Oriental *Trypogeus* Lacordaire, but Danilevsky (1979 b) included only *Apatophysis* in the new subfamily (defined predominantly on larvae) because immature stages of the other two genera are unknown. Svacha (in Svacha & Danilevsky 1987) added to Apatophyseinae the Afrotropical genus *Dorcasomus*, the larvae of which were previously erroneously characterized as “undoubtedly lepturine” by Duffy (1957, 1980), and suggested that the rich fauna of “Lepturinae” in Madagascar and some adjacent islands may in fact belong to the same subfamily. Many dorcasomine and no leptu-

rine larvae were later collected in Madagascar (Svacha *et al.* 1997: 364) and some were reared to adults of typical Madagascan formerly “lepturine” genera (*Mastododera*, *Toxitiades*, *Logisticus*, *Artelida*, *Eccrisis* Pascoe and several others) plus some less typical (*Zulphis*, *Zulphisoma*, *Criocerinus*). A living dorcasomine larva received from South Africa was reared to an adult of *Otteissa sericea*.

Villiers *et al.* (2011) revised the rich dorcasomine fauna of Madagascar and the Comores. *Trigonarthron* Boppe (Fig. 2.4.3 M) and *Varieras* Villiers from Madagascar were not included but might be also dorcasomine. Villiers (1984) created for them a separate tribe Trigonarthrini of Cerambycinae (not listed in Bousquet *et al.* 2009 and Bouchard *et al.* 2011) considered related to Protaxini Gahan (here regarded as a synonym of Apatophyseini, see below). *Trigonarthron* was placed in Apatophyseinae without comment by Jeniš (2001), and is currently being placed, together with the Oriental *Protaxis* (Fig. 2.4.3 I, J), in Protaxini in some online databases.

Continental Afrotropical dorcasomine genera include *Dorcasomus* Audinet-Serville (Dorcasomini; eight species in southern, central and eastern Africa), *Afroartelida* Vives & Adlbauer (*A. tenuisenni* Vives & Adlbauer from Zimbabwe, Namibia, and RSA, *A. quentini* Vives from Malawi, and an undescribed species from Somalia that is the northernmost known occurrence of the Apatophyseini in sub-Saharan Africa; K. Adlbauer, personal communication), and several monotypic genera: *Afroccrisis perissinottoi* Vives (RSA), *Apterotoxitiades vivesi* Adlbauer (RSA; Fig. 2.4.3 K), *Capetoxotus rugosus* Tippmann (RSA; Fig. 2.4.3 C), *Kudekanye suidafrika* Rice (RSA), *Otteissa sericea* Pascoe (Namibia, RSA), *Pachyticon brunneum* J. Thomson (RSA; unknown to us), and *Urasomus elongatissimus* Adlbauer (RSA; see Adlbauer 2012, the presumed female is strongly brachelytrous and wingless; male of this species was originally misidentified as *Uracanthus inermis* Aurivillius in Adlbauer 2000 and therefore presumed to have been introduced from Australia). Two very poorly known taxa probably also belong here, but types have not been studied (Vives 2009 a): *Micrometopus punctipennis* Quedenfeldt (Angola; unknown to us) and *Aristogitus* J. Thomson with *A. cylindricus* (J. Thomson) (RSA; according to K. Adlbauer possibly a male and thus a senior synonym of *Capetoxotus*).

Palearctic and Oriental taxa. Three Oriental genera were described (*Borneophysis* Vives & Heffern, Sabah, Borneo) or elevated from subgenera of *Apatophysis* Chevrolat (*Paratophysis* Gressitt & Rondon and *Epitophysis* Gressitt & Rondon, both Laos) by Vives & Heffern (2006); note that their Fig. 3 and 4 depicting holotypes are reversed, Fig. 3 is *Epitophysis substriata* (Gressitt & Rondon), Fig. 4 is *Paratophysis sericea* (Gressitt & Rondon). Danilevsky (2011) raised also *Protapatophysis* Semenov & Shchegoleva-Barovskaya (NE Afghanistan, N Pakistan, N India) to a separate genus differing from



*Apatophysis* among other by the fully winged females with elytra completely covering abdomen. *Apatophysis* in the present narrow sense occurs predominantly in southern Palaearctic (including North Africa), reaching the continental Oriental Region; species of the former USSR, Mongolia, China and Turkey were revised by Danilevsky (2008). The Oriental *Formosotoxotus* Hayashi was placed in Apatophyseinae by Ohbayashi (2007), and Vives (2007) returned there also *Trypogeus*. *Protaxis* is another Oriental member, obviously closely related if not synonymous to *Epitophysis* (compare Fig. 2.4.3 H–J). Of all those genera, only larvae of three species of *Apatophysis* are known.

Dorcasominae are related to Cerambycinae (see Phylogeny and Taxonomy of the family Cerambycidae) but do not have any obvious apomorphies. Larvae differ only by the lack of the cerambycine apomorphies (constricted clypeus and round “gouge-like” apical part of mandible). Dorcasomine larvae can be easily distinguished from all subfamilies other than Cerambycinae by the combination of a very narrow tentorial bridge and a distinct postnotum. Even definition of the subfamily is problematic on adult morphology; there are virtually no characters that could distinguish it from the Cerambycinae, and some genera with unknown larvae may still be misclassified. Adult differences from all or at least typical Lepturinae with which most dorcasomines were long associated include antennal sockets usually facing laterally (but with distinct anterior emarginations in some specialized floricolous taxa such as *Sagridola*, *Eccrisis* or *Anthribola*), pretentorial pits lateral or at most laterodorsal and less distinct, or mandible without a molar plate (cf. Fig. 2.4.12 K, L). Wings in macropterous Lepturinae rarely have only four veins in the medial wing field and never have three, and the wedge cell, present in some Lepturinae, is invariably absent in dorcasomines. Pre- and metatentorium (studied in very few species) firmly connected even in cleared specimens of Lepturinae, disconnected in similarly treated Dorcasominae.

Tribal classification has received little attention. The genus *Dorcasomus* differs by several larval characters (relatively distinct metatentorial pits, presence of small mandibular pseudomola) from all other known larvae, and the subfamily may be preliminarily divided into monogeneric Dorcasomini (Central, East and South Africa; revised by Quentin & Villiers 1970) and Apatophyseini (Oriental, South Palaearctic, Afrotropical incl. Madagascan). The Madagascan, continental Afrotropical, and Palaearctic-Oriental faunas currently do not share any generic names (except for Jeniš 2001 using *Apatophysis* for some Madagascan species belonging to *Boppeus* Villiers without further explanation), but a comprehensive revision might reveal some generic overlaps. Vives in Villiers *et al.* (2011: 18) suggests that a separate tribe should be created for *Trypo-*

*geus*, but it has not been formally proposed and we retain the genus in Apatophyseini. Protaxini (an incorrect spelling of Protaxeini considered as being in prevailing usage by Bousquet *et al.* 2009) is here regarded as a younger synonym of Apatophyseini because of the similarity of *Protaxis* and *Epitophysis*. Status and subfamily placement of Trigonarthrini require clarification.

Some taxa were erroneously associated with dorcasomines. Although Audinet-Serville (1834, 1835) described *Dorcasomus* in Cerambyciens while placing the North American genus *Desmocerus* in Lepturiens, Thomson (1860–1861) and some later authors regarded the two genera as related (see Quentin & Villiers 1969; Linsley & Chemsak 1972); the larvae of *Desmocerus* are typically lepturine (Craighead 1923; Svacha & Danilevsky 1989: 15). Gressitt (1947, 1951) downgraded *Apatophysis* to a subgenus of the North American *Centrodera* LeConte, but it was reinstated later (Gressitt *et al.* 1970); the two genera are unrelated and *Centrodera* is a true lepturine. The Oriental *Peithona* Gahan was considered as closely related to *Apatophysis* by Gahan (1906), but it is retained in Lepturinae here (discussed under that subfamily). Some authors (e.g., Özdikmen 2008) incorrectly include the lepturine genera *Apioccephalus*, *Capnolymma* and *Acapnolymma* Gressitt & Rondon (see Lepturinae). The continental Afrotropical genus *Lycosomus* Aurivillius, occasionally listed as a dorcasomine in current online databases, was synonymized with *Kuilua* Jacoby (Megalopodidae) by Kuntzen (1925).

## Cerambycinae Latreille, 1802

**Distribution.** Worldwide and the second largest subfamily with approximately 1700 genera and 11,000 species, and the most speciose subfamily in Australia, southern South America, and North America (e.g., Forchhammer & Wang 1987).

**Biology and Ecology.** The distinctive cerambycine larval mouthparts (Fig. 2.4.21 J, 2.4.25 E, F) are well suited for work on hard compact material, and larvae do not occur in soft rotten wood or in soil; species feeding in soft herbs are few. The round larval mandibles are specialized for removing small pieces of host material, often leaving characteristic patterns on gallery walls, but are not suitable for producing long fibers often used by larvae of other subfamilies, particularly in constructing pupal chambers (exceptions are uncommon, e.g., larvae of *Axinopalpis* Dejean can produce such fibers). Although many cerambycine larvae are partly subcortical, the larval morphology (particularly the deeply retracted head with at most slightly internalized tentorial bridge) does not allow evolution of extremely depressed “interstitial” body forms known in some Lepturinae. As in

the Lamiinae, larvae developing in thin branches and twigs (where they generally maintain a long hollow gallery enabling quick locomotion) typically are long and slender, often with expanded “intersegmental” zones or pseudosegmentation (Fig. 2.4.20 G). Adults are extremely diverse, from dark nocturnal forms to brightly colored mimetic diurnal species. Floricolous species are common. Wing reduction is rare and mostly occurs in both sexes, seldom restricted to males (*Thaumasus*, Torneutini). Brachelytrous forms more or less resembling hymenopterans (and sometimes misclassified as Necydalinae) have evolved in several lineages.

**Morphology, Adults** (Fig. 2.4.3 N–S, 2.4.4, 2.4.5 A–Q). Small to large (about 2.5–90 mm), habitus variable, but body rarely broad and short, usually elongate.

Head prognathous to subvertical, seldom distinctly rostrate (Fig. 2.4.5 B); may be gradually narrowing to abruptly constricted behind eyes but seldom with prominent “temples” followed by a constricted “neck” (e.g., *Erlandia* Aurivillius, Fig. 2.4.4 J, or the ant-mimicking tribe Pseudoceraphalini with inflated and abruptly constricted head). Median frontal groove and associated endocarina often present but seldom continuing posteriorly and approaching hind cranial margin except for some southern taxa; frontoclypeal border (if distinct) often with two deep paramedian impressions (Fig. 2.4.11 H; not to be confused with pretentorial pits). Modified dorsal mandibular articulation followed by a more or less deep excavation with a tongue-shaped process (Fig. 2.4.12 I) or a brush of setae occurs in some southern genera (e.g., *Stenoderus*, *Syllitus* Pascoe, *Tropocalymma* J. Thomson); the structure is connected with a large intracranial pocket (gland reservoir?) placed behind the lateral part of mandible (*Stenoderus* dissected). Postclypeus of variable shape, elongate-triangular in some rostrate heads, anteclypeus usually short and flat; labrum free but of limited mobility, often transverse and straight or emarginate anteriorly. Position and orientation of antennal sockets variable (Fig. 2.4.11 G, H, 2.4.12 C), but rarely close to mandibular condyles, often far from them and both structures may be connected by a pair of longitudinal elevations or ridges; pretentorial pits usually lateral (remain on lateral side of those elevations) and occasionally indistinct, rarely distinctly frontal (Fig. 2.4.12 C). Eyes variable, seldom divided, may approach dorsally and seldom also ventrally, occasionally slightly protruding between antennal sockets and mandibular articulations; a trilobate eye present in Australian *Tricheops* Newman (Fig. 2.4.10 H). Antennae variable, usually 11-segmented, rarely with more than 12 antennomeres (males of *Pleiarthrocerus* Bruch). Mandibles seldom distinctly enlarged (e.g., large males of *Trachyderes mandibularis*, Fig. 2.4.4 A, *Gnathopraxitheia sarryi*

*Seabra* & Tavakilian, *Parandrocephalus* Heller, and a few Cerambycini), without a distinct molar plate, incisor edge with pubescent fringe very distinct to absent, apex usually simple, rarely broad and scalpriform. Maxillae and labium variable, lacinia usually well-developed, intermaxillary process moderately long to absent, ligula variable, but seldom reduced and sclerotized, terminal segments of both palps usually with at least a moderately large sensory area and thus more or less truncate, in extreme cases broadly securiform. Tentorial bridge broad to narrow, pre- and metatentorium firmly connected (*Oplatocera* White or some forms from Southern Hemisphere) to disconnected. Cervical sclerites present to absent.

Pronotum sometimes with lateral spine, mostly without distinct lateral carina or it is incomplete and running from posterior angles toward lateral extremities of procoxal sockets, exceptionally a distinct complete carina occurs in flattened forms with shield-like pronotum (e.g., Neotropical trachyderine genus *Allocerus* Lacordaire, Fig. 2.4.4 D). Notosternal suture rarely complete, usually indistinct or incomplete anteriorly, or absent. Prosternum may be very long before coxae, prosternal process from very broad to absent, procoxal cavities variable (from transverse to round with closed lateral angles), at least narrowly closed internally (very rarely bridge rudimentary), open or closed posteriorly. Mesoscutum with median endocarina complete to absent (rudiments usually remain on anterior vertical phragma and apparently may return to mesoscutal region when stridulatory file is lost); stridulatory file, if present, usually undivided, seldom divided (more often in southern taxa), usually symmetrical, rarely asymmetrical (a few Australasian genera, Fig. 2.4.14 F). Mesocoxal cavities open or closed laterally. Metendosternite usually with laminae. Wing (Fig. 2.4.17 A–D) with RP variable, particularly in northern taxa usually short basally and not or hardly surpassing crossvein r<sub>4</sub>, latter crossvein with spur distinct to absent; wedge cell invariably absent, medial field usually with four or three regular free veins, seldom five, CuA<sub>2</sub>, if present, usually remains connected with MP<sub>3+4</sub> (CuA<sub>1</sub> present) but mostly disconnected from CuA stem (CuA<sub>1+2</sub> absent or distinctly interrupted basally), and wing venation may be strongly reduced in some small or stenelytrous taxa; the most complete venations are retained in certain southern groups (Fig. 2.4.17 A). Procoxae of variable shape, but seldom strongly projecting below prosternal process. Tarsi mostly pseudotetramerous and padded beneath, reduction of all pads and lobes of tarsomere 3 occurs in some strongly modified taxa (particularly *Thaumasus*). Empodium usually indistinct or small (then bearing at most two setae).

Ovipositor mostly elongate and poorly sclerotized with styli apical, very short ovipositor of some groups such as Trachyderini and relatives (Fragoso

*et al.* 1987) or Obriini *sensu lato* (Saito 1992) is often combined with female ventral abdominal combs or brushes.

**Morphology, Larvae** (Fig. 2.4.20 G–I). Subcylindrical to moderately depressed. Head deeply retracted, pale colored posteriorly (rarely with dark spots on posterior angles), cranium transverse to subquadrate, posterior margin shallowly emarginate to straight, epicranial halves completely fused dorsally, frontal arms (if distinct) enter separately dorsomedian duplicate cranial region, latter without a deep intracranial carina, transfrontal line absent. Epistoma rarely slightly projecting over clypeus (e.g., *Hoplocerambyx* J. Thomson of Cerambycini), frontal and postcondylar carinae absent or entirely rudimentary; medial pair of epistomal setae far from basal clypeal margin and appears to be frontal (arrowheads in Fig. 2.4.25 E, I) Clypeus abruptly constricted and thus narrow and not filling space between mandibular articulation (but slender basal clypeal extensions reaching those articulations are mostly distinct, Fig. 2.4.21 J, 2.4.25 E, I; seldom sclerotized and fused with epistomal margin); labrum small. Stemmata from six pairs to absent. Antennae short to moderately long, mostly trimerous, rarely antennomere 3 reduced and knob-shaped (some *Phymatodes* Mulsant of Callidiini) or 1 and 2 fused (some Molorchini or *Nathrius*); sensorium conical (flat in *Icosium*). Mandibles strongly apomorphic; apex, dorsal angle and inner keels lost or entirely rudimentary, apical part round, excavated from inner side, “gouge-like” with sharp edge (Fig. 2.4.21 J, 2.4.25 E, F). Cardo free, movable, large to extremely large (Fig. 2.4.24 B, 2.4.25 J) except in Opsimini (Fig. 2.4.24 F) having very unusual apomorphic maxillolabial complex; maxillary articulating area may be divided, mala broadly triangular to cylindrical but never very slender and arising exclusively from palpiger, latter mostly with distinct laterodorsal sensory process, first palpal segment often with a similar process, palps tri- or rarely dimerous; ligula from broad and setose to very small or nearly absent and labial palps subcontiguous. Hypostomal lines usually slightly converging posteriorly (but sometimes only short initial sections remain), hypostomal plates shorter than in Prioninae yet much longer than the relatively small gula, which may rarely be partly covered posteriorly by a membranous postgular lobe (the Oemini-Methiini complex) or partly covered anteriorly by expanded slightly sclerotized submentum (*Teratoclytus* Zaitzev of Clytini). Metatentorial arms invaginated virtually on posterior hypostomal margin (and tentorial pits therefore at most very indistinct), their broader basal parts more or less in same plane with hypostoma, bridge firm but narrow (narrower than length of gula and much narrower than in any Prioninae or Parandrinae) and often

slightly countersunk, visible in ventral view, making occipital foramen “divided” (Fig. 2.4.24 B); absence of tentorial bridge was erroneously claimed or figured for *Neoclosterus boppei* Quentin & Villiers (Duffy 1980) and *Phymatodes albicinctus* Bates (Kojima 1959 and some later publications).

Pronotum delimited by distinct lateral furrows that always interrupt anterior protergal pigmentation if distinct (Fig. 2.4.21 J), pronotal base may be (micro)asperate or variously characteristically sculptured. Proepipleuron anteriorly incompletely ventrally delimited except for Cerambycini where it is distinct and tapering anteriorly. Proepisternum not remarkably thickened, epimeron more or less fused with posterior epipleural angle and, in derived forms, often more or less also with coxosternal and sternellar regions to form a long transverse fold across entire hind margin of prothoracic venter (Fig. 2.4.29 B). Coxosternal halves, if defined, approaching medially, mediopresternum distinct to non-defined. Postnotum present (Fig. 2.4.29 B), rarely absent (Opsimini and the “true” Oemini-Methiini complex, which excludes Xystrocerini and some other misclassified forms), meso- and metathoracic pleuron entire and broadly separating coxae from epipleuron, or fused with coxae. Legs short to absent, pretarsus without setae.

Abdomen with dorsal and ventral ampullae usually on segments I–VII (at least in some Hexoplonini on I–VI: Casari & Steffanello 2010; Fuhrmann *et al.* 2012), both usually with one pair of lateral impressions, but dividing pattern may be modified or simplified. Epipleuron protuberant on segments VII–IX or rarely only VIII and IX, a few anterior abdominal segments may bear epipleural discs (Fig. 2.4.30 E, F) which are at most finely indistinctly radially striate. Segment IX short to moderate, rarely long, tergum usually unarmed, a few species bear urogomphi (*Vandykea* Linsley) or other type of sclerotized armature; segment X separate, short and subterminal, rarely longer, posteroventral and bearing sclerotizations on dorsal side (e.g., some Uracanthini); anus triradiate. Foregut may rarely bear a proventriculus, anterior midgut lacking crypts with symbionts, cryptonephridial part of hindgut usually long (Fig. 2.4.19 J, K).

First instars with at most short legs, without cephalic and also pterothoracic egg bursters, only lateral abdominal egg bursters may be present.

**Phylogeny and Taxonomy.** This is the second largest subfamily with thousands of described species, extremely diversified adults and with an unsettled tribal classification. Whereas larvae are easily recognized by their apomorphic rounded mandibles and abruptly constricted clypeus (Fig. 2.4.21 J, 2.4.25 E, I), no adult apomorphies have been identified, and even definition of the subfamily on adult characters is difficult. The usual lack

of a distinct pronotal margin will distinguish Cerambycinae from Parandrinae and most Prioninae, the absence of a wedge cell will separate it from almost all Prioninae and some Lepturinae and Spondylidinae, and in the Northern Hemisphere, the prevailing presence of four or less free veins in the medial region and usually lacking or rudimentary  $CuA_{1+2}$  will distinguish cerambycines from most Lepturinae and Spondylidinae (the rich cerambycine venations occur in certain southern regions where the Lepturinae and Spondylidinae almost do not occur). The usual absence of median mesoscutal endocarina (and thus an undivided stridulatory plate, if present) will be helpful for distinguishing cerambycines from many Spondylidinae and Lepturinae, but exceptions exist on both sides and the character again becomes unusable in the Southern Hemisphere where many Cerambycinae possess the endocarina. The lack of protuberant temples in most species and absence of mandibular molar plate will separate Cerambycinae from most Nedydalinae and Lepturinae. Lamiinae have many adult apomorphies separating them from other groups including cerambycines. There are no adult differences between Cerambycinae and Dorcasominae, apart from the lepturine-like habitus of many dorcasomines.

Some Cerambycinae have been misclassified in Spondylidinae, Nedydalinae and Lepturinae (see under those subfamilies). The almost certainly cerambycine New Caledonian genus *Acideres* Guérin-Méneville has been often classified in Prioninae (Vives *et al.* 2008; see the wing venation depicted in that publication); for comments on *Cycloprionus* see Prioninae. Perhaps the only larval misclassification was placement of the aberrant and legless larva of *Opsimus* Mannerheim (Cerambycinae: Opsimini; Fig. 2.4.24 E–G) in Spondylidinae (= Aseminae) by Craighead (1923), although regarded as a transitional form to Cerambycinae. *Opsimus* has both principal cerambycine larval apomorphies (round mandible and constricted clypeus) and also shares with Cerambycinae and Dorcasominae the apomorphic posterior shift of the medial pair of epistomal setae, but differs from all known cerambycine and dorcasomine larvae by an unusual maxillolabial complex with an expanded connecting region, reduced laterally displaced cardo and a peculiar flat, lanceolate mala fringed with long setae; contrary to Craighead (1923), the mala is not borne on palpiger as in Spondylidinae (*cf.* Fig. 2.4.24 F, G, I). However, the maxillolabial complex is entirely dissimilar to anything known in other subfamilies (including Spondylidinae) and is undoubtedly autapomorphic. Hypostomal plates are much longer than gula and metatentorial pits are indistinct as in all Cerambycinae (Fig. 2.4.24 F; *cf.* Fig. 2.4.24 I). Legless larvae are known only in Cerambycinae and Lamiinae, legs are always distinct in Spondylidinae. Postnotum is absent in *Opsimus*, but also in some other Cerambycinae (see larval

morphology). Wing venation in adult *Opsimus* (Fig. 2.4.17 C) is more reduced than in any Spondylidinae. The tribe Opsimini, remarkable by unusually long antennal pedicel in adults (about 2.5–3 times as long as broad; Fig. 2.4.5 P), contains the North American *Opsimus* Mannerheim (one species) and *Dicentrus* LeConte (two species) and the Oriental *Japonopsimus* Matsushita with three species, including the generically misplaced *Hypoeschrus simplex* Gressitt & Rondon (Gressitt *et al.* 1970; Hua *et al.* 2009; Löbl & Smetana 2010, as *Noserius* Pascoe; photographs in the former two books suggest a species of *Japonopsimus*). *Japonopsimus* has been also misplaced in Spondylidinae: Saphanini (e.g., Gressitt 1951; Nakamura *et al.* 1992; Chou 2004).

### Spondylidinae Audinet-Serville, 1832

**Distribution.** The subfamily as accepted here (see Table 2.4.1) is distributed mainly in the Northern Hemisphere, predominantly Holarctic. Consisting of approximately 100 species, two-thirds of them in Asemini. Of the “saphanine branch”, Anisarthrini are western Palaearctic (*Anisarthron*, *Schurmannia*, *Alocerus moesiacus* Fivaldsky) and Afro-tropical (*Pectoctenus* and *Alocerus bicolor* Distant, the former also on Madagascar), Saphanini are western Palaearctic (*Saphanus* and *Drymochares*) and eastern Nearctic (*Michthisoma*), and Atimiini are predominantly western Nearctic and eastern Palaearctic/Oriental, except for *Oxypleurus*, which occurs in the western Palaearctic (Black Sea, Mediterranean region, Canary Islands, Madeira) and was probably introduced to the Cape region of South Africa (Duffy 1957). The “spondylidine branch” (Spondylidini + Asemini) is generally Holarctic with Central American and Oriental extensions. *Arhopalus fesus* (Mulsant) was introduced to Namibia (Adlbauer 2001), three species of *Arhopalus* to the Australasian Region (Wang & Leschen 2003), and two to Argentina (López *et al.* 2008).

**Biology and Ecology.** Saphanini (excluding *Oxypleurus*, here placed in Atimiini) and Anisarthrini are dead wood feeders known almost exclusively from angiosperms (only the polyphagous *Saphanus* has been recorded from conifers), whereas the remaining three tribes feed in conifers. Larvae of Anisarthrini (*Pectoctenus*, *Alocerus*, *Schurmannia* and *Anisarthron*) feed in dead wood of living trees (small hollows, wound scars, moist bases of dead branches) without a subcortical phase. *Saphanus* and *Drymochares* develop in dead or dying wood of underground parts of trees and shrubs, but at least in *Saphanus* both oviposition and emergence occur at ground level and young larvae may feed subcortically for some time. *Michthisoma* was found in “dead sapwood of hickory stumps” (Craighead 1923). Of Atimiini, *Oxypleurus* feeds in dead pine wood above ground with an occasional, but short,

Table 2.4.1 Genera and number of species of Spondylidinae (introduced taxa are not considered).

Tribe	Genus	Old World	Shared	New World
Anisarthrini	<i>Alocerus</i> Mulsant	2	0	0
	<i>Schurmannia</i> Sama	1	0	0
	<i>Pectoctenus</i> Fairmaire	3(2?)	0	0
	<i>Anisarthron</i> Dejean	2	0	0
Saphanini	<i>Saphanus</i> Audinet-Serville	2	0	0
	<i>Drymochares</i> Mulsant	3	0	0
	<i>Michthisoma</i> LeConte	0	0	1
Atimiini	<i>Oxypleurus</i> Mulsant	1(2?)	0	0
	<i>Proatimia</i> Gressitt	1	0	0
	<i>Paratimia</i> Haldeman	0	0	1
	<i>Atimia</i> Haldeman	6	0	7
Asemini	<i>Asemum</i> Eschscholtz	5	1	5
	<i>Megasemum</i> Kraatz	1	0	1
	<i>Arhopalus</i> Audinet-Serville	14	1	6
	<i>Cephalallus</i> Sharp	3	0	0
	<i>Tetropium</i> Kirby	13	0	13
	<i>Nothorhina</i> Redtenbacher	2	0	0
	<i>Spondylis</i> Fabricius	1	0	0
Spondylidini	<i>Neospondylis</i> Sama	0	0	2
	<i>Scaphinus</i> LeConte	0	0	1
Total		59–61	2	37

The North American species currently placed in *Megasemum* may be misclassified. *Pectoctenus bryanti* Lepesme may be a synonym of *Alocerus bicolor* (Distant) (pers. comm., K. Adlbauer). *Schurmannia* is sometimes considered synonymous with *Alocerus*, and *Cephalallus* placed as a subgenus of *Arhopalus*. The population of *Oxypleurus* from Canary Islands is accepted by some authors as a separate species *O. pinicola* Wollaston. *Saphanus* is sometimes treated as single species *S. piceus* (Laicharting) with subspecies, but this is in our opinion incorrect at least for the populations from southern Balkans.

initial subcortical phase. *Pinus yunnanensis* is the host of *Proatimia pinivora* Gressitt (Gressitt 1951). *Paratimia* develops in pinecones, and *Atimia* feeds on Cupressaceae, where larvae can be found under bark for much or all of their development. Asemini and Spondylidini generally do not oviposit on barkless wood, and at least a short initial larval period is usually spent under bark; larval feeding (but often not pupation) of *Tetropium* is completely subcortical, sometimes in freshly dead or live trees. Species of *Nothorhina* (feeding on *Pinus*) and *Tetropium aquilonium* (feeding on *Picea*; Heliövaara *et al.* 2004) develop exclusively within the bark of large standing living trees that, at least in *Nothorhina*, often survive for decades and host many generations. Larvae of many Asemini may penetrate into underground parts of the host tree; Spondylidini (unknown for *Scaphinus*) are specialized root feeders, working from distal roots toward the tree base so that mature larvae may reach it and adults may emerge from stem or stump bases above ground. Female *Spondylis* dig into the soil and oviposit directly on the root bark (Cherepanov 1979). All taxa pupate in the food material. Known Atimiini (including *Oxypleurus*: Sama 2002) overwinter mostly as adults either inside or outside of their pupal chambers, whereas other taxa overwinter as larvae. Adults are predominantly crepuscular and nocturnal, usually somber-colored,

non-feeding and short-lived. The Saphanini tend toward flightlessness; *Saphanus* is macropterous but at least females of some, if not all, populations do not fly and beetles are frequently collected in pitfall traps; *Drymochares* and *Michthisoma* are micropterous.

**Morphology, Adults** (Fig. 2.4.5 R–T, 2.4.6 A–J). Moderately large (5–35 mm), subcylindrical (Spondylidini) to flat.

Head may be constricted behind eyes, but without prominent temples; anteriorly short, never rostrate; mouthparts moderately to strongly oblique (Fig. 2.4.10 B). Median frontal endocarina and associated groove present to reduced or absent (mainly Spondylidini, *Tetropium*, *Nothorhina*, and *Michthisoma*), disappearing on vertex. Frontoclypeal suture complete or obliterated medially, postclypeus strongly transverse to shortly triangular, pretentorial pits mostly distinct, sublateral to dorsal/frontal, anteclypeus small, reduced in Spondylidini. Labrum separate but often short and transverse. Antennal sockets broadly separate, relatively distant from mandibular condyles and facing laterally in the saphanine branch (Anisarthrini, Saphanini and Atimiini), usually closer to condyles and facing slightly anteriorly in Asemini and Spondylidini. Eyes very large (*Pectoctenus*; Fig. 2.4.6 A) to very small (*Michthisoma*; Fig. 2.4.6 F); more or less

emarginate, in some cases strongly constricted or divided into two parts (*Tetropium*); may reach far dorsally and/or ventrally but not closely approximated; in the saphanine branch eyes in some species slightly protruding between mandibular articulation and antennal socket. Antennae at most slightly longer than body, very short in Spondylidini (Fig. 2.4.5 T); simple to very strongly serrate or almost pectinate (*Pectoctenus*; Fig. 2.4.6 A); usually 11-segmented but terminal flagellomere may be incompletely subdivided in some (particularly male) Anisarthrini and *Saphanus*, and is completely divided in both sexes of *Pectoctenus scalabrii* Fairmaire (Fig. 2.4.6 A). Mandibles usually short, but longer (Fig. 2.4.5 T) or even sickle-shaped particularly in males of Spondylidini; molar region with very fine and short pubescence and occasionally partly desclerotized but without a molar plate; incisor edge without a fringe of long hairs; apex mostly simple, but a blunt supplementary ventral tooth present in *Nothorhina*. Maxillae and labium relatively small, but palps long in some cases; lacinia distinct; intermaxillary process very short or lacking; ligula variable (membranous or sclerotized); terminal segments of both palps narrowly spindle-shaped in Anisarthrini, slightly truncate to broad and securiform (strongly so in flightless *Drymochares* and *Michthisoma*) in remaining tribes. Tentorial bridge narrow; pre- and metatentorium connected (branches of the latter extremely thin and ligamentous in Anisarthrini; *Anisarthron* and *Pectoctenus* dissected). Cervical sclerites moderately sized to absent (always absent in the spondylidine branch).

Pronotum without lateral carina or at most oblique individually variable vestiges present at hind angles. Notosternal suture fine or obliterated anteriorly. Prosternal process present. Procoxal cavities of variable shape, closed internally, open or closed posteriorly; lateral procoxa and trochantin at least partly exposed. Procoxae moderately transverse to subglobular, at most slightly projecting below prosternal process. Mesoscutum with distinct median endocarina; stridulatory plate (if present) divided. Mesocoxal cavities open or narrowly closed laterally (Atimiini including *Oxypleurus* and *Proatimia*, *Michthisoma*). Metendosternite usually with laminae (reduced in *Michthisoma*). *Drymochares* and *Michthisoma* are micropterous; wing in macropterous taxa (Fig. 2.4.16 I, J) with radial cell closed proximally; RP proximally distinctly surpassing crossvein r<sub>4</sub>; spur of r<sub>4</sub> short to absent; wedge cell absent in the spondylidine branch, usually present and distinct to extremely narrow in the saphanine branch (absent in some specimens or possibly populations of *Saphanus*, may be extremely narrow to virtually lost also in some individuals of certain Anisarthrini and *Oxypleurus*); medial field usually with five free veins (venation of this region often strongly individually variable; see Saalas 1936), seldom regularly with four veins (*Neospondylis*, *Megasemum*); CuA<sub>2</sub> either connected with both

neighboring veins (CuA<sub>1+2</sub> and CuA<sub>1</sub> present), or CuA<sub>1+2</sub> more or less broadly interrupted basally. Tibial spurs 2-2-2 or reduced to 1-2-2 in *Anisarthron*, *Pectoctenus*, *Oxypleurus*, *Proatimia*, *Paratimia*, *Arhopalus*, *Cephalallus* and *Megasemum quadricostulatum* Kraatz but not *M. asperum* (LeConte); tarsi pseudotetramerous and padded beneath; claws divaricate; empodium small and bisetose to indistinct; legs modified in Spondylidini, short and stout with slightly compressed dentate tibiae, somewhat reduced tarsal pads and enlarged fourth tarsomere.

Ovipositor usually with styli apical, but coxites somewhat sclerotized and styli shifted laterally in Spondylidini and also slightly so in *Tetropium* (Saito 1990).

**Morphology, Larvae** (Fig. 2.4.20 J, K; unknown in *Proatimia* and *Scaphinus*). Body broadest and often moderately depressed at thorax; abdomen subcylindrical. Head (Fig. 2.4.21 H, I, 2.4.24 H, I) deeply retracted and pale except for anterior margin in Anisarthrini and Saphanini, moderately to weakly retracted and pigmentation usually more extensive (involving hypostoma and gula) in remaining taxa; cranium slightly to distinctly transverse, at most very shallowly and broadly emarginated posteriorly; epicranial halves completely fused dorsally; gena and anterior epicranial region often with dense setation. Frontal arms posteriorly separately entering duplicated dorsomedian cranial region which lacks a deep intracranial carina; anteriorly enter antennal sockets and usually reach anterior cranial margin; transfrontal line absent. Epistomal, frontal and postcondylar carinae absent. Medial pair of epistomal setae close to clypeal border, or both medial and middle pair slightly removed from it. Clypeus trapezoidal, not abruptly constricted. Labrum variable; long cordate labrum (Fig. 2.4.21 I) correlated with presence of large mandibular pseudomola in most genera of the spondylidine branch; labrum transverse and pseudomola reduced in *Nothorhina*, *Tetropium*, *Neospondylis* and the saphanine branch. Stemmata from five pairs to absent (at most two pairs of main stemmata present, no larvae known with three). Antennae usually short and trimerous, rarely moderately long but with antennomere 3 lost (*Nothorhina* of Asemini); sensorium conical. Mandibles short, with or without pseudomola; apex unidentate; inner face with three or two inner keels (occasionally indistinct). Maxillolabial complex with small free cardo and maxillary articulating area undivided; mala slender and finger-like and borne on palpiger; in the saphanine branch palpiger with small laterodorsal sensory process; maxillary palps trimerous; ligula well-developed, with variable pattern of setae and microtrichia. Hypostomal lines subparallel. Gula exposed, moderately sized to long. Hypostoma not much longer than gula, both regions may be fused almost without traces, the fused sclerite forming a more or less distinct transverse bulge posteriorly in Atimiini (including *Oxypleurus*). Metatentorium



very slender, more or less oblique (usually partly visible in ventral view, scarcely visible in Spondylidini and in some Asemini with a long gula); bridge very thin; pits from poorly defined and very close to hind margin to distinct.

Pronotum delimited by distinct lateral furrows that interrupt anterior protergal pigmentation (Fig. 2.4.21 H, I); base may bear fine asperities or microtrichia but never coarse sclerotized granules. Proepipleuron fused with lateropresternum and at most indistinctly separated from pleural region; episternum without thickened cuticle, sometimes not distinctly defined anteriorly. Coxosternal halves (if distinct) approach medially, mediopresternum fully separate to fused with lateropresternum. Postnotum absent. Mesothoracic spiracle not protruding into prothorax. Meso- and metathoracic pleuron entire and broadly separating coxae (the latter sometimes poorly defined) from epipleuron. Legs short but with full number of segments; trochanter small and occasionally poorly separate from femur; pretarsus slender, without setae.

Abdomen with dorsal and ventral ampullae on segments I–VII; dorsal ampullae usually with two pairs of lateral impressions (pattern may be considerably simplified; Fig. 2.4.29 I, J), one pair of impressions in *Pectoctenus*. Epipleuron protuberant on segments VII–IX (Fig. 2.4.20 K). Segments I–VI without distinct epipleural discs. Segment IX not enlarged, tergum almost always with urogomphi, sometimes with common prominent base and/or contiguous to almost fused; urogomphi virtually absent in some specimens of *Nothorhina punctata* (Fabricius) but distinct in *N. gardneri* Plavilstshikov. Segment X short, subterminal; anus triradiate. Anterior midgut bears mycetomes (Fig. 2.4.19 L).

First instars with short legs, but pretarsus in Spondylidini and Asemini extremely long and flagelliform (Fig. 2.4.31 L); cephalic egg bursters absent; urogomphi present or absent.

**Phylogeny and Taxonomy.** The subfamily as recognized here (Table 2.4.1) contains separate subfamilies Spondylidinae and Aseminae of some authors. It does not have obvious larval or adult apomorphies. The spinose pupal antennae or at least some basal antennomeres may be apomorphic (Fig. 2.4.32 G–J); spines occur in pupae of all five tribes (completely absent in *Megasemum* of Asemini: Cherepanov 1979; Nakamura 1981), but to a variable extent; antennal spines are rare in other subfamilies. Preliminary unpublished molecular data (Sýkorová 2008) tend to support monophyly of the subfamily and typically show it divided in two major branches that can be named spondylidinae (Asemini + Spondylidini, the latter often an ingroup of the former) and saphaninae (Anisarthrini + Saphanini + Atimiini). Within the branches, tribes are not well-defined (in particular the Anisarthrini and Asemini may be paraphyletic). The spondylidinae branch is defined by some apomorphies

(universal lack of cervical sclerites or wedge cell in the wing, long flagelliform pretarsus in first-instar larvae) whereas the saphaninae branch retained many plesiomorphies.

Tribal classification (see Table 2.4.1 and Bousquet *et al.* 2009). We accept five tribes: Anisarthrini, Saphanini, Atimiini, Asemini and Spondylidini. Saphanini include Michthisomatini (*Michthisoma*). Anisarthrini include the Afrotropical *Pectoctenus*, the larvae of which have simple lateral impressions on dorsal ampullae (a potential plesiomorphy compared with all other Spondylidinae), but otherwise are similar to *Alocerus* or *Schurmannia* and share the anisarthrine habits of development in dead parts of living trees (Duffy 1957) that may also be plesiomorphic. *Oxypleurus* is usually classified in Saphanini, but some larval characters (e.g., the raised hypostoma or dense recurved genal setae), feeding in *Pinus*, or overwintering of adults may indicate relations to Atimiini; the adult beetle is extremely similar to the Chinese *Proatimia pinivora* Gressitt (*cf.* Fig. 2.4.6 G, H–J) placed in Atimiini (Gressitt 1951), and the two genera should be possibly synonymized (personal communication by N. Ohbayashi and M. Lin). *Oxypleurus*, *Proatimia* and *Paratimia* share the derived 1–2 tibial spur pattern (otherwise occurring only in some Anisarthrini and Asemini). *Oxypleurus* is therefore moved to Atimiini, but placement and relationships of those two related genera need further study. Asemini have no apomorphies and may be paraphyletic in terms of Spondylidini. Moreover, *Spondylis* and *Neospondylis* show distinct differences in their larval morphology (Svacha & Danilevsky 1987: 170), wing venation (Saalas 1936) and other characters (Sama 2005). The monophyly of Spondylidini is therefore also questionable as the partly subterranean fossorial habits and associated adult modifications may have developed parallelly.

Some Spondylidinae have been often confused with Cerambycinae. Subfamily classification of the genera listed in Table 2.4.1 is supported by larval morphology except for *Proatimia* and *Scaphinus*, the larvae of which are unknown. The following genera occasionally associated in some way with spondylidinae taxa are known to have cerambycine larvae (partly unpublished observation by P. Svacha): *Blabinotus* Wollaston, *Daramus* Fairmaire, *Hybometopia*, *Lucasianus* Pic, *Opsimus* (see comments on Opsimini under Cerambycinae), *Smodicum* Haldeman, *Tetropiopsis* Chobaut, and *Zamium* Pascoe. The Chilean monospecific genus *Marileus* Germain, often classified in “Aseminae” by earlier authors (e.g., Blackwelder 1946; Cerda 1986), was later placed in the cerambycine tribe Phlyctaenodini (Martins 1998; Monné 2005 a) and Barriga & Cepeda (2007) synonymized *M. chilensis* Germain with the New Zealand phlyctaenodine *Ambeodontus tristis* (Fabricius). Several other mainly African and Madagascan genera directly or indirectly associated by some authors with the present subfamily may all be cerambycine, but

they remain without larval descriptions and adults have not been critically revised; until the discovery of larvae, wing venation should be helpful in placing them in the appropriate subfamily as the Saphanini and Anisarthrini (with which various habitually similar Cerambycinae have been most often associated) usually possess at least a small wedge cell and five veins in the medial wing field, characters unknown and uncommon, respectively, in the Cerambycinae.

The erroneous placement of the North American genus *Vandykea* in "Aseminae" by Svacha (in Svacha & Danilevsky 1987) was based on a misidentified larva, possibly of *Atimia helenae* Linsley (see erratum in Svacha & Danilevsky 1988).

### Necydalinae Latreille, 1825

**Distribution.** Mostly Northern Hemisphere: North America (reaching Mexico), Palaearctic and northern part of Oriental Regions (two species of *Necydalis* are known from Borneo and Java). There are only two genera. *Necydalis* contains close to 70 species occurring in the entire range of the subfamily; numerous species have been recently described from southeast Asia (China, northern Vietnam, northern Laos, northern Thailand and Nepal). *Ulochaetes* has one species in western North America and two nominal species (possibly synonyms) in the Himalayan region (China, northern India, Bhutan, certainly Nepal as specimens have been collected close to the Indian-Nepalese border). All other genera classified in Necydalinae or Necydalini are very probably cerambycines (see Phylogeny and Taxonomy).

**Biology and Ecology.** Larvae develop in dead wood, occasionally of living trees and/or with specific fungal infestation (e.g., Rejzek & Vlasák 2000), without an obligatory initial subcortical phase. Pupation occurs in the host in the spring or summer of the year of adult emergence. Species of *Necydalis* are known from broadleaved and coniferous trees, whereas *Ulochaetes* is restricted to conifers. Adults morphologically and behaviorally mimic hymenopterans (*Necydalis* larger wasps, *Ulochaetes* resembles bumblebees). Some species of *Necydalis* visit flowers.

**Morphology, Adults** (Fig. 2.4.6 K, L). Moderately large beetles (12–35 mm) with shortened elytra covering only the pterothorax, exposed wings with unfolded apex, and a free and (particularly in *Necydalis*) basally constricted flexible abdomen capable of extensive vertical movements.

Head short, with mouthparts directed obliquely ventrad (strongly so in *Ulochaetes*), temples abruptly protuberant (sometimes with a vertical carina) and a constricted neck. Median frontal groove present but disappearing before occipital region. Postclypeus semi-oval, frontoclypeal suture may

be indistinct medially; pretentorial pits large, frontal, placed mesad of a fine carina more or less completely connecting mandibular condyle with antennal socket; anteclypeus moderately sized; labrum free. Antennal insertions high on head, distant from mandibular condyles; antennal sockets usually facing laterally or laterodorsally, sometimes slightly anteriorly. Eyes deeply emarginate, lower half larger, not extending to ventral side of cranium and not reaching anterior cranial margin. Antennae with 11 segments (last flagellomere at most indistinctly subdivided), filiform, rarely (males of *Ulochaetes*) longer than body. Mandibles short, triangular, with small molar plate (reduced and tending to fuse with dorsal mandibular cuticle in some species) and distinct fringe of hairs along incisor edge; apex simple. Maxillae and labium well-developed; lacinia distinct; gulamentum with short intermaxillary process; ligula membranous, bilobed; terminal segments of both palps more or less truncate. Tentorial bridge narrow, pre- and metatentorium connected, arms of the latter relatively solid. Cervical sclerites present.

Pronotum without lateral carina. Notosternal suture fine or incomplete. Procoxal cavities closed internally and broadly open to narrowly closed posteriorly (Fig. 2.4.13 F). Prosternal process present, narrow. Procoxae moderately transverse, prominent, projecting below prosternal process, exposed laterally including trochantin. Mesoscutum without median endocarina (latter restricted to anterior vertical phragma) and bearing undivided stridulatory plate. Mesocoxal cavities open laterally. Metendosternite with laminae. Elytra rounded or slightly pointed posteriorly. Wing (Fig. 2.4.16 K) with radial cell closed proximally; RP extends far proximally beyond crossvein r<sub>4</sub>, latter sometimes with short spur; wedge cell absent; medial field mostly with five or four free veins; CuA<sub>1+2</sub> branching off far proximally (about level of attachment of AA<sub>3</sub>) and fused with MP<sub>3+4</sub> (a separate CuA<sub>1</sub> is therefore absent); base of MP<sub>3+4</sub> weakened to absent proximally to CuA<sub>1+2</sub> fusion. Tarsi pseudotetramerous and padded beneath; first hind tarsomere often very long (Fig. 2.4.6 K) and pad strongly reduced; empodium variable, in some cases distinct and multisetose.

Abdominal sternum III without intercoxal process and sternum II visible between hind coxae. Ovipositor long and flexible; apex not sclerotized, styli inserted apically.

**Morphology, Larvae.** Similar to Lepturinae, differences and restrictions are as follows. Body subcylindrical. Head (Fig. 2.4.21 K) half-retracted, pale except for dark mouth frame; cranium moderately transverse; epicranial halves shortly fused, posterodorsal margin deeply notched. Frontal arms often poorly visible on pale cuticle; transfrontal line absent. Epistomal margin and anterior frons without projections. Labrum slightly transverse.

One to three pairs of small (often indistinct) main stemmata (if three, then without distinctly separate corneal lenses), other stemmata indiscernible. Antennae relatively long, deeply retractile, trimerous. Mandibles short and robust; pseudomola moderately sized and non-striate to rudimentary; apex unidentate; apical part with three distinct inner keels. Maxillolabial complex with basal parts well separate; cardo larger than in most Lepturinae; mala from broadly triangular to cylindrical but never very slender; ligula bearing a combination of setae and microtrichia. Hypostomal lines subparallel to slightly converging, gula moderately long, with raised lateral margins.

Pronotum with lateral furrows distinct in basal half, which bears asperities; they are fine and restricted to lateral and sometimes posterior margins (*Necydalis*) or widespread and moderately coarse (*Ulochaetes*). Pterothoracic coxae poorly defined and tend to fuse with neighboring areas. Legs in later instars moderately long.

Abdomen with dorsal and ventral ampullae on segments I–VII, both with two pairs of lateral impressions (Fig. 2.4.30 A, B). Epipleuron protuberant on segments I–IX in *Ulochaetes*, but not or poorly so (partly depends on preservation) on a few anterior segments in *Necydalis*. Tergum IX unarmed. Segment X separate, subterminal. Midgut with very large mycetomes (*Necydalis*, Fig. 2.4.19 M).

**Phylogeny and Taxonomy.** The subfamily, comprising *Necydalis* Linnaeus and *Ulochaetes* LeConte (for probably misclassified taxa see below), was often treated as a tribe of Lepturinae; it does not share the possible apomorphy of other lepturines (strong reduction or absence of larval pronotal lateral furrows), and the duplicate lateral impressions of the ventral ambulatory ampullae (Fig. 2.4.30 A, B) may be a necydaline larval apomorphy as they are virtually unique in the entire family. The derived adults (brachelytrous hymenopteran mimics with unfolded wing apex and modified wing venation; Fig. 2.4.6 K, L) also suggest monophyly but at the same time show no characters that could be labelled as undoubted plesiomorphies compared with Lepturinae. Craighead's (1923) note that on larvae "Necydalini could be as well placed with the Aseminae as in the true Lepturinae" does not seem justified.

Extensive parallelisms occur in certain adult Cerambycinae (cf. Fig. 2.4.4 L, U, 2.4.5 J, N), and some of those taxa have been or still are erroneously classified in Necydalinae or Necydalini. After the placement of *Psebena* Gahan from Borneo in Cerambycinae (Thraniini) by Vives (2006), the last remaining taxa misclassified in Necydalinae appear to be the New World genera other than *Necydalis* and *Ulochaetes* (Bezark & Monné 2013); all are South American, a few species of *Rhathymoscelis* reaching Central America. Those genera form at least two (but probably more) unrelated groups (P. Svacha,

personal observation; adults of asterisked genera were studied, larvae are known in *Callisphyris* and ?*Hephaestion*): 1. *Atelopteryx* Lacordaire, \**Callisphyris* Newman (Fig. 2.4.4 U), \**Hephaestion* Newman, *Parahephaestion* Melzer, \**Planopus* Bosq, possibly *Hephaestioides* Zajciw (unknown to us) and \**Stenorhopalus* Blanchard in Gay. Adults show all transitions from forms very similar to certain Holopterini (to which also the known larvae are undoubtedly related) to the rather *Necydalis*-like *Callisphyris*. Mandible without molar plate. Elytra always surpassing posterior pterothorax at least by narrow projections; wing venation different. Only some species have more or less reduced abdominal intercoxal process. Mesoscutum in available genera with median endocarina (and thus divided stridulatory plate) except for *Stenorhopalus*. Ovipositor extremely short (indicating surface oviposition). The very slender larvae develop in fresh branches and are typically cerambycine (Fig. 2.4.24 D) with postnotum, rounded mandibles and constricted clypeus; they share with Holopterini the apomorphic spiracle with extensive field of long narrow marginal chambers (Duffy 1960: 317; Fig. 2.4.30 K, L). 2. \**Cauarana* Lane (Fig. 2.4.5 N, 2.4.17 L), *Mendesina* Lane, *Rhathymoscelis* J. Thomson. Larvae unknown, no adults were available for dissection. They share with Necydalinae the apically completely unfolded wings, extremely short elytra covering only pterothorax, and abruptly protuberant temples. Wing venation with RP absent proximally of r<sub>4</sub>; only three free veins in medial region as MP<sub>3+4</sub> is unbranched (but long basally, not reduced as in Necydalinae) and entire CuA<sub>1+2</sub> complex is lost. The head and mouthparts of *Cauarana* are very different from Necydalinae (e.g., pretentorial pits indistinct, apparently lateral), the prosternal process is absent, and the abdominal base is strongly derived as segment II is secondarily well-developed (sternum relatively long, much more distinct than in any studied Necydalinae, and surpassing coxae) and segment III forms a petiolus-like basal piece (Fig. 2.4.17 L). However, at least some species of *Rhathymoscelis* have a normal abdominal base with a well-developed intercoxal process.

### Lepturinae Latreille, 1802

**Distribution.** A moderately large subfamily with ca. 200 genera and 1500 species. Most abundant in the Holarctic Region (e.g., about 20% of the cerambycid fauna of America north of Mexico), penetrating into Neotropical (see Monné & Monné 2008) and Oriental regions. There is only one Afrotropical species (*Apioccephalus punctipennis* Gahan from eastern Africa, another congener in northwestern India and the related genus *Capnolymma* is Oriental). The group reaches Wallacea; *Elacomia* Heller of Lepturini occurs in Misool and Ceram Islands, and two undescribed species (one *Elacomia*) in Madang region of Papua New Guinea (personal

communication, P. Pokluda). For taxa from other regions misclassified in Lepturinae, see Phylogeny and Taxonomy.

**Biology and Ecology.** Larvae often feed in dead wood and, like in Anisarthrini (Spondylidinae), some taxa develop in dead rotting moist wood of living trees that may be primitive for the group. Subcortical larval feeding and strongly flattened larval forms are widespread in Rhagiini but rare (Lepturini) or unknown in other tribes. Other types of larval feeding are much more restricted. Larvae of many species may penetrate into the roots, and in specialized root feeders (*Pachyta*, *Stenocorus*, *Akimerus*) the larvae almost invariably start feeding in thinner distal roots and proceed toward the thicker proximal ones. Larvae of *Pidonia* Mulsant are also frequently subterranean, and related taxa (*Pseudosieversia* Pic, *Macropidonia* Pic) appear to be at least partly terricolous, feeding on the roots externally (Cherepanov 1979). *Encyclops* Newman and some *Pidonia* develop in thick outer bark of living trees, but feeding within living tissues of woody plants is uncommon (*Pseudogaurotina* Plavilstshikov, *Desmocerus*). A few groups develop in or on the underground parts of living herbs (*Brachyta* Fairmaire, many *Cortodera*, *Brachysomida* Casey, *Vadonia* Mulsant, some *Typocerus*), other *Cortodera* feed in wood fragments or conifer cones buried in humus – typical food items for *C. femorata* (Fabricius). Some dead wood feeders are associated with specific fungi, and *Pseudovadonia livida* appears unique among all cerambycids in tunnelling in humus with mycelium of the fungus *Marasmius oreades*. Eggs are usually laid on or in the food material without special preparation of the oviposition site. However, females of some specialized root feeders oviposit in, on or above ground and first instar larvae dig into the soil and search for the roots. The pupal chamber is typically constructed in the host plant, but several groups pupate in soil: all terricolous groups, some or all specimens of most species with underground endophytic larvae, some Rhagiini developing under very loose bark, and all known Oxymerini. Adults are often floricolous and head and mouthpart morphology of many taxa is strongly adapted to pollen and nectar feeding (somewhat rostrate head, long mandibles extensively fringed with hairs and bearing a large variously sculptured molar plate, maxillary galea and lacinia large and provided with specialized pollen-collecting armature of long and/or curved hairs). Floricolous is unknown or infrequent in some presumably basal groups and may not belong to the lepturine groundplan; even species with flower records are often only occasional flower visitors, and the mouthpart adaptations might originally serve other purposes, such as collecting spores or anemophilous pollen. Dissection of adult gut of *Aredolpona rubra*, frequently collected from flowers, revealed fungal material (Kinmark 1924, *vide* Butovitsch 1939). However, floricolous or pollinophagy may occur (and remain unknown) in crepuscular or nocturnal spe-

cies, as was the case in *Enoploderes sanguineum* (Danilevsky & Miroshnikov 1981). Leech (1963) often found pollen from anemophilous (*Pinus*) and entomophilous trees (possibly *Lithocarpus* or *Castanopsis* of Fagaceae) on predominantly nocturnal adults of *Centrodera spurca* (LeConte) and its relatives that lack solid floral records.

**Morphology, Adults** (Fig. 2.4.6 M–P, 2.4.7 A–S). Small to moderately large (3.5–35 mm), slender to moderately robust, with cursorial legs; elytra may be narrow and dehiscent, occasionally slightly abbreviated, but never covering only pterothorax.

Head more or less prognathous, mouthparts moderately oblique with rare exceptions (*Desmocerus* with deflexed anterior head and strongly oblique mouthparts); region behind eyes usually with prominent temples followed by a constricted neck (Fig. 2.4.10 C, 2.4.11 J) or abruptly to gradually narrowing, seldom subparallel (e.g., *Peithona*, *Piodes* LeConte). Median frontal groove usually present but disappearing before occipital region. Frontoclypeal suture often poorly defined at middle. Pretentorial pits distinct, usually dorsal or laterodorsal, lying behind mandibular condyles (Fig. 2.4.11 K), rarely more or less lateral. Postclypeus never long (transversely triangular even in some slightly rostrate heads of Lepturini); anteclypeus often large and slightly convex. Labrum free. Antennal insertions moderately to very far from mandibular condyles; antennal sockets facing laterally to laterodorsally and almost always also broadly open anteriorly (Fig. 2.4.11 K). Eyes of variable size, entire or more or less emarginate, never divided into two parts or approximate dorsally or ventrally. Antennae of variable length, hardly surpassing pronotal base in females of *Piodes* (Fig. 2.4.7 O), nearly twice as long as the body in male *Peithona* (Fig. 2.4.6 O); usually filiform, seldom strongly serrate. Mandibles never enlarged, usually with distinct molar plate (rudimentary in *Peithona*); incisor edge usually with more or less extensive fringe of long hairs; apex simple, somewhat scalpriform in *Desmocerus*. Maxillae and labium well-developed; lacinia distinct; gumentum forming short to long intermaxillary process (Fig. 2.4.11 J); ligula usually large, membranous, emarginate or bilobed; terminal segments of both palps usually truncate. Tentorial bridge narrow, pre- and metatentorium firmly connected, the latter often with distinct dorsal arms (Fig. 2.4.12 F). Cervical sclerites present (Fig. 2.4.11 J).

Pronotum without lateral carina, at most with a tubercle or spine, the latter flattened and with a sharp margin in *Enoploderes*. Notosternal suture fine to indistinct. Procoxal cavities angulate laterally, closed internally, open or narrowly closed posteriorly. Prosternal process moderately broad to (usually) narrow, occasionally shortened. Procoxae prominent, strongly projecting below prosternal process unless this is also strongly prominent (*Rhagium* Fabricius).

Mesoscutum usually with complete median (rarely asymmetrical) endocarina and stridulatory plate (if present) divided; rarely (*Capnolymma*) striation not interrupted; in a few cases (such as some Xylosteini) endocarina restricted to anterior perpendicular phragma and plate undivided; in *Pseudovadonia livida* divided by strongly asymmetrical smooth line not associated with endocarina. Mesocoxal cavities open laterally. Metendosternite usually with laminae (virtually absent in flightless *Teledapus*). Elytra not or at most slightly shortened, but may be narrow and dehiscent. Wings rarely reduced, either in females (*Xylosteus*; Fig. 2.4.6 M, N) or in both sexes (*Teledapus* and its relatives, Fig. 2.4.7 A, B); females of some other genera such as *Katarinia* Holzschuh (Fig. 2.4.7 N) or *Piodes* (Fig. 2.4.7 O) are more or less macropterous but probably flightless and may be slightly physogastric. Wings (Fig. 2.4.6 Q, 2.4.15 E, G, H, 2.4.16 L) with radial cell usually closed proximally; RP extends more or less beyond crossvein r4 which mostly bears a distinct spur; wedge cell large to absent; medial field usually with five free veins; rarely regularly with four (usually MP<sub>4</sub> absent or reduced to basal stub; e.g., *Evodinus* LeConte, *Brachyta*, *Capnolymma*, *Apioccephalus*, some members of the *Acmaeops*-complex, *Centrodera sublineata* LeConte); CuA<sub>1+2</sub> complete or only narrowly interrupted at base; CuA<sub>1</sub> present. Tarsi pseudotetramerous and padded beneath; claws divaricate to moderately divergent, always free; empodium variable.

Ovipositor (Saito 1989 a, b; Fig. 2.4.18 H–J, 2.4.19 O) usually moderately developed to long, poorly sclerotized; styli apical, seldom slightly shifted laterally; ovipositor short in *Toxotinus* Bates. Male genitalia (particularly parameres) more or less robust and complex in Oxymirini (Fig. 2.4.18 B; S. Laplante, personal communication).

**Morphology, Larvae** (Fig. 2.4.20 L–Q). Subcylindrical to extremely depressed (Fig. 2.4.24 L, 2.4.31 A, B); strongly flattened subcortical forms occur mainly in Rhagiini. Head from deeply retracted to largely exposed, pigmentation variable. Cranium slightly to strongly transverse; epicranial halves mostly fused along a short distance or virtually at “one point” (i.e., duplicated dorsomedian region short to absent and cranium deeply emarginate or notched posteriorly, Fig. 2.4.22 B), rarely (some Xylosteini) broadly fused and posterior cranial margin shallowly emarginate. Frontal arms usually distinct (sometimes diffuse) and almost meeting at frontal base; transfrontal line in some later-instar larvae very distinct (Fig. 2.4.20 Q, 2.4.22 B), but absent or poorly developed in early instars. Epistomal, frontal and postcondylar carinae absent, rarely epistomal margin with moderate paramedian protuberances; medial pair of epistomal setae slightly removed from clypeal border in some strongly flattened heads (*Dinoptera*). Clypeus trapezoidal, not constricted. Labrum variable; long and cordate in species with well-developed mandibular pseudomola. Stemmata

from six pairs to absent; very large in some forms living under loose bark. Antennae moderately long to minute, from trimerous through various stages of reduction to monomerous rudiments; sensorium conical. Mandibles variable (long and slender in some flat subcortical Rhagiini); with (Fig. 2.4.26 G, H) or without pseudomola; apex usually unidentate, rarely bidentate (within this subfamily undoubtedly apomorphic), apical part with three distinct inner keels (Fig. 2.4.26 H) or they are reduced to two (Rhagiini and Lepturini) and occasionally indistinct. Maxillolabial complex with moderately large free cardo; maxillary articulating area undivided, fused with submentum in some depressed forms; mala usually slender and apparently inserted on palpiger, rarely (*Enoploeres*, *Rhamnusium*, *Teledapus*) broad and triangular; palpiger lacks laterodorsal sensory process; maxillary palps trimerous; ligula distinct, its vestiture variable (setae or various combinations with microtrichia). Hypostomal lines subparallel or diverging. Gula exposed, moderately to very long. Hypostoma not much longer than gula, both regions may be fused and gular borders lost. Metatentorium (Fig. 2.4.26 O, 2.4.27 H) delicate, strongly oblique and (almost) invisible in ventral view; bridge thin; pits distinct.

Thorax (Fig. 2.4.28 B, D, F) with lateral pronotal furrows reduced to basal rudiments or lacking; anterior protergal pigmentation not interrupted (Fig. 2.4.21 L); base occasionally with a field of microasperities. Anterior proepipleuron fully delimited ventrally and tapering anteriorly. Pleural and sternal prothoracic components well-defined; proepisternum not thickened; coxosternal halves approaching medially. Postnotum absent. Mesothoracic spiracle not protruding into prothorax. Pterothoracic pleuron divided by constriction into episternum and epimeron; coxae at that constriction almost touching epipleuron. Legs with full number of segments; primarily slender and usually moderately long, rarely extremely long (Fig. 2.4.20 P); pretarsus bearing a distinct seta (absent in *Pyrocalymma*) and often a distinctly sclerotized claw (Fig. 2.4.29 G).

Abdomen (Fig. 2.4.28 B, D, F) with ambulatory ampullae on segments I–VII, rarely dorsal or both ampullae absent on VII; ampullae with one pair of lateral impressions and occasionally with a duplicated anterior transverse line (Fig. 2.4.29 H). Epipleuron protuberant on segments I–IX, sometimes less distinctly so on a few anterior segments in stout cylindrical larvae; epipleural discs absent; epipleural tubercles present on segments I–VIII. Segment IX not enlarged; tergum rarely with paired urogomphal spines [*Centrodera decolorata* (Harris), Oxymirini, *Caraphia* Gahan]; sometimes with unpaired caudal spine, often on triangular more or less sclerotized base; rarely with other types of armature (Fig. 2.4.30 Q). Segment X unarmed, variable; in some depressed subcortical larvae posteroventral and used as pseudopod; rarely (*Enoploeres*) fused with IX; anus triradiate.

Anterior midgut mostly bearing crypts with yeast-like endosymbionts.

First-instar larvae (Fig. 2.4.31 J, K) without transfrontal line; with long to very long legs; cephalic egg bursters absent, pterothoracic egg bursters often present.

The aberrant flattened larvae of *Apiiocephalus* and *Capnolymma* (Fig. 2.4.31 A–E) show numerous unique apomorphies not covered by the general larval description. Cranium with long posterior internal projections and bearing variously shaped anterior processes; antennae placed ventroapically on medial process and far from pleurostoma; median frontal endocarina lacking; frontal lines absent in *Apiiocephalus* and some unidentified larvae from southeastern Asia (*Capnolymma* has both frontal and transfrontal lines); epistomal margin bearing a pair of conical tubercles. Prothorax extremely flattened and strongly modified (e.g., without a defined mediopresternum), extensively sclerotized (anterior pronotum and entire alar lobes that are separated from one another by paired anterolateral desclerotized lines; virtually entire epipleuron and presternum). Ambulatory ampullae very flat, with modified dividing pattern, but in slightly reduced form present also on segment VIII; epipleural tubercles poorly delimited but projecting as moderately sclerotized, apically dentate processes bearing a few setae and, at least in some species, one long thin trichobothrium (Fig. 2.4.31 C; usually broken off in preserved specimens); anal segment reduced and ventral; only two ventral anal papillae distinct, dorsal papilla tends to fuse with tergum IX.

**Phylogeny and Taxonomy.** The vestigial or missing larval lateral pronotal furrows (much more reduced than in any Necydalinae) may be a lepturine apomorphy in terms of Necydalinae. The tribal classification is unstable (Table 2.4.2). American authors (Linsley & Chemsak 1972; Monné & Giesbert 1995; Monné 2006) often included Necydalini as a tribe and classified all present Lepturinae as one tribe, Lepturini, except for the genus *Desmocerus* (separated in Desmocerini). Authors working primarily with the Old World fauna often separated Necydalinae as a subfamily, and this approach is preferred here and has been accepted also in several recent American works (Bousquet *et al.* 2009; Bezark & Monné 2013). The remaining classification is variable and confusing. A number of genera related to *Leptura* Linnaeus (represented by several genera at the bottom of Table 2.4.2) have always been placed in Lepturini, but other tribal names were used very inconsistently and often without explanation. Particularly the tribe Xylosteini, defined by having coarsely faceted eyes, was often used as a polyphyletic wastebasket occasionally including some Dorcasominae.

Svacha (*in* Svacha & Danilevsky 1989) tentatively proposed a tribal classification of Lepturinae, exclusive of Necydalinae, based on larval characters and

consisting of six tribes (those for which no formal name was available were left unnamed). I. Xylosteini (*Xylosteus*, *Leptorhabdium* Kraatz, *Centrodera*); II. unnamed (*Rhamnusia*, *Enoploderes*; the former genus was placed in a separate tribe Rhamnusiini by Sama *in* Sama & Sudre 2009); III. unnamed (*Oxymirus* Mulsant, *Anthophylax* LeConte, *Neanthophylax* Linsley & Chemsak; named Oxymirini by Danilevsky *in* Althoff & Danilevsky 1997); IV. unnamed (*Sachalinobia* Jakobson, *Xenoleptura* Danilevsky, Lobanov & Murzin; the former was placed in Sachalinobiini by Danilevsky *in* Löbl & Smetana 2010); V. Rhagiini (including *Centrodera spurca*, *Cortodera*, *Grammoptera* Audinet-Serville, and *Strophiona* Casey, which are usually placed in Lepturini, *Encyclops*, often placed in Encyclopiini, and *Desmocerus*); VI. Lepturini. The first four groups have retained plesiomorphic three inner mandibular larval keels, whereas only two are present in Rhagiini and Lepturini. Xylosteini were considered possibly the basalmost tribe because of the relatively distinctly impressed rudiments of the lateral pronotal furrows. Since proposing that classification, larvae of several genera have been studied that cannot be unambiguously placed in any of these six tribes: two species of *Teledapus* (for species see Holzschuh 1989, 1999, 2003, 2007; Miroshnikov 2000), *Carpaphia lepturoides* (Matsushita), and an undescribed Chinese species of *Palaeoxylosteus* Ohbayashi & Shimomura.

Of the above larval classification, placement of *Grammoptera* and *Strophiona* in Rhagiini was undoubtedly incorrect (probably based on larval parallelisms associated with flattened subcortical larvae), and the genera should be returned to Lepturini; surprisingly, *Desmocerus* also occurred in the (usually monophyletic even if not strongly supported) Lepturini (Sýkorová 2008). Lepturini (comprising the genera *Pseudalosterna* Plavilstshikov through *Judolia* Mulsant in the cladogram) were also monophyletic in Saito & Saito (2003); “*Grammoptera*” (actually *Alosterna* Mulsant) and *Kanekoa* Matsushita & Tamanuki occurring outside the tribe were based on misidentified sequences (personal observation, P. Svacha); *Desmocerus*, *Grammoptera* and *Strophiona* were not included. Other tribes are so far not supported by molecular data, and the position of many important taxa (including Necydalinae) is variable.

The Oriental monospecific *Peithona* (Fig. 2.4.6 O–R) was regarded as closely related to *Apatophysis* (here in Dorcasominae) by Gahan (1906), but we retain it in Lepturinae as a genus *incertae sedis*; classification of *Peithona* in Xylosteini (e.g., Löbl & Smetana 2010) is questionable. The larva is unknown, but the wing venation is more complete than in any studied dorcasomine (five veins in medial field due to long separate MP<sub>3</sub> and MP<sub>4</sub>, CuA<sub>1+2</sub> only narrowly interrupted at base), pre- and metatorial pits are very large, pre- and metatorial arms are robust and firmly connected, and although mandibles are not typically lepturine, particularly the right mandible of the studied



Table 2.4-2 Placement of *Necydalis* and selected genera of Lepturinae by various authors.

Genus	Linsley & Chemsak 1972, 1976	Cherepanov 1979	Sama 1988	Svacha & Danilevsky 1989	Ohbayashi et al. 1992, 2007	Monné & Giesbert 1995	Althoff & Danilevsky 1997	Vives 2000	Chiang & Chen 2001	Löbl & Smetana 2010	Bezark & Monné 2013
<i>Necydalis</i>	NEI	NEI	NEI	NEE	NEE	NEI	NEE	NEE	NEE	NEE	NEE
( <i>Pseudo</i> ) <i>Xylosteus</i>	LEP		XYL	XYL		LEP	XYL			XYL	XYL
<i>Leptorhabditum</i>	LEP		XYL	XYL		LEP	XYL			XYL	XYL
<i>Centrodra decolorata</i>	LEP			XYL		LEP					RHA
<i>Teledapus</i>											
<i>Oxymirus</i>				OXY			OXY	STE		OXY	
<i>Anthophylax</i>	LEP	RHA	RHA	OXY		LEP					RHA
<i>Rhamnusium</i>		RHA	RHA	OXY							
<i>Enoploides</i>	LEP	RHA		RHM	RHA	LEP	RHM	RHA		RHM	
<i>Sachalinobia</i>	LEP	RHA		RHM	RHA	LEP	ENO		XYL	RHA	ENC
<i>Xenoleptura</i>	LEP	RHA		SAC		LEP				SAC	SAC
<i>Caraphia</i>				SAC						LEP	
<i>Centrodra spurca</i>	LEP			RHA	LEP	LEP			XYL	LEP	
<i>Rhagium</i>	LEP	RHA	RHA	RHA	RHA	LEP			RHA	RHA	RHA
<i>Stenocorus</i>	LEP	RHA	RHA	RHA	RHA	LEP			RHA	RHA	RHA
<i>Pachyta</i>	LEP	RHA	RHA	RHA	RHA	LEP			STE	RHA	RHA
<i>Evodinus</i>	LEP	RHA	RHA	RHA	RHA	LEP			STE	RHA	RHA
<i>Gaurotes sensu lato</i>	LEP	RHA	RHA	RHA	RHA	LEP			STE	RHA	RHA
<i>Acnaeops</i>	LEP	RHA	RHA	RHA	RHA	LEP			STE	RHA	RHA
<i>Desmocerus</i>	DES			RHA	RHA	DES			STE	RHA	DES
<i>Encyclops</i>	LEP	XYL		RHA	RHA	LEP			STE	ENC	ENC
<i>Pitonia</i>	LEP	RHA	RHA	RHA	RHA	LEP			STE	RHA	RHA
<i>Cortodera</i>	LEP	LEP	LEP	RHA		LEP				RHA	RHA
<i>Grammoptera</i>	LEP	LEP	LEP	RHA		LEP		LEP	STE	LEP	LEP
<i>Pedostrangalia</i>	LEP	LEP	LEP	LEP	LEP	LEP		LEP	STE	LEP	LEP
<i>Etorofus</i>	LEP	LEP	LEP	LEP	LEP	LEP		LEP	STE	LEP	LEP
<i>Lepturobosca</i>	LEP	LEP	LEP	LEP	LEP	LEP		LEP	STE	LEP	LEP
<i>Judolia</i>	LEP	LEP	LEP	LEP	LEP	LEP		LEP	STE	LEP	LEP
<i>Anastrangalia</i>	LEP	LEP	LEP	LEP	LEP	LEP		LEP	STE	LEP	LEP
<i>Stictoleptura</i>	LEP	LEP	LEP	LEP	LEP	LEP		LEP	STE	LEP	LEP
<i>Leptura</i>	LEP	LEP	LEP	LEP	LEP	LEP		LEP	STE	LEP	LEP
<i>Strangalia</i>	LEP	LEP	LEP	LEP	LEP	LEP		LEP	STE	LEP	LEP

Some genera were included under different names (*Enoploides* = *Pyrorichius*; *Lepturobosca* = *Cosmosalia*; American authors place species related to *Etorofus* in *Leptura* and species related to *Leptura* in *Typocerus*). NEI, Necydalini (of Lepturinae); NEE, Necydalinae; DES, Desmocerini; ENC, Encyclopinii; ENO, Enoploiderini (*nomen nudum*, not yet validated); LEP, Lepturini; OXY, Oxymirini (unnamed in Svacha & Danilevsky 1989); RHA, Rhagiini; RHM, Rhamnusiini (unnamed in Svacha & Danilevsky 1989, *nomen nudum* in Althoff & Danilevsky 1997, validated by Sama in Sama & Sudre 2009); SAC, Sachalinobiini (unnamed in Svacha & Danilevsky 1989); STE, Stenocorini; XYL, Xylosteini; blank, not treated.

female bears small rudiments of the molar plate. A 16S rDNA mitochondrial sequence (P. Svacha, unpublished data) likewise places the genus in the Lepturinae-Necydalinae cluster, although without any specific relationship.

The genera *Apiocephalus* (northwestern India, Afrotropical) and *Capnolymma* (including the subgenus *Acapnolymma*; Oriental) have been sometimes classified close to genera now known or suspected to be dorcasomine, and both groups are often placed in the lepturine tribe Xylosteini (Gressitt *et al.* 1970; Chiang & Chen 2001). Their larvae, although extremely aberrant, are clearly lepturine (Böving & Craighead 1931, unidentified lepturine larva, Fig. K in Plate 100 is a ventral view; Gardner 1931 b; Duffy 1957, 1968; Nakamura & Kojima 1983; Fig. 2.4.31 A–E); *Capnolymma* has a distinct transfrontal line, a derived character unknown outside Lepturinae. Adult *Capnolymma* have a distinct mandibular molar plate. The genera might be preliminarily placed in Rhagiini (the larvae do not support classification in Xylosteini) and, as pointed out already by Duffy (1953, 1957, 1968), slight modifications in a similar direction occur in strongly flattened larvae of the Palaearctic genus *Dinoptera* Mulsant (Fig. 2.4.20 Q).

Taxa more recently misplaced in Lepturinae include *Vesperus* and *Vesperoctenus* (see Vesperidae). Almost universally until Danilevsky (1979 b), the Apatophyseini of Dorcasominae were placed in Lepturinae, and even within some of the lepturine tribes if the authors used tribal classification (Xylosteini: Gressitt 1951 and others; “Toxotini”: Ferreira & Veiga-Ferreira 1959 a, b). Duffy (1957, 1980) placed Dorcasomini (*Dorcasomus*) in Lepturinae. The Neotropical genus *Holopterus* Blanchard in Gay (Holopterini; replaced by *Proholopterus* and *Proholopterini* by Monné 2012, but the replacement names may not be necessary), generally placed in Cerambycinae, has been included in Lepturinae by Vitali (2002) based on head somewhat rostrate anteriorly and constricted behind the eyes, “eyes not deeply emarginate”, intermaxillary process distinct, procoxae prominent and conical, procoxal sockets open posteriorly and angulate laterally, divided mesoscutal stridulatory plate, and five free veins in the medial wing region (although  $CuA_{1+2}$  is lacking, unlike most Lepturinae). All those characters are not uncommon in Cerambycinae from the Southern Hemisphere. Adults of *Holopterus* lack a mandibular molar plate and larvae show a typical cerambycine morphology (postnotum present, rounded mandibles, constricted clypeus; Fig. 2.4.24 C). Lacordaire (1868) placed the Oriental lepturine genus *Pyrocalymma* (Fig. 2.4.7 L) in “Éroschémides” based on the dense bright red body pubescence and lycid-like appearance that it shares with the Australian cerambycine genus *Eroschema* Pascoe (Fig. 2.4.5 M). Later authors added two other East Asian lepturine genera with similar red pubescence (*Corennys* Bates and *Formosopyrrhona* Hayashi) to this group. Gressitt (1951) was apparently the first to place Eroschematini

(= Eroschemini) in Lepturinae and several other publications covering East Asian fauna followed until Ohbayashi (1992) moved the latter two genera to Lepturini; see Ohbayashi & Niisato (2009) for further comments. The genera *Blosyropus* (New Zealand; Fig. 2.4.5 K) and *Montrouzierina* Vives, Sudre, Mille & Cazères (New Caledonia, earlier also treated in *Blosyropus*), classified by early authors among lepturines (e.g., Aurivillius 1912; Hayashi 1961), belong to Cerambycinae (Duffy 1963 for *Blosyropus*) and are currently usually placed in the Phlyctaenodini. The New Guinean *Papuleptura* Gressitt, placed by its author in Lepturinae (Gressitt 1959), was recently synonymized with *Zeugophora* Kunze of the Megalopodidae: Zeugophorinae and both its species were placed in that subfamily as *Zeugophora alticola* (Gressitt) and *Zeugophorella elongata* (Gressitt) (Sekerka & Vives 2013).

### Lamiinae Latreille, 1825

**Distribution.** The largest subfamily containing more than half of described cerambycid species (currently about 3000 genera with over 20,000 species). Worldwide, particularly diverse in the tropics. The species-richest subfamily in most regions but outnumbered by the Cerambycinae in some southern regions (Australia, southern South America) and North America (Forchhammer & Wang 1987).

**Biology and Ecology.** Lamiinae are biologically specialized and many specific comments can be found in the general section on cerambycid biology; only some aspects will be briefly reviewed here. Larvae lack midgut mycetomes with intracellular yeast-like symbionts, have a relatively short cryptonephridial part of the hindgut and typically develop in fresh or living woody and herbaceous hosts. Some (e.g., Dorcadiini) are terricolous and feed externally on underground parts of plants; species developing within dead wood require at least moderate moisture, and some also the presence of fungi. Lamiine larvae are very rarely found in strongly rotten wood (*Rhodopina* is an exception) and in dry hard long-dead wood, including seasoned construction timber. Females never oviposit on barkless wood and almost always prepare or modify the oviposition site with the mandibles. Eggs are laid singly or in small groups and are often relatively larger than in other subfamilies. Development may be rapid, sometimes with a relatively low number of instars (as few as three are possible). Except for terricolous larvae, pupation almost always occurs in the host, though some species feeding in lianas enter the support tree for pupation. Adults feed on fresh plant tissue, bark or fungi; almost no specialized pollen or nectar feeders are known, although flower parts may be consumed. Active adult lifespan may be relatively long, up to several months in some large species. Flightlessness is not infrequent and obviously of

multiple origin (resulting in very similar morphological modifications that often led to misclassifications) and apparently always concerns both sexes. Generally, sexual dimorphism is at most moderate; male antennae may be very long but almost never distinctly modified for improved olfactory sensitivity (serrate, pectinate or flabellate), indicating probable absence of female long-range pheromones; known volatile products are short-range and male-produced. Visual stimuli may be used in host and mate location. Crepuscular or nocturnal habits are widespread, mimetic species are more often cryptic, Batesian mimicry is much rarer than in Cerambycinae but occurs, e.g., in many Neotropical Hemilophini or some Colobotheini, which mimic lycids; wasp-mimicking brachelytry with exposed wings is unknown, although stenelytrous forms do occur in some taxa (e.g., Phytoeciini).

**Morphology, Adults** (Fig. 2.4.7 T, 2.4.8, 2.4.9). Small to large (2.4 to approximately 100 mm in the Oriental *Pseudomeges* Breuning), habitus extremely variable.

Head (Fig. 2.4.10 D–G, I, 2.4.11 I) usually with at most a moderately constricted neck region, except in some forms with enlarged heads, such as Laticraniini, males of some Phytoeciini, males of *Enicodes* J. Thomson (Fig. 2.4.9 H, 2.4.12 D), shield-headed Tapeinini (Fig. 2.4.8 E), or some ant mimics (e.g., Vives 2012). Frons large (but occasionally constricted by eye lobes) and vertical to receding; mouthparts oriented ventrally to posteroventrally; a strongly opisthognathous head with the antennae-bearing part projecting anteriorly occurs in some Agapanthiini (Fig. 2.4.10 E; antennae in such forms generally point anteriorly when at rest); rarely anterior head and mouthparts oblique to nearly prognathous (some Acanthoderini, Mesosini, Pteropliini, Homonoeciini, and many southeast Asian and Australasian Tmesisternini; Fig. 2.4.8 P). Median frontal groove or line almost always present, continuing posteriorly and approaching or reaching posterior cranial margin, forming a more or less deeply reaching carina (Fig. 2.4.12 G). Frontoclypeal border never V-shaped; postclypeus very short, strongly transverse, occasionally bulging or even projecting above anteclypeus (Fig. 2.4.10 G), in males of some Anisocerini and particularly Mauesiini bearing a pair of lateral projections or rarely long horns (Julio 2003); pretentorial pits distinct, usually present as blind oblique slits, always on frontal side of head (Fig. 2.4.11 I). Labrum free. Antennal sockets high on head, far from mandibular condyles, usually more or less surrounded by the eyes. Compound eyes may be strongly constricted or divided into two parts (Fig. 2.4.10 E, G) and may be approximated both dorsally and between the antennal sockets and mandibular articulations, but never extend onto the ventral side of the head. Antennal tubercles in males of some Onciderini projecting as short anterior horns. Antennae often very long, mostly 11- or 12-segmented; rarely terminal flagellomeres (3–9) partly and usually irregularly fused; flagellum usu-

ally simple, never pectinate or flabellate; very rarely several flagellomeres broad and flattened but then this concerns both sexes (*Hemicladius* Buquet, Fig. 2.4.8 C; *Cloniocerus* Dejean); some antennomeres may be swollen or bear spines or tufts of hairs (Fig. 2.4.8 B, 2.4.9 C). Mandibles never distinctly enlarged or sickle-shaped but may bear anterior processes or rarely long anterior horns in males (Fig. 2.4.10 I); incisor edge without fringe of hairs or distinct molar plate; apex simple to scalpriform or bidentate. Maxillae and labium well-developed; lacinia present; galea and lacinia without long hairs of specialized floricoles; gulamentum typically short and usually forming a short intermaxillary process; ligula well-developed; terminal segments of both palps usually with very small apical sensory area and thus pointed or at least subcylindrical; truncate or pronouncedly securiform palps occur in males of some species or even higher taxa such as Gyaritini (personal communication, C. Holzschuh), and the terminal palpomeres of *Phantasis* are strongly securiform in males (Fig. 2.4.8 K) and flattened and moderately truncate in females. Tentorial bridge narrow to rudimentary; pretentorial arms robust and sclerotized; metatentorial arms thin to almost ligamentous yet in studied species connected with pretentorium (usually at an angle due to perpendicular anterior head) (Fig. 2.4.12 G). Cervical sclerites rudimentary or absent.

Prothorax (Fig. 2.4.10 D–F) short to very long, pronotum laterally simple or with pair of tubercles, spines or occasionally more complex processes; a more or less continuous “lateral margin” of some species (prominent in males of some flattened Tmesisternini with a shield-like pronotum) develops above the lateral spines (Fig. 2.4.13 J). Notosternal suture variable. Procoxal cavities closed internally, open or closed posteriorly. Prosternal process present, variable. Procoxae laterally exposed to almost completely concealed, and in some taxa projecting below prosternal process, sometimes with secondary articulation on that process. Mesoscutum usually with both stridulatory plate and complete endocarina; endocarina with strongly asymmetrical line of invagination (Fig. 2.4.14 G), usually displaced leftward, but both alternatives can be found in the same species; the stridulatory plate is thus effectively “undivided” (only one half is functional, the other vestigial or lost); in some derived lamiines endocarina may become reduced. Mesocoxal cavities open or closed laterally. Metendosternite with laminae present or absent. Wing in macropterous specimens with radial cell usually closed proximally; RP usually (but not always) short, not or only slightly surpassing crossvein r<sub>4</sub>; spur on latter crossvein short to absent; wedge cell absent; medial field in plesiomorphic situations with five free veins reaching wing margin; CuA<sub>1+2</sub> stem absent (probably missing in the groundplan) and CuA<sub>2</sub> only connected with MP<sub>3+4</sub> (i.e., CuA<sub>1</sub> present), which thus appears to have three branches (Fig. 2.4.16 M); the common MP<sub>3+4</sub> base often disappears, and the three veins become disconnected, and/or some may be lost, as

well as  $AA_4$ ; in some reduced venations, the presumed  $CuA_2$  is reconnected with the  $CuA$  stem (Sternotomini, Tragocephalini; Fig. 2.4.16 N). Forelegs (especially in males of some species) may be disproportionately long (e.g., *Acrocinus*; Fig. 2.4.9 E); basal sclerite of tibial flexor apodeme always prominent and bilobed to bispinose (Fig. 2.4.17 G); protibia almost always with a medial cleaning brush, mostly combined with an oblique groove or emargination; sometimes mesotibia and rarely also metatibia with a similar cleaning structure on the outer side (Fig. 2.4.8 D); tarsi usually pseudotetramerous and padded beneath, but tetramerous (tarsomeres 4 and 5 completely fused, Fig. 2.4.17 I) in some groups (e.g., Tetraopini, Tetrocini and Astathini, Dorcaschematini, or a cluster of tribes around Lamiini but excluding some Monochamini: *Mecynippus* Bates, *Psacotheta* Gahan, *Macrochenus* Guérin-Méneville, *Epepeotes* Pascoe, or *Parepepeotes* Breuning); claws divaricate to subparallel; empodium absent.

Males of some taxa (Lamiini, Monochamini, Batocerini, Dorcadiini, Gnomini, Petrognathini) have more or less completely paired genital outlets (ejaculatory ducts), often up to the gonopore on the internal sac (Fig. 2.4.18 F; Sharp & Muir 1912: 569; Ehara 1954; Marinoni 1979). Ovipositor short to moderately long (but may be strongly protrusible); segment VIII may be long, tubular, projecting from abdomen and covered by posterior sternal and tergal projections of segment VII (e.g., in some Acanthocinini); basal parts (paraproct) always short and without supporting sclerotized rods (baculi); distal parts of coxites long and slender, giving the ovipositor a more or less deeply cleft appearance (Fig. 2.4.19 Q); styli apical to slightly lateral, small to almost integrated in coxites. Anterior margin of tergum VII in females often projecting into large usually bilobed apodeme lying flat below tergum VI (Fig. 2.4.17 N). Stomodaeal valve occasionally with sclerotized armature (Fig. 2.4.12 M); midgut well developed.

**Morphology, Larvae** (Fig. 2.4.20 R–T, 2.4.21 A–D). Subcylindrical to distinctly flattened, sometimes C-shaped. Head (Fig. 2.4.21 M, N, 2.4.24 J, K, 2.4.25 A–D) from deeply retracted to largely exposed (e.g., in many Agapanthiini); pigmentation variable. Cranium almost always distinctly elongate (rarely subquadrate); epicranial halves entirely fused and jointly rounded posteriorly; ventral layer of dorsomedian duplicate region forming a deep intracranial crest (Fig. 2.4.21 F, 2.4.25 B; a continuation of frontal endocarina). Frontal arms (if distinct) enter separately duplicated region, rarely subparallel posteriorly and almost meeting at frontal base in forms with very long frons (Fig. 2.4.25 C); anteriorly reaching antennal sockets or not; transfrontal line absent. Epistomal, frontal and postcondylar carinae absent; epistomal margin almost always without other projections (rarely with low paired tubercles); epistomal setae close to clypeal border. Clypeus trapezoidal, not constricted. Labrum slightly

to strongly transverse. At most, four pairs of stemmata; original three main stemmata always fused, but three pigment spots may be distinguishable. Antennae at most moderately long, from trimerous through various stages of reduction to scarcely projecting knob-shaped monomerous rudiments; sensorium conical. Mandibles of variable shape, without pseudomola; apex usually unidentate, seldom bidentate (Fig. 2.4.21 N), with two inner keels (Fig. 2.4.26 L; sometimes indistinct) or the third (middle) keel rudimentary. Maxillolabial complex with base fused and attached along its entire width to cranium, cardo strongly reduced, displaced laterally, immobilized (Fig. 2.4.25 K); mala more or less cylindrical at base and appears to originate entirely from palpiger, which is large and without a dorsolateral sensory process; maxillary palps trimerous or rarely dimerous; mentum occasionally fused with submentum; ligula broad, almost always bearing numerous setae, microtrichia usually restricted to dorsal and lateral areas and (almost) invisible in ventral view. Hypostomal lines subparallel to moderately converging posteriorly, occasionally short or even reduced to basal rudiments (Fig. 2.4.21 N). Gula exposed, moderately to very long. Metatentorium (Fig. 2.4.26 P) moderately oblique and at least partly visible in ventral view; bases in some Dorcadiini with very long posterior apodemes (Fig. 2.4.26 Q); bridge extremely thin, arms on bridge rudimentary; pits distinct but often very close to posterior cranial margin.

Pronotum with lateral furrows usually distinct in the basal half but rarely interrupting anterior pigmentation; seldom reduced or absent (e.g., in *Agapanthia* with protracted head); pronotal base may bear fine to extremely coarse asperities, in some *Batocera* Laporte de Castelnau pronotum with a separate posterior fold non-homologous to postnotum (Fig. 2.4.27 M); sublateral impressions may be very distinct, in Phytoeciini (including Obereini of some authors) they form long oblique sclerotized rods (Fig. 2.4.21 M). Proepipleuron fused with episternum and lateropresternum, fused area often broadly sclerotized; epimeron may be separate, but often fuses with epipleuron and/or coxosternal region; the latter always fused with sternellar fold; mediopresternum from distinct to fused with lateropresternum; some groups possess secondary impressions mimicking the lost medio-presternal borders. Postnotum absent, or rarely a poorly developed similar fold present (*Sophronica* Blanchard and a few genera related to *Sybra* Pascoe). Mesothoracic spiracle may protrude into prothorax (e.g., Fig. 2.4.20 R, 2.4.29 C). Broad pterothoracic pleuron tends to fuse with coxal region, which is integrated into the body wall and poorly defined. Legs as minute rudiments consisting of two or rarely three segments, or absent.

Abdomen with dorsal ampullae almost always present on segments I–VII, exceptionally on I–VI or reduced on some middle segments; dorsal ampullae in groundplan with two pairs of lateral

impressions (Fig. 2.4.29 K, L) but dividing pattern may be reduced up to a simple or incomplete transverse line. Ventral ampullae present on segments I–VII or absent on some or all of those (mainly in the C-shaped *Agapanthia* larval type), never with two distinctly separate lateral impressions. Occurrence of protuberant epipleuron variable (up to all nine anterior segments, although usually less distinct on at least I and II); epipleural discs absent; epipleural tubercles usually distinct and present on segments I–VIII (rarely ill-defined on some); some groups bear sclerotized pits or apodemes at one or both ends; in Pogonocherini tubercles I–VII uniquely modified, small, finely sclerotized and with a broad internal apodeme at the anteroventral end (Fig. 2.4.29 C, 2.4.30 G, H). Abdominal apex variable; tergum IX may bear urogomphi or another type of armature (sometimes elaborate, in exceptional cases almost entirely sclerotized and “operculate”; Fig. 2.4.21 A, B); rarely limited sclerotizations also present on some preceding segments or on segment X. Anus from triradiate to transverse slit (gradual reduction of ventral radius; Fig. 2.4.30 N–P). Midgut lacking crypts with symbionts, cryptonephridial part of hindgut generally shorter than in other subfamilies (Fig. 2.4.19 N).

First instars with legs at most rudimentary, sometimes (but not always) with cephalic egg bursters (Fig. 2.4.31 F, G); lateral egg bursters usually present but rarely on pterothorax; dorsal ampullae in some *Agapanthia* bilobed and functioning as dorsal pseudopods (Fig. 2.4.31 M, N).

**Phylogeny and Taxonomy.** The subfamily is monophyletic. Larvae can be easily identified by their rudimentary legs combined with the lack of cerambycine apomorphies (round mandibles and constricted clypeus). Unique larval apomorphies include the elongate cranium with the epicranial halves completely fused dorsally and jointly rounded posteriorly, the duplicated dorsomedian region bearing a deep intracranial crest, and the extremely reduced and laterally displaced fixed cardo (resulting in the firm attachment of the maxillolabial complex along the entire basal width). Adult groundplan apomorphies include the perpendicular frons (oblique heads of Tmesisternini and some other taxa are due to reversals), the narrow and pointed terminal palpal segments (rare in other subfamilies), the antennal cleaner of the anterior tibiae (a similar structure occurs in some Cerambycinae such as Methiini, and in most Disteniidae), the asymmetrical morphology of the mesoscutal stridulatory plate, and the unique protuberant bilobed basal sclerite of the tibial flexor apodeme (Marinoni 1979; the sclerite is flat and usually less distinct in other subfamilies; G. Sama, personal communication). Misclassifications are rare and currently include some strongly derived and poorly known forms (e.g., the ant-mimicking *Falshomaemota* Hayashi described as a cerambycine

but probably a lamiine; see Vives *et al.* 2011; Vives 2012; Fig. 2.4.8 G).

Tribal classification will not be discussed as it is unsatisfactory, unstable and in many points obviously non-phylogenetic. In particular, absolute dichotomic use of single arbitrarily selected adult characters (such as presence or absence of antennal cicatrix or certain cleaning devices, claw morphology, or modifications associated with the loss of flight capacity) disregarding possible parallelisms has been frequent in taxonomic history of this subfamily. A complete revision of the higher classification is warranted. In a recent revision of Australian Lamiinae (Ślipiński & Escalona 2013), the number of species increased to about 550 but genera were reduced to 74 (approximately 440 species in ca. 100 genera in McKeown 1947).

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