Handbook of Zoology
Arthropoda: Insecta

Coleoptera, Beetles
Volume 3: Morphology and Systematics
(Phytophaga)

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Founded by Willy Kükenthal
Editor-in-chief Andreas Schmidt-Rhaesa

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DE GRUYTER

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(Volume Editors)

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ISBN 978-3-11-027370-0
e-ISBN 978-3-11-027446-2
ISSN 2193-4231

Library of Congress Cataloging-in-Publication Data
A CIP catalogue record for this book is available from the Library of Congress.

Bibliografic information published by the Deutsche Nationalbibliothek

The Deutsche Nationalbibliothek lists this publication in the Deutsche Nationalbibliografie; detailed bibliographic data are available in the Internet at http://dnb.dnb.de

Typesetting: Compuscript Ltd., Shannon, Ireland
Printing and Binding: Hubert & Co. GmbH & Co. KG, Göttingen
Printed in Germany
www.degruyter.com

2.1 Vesperidae Mulsant, 1839

Petr Svacha and John F. Lawrence

Distribution. The family comprises 17 described genera with nearly 80 species. As defined by Svacha *et al.* (1997), it is composed of four relatively different completely allopatric groups, Vesperinae, Philinae, Anoplodermatinae and the tribe Vesperoctenini of uncertain taxonomic position. Vesperinae (single genus *Vesperus* Dejean, ca. 20 spp.) is Mediterranean (southern Europe, North Africa and Asia Minor). The predominantly Oriental subfamily Philinae includes five described genera, two of which are known exclusively from China, *Spiniphilus* Lin & Bi (two spp., one undescribed) from Yunnan (Lin & Bi 2011) and *Heterophilus* Pu (three spp.) from Xizang (Tibet) (Pu 1988; Chiang *et al.* 1996). *Mantitheus* Fairmaire (four spp.) is widely distributed in the eastern half of China and in Mongolia. It is the genus with the most extensive Palaearctic presence (Löbl & Smetana 2010). The genera *Philus* Saunders and *Doesus* Pascoe (together ca. ten spp.) contain a chain of transitional forms. The group occurs in India, Sri Lanka, southeastern China (including Hainan Island), mainland Southeast Asia (reaching Malay Peninsula), Taiwan, Philippines, Borneo and Sumatra. One species of *Doesus*, currently considered conspecific with the type species *D. telephoroides* Pascoe from India, occurs in tropical Africa. A species from North India and Burma, generally listed as *Philus globulicollis* J. Thomson, cannot be accommodated in any existing genus (Svacha *et al.* 1997; see under Philinae). The subfamily Anoplodermatinae contains two or, if Hypocephalini is recognized, three tribes with ten genera (Dias 1984–1988; Bezark & Monné 2013) and is exclusively Neotropical and restricted to southern South America: the southern part of Brazil, southern Peru, Bolivia, Paraguay, Argentina (to slightly over 40° latitude) and Uruguay. No species is known from Chile, although some occur relatively close to the border on the Argentinian side. *Vesperoctenus flohri* Bates, placed as a taxon *incertae sedis* in Vesperidae by Svacha *et al.* (1997) and in a separate tribe Vesperoctenini by Vives (2005), is known exclusively from Mexico (Baja California Sur, Durango, Nuevo León; Vives 2001). Presumably in connection with their larval subterranean habits requiring deeper finer soils, vesperids generally prefer relatively flat landscapes, although such landscapes may occur at very high altitudes (e.g., *Heterophilus* on the Tibetan plateau).

Biology and Ecology. Adult beetles are moderately sized to large, with a relatively monotonous straw-yellow to black coloration. They are usually nocturnal (although copulation and oviposition may also occur during the day), but at least males of some Anoplodermatini are diurnal (the circadian activity regime in females is poorly known). As far as known, adults do not feed (and no food was found in the gut of dissected specimens) and some live for only a very short time after emergence. Females of Vesperinae (except for *Vesperus macropterus* Sama, in which females are macropterous but cannot actively fly – see biology of the subfamily), Anoplodermatinae, Vesperoctenini, and of the genera *Mantitheus* and *Heterophilus* of Philinae are slightly brachypterous to apterous and occasionally also brachelytrous and/or physogastric (Fig. 2.1.1 C, 2.1.3 B). Females of the remaining Philinae (*Philus*, *Doesus*, *Spiniphilus*, and *Philus globulicollis*) are macropterous, yet in some cases apparently also flightless (*Philus antennatus* Gyllenhal; Svacha *et al.* 1997). Males are winged and capable of flight, except for the strongly derived *Hypocephalus* Desmarest of Anoplodermatinae (Fig. 2.1.2 H, I) with both sexes wingless. Although males of the species with flightless females are mostly more numerous in collections, as they are more active and in the crepuscular and nocturnal species they often fly to light, the sex ratio of adults of *Vesperus sanzi* taken from soil pupal chambers was close to 1 (Calvo Sánchez 2007). Females appear to be even much more numerous in *Philus antennatus* as the male to female ratio of adults hand-collected during an outbreak was approximately 1 to 90–100 (Svacha *et al.* 1997). If this reflects the true situation, such a ratio might even indicate at least partial parthenogenesis. Females of Anoplodermatinae are particularly rarely encountered (unknown in some species) as they apparently spend much of their lifespan in soil burrows.

Long-range female pheromones were found in *Migdolus* and *Vesperus*, but the compounds (and possibly also the location of glands) are different: in *Migdolus fryanus* Westwood, the glands appear to be on the female prothorax (Bento *et al.* 1992), and the active compound was identified as an amide, N-(2'S)-methylbutanoyl 2-methylbutylamine (Leal *et al.* 1994). In *Vesperus xatarti* Mulsant, the source is unknown, and the pheromone is a monoterpene, (S)-10-oxoisopiperitenone (named vesperal: Boyer *et al.* 1997). Vesperal appeared to be slightly cross-attractive to males of *V. aragonicus* Baraud but not to *V. creticus* Ganglbauer (Peslier & Mazel 2009). Females of Vesperinae and Philinae often climb to elevated places (tree stems, stones, etc.) for mating and oviposition. In known species, they lay numerous eggs and typically oviposit in batches. Eggs are laid under bark scales or on various objects above ground level and first instar larvae fall or descend to the ground after eclosion to enter the soil. Artificial materials are not avoided. In the Beijing Botanical Garden, *Mantitheus* frequently oviposits under plastic bands wrapped around tree stems as a protection from pests (Fig. 2.1.8 A), and vineyard owners in some regions wrap the tops of vineyard posts

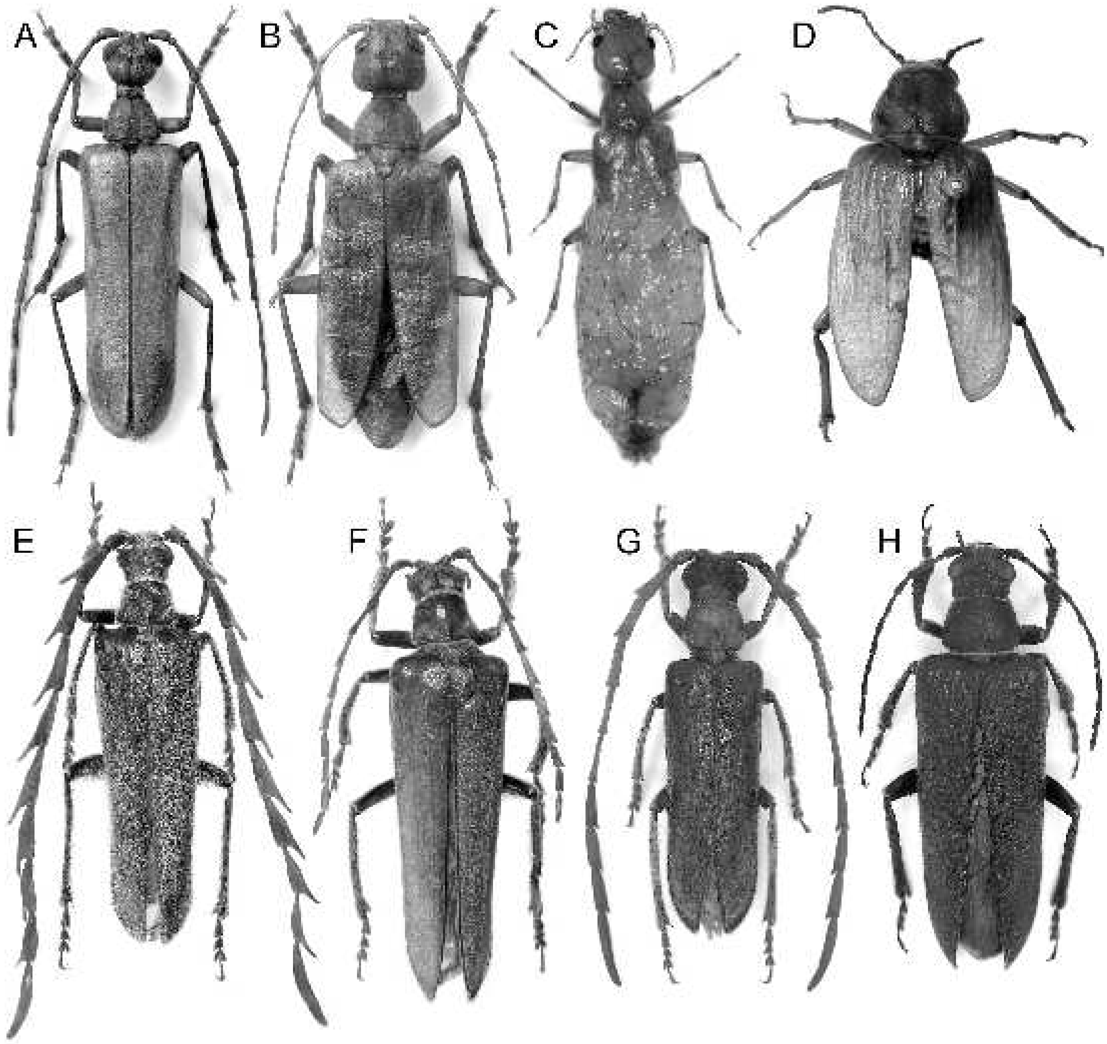

Fig. 2.1.1 Adults of Vesperinae (A–C) and Philinae (D–H), dorsal view. A, *Vesperus strepens* (Fabricius), male, 21 mm (© I. Jeniš); B, *V. strepens*, female, 23 mm (© I. Jeniš); C, *V. jertensis* Bercedo & Bahillo, female with incomplete antennae, 17.5 mm (from Calvo Sánchez 2008, © F. Calvo Sánchez); D, *Heterophilus* sp., one of two known females (from Lin & Bi 2011, © Meiying Lin); E, *Spiniphilus spinicornis* Lin & Bi, male, 26 mm (from Lin & Bi 2011, © Meiying Lin); F, *S. spinicornis*, female, 37 mm (from Lin & Bi 2011, © Meiying Lin); G, *Philus globulicollis* Thomson, male from Burma, 22 mm; H, *Philus antennatus* (Gyllenhal), female, 30 mm.

with fabric to stimulate oviposition of *Vesperus* females, and then destroy the eggs (Peslier & Mazel 2009). Oviposition may occur at the ground level or in surface soil in species developing in grasslands. Females of *Migdolus* (Anoplodermatinae) ascend in their soil burrows to copulate at the entrances and then return deeper into the soil where they oviposit.

Known vesperid larvae (*Vesperus*, *Philus*, *Heterophilus*, *Mantitheus*, and *Migdolus*), are terricolous and feed externally on living rootlets and thinner roots of various plants. The spectrum of known host plants is very wide (conifers and both monocot and dicot angiosperms), and the few species with relatively extensive available biological data are remarkably polyphagous. At least *Philus antennatus* and *Migdolus fryanus* (and probably also some species of *Vesperus*) can feed on both gymnosperms and angiosperms (Svacha *et al.* 1997; Monné 2002; Lin *et al.* 2004; Vives 2005; Wilcken *et al.* 2005). Pupation occurs in soil. Some species may occasionally become pests of cultured plants.

Recorded enemies are usually unspecific. Flying males of *Vesperus* are apparently attacked by bats, as Peslier & Mazel (2009) observed numerous living males lying on the ground with missing abdomens and mutilated thoraces. Night-active ants and, less frequently, scorpions and solifuges were the main predators of the flightless females of *V. sanzi* Reitter (Calvo Sánchez 2007), and various spiders (including orb-web builders in the case of males) captured *V. macropterus* (Sechi 2011). *Philus* adults were preyed upon by birds, and specimens were seen naturally infested by the entomopathogenic fungus *Beauveria bassiana* (Svacha *et al.* 1997). Adults of *Migdolus* (mostly the active free-living males) may be parasitized by flies of the family Sarcophagidae (Botelho & Degaspari 1980). Terricolous immature stages of *Philus* and *Migdolus* are susceptible to infection by parasitic nematodes (Svacha *et al.* 1997; Machado *et al.* 2005).

The two known karyotypes show high or extremely high numbers of chromosomes compared with the presumptive ancestral condition in Polyphaga (2n, 20) and with the known range in Cerambycidae (2n, 10 – 36, with 20 being most frequent). *Migdolus fryanus* has a karyotype of 2n, 28 with 13 pairs of autosomes and a pair of Xy_p sex chromosomes in males; a small y chromosome forms a "parachute" pattern with the X chromosome at the meiotic metaphase I (this type is also typical for cerambycids); females have not been studied yet (Mesa & Martins 1992). *Vesperus xatarti* has a very unusual karyotype, presumably resulting from fragmentation (Dutrillaux *et al.* 2007): 54 chromosomes in females (26 pairs of autosomes + XX sex chromosomes) and 53 chromosomes in males, interpreted by the authors as 24 paired and two unpaired autosomes and multiple XY1Y2 sex chromosomes (none of the two Y chromosomes is small). The presumed multiple male sex chromosomes probably resulted from complex rearrangements involving fusion(s) with autosome(s).

Morphology, Adults (Fig. 2.1.1, 2.1.2). Length 8–50 mm. Body approximately 2.25–4 times as long as wide, parallel-sided and moderately flattened to stout and convex. Surface usually more or less pubescent (pubescence is extremely long in males of *Vesperoctenus* Bates and of some Anoplodermatinae) except for some largely glabrous flightless forms; elytral disc always glabrous in Anoplodermatinae.

Head almost prognathous to nearly hypognathous, but then extensively movable vertically (particularly in some Anoplodematini); abruptly constricted posteriorly to form short neck in *Vesperus* and *Vesperoctenus* (different from the configuration in lepturine Cerambycidae where both genera were often classified as the neck does not involve posterior gula and metatentorial invaginations; *cf.* Fig. 2.1.3 A and 2.4.11 J). Occipital region without transverse ridge (except *Hypocephalus*) or stridulatory file. Frons and vertex with both the median impression and corresponding endocarina indistinct or absent. Eyes very large to small, often strongly convex, not to moderately emarginated; finely or coarsely facetted; interfacetal setae absent or sparse and short except for *Vesperoctenus*, where they are long and numerous; ommatidial structure unknown. Antennal insertions usually partly exposed from above and medially supported by raised tubercles; tubercles less prominent in Anoplodermatinae and sockets more or less concealed dorsally; without distinct tubercles in *Hypocephalus*; subantennal groove absent or weakly developed. Frontoclypeal (epistomal) sulcus, if distinct (usually less so medially), may be strongly curved, V-shaped or somewhat lyriform, without deep paramedian impressions; it is strongly reduced or absent in some Anoplodermatinae. Pretentorial pits large to moderately sized, usually not slit-like, placed laterally and close to mandibular articulations. Clypeus variable; anteclypeus and labrum more or less covered by sclerotized postclypeal projection in some Anoplodermatinae. Variously shaped labrum more or less separate (even if concealed) except for *Sypilus* Guérin-Méneville. Antennae usually 11-segmented, eight to ten-segmented in females of some Anoplodermatinae, 12-segmented in both sexes of *Vesperoctenus*; longer than body in some males, short to very short in females of Anoplodermatinae and some *Vesperus* and particularly in both sexes of *Hypocephalus*; filiform, moniliform, serrate or pectinate; scape moderately sized to small (always much shorter than head); pedicel ring-like to slightly longer than broad; flagellum without long setae and without sharply defined sensory areas. Mandibles (Fig. 2.1.4 A–C) symmetrical to slightly asymmetrical, moderately long to very elongate, usually slightly and gradually to strongly and abruptly curved mesally (not curved and parallel in *Hypocephalus*), with simple apex; often extensively overlapping when closed, usually with left mandible in upper position; outer face sometimes with blunt projection; incisor edge without long pubescence, simple or with one or several teeth; mola and prostheca absent. Maxilla with setose galea and lacinia, the latter much more basal, without uncus, sometimes highly reduced; palps long, four-segmented, with cylindrical or fusiform to slightly expanded and truncate apical palpomere. Prementum narrow, with small to virtually missing ligula; if present, ligula simple or moderately emarginate, sometimes projecting anterolaterally; palps long (up to almost as long as maxillary palps), three-segmented; apical palpomere generally similar to that of maxillary palps. Ventral side without paired subgenal ridges; lower part of gena (bearing mandibular pit) projecting into conical ventral process in *Hypocephalus* (particularly large in male). Metatentorial slits widely separated, continuing anteriorly as more or less distinct gular sutures reaching anterior cranial margin (gula constricted by ventral eye lobes in Mysteriini of Anoplodermatinae, Fig. 2.1.4 E); intermaxillary process absent or short; tentorial bridge broad, roof-like; pre- and metatentorium connected; at least bases of dorsal arms present (Fig. 2.1.4 E, F). Cervical sclerites present.

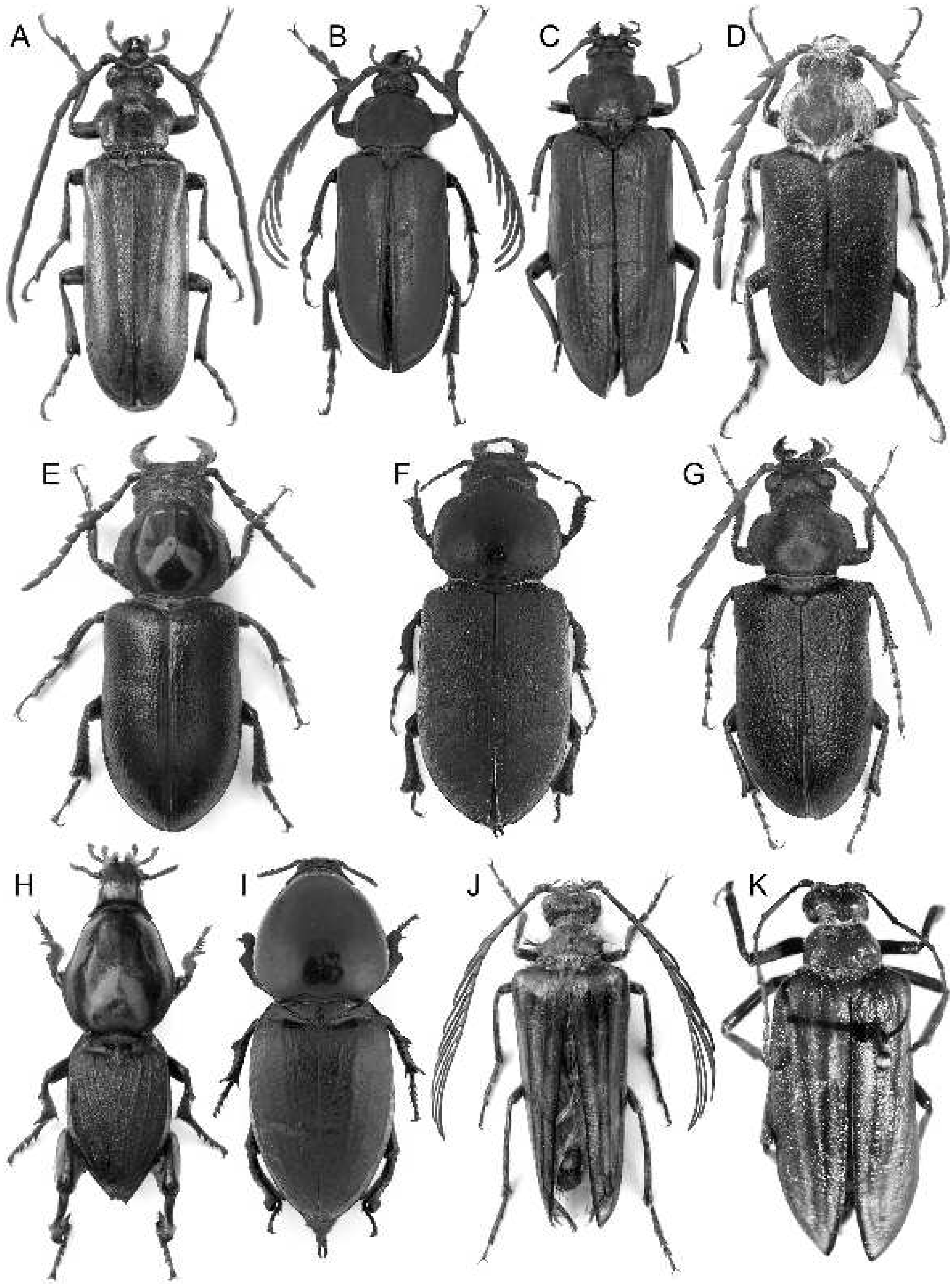

Fig. 2.1.2 Adults of Anoplodermatinae (A–I) and Vesperoctenini (J, K), dorsal view. A, *Mysteria minuta* Dias, male, 15.5 mm; B, *Pseudopathocerus humboldti* (Lameere), male, 21 mm; C, *Pathocerus wagneri* Waterhouse, damaged female, 49 mm; D, *Sypilus orbignyi* Guérin-Méneville, male, 19 mm (© I. Jeniš); E, *Migdolus fryanus* Westwood, male, 35 mm (© I. Jeniš); F, *M. fryanus*, female, 37 mm; G, *Anoploderma breueri* Lameere, male, 19.5 mm; H, *Hypocephalus armatus* Desmarest, male, 44 mm (© I. Jeniš); I, *H. armatus*, female, 47 mm; J, *Vesperoctenus flohri* Bates, male, 22 mm (© I. Jeniš); K, *V. flohri*, lectotype female, 27 mm (© E. Vives).

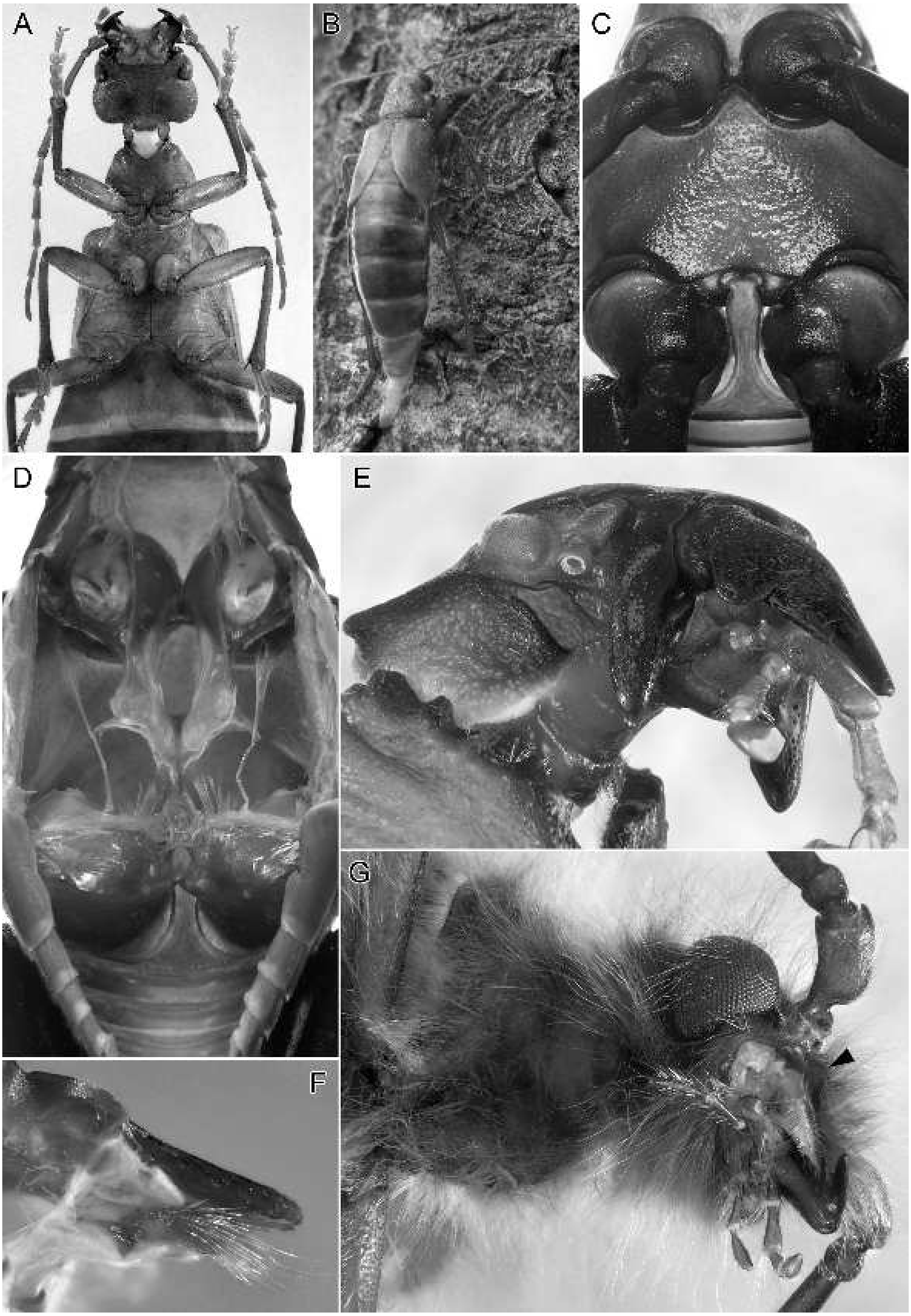

Fig. 2.1.3 A, *Vesperus strepens*, female, ventral view; B, *Mantitheus pekinensis* Fairmaire, female ovipositing in bark of a fruit tree (© E. Kučera); C, *Hypocephalus armatus*, male, pterothorax and base of abdomen, ventral view; D, *H. armatus*, male, pterothoracic endoskeleton, dorsal view; E, *H. armatus*, male, head, lateroventral view (right antennal flagellum and three distal segments of right maxillary palp removed); F, *Pathocerus wagneri*, male, postclypeal projection covering anteclypeus and labrum, lateral view; G, *Vesperoctenus flohri*, male, head, anterolateral view (right mandible and maxillary palp removed, arrowhead points to right lobe of the bilobed postclypeal projection above anteclypeus).

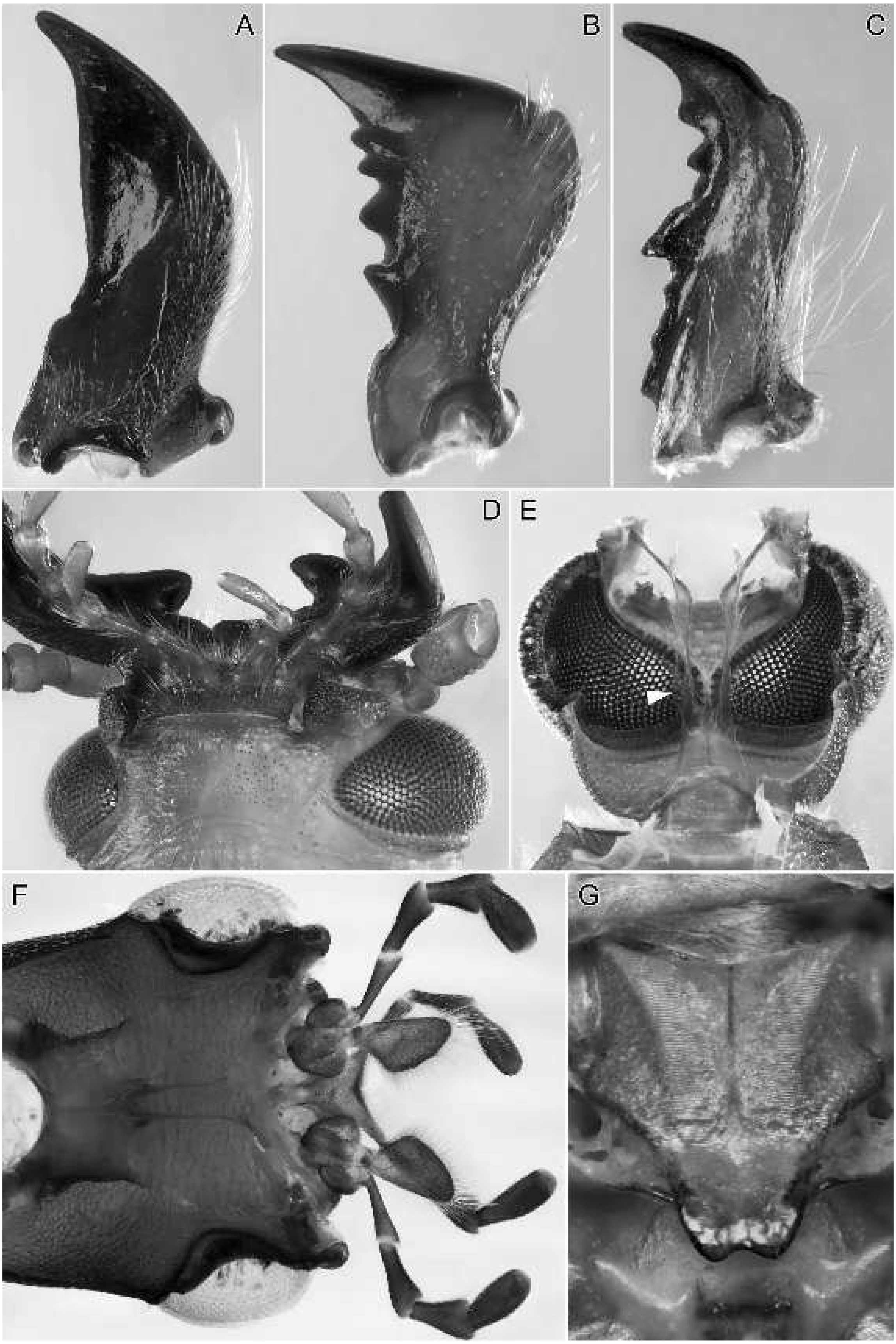

Fig. 2.1.4 A, *Philus antennatus*, female, right mandible, dorsal view; B, *Pseudopathocerus humboldti*, male, right mandible, dorsal view; C, *Vesperoctenus flohri*, male, right mandible, dorsal view; D, *Anoploderma breueri*, male, anterior head, lateroventral view; E, *Pathocerus wagneri*, male, ventral cranium with tentorium, dorsal view (arrowhead points to thin anterolateral projection of corpotentorium, removed on right side); F, *Philus antennatus*, female, ventral cranium with maxillolabial complex, dorsal view; G, *Vesperus conicicollis hispalensis* Fuente, male, mesoscutum with distinct rudiments of stridulatory file, dorsal view.

Pronotum about 0.5–1.4 times as long as wide; base distinctly to very slightly narrower than elytral base, or (*Hypocephalus*) elytral and pronotal bases both narrowed; lateral pronotal margins complete and often with distinct bead in Anoplodermatinae; usually incomplete to virtually absent in Vesperinae and Philinae, absent in *Vesperoctenus*; anterior pronotal angles usually not produced; posterior angles broadly rounded to square; posterior edge more or less straight or evenly rounded; disc without paired basal impressions or median longitudinal groove, simple or with pair of tubercles. Prosternum in front of coxae usually longer than shortest diameter of procoxal cavity (shorter in some Anoplodermatinae), sloping, flat or convex. Prosternal process variable, complete to slightly shortened; in some cases with secondary coxal articulation if strongly elevated; apex acute to broadly rounded or emarginate. Notosternal sutures complete. Procoxae not concealed laterally (trochantins at least partly exposed), projecting well below reduced compressed prosternal process in *Vesperus* and *Vesperoctenus*, and also in *Hypocephalus*, where the prosternal process is well developed. Procoxal cavities slightly to strongly transverse and extended laterally, contiguous to moderately widely separated; internally closed (sometimes only by a very narrow fine bridge); externally narrowly closed in Anoplodermatinae, narrowly or broadly open in Philinae, *Vesperus* and *Vesperoctenus*. Mesoscutum broadly emarginate anteriorly, usually with more or less complete median endocarina (nearly straight and without endocarina in *Hypocephalus*); indistinct stridulatory plate present in some Philinae and vestiges in some *Vesperus*. Scutellar shield not abruptly elevated above and/or separated from mesoscutum; anteriorly simple, posteriorly acute, rounded or bilobed. Elytra fully developed or (females of *Heterophilus*, *Mantitheus* and most *Vesperus*) more or less strongly shortened, 0.8–3.2 times as long as combined width and 1–8 times as long as pronotum; irregularly punctate or rugose, without scutellary striole; apices meeting at suture or (always in brachelytrous females) independently rounded and dehiscent; epipleura variable. Mesoventrite separated by complete sutures from mesanepisterna, which are distinctly separated at midline; anterior margin on same plane as metaventrite or more or less sloping; paired procoxal rests indistinct or missing. Mesoventral cavity absent. Mesocoxal sockets circular to slightly obliquely extended, narrowly separated, broadly open laterally to mesepimeron; mesocoxae somewhat conical and moderately projecting posteriorly in Vesperinae, Philinae and *Vesperoctenus* (mesocoxal cavities in those groups with poorly defined posterior margin); in Anoplodermatinae less prominent, with well-defined sockets and occasionally a secondary articulation on the mesoventral process. Mesometaventral junction narrow, occasionally missing when the metaventral projection is reduced. Metaventrite with discrimen usually moderately to very long (absent in *Hypocephalus* and short in some Philinae); postcoxal lines absent; exposed portion of metanepisternum usually moderately elongate (short and broad in *Vesperoctenus*), strongly tapering posteriorly to subparallel; completely fused with metaventrite in *Hypocephalus* (unique among cerambycoids). Metacoxae usually contiguous or narrowly separated (widely separated in some flightless females); somewhat oblique in *Vesperoctenus*, enlarged and projecting (particularly in males) in *Hypocephalus*; extending laterally to meet elytra or separated from them; plates absent. Metendosternite with lateral arms moderately to very long; laminae absent in Anoplodermatinae, present in remaining groups; anterior process short or absent; anterior tendons narrowly to moderately broadly separated; pterothoracic sternal endoskeleton strongly modified in *Hypocephalus* (see description of that taxon and Fig. 2.1.3 D). Hind wing in macropterous specimens with moderately large apical field bearing two (Philinae; Fig. 2.1.5 A) or only one (other groups, Fig. 2.1.5 B–G) distinct sclerotized radial vein remnants; radial cell moderate to small, closed or (some Anoplodermatinae) open proximally; crossvein r3 present (then oblique) or absent; r4 present and with spur very short or, most often, absent; basal portion of RP moderately long, far overreaching r4 proximally; medial field with five free veins in most Philinae (four in *Mantitheus* and *Heterophilus*) and typically in *Vesperus*; usually four in *Vesperoctenus* and Anoplodermatinae (either unbranched MP_{3+4} or reduced MP_3); more or less distinct medial fleck present in some Anoplodermatini; wedge cell well-developed in Philinae, narrow but distinct in *Vesperoctenus*, narrow, rudimentary or absent in *Vesperus*, invariably absent in Anoplodermatinae; anal lobe well-developed, often enlarged, without embayment. Wings more or less reduced in females of *Mantitheus* and *Heterophilus* of Philinae, of almost all species of *Vesperus*, and of all known Anoplodermatini (absent in both sexes of *Hypocephalus*). Legs moderately long and slender in Vesperinae, Philinae, *Vesperoctenus* and some Anoplodermatinae (particularly some Mysteriini); shorter and stronger to pronouncedly fossorial in remaining Anoplodermatinae, extremely modified in *Hypocephalus*; trochanterofemoral joint moderately to strongly oblique but base of femur remains separated from coxa; distal end of hind trochanter in males of *Paramigdolus* Dias projecting into a spine usually surpassing middle of femur; metafemora greatly enlarged in *Hypocephalus*; apices of all or at least fore tibiae with flattened outer teeth in some Philinae and all Anoplodermatinae; moderately to strongly widened apically in most Anoplodermatinae, where the apical area bearing the tarsus and spurs is surrounded by a palisade of dense setae; tibial spurs 2-2-2 in Vesperinae, 1-2-2 (*Philus*, *Doesus*, *Heterophilus*) or 2-2-2 (remaining genera) in Philinae, and 2-2-1 in *Vesperoctenus*

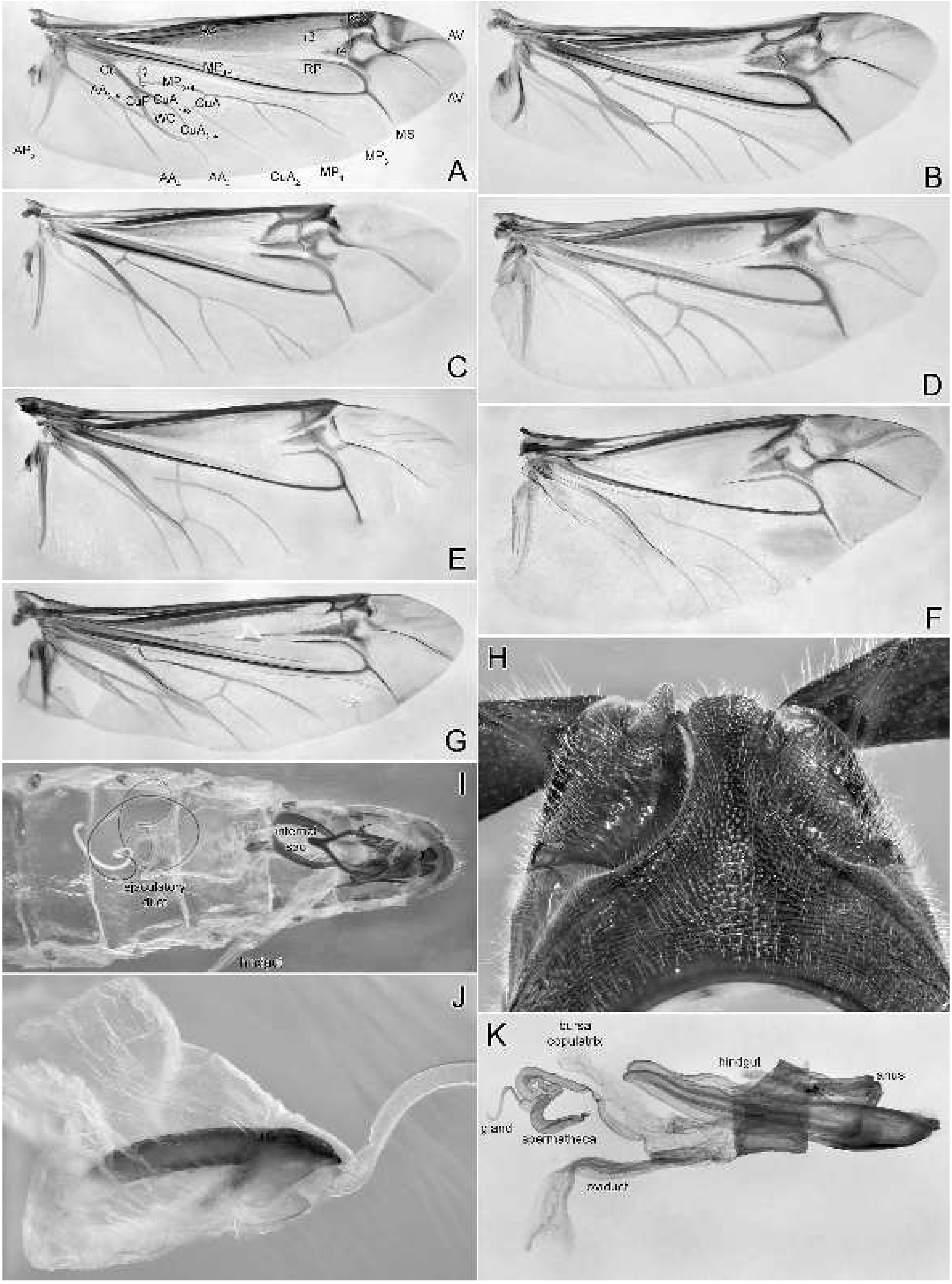

Fig. 2.1.5 A–G, right wing: A, *Philus pallescens* Bates, female; B, *Vesperus conicicollis hispalensis*, male; C, *V. strepens*, male; D, *Mysteria minuta*, male; E, *Pathocerus wagneri*, male; F, *Migdolus fryanus*, male; G, *Vesperoctenus flohri*, male; H, *Philus antennatus*, female, procoxae and prosternal process, anterior view (apex of left coxa exposed to show articulating tubercle); I, *Pathocerus wagneri*, male genitalia, ventral view (sterna removed); J, *P. wagneri*, male, base of retracted internal sac, gonopore projecting into strong spine; K, *Migdolus fryanus*, female genitalia, left lateral view (parts of sclerotized apices of coxites broken). AV, veins in apical region (all are presumably of radial origin); MS, medial spur; RC, radial cell; WC, wedge cell; *, mp_{3+4}-cu; ?, a vein of uncertain homology (either a crossvein or base of MP_{3+4}).

and most Anoplodermatinae (further reduced in some anoplodermatine females and in both sexes of *Hypocephalus*); tarsi 5-5-5 in both sexes, more or less pseudotetramerous (with emarginate tarsomere 3 partly hiding small 4 and with distinct ventral pads on first three tarsomeres) in Vesperinae, Philinae and some Anoplodermatinae (particularly fore and mid tarsi of *Pseudopathocerus*); transitional in *Vesperoctenus* and many Anoplodermatinae, and clearly pentamerous (without lobes and pads and with distinct exposed tarsomere 4) in some female anoplodermatines and in both sexes of *Hypocephalus*; pretarsal claws simple, extensively movable, lacking setae; empodium from large and multisetose to small and hidden when claws are flexed.

Abdomen usually with five visible sterna (III–VII); first not much longer than second, without postcoxal lines; intercoxal process usually acute or narrowly rounded, but broadly rounded in *Hypocephalus*; reduced in *Vesperoctenus* and some Vesperinae and Philinae, partly exposing sternum II, particularly in females with broadly separate hind coxae; sternum II large and visible along entire abdominal width in physogastric females of some Vesperinae and *Mantitheus*. Functional spiracles present on segments I–VII or rarely I–VI (female of *Migdolus*), located in lateral membrane. Males with anterior edge of sternum VIII bearing median strut; anterior edge of sternum IX with spiculum gastrale; terga IX and X completely fused and membranous. Aedeagus cucujiform, symmetrical; anterior edge of tegmen usually with single strut; parameres mostly separate (completely fused in *Pseudopathocerus* and nearly so in *Pathocerus*), fused to phallobase or at most more flexible basally; anterior edge of penis with paired struts. Gonopore may project into a spiculum; ejaculatory duct unpaired and usually containing long sclerotized tube or rod within much of its distal portion (Fig. 2.1.5 I; absent in *Philus*, *Doesus*, *Spiniphilus* and some *Vesperus*; not depicted in *Vesperoctenus* by Vives 2001). Female sternum VIII with spiculum ventrale. Ovipositor in Vesperinae and Philinae (Fig. 2.1.6 B) long and flexible; coxites with thick baculi and free terminal styli; dorsal baculi short; paraproct and its baculi long; proctiger very long and with two pairs of thin baculi; a flexible ovipositor may also occur in *Vesperoctenus* as the styli are apparently terminal (judging from Vives 2001); “digging” ovipositors of Anoplodermatinae (Fig. 2.1.5 K) are short, with coxites extensively and heavily sclerotized (expanded coxital baculi or also distal parts of dorsal baculi), not subdivided, with styli (dorso)lateral and reduced or more or less sunken in coxites, paraproctal baculi thick and forming long internal apodemes, proctiger membranous and without baculi. Small “intersegmental pouches” at the ovipositor base (Schomann 1937) occur in *Vesperus* and Philinae, but Schomann did not find symbionts in them in the former genus (Philinae were not studied). Internal female genitalia very similar and uniquely modified in *Vesperus* and Philinae, which lack a sclerotized spermatheca; their vagina bears only one membranous sac on a more or less narrow duct, which was interpreted as a desclerotized spermatheca without spermathecal gland by Saito (1990) (Fig. 2.1.6 B); alternatively, it might be the bursa copulatrix and the spermatheca would be absent. Anoplodermatinae (*Pathocerus* and *Migdolus* dissected) with sac-like bursa copulatrix bearing distinct sclerotized spermatheca; associated sclerotized variously coiled distal part of spermathecal duct bears spermathecal gland (Fig. 2.1.5 K; situation resembles some Disteniidae). Internal female genitalia unknown in *Vesperoctenus*.

Morphology, Larvae (Fig. 2.1.6 D–F, 2.1.8 B–F; based on *Vesperus* of Vesperinae, *Migdolus* of Anoplodermatinae and three genera of Philinae; larvae of the three subfamilies are rather different). Body soft, white or yellowish, not depressed; in Philinae and *Migdolus* moderately elongate, broadest at thorax or anterior abdomen, covered with locally dense short setae and extensive vestiture of very fine microtrichia; in *Vesperus* very stout and pyriform, broadest and highest posteriorly and without extensive microtrichia.

Head distinctly narrower than prothorax, almost completely retracted, prognathous and with short frons and no exposed coronal stem in Philinae and *Migdolus*; oblique and with frons longer and coronal stem present in *Vesperus* (presence of exposed coronal stem unique among cerambycoids, possibly secondary and associated with stout and very high body and oblique head). Cranium slightly transverse to approximately as long as broad, almost completely lacking strongly sclerotized and pigmented areas, subparallel or slightly convex laterally; medial cranial duplicature at frontal base short or absent. Frontal lines indistinct, often only traceable from splits on larval exuviae (splits may be irregular laterally, apparently not following original frontal lines; exuviae not available in *Migdolus*). Frons in Philinae and *Vesperus* with median endocarina, clypeus not sharply separated from frons, large, complete and with postclypeal setae (i.e., postclypeus not fused with frons to form strengthened epistomal margin); in *Migdolus* frons extremely short, without endocarina and separated from clypeus by strengthened infolding that may not be homologous to the epistomal margin of Disteniidae and Cerambycidae as it bears no distinct epistomal (= postclypeal) setae, whereas a row of strong pointed setae is present on the clypeus (Fig. 2.1.7 B). Pretentorium similar to that of Cerambycidae, with slender arms pointing posteriorly; arms prolonged in Philinae and *Migdolus* where they follow the extremely long antennal muscles for much of their length; pretentorial pits not distinct. Labrum free, transverse, densely setose, at least along margin. Epipharynx as in Fig. 2.1.7 C–E

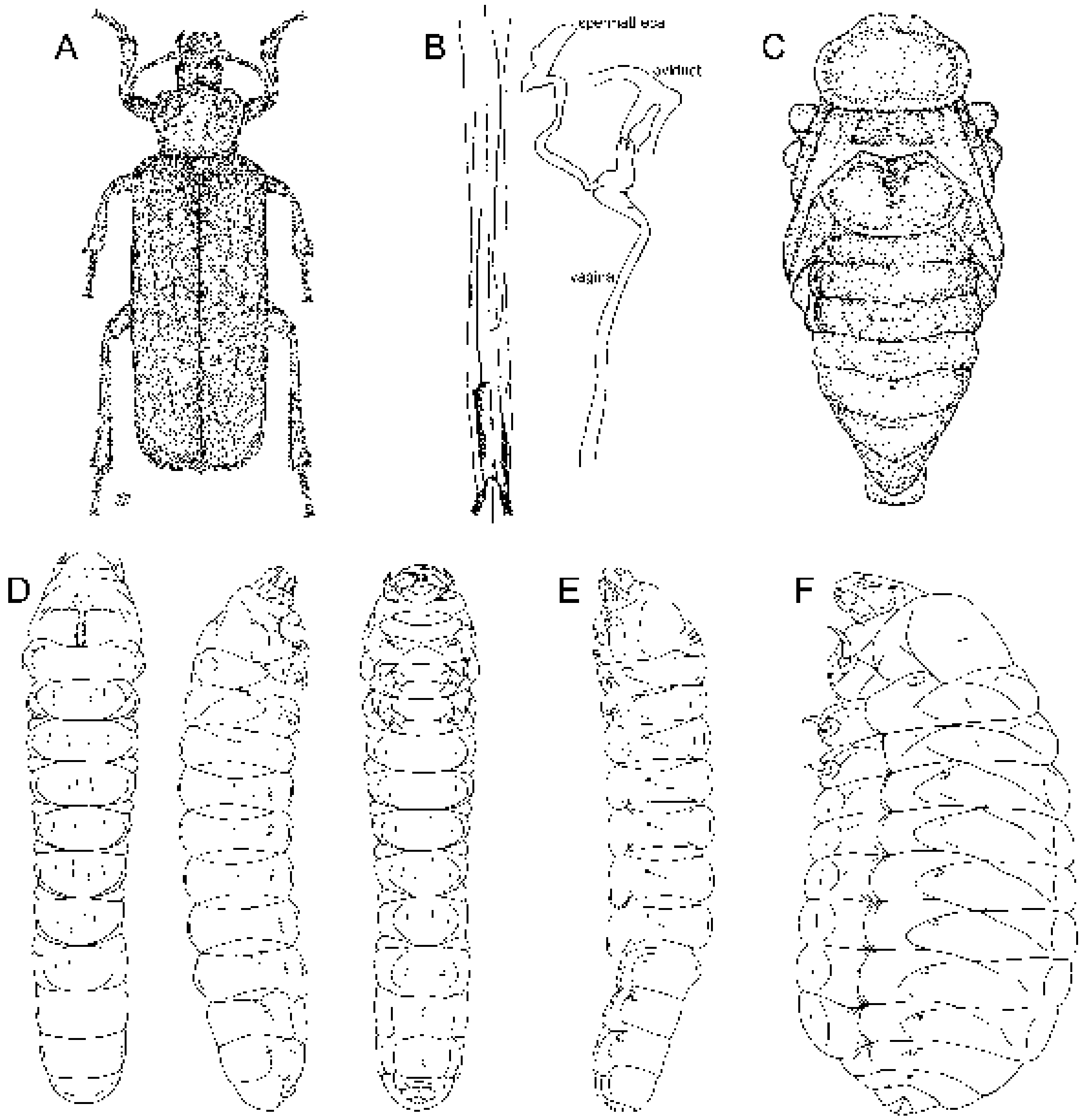

Fig. 2.1.6 A, *Mysteria darwini* (Lameere), female, dorsal view, 37 mm (from Dias 2004); B, *Vesperus strepens*, female, ovipositor (left half ventral view, right half dorsal view) and internal genitalia (from Saito 1990); C, *Migdolus fryanus*, pupa, dorsal view (from Costa *et al.* 1988); D, *Philus antennatus*, larva, dorsal (left), lateral (middle) and ventral view (right), drawn from slightly extended specimen; E, *Migdolus fryanus*, larva, lateral view; F, *Vesperus xatarti*, larva, lateral view, drawn from slightly extended specimen (D–F from Svacha *et al.* 1997).

(longitudinally compressed and with the group of five paired sensilla strongly shifted anteriorly in Philinae and *Migdolus*). Pleurostomal region not swollen or strongly sclerotized. Stemmata absent or very small pigment spots of three main stemmata present but without distinct lenses. Antennal socket without sclerotized ring. Antenna trimerous, very long; completely retractile in Philinae and *Migdolus* (antennal muscles extremely long and attached to dorsal cranium slightly beyond its midlength), not retractile in *Vesperus*; first antennomere strongly elongate, with secondary flexion zone in Philinae; third antennomere very small; sensorium flat to very shortly conical. Mandibles symmetrical, long, with basal parts broad and distant from each other (Fig. 2.1.9 F), without molar armature or prostheca; distal part flat, shovel-like and carinate dorsally and ventrally; apical structures often abraded; in intact mandibles of Philinae and *Vesperus* (particularly in first instars), apical edge forms three teeth (the two ventral teeth may be very poorly defined or indistinct), and at least the dorsal tooth is separated by a distinct incision (Fig. 2.1.9 C, F, H, 2.1.10 I), later instars of *Migdolus* have truncate mandibular apex (first instars not available). Maxillolabial complex very large, not retracted (depending on position of large

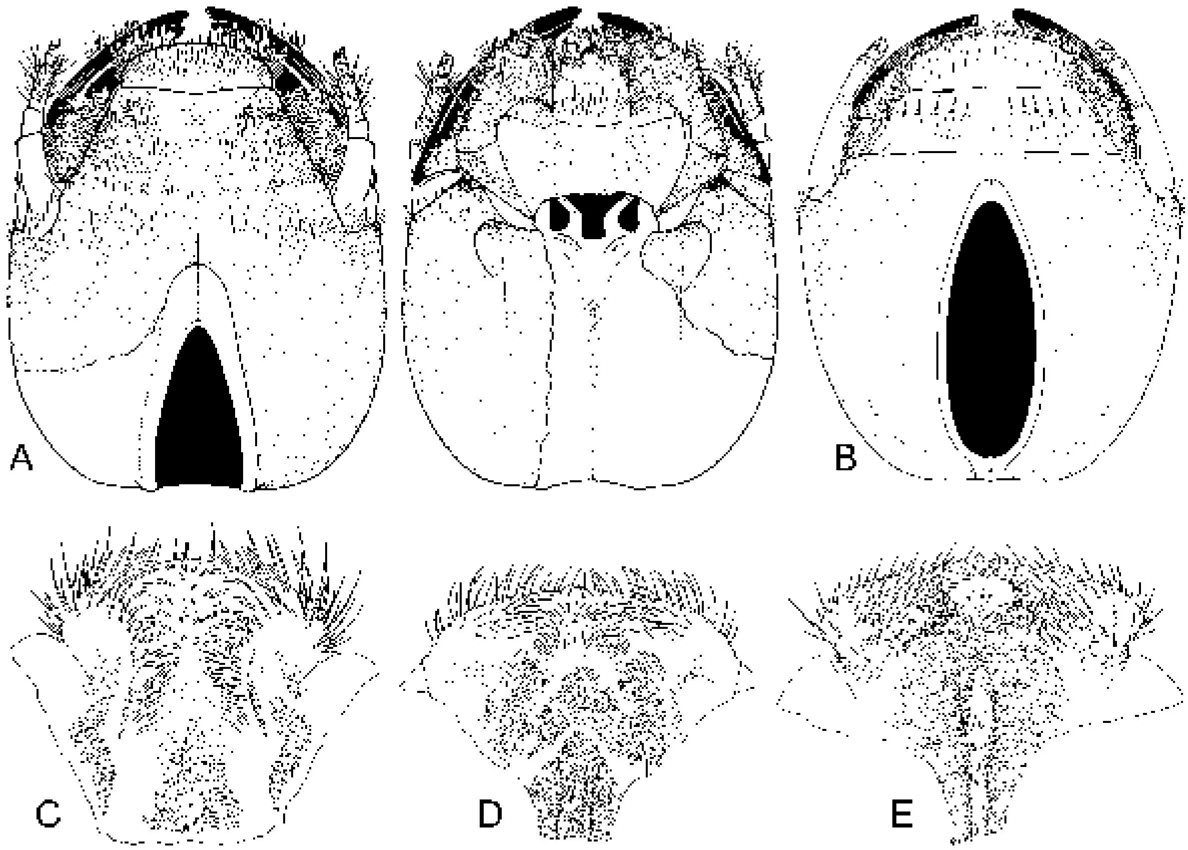

Fig. 2.1.7 Larvae. A, *Philus antennatus*, head, dorsal (left) and ventral view (right); B, *Migdolus fryanus*, head, dorsal view; C, *Vesperus luridus* (Rossi), epipharynx; D, *Philus antennatus*, epipharynx; E, *Migdolus fryanus*, epipharynx (all figures from Svacha *et al*. 1997).

movable cardo, cardo/stipital border slightly anterad to slightly posterad of level of ventral mandibular condyle in ventral view). Maxillary articulating area large, sharply divided in Philinae and *Vesperus*, not distinctly divided in *Migdolus*. Cardo large, free, not distinctly sclerotized or divided; stipes large and without basal sclerotized band; palpiger incompletely separated from stipes by lateral notch, densely setose; palps trimerous; palpiger and first palpomere without laterodorsal process; mala fixed, with inner side carinate and inserted obliquely above distal labium, bearing strong setae and tubercle with two closely adjacent more or less embedded smaller sensilla (Fig. 2.1.10 E–H). Labium variable (modified in *Migdolus*); palps dimerous. Hypopharyngeal sclerome and hypopharyngeal bracon absent. Hypostomal rods ending blindly posteriorly, missing in *Vesperus*; ventral epicranial ridges absent. Gula absent (labial base and prosternum connected by membrane). Metatentorial pits not distinct, metatentorium invaginates extremely broadly (Fig. 2.1.7 A, 2.1.9 B) along lateral margin of ventral and in *Migdolus* also posterior part of occipital foramen and fuses into plate-like tentorial bridge (that of *Migdolus* is apparently the broadest known in beetle larvae; Fig. 2.1.7 B, 2.1.9 E); its anterior margin bears distinct arms running toward dorsal cranium but not connected with pretentorial arms.

Prothorax enlarged, nearly as long as pterothoracic segments combined; with moderate sclerotizations at most; pronotum and prosternum in *Migdolus* with transverse sclerotized ridges. Pronotum not or incompletely delimited laterally; in Philinae and *Migdolus*, slightly expanding posteriorly at middle, thus reducing size of mesonotum. Epipleuron more or less separate; pleurosternal region differing between subfamilies (also differing from the presumptive cerambycid ground plan and often difficult to homologize). Pleural apodeme always well-developed. Furca and spina distinct to strongly reduced (Fig. 2.1.11 B, D, F). Meso- and metathorax short; alar lobes without wing discs; epipleuron defined. Mesothoracic spiracle without marginal chambers, not (*Migdolus*) to slightly (*Vesperus*) protruding into prothorax; rudiments of metathoracic spiracle distinct. Pleural and sternal parts variable, tending to fuse into one transverse fold in *Migdolus*; sternal endoskeleton indistinct or mesothoracic spina present. Coxa more or less defined, without sclerotized rod supporting coxotrochanteral articulation even if slightly projecting (*Vesperus* and forelegs in *Migdolus*); distal legs short to

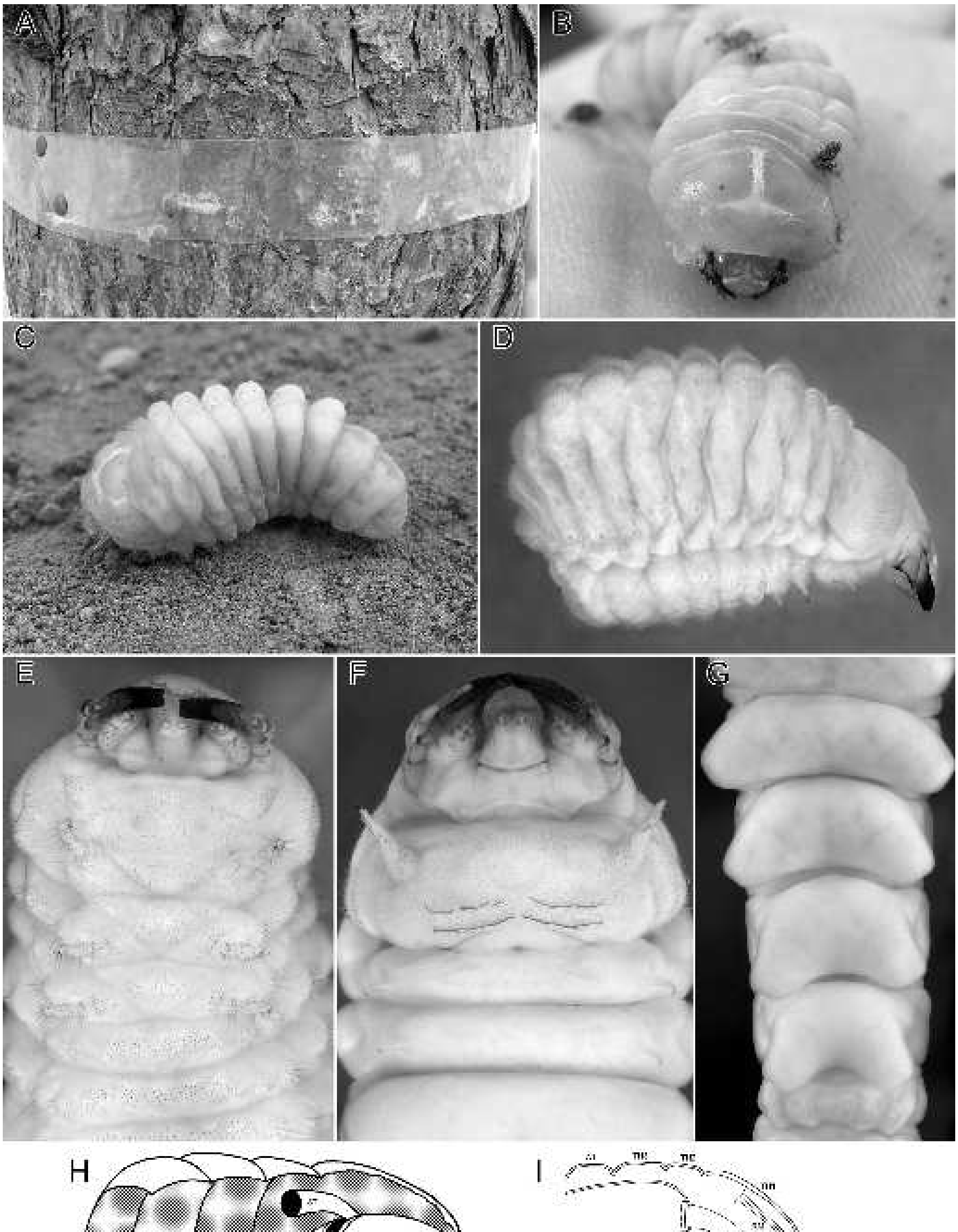

Fig. 2.1.8 A, *Mantitheus pekinensis*, hatched egg batches under protective plastic band on a pine tree in Beijing Botanical Garden (© W. Bi); B–I, larvae: B and C, *M. pekinensis*, living specimen, anterior (B) and lateral view (C) (© W. Bi); D, *Vesperus sanzi* Reitter, lateral view; E, *V. sanzi*, head, thorax and first two abdominal segments, ventral view; F, *Migdolus fryanus*, head, thorax and first abdominal segment, ventral view; G, *M. fryanus*, pseudopods on abdominal segments 2–5, ventral view; H, Philinae, head, thorax and first abdominal segment, posterolateral view, diagrammatic (right lateral part of body wall removed to show relative position of some internal structures, deeply retracted head inserted in membranous prothoracic pocket, and unusually broad tentorial bridge widely separating the "neural" and "stomodaeal" parts of the occipital foramen and making the latter posterodorsal); I, *Philus antennatus*, semidiagrammatic submedial section through head, thorax and first abdominal segment (showing the absence of gula and very broad tentorial bridge) (H and I from Svacha *et al*. 1997). A1, first abdominal segment; ANT, antenna; CL, clypeus; CRD, concealed cranial duplicature; ENC, median frontal endocarina (continues also on CRD); FR, frons; LBI, labium; LBR, labrum; MD, mandible; MES, mesenteron; NC, nerve cord; PP, prothoracic membranous pocket embracing the deeply retracted head; RM, main dorsal head retractor muscles (diagrammatic); ST, stomodaeum; TB, tentorial bridge; TH1–3, pro-, meso- and metathorax.

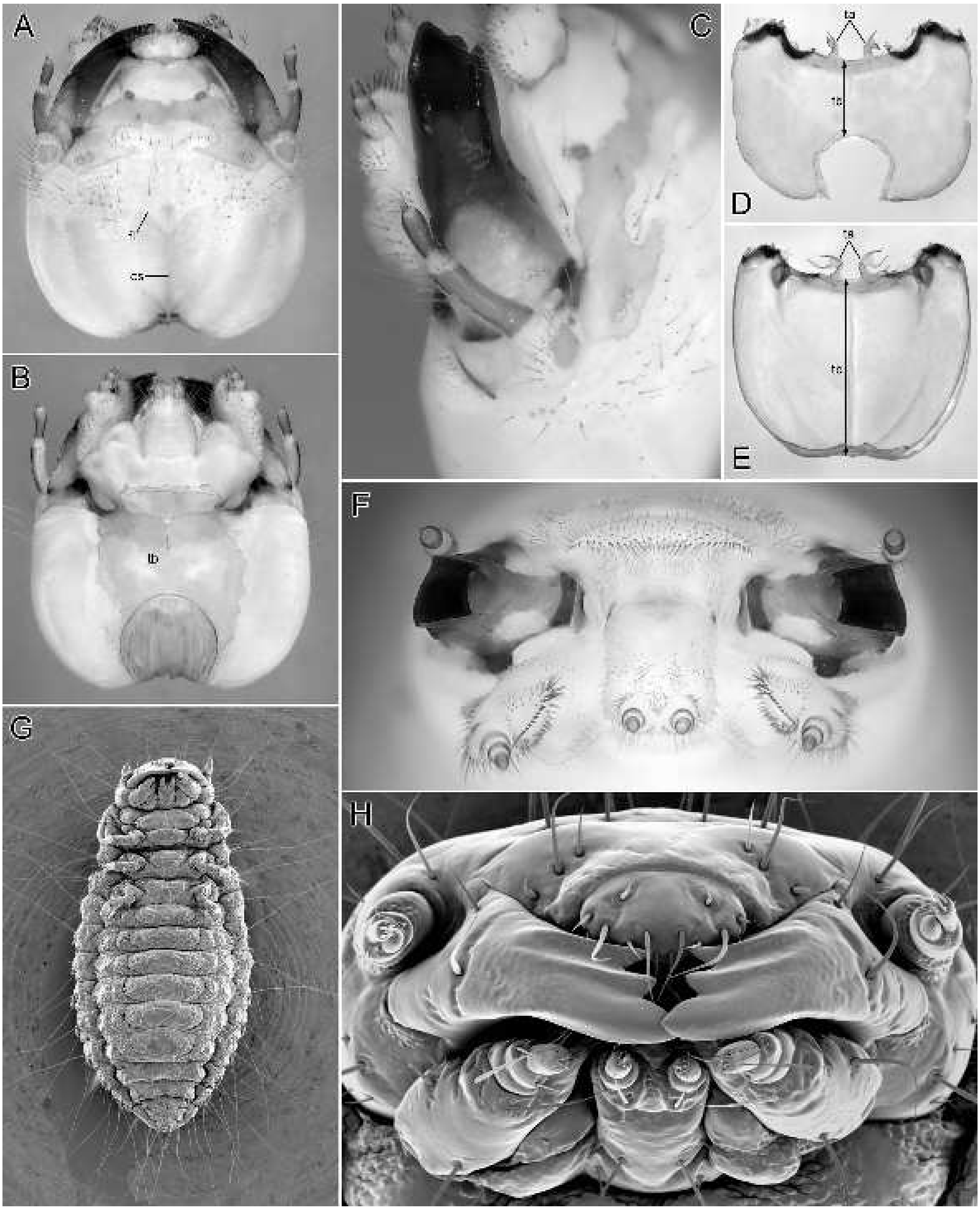

Fig. 2.1.9 Larvae. A, *Vesperus sanzi*, head, dorsal view; B, *V. sanzi*, head, ventral view; C, *V. sanzi*, head, anterolateral view; D, *V. luridus*, ventral half of cranium, dorsal view (tentorial arms on anterior margin of tentorial bridge cut to short stubs); E, *Migdolus fryanus*, dtto.; F, *Mantitheus pekinensis*, head, anterior view (mouthparts broadly open by artificial internal pressure); G, *Vesperus luridus*, first instar, ventral view (SEM); H, *V. luridus*, first instar, head, anterior view (SEM) (G and H from Svacha *et al.* 1997). cs, coronal stem; fl, frontal lines; ta, metatentorial arms arising on anterior margin of tentorial bridge; tb, tentorial bridge.

moderately long (forelegs remarkably enlarged, modified and shifted anteriorly in *Migdolus*); trochanter without distinct basal sclerotized ring; pretarsus with needle-shaped sclerotized claw (flattened in forelegs of *Migdolus*), and one or (*Migdolus*) two basal setae from inner side.

Abdomen in Philinae and *Migdolus* with poorly defined dorsal ambulatory ampullae on segments I–VI; ventral ampullae absent on VI and strongly modified on II–V in *Migdolus* (Fig. 2.1.8 G, 2.1.11 E); *Vesperus* lacks distinct ampullae and terga and sterna I–VI are broad, plate-like and bearing a

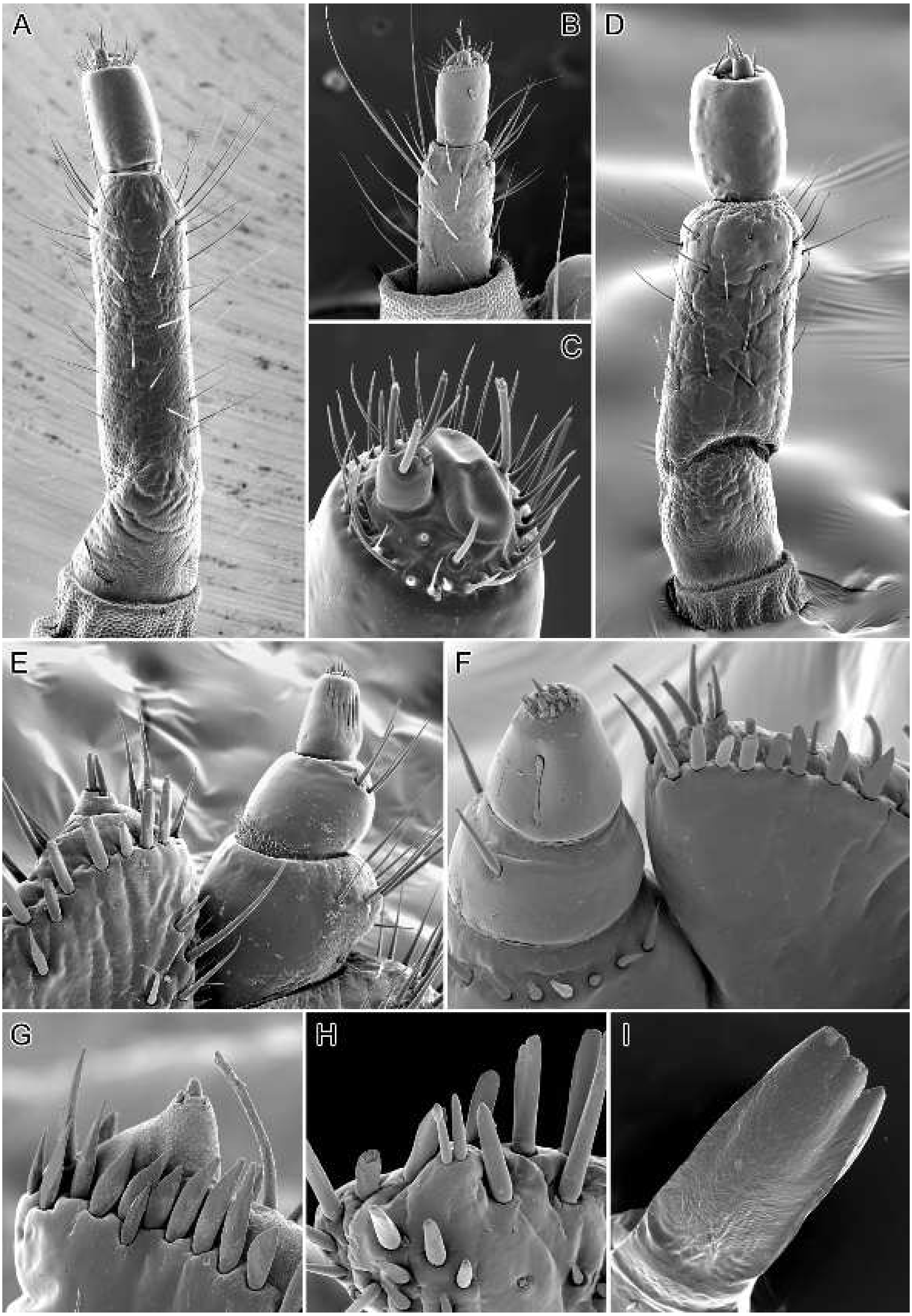

Fig. 2.1.10 Larvae, SEM. A, *Philus antennatus*, right antenna fully protracted, dorsal view; B, *P. antennatus*, left antenna half-retracted, dorsal view; C, *P. antennatus*, same specimen as in A, antennal apex, anterolateral view; D, *Heterophilus punctulatus* Chiang, Chen & Zhang, left antenna fully protracted, dorsal view; E, *Philus antennatus*, apical part of right maxilla, dorsal view; F, *Migdolus fryanus*, apical part of left maxilla, dorsal view; G, *Heterophilus punctulatus*, apex of left mala, dorsal view; H, *Vesperus luridus*, apex of right mala, anteroventral view; I, *Philus antennatus*, apical part of unabraded left mandible, lateral view (all except F from Svacha *et al*. 1997).

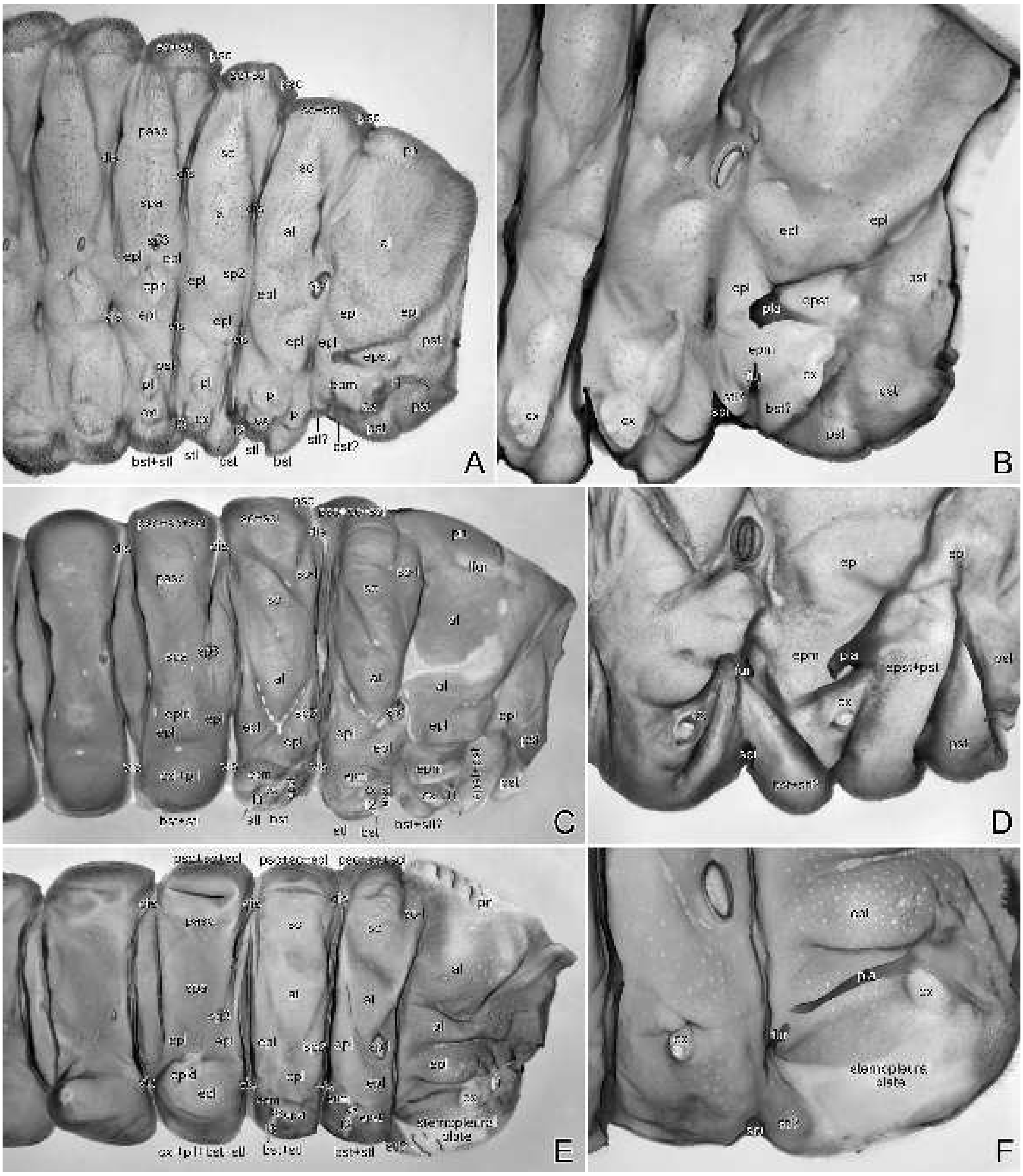

Fig. 2.1.11 Larvae, anterior part of body, cleaned cuticle stained with Chlorazol Black E. A, *Vesperus luridus*, right half of thorax and abdominal segments I and II, lateral view; B, *V. luridus*, left half of thorax, mesal view; C, *Philus antennatus*, right half of thorax and abdominal segments I and II, lateral view; D, *P. antennatus*, lower part of left half of pro- and mesothorax, mesal view; E, *Migdolus fryanus*, left half of thorax and abdominal segments I and II, lateral view (electronically horizontally reverted); F, *M. fryanus*, lower part of left half of pro- and mesothorax, mesal view. al, alar lobe; bst, basisternum; cx, coxa; dis, dorsal intersegmental zone; epl, epipleuron; epld, epipleural disc; eplt, epipleural tubercle; epm, epimeron; epst, episternum; fur, prosternal furca; l1, l2, l3, distal part of pro-, meso- and metathoracic legs (without coxa); lfur, lateral pronotal furrows; pasc, parascutum (abdominal homologue of lateral part of pterothoracic scuta); pl, pleuron (fused episternum and epimeron); pla, propleural apodeme; pll, pleural lobe (on abdominal segments); pn, pronotum; psc, prescutum; pst, presternum (usually reduced and not labelled on segments other than prothorax); sc, scutum; sc-I, scutum-I; scl, scutellum; sp1, sp2, sp3, mesothoracic, metathoracic (rudimentary and closed) and first abdominal spiracle; spa, spiracular area (presumed abdominal homologue of pterothoracic alar lobes); spi, prosternal spina; stl, sternellum; vis, ventral intersegmental zone. For a more detailed discussion of terminology see Cerambycidae.

combination of normal and short spine-like setae (Fig. 2.1.8 E). Intersegmental regions variable (virtually simple continuous infoldings in *Vesperus*). Spiracles I–VIII similar to those of mesothorax but much smaller. Epipleuron without tubercles and protuberant on several posterior segments in Philinae and *Migdolus*; slightly protuberant on all nine segments and with incompletely defined epipleural tubercles on five anterior segments in *Vesperus*. Segments VII–IX reduced in *Vesperus*; in live larvae more or less telescoped, rendering the abdomen truncate posteriorly. Tergum IX unarmed. Segment X separate from IX, not projecting, without sclerotizations. Anus triradiate or (*Vesperus*) transverse. Digestive tract as shown in Fig. 2.1.13, simplified in *Migdolus*. Proventriculus absent; posterior foregut slightly distensible and forming a small crop (more distinct in *Vesperus*); anterior midgut without mycetomes. Six Malpighian tubules enter gut in two groups of three. Nerve cord with eight abdominal ganglia; abdominal connectives closely adjacent, tending to fuse; long in *Migdolus* and Philinae (last ganglion reaching segment VII); extremely short in *Vesperus*, last ganglion hardly surpassing border between segments II and III in *V. luridus* (Rossi) (only species studied).

First instars (Fig. 2.1.9 G, H, 2.1.12 C, D) known of *Vesperus luridus* (Rossi) (Vesperinae) and *Mantitheus pekinensis* Fairmaire (Philinae). Basically similar to later instars but slightly more elongate in *Vesperus* (terminal abdominal segments not telescoped). Setation sparse; some dorsal and particularly lateral setae very long. Only three pairs present on clypeus. Main stemmata with large pigment spots and more or less convex corneae. Antennae shorter and much thicker; sensorium prominent and conical. Mandible distinctly tridentate in *Vesperus* (Fig. 2.1.9 H), in *Mantitheus* dorsal tooth smaller. Legs relatively long in both genera (in *Mantitheus* thus much longer than in later instars). Spiracles without broadly open atrium and with two marginal chambers (Fig. 2.1.12 C). Spine-like egg bursters (Fig. 2.1.12 D) present above spiracles on abdominal segments I–IV in *Vesperus*, and I–VI (last one smaller or occasionally absent) in *Mantitheus*. Low resolution photograph of first instar larva of *Migdolus* in Machado *et al.* (2006 b: Fig. 5b) shows that it is apparently similar to later instars including abdominal pseudopods.

Morphology, Pupae. Only pupae of *Vesperus sanzi* are available (Fig. 2.1.14; see also Calvo Sánchez 2007). Photograph of an ~~I agree, the readers will know~~ apparently strongly malformed pupa of *Philus ?antennatus* in ventral view was published in Lin *et al.* (2004), and a line drawing of *Migdolus fryanus* in dorsal view in Costa *et al.* (1988; present Fig. 2.1.6 C). Pupae are exarate, white or cream-colored, unsclerotized, without spines and largely devoid of setae except for some dorsal setose areas in *Vesperus* (however, setation was possibly omitted from the habitus drawing of *Migdolus* and complete absence of setae is unlikely even if the pupa is described as "glabrous"). Head strongly bent ventrally and mouthparts directed posteriorly. In *Vesperus sanzi*, body with extremely sparse, inconspicuous and very short setae except for broad central setose protuberance on pronotum and paired setose tubercles on first three abdominal terga (pupa lies on its back in pupal chamber). Both antennae combine in male to form single oval loop (like in Disteniidae and unlike most Cerambycidae where they are looped or coiled separately); female antennae very short. Abdomen without gin traps. Functional abdominal spiracles present on segments I–V; spiracles VI and VII reduced and apparently closed and non-functional (not visible in male specimen which is a moulting pharate adult with shrunken posterior abdominal cuticle); tergum IX bearing small soft urogomphi (Fig. 2.1.14 B). Female pupa with reduced short elytra and wings.

Phylogeny and Taxonomy (for family classification see also the general discussion under Cerambycidae). Vesperidae is perhaps the most problematic family of the cerambycoid assemblage, and its monophyly requires further testing. In some recent studies (e.g., Bousquet *et al.* 2009; Bouchard *et al.* 2011), its subgroups are still treated separately within a broader cerambycid concept. It is beyond the scope of this chapter to follow in detail the variegated taxonomic history of individual taxa here classified in Vesperidae. The extremely derived anoplodermatine genus *Hypocephalus* in particular was subject to shifts between what are today various beetle superfamilies, or even occasionally excluded from beetles in earlier studies (overview in Thomson 1861: 263–269; Lacordaire 1868: 29; LeConte 1876). However, an association of *Hypocephalus* with anoplodermatines was indicated at least as an alternative by some earlier authors. The genus was mostly placed with or near the other anoplodermatine genera since Lameere (1902), who argued that the extreme modifications are actually specializations for subterranean life and that transitional states can be found in the flightless females of some other anoplodermatines such as *Migdolus*. His position was not universally accepted (e.g., Lane 1937 or Prosen 1960). A placement of *Vesperoctenus* in "Rhipiceridae" near to *Callirhipis* Latreille (now Callirhipidae) by Horn (1894) was swiftly rejected by Gahan (1895; see rebuttal by Horn 1895).*Vesperus* was given a high rank in a comprehensive cerambycid classification as early as in Schiødte (1864), who divided cerambycids into Prionini, Vesperini, Asemini, Cerambycini, Lepturini and Lamiini. Nevertheless, the genera *Vesperus* and later also *Vesperoctenus* were most often placed with forms belonging to or resembling the cerambycid subfamily Lepturinae, primarily because of the strongly constricted neck and prominent fore coxae. It was not taken into account that the neck is constructed differently from Lepturinae (not involving the posterior gular region and metatentorial slits), and both genera differ from most or all lepturines

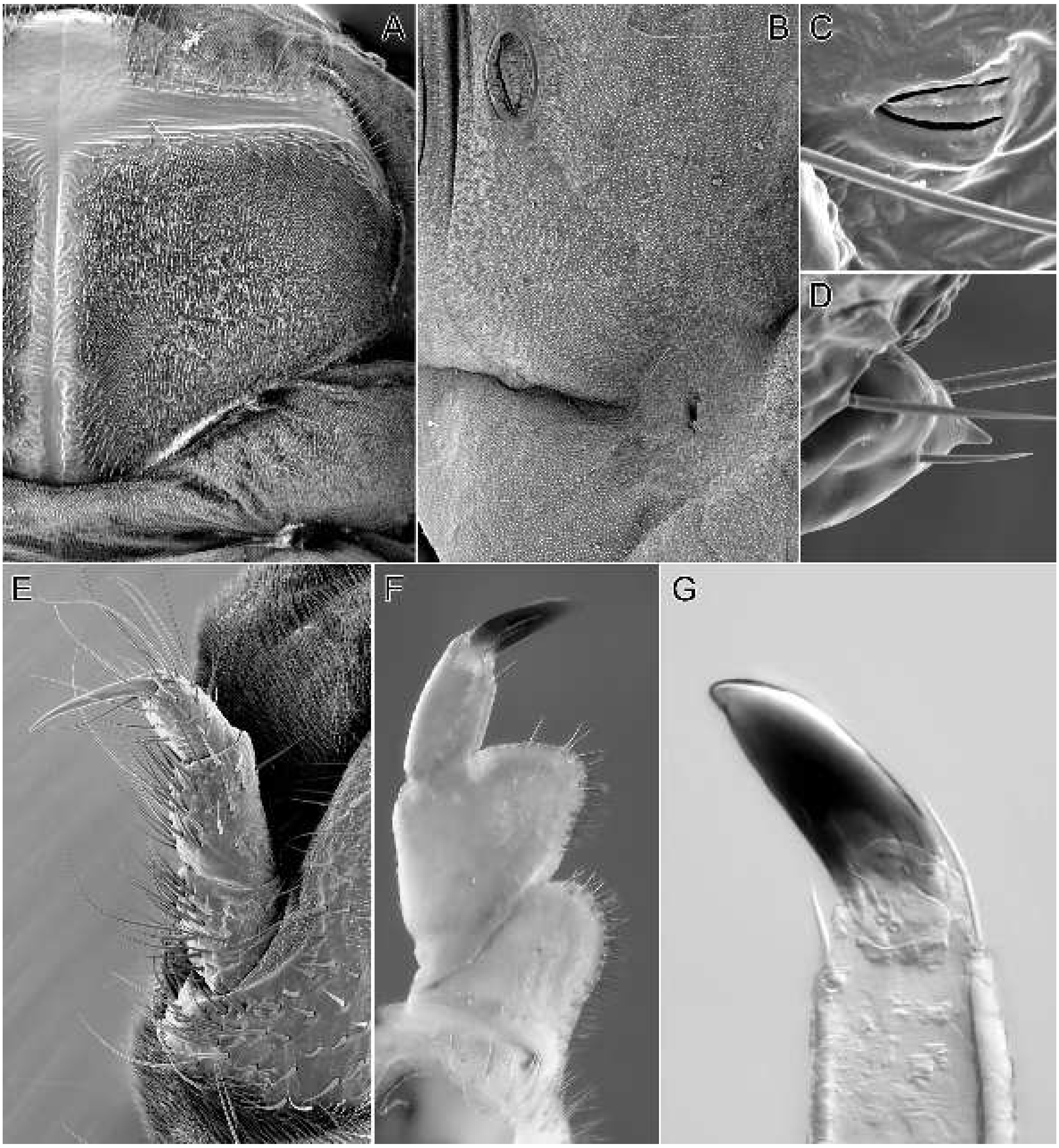

Fig. 2.1.12 Larvae. A, *Philus antennatus*, right half of pro- and mesonotum (SEM); B, *Heterophilus punctulatus*, left lateral part of abdominal segment I with spiracle and epipleural disc (SEM); C, *Vesperus luridus*, first instar, left abdominal spiracle VI (SEM); D, *V. luridus*, first instar, left egg burster on abdominal segment IV, ventral view (SEM); E, *Philus antennatus*, right fore leg, anterior view (SEM); F, *Migdolus fryanus*, left fore leg, mesal view (fore legs are directed anteriorly); G, *M. fryanus*, left fore pretarsus, ventrolateral view (showing two minute basal setae) (A–E from Svacha *et al*. 1997).

in many other characters: mandible without molar plate; very different maxillolabial complex (indicating adult aphagy) with small and proximally shifted lacinia, small ligula and long palps; gulamentum not forming intermaxillary process; and tentorial bridge broad and roof-like. Alternatively, in Lacordaire's (1869) classification, the Vesperides and Apatophysides composed the cohort "Cérambycides vrais souterrains", and *Vesperus* was thus far from Lepturinae, which were placed in Section B of "Cérambycides vrais sylvains". Differences between *Vesperus* and Apatophyseini (here a tribe in the cerambycid subfamily Dorcasominae) are likewise numerous, including features of the cranium, maxillolabial complex (differences similar to those from Lepturinae), wing venation (always without wedge cell in Dorcasominae), etc. Both Vesperinae and Philinae differ from virtually all remaining cerambycoids (including Anoplodermatinae; female reproductive tract unknown in Vesperoctenini) by the desclerotized sac-like spermatheca (Saito 1990; Fig. 2.1.6 B).

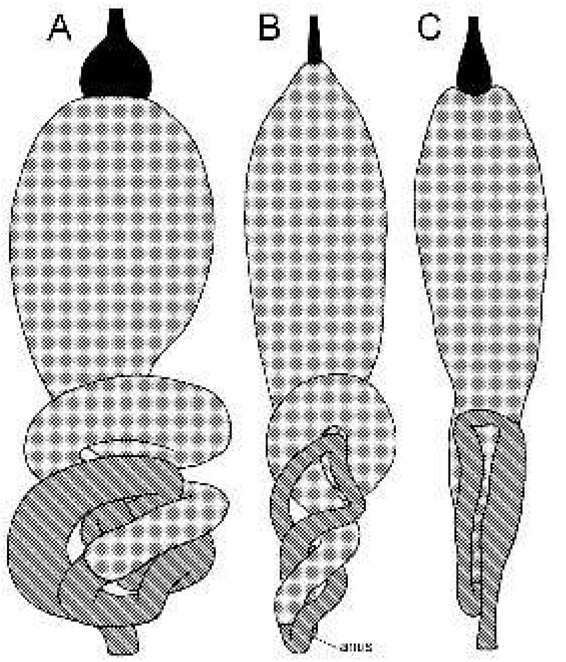

Fig. 2.1.13 Gross morphology of larval gut, diagrammatic, dorsal view. A, *Vesperus luridus*; B, *Philus antennatus*; C, *Migdolus fryanus*. Foregut black, midgut stippled, hindgut crosshatched (from Svacha *et al*. 1997).

Philinae were associated either with Prioninae because of the distinct (even if usually incomplete) pronotal margin of some genera, or with the rather heterogeneous lepturine assemblage, particularly when this grouping contained *Vesperus*. The genera of Philinae were not always placed together, as *Mantitheus* with its *Vesperus*-like brachelytrous females was occasionally classified with Lepturinae, whereas *Philus* and *Doesus* were kept outside it (e.g., as a separate tribe Philini of Cerambycinae placed before Lepturini with *Mantitheus* in Aurivillius 1912). Separating Philinae and Prioninae based on adult morphology is not easy due to many retained plesiomorphic characters; the wing characters sometimes used (e.g., Gressitt & Rondon 1970) are no longer valid because of some variability in the Philinae (Svacha *et al*. 1997; Lin & Bi 2011) and the more complete wing venations found in some "southern" Prioninae. In addition to the abovementioned "universal" difference of Philinae and Vesperinae from other cerambycoids in the lack of a sclerotized spermatheca, Philinae differ from most Prioninae by internally closed procoxal cavities (extremely narrowly and finely) and by the presence of a more or less distinct mesoscutal stridulatory file in some genera (absent in prionines). Differences between Philinae and most or all true Lepturinae are similar to those listed above for Vesperinae *vs*. Lepturinae. From the Dorcasominae (until recently mostly placed in Lepturinae), which do not possess the mandibular mola and may have a broad tentorial bridge, philines additionally differ by wings with a large wedge cell (absent in dorcasomines).

Thomson (1860–61) placed the present Anoplodermatinae (except *Hypocephalus*) in his very heterogeneous Cerambycitae: Spondylitae containing, besides Spondylitae verae (now Spondylidinae: Spondylidini), and Anoplodermitae, also Torneutitae (now Torneutini of Cerambycinae), Erichsonitae (now a tribe of Parandrinae), and Cantharocnemitae (now in Prioninae). *Hypocephalus* was

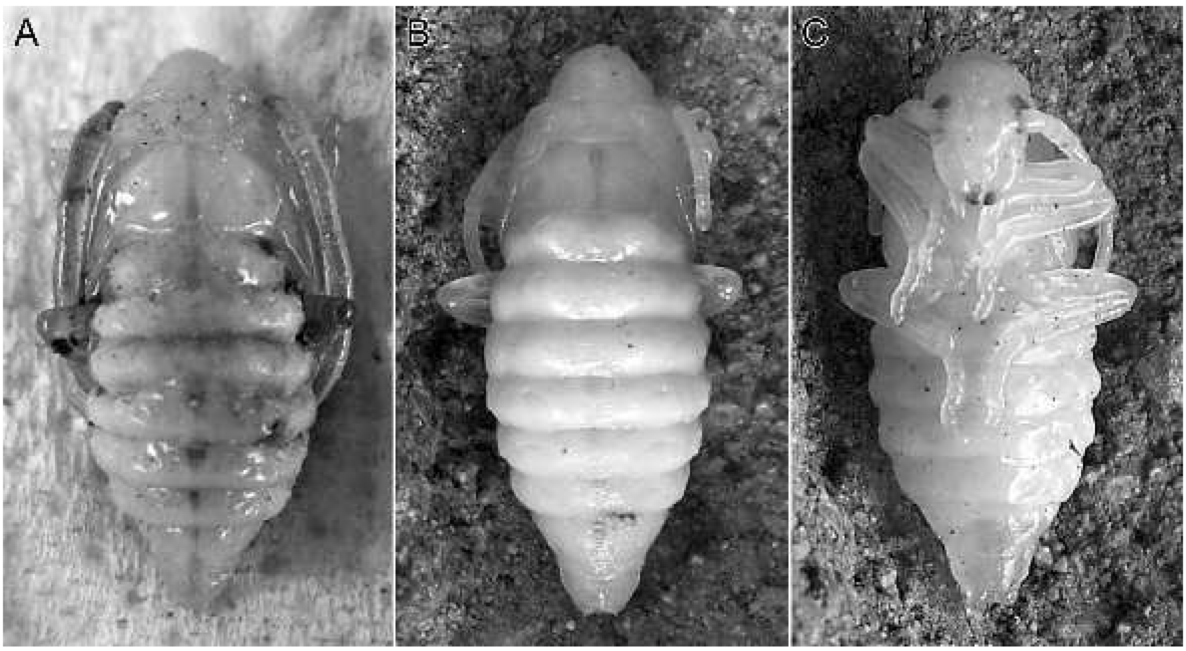

Fig. 2.1.14 *Vesperus sanzi*, pupa (© F. Calvo Sánchez). A, male, dorsal view; B, slightly malformed female, dorsal view; C, same, ventral view.

excluded from cerambycids as a separate family. The same author (Thomson 1864–65) placed both Anoplodermatides and Hypocephalides outside cerambycids among his “familles limitrophes”. However, other authors usually associated Anoplodermatinae with the cerambycid subfamilies Prioninae and Parandrinae because of their mostly distinct and complete lateral pronotal margin, the universal lack of the mesoscutal stridulatory plate, and a prionine-like habitus. The polarity, degree of homoplasy and the phylogenetic significance of the lateral pronotal margin in chrysomeloids is problematic (Reid 1995). Its reduced and incomplete state in some Prioninae (e.g., many Aegosomatini, Fig. 2.4.13 H) and most Philinae indicates that the long and complete lateral margin distant from the procoxal sockets (as present in anoplodermatines and many prionines) may be derived. However, placing Anoplodermatinae within Prioninae would meet serious problems (see below) even disregarding the fundamentally different larvae. Also the stridulatory file was obviously lost (or possibly also regained) many times in cerambycoids, including some Philinae and most Vesperinae (may be present even if vestigial in the latter, see Fig. 2.1.4 G). Napp (1994: 406) proposed the following additional characters holding together the Anoplodermatinae, Prioninae and Parandrinae: reduction of galea (not universal in either Prioninae or Anoplodermatinae, within Parandrinae relatively large in Erichsoniini, size also variable in Parandrini, e.g., Santos-Silva *et al.* 2010); the poorly developed corneous labrum (labral morphology very variable in both Anoplodermatinae and Prioninae); metendosternite without laminae (laminae present in some Prioninae and lost also in some other cerambycids and in Disteniidae); reduction of the vein r3 (sector vein of Napp; variable in these groups and present in Anoplodermatinae as admitted by Napp herself on p. 320 and shown in Fig. 194). Anoplodermatinae differ from Parandrinae and nearly all Prioninae by the plesiomorphic internal closure of the procoxal cavities and gulamentum slightly projecting between maxillary bases. The possibly plesiomorphic sclerotized rod or tube in the ejaculatory duct (occurring also in Disteniidae and Oxypeltidae and observed in several unrelated taxa in a randomly selected sample of other chrysomeloid families) was not found in Prioninae and Parandrinae (and nearly all other studied cerambycids except for a few Lamiinae). At the same time, anoplodermatines possess some apomorphies compared with Prioninae and/or Parandrinae: lack of wedge cell in the wing, the 2-2-1 ground plan pattern of tibial spurs, and possibly the externally closed procoxal cavities, which are uncommon and probably parallelly developed in the prionine branch (some Parandrinae) and do not occur in the very few prionines having the internal closure (*Anoeme* Gahan). Unlike in the Prioninae and Parandrinae, in the nerve cord of adults of *Migdolus* and *Hypocephalus* the abdominal ganglion V is fused with the terminal ganglionic complex (Penteado-Dias 1984), but very few species were studied.

Relationships of *Vesperus* with the “old” genera of Philinae (*Philus*, *Doesus* and *Mantitheus*) were suggested by some earlier authors (e.g., Gahan 1906: 55) and *Vesperoctenus* was compared to *Vesperus* in the original description (Bates 1891). The two genera were grouped together in the world catalogues of Aurivillius (1912) and Boppe (1921). However, the modern taxonomic history of this family began in the 1950–60s and was in part connected with (re)descriptions of the larvae. Crowson (1955) recognized Anoploderminae (a misspelling) and Philinae as separate cerambycid subfamilies (retaining *Vesperus* provisionally in Lepturinae), and later (1967) he mentioned that, following Duffy’s (1960) elevation of the Oxypeltinae to subfamily status based on larval morphology, “a good case could be made out for a separate subfamily also for *Vesperus*, whose larva is also described by Duffy (1957)”. Obviously this proposition was based on larval morphology of later instars and not on the then incorrectly accepted “hypermetamorphic” differences of first instars of *Vesperus* (as implied by Vives 2005: 439) because Duffy did not have first instars available and just cited data from old imprecise sources. Finally Crowson (1981), perhaps following the exclusion of Disteniidae from the Cerambycidae by Linsley (1961, 1962), accepted a broad separate family Disteniidae, including also Oxypeltinae, Philinae and Vesperinae as subfamilies (for priority reasons the name of the family should have been Vesperidae). Crowson (1981) retained Anoplodermatinae in the Cerambycidae, possibly because the available larval description of *Migdolus* (Fonseca 1959) was not sufficiently detailed.

Svacha *in* Svacha & Danilevsky (1987) redescribed larvae of *Vesperus* and *Migdolus* (larvae of the Philinae were unknown) and accepted Vesperidae and Anoplodermatidae (together with Oxypeltidae and Disteniidae) as separate families because he did not find any common larval characters beyond the plesiomorphic lack of the gula (whose presence defined his Cerambycidae *s.str.*). Saito (1990) studied female genitalia of *Vesperus*, *Philus* and *Mantitheus*. She accepted the separate family Vesperidae and included the Philinae (as a tribe Philini) based on the very similar and very unusual (probably apomorphic) female genitalia with extremely long proctiger and desclerotized spermatheca. Larvae of Philinae were described by Yin (1994) and redescribed by Svacha (in Svacha *et al.* 1997), who accepted Saito’s placement of Philinae (treated by him as a subfamily) in Vesperidae and added also the Anoplodermatinae, using the similarities of the newly discovered philine larvae to both *Vesperus* and *Migdolus*, thus creating the family Vesperidae as accepted here. As Svacha defined Vesperidae mainly based on larval characters, he preliminarily placed *Vesperoctenus* (larvae unknown) in Vesperidae as a genus *incertae sedis*, possibly related to Anoplodermatinae (see below). Definition of Vesperidae on adult characters is very difficult as Philinae have retained an extensive set of plesiomorphies probably close to the chrysomeloid ground plan. The undoubtedly apomorphic absence of a sclerotized spermatheca in Vesperinae and Philinae is not shared by the Anoplodermatinae (present data). The tendency for flightless females (Vesperinae, Anoplodermatinae, Vesperoctenini, some Philinae; see Svacha *et al.* 1997) is not universal because at least some females of *Philus* can fly (C. Chen and Y. Lin, personal communication for two species of *Philus* occurring in Taiwan) and female flightlessness is shared by the Oxypeltidae. Vesperid larvae differ fundamentally from those of all other cerambycoid groups, but many of their features may be plesiomorphic. The following presumed larval apomorphies were used by Svacha (in Svacha *et al.* 1997) to define Vesperidae: "Very long antennae [concerns later instars, antennae are shorter in first instars]; twin malar sensory organ [see comments below]; spiracles in later instars without marginal chambers; terricolous habits (probably including *Vesperoctenus*). Perhaps also long digging mandibles and later instar larvae with stemmata inconspicuous or absent". The "malar organ" (Fig. 2.1.10 E–H) comprises two sensilla widespread (possibly universally present) in cerambycoids and other Chrysomeloidea (and occuring also in other beetle groups). They are homologous to the "lateral and medial galeal sensilla" described in chrysomelids (e.g., Mitchell *et al.* 1979); at least one of these sensilla was identified as a contact chemoreceptor (whereas the surrounding sensilla are generally mechanoreceptive setae). In Vesperidae, the two sensilla are placed on a more or less prominent common tubercle. However, an inconspicuous tubercle bearing these sensilla has been since observed also in some Cerambycidae.

Svacha (in Svacha *et al.* 1997) proposed the following apomorphic larval characters joining Philinae and Anoplodermatinae as opposed to Vesperinae: "Extremely hypertrophied metatentorial bridge; very short frons (convergently also in some Cerambycidae); epipharynx longitudinally compressed and sensilla shifted anteriorly; abdomen with lateral more or less completely delimited intersegmental folds. Perhaps also the body almost completely covered with microtrichia". The only potential adult synapomorpy of Philinae and Anoplodermatinae is the secondary procoxal articulation on the prosternal process (some Anoplodermatinae, possibly all Philinae; Fig. 2.1.5 H). However, such structures are not uncommon in Cerambycidae and may have evolved several times independently and/or become secondarily reduced in some taxa. Adult structural affinities between Philinae and Vesperinae are more numerous. Although most of them are probably plesiomorphies (mentum not broad and plate-like and not partly covering maxillary base; retained vestiges of the mesoscutal stridulatory file in some taxa; wing with connection between MP_{1+2} and MP_{3+4} not shifted distally and in some taxa with a wedge cell and five free veins in the medial field; metendosternite with laminae; hind tibia with two spurs; females with long flexible ovipositor bearing apical styli, etc.), the gulamentum not forming an intermaxillary process and particularly the abovementioned similar female reproductive organs without a sclerotized spermatheca may be synapomorphies (however, the lack of intermaxillary process is shared with Parandrinae and Prioninae). If Vesperinae and Philinae were sister groups, the larvae of *Vesperus* (distinguished from all other cerambycoid larvae by a short pyriform body, lack of true ambulatory ampullae, simple lateral borders between abdominal segments, long exposed coronal stem, very long *and* non-retractile antennae, etc.) may actually be highly derived, and the similarities of larvae of Philinae and Anoplodermatinae used by Svacha might be either plesiomorphies within Vesperidae, or parallelisms resulting from similar terricolous habits (at least the body covered with microtrichia is shared by some terricolous larvae of Prionini) but missing in likewise terricolous *Vesperus*. Thus the relationships of the three vesperid subfamilies, or indeed the monophyly of the Vesperidae in the present sense, require further study.

The tribe Vesperoctenini was erected by Vives (2005) for the enigmatic Mexican genus *Vesperoctenus* containing a single species, *V. flohri*. The genus differs from all other Vesperidae by the apomorphic 12-segmented antennae in both sexes (in the other groups the terminal flagellomere may be appendiculate but never divided). The original description (Bates 1891) did not assign the genus to any particular cerambycid group but proposed relationships to the Old World *Vesperus*. *Vesperoctenus* was therefore later placed with the cerambycid subfamily Lepturinae or equivalents, with similar problems as in the case of *Vesperus* (see above). Svacha (in Svacha *et al.* 1997) considered the genus as a taxon *incertae sedis* in the newly defined Vesperidae, based mainly on the presumed subterranean root-feeding larval habits and the derived 2-2-1 formula of tibial spurs shared with most Anoplodermatinae (Dias 1984–1988; further reduced in some females and both sexes of *Hypocephalus*), but unknown in Vesperinae (2-2-2) or Philinae (2-2-2 or 1-2-2); Napp (1994) is incorrect in stating that *Philus* has only one spur on the hind tibia. Oxypeltidae and Disteniidae also have two spurs on all tibiae, and the 2-2-1 formula is very uncommon in Cerambycidae. Reviewing *Vesperoctenus*, Vives (2001) questioned the concept of the family Vesperidae in the present sense (indeed its monophyly is by no means well supported, see above and in Cerambycidae) and used another set of characters to advocate a relationship of *Vesperoctenus* to *Vesperus* as proposed in the original description (Bates 1981). Similarities to *Vesperus* (possible apomorphies marked by "A", characters shared also with the Philinae marked by "Ph") include the constricted neck (A), a mentum not expanded and not covering the maxillary base (Ph), the lack of an intermaxillary process (A?, Ph), well-developed broad dorsal tentorial arms (verification needed; Ph), a pronotum without a lateral carina (A?), procoxal cavities externally open (Ph), procoxae projecting above very narrow prosternal process (A?; polarity uncertain, see discussion of secondary procoxal articulation above), mesocoxal cavities not sharply defined posteriorly (A?, Ph), wings with wedge cell (Ph; present in Philinae and some Vesperinae, universally absent in Anoplodermatinae) and with the connection between MP_{1+2} and MP_{3+4} not shifted distally (Ph), the presence of metendosternal laminae (Ph), and possibly an unmodified ovipositor with terminal styli (more data needed; Ph). It will be of interest whether females share the apomorphic absence of a sclerotized spermatheca as is the case in Vesperinae and Philinae. Although it can be deduced from the previous list that *Vesperoctenus* lacks many of the anoplodermatine apomorphies, such as the broad plate-like mentum covering the maxillary base, procoxal cavities closed externally; wing without wedge cell and with the connection between MP_{1+2} and MP_{3+4} shifted distally, the absence of metendosternal laminae, and possibly the modified sclerotized ovipositor, it displays some similarities to all or some Anoplodermatinae. This includes a postclypeus projecting above the anteclypeus (A), mandibles with a dentate incisor edge and a small external projection (A?), a medial field of the hind wing with only four free veins (A), a 2-2-1 tibial spur pattern (A), and possibly also the extremely setose body and pectinate antennae of males (A?; one or both occur in some Anoplodermatinae, but pectinate antennae also occur in males of the philine genus *Spiniphilus*). Thus, relationships of *Vesperoctenus* also remain obscure. However, the placement of Vesperoctenini (but not any other of the present subgroups of Vesperidae) in the cerambycid subfamily Prioninae (Bousquet *et al.* 2009; Bouchard *et al.* 2011; accepted in Bezark & Monné 2013) is entirely unsupported.

Vesperinae Mulsant, 1839

Biology and Ecology. Based mainly on the summary in Vives (2005), a very detailed account of the biology of *Vesperus sanzi* Reitter (one of the smaller species developing predominantly in grasslands; Calvo Sánchez 2007), and data for *V. macropterus* (Sechi 2011). Adults are crepuscular and nocturnal, with males and occasionally also females attracted to light; males usually fly during the hours immediately after sunset. Females are flightless but not subterranean, although they are mostly hidden during the day and not frequently encountered, whereas males may be abundantly collected during the flight period. In contrast to this, the number of males and females of *V. sanzi* collected from the soil pupal chambers was not significantly different. Females of *V. xatarti* produce a long-range pheromone. Males of *V. sanzi* often perch on grass stems or other higher plants with the head upward and antennae outstretched, apparently trying to detect the female pheromone. They were also observed patrolling on the ground in areas of female emergence, occasionally violently pulling out the emerging female and immediately attempting to copulate. Males may battle for mates. Females of *V. sanzi* were not seen to climb on plants or other elevated objects. Copulation lasted several minutes and could occur repeatedly with the same female. Unmated males and females of *V. sanzi* lived for about 4 and 8 days, respectively, but both sexes died within a day or two after copulation or oviposition. Females of *V. macropterus* apparently lay all eggs during one night and die soon after, and males may be even more ephemeral. The period of adult activity differs among species, those occurring at low altitudes may be active in winter. Some species lay eggs in or on various objects above ground level, such as stones or tree bark (Butovitsch 1939). Oviposition in dry inflorescences of dead herbs up to 1.5 m tall was observed in *V. macropterus*; in suitable plants, the newly-emerged larvae at least partly bored down through the soft pith of the plant stem, thus avoiding exposure before entering soil. The macropterous females cannot fly but may use the well-developed elytra and wings to "parachute" from the dry plants (e.g., when disturbed). Other species, particularly those developing in grasslands (such as *V. sanzi*), oviposit in cavities in the soil, among roots, or in grass sods. *Vesperus sanzi* often oviposits in its own emergence galleries. Eggs are mostly laid in batches and covered and held together by a sticky substance (not in *V. macropterus*). One female lays over 100 and usually several hundred eggs (the ovipositor may become non-functional before all eggs are laid). In *V. sanzi,* in which adults are active in summer, the egg incubation period in the laboratory was 25–28 days, but egg hatching is delayed in species with winter activity. Rain might be a stimulus for egg hatching in *V. macropterus*, presumably to avoid desiccation of the minute first instar larvae and to facilitate entering the otherwise dry hard soil. The egg chorion is split longitudinally in *V. sanzi*, probably by the lateral egg bursters (see larval morphology and Fig. 2.1.12 D), and larvae leave the egg through that lateral split. The first instars (Fig. 2.1.9 G; see also Vives 2005) differ distinctly from the later stages: they are slightly more slender and elongate, their terminal abdominal segments are less retracted (*cf.* Fig. 2.1.7 F and 2.1.8 D), the setae are arranged more sparsely (some of them are very long) and the antennae are shorter. However, these differences are comparable to those between first and later instars in many other species. Mayet's old figure of first instar larva reprinted in Duffy (1953, 1957) is very inaccurate, undoubtedly depicting a strongly inflated specimen, and suggestions of considerable larval differences amounting to hypermetamorphosis are incorrect. First instars search for suitable roots in soil. In *V. sanzi* they are able to survive for over a month without food. At least *V. strepens* (Fabricius) and *V. luridus* (Rossi) are apparently very broadly polyphagous on various trees and herbs (Vives 2005). *Vesperus sanzi* developing in grasslands feeds on roots of herbs of several families. Some species are pests in vineyards. Larval development takes several years. Larvae of *V. sanzi* actively feed in spring and early autumn, with periods of inactivity during the hot dry summer and winter when the larvae are dormant in soil chambers at depths of up to 50 cm. In the laboratory, larvae moulted at least twice a year (after each dormant period) and were estimated to undergo at least a total of ten moults during a life cycle of 5 years. Pupation occurs in soil. In June, the mature larva of *V. sanzi* descends from a superficial layer to depths of 10–20 cm where it constructs an ellipsoid oblique pupal chamber with smoothened walls. The descending larval gallery remains largely empty and serves for the emergence of adults (which have no fossorial adaptations). The pupal stage of *V. sanzi* lasts 18–20 days, with adults emerging in August.

Morphology, Adults (Fig. 2.1.1 A–C, 2.1.3 A). Body length 8–35 mm. Lightly sclerotized, not depressed. Coloration straw-yellow to brown or red-brown. With distinct sexual dimorphism: males slender, with antennae approaching to surpassing the end of body, complete elytra and functional wings; females broader and generally heavier, with antennae much shorter than body and sometimes hardly attaining posterior pronotal margin, always flightless and usually with more or less reduced elytra and wings, pronouncedly physogastric in some species (e.g., Calvo Sánchez 2008). Pubescence covering most body parts (including elytra in males), except setae, at most, moderately long and never very dense and obscuring body details.

Head large, more or less oblique (but extensively movable). Cranium subquadrate to elongate; occipital region strongly inflated and abruptly constricted posteriorly into a short narrow neck not involving the gular region with metatentorial slits. Eyes moderately sized to large, lateral, not approaching each other dorsally or ventrally, at most moderately emarginated; coarsely facetted, interfacetal setae absent or very short and sparse. Antennal sockets moderately broadly separated, close (but not immediately adjacent) to mandibular articulation, supported by distinct medial tubercles and facing almost laterally. Frontoclypeal sulcus broadly V-shaped, less distinct medially. Pretentorial pits lateral, close to mandibular articulations, not slit-like. Postclypeus not projecting above anteclypeus, which is narrow, flat, and membranous anteriorly. Labrum separate, approximately as long as broad or shorter, moderately sclerotized, bearing numerous setae. Antennae 11-segmented, very short in some females; filiform or in some males flagellum flattened and slightly serrate. Mandibles long, strongly evenly curved mesally, broadly overlapping when closed, without outer projections or distinct incisor teeth; basal part bearing numerous lateral setae. Maxillolabial complex moderately large. Lacinia present but much more basal than galea; maxillary palps longer than half of width of head; terminal palpomere truncate. Mentum trapezoidal, not distinctly sclerotized and not covering maxillary bases; prementum narrow, with small ligula sometimes bearing lateral projections; palps slightly shorter than those of maxillae, with truncate terminal palpomere. Intermaxillary process absent. Dorsal tentorial arms long, flat and broad.

Prothorax more or less distinctly narrower than base of elytra, transverse to slightly longer than broad, bell-shaped, tapering anteriorly. Pronotum without lateral margins or just rudiments present at hind angles. Prosternal process strongly compressed laterally and hidden between prominent conical subcontiguous coxae. Prosternum before coxae long and sloping. Procoxal cavities open externally. Mesoscutum broadly emarginate anteriorly, with median endocarina and usually without a stridulatory plate (but distinct paired remnants of striation were found in male *V. conicicollis* Fairmaire & Coquerel; Fig. 2.1.4 G); scutellar shield of variable shape. Elytra usually reduced to various degrees in females; in males subparallel to moderately tapering posteriorly. Mesocoxal sockets poorly defined posteriorly, narrowly separated to subcontiguous. Mesocoxae slightly projecting. Mesometaventral junction very narrow or its metathoracic component absent. Exposed metanepisternum triangular. Metaventrite with long discrimen. Metacoxae moderately or (females, Fig. 2.1.3 A) broadly separate. Metendosternite with laminae. Wing (Fig. 2.1.5 B, C) in macropterous specimens with one distinct vein in apical field; radial cell narrow, closed; oblique r3 present; r4 attached on radial cell and with, at most, a rudimentary spur; medial field typically with five free veins; wedge cell narrow to absent; CuA_1 present but CuA_{1+2} may be absent and MP_{3+4} then appears to have three branches; connection between MP_{1+2} and MP_{3+4} not shifted distally; medial fleck absent. Legs moderately long, slender, without fossorial adaptations; tibiae not distinctly expanded apically and without pronounced apical fringe of setae; tibial spurs 2-2-2, not placed in distinct notches; tarsus pseudotetramerous and padded beneath, with plurisetose empodium.

Sternum III is usually the first visible, but intercoxal process may be reduced particularly in females, where sternum II may be more or less visible between (Fig. 2.1.3 A) and, in extreme cases, also behind the broadly separated coxae. Male terminalia with distinct paired parameres; gonopore without spiculum; ejaculatory duct usually with long internal sclerotized rod; latter missing in *V. conicicollis* and according to Vives (2005), who refers to this structure as a flagellum, also in *V. bolivari* Oliveira, *V. fuentei* Pic, *V. serranoi* Zuzarte, and probably *V. macropterus* (treated by Vives as a subspecies of *V. conicicollis*). Female genitalia (Saito 1990) similar to Philinae: ovipositor long, flexible, with very long proctiger and distinct apical styli; small "intersegmental pouches" (but without symbionts) were found in an unidentified species of *Vesperus* by Schomann (1937); sclerotized spermatheca absent; vagina bearing only one petiolate membranous sac (Fig. 2.1.6 B) interpreted by Saito as a desclerotized spermatheca without gland.

Morphology, Larvae (Duffy 1957; Svacha & Danilevsky 1987). Body (Fig. 2.1.6 F, 2.1.8 D, E, 2.1.11 A, B) extremely short and robust, broadest and highest at mid-abdomen, setose and with only limited soft areas bearing microtrichia, many regions forming more or less distinct setose protuberances.

Head (Fig. 2.1.9 A–D) oblique to almost orthognathous, almost entire dorsal part exposable. Cranium slightly transverse (width/length ratio about 1.3), moderately depressed, poorly sclerotized and pale or with slightly darker yellowish areas at dorsal mandibular articulations. Posterior part nearly glabrous except for paired row of minute setae; anterior part more or less densely setose. Dorsal cranium shallowly notched posteriorly, without duplicate region, but with long unpaired coronal stem with low median endocarina that continues along much of frontal length but does not reach clypeus. Only mesal parts of frontal lines more or less visible, fusing slightly before cranial midlength; cleavage lines in single damaged exuviae laterally irregular and medially running along frontal lines, then along coronal stem on one side of median endocarina. Clypeus very large, trapezoidal, long and strongly tapering, indistinctly separated from frons (without infolded strengthened epistomal margin); finely sclerotized in basal half, with paired spots at midlength; setae arranged in two paired groups (smaller at paired spots and larger before posterolateral corners). Labrum transversely elliptical and constricted at base, almost unpigmented; setae mostly marginal except for one discal pair. Epipharynx (Fig. 2.1.7 C) much more elongate compared with the other two subfamilies; five pairs of sunken sensilla placed far behind level of clypeolabral border. Three small pigment spots of main stemmata often visible behind antennal sockets, but without cuticular lenses. Antenna very long, connected with cranium by short finely sclerotized setose basal piece not allowing any retraction; antennomere 1 strongly elongate, curved, sclerotized, with several distinct setae; antennomere 2 shorter yet also elongate, devoid of setae; sensorium subcircular to broadly oval, flat or (*V. sanzi*) very shortly conical; antennomere 3 minute. Mandible with outer basal part paler than the rest and bearing groups of one to several setae at dorsal mandibular articulation and anterior margin; apical part with dorsal angle separated by incision, two ventral teeth in later instars poorly defined. Maxillolabial complex at most slightly sclerotized, except for ring-shaped sclerites of all maxillary and terminal labial palpomeres; maxillary articulating area divided and posterior part not clearly separated from submentum. Cardo without setae; apical maxillary palpomere with single digitiform sensillum. Prementum not wedged into mentum; ligula small, entire, setose. Hypostomal rods lost. Tentorial bridge extremely broad and plate-like, yet not extended to posterior cranial margin; part of occipital foramen behind the bridge posteroventral (Fig. 2.1.9 D).

Pronotum without sclerotized ridges, fused with alar lobes into large transverse area. Presternal region with two prominent areas possibly homologous to those of Philinae (Fig. 2.1.8 E, 2.1.11 A); posterior area is wedged between coxae and was probably erroneously considered basisternal by Svacha (in Svacha & Danilevsky 1987); anterior area with two broad shallow slightly sclerotized pits; episterna separate. Procoxae moderately protuberant and densely setose. Posterior sternal region reduced yet bearing slender but distinct furcal arms and distinct spina; pleural apodeme broad and well-developed (Fig. 2.1.11 B). Pterothoracic nota with well-separated prescutum; scutum-I indistinct; both parascuta and alar lobes forming setose protuberances. Mesothoracic spiracle slightly protruding into prothorax. Pterothoracic coxae protuberant and setose mesally. Pleuron undivided, broad and with a setose tubercle; basisterna (particularly of the mesosternum) also with prominent central setose area. Mesothoracic furca and spina distinct, both originating on posterior segmental margin. Distal part of legs approximately as long as antennae (fore legs slightly longer and directed obliquely anteriorly), densely setose; pretarsus slender with needle-shaped claw and one median seta at base.

Abdomen with all intersegmental zones continuous and simple. Terga and sterna I–VI flat and densely covered with setae, some of which are short and spine-like; coxal and pleural lobes of those segments forming separate setose protuberances. Segments VII–X reduced and more or less telescoped in living larvae. Spiracle VIII distinctly reduced in size. Abdominal epipleura slightly protuberant on I–VIII, I-V with gradually less distinct setose epipleural tubercles with short dorsal slits projecting into a small apodeme (Fig. 2.1.11 A, eplt); epipleural discs absent. Anal opening transverse.

Taxonomy. This monogeneric subfamily contains the Mediterranean genus *Vesperus* Dejean with approximately 20 species that were revised by Vives (2005). An updated catalogue is provided by Löbl & Smetana (2010), though it does not include *Vesperus barredai* Verdugo (Verdugo-Páez 2009).

Philinae J. Thomson, 1861

Biology and Ecology. Adults are predominantly nocturnal although copulation and oviposition was also observed during the day. Females emerge from soil and live freely. Those of *Heterophilus* and *Mantitheus* are brachy- or micropterous (Lin & Bi 2011; Fig. 2.1.1 D, 2.1.3 B), whereas they are macropterous in the remaining genera. Females of a Chinese population of *Philus antennatus* (Gyllenhal) do not fly (Svacha *et al.* 1997), but flight was observed in two species of *Philus* occuring in Taiwan (C. Chen, Y. Lin, personal communication; one of the Taiwanese species is possibly incorrectly classified as *P. antennatus*). Eggs are typically laid in bark crevices of the host trees in *Philus antennatus* (Svacha *et al.* 1997) and *Mantitheus pekinensis* (Fig. 2.1.3 B, 2.1.8 A). First instar larvae fall to the ground after eclosion. *Philus pallescens* Bates is known to damage roots of herbs such as sugar cane (Gressitt 1951), and larvae of *Heterophilus punctulatus* Pu were found on roots of congograss (*Imperata cylindrica*, Poaceae) on the Tibetan plateau (Svacha *et al.* 1997). The mode of oviposition in those cases is unknown. Larvae feed underground on rootlets or root bark. More detailed biological information is only available for *Philus antennatus* (Svacha *et al.* 1997; Lin *et al.* 2004). The life cycle lasts at least two years in southern China. Emergence was observed in late March and April in China (adults usually emerged from the soil during the night) and in May in Taiwan. Adults live for about a week following emergence. Mating lasted 1.5–3 h, oviposition followed 2–3 days later. Hand-collected adults in China showed strong female bias (about 90–100 females per one male). Fecundity is high; 509.3 ± 118.2 eggs per female were counted for a Taiwanese sample, and up to 150 eggs per laid egg batch in China. Eggs are whitish, elongate, spindle-shaped and measure about 3.7 mm (apparently smaller, about 3 mm, in the Taiwanese population, see Fig. 1 in Lin *et al.* 2004). Larvae are polyphagous as they can feed *en masse* both on conifers (*Pinus* plantations in China) and broadleaved trees (*Citrus* orchards in Taiwan). They were observed at depths up to approximately 1 m depending on the season (deeper in dry parts of the year) and can tolerate hypoxia caused by flooding. When the original host tree dies (which is not uncommon in the case of small trees and high infestations), larvae can spread through the soil to neighboring trees, sometimes causing larger continuous areas with dead trees. In the Chinese population, pupae were observed in October. The duration of the pupal stage was approximately 10–15 days, and adults overwintered in their pupal chambers in the soil.

Morphology, Adults (Fig. 2.1.1 D–H, 2.1.3 B). Length 13–37 mm. Body in males elongate and subparallel, in females more robust and variable, not or moderately depressed. Coloration yellow-brown to brown-black. Macropterous specimens (particularly males) extensively covered by sparse to locally dense short pubescence (including elytra); pubescence sparser in brachelytrous flightless females and some regions are more or less glabrous.

Head slightly to (some females) strongly oblique, at most moderately tapering behind eyes, without temples or a constricted neck. Eyes lateral, close to (sometimes almost touching) anterior cranial margin, moderately emarginate, coarsely facetted and without interfacetal setae, moderately to (males) very large and projecting from cranial outline, may approach each other dorsally and ventrally in males but always remain distinctly separated. Antennal sockets close to mandibular articulations, supported by medial tubercles and facing laterally. Pretentorial pits lateral, not slit-like. Postclypeus never projecting above anteclypeus; anteclypeus narrow and membranous anteriorly. Labrum weakly sclerotized, setose, not strongly transverse. Antennae 11-segmented, pectinate (males of *Spiniphilus*), serrate or filiform, approximately as long as the body length or longer in males, shorter in females (hardly surpassing the base of pronotum in *Heterophilus*). Mandibles (Fig. 2.1.4 A) long, crossed when closed, slightly asymmetrical, with pointed gradually incurved apex; incisor edge without teeth or with one before base (seen on left mandible), outer face setose basally and at most slightly bulging, lacking a projection. Maxillolabial complex small. Maxilla with long palps; last palpal segment truncate to slightly tapering; galea well-developed, lacinia small and basal (Fig. 2.1.4 F), completely hidden behind labium at rest. Mentum trapezoidal and not covering maxillary base; prementum narrow; ligula reduced but in some cases with anterolateral projections. Gulamentum not forming intermaxillary process. Dorsal tentorial arms in *Philus* long, broad and flat.

Prothorax narrower than base of elytra, at most moderately tapering anteriorly, about as long as broad to distinctly transverse (females of *Heterophilus*). Lateral pronotal carina oblique but not touching procoxal sockets, usually incomplete anteriorly (complete in females of *Heterophilus*), virtually absent in some males; pronotal disc may bear a pair of tubercles in anterior half. Procoxae prominent but not surpassing elevated prosternal process; somewhat broadened top of prosternal process with secondary coxal articulation (Fig. 2.1.5 H), consequently procoxa rotating along single axis; procoxal sockets open externally; internal closure present but very narrow and fine. Mesoscutum with median endocarina (may be incomplete posteriorly, apparently absent in *Heterophilus* but material not available), in some taxa bearing a more or less distinctly striate stridulatory file; scutellar shield small, subtriangular to broadly bilobed. Elytra covering abdomen or (females of *Heterophilus* and *Mantitheus*) more or less shortened and dehiscent. Mesocoxal sockets very narrowly separated, not sharply defined posteriorly. Mesocoxae slightly conical and projecting, may be contiguous when mesometaventral junction is reduced. Mesometaventral junction very narrow or its metathoracic component reduced and mesoventral process ending freely between coxae. Exposed metanepisternum subtriangular, tapering posteriorly. Metaventrite with discrimen incomplete anteriorly (only short posterior rudiments in some taxa). Metacoxae contiguous to narrowly separated in macropterous specimens, more broadly separated in females with reduced wings. Metendosternite with laminae. Females in *Heterophilus* strongly brachypterous, micropterous in *Mantitheus*; wing in macropterous specimens with very complete venation (Fig. 2.1.5 A) except for males of *Heterophilus* and *Mantitheus* having unbranched MP_{3+4} and the latter also lacking CuA_{1+2} (Lin & Bi 2011); apical field with two distinct veins; radial cell closed; r3 short or absent, r4 attached on radial cell and with at most rudimentary spur; connection between MP_{1+2} and MP_{3+4} not shifted distally; medial fleck absent; wedge cell large. Legs moderately long, without distinct fossorial modifications (although outer side of tibiae dentate in some cases); tibial ends not remarkably expanded, without thick setal fringes along apical edge; tibial spurs 2-2-2 (*Spiniphilus*, *Mantitheus*, *Philus globulicollis*) or 1-2-2 (*Philus*, *Doesus*, *Heterophilus*); tarsi pseudotetramerous and tarsomeres 1–3 padded (apparently slightly reduced in females of *Heterophilus*); plurisetose empodium present.

Abdominal base with intercoxal process small and more or less sunken below metacoxae to absent; sternum II large and broadly exposed behind coxae in the slightly physogastric females of *Mantitheus* (female abdominal morphology unknown in *Heterophilus*). Male genitalia with long paired setose parameres; gonopore without spiculum; internal sclerotized tube or rod of ejaculatory duct present in *Mantitheus* and *Heterophilus*, but absent in *Philus* and *Spiniphilus* (pers. comm. Meiying Lin for *Heterophilus* and *Spiniphilus*). Ovipositor long and flexible, with very long proctiger and apical styli; small "intersegmental pouches" present (*Philus* and *Mantitheus* studied); sclerotized spermatheca absent; vagina bearing only one petiolate membranous sac interpreted by Saito (1990) as a desclerotized spermatheca without gland.

Morphology, Larvae. (*Philus*, *Heterophilus* and *Mantitheus*, latter undescribed; Yin 1994; Svacha *et al.* 1997; Lin *et al.* 2004). Body (Fig. 2.1.6 D, 2.1.8 B, C, 2.1.11 C) moderately elongate, robust, not depressed, broadest at thorax. Body surface with very fine short setae, becoming stronger and denser on some regions and particularly on legs; with dense vestiture of short to spine-like microtrichia except for legs and some limited areas on thorax and abdomen.

Head (Fig. 2.1.7 A, 2.1.8 H, I, 2.1.9 F) prognathous, very deeply retracted, only short anterior part with mouthparts and antennae exposed. Cranium subquadrate (width/length ratio about 1.2), moderately depressed, almost unpigmented. Posterior part glabrous, anterior part with numerous very short setae. Dorsal cranium deeply notched posteriorly; exposed part of frons very short medially and followed by equally short duplicate region, both spanned by a median endocarina gradually reduced anteriorly before reaching clypeal base; frontal lines indistinct, cleavage lines in exuviae laterally not approaching antennal sockets, medially entering duplicate region separately and running posteriorly on both sides of median endocarina, meeting immediately before hind cranial margin (i.e., unpaired coronal stem absent). Clypeus very large, trapezoidal, indistinctly separated from frons (without infolded strengthened epistomal margin), bearing numerous setae and in later instars with paired reddish spots in anterior half. Labrum strongly transverse, semielliptical, almost unpigmented, setose. Epipharynx anteriorly (labral part) bearing numerous stout short setae and median group of usually six large sunken sensilla; two paired groups of five sunken sensilla shifted strongly anteriorly towards level of clypeolabral border. Stemmata absent or (*Mantitheus*) small pigment spots of three main stemmata visible behind pleurostoma. Antenna (Fig. 2.1.10 A–D) very long, connected by extremely large and glabrous (except for few fine short setae at base) articulating membrane making antenna entirely retractile. Antennomere 1 strongly elongate, particularly in mature larvae where it is indistinctly subdivided; distal part setose; antennomere 2 at most moderately elongate, sclerotized and without setae; apical membranous region surrounded by ring of minute trichoid structures in *Philus*; antennal sensorium large, broadly oval to strongly elongate in apical view, at most very shortly conical; third antennomere minute, barrel- to knob-shaped. Basal part of mandible with four desclerotized areas (two mesal ones visible in Fig. 2.1.9 F), the laterodorsal and lateroventral areas setose; single isolated lateral seta may be present on sclerotized part; apex in intact specimens with three more or less distinct teeth; dorsal tooth separated by incision. Maxillolabial complex at most lightly sclerotized except for mala and palpal segments; maxillary articulating area divided and posterior part not clearly separated from submentum. Cardo bearing numerous setae; apical maxillary palpomere with several digitiform sensilla (Fig. 2.1.10 E). Free labium short; prementum not wedged into mentum; ligula small, entire, setose. Hypostomal rods present. Tentorial bridge extremely broad, plate-like; part of occipital foramen behind bridge posterodorsal, virtually invisible in ventral view.

Prothorax broadest posteriorly. Pronotum without sclerotized ridges, expanded backward in middle, thus slightly constricting mesonotum; with distinct median furrow and anterior transverse zone slightly sclerotized; lined with short setae and devoid of microtrichia (Fig. 2.1.12 A); lateral furrows delimiting pronotum present, incomplete anteriorly. Alar lobes with strengthened oblique internal ledge (Fig. 2.1.11 C). Presternal region with two transverse areas, posterior one including also episterna; anterior transverse area with pair of broad flat depressions. Coxae flat and poorly defined medially. Posterior sternal region with recurved impressed line, its lateral extremities pointing toward very strongly reduced furcal pits located very near to posterior prothoracic margin. Sternal endoskeleton (furca and spina) reduced (small internal tubercles); propleural apodeme well-developed, slender, arising at lateral coxal extremity and reaching obliquely posteromedially across much of coxal width (Fig. 2.1.11 D). Mesonotum almost undivided. Metanotum with more or less distinctly separated triangular prescutum. Scutum-I distinct on both pterothoracic segments. Alar lobes not remarkably protuberant, deeply wedged into epipleural region. Mesothoracic spiracle very slightly protruding into prothorax. Pterothoracic coxae flat, poorly defined posteriorly, extended and angular anterolaterally, almost touching epipleural region (pleural sulcus very short). Epimeron posterolateral to coxa, distinctly protuberant; episternum anterior to coxa; both pleural divisions not distinctly separated from adjacent sternal parts. Transsternal line incomplete medially. Pterothoracic endoskeleton absent. Distal parts of legs (Fig. 2.1.12 E) short, much shorter than half of basal distance between trochanters, devoid of microtrichia; fore legs not distinctly enlarged or modified; pretarsus slender, with needle-shaped claw and one medial seta at base.

Abdominal segments I–VI with moderately protuberant broad ambulatory ampullae without conspicuous sculpture; ventral ampullae shallowly separated from epipleuron. Terga and sterna VII and VIII simple, almost undivided. Abdominal epipleura distinctly protuberant on VII to IX, poorly so on VI; epipleural tubercles indistinct; segment I with inconspicuous but relatively large epipleural disc, smaller and much less distinct discs also present on II–V (Fig. 2.1.11 C, 2.1.12 B). Lateral intersegmental zone between metathorax and abdominal segment I simple, but with oblique impressed line running posteroventrally and ending blindly at abdominal spiracle I; those between segments I to VI with more or less complete lateral intersegmental fold (last may be intermediate); border following VI with forked dorsal line embracing single ventral line (rather indistinct in *Mantitheus*). Segment IX hood-shaped, with enlarged dorsolateral and small ventral part; anal segment facing posteroventrally, invisible from above; anal opening triradiate.

Taxonomy. A key to genera is found in Lin & Bi (2011). The subfamily consists of five described genera and approximately 20 species (one unplaced). *Philus* Saunders comprises eight species or subspecies (a revision needed as some are transitional to *Doesus*); species were listed in Svacha *et al.* (1997), but two names were overlooked (*Philus longipennis* Pic from Cambodia and *P. lumawigi* Hüdepohl from Philippines). *Doesus* Pascoe has two species (*D. telephoroides* Pascoe from India and tropical Africa and *D. taprobanicus* Gahan from Ceylon). *Heterophilus* Pu contains three species known exclusively from the Tibetan plateau. Four species of *Mantitheus* Fairmaire were listed in Löbl & Smetana (2010), but the status of *M. acuminatus* Pic may require verification as it was described from a specimen accidentally imported in Belgium; all species occur in China and *M. pekinensis* Fairmaire also in Mongolia. *Spiniphilus* Lin & Bi has one described and one undescribed species, both from Yunnan, China. *Philus globulicollis* J. Thomson from North India and Burma (Fig. 2.1.1 G) cannot be accommodated in any existing genus; it differs from the first three genera by the plesiomorphic 2-2-2 set of tibial spurs, from *Mantitheus* by complete wing venation and normal winged females, and from *Spiniphilus* by male antennae just slightly serrate.

Anoplodermatinae Guérin-Méneville, 1840

Biology and Ecology. Very little biological information is available for Mysteriini. Adults are nocturnal and attracted to light (Dias 1988; S. Lingafelter, personal communication for *Pathocerus*). *Acacia cavenia* (Mimosaceae) was listed as a host for *Pathocerus wagneri* Waterhouse by Duffy 1960 (record attributed to F. Monrós and questioned by Di Iorio 2004). What little is known about *Hypocephalus armatus* Desmarest (placed either in Anoplodermatini or in a separate tribe Hypocephalini) comes mainly from Gounelle (1905) and was reviewed by Araujo (1954) and Duffy (1960). Both sexes are apterous, with fossorial habits. The species' occurrence is very localized but where it occurs, it may not be rare. Emergence usually starts in December after beginning of rainfall. Adults are found crawling or hidden under various objects in largely open areas with some deciduous scrub but devoid of trees or continuous vegetation cover, on clay and sandy soils with quartz fragments. As in all anoplodermatines, females are rarely encountered and probably remain in the soil for most of their life. At least the males are not strictly nocturnal. Larvae are unknown but are very likely subterranean. Of Anoplodermatini, the biology is known for *Migdolus fryanus* (the only anoplodermatine with known larval development) damaging sugar cane and some other cultured plants in Brazil (a summary with references can be found in Machado & Habib 2006; see also Bento *et al.* 1993, 1995; Botelho & Degaspari 1980 (*M. fonsecai* Lane, misspelled by the authors as *fonsecae*, is a synonym of *M. fryanus*); Fonseca 1959 (misidentified as *M. morretesi* Lane); Machado *et al.* 2006 a, b). Emerged males are short-lived (3–9 days in the laboratory), whereas active females live up to 38 days. The flight period is a week long, and timing differs depending upon region (October to March, usually following rainfall). Males are diurnal and fly and search for females mainly during forenoon. Females remain in their soil burrows, coming to the surface only for copulation, and attract males with a long-range sex pheromone (males often gather at the burrow entrance before the female appears on the surface). Copulation lasts 5–30 seconds. Females oviposit underground. In the laboratory a single female can lay up to approximately 50 elongate-oval, relatively large eggs (length up to 5 mm). The incubation period was 17–25 days. Larvae live in soil at depths up to 5 m, depending on the season of the year, and feed externally on plant roots; they are extremely polyphagous and were found damaging such taxonomically diverse plants as *Pinus*, *Eucalyptus* and *Saccharum*. Pupation occurs in soil at a considerable depth (typically 3–4 m) and adults remain in their pupal cells for some time before emergence (freshly moulted adults collected from soil have enlarged abdomens with fat reserves and can be kept alive in the laboratory for up to 4 months). Development period is from 1 to 3 years. Larvae reared in laboratory on semisynthetic diet for 2 years attained lengths of 4–5 cm and underwent 6–7 moults without reaching the pupal stage. Very little is known about other genera of Anoplodermatini, except that at least some of them are nocturnal and males fly to light (*Anoploderma breueri*: S. Lingafelter, personal communication).

Morphology, Adults (Fig. 2.1.2 A–I; the strongly derived *Hypocephalus* is not fully covered, see separate description below). Length 8.5–50 mm, with remarkable individual variability (males of *Migdolus fryanus* measure 12–37 mm; Dias 1984); females typically larger than males. Body slender and parallel-sided (most males of Mysteriini; Fig. 2.1.2 A) to very stout, at most moderately depressed. Usually more or less uniformly yellow-brown to black, seldom elytra much paler than rest of body (*Cherrocrius*). Pubescence variable but virtually absent on elytral disc, even in very hairy species.

Head prognathous to subvertical, without distinct temples or a constricted neck. Eyes variable (small and lateral to very large and approaching or touching each other ventrally), more distant from anterior cranial margin than antennal sockets; usually coarsely facetted (relatively finely in some at least partly diurnal Anoplodermatini, including *Hypocephalus*), without interfacetal setae. Antennal sockets very close to mandibular articulation (slightly removed in *Hypocephalus*), broadly separate, facing (antero)laterally; tubercles low or absent. Pretentorial pits lateral, close to mandibular articulations. Clypeus and labrum variable; labrum separate except for *Sypilus* but may be small and covered by a sclerotized projecting postclypeus (all Mysteriini and nearly so in *Anoploderma*). Antennae usually 11-segmented (last flagellomere slightly appendiculate in some cases), always so in males, where they attain about one-half to three-fourths of the body length (except *Hypocephalus*) and may be serrate or pectinate; in females very short and more or less simple, usually not reaching posterior pronotal margin; with eight to 11 segments (some flagellomeres may be more or less completely fused); first flagellomere very short in both sexes of *Sypilus* (Fig. 2.1.2 D). Mandibles long, variably shaped; strongly modified in *Hypocephalus*. Functional mouth and maxillolabial complex narrow to broad. Galea well-developed to small; lacinia reduced and placed basally. Mentum broad, sclerotized, plate-like and usually more or less covering maxillary base (Fig. 2.1.4 D); prementum narrow, even if the mentum is very broad; ligula reduced (with or without anterolateral projections) to virtually absent. Short intermaxillary process present (Fig. 2.1.4 D), but in some Anoplodermatini almost fused with cranium laterally, thus completing the ventral cover of the maxillary base. Dorsal tentorial arms present but not broad and flat (Fig. 2.1.4 E).

Prothorax variable, strongly narrower to not narrower than elytral base, moderately transverse to (males of *Hypocephalus*) distinctly longer than broad and as long as elytra. Pronotum simple and with usually distinct and complete non-dentate lateral carina distant from procoxal sockets. Procoxae transverse, moderately prominent, but (except in *Hypocephalus*) inserted under strongly elevated prosternal process; in some taxa articulating on that process by a tubercle as in Philinae (Fig. 2.1.5 H). Procoxal sockets closed internally and externally. Mesoscutum with more or less complete median endocarina (absent in *Hypocephalus*) and without stridulatory file; scutellar shield subtriangular to broadly linguiform. Elytra complete and covering abdomen even in flightless forms (in these cases often locked together at suture). Mesocoxal sockets broadly oval to subcircular, sharply delimited posteriorly, separated by narrow mesometaventral junction. Mesocoxae not prominent, in some cases articulating by a tubercle on the mesoventral process. Exposed metanepisternum triangular to subparallel, metaventrite with long discrimen (metanepisternum and metaventrite uniquely fused without traces and discrimen absent in *Hypocephalus*). Metacoxae narrowly to (some females) broadly separate, strongly hypertrophied in *Hypocephalus* (particularly in males). Metendosternite without laminae (pterothoracic endoskeleton uniquely modified in *Hypocephalus*). Females flightless and very slightly (e.g., *Pathocerus*) to strongly brachypterous; both sexes of *Hypocephalus* virtually apterous. Wing in macropterous specimens (Fig. 2.1.5 D–F) with one distinct vein in apical field; radial cell open or closed; short r3 present; r4 attached on radial cell and with spur short to absent; medial field typically with four free veins (MP_{3+4} with only one branch); wedge cell absent; CuA_{1+2} and CuA_1 present or the former or both more or less reduced (*Migdolus*); connection between MP_{1+2} and MP_{3+4} shifted distally and relatively close to (occasionally directly adjacent to) CuA_1; fine medial fleck present in some

Anoplodermatini (Fig. 2.1.5 F). Legs moderately long and relatively unmodified in Mysteriini and *Cherrocrius*, and with increasing fossorial modifications (shorter stronger legs, tibial teeth or external carinae) in remaining Anoplodermatini; extremely modified in *Hypocephalus*; hind trochanterofemoral border very strongly oblique in some Anoplodermatini; hind trochanter projecting into a long spine in males of *Paramigdolus*; tibiae slightly to very strongly expanded distally; apical edge at least partly fringed with dense setae, sometimes entire enlarged apical area densely pubescent; tibial spurs 2-2-1, 2-2-0 (females of some Anoplodermatini and both sexes of *Hypocephalus*), or 1-1-0 (females of *Sypilus*); tarsi variable, from pseudotetramerous and densely and continuously padded beneath (e.g., fore and mid tarsi of *Pseudopathocerus*; ventral padding always less developed on hind tarsi) to pentamerous and without pads (*Hypocephalus* and many females); mid tarsi longest in most Anoplodermatini, including *Hypocephalus*; empodium from distinct and plurisetose to small, hidden and lacking setae.

Abdomen with five visible sterna (III–VII), first forming distinct intercoxal process. Spiracles VI and VII smaller in some cases, VII rudimentary and apparently non-functional in female of *Migdolus*. Male genitalia with large setose parameres (nearly fused in *Pathocerus* and completely so in *Pseudopathocerus*); gonopore often with spine (Fig. 2.1.5 J); ejaculatory duct in all studied genera (all Mysteriini, *Anoploderma*, *Migdolus*, *Hypocephalus*) containing sclerotized tube or rod (Fig. 2.1.5 I). Females with ovipositor strongly sclerotized apically and bearing small lateral and sometimes partly sunken styli (Dias 1984–1988); *Pathocerus* and *Migdolus* (only genera dissected) with bursa copulatrix bearing distinct complex sclerotized spermatheca on thin duct (probably a distal sclerotized portion of the duct is associated with the original C-shaped spermathecal capsule and that part of the duct bears the spermathecal gland; Fig. 2.1.5 K). Hindgut in dissected specimens usually long and thin, never containing distinct food particles.

Morphology, Larvae (based on *Migdolus*; Fig. 2.1.6 E, 2.1.8 F, G). Body moderately elongate, not depressed, broadest at thorax. With vestiture of very fine short setae; very sparse on most body regions but very dense (and in part stronger) on much of the prothorax and some parts of the enlarged fore legs; almost entire body except for legs and densely setose prothoracic regions covered with dense, short spine-like microtrichia.

Head (Fig. 2.1.7 B, 2.1.8 F) prognathous, entirely retracted. Cranium subquadrate (width/length ratio about 1.2), moderately depressed, slightly tapering posteriorly, unpigmented except for very limited regions at anterior margin. Setae extremely short, pale and inconspicuous, restricted to anterior third and more numerous laterally. Dorsal cranium very deeply notched posteriorly, frons at midline and duplicate region both extremely short (about 3 times shorter than in Philinae) and without median endocarina. Frontal lines indistinguishable, cleavage lines unknown; frontal region separated from clypeus by strengthened but unpigmented cuticular infolding (presumably not homologous to epistomal margin of postclypeal origin in Cerambycidae and Disteniidae as it lacks epistomal setae whereas strongly developed clypeal setae are present). Clypeus very broad but shorter than in other subfamilies, trapezoidal, unsclerotized; with transverse row of anteriorly directed strong setae and some additional lateral small setae and sunken sensilla. Labrum broad, flat, strongly transverse, abruptly constricted at base, unpigmented, setose. Epipharynx (Fig. 2.1.7 E) anteriorly (labral part) bearing numerous stout short setae and a median group of usually six large and some small sunken sensilla; two paired groups of five sunken sensilla strongly shifted anteriorly, approximately to the level of the clypeolabral border. Stemmata absent. Antenna very long, entirely retractile; articulating membrane extremely large, as long as antenna (Fig. 2.1.7 B shows fully protracted antennae); membrane glabrous including slightly firmer base; antennomere 1 strongly elongate, with limited fine sclerotization and few minute setae on apical part; antennomere 2 slightly longer than broad, sclerotized, without setae; sensorium shortly conical and tilted toward small cylindrical antennomere 3. Basal part of mandible with four desclerotized patches and only one laterodorsal seta shortly before mandibular condyle; apical part in intact specimens obliquely truncate and without incision; dorsal and ventral edges very strongly carinate; outer face coarsely longitudinally striate. Maxillolabial complex (Fig. 2.1.8 F) without distinct sclerotizations except for mala, palpomeres, narrow band along base of mentum and small lateral sclerite on labial palpigers; maxillary articulating area very lightly sclerotized, not distinctly divided and more or less separate from submentum. Cardo bearing sparse minute setae; last maxillary palpomere with single digitiform sensillum (Fig. 2.1.10 F). Submentum broad, with round emargination posteriorly; mentum broad basally and tapering anteriorly; base of prementum deeply inserted in mentum; dorsal hypopharyngeal impression reaching far anteriorly, small ligula thus appearing bilobed. Short hypostomal rods present. Tentorial bridge extremely broad, plate-like, entirely closing cranial cavity ventrally and posteriorly so that the posterior part of occipital foramen opens dorsally (Fig. 2.1.7 B, 2.1.9 E).

Prothorax (Fig. 2.1.11 E) broadest posteriorly; large areas very densely setose and without microtrichia. Pronotum fused with alar lobes (lateral furrows absent), expanded posteromedially, thus slightly constricting mesonotum; in posterior half with several transverse sclerotized ridges interrupted by median line; lateral part of alar lobe forming separate fold above epipleural region. Prothoracic venter strongly modified and difficult to homologize, most parts (presternum, episternum, epimeron, basisternum) fused into large plate anteriorly bearing ventral part of the membranous collar surrounding head and in basal half with several transverse sclerotized ridges (Fig. 2.1.8 F); fore legs strongly shifted anterolaterally to anterior angles of that plate, virtually touching epipleural region, thus strongly reducing pleural sulcus; procoxa round, sharply defined, densely setose. Posterior prosternal margin with separate bilobed laterally tapering area (?sternellum) bearing short but distinct furcal rudiments at lateral extremities and a median spina on posterior margin; pleural apodeme narrow, rod-like but very long, originating at anterior procoxal margin and almost reaching furcal arms (Fig. 2.1.11 F). Mesonotum almost undivided. Metanotum with indistinct X-shaped lines and with scutum I indistinct. Alar lobes not protuberant. Mesothoracic spiracle not protruding into prothorax; spiracle-bearing epipleural triangle tends to fuse with alar lobe. Coxae small, flat, close to epipleural region (i.e., pleural sulcus short); otherwise all pleural and sternal regions more or less fused into one transverse fold. Small mesothoracic spina present. Fore legs (Fig. 2.1.12 F) enlarged, directed obliquely anteriorly; trochanter and femur large, with produced carinate inner side bearing row of short stout setae; pretarsal claw flattened; middle and hind legs much smaller, unmodified, with sparse fine setae and needle-shaped claw; pretarsus of all legs with two minute adjacent setae at base, one usually much smaller and hardly visible (Fig. 2.1.12 G; overlooked in Svacha & Danilevsky 1987; described in Costa *et al.* 1988).

Abdominal segments I–VI with dorsal ambulatory ampullae (large on I–V, much smaller on VI), each with two pairs of lateral impressions; ventral ampulla VI absent, those on segments I–V fused with ventral part of epipleural fold, projecting posterolaterally as pseudopods bearing epipleural discs; pseudopods on segment I shaped as round protuberances with discs on dorsal side, those on II–V longer and with epipleural discs on their tips (Fig. 2.1.11 E). Terga VI–IX simple; epipleura VI–IX protuberant, without epipleural tubercles or discs. Venter on segments VI–IX entire, simple or (VI–VII) with fine transverse line. Lateral intersegmental zones following metathorax and abdominal segments I–IV similar to those in Philinae, those following V with bifurcate dorsal furrow embracing single ventral furrow; VI and VII followed by standard intersegments with dorsal and ventral zones slightly overlapping and the former more anterior. Anal segment retracted, terminal; anus triradiate. Digestive tract (Fig. 2.1.13 C) simplified; posterior foregut slightly distensible but without distinct crop and without blind ventral process, that described by Svacha (in Svacha & Danilevsky 1987) was a malformation and not found in additional dissected specimens; midgut without loop and posteriorly with numerous elongate crypts (Fonseca-Gessner 1990).

Taxonomy. The group was revised by Dias (1984–1988; female of *Mysteria* described by Dias 2004) and contains ten genera and 37 species placed by Dias in two tribes as follows: Mysteriini Prosen, 1960 (Fig. 2.1.2 A–C, 2.1.6 A). Males slender, parallel-sided and slightly flattened (less so in *Pseudopathocerus*). Head prognathous. Eyes coarsely facetted, in males very large, approaching or touching each other dorsally and particularly ventrally, constricting the gula (Fig. 2.1.4 E). Antenna in males serrate or (*Pathocerus* and *Pseudopathocerus*) pectinate including first flagellomere. Postclypeus with a flattened conical projection covering small anteclypeus and labrum (Fig. 2.1.3 F). Mandibles broad and flat, not sickle-shaped; apical part abruptly curved mesad; usually with several incisor teeth and an external protuberance or process (Fig. 2.1.4 B). Functional mouth and maxillolabial complex narrow. Pronotum narrower than elytra, subcordate, with sharp prominent lateral carina. Legs moderately long, in males cursorial or (*Pseudopathocerus*) slightly strengthened; tibial spurs 2-2-1 in both sexes; mid tarsi not distinctly longer than hind tarsi. Immatures unknown. Three genera and seven species: *Mysteria* Thomson with five species, *Pathocerus* Waterhouse with *P. wagneri* Waterhouse, and *Pseudopathocerus* Dias with *P. humboldti* (Lameere). Anoplodermatini Guérin-Méneville, 1840 (Fig. 2.1.2 D–G). Seven genera with 20 species. The monospecific *Cherrocrius* and *Hypocephalus* are treated separately below. The remaining five genera form a relatively coherent group: body stout, convex; males of *Sypilus* with extremely long dense yellowish pubescence (Fig. 2.1.2 D; often abraded on pronotum) except for glabrous elytra. Head broad to very broad, strongly oblique to subvertical (but relatively extensively movable vertically). Eyes always well separated, in some cases relatively finely facetted. Labrum transverse and visible or (*Anoploderma*) hidden in dorsal view under sclerotized flat projecting clypeus, but postclypeus never forms a conical projection; in *Sypilus*, labrum apparently both partly hidden by and fused to clypeus. Antennae in males serrate, slightly pectinate in *Sypilus* but first flagellomere strongly reduced and without process. Mandibles more slender and sickle-shaped, with only one incisor tooth either at midlength (*Migdolus*; Fig. 2.1.2 E, F) or close to base and more or less blocking mouth when mandibles are closed (remaining four genera; Fig. 2.1.2 G, 2.1.4 D); outer process small or absent. Functional mouth and maxillolabial base (particularly mentum) broad. Pronotum larger than in Mysteriini, convex, occasionally almost as broad as base of elytra; lateral carina relatively blunt in some cases. Legs shorter and stouter, with more or less distinct fossorial modifications; tibial spurs 2-2-1 in males, 2-2-0 or (*Sypilus*) 1-1-0 in known females; mid tarsi more or less distinctly longer than others (very slightly so in *Sypilus*). Larvae known only of *Migdolus*. Genera: *Acanthomigdolus* Bruch with *A. quadricollis* (Bates), *Anoploderma* Guérin-Méneville with three species, *Migdolus* Westwood with ten species, *Paramigdolus* Dias with *P. tetropioides* (Fairmaire), and *Sypilus* Guérin-Méneville with three species. *Cherrocrius bruchi* Berg (based on Dias 1987). Males differ from those of the five genera treated above by the bicolored appearance with the body black-brown (with very long dark pubescence) and the elytra yellow-brown (and glabrous as in all Anoplodermatinae), by a narrower head, flat and straight mandibles (more similar in shape to those of Mysteriini except for the absence of distinct incisor teeth) and exposed and triangular labrum, antenna distinctly pectinate including a well-developed first flagellomere, slender legs with only slight modifications (tibial apices with flat teeth and outer side of fore tibia slightly dentate), and mid tarsi not distinctly longer than the hind tarsi. Immatures unknown. Prosen (1960) created a subfamily Cherrocriinae for this genus in his Anoplodermatidae (some South American authors accepted cerambycoids as a superfamily containing a number of families more or less corresponding to subfamilies of other authors). *Hypocephalus armatus* Desmarest (Fig. 2.1.2 H, I). This extremely specialized spe cies of rich taxonomic history (see systematic discussion of the family Vesperidae) was placed in Anoplodermatini by Dias (1987), but it is often singled out in a separate tribe, Hypocephalini Blanchard, 1845 (recently for instance in Bousquet *et al.* 2009 and Bezark & Monné 2013), as it makes any group in which it would be classified almost impossible to characterize. Body length 33–50 mm or more (size depends on position of head). Cylindrical, strongly sclerotized; black to black-brown, with very restricted and short pubescence. Head (Fig. 2.1.3 E) of unique shape and extensively movable vertically, may be flexed on prosternum (apparently a defensive position protecting large ventral membranous area between head and prosternum) or lifted to an almost prognathous position (Sharp 1902), although mouthparts even then point obliquely ventrally due to cranium being abruptly bent down in anterior half. Eyes small, oval, lateral, finely facetted, far from anterior cranial margin and placed above deep excavations. Antennal sockets without tubercles, lateral, slightly separated from mandibular articulation. Frontoclypeal region smooth; frontoclypeal sulcus obliterated; pretentorial pits small, lateral, connected by sulcus with antennal sockets; anteclypeus small and abruptly deflexed. Labrum separate, long (about twice as long as broad in males), almost perpendicular between mandibular bases. Antennae 11-segmented, extremely short, even in male shorter than head. Mandibles straight, vertical, parallel and of limited mobility (not working against each other); sharply pointed and with lateral projection; vestiture of setae reduced to several small patches. Gena bearing large (males) or small (females) ventral conical projections. Galea well-developed. Mentum strongly transverse but scarcely covering bases of maxillae; ligula reduced but with anterolateral projections. Tentorial bridge broad and roof-like; pre- and metatentorial arms connected at an angle due to ventrally curved anterior cranium. Pronotum extremely large, as broad as elytra and in males also as long; prosternum before coxae very long and emarginate anteriorly to accommodate head when flexed ventrally; emargination with series of round notches, particularly distinct in males. Procoxae project above prosternal process, not articulating on it. Mesoscutum externally with smooth median line but without internal endocarina, largely exposed except when prothorax raised and its posterior margin covering both mesoscutum and flat elytral bases. Scutellar shield minute. Elytra locked together at suture, subparallel and then converging, in males each with an acute tip. Hind wings absent. Metanepisternum fused without traces with metaventrite which lacks a discrimen (Fig. 2.1.3 C). Pterothoracic endoskeleton extremely hypertrophied and modified; mesofurca with two posteriorly directed very broad flaps dorsally attached on extremely broad metendosternal branches arising from very high laterally compressed metendosternal shaft (Fig. 2.1.3 D). All legs strongly fossorial; hind legs extremely hypertrophied in males; tibial spurs 2-2-0 in both sexes; hind tibia with densely pubescent terminal area; tarsi pentamerous, mid tarsi distinctly longer than others; empodium present, usually multisetose. Abdomen small; intercoxal process in male very long, slightly expanded apically and locked on both sides by processes of metaventrite (Fig. 2.1.3 C); in female shorter, broader and less distinctly locked. Males with strut on sternum VIII vestigial; ejaculatory duct with thick internal sclerotized tube. Female not dissected. Immatures unknown.

Incertae Sedis: Vesperoctenini Vives, 2005

Biology and Ecology. The single species of *Vesperoctenus* Bates, *Vesperoctenus flohri*, occurs exclusively in Mexico and is seldom collected. Very little is known about its biology (Vives 2001). Males (Fig. 2.1.2 J) are winged. Females (Fig. 2.1.2 K), which are much rarer in collections, are brachypterous but without distinct fossorial adaptations. Adults are nocturnal and attracted to light. The larval development is presumably subterranean. In the original description Bates (1891) writes: “Mr. Flohr informs me that the specimens were taken by Mr. Becker at night, by spreading a white sheet on the ground and lighting a fire, which attracts them; they come out of the ground after the manner of the *Cebrios* and *Scaptoleni*. Their habits are, no doubt, similar to those of the *Vesperi*, which are subterranean in their early stages". The species occurs in sparse oak and mixed groves usually above 1000 m and up to at least 2000 m altitude. Adults (obviously males) were also beaten from branches of *Quercus devia* in Baja California (Hovore 1988).

Morphology, Adults. Males (Fig. 2.1.2 J). Length 20–28 mm (Vives 2001). Moderately elongate, not depressed. Colored in various shades of brown. Nearly entire body surface, particularly head and thorax (including dorsal surface under elytra and wings), bearing unusually long and dense brownish pubescence obscuring body details (Fig. 2.1.3 G); only elytral disc with sparse vestiture of short setae.

Head obliquely prognathous, subquadrate, posteriorly abruptly constricted to form a short narrow neck not involving ventral (gular) region. Eyes lateral, not approaching each other dorsally or ventrally, nearly without emargination, narrowly separated from anterior cranial margin; ommatidial lenses convex; numerous long interfacetal setae present. Antennal sockets moderately broadly separated, facing anterolaterally and slightly dorsally; articulation supported by mesal tubercles connected by slight transverse protuberance; tubercles project into spine above antennal condyle. Pretentorial pits almost lateral, close to mandibular articulations, forming short slit. Anteclypeus not sclerotized and completely covered laterally by large bilobed sclerotized postclypeal projection (Fig. 2.1.3 G). Labrum separate, strongly transverse, setose. Antennae 12-segmented, reaching posterior third of elytra; scape subcylindrical and abruptly constricted basally; flagellum strongly pectinate. Mandible (Fig. 2.1.4 C) long, with apical part abruptly curved mesad and outer margin at this point with small protuberance; basal part bearing numerous lateral setae; incisor edge with several bilaterally asymmetrical teeth. Maxillolabial complex small. Galea and lacinia small, latter shifted strongly basally; galea desclerotized at base and passively articulated; maxillary palps longer than half of width of head. Mentum trapezoidal, not broad and plate-like and not covering maxillary base; prementum very narrow; ligula small, without lateral projections, moderately sclerotized; palps slightly shorter than those of maxillae; terminal palpomeres in both cases fusiform and pointed. Intermaxillary process absent. Dorsal tentorial arms (as visible through the occipital foramen in a cleared but intact head) apparently long, broad and flat.

Pronotum much narrower than elytral base, transverse, tapering anteriorly, without lateral carina. Procoxae subcontiguous, prominent, projecting above prosternal process, which is compressed and hidden between the coxae but not distinctly shortened. Procoxal cavities open externally. Mesoscutum with median endocarina and lacking stridulatory plate; scutellar shield tongue-shaped. Elytra strongly tapering posteriorly, finely rugose; each elytron with three low darker costae. Mesocoxal sockets broadly elliptical, not sharply defined posteriorly, narrowly separate (mesometaventral junction very narrow). Mesocoxae moderately prominent. Exposed metanepisternum triangular, broad anteriorly. Metaventrite with long discrimen. Metacoxae narrowly separated. Metendosternite bearing large laminae. Males macropterous; hind wing (Fig. 2.1.5 G) with only one distinct vein in the apical field; radial cell closed; short r3 present; r4 attached on radial cell and without spur; medial field with four free veins (MP_{3+4} with only one branch) and with narrow yet distinct wedge cell; CuA_{1+2} present, CuA_1 present or (Fig. 7 in Vives 2001) absent; connection between MP_{1+2} and MP_{3+4} not shifted distally; medial fleck absent. Legs moderately long, slender, without fossorial adaptations; tibiae not distinctly expanded apically, with dense apical fringe of setae; tibial spurs 2-2-1 and placed in notches; tarsus pseudotetramerous but lobes of tarsomere 3 small; ventral pads moderately sized and divided medially; distinct plurisetose empodium present.

First visible abdominal sternum (sternum III) with intercoxal process reduced. Male terminalia with distally paired slender parameres on broad conical base.

The female morphology was redescribed by Vives (2001). Length of lectotype female (Fig. 2.1.2 K) 27 mm; body more robust and without exceptionally long and dense pubescence. Antennae 12-segmented as in male but hardly attaining mid length of elytra; segments moderately dentate externally from antennomere 5 onward. Elytra subparallel anteriorly and distinctly dehiscent posteriorly. Brachypterous. Ovipositor apparently with apical styli and thus possibly not strongly sclerotized ("ovipositor slightly extruding, with two segments in the lateral lobes": Vives 2001: 36). Other details of genitalic morphology (in particular the presence or absence of a sclerotized spermatheca) unknown.

Acknowledgments

The authors are grateful to W. Bi (Shanghai, China), F. Calvo Sánchez (Errenteria, Spain), I. Jeniš (Náklo, Czech Republic), E. Kučera (Soběslav, Czech Republic), Meiying Lin (Institute of Zoology, Chinese Academy of Sciences, Beijing) and E. Vives (Terrassa, Spain) for permission to use their photographs; to F. Calvo Sánchez, J. Hájek (Department of Entomology, National Museum, Prague), Meiying Lin, S. W. Lingafelter (Systematic Entomology Laboratory, National Museum of Natural History, Washington, DC) and U. R. Martins (Museum of Zoology, University of São Paulo) for the gift or loan of material and for biological information; and to C. Chen (Tianjin, China) and Y. Lin (Taipei, Taiwan) for information on the flight capacity of females of Taiwanese species of *Philus*. P. Svacha acknowledges support from the Institute of Entomology (RVO:60077344).

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Biology and Ecology. Oyxpeltid beetles are diurnal and can be usually found on or around their larval hosts. Adult feeding has not been reported in literature. The morphology of adult mouthparts does not suggest non-feeding or floricoly and appears compatible with feeding on solid plant tissues. The gut of a dissected female of *C. childreni* contained distinct fibrous plant fragments, and the beetles may possibly feed on fresh bark or other tissues of their host trees. In captivity, females of *C. childreni* occasionally fed on apples (Cameron & Real 1974). Males are strong fliers, whereas females, although winged, almost do not fly and, at least in *C. childreni*, probably produce a long-range pheromone because males are attracted to virgin females (Cerda 1972; Cameron & Real 1974; Gara *et al.* 1978; J. E. Barriga, personal communication). Larvae of all three species develop in living *Nothofagus* trees. *Quercus* and *Myrtus* (currently *Amomyrtus*) *luma* have been also cited for *C. childreni* (Germain 1900: 86–104, *fide* Duffy 1960), but although the local name "coleóptero de la luma" would imply an association with *Amomyrtus luma* (or some other Myrtaceae growing in the region), no reliable data confirming development in this species were found (Cerda 1972). The record from *Quercus* might also require confirmation. The following hosts were listed in Monné (2002): *Nothofagus antarctica*, *N. dombeyi*, *N. procera* and *N. pumilio* for *O. quadrispinosus*, *N. dombeyi*, *N. obliqua* and *Quercus* sp. (probably the above record) for *C. childreni* and *N. pumilio* and *N. antarctica* for *C. penai*. *Nothofagus antarctica* should probably be excluded for the latter species as it was erroneously listed in Kuschel's (1955) original description of *C. penai* based on material actually collected by Luis Peña on *N. pumilio* (Cerda 1972 and references therein). According to Cameron & Real (1974), females of *C. childreni* attach eggs solitarily on the bark of stems and branch bases of living *Nothofagus* trees. The peculiar reduced female external genitalia serve for collecting debris from the bark surface. At oviposition, the collected material is used for camouflaging the egg. The egg stage lasts several months. Larvae penetrate the bark and gradually excavate a J-shaped gallery oriented upward and leading deep into the wood. That gallery serves as a shelter, and the larva returns for feeding to a broadened flat subcortical cavity around the entrance. Healing tissue produced by the host plant causes a swelling around that cavity and probably serves as the main larval food because the subcortical cavity is of limited size. The gallery is gradually enlarged as the larva grows and long wooden fibers are expelled through a small hole in the bark at the original oviposition site. The larval development is completed after approximately 5–6 years. Pupation occurs at the top of the larval gallery, and the pupal chamber is separated by a wad of wood fibers; the pupa lies in the cell with its head downward. Pupae were found from September to January, adults from November to May. According to E. Krahmer and J. E. Barriga (personal communication), larvae of *Oxypeltus* develop for at least 2 years in living *Notho-fagus* and pupate in April and May in branches. The pupal chamber is constructed in late summer. It is plugged at both ends with long wood fibers and separated by two girdles (Fig. 2.2.7 C) so that, particularly in thinner branches up to approximately 2 cm, the part with the pupal cell usually is broken off by wind and falls to the ground. Adults overwinter in the fallen branch fragments and emerge the next summer.

Morphology, Adults. Moderately sized to large (13–45 mm), robust, not depressed. Surface shiny metallic. Various parts green to blue; elytra with red tinge; color partly depending on viewing angle (Fig. 2.2.1 A, C). Body approximately 2.65–3 times as long as wide. Head, pronotum, scutellar shield and undersurfaces clothed with pale long hairs (Fig. 2.2.1 B) (shorter, sparser and less widespread, particularly in females of *Cheloderus childreni*); elytra and middle of abdominal venter largely glabrous.

Head moderately declined in *Oxypeltus*, strongly so (with mouthparts pointing almost ventrally) in *Cheloderus*; with small slightly protuberant temples behind and slightly below the eyes (often poorly visible dorsally), in *Oxypeltus* moderately constricted behind eyes to form a broad neck. Occipital region without transverse ridge and without median groove. Frontal region more or less impressed medially but without distinct median endocarina. Eyes moderately large, deeply emarginate, with ventral lobes much larger and almost touching anterior cranial margin but not extending onto ventral side; finely facetted, without interfacetal setae; ommatidial structure unknown. Antennal insertions exposed from above, moderately distant from mandibular articulations, located within eye emarginations, supported medially by raised tubercles; facing laterally or anterolaterally, not connected with mandibular articulation by a distinct elevation but a more or less distinct sulcus connecting antennifer to frontoclypeal boundary (epistomal suture); subantennal groove absent. Frontoclypeal sulcus distinct, curved to broadly V-shaped, without deep paramedian impressions; pretentorial pits laterodorsal, close to mandibular articulations, broadly open. Clypeus large, extensively sclerotized. Labrum free, partly retractile, transverse, rounded anteriorly. Antennae in both sexes shorter than body, 11-segmented (last flagellomere may be appendiculate); scape short, curved and dilated distally; pedicel very short and ring-like; flagellum slightly flattened and serrate, without long pilosity; first flagellomere short (clearly shortest of all, particularly in *C. childreni*) and its apical margin emarginate anteroventrally (Fig. 2.2.1 B). Mandible (Fig. 2.2.1 B, D) short and broad, moderately to strongly curved mesally, with bidentate apex; incisor edge simple, without row of

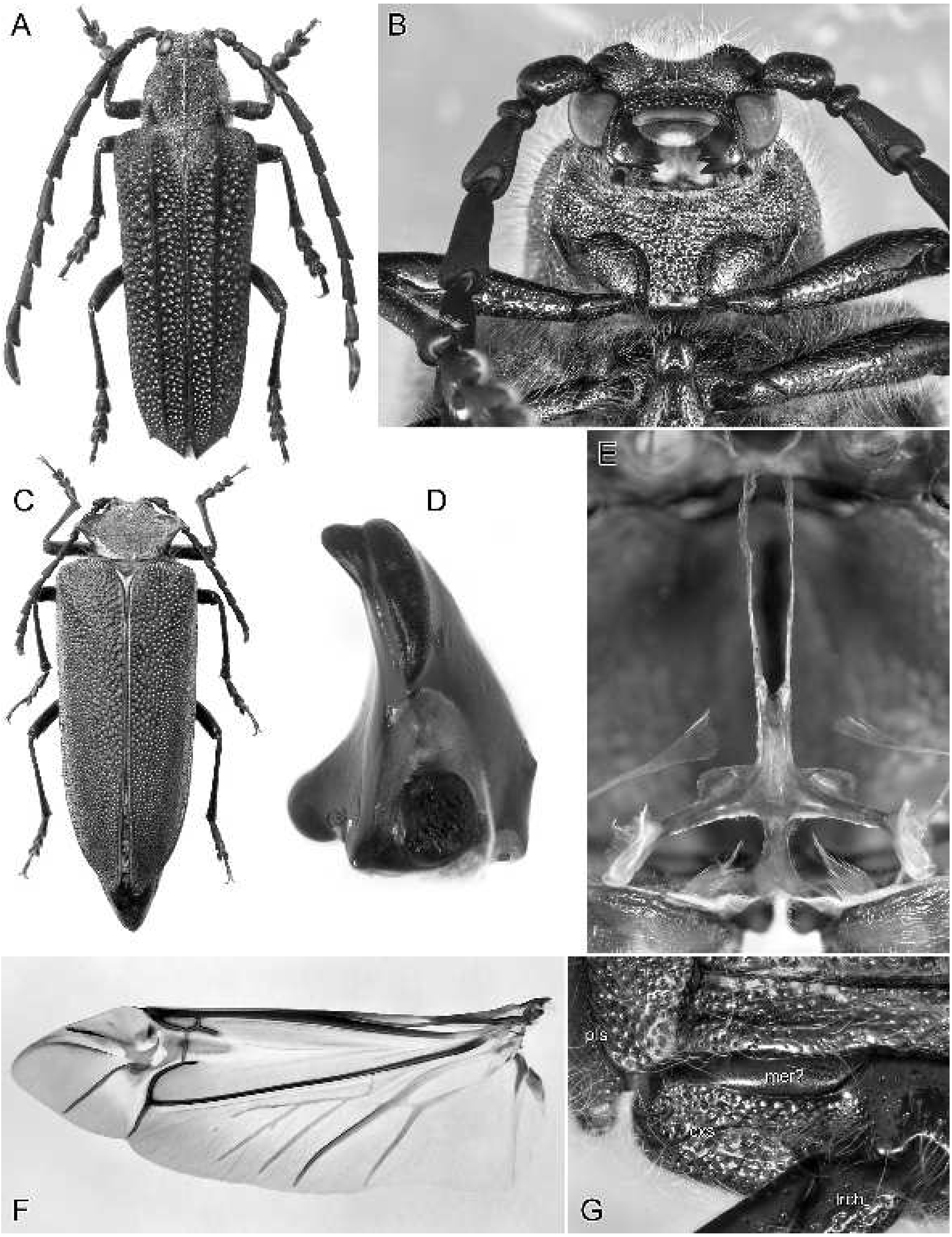

Fig. 2.2.1 Adults. A, *Oxypeltus quadrispinosus* Blanchard in Gay, male, dorsal view, 17 mm (© I. Jeniš); B, *O. quadrispinosus*, male, head and anterior thorax, ventral view; C, *Cheloderus childreni* Gray in Griffith, female, dorsal view, 41 mm (© I. Jeniš); D, *C. childreni*, male, right mandible, mesal view; E, *O. quadrispinosus*, female, metendosternite, dorsal view; F, *O. quadrispinosus*, male, left wing (particularly the conformation of MP_{3+4} is strongly individually variable); G, *O. quadrispinosus*, right hind coxal region, ventral view. cxs, coxal sulcus; mer?, enlarged distinctly delimited region probably belonging to coxal meron; pls, metapleural sulcus; trch, trochanter.

hairs; molar plate well-developed, subcircular and coarsely rugose; anteriorly largely enclosed by membranous region bearing dense microtrichia but not projecting into a prostheca. Maxilla with distinct, densely setose galea and lacinia, the latter shorter and without uncus. Labial ligula membranous, bilobed, moderately large. Maxillary palp tetramerous, labial palp trimerous, both short and with fusiform terminal segments. Subgenal ridges absent. Metatentorial slits widely separate. Gular sutures more or less distinct along entire gular length; gula fused with submentum, which projects slightly between maxillary bases. Tentorial bridge intermediate, firm but not broad and roof-like; pre- and metatentorium connected; dorsal tentorial arms present. Cervical sclerites very large.

Pronotum subquadrate or slightly transverse; pair of large flattened triangular laterodorsal projections present in *Cheloderus* (Fig. 2.2.1 C), apparently homologous to paired smooth elongate protuberances in *Oxypeltus* (certainly non-homologous to lateral pronotal carinae of some other cerambycoids); base distinctly narrower than elytra; sides without spines, lateral pronotal carinae absent or vestigial; anterior pronotal angles not produced; posterior angles broadly rounded to subacute; disc without paired basal impressions. Prosternum in front of coxae flat and shorter than shortest diameter of coxal cavity, particularly short in *Cheloderus*. Prosternal process complete, broad, parallel-sided, strongly elevated between and receding dorsally behind coxae. Notosternal sutures complete. Procoxal cavities moderately broadly separated, strongly transverse, angulate laterally, not concealing lateral coxal angles and trochantins, externally open (*Cheloderus*) or closed (*Oxypeltus*), internally closed. Procoxae prominent but not projecting below elevated prosternal process (Fig. 2.2.1 B), without secondary articulation. Mesoscutum short, with broad, shallow emargination anteriorly; with median endocarina; without stridulatory plate; scutellar shield large, acutely triangular, not sharply separated from or abruptly elevated above mesoscutum. Elytra covering abdomen (in some cases slightly dehiscent posteriorly), 2.2–2.5 times as long as combined width; irregularly punctate, without scutellary striole, epipleura very short or absent; elytra of *Oxypeltus* with paired longitudinal ridges terminated anteriorly by prominent parascutellar tubercles, also with tuberculate humeri. Elytral apices distinctly bispinose in *Oxypeltus* and more or less distinctly so in males of *Cheloderus*, whereas in females particularly the outer spine is usually reduced. Mesoventrite separated by complete sutures from mesanepisterna, the latter broadly separated at midline; sharply sloping, anterior edge on different plane than metaventrite, without paired procoxal rests. Mesocoxae subglobular with short lateral angle, moderately projecting, separated by much less than own width; cavities very broadly open laterally to mesepimeron. Mesometaventral junction strongly raised, as high as or raised above mesocoxae; junction complex, with metaventral knob fitting into mesoventral cavity (Fig. 2.2.1 B). Metaventrite with very long discrimen; postcoxal lines absent; transverse (katepisternal) suture more or less complete; exposed portion of metanepisternum short and broad anteriorly. Metacoxae narrowly separate, horizontally oriented, may or (particularly in females of *Cheloderus*) may not extend laterally to elytral margins; anteriorly with large and well-defined separate area, possibly a posterior expansion of otherwise hidden metacoxal meron (Fig. 2.2.1 G; it is small or usually indistinct in other cerambycoids); coxal plates absent. Metendosternite with lateral arms moderately long; laminae reduced; anterior process present, moderately long and bearing closely associated anterior tendons (Fig. 2.2.1 E). Wings (Fig. 2.2.1 F) present; apical field relatively short (very short and not completely folded in females of *Cheloderus*), with short sclerite just apicad of radial cell, three radial vein remnants and longitudinal sclerite crossing r4; radial cell moderately large, elongate, closed proximally; r3 (at least its distinct part) not longer than cell and longitudinal; r4 with spur rudimentary to absent; basal portion of RP only shortly surpassing r4; medial spur reaching wing margin at a distinct embayment; medial field without medial fleck and usually with five free veins (but number individually variable); at least rudiments of mp_{3+4}-cu present; CuA_2 attached only to MP_{3+4} before its fork; CuA_{1+2} in studied specimens vestigial or absent (and MP_{3+4} thus appears to have typically three branches, although venation of this region is rather variable and veins may be added or lost); wedge cell absent; anal lobe large, without embayment. Legs moderately long, slender; trochanterofemoral joint strongly oblique yet base of femur separated from coxa; tibiae only slightly expanded apically, each with well-developed spurs (2-2-2); fore and mid tibiae without antennal cleaners; tarsi 5-5-5, pseudotetramerous (tarsomere 4 very small and sunken in cavity of tarsomere 3); tarsomeres 1–3 broad, with dense ventral pads, tarsomere 3 deeply bilobed; pretarsal claws simple, without setae, free, moderately divergent; empodium very small (concealed when claws are flexed) and asetose.

Abdomen with five visible sterna (III–VII); first not much longer than second, without postcoxal lines; intercoxal process acute; sternum II invisible. Functional spiracles present on segments I–VII, located in lateral membrane. Terga I–VII well-sclerotized, with metallic coloration. Terminalia strongly modified and very different from remaining cerambycoids (see also Fragoso 1985). Males (Fig. 2.2.2 A, 2.2.3 A–C) with tergum VIII sclerotized and forming genital capsule; sternum VIII desclerotized and without apodeme. Segments IX and X reduced and membranous; sternum IX without spiculum gastrale. Aedeagus of reduced cucujiform type, symmetrical; tegmen ring-like with long anterior strut; parameres fused into small unpaired process (*Cheloderus*, Fig. 2.2.3 B, C) or completely lost (*Oxypeltus*, Fig. 2.2.3 A); penis more or less evenly sclerotized, slightly flattened and ventrally curved, with long narrow paired anterior struts; endophallus (internal sac) entirely within sclerotized distal capsule of penis when inverted, short and bulbous when everted, with a sclerotized apical rod (Kasatkin 2006). Ejaculatory duct thin, unpaired, containing a very long sclerotized rod (Fig. 2.2.3 A, B). Female terminalia (Fig. 2.2.2 B–D,

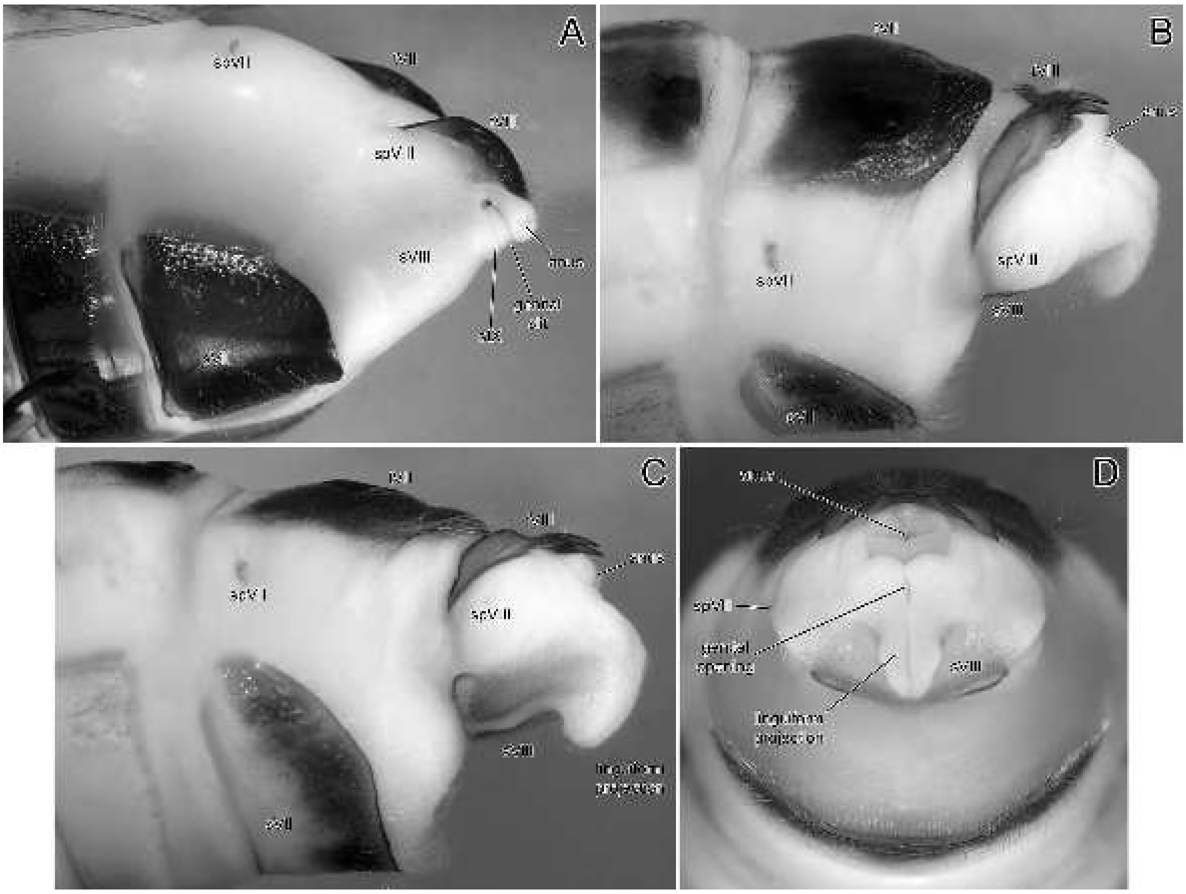

Fig. 2.2.2 *Oxypeltus quadrispinosus*, abdominal end of freshly moulted adults before the fat reserves are resorbed and membranes infolded. A, male, lateroventral view; B–D, female: B, laterodorsal view; C, lateroventral view; D, caudal view. s, sternum; sp, spiracle (vestigial on segment VIII); t, tergum.

2.2.3 D–F) with sclerotized and posteriorly dentate tergum VIII (a structure scraping debris for egg masking); membrane between sterna VII and VIII enlarged ("debris pocket" of Fragoso 1985); sternum VIII with anterior apodeme (spiculum ventrale), desclerotized along midline; posteriorly forming fleshy linguiform projection lateroventrally surrounding a simple membranous egg outlet (no distinct sclerotized ovipositor present). Vagina broad; bursa copulatrix virtually absent; spermathecal duct coiled and slightly sclerotized distally; spermatheca sclerotized, C-shaped, with moderately long gland on distalmost part of duct in *Cheloderus* (Fig. 2.2.3 F); *Oxypeltus* with small, spindle-shaped, poorly sclerotized capsule and a small gland far from terminal capsule (Fig. 2.2.3 D, E). Gut functional (hindgut often filled with food particles).

Morphology, Larvae (Duffy 1960; Svacha & Danilevsky 1987; Svacha *et al*. 1997). Body (Fig. 2.2.4 A, 2.2.6 A, B) soft, white, non-depressed, moderately elongate, almost parallel-sided. Setae simple, sparse and very short. Large body areas [posterior pronotum, posterior margin of prosternum, prothoracic coxal area and pleuron, pterothoracic terga and sterna, ambulatory ampullae (Fig. 2.2.6 E), and some others] covered with microspines, on some sclerotized prothoracic regions in the form of small sclerotized granules.

Head (Fig. 2.2.4 B, 2.2.5 A, B; for terminology see Fig. 2.4.22) narrow and deeply retracted, prognathous; cranium elongate due to posteriorly expanded epicranial lobes with parallel and approximate dorsal inner margins (not fused as stated in Duffy 1960; i.e., without cranial duplicature behind frontal base and with epicranial halves touching dorsally at "one point" immediately behind fusion of frontal lines; coronal suture absent); shape of posterior cranium individually variable. Frontal arms distinct, functioning as cleavage lines (at least during larval/pupal ecdysis), in part secondary as in Cerambycidae (see Fig. 2.4.27 E–I and cerambycid larval description); strongly curved to almost angulate, meeting at nearly 180°, anteriorly passing below antennae (not entering antennal openings) and (almost) reaching cranial margin. Frons entirely sclerotized, rugose and bearing a procurved transverse protuberance (its lateral ends more anterior), with distinct median endocarina; labrum and clypeus also sclerotized and fused with each other and with frons, forming a broadly trapezoidal nasale. Pretentorium as in Cerambycidae; pretentorial pits unusually

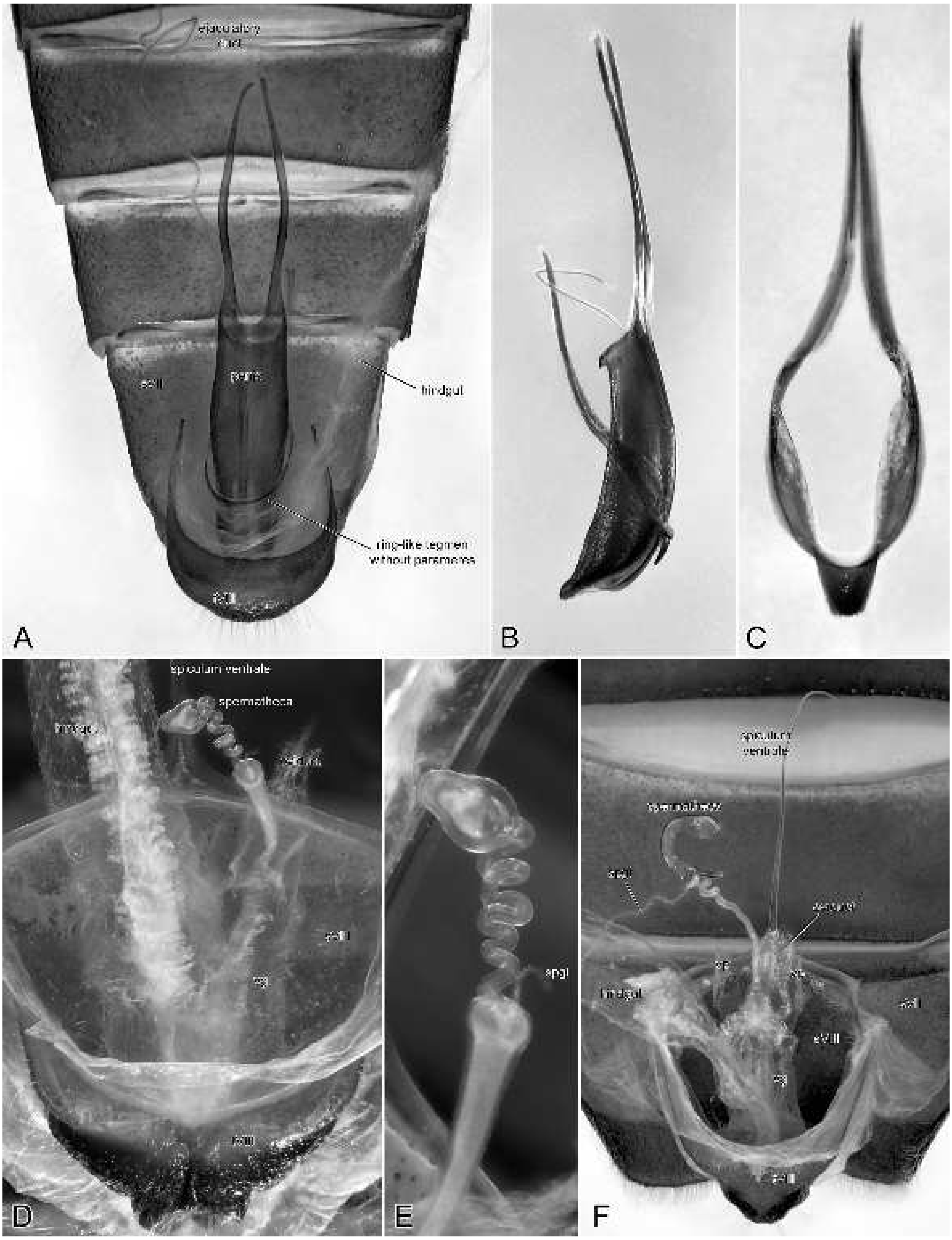

Fig. 2.2.3 Genitalia. A, *Oxypeltus quadrispinosus*, male, end of abdomen, dorsal view (terga removed except for VIII); B, *Cheloderus childreni*, penis (with part of ejaculatory duct) and tegmen, left lateral view (membranes removed); C, *C. childreni*, tegmen, dorsal view; D, *O. quadrispinosus*, female, end of abdomen, dorsal view (terga removed except for VIII); E, *O. quadrispinosus*, detail of spermatheca and spermathecal gland (may not be complete); F, *C. childreni*, female, end of abdomen, dorsal view (terga removed except for VIII). s, sternum; spgl, spermathecal gland; t, tergum; vp, paired vaginal plates (apodemes at anterior end of vagina, see Saito 1989); vg, vagina.

distinct (Fig. 2.2.5 B). Pleurostomal region swollen, without setae and subfossal process; low longitudinal ridge runs from ventral mandibular articulation posteriorly. Six stemmata on each side arranged in three groups (Fig. 2.2.5 B), three in an oblique row laterad of the antennal socket (lower two with cornea contiguous to fused, although pigment spots often remain distinguishable), two

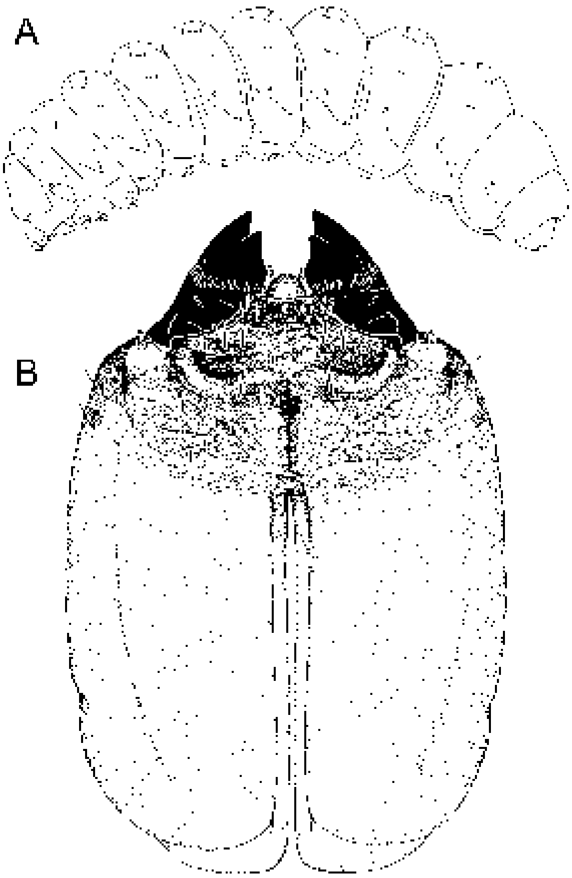

Fig. 2.2.4 Larvae. A, *Oxypeltus quadrispinosus*, larval habitus, left lateral view (from Svacha *et al.* 1997); B, *Cheloderus childreni*, head, dorsal view (from Svacha & Danilevsky 1987).

posterodorsally and one posteroventrally to the first group. Antenna trimerous, moderately long, with large connecting membrane and therefore deeply retractile; membrane smoothly continuous with cranial cuticle that does not form a distinct antennal ring; sensorium conical; antennal retractors attached on posterior frontal margin (Fig. 2.2.5 B, asterisk). Mandibles (Fig. 2.2.5 C, D) symmetrical, strongly sclerotized, with two dorsolateral setae on basal part (ventral one much more distal) and no mesal molar armature or articulated appendage; apical part with apex simple and separated from flat and shallowly bilobed dorsal edge by a distinct incision; in *Oxypeltus* medioapical face at base with cushion of short trichoid structures (Fig. 2.2.5 D; sometimes strongly abraded); position different from the penicillus of some Chrysomelidae (the structure was not found in a single, relatively intact mandible of *Cheloderus* that was studied). Maxillolabial complex (Fig. 2.2.5 A) more retracted than in Cerambycidae (cardo/stipes border distinctly behind mandibular condyle). Maxillary articulating area sharply divided in two parts, with larger posterior plate-like part fused with submentum and entire fused region slightly sclerotized. Cardo large, free, bearing one short lateral seta, sclerite not distinctly divided; stipes long, maxillary palpiger small, poorly defined, without laterodorsal process (Fig. 2.2.5 B); palp trimerous; last palpomere with one digitiform sensillum; mala with somewhat carinate inner face, extensively covered with dense long microtrichia with sparse interspersed setae. Distal labium slender; mentum long, almost fused with submentum; pigmentation of labial palpigers not fused medially; ligula entire, lacking setae and densely covered with microtrichia reaching far posteriorly along dorsolateral margin; hypopharyngeal part narrow and abruptly raised, without sclerome. Hypopharyngeal bracon absent. Short hypostomal rods present (ending blindly posteriorly); hypostomal plates not bridged by a sclerotized gula (i.e., connection between labial part of maxillolabial base and prosternum remains membranous). Metatentorial pits not distinct, metatentorial invaginations very broad, fusing into a plate-like tentorial bridge (lying in same plane as hypostomal plates and misinterpreted by Duffy 1960 as a "concealed hypostoma") and anteriorly bearing paired fine branches reaching deep into the cranial cavity toward the frontal region but not connected with pretentorial arms (Fig. 2.2.5 A, E).

Prothorax moderately enlarged and not broader than other body segments. Protergum large, strongly inclined, broadly pigmented; pronotum not distinctly delimited except for posterior indistinct rudiments of what may be homologues of cerambycid lateral furrows; sclerotization divided by a soft and flexible median zone, anteriorly with a pair of notches and posteriorly with a pair of paler protuberances just mesad of the rudiments of the lateral furrows; alar lobes partly divided posterioly by longitudinal impression (indistinct in inflated specimens) laterally delimiting protergal sclerotization. Epipleuron broadly pigmented and delimited by anteriorly diverging lines. Propleuron separate; pleural sulcus indistinct except for deep invagination at upper margin (Fig. 2.2.6 A), projecting internally into a short pleural apodeme. Sternal region (Fig. 2.2.6 B) composed of large and broadly sclerotized anterior plate and narrow, medially constricted posterior fold (possibly sternellum) with laterally adjacent procoxae; posterior fold constricted medially at short but distinct internal process, possibly representing a spina; other sternal endoskeletal elements absent. Pterothorax with mesonotum not distinctly subdivided; postnotum not developed; metanotum divided by two feeble transverse lines. Wing discs absent. Mesothoracic spiracle not protruding into prothorax, narrowly oval, annular-biforous, with two small marginal chambers at upper end; vestiges of metathoracic spiracle distinct. Meso- and metapleuron large, undivided, broadly separating coxa from epipleuron. Mesosternum divided by single trans-sternal line with incomplete anterior oblique branches. Metasternum with (partly) duplicate transverse line. Small but distinct spina present between meso- and metasternum. Coxae poorly defined, unsclerotized; distal legs short (slightly longer than maxillary palps), stout, without any sclerotized articulating points; trochanter unsclerotized and extremely reduced

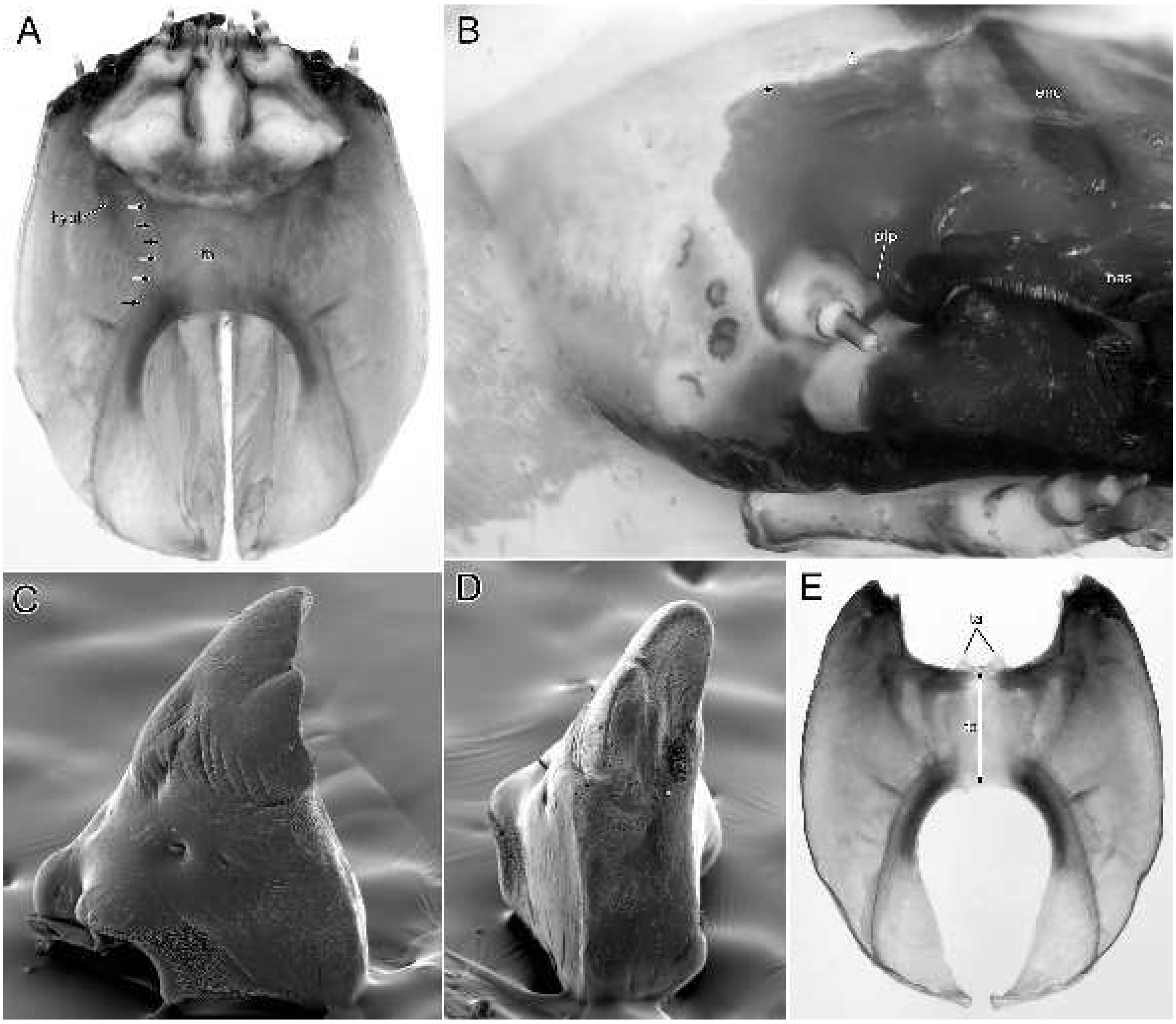

Fig. 2.2.5 *Oxypeltus quadrispinosus*, larva. A, head, ventral view; B, head, anterolateral view; C, left mandible, dorsal view; D, same, mesal view (C and D from Svacha *et al.* 1997); E, ventral half of cranium, dorsal view. enc, median frontal endocarina; fl, right frontal line; hypl, hypostomal lines; nas, sclerotized nasale; ptp; right pretentorial pit; ta, slender metatentorial arms on anterior margin of tentorial bridge, cut to short stubs; tb, tentorial bridge; *, point of attachment of retractors of right antenna; arrows in A, broad metatentorial invagination.

laterally; femur annular; tibiotarsus slightly longer than broad; pretarsus stoutly conical, sclerotized and rugulose distally, without setae; desclerotized mesal side of femur and usually adjacent part of trochanter bearing patches of microspines.

Abdomen with broad, flat and poorly delimited dorsal and ventral ambulatory ampullae on segments I–VII (ventral ampullae not distinctly separate from protuberant epipleuron), both divided by two laterally converging transverse lines delimited by one distinct pair of lateral impressions (Fig. 2.2.6 E). Spiracles on segments I–VIII (Fig. 2.2.6 C) similar to mesothoracic spiracles but smaller. Epipleuron protuberant on segments I–IX; epipleural tubercles or discs not defined. Lateral intersegmental zones behind segments I–VI with dorsal infolding forked and embracing dorsal end of ventral infolding (Fig. 2.2.4 A, 2.2.6 A, F). Pleural lobes small, indistinct, posterolateral. Segments IX and X small, subterminal, tergum IX unarmed. Anus triradiate, ventral radius long. Internal organs (*Oxypeltus* dissected): Foregut slightly asymmetrical, forming a moderately voluminous crop (Fig. 2.2.6 D); midgut not looped posteriorly; with broader anterior part without mycetomes and a posterior part bearing numerous small globular crypts; only very short distal parts of Malpighian tubules forming cryptonephric complex; hindgut simply looped, first fold not twisted above anus. Eight abdominal ganglia distinctly separated, connected by paired connectives; ganglionic complex VIII moved to posterior region of segment VII yet fully separate from seventh ganglion. First-instar larvae unknown.

Morphology, Pupae. Information based on female pupa of *Oxypeltus* (Fig. 2.2.7 A, B). The description and photograph of *C. childreni* in Cameron & Real (1974) is insufficient. Exarate (all appendages free), only very slightly depressed, white, soft, almost

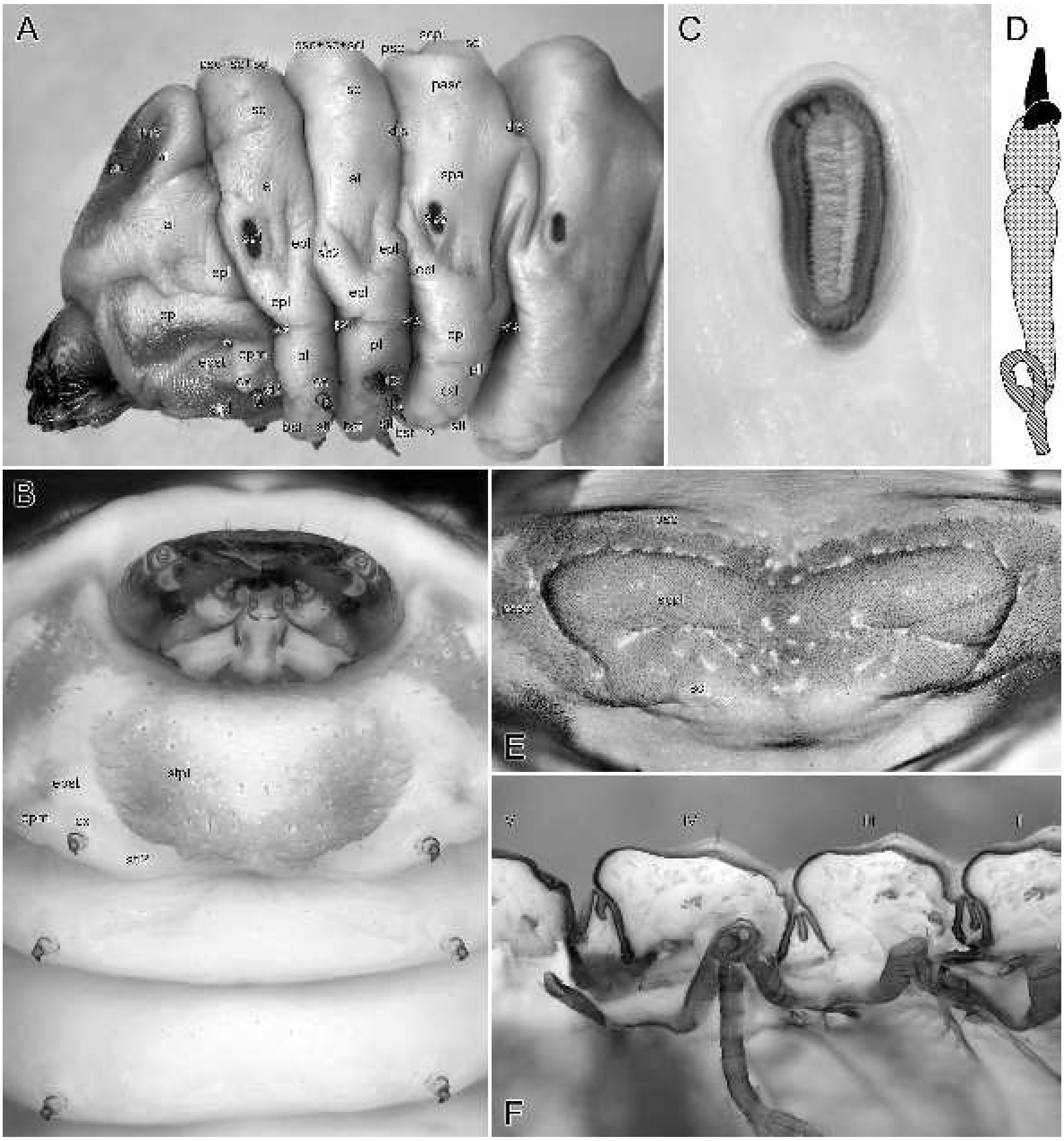

Fig. 2.2.6 Larvae. A, *Cheloderus childreni*, head, thorax and first two abdominal segments, left lateral view; B, *Oxypeltus quadrispinosus*, head and thorax, ventral view; C, *O. quadrispinosus*, 7th right abdominal spiracle; D, *O. quadrispinosus*, gross morphology of larval gut, diagrammatic, dorsal view (foregut black, midgut stippled, hindgut crosshatched; from Svacha *et al*. 1997); E, *O. quadrispinosus*, fifth dorsal abdominal ampulla, cleaned cuticle stained with Chlorazol Black E; F, *O. quadrispinosus*, right side of abdomen cut horizontally immediately above spiracles, dorsal part viewed ventrally, showing intersegmental folds following segments II, III and IV. al, alar lobe; bst, basisternum; cx, coxa; dis, dorsal intersegmental zone; epl, epipleuron; epm, epimeron; epst, episternum; l1, l2, l3, pro-, meso- and metathoracic distal legs (without coxa); lfur?, possible homologues of lateral pronotal furrows of the Cerambycidae; pasc, parascutum (abdominal homologue of lateral part of pterothoracic scuta); pl, pleuron (fused episternum and epimeron); pll, pleural lobe (on abdominal segments); pn, pronotum; psc, prescutum; pst, presternum; sc, scutum; scl, scutellum; sp1, sp2, sp3, mesothoracic, metathoracic (vestigial and closed) and first abdominal spiracle; scpl, scutal plate of dorsal abdominal ampulla; spa, spiracular area (presumed abdominal homologue of pterothoracic alar lobes); stl?, presumed sternellum; stpl, prosternal plate of uncertain homology; vis, ventral intersegmental zone; *, invagination of propleural apodeme; ?, separate transverse fold on ventral abdominal ampulla (may belong to either basisternum or sternellum). For a more detailed discussion of terminology see Cerambycidae.

glabrous (minute setae present on some small tubercles/processes on abdominal terga I–VI). Head bent ventrally, with mouthparts pointing obliquely caudad. Antennae looped separately between mid and hind legs, not coiled, without spines. Pronotum bears paired round and fleshy processes. Abdomen with functional spiracles on segments I–V (those on VI and VII distinct but

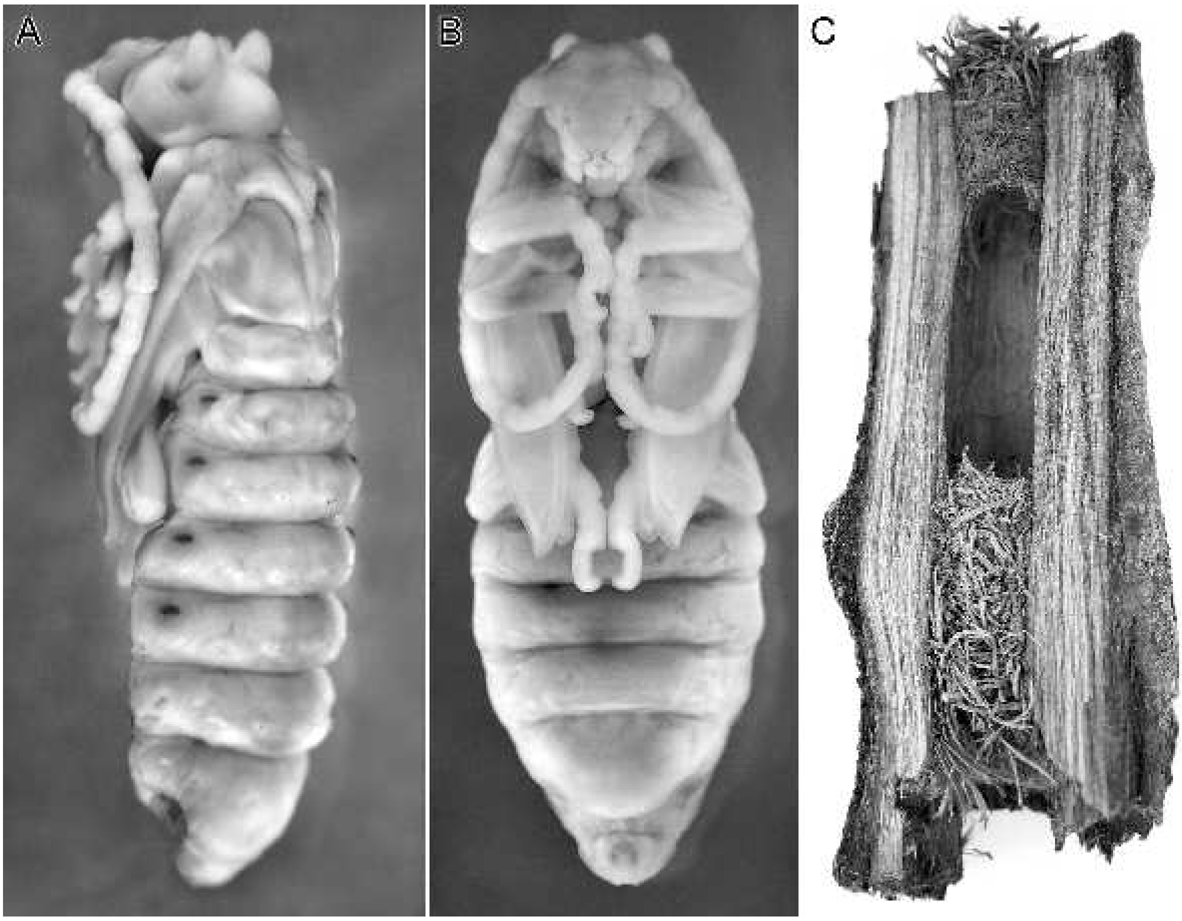

Fig. 2.2.7 *Oxypeltus quadrispinosus*. A, female pupa, dorsolateral view; B, same, ventral view; C, pupal chamber in about 2 cm thick girdled branch fragment of *Nothofagus dombeyi*.

obviously closed, VIII much less distinct), without gin traps; in female, sternum VIII very soft, wrinkled and with slightly marked prospective lingular process; segment IX reduced, tergum without urogomphi or spine, venter without paired lobes (corresponding with absence of ovipositor).

Phylogeny and Taxonomy. The group was revised by Cerda (1972). Both genera were originally classified as an aberrant, problematic group with possible affinities to members of the cerambycid subfamily Prioninae (in part because of the flat pronotal projections of *Cheloderus*, which are not homologous to the prionine lateral pronotal carinae). This concept was accepted by Thomson (1861), but later Thomson (1864) and Lacordaire (1868) removed the two genera from prionines. Thomson (1864) placed them in his Tribus Lepturitae and Division Necydalitae. This was a remarkably heterogeneous group containing (in addition to *Oxypeltus* and *Cheloderus*) 23 other genera currently belonging to three or (if Necydalinae and Lepturinae are separate) four different subfamilies of Cerambycidae. Lacordaire introduced a group named Oxypeltides in his broad subfamily named Cérambycides. Afterward, the group was generally classified in the non-prionine and non-lamiine parts of the Cerambycidae or its equivalents (e.g., "Longicornia"), frequently close to forms belonging to or resembling Lepturinae. Crowson (1955) also provisionally placed *Oxypeltus* and *Cheloderus* in his Lepturinae (characterized by himself as "a fairly extensive subfamily of rather uncertain limits" and containing present Dorcasominae and the genera *Vesperus* Dejean and *Mantitheus* Fairmaire of Vesperidae), mentioning that they have "Prionid-like facies, little posterior constriction of the head, and no mesonotal stridulatory file". Discovery of the extraordinary larvae prompted Duffy (1960), who was otherwise very reserved concerning taxonomic changes, to elevate their rank to a cerambycid subfamily Oxypeltinae. The subfamily rank was accepted by other researchers, such as Cerda (1972, 1986), Monné (1994, 2002, 2006), Lawrence & Newton (1995), and Bousquet *et al.* (2009). Crowson (1981) combined the subfamily with Philinae, Vesperinae and Disteniinae in his family Disteniidae (though it should have been named Vesperidae based on priority). Based primarily on larval characters, Svacha & Danilevsky (1987) and Svacha *et al.* (1997) treated Oxypeltidae as a separate family (followed by Lawrence *et al.* 1999 b). Napp (1994) accepted this concept, although it was not clearly supported by her analysis of adult characters. Even though Monné & Giesbert (1994) placed Oxypeltini as a tribe in their cerambycid subfamily Aseminae without explanation, recent works (Monné 2012; Bezark & Monné 2013) support the group as a family. Oxypeltidae is undoubtedly a monophyletic taxon bearing some striking apomorphies, which are either unique or have evolved in parallel in unrelated chrysomeloid groups. These characters are as follows: adult males with reduced or lost parameres (Fig. 2.2.3 A–C) and with sterna VIII and IX lacking apodemes; adult females without any traces of a sclerotized ovipositor (Fig. 2.2.2 B–D); elongated larval head with epicranial halves extended posteriorly, with approximated but separate parallel dorsomesal margins (Fig. 2.2.4 B, 2.2.5 A); maxillary mala covered with dense long microtrichia and only few scattered setae; completely fused and sclerotized nasale (Fig. 2.2.4 B, 2.2.5 B). Relationships to other chrysomeloid families are unclear. Oxypeltids were always classified in the cerambycoid assemblage (i.e., together with the presently recognized families Vesperidae, Disteniidae and Cerambycidae), but monophyly of that assemblage is not reliably supported, and some larval characters (such as the tendency toward increased sclerotization and fusion of the labrum and clypeus, also occurring but less pronounced in the megalopodid subfamily Palophaginae) or preliminary unpublished molecular data (D. McKenna *et al.*, in preparation) suggest possible closer relationships with the Megalopodidae.

Acknowledgments

J. E. Barriga (Curicó, Chile) and the late E. Krahmer (Valdivia, Chile) provided valuable material and information about biology. I. Jeniš (Náklo, Czech Republic) permitted the use of his photographs (mentioned in legends). P. Svacha acknowledges support from the Institute of Entomology (RVO:60077344).

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2.3 Disteniidae J. Thomson, 1861

Petr Svacha and John F. Lawrence

Distribution. A moderately large (over 300 species) and widely distributed family (absent from New Zealand and Australia) that is predominantly tropical and subtropical, with only a few species penetrating into temperate areas, exceptionally surpassing 45° latitude (*Distenia japonica* Bates in Sakhalin). Arid zones are avoided. Disteniids are present in South America (except for Chile and Uruguay; in Argentina known only from Misiones; Di Iorio 2005), Central America (including some Caribbean islands), southern North America (numerous species in Mexico but only one in the eastern United States), the Afrotropical region (including Madagascar and some adjacent islands), the eastern Palaearctic region (northeastern China, Korean Peninsula, Japan and the Ussuri region, Sakhalin and Kurile Islands in Russia; absent from the western Palaearctic and Siberia), the Oriental region including southeastern Asian islands and some Melanesian islands (New Britain, Bougainville, several islands of Fiji; not known from New Guinea or New Caledonia; Lingafelter 2007).

Biology and Ecology. The larval biology of Cyrtonopini and Heteropalpini is unknown. The slender larvae of Disteniini feed in or under bark and sometimes later in the sapwood of dead or dying trees and shrubs, often assuming a characteristic curved position resembling some buprestid larvae. A Madagascan species of *Nethinius* Fairmaire was also found in a half-dead liana. Pupation occurs usually in sapwood. The relatively well known East Asian island species *Distenia japonica* (sometimes incorrectly treated as a synonym of *D. gracilis*; Danilevsky 2012) is polyphagous on broadleaved trees and conifers (see Gressitt 1951; Ohbayashi & Niisato 2007); the mainland *D. gracilis* feeds underground on roots of broadleaved trees, although larvae return to root bases for pupation (Cherepanov & Cherepanova 1975). The North American *Elytrimitatrix undata* (Fabricius) also feeds on roots (Craighead 1923). The Oriental *Dynamostes audax* Pascoe (Dynamostini) was recently found in Yunnan (Lin *et al.* 2010), and some specimens were reared from larvae found in May in rainforest at approximately 1000 m in a standing half-dead stem of an unidentified broadleaved tree about 30–40 cm in diameter; larvae fed under dead bark together with some cerambycids; pupation was not observed (X. Zhu, personal communication). Disteniid adults are usually winged and both sexes are capable of flight (verified in some Disteniini); only two related wingless Oriental genera are known: *Clytomelegena* Pic (Fig. 2.3.1 F, 2.3.2 C; Lin & Murzin 2012) and *Olemehlia* Holzschuh. Adults of some species (e.g., some Madagascan *Nethinius*) are at least partly diurnal, but many disteniids are predominantly crepuscular or nocturnal and are often attracted to light. Very little is known about adult feeding; some taxa possibly do not feed at all (?*Cyrtonops* White), but captive adults of Madagascan *Nethinius* sp. fed on honey, whereas pellets of unidentified particulate food (but not pollen) were found in the guts of several Disteniini (*America* Santos-Silva & Tavakilian, *Elytrimitatrix* Santos-Silva & Hovore, *Distenia* Le Peletier & Audinet-Serville).

Morphology, Adults (Fig. 2.3.1, 2.3.2; no specimens of Heteropalpini were available for dissection). Length 5–40 mm; body about 2.7–6 times as long as wide; sides subparallel or elytra distinctly tapering (expanded behind middle in flightless myrmecoform *Clytomelegena* and *Olemehlia*). Coloration usually brownish to black, occasionally metallic and/or variegated. Upper surfaces bearing longer erect setae and/or short decumbent hairs, the latter sometimes forming patterns on the elytra.

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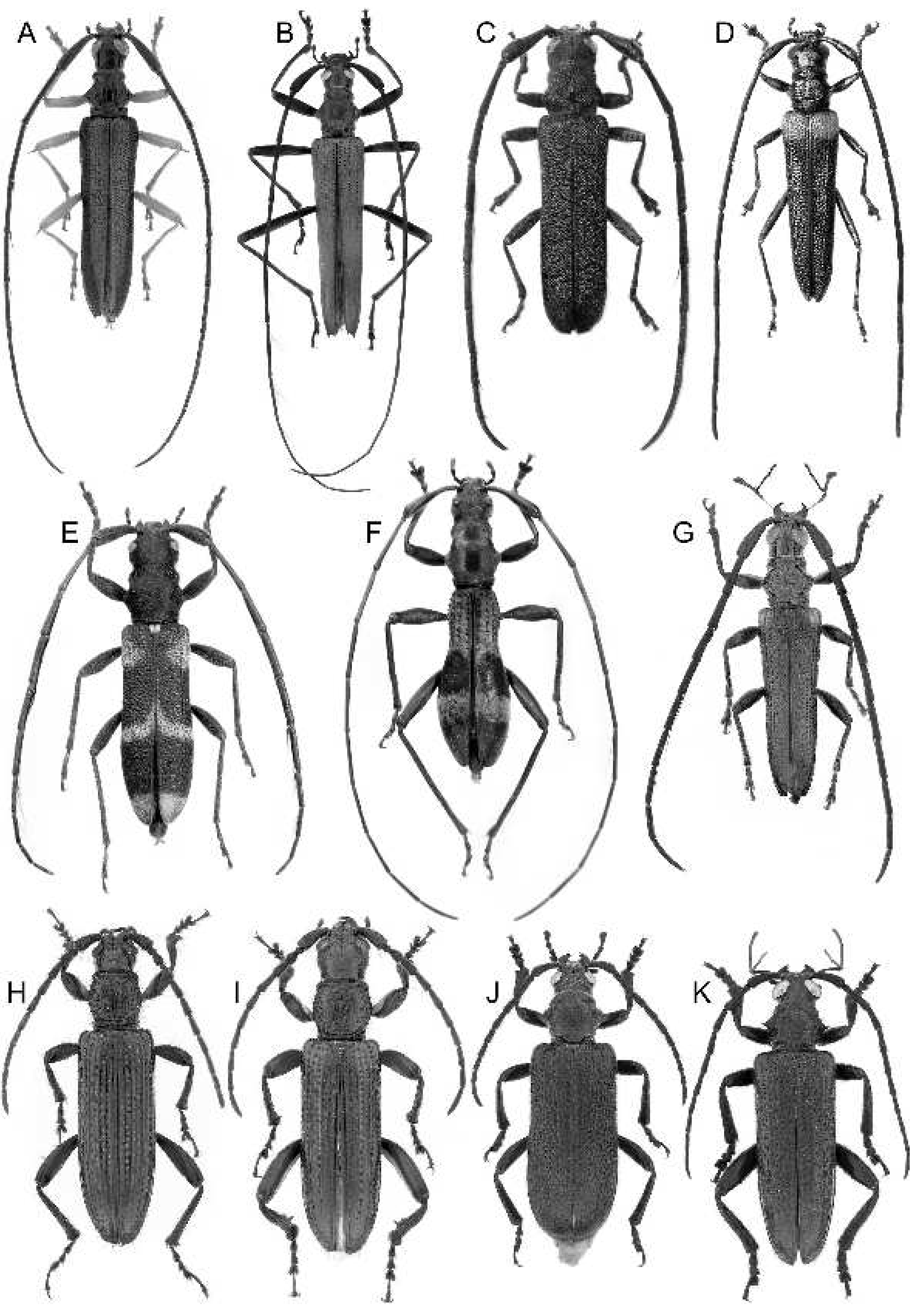

Fig. 2.3.1 Adults of Disteniini (A–F), Heteropalpini (G), Dynamostini (H, I), and Cyrtonopini (J, K), dorsal view. A, *Distenia suturalis* Bates, female, 20 mm; B, *Typodryas callichromoides* J. Thomson, male, 23 mm; C, *Cometes hirticornis* Le Peletier & Audinet-Serville in Latreille, male, 9 mm (© I. Jeniš); D, *Paracometes acutipennis* (Buquet), male, 12 mm (© I. Jeniš); E, *Tengius ohkuboi* Matsushita, female, 8 mm; F, *Clytomelegena kabakovi* (Murzin), female, 11 mm; G, *Pseudocometes argutulus* (Buquet), male, 13 mm; H, *Dynamostes audax* Pascoe, female, 19 mm; I, *D. audax*, male, 20 mm; J, *Cyrtonops metallicus* Hüdepohl, female, 19 mm; K, *Cyrtonops* sp. (Sri Lanka), male, 25 mm.

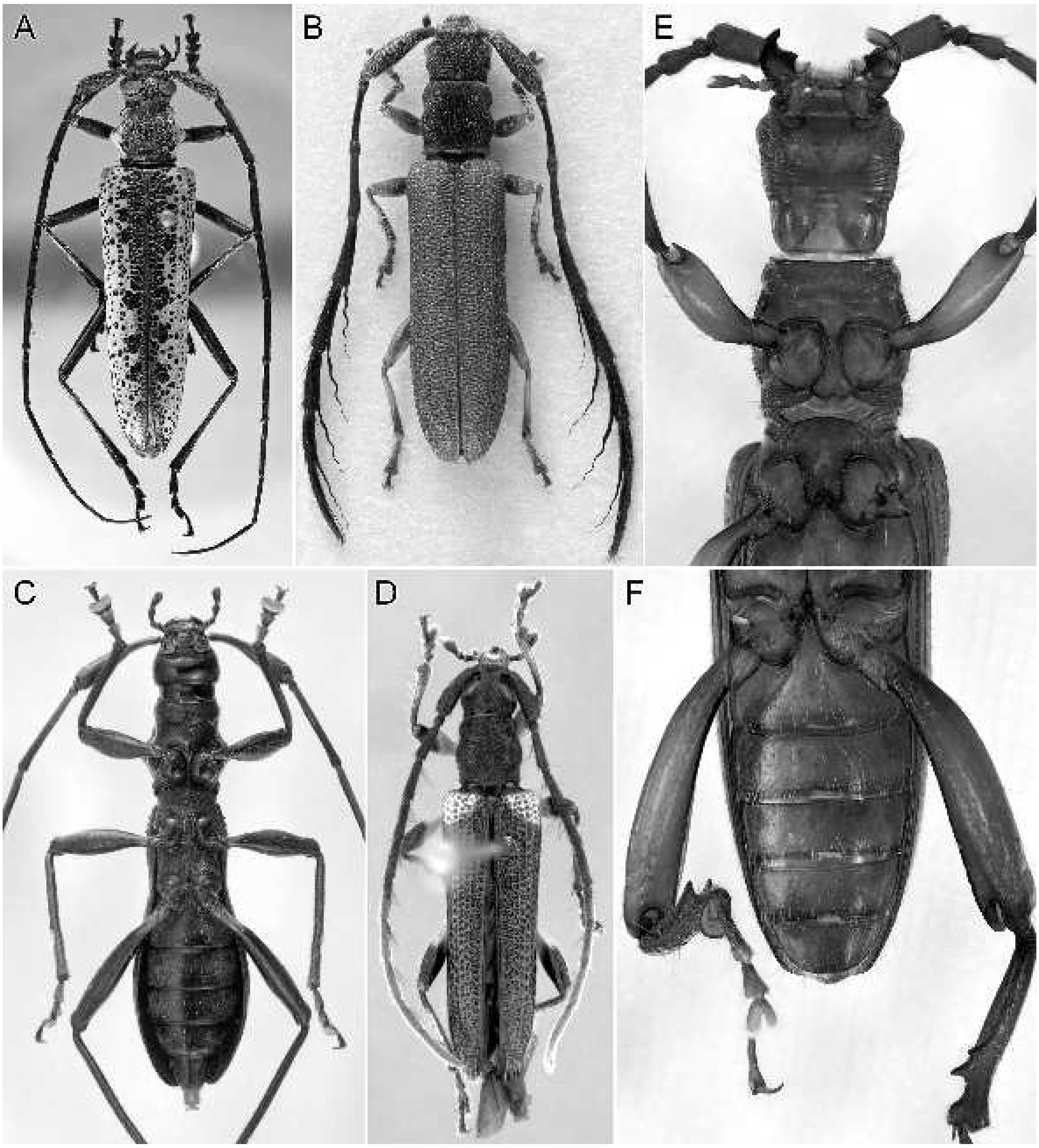

Fig. 2.3.2 Adults of Disteniini (A–C) and Dynamostini (D–F). A, *Disteniazteca pilati* (Chevrolat), female, dorsal view (© N. P. Lord & E. H. Nearns); B, *Villiersicometes wagneri* (Gounelle), ?male, dorsal view (© N. P. Lord & E. H. Nearns); C, *Clytomelegena kabakovi*, female, 11 mm, ventral view; D, *Aiurasyma potira* Martins & Galileo, male, 8.4 mm, dorsal view (© G. Biffi); E, *Dynamostes audax*, male, head, pro- and mesothorax, ventral view; F, *D. audax*, male, hind legs and abdomen, ventral view.

Head prognathous, short to moderately elongate, not or only slightly constricted posteriorly; sometimes forming a very broad neck and long, weakly defined temples. Occipital region without transverse ridge or stridulatory file. Frontal region not to moderately, gradually declined except for steeply declivous anterior margin; with median groove or line (marking deep internal carina) that may continue behind the eyes but does not reach the posterior cranial margin. Eyes small to large, slightly to strongly protuberant, usually shallowly emarginate (may be entire when small); finely or coarsely facetted, without interfacetal setae. *Distenia japonica* (described by Gokan & Hosobuchi 1979 as *D. gracilis*) has acone ommatidia with biconvex corneal lens and a large open rhabdom (corresponding with nocturnal habits) formed by two central and six peripheral retinula cells; central rhabdom fused at both ends with continuous circular peripheral rhabdom. Antennal insertions exposed from above, very close to mandibular articulations, facing laterally and more or less anteriorly; supported medially by prominent tubercles connected by more or less complete transverse protuberance, sharply declivous anteriorly toward (and usually partly involving) postclypeus; short carina usually present behind antennal sockets; subantennal groove absent. Frontoclypeal ridge distinctly impressed, transverse or slightly V-shaped; pretentorial pits distinct and positioned in narrow space between antennal sockets and lateral postclypeus with mandibular articulations (Fig. 2.3.3 A). Anterior clypeus membranous; postclypeal sclerotization reaching more or less anterior to mandibular articulations; with straight or (*Cyrtonops*, Fig. 2.3.3 B) slightly raised and emarginate anterior margin. Labrum free, moderately to strongly transverse, broadly rounded to truncate or slightly emarginate. Antennae 11-segmented, filiform; usually surpassing elytral apices, distinctly shorter than body in both sexes of *Cyrtonops* and *Dynamostes* Pascoe; scape long (occasionally almost reaching posterior margin of prothorax) and thickening distad, occasionally spinose; pedicel small (at most slightly longer than broad) but with large condyle fitting in broad distal opening of scape; all or at least some flagellomeres usually bearing characteristic long recumbent setae in large sockets placed in shallow longitudinal groove on posterior antennal face and typically

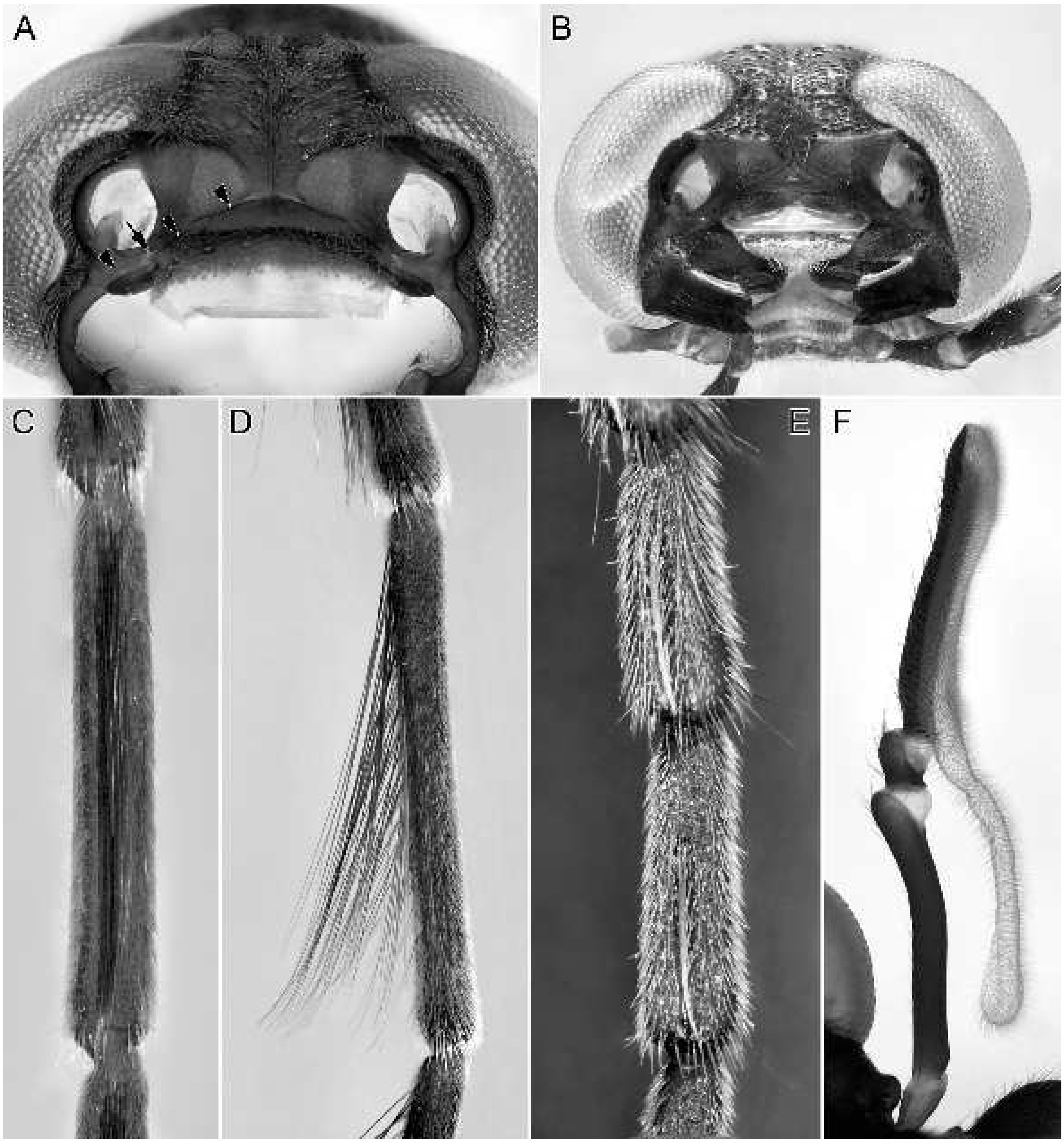

Fig. 2.3.3 Adults. A, *Elytrimitatrix undata* (Fabricius), female, head, anterior view (arrowheads mark the frontoclypeal sulcus, arrow points to right pretentorial pit); B, *Cyrtonops punctipennis* White, male, head, anterior view; C, *Elytrimitatrix undata*, female, fifth right flagellomere, posterior view (long setae in shallow groove); D, *E. undata*, male, sixth right flagellomere, dorsal view (long setae partly erect); E, *Dynamostes audax*, male, sixth and seventh right flagellomeres, posterior view (showing reduced but present long setae); F, *Cyrtonops punctipennis*, male, left maxillary palp, dorsal view.

surpassing distal end of flagellomere (Fig. 2.3.3 C, D); those setae are absent on flagellomere 1 in *Tengius* Matsushita, are fewer and shorter (not surpassing segments) in Dynamostini, particularly in *Dynamostes* where present only on flagellomeres 2–8 (Fig. 2.3.3 E), and are absent in Cyrtonopini. Mandible short and broad to moderately long (*Dynamostes*, Fig. 2.3.2 E), more or less abruptly curved mesally; apex bidentate (*Cyrtonops*, Fig. 2.3.3 B), more or less broadly truncate or rounded (most species, Fig. 2.3.4 A), or sharply pointed (*Nethinius*; mandible in latter genus also with particularly prominent, longitudinal lateroventral carina, Fig. 2.3.4 B); incisor edge simple or with one or two teeth, in some cases with row of long hairs; molar plate usually well-defined (often finely striate or with other microsculpture), surrounded anteriorly by desclerotized area with fine microtrichia (Fig. 2.3.4 A, B); molar plate less distinct in Dynamostini, with only small central area of distinct microsculpture and smaller desclerotized area in *Dynamostes*; both structures absent in *Cyrtonops* (molar region partly visible in Fig. 2.3.3 B); prostheca absent. Maxilla with distinct, setose galea and lacinia without obvious pollinophagous modifications (such as elongate bases and long curved setae), both relatively small in *Cyrtonops*; lacinia without uncus; palps tetramerous; terminal palpomere always with larger sensory area in males, often fusiform or moderately truncate in females and apically expanded and more or less triangular in males; in Cyrtonopini and Heteropalpini broadened in females and uniquely modified in males (Fig. 2.3.1 G, K, 2.3.3 F) where palpomere 2 is long, 3 very short, 4 (terminal) again long with sensory area expanded along its entire mesal face and projecting basally into a finger-like process. Ligula with more or less broad membranous anteriorly straight or very shallowly emarginate apical flap (small in *Cyrtonops*); never typically bilobed but in *Nethinius* with paired membranous lobes sharply folded back on ventral side; labial palps trimerous; terminal palpomere normal, fusiform (some females) to strongly expanded apically (many males). Metatentorial slits oblique and converging, broadly separated to virtually touching anteriorly. Gula not defined laterally

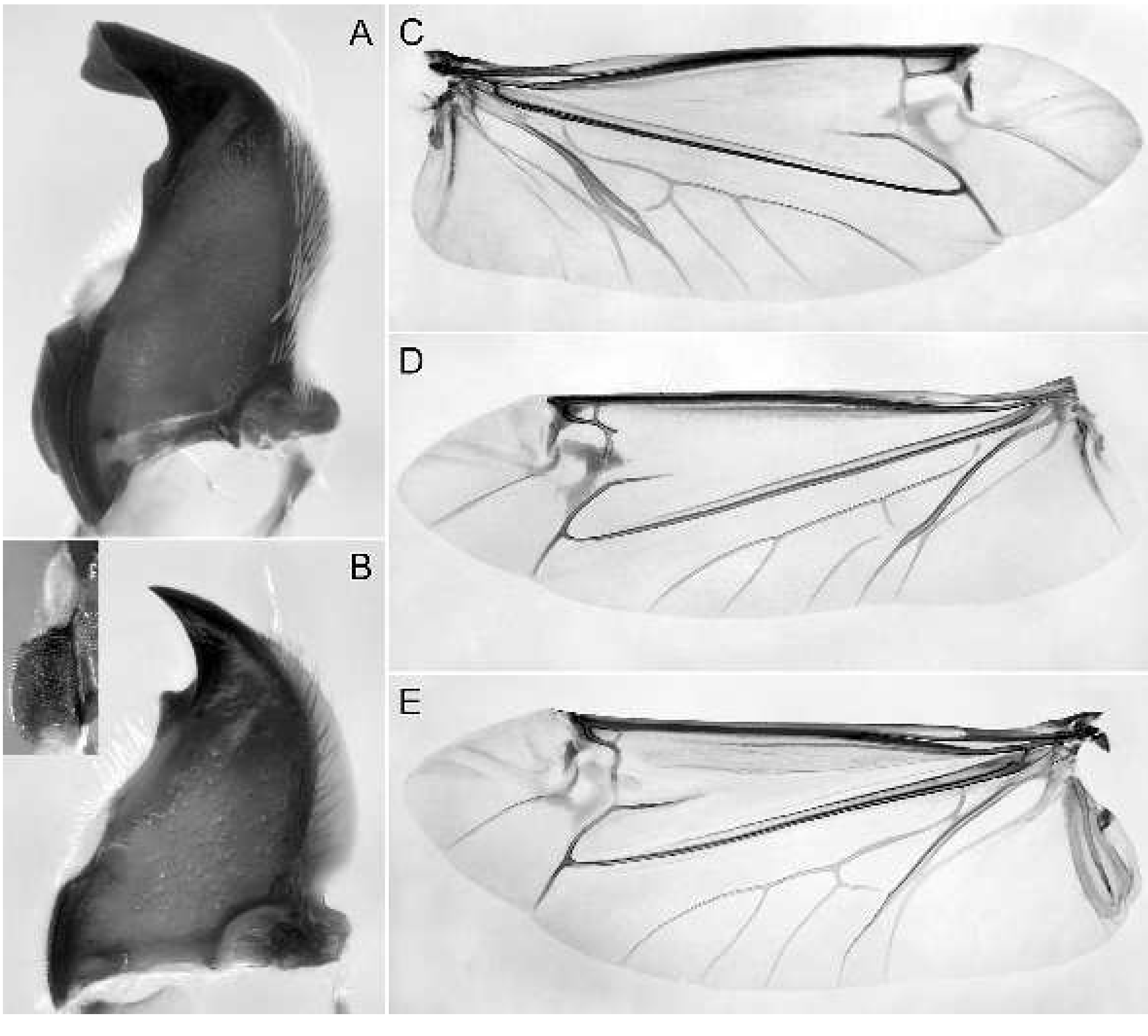

Fig. 2.3.4 Adults. A, *Elytrimitatrix undata*, female, right mandible, dorsal view; B, *Nethinius* sp., male, right mandible, dorsal view (inset shows molar plate in dorsomedial view); C, *Elytrimitatrix undata*, female, right wing; D, *Distenia japonica* Bates, female, left wing; E, *Cyrtonops* sp. (Sri Lanka), male, left wing.

anterior to those slits, fused with submentum; the latter strongly projecting between maxillary bases. Tentorial bridge broad, roof-like or, in taxa with approximate metatentorial slits, almost cylindrical anteriorly where the bases of metatentorium become subcontiguous; pre- and metatentorial arms sclerotized and firmly fused with each other; dorsal arms absent or only bases distinctly sclerotized. Cervical sclerites rudimentary or absent.

Prothorax 0.65–1.2 times as long as wide, usually widest and bearing a lateral spine or distinct tubercle at approximately the middle (sides broadly rounded and without tubercle in Dynamostini and *Micronoemia* Aurivillius of Disteniini); often constricted anteriorly and less distinctly posteriorly; base distinctly narrower than elytral bases except for flightless *Clytomelegena* (Fig. 2.3.1 F, 2.3.2 C) and *Olemehlia*; pronotum not explanate or margined laterally, without produced anterior angles; anterior edge usually with narrow margin or bead; posterior angles obtuse or right, posterior edge more or less straight or evenly rounded; disc frequently with smooth or otherwise distinguished raised areas, without paired basal impressions. Prosternum in front of coxae slightly shorter to slightly longer than shortest diameter of procoxal cavity, flat to moderately convex. Prosternal process usually more or less complete, narrow, parallel-sided and rounded, truncate or slightly expanded at apex; very short and pointed in *Cyrtonops*, broader and strongly expanded apically in *Dynamostes* and *Aiurasyma* Martins & Galileo. Notosternal sutures incomplete or indistinct. Procoxal cavities usually narrowly separated and more or less circular (lateral coxal angles completely covered by prosternal flaps), confluent and lateral angles and trochantins partly exposed in *Cyrtonops*; open externally except for *Dynamostes* (Fig. 2.3.2 E) and *Aiurasyma*, broadly closed internally; visible procoxae usually subglobular and moderately projecting below prosternum, but strongly prominent in *Cyrtonops*. Mesoscutum straight or shallowly emarginate anteriorly, with median endocarina and divided and usually large stridulatory plate (Fig. 2.3.5 A); endocarina slightly shifted to left side (making division asymmetrical) in single available specimen of *Saphanodes* Hintz (holotype of *S. apicalis* [Chevrolat]). Scutellar shield small, more or less abruptly elevated above mesoscutum, anteriorly simple, posteriorly broadly rounded to truncate. Elytra fully covering abdomen, 2.2–4.2 times as long as combined width and 2.7–5 times as long as pronotum; irregularly punctate, or with as many as ten puncture rows (often obliterated posteriorly); rarely punctation indistinct (*Thaigena* Holzschuh); scutellary striole missing; elytral apices meeting or almost meeting at suture, in some cases with inner (sutural) and/or outer spines; epipleura absent or incomplete. Mesoventrite separated by complete sutures from mesanepisterna, which are broadly separated at midline; anterior edge on same plane as metaventrite, in species with externally open procoxal cavities usually with paired horizontal or slightly declined procoxal rests; mesoventral cavity absent. Mesocoxal sockets subcircular, moderately to widely separated; broadly open laterally in *Cyrtonops*, narrowly open to closed in Disteniini and Heteropalpini, closed in Dynamostini; mesocoxae round, moderately projecting. Mesometaventral junction a complex fitting. Metaventrite with discrimen moderately to very long; postcoxal lines absent; exposed portion of metanepisternum very long and narrow. Metacoxae contiguous or narrowly separated, horizontally oriented, extending laterally to meet elytra; plates absent. Metendosternite (Fig. 2.3.5 B) with lateral arms moderately to very long; laminae and anterior process absent; anterior tendons fine and placed more or less far apart on lateral arms. Hind wing (Fig. 2.3.4 C–E) fully developed except for apterous *Clytomelegena* and *Olemehlia*; apical field moderately long, with only one (posteriormost) distinct sclerotized radial vein remnant; radial cell proximally closed (see remark under Dynamostini), with posterobasal angle right or obtuse; crossvein r3 short or absent and often fused for most/all of its length with r4; r4 in some cases interrupted before reaching RP; spur usually short or absent (relatively distinct in some *Nethinius*, but variable even between right and left wing of the same specimen); RP surpassing r4 proximally, moderately long; medial field with five free veins and no medial fleck; mp_{3+4}-cu often absent; CuA_{1+2} and CuA_1 present but former often interrupted basally; CuA_2 in some cases also disconnected (Fig. 2.3.4 D); wedge cell usually absent but narrow yet distinct in *Elytrimitatrix undata* (Fig. 2.3.4 C) and rudiments present in several other Disteniini (Santos-Silva & Hovore 2007 a); anal lobe well-developed, without embayment; AP_3 may be more or less surrounded by sclerotization in *Cyrtonops* (Fig. 2.3.4 E). Legs moderately to very long, usually slender; strong particularly in males of *Cyrtonops* and *Dynamostes*; trochanterofemoral joint strongly oblique, with base of femur sometimes abutting coxa; femur, particularly in some American taxa, with apical spine on anterior side (Fig. 2.3.1 A); tibial spurs 2-2-2; inner protibia and outer mesotibia near apex usually with oblique, hairy grooves (antenna cleaners similar to those in cerambycid subfamily Lamiinae; reduced in *Cyrtonops*, possibly in connection with loss of long flagellar setae); hind legs enlarged in males of *Dynamostes* and some *Cyrtonops*, in former hind tibiae with two large teeth on inner side, in latter inner edges of femora and tibiae tuberculate or spinose. Tarsi 5-5-5, pseudotetramerous with tarsomere 4 strongly reduced and tarsomere 3 enlarged and ventrally (bi)lobed; tarsomeres 1–3 each with dense ventral pads (slightly reduced on tarsomere 1 in some species); pretarsal claws simple, without setae, divaricate; empodium present, bi- or usually multisetose.

Abdomen with five visible sterna (III–VII), first not much longer than second, without postcoxal lines; intercoxal process acute or narrowly rounded, completely hiding sternum II. Functional spiracles located in lateral membranes of

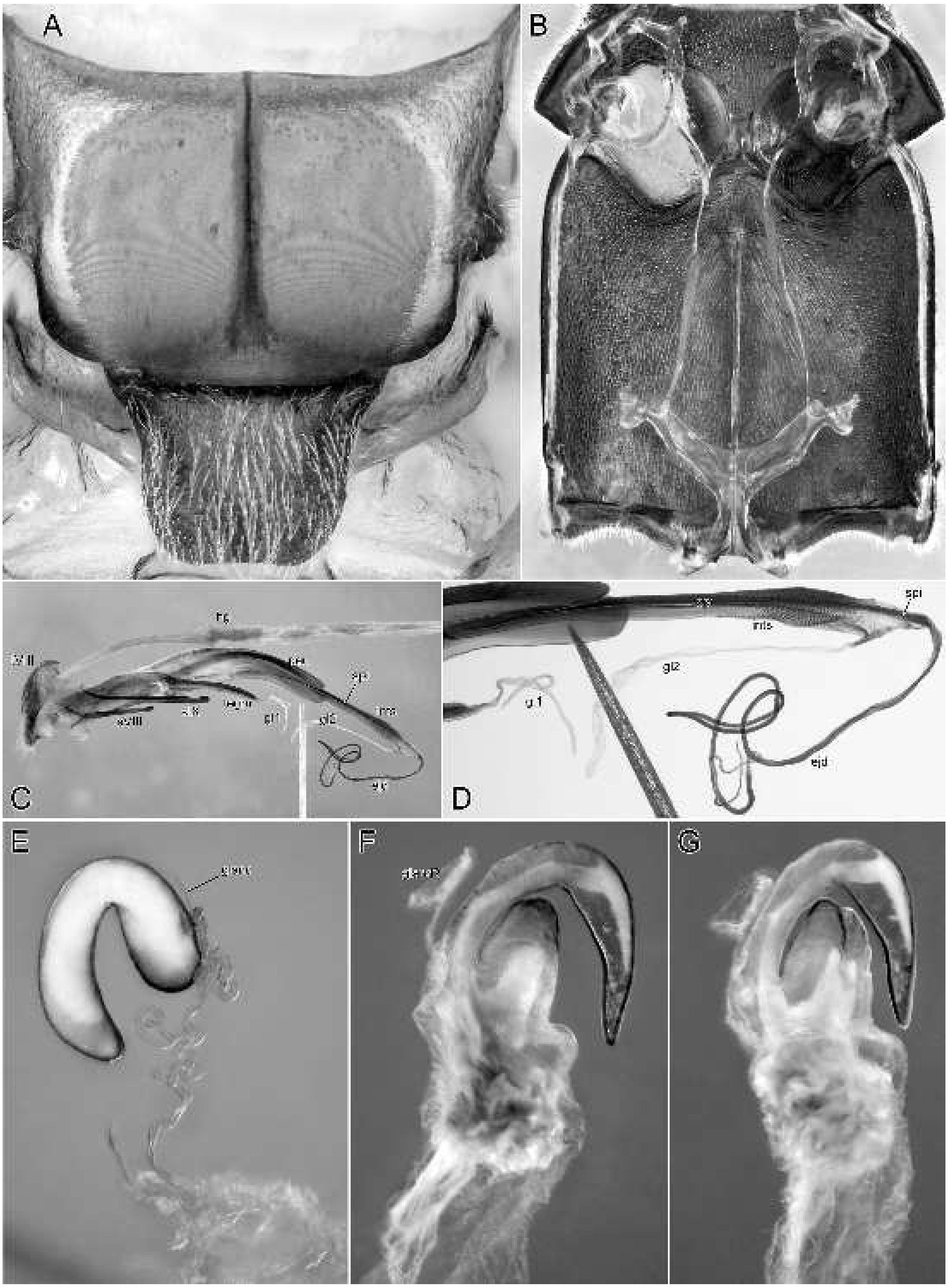

Fig. 2.3.5 Adults. A, *Distenia japonica*, female, mesoscutum with divided stridulatory file and scutellum, dorsal view; B, *Elytrimitatrix undata*, female, meso- and metathoracic venter, dorsal view (showing metendosternite with broadly separate anterior tendons approaching posterior tendons of mesothoracic endoskeleton); C, *E. undata*, dissected male terminalia, lateral view; D, *E. undata*, same preparation as in C, different illumination; E, *America berkovi* Santos-Silva & Tavakilian, female, spermatheca (spermathecal gland only partly visible, opens into distalmost part of slightly sclerotized coiled duct); F and G, *Cyrtonops ?piceatus* Holzschuh, female, spermatheca, lateral (F) and lateroventral (G) view. ejd, ejaculatory duct (containing a sclerotized rod along most of its length, which enters the canal in the spine on internal sac, visible in D); gl1, bifurcate gland (?) opening at anterior tip of tegmen; gl2 (held down by a pin), unpaired gland (?) opening at base of retracted internal sac (close to secondary gonopore) and thus at its apex when everted; hg, hindgut; ints, internal sac; pen, penis; sVIII, anterior apodeme of sternum VIII; sIX, anterior apodeme of sternum IX (spiculum gastrale); spi, spine projecting at secondary gonopore (terminal genital opening on everted internal sac); tVIII, tergum VIII; tegm, anterior tip of tegmen.

segments I–VII. Male terminalia (Villiers 1980; Lin *et al.* 2010 for *Dynamostes*; Fig. 2.3.5 C, D): Tergum VIII sclerotized; anterior edge of sternum VIII with median strut and anterior edge of sternum IX with spiculum gastrale. Terga IX and X fused and membranous. Aedeagus cucujiform, symmetrical; anterior edge of phallobase without strut; parameres fused to phallobase but free from each other; broad struts on anterior edge of penis present but sometimes fused except for apices (*Cyrtonops*); internal sac variable; ejaculatory duct unpaired, containing long sclerotized rod; gonopore projects into a sclerotized spine (usually very long as in Fig. 2.3.5 D, but very short in *Nethinius*). Female terminalia (Villiers 1980; Saito 1990; Lin *et al.* 2010 for *Dynamostes*; Fig. 2.3.6 A) with sternum VIII bearing anterior apodeme (spiculum ventrale) and segment VIII not protruding; ovipositor moderately long, virtually without basal paired pockets; four pairs of baculi present (proctigeral, dorsal, paraproctal and usually broad coxital baculi; *cf.* Fig. 2.4.19 O); styli distinct, terminal. Vagina broad; bursa copulatrix short; spermatheca (Fig. 2.3.5 E–G, 2.3.6 A) present, terminally attached on bursa; duct present or absent, occasionally with its distal part sclerotized, thickened and closely associated with spermatheca, making it appear very complex; spermathecal gland small, inserted on distal spermathecal duct or its sclerotized derivatives. Single dissected female of *Cyrtonops* lacking distinct spermathecal duct; simple sickle-shaped spermatheca attached to anterior tip of bursa copulatrix, which terminates as peculiar sclerotized bilobed knob (Fig. 2.3.5 F, G). Gut usually functional (hindgut well-developed and often containing food pellets; slightly reduced and not containing food in dissected *Cyrtonops*); stomodeal valve (posterior end of foregut) in dissected species without sclerotized armature.

Morphology, Larvae (Fig. 2.3.6 B). Known only in Disteniini. Described for *Elytrimitatrix* and *Distenia* (e.g., Craighead 1923; Gardner 1931; Kojima 1959; Duffy 1968; Mamaev & Danilevsky 1975; Cherepanov 1979; Svacha & Danilevsky 1987; Svacha *et al.* 1997; Lawrence *et al.* 1999 a), undescribed material available also for *Tengius* (two sp.), *Noemia incompta* Gressitt and several Madagascan species of *Nethinius*.

Body unsclerotized, extremely elongate, with slightly broader and flattened thorax and subcylindrical abdomen. All surfaces lightly pigmented, except for mouth frame (anterior cranial margin supporting mouthparts) and mandibles. Vestiture consisting of moderately dense, short, simple setae, and large fields of fine spine-like microtrichia on some body regions contacting gallery walls.

Head (Fig. 2.3.6 C, 2.3.8 C; for terminology see Fig. 2.4.22) prognathous, about half of it retracted into prothorax; cranium transverse, distinctly flattened, widest behind the middle, with sides evenly rounded; posterodorsally deeply notched; epicranial halves meeting almost at one point at frontal base, duplicate dorsomedian region and coronal suture absent; frontal arms broadly V-shaped, indistinct in posterior pale frontal region (yet functioning as cleavage lines at ecdysis); anteriorly reaching cranial margin below antennal sockets, not interrupting their sclerotized rings. Median frontal endocarina complete, reaching epistomal margin, which is constructed as in Cerambycidae (i.e., incorporating postclypeus), sclerotized and sloping to step-like, without epistomal or frontal carinae; bearing six main and often several supplementary epistomal setae, median main pair not shifted posteriorly. Pretentorial pits indistinct; pretentorial arms as in Cerambycidae (short posteromedial rods). Clypeus membranous, trapezoidal, filling space between mandibular articulations, lacking setae. Labrum free, strongly transverse, sclerotized basally, broadly rounded and setose anteriorly; epipharynx with long tormae curved backward and reaching to sides of posterior raised epipharyngeal region. Pleurostoma sclerotized and moderately raised, without subfossal process. One fused composite main stemma present on each side (indistinct in *Elytrimitatrix*); small dorsal additional stemma visible in some specimens of *Nethinius*; ventral stemma absent. Antennae short, moderately retractile, three-segmented; antennomere 2 shorter than broad to ring-like, bearing prominent conical sensorium. Mandibles symmetrical, short and broad; basal part bearing two lateral setae; inner face simple, without molar plate; apical part with simple blunt apex, straight cutting edge, and two distinct inner keels (occasionally with some transverse connecting ridges; Fig. 2.3.7 A); pseudomola not distinctly developed, only present as small rudiment at dorsal angle (not visible in dorsal view). Maxillolabial complex (Fig. 2.3.8 D) more retracted than in Cerambycidae (cardo/stipes border distinctly posterad of mandibular condyle); maxillary articulating area large and divided into two parts; posterior portion larger and fused with submentum. Cardo large, free, with extensive undivided sclerotization, in some cases with minute lateral seta; stipes distinctly longer than wide; mala fixed, stout, subcylindrical, apically rounded, densely setose; not arising from palpiger, which is distinct and lacks a dorsolateral process; palp moderately long, three- or (*Noemia* Pascoe and some *Nethinius*) two-segmented; terminal palpomere with one lateral digitiform sensillum. Mentum not fused with submentum; labial palpigers widely separated; palps two-segmented; ligula well-developed, broadly rounded, with sparse ventroapical setae and broad apical and dorsolateral area of microtrichia; dorsal ligula and hypopharyngeal region very lightly sclerotized (hypopharyngeal sclerome absent) and separated from each other by narrow membranous zone. Hypopharyngeal bracon absent. Hypostomal rods absent, hypostomal region fused with epicranium. Gula absent. Metatentorial pits not distinct, metatentorial invaginations extremely broad, occupying entire lateral margin of ventral part of occipital foramen and fusing into a plate-like tentorial bridge lying in

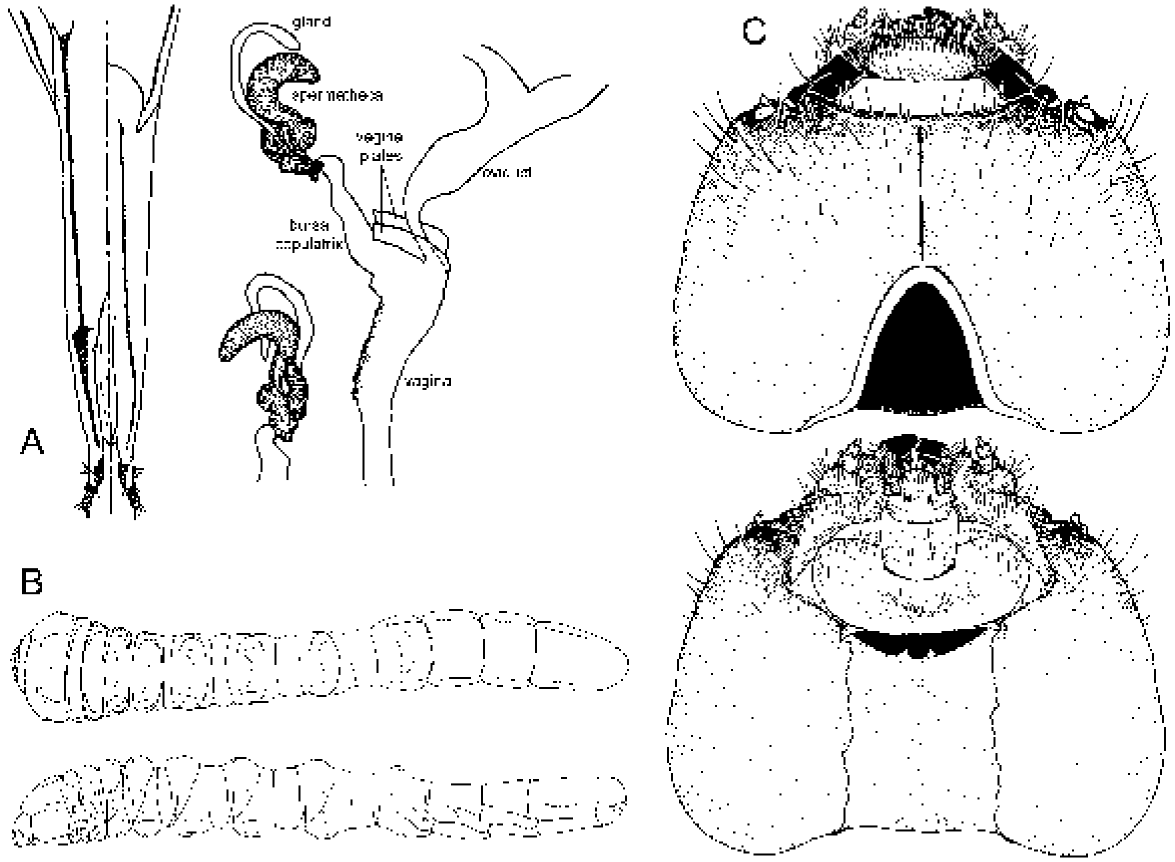

Fig. 2.3.6 A, *Distenia japonica*, female, ovipositor (left half in ventral view, right half in dorsal view) and internal genitalia showing a complex spermatheca with associated sclerotized coiled duct (from Saito 1990, as *D. gracilis*); B, *D. japonica*, larva, dorsal and lateral view; C, *D. japonica*, larva, head in dorsal and ventral view (B and C modified from Svacha & Danilevsky 1987).

the same plane with hypostomal region and anteriorly bearing paired fine branches reaching inside the cranial cavity toward the frontal region but not connected with pretentorial arms (Fig. 2.3.6 C, 2.3.8 B).

Thorax (Fig. 2.3.9 C) broadened and flattened. Prothorax about as long as meso- and metathorax combined and slightly wider. Pronotum delimited by long lateral furrows that slightly converge anteriorly; anterior protergal pigmentation missing or very pale (and then interrupted by lateral furrows); posterior pronotum and small adjacent lateral regions microspiculate (Fig. 2.3.9 A). Prothoracic venter (Fig. 2.3.9 B) with more or less separate epimeron and nearly fused coxal, basisternal and sternellar regions (faint oblique impressions divide this fold into what may be homologues of the cerambycid coxosternum and sternellar fold, both of composite origin), and with fused epipleuron, episternum and lateral presternum; median presternal region separated by anteriorly converging impressions (homology with cerambycid mediopresternal limits uncertain); base of median region always distinctly microspiculate; spinasternum indistinct; spina at most present as rudimentary fovea; other prosternal endoskeletal elements and pleural apodeme absent. Meso- and metanota simple or (metanotum) with indistinct lateral impressions; usually microspiculate; particularly mesonotum with narrow anterior separate region. Wing discs absent. Epipleuron divided into two parts; mesoepipleural spiracle-bearing area not protruding into prothorax; mesothoracic spiracle placed on border with alar lobe, annular-multiforous, with broadly oval peritreme and variable number of distinct marginal chambers (Fig. 2.3.9 D); vestigial metathoracic spiracle present. Pleuron undivided and broadly separating coxal region from epipleuron. Sterna usually microspiculate; transsternal lines present as indistinct lateral rudiments. Coxa not prominent, without sclerotizations and incompletely defined, medially separated from sternum by distinct impression. Distal legs (Fig. 2.3.10 B) small and very widely separated; trochanter small, distinct medially, reduced laterally; femur and tibiotarsus weakly sclerotized; pretarsus narrowly conical, very weakly sclerotized but microasperate, lacking setae.

Abdomen (Fig. 2.3.6 B, 2.3.9 C) long and narrow, more than five times as long as thorax; anteriorly distinctly pseudosegmented; dorsal and ventral intersegmental zones overlapping and dorsal one more anterior (as in Cerambycidae); dorsal intersegmental area expanded and forming more or less complete intersegments anterior to abdominal segments I–VI; intersegments very large anterior to segments IV–VI (Fig. 2.3.8 A). Dorsal and ventral

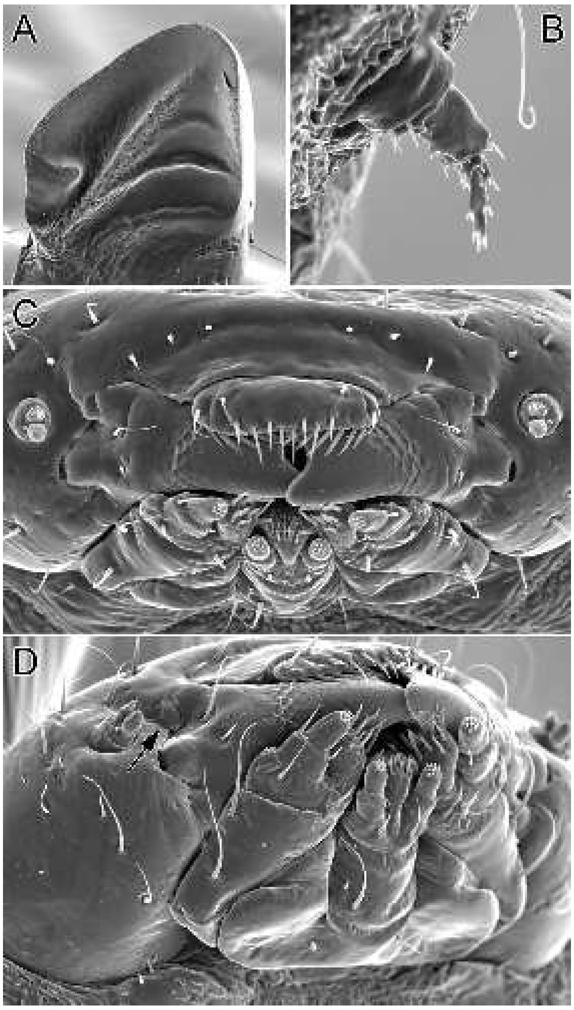

Fig. 2.3.7 SEM. A, *Distenia japonica*, later instar, apical part of left mandible, mesal view; B–D, *Nethinius* sp., first instar larva, left hind leg, anterior view (B), head, anterior view (C) and lateroventral view (D, arrow points to very inconspicuous pretentorial pit) (A and C from Svacha *et al*. 1997).

microasperate or microgranulate/microrugose ambulatory ampullae present on segments I–VI, those on II–V strongly prominent laterally and impressed in the middle; sixth ampullae much smaller; all with distinct lateral impressions and usually a pair of faint oblique discal impressions. Functional spiracles present on segments I–VIII, subequal, much smaller than mesothoracic spiracle and with marginal chambers on average fewer (some spiracles may bear only two in small species and/or early larval instars). Epipleuron distinctly protuberant on segments VII–IX and posteriorly on VI; fused with spiracular area on I–V; fused region divided by oblique furrow, particularly on II–V; poorly defined epipleural tubercles present on segments I and VI; virtually not defined on other segments but original posterodorsal extremity marked by small invaginated sclerite on I–VII; invaginated sclerites not surrounded by pleural discs (Fig. 2.3.9 C). Segments VII–IX long (IX much longer than wide), with simple terga and sterna; tergum IX without sclerotized armature. Segment X subterminal, short and round, partly fused with IX. Anus slightly shifted posteroventrally, triradiate with very short ventral radius (relatively distinct in *Noemia*) to transverse. Digestive tube (Danilevsky 1976; Semenova & Danilevsky 1977; Svacha *et al.* 1997; Fig. 2.3.10 A) without defined crop or proventriculus; midgut straight (not looped as in Cerambycidae), without anterior mycetomes; first hindgut fold may be twisted above anus. Six Malpighian tubules present; crytonephridial condition weakly developed. Nerve cord with eight abdominal ganglia; ganglionic complex VIII shifted to segment VII; connectives paired.

First instars (Fig. 2.3.7 B–D) available for *Distenia japonica* and *Nethinius*. Basically similar to later instars, but much less elongate (larvae before hatching lie straight in fusiform eggs). Intersegments very short. Abdominal segments VII–IX transverse in larvae which are not inflated. Setation sparse, some setae longer. Legs basically similar to later instars, not distinctly longer. Spiracles with two marginal chambers and without a broadly open atrium. Egg bursters not identified; empty egg shells were possibly opened by mandibles (hatching not observed). In species of *Nethinius* with two-segmented maxillary palps, the reduction occurs also in first instars (Fig. 2.3.7 C, D).

Morphology, Pupae (Fig. 2.3.10 C–E). Described for *Distenia* (Cherepanov & Cherepanova 1975; Cherepanov 1979; Nakamura 1981), available also for *Nethinius*. Exarate, moderately depressed. Integument thin and unsclerotized except for small abdominal tergal spines; setae short and sparse, present also on distal femora, absent on antennae. Head bent ventrally, with the mouthparts pointing caudally. Both antennae looped together in a joint oval (not separately as in most Cerambycidae). Functional abdominal spiracles present on segments I–VI. Abdominal dorsum with sparse (*Nethinius*) or numerous (*Distenia*) small sclerotized spines that may become larger on terminal abdominal region but tergum IX without distinct urogomphi or unpaired caudal spine.

Phylogeny and Taxonomy. Disteniidae J. Thomson, 1861 is considered a *nomen protectum* and Cométites Blanchard, 1845 (derived from *Cometes* Le Peletier & Audinet-Serville, a genus currently classified in Disteniini) a *nomen oblitum* (Monné & Santos-Silva 2008).

The group was traditionally treated within Cerambycinae (when that subfamily was accepted in a broad sense, including all current cerambycid subfamilies except for Prioninae, Parandrinae and Lamiinae) either close to the present Lepturinae, or to various groups of then uncertain position. Gahan (1906) and many subsequent authors listed Disteniinae as a separate subfamily, and it was explicitly excluded from Cerambycidae by Linsley (1961, 1962) based on "scalpriform mandibles, the clypeus oblique to the frons, a nonhylecoetoid metendosternite, wings lacking a spur in the

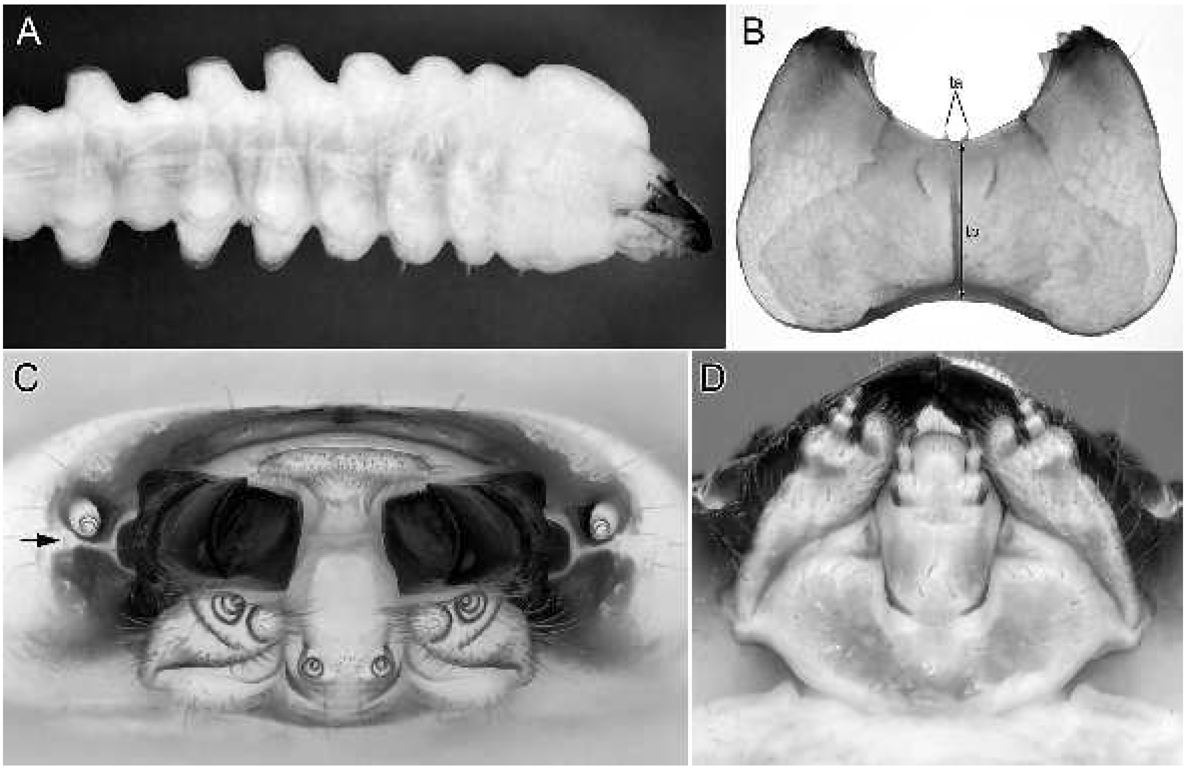

Fig. 2.3.8 Larvae. A, *Nethinius* sp., later instar, lateroventral view (showing large pigment spot of main stemma and first three of the strongly protuberant bilobed ambulatory ampullae on abdominal segments II–V); B, *Distenia japonica*, ventral half of cranium, dorsal view; C, *D. japonica*, head, anterior view (arrow points to small main stemma); D, *D. formosana*, maxillolabial complex, ventral view. ta, slender metatentorial arms on anterior margin of tentorial bridge, cut to short stubs; tb, tentorial bridge.

radio-medial crossvein [present crossvein r4; the lack of spur was incorrectly regarded as unique among Phytophaga], and larvae with retracted ventral mouthparts, the gula and hypostoma absent, and the skin of the prothorax attached directly to the submentum".

Although the group's position had been questioned prior to Linsley (since the early 20th century), conclusions were sometimes based on poor knowledge of character variation in Disteniidae and Cerambycidae (see also Villiers 1980). Forbes' (1922) comment on wing venation of *Distenia undata* (currently in *Elytrimitatrix*) as violating all definitions of Phytophaga stemmed from his poor knowledge of cerambycoid wings, as disteniid wings possess no characters unknown in cerambycids. Linsley's interpretation of the disteniid metendosternite as nonhylecoetoid (Linsley 1961, 1962; *contra* Villiers 1980: 19) implies a nonhylecoetoid metendosternite also in Parandrinae and many Prioninae (see Crowson 1938; the hylecoetoid metendosternite with laminae occurs in some Prioninae not known to Crowson). The broadly separated disteniid anterior tendons (Fig. 2.3.5 B) are unusual but present in some cerambycids. Thus, what remains to exclude disteniids from Cerambycidae is mainly the lack of the larval gula (Craighead 1923; Böving & Craighead 1931 and others), a presumed plesiomorphy as there are no obvious reasons to suspect the homology of the gula within Cerambycidae. Some later authors (Nakamura 1981: 7; Lawrence & Newton 1982: 283) misinterpreted the broad tentorial bridge, an internal structure positioned above the nerve cord (Fig. 2.3.8 B), as a "concealed" gula or hypostoma. Larvae also differ from all known cerambycids by a straight midgut without a loop (polarity uncertain, possibly an apomorphy of slender disteniid larvae). The broad and bilobed or "scalpriform" adult mandibular apex (the simple apex in *Nethinius* and some other Disteniini may be derived), the approximate antennal sockets and mandibular articulations, and antennal tubercles associated with a protuberance abruptly sloping toward the postclypeus (Fig. 2.3.3 A, B) remain useful but are not diagnostic, and the polarity is uncertain. The characteristic long recumbent flagellar setae (Fig. 2.3.3 C–E) are probably autapomorphic for disteniids, but reduced in *Dynamostes* and absent in Cyrtonopini.

Unlike in Oxypeltidae and Vesperidae as presently defined (and most other chrysomeloids), the disteniid larval epistomal margin (postclypeus with its setae fused with and forming the anterior margin of the frontal region) is constructed exactly as in Cerambycidae and may be a synapomorphy of the two families. Late instar disteniid larvae also have annular-multiforous spiracles (annular-biforous in Oxypeltidae and Megalopodidae, annular without marginal chambers in Vesperidae), lateral pronotal furrows, apparently homologizable mandibular and prosternal morphology, and a similar construction of the overlapping

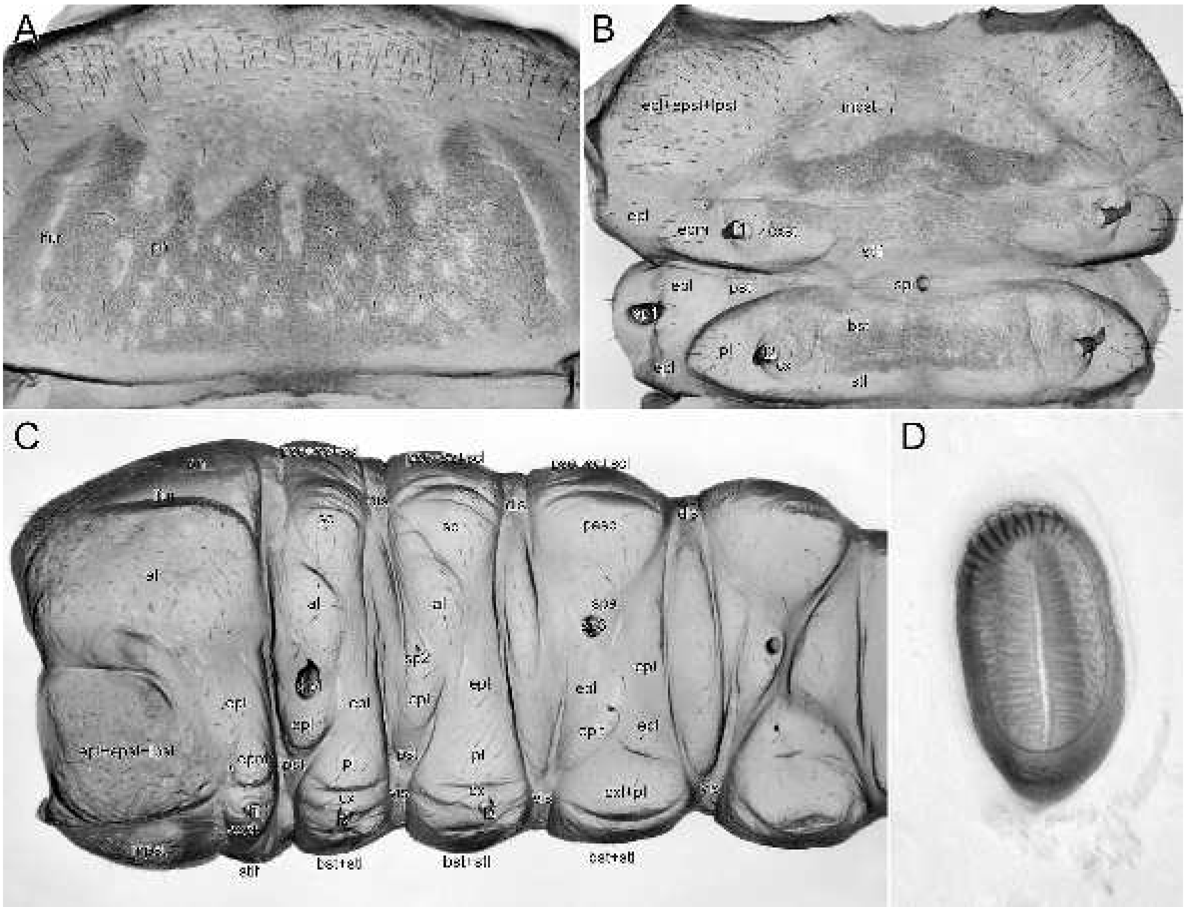

Fig. 2.3.9 *Distenia japonica*, larva (all figures from cleared cuticular preparations stained with Chlorazol Black E). A, pronotum; B, venter of pro- and mesothorax; C, thorax and abdominal segments I and II, lateral view; D, left mesothoracic spiracle. al, alar lobe; bst, basisternum; cx, coxa; cxst, coxosternum (on prothorax); dis, dorsal intersegmental zone; epl, epipleuron; eplt, epipleural tubercle; epm, epimeron; epst, episternum; l1, l2, l3, distal parts of pro-, meso- and metathoracic legs (without coxae); lfur, lateral pronotal furrows; lpst, lateropresternum (on prothorax); mpst, mediopresternum (on prothorax); pasc, parascutum (abdominal homologue of lateral part of pterothoracic scuta); pl, pleuron (fused episternum and epimeron); pll, pleural lobe (on abdominal segments); pn, pronotum; psc, prescutum; pst, presternum (not distinct on abdomen); sc, scutum; scl, scutellum; sp1, sp2, sp3, mesothoracic, metathoracic (rudimentary and closed) and first abdominal spiracle; spa, spiracular area (presumed abdominal homologue of pterothoracic alar lobes); spi, prosternal spina; stl, sternellum; stlf, sternellar fold (on prothorax); vis, ventral intersegmental zone; *, propleural sulcus (in known disteniid larvae not invaginated into propleural apodeme). For a more detailed discussion of terminology see Cerambycidae.

intersegmental zones between the anterior abdominal segments (in Vesperidae mostly simple or fused, in Oxypeltidae different from cerambycids and similar to some megalopodids; *cf.* Fig. 2.1.6 D–F, 2.1.11 A, C, E; 2.2.4 A, 2.2.6 A). Some or all of these characters belong to the cerambycid ground plan, but their polarity remains uncertain; in particular the cerambycid intersegmental morphology may be plesiomorphic as a similar configuration is rather widespread in Chrysomeloidea and Cucujoidea. The hypertrophied larval tentorial bridge could be interpreted as a synapomorphy with Oxypeltidae and/or Vesperidae. However, such phylogenetic interpretation could be supported by only very few other characters, and the relatively broad tentorial bridge (and very short gula) in Prioninae and Parandrinae indicates that a primarily broad bridge may have been reduced in correlation with the origin and expansion of the larval gula. No obvious disteniid adult synapomorphies with Cerambycidae or any other group are presently known.

Crowson (1981) accepted a separate family Disteniidae, including Oxypeltinae, Vesperinae and Philinae (see the families Oxypeltidae and Vesperidae in the current volume; Anoplodermatinae were retained by him in Cerambycidae), though Vesperidae had priority. Although Crowson did not provide reasons for his grouping, the broadly defined family Disteniidae may have been based on the absence of a larval gula because in the larval key to chrysomeloid families and subfamilies in Mann & Crowson (1981) the cerambycoid assemblage was divided into Cerambycidae and Disteniidae, and the former was distinguished from the latter (and all remaining chrysomeloids) only by the presence of the larval gula (a sclerotized bar or plate *externally*

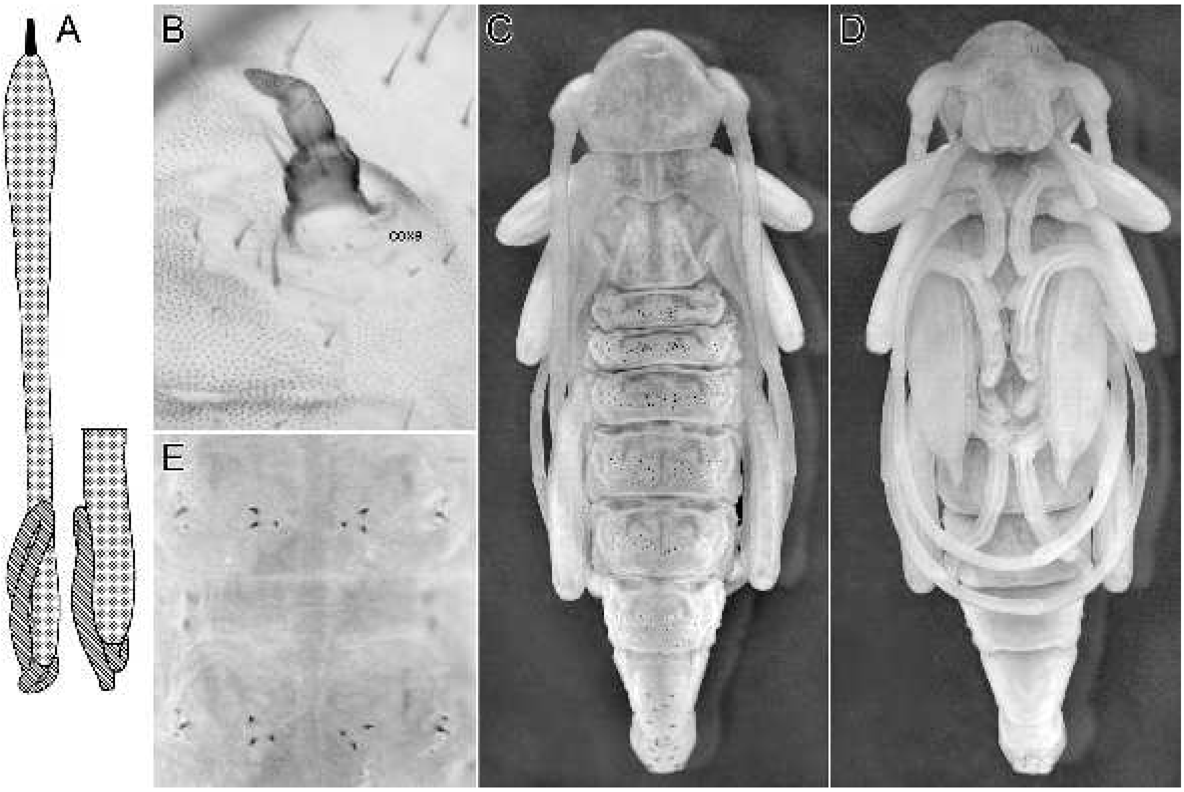

Fig. 2.3.10 A, larval digestive tract, diagrammatic, dorsal view, *Tengius* (left) and posterior part of gut of *Distenia* (right), foregut black, midgut stippled, hindgut crosshatched (from Svacha *et al.* 1997); B, *Distenia japonica*, larva, left middle leg, posteroventral view; C and D, *D. japonica*, female pupa, dorsal (C) and ventral view (D); E, *Nethinius* sp., female pupa, spines on abdominal terga III and IV.

bridging both hypostomal regions and separating the maxillolabial base from the prosternum). Larvae of Anoplodermatinae, which also lack a gula, were then very poorly known. Larvae of Philinae were unknown but the group's relationship to *Vesperus* had been repeatedly suggested before.

Taxa incorrectly placed in Disteniidae or its equivalents include *Dandamis* Gahan, containing *D. nigropunctatus* (Aurivillius), which was originally placed conditionally in *Cyrtonops* and is still occasionally treated in Disteniidae; it was considered a prionine cerambycid "allied to *Aegosoma* and *Sarmydus*" by Gahan (1906), and the larva described by Duffy (1953, as *Megopis*) is unquestionably prionine. Duffy (1968: 53) later questioned the identification solely because the larva was not similar to other Aegosomatini, but it was actually similar to *Sarmydus* Pascoe, and the reliably identified pupae with an almost prognathous head confirm a placement within the Prioninae because among the cerambycoids, prognathous pupae are known only in some prionines. Three Madagascan genera (*Apharsatus* and *Zulphis*: Fairmaire 1893; *Eupalelius*: Fairmaire 1896) were usually misplaced among disteniids in catalogues (e.g., Aurivillius 1912; Boppe 1921; Ferreira & Veiga-Ferreira 1959) because Fairmaire inappropriately compared them in the original descriptions with the disteniid genera *Phelocalocera* Blanchard and *Nethinius*. *Eupalelius* and *Zulphis* are now classified in Dorcasominae (Villiers *et al.* 2011; larvae of *Zulphis* are available and support that placement). The position of *Apharsatus* has never been revised and the genus is still usually placed in Disteniini although it very probably does not belong there (as noted by Boppe 1921: 3) because according to the original description it does not share the universal disteniid placement of antennal sockets before eyes and approximate to the mandibular articulations.

The group is usually divided into four tribes (Bousquet *et al.* 2009, Löbl & Smetana 2010, both as Disteniinae; Bezark & Monné 2013): Disteniini, Dynamostini, Heteropalpini, and Cyrtonopini. Disteniini may be paraphyletic as they are defined solely by lacking apomorphic characters present in the other tribes (such as the externally closed procoxal cavities of Dynamostini and uniquely modified male maxillary palps of Heteropalpini and Cyrtonopini). The phylogenetic placement of *Cyrtonops* is ambiguous; depending on interpretation of characters, it could be basal or derived, and both alternatives would imply reversals and/or parallelisms. At present, we prefer the derived position as the large prominent pro- and mesocoxae may be apomorphic and responsible for the partly exposed lateral procoxal angles and broadly open mesocoxal sockets. The antennal grooves with long recumbent setae may be a plesiomorphic character within the family and its absence (associated with absence of the pro- and mesotibial cleaners) in *Cyrtonops* may be secondary. Regardless of some authors claiming absence of those setae also in Dynamostini (Gahan 1906;

Gressitt 1940; Villiers 1980; Martins & Galileo 2001 for *Aiurasyma*), the setae are present (even if reduced) at least on several middle flagellomeres (Fig. 2.3.2 D, 2.3.3 E; A. Santos-Silva, personal communication for *Aiurasyma*), and also the tibial cleaners are distinct. The unique male maxillary palps shared between Cyrtonopini and Heteropalpini may be a synapomorphy, even if the adults are dissimilar.

Disteniini J. Thomson, 1861. Distribution that of the family. The largest tribe with approximately 300 species; generic classification unsatisfactory and in need of revision in many regions; recent comprehensive taxonomic studies are available only for the New World taxa (Santos-Silva & Hovore 2007 a–d, 2008 a, b; Santos-Silva & Tavakilian 2009; Santos-Silva & Martins *in* Martins 2010). The only generic name currently used for both Old World and New World species of Disteniini is *Distenia* Le Peletier & Audinet-Serville (synn. *Apheles* Blessig; *Sakuntala* Lameere; *Thelxiope* J. Thomson, preoccupied; *Thomsonistenia* Santos-Silva & Hovore, *nom. nov. pro Thelxiope*). Old World genera currently in use: *Capnethinius* Adlbauer (Afrotropical: South Africa); *Clytomelegena* Pic (Oriental; syn. *Noeconia* Murzin: Lin & Murzin 2012); *Melegena* Pascoe (Oriental); *Micronoemia* Aurivillius (Seychelles); *Nericonia* Pascoe (Oriental); *Nethinius* Fairmaire (Afrotropical: Madagascar and adjacent islands; occasionally treated as a synonym of *Noemia*); *Noemia* Pascoe (Oriental); *Nupseranodes* Adlbauer (Afrotropical: South Africa); *Olemehlia* Holzschuh (Oriental: Vietnam); *Phelocalocera* Blanchard (Mauritius, Reunion); *Phelocalocerella* Villiers (Mauritius, Reunion); *Saphanodes* Hintz (Afrotropical); *Tengius* Matsushita (Japan); *Thaigena* Holzschuh (Oriental: Thailand); *Typodryas* J. Thomson (Oriental; syn. *Psalanta* Pascoe). New World genera and subgenera currently in use (Santos-Silva & Martins *in* Martins 2010; Bezark & Monné 2013): *Abauba* Santos-Silva & Tavakilian; *America* Santos-Silva & Tavakilian; *Arietocometes* Santos-Silva & Tavakilian; *Cometes* Le Peletier & Audinet-Serville; *Cupecuara* Santos-Silva & Tavakilian; *Basisvallis* Santos-Silva & Hovore (subgenus of *Distenia*); *Disteniazteca* Santos-Silva & Hovore; *Elytrimitatrix* Santos-Silva & Hovore; *Grossifemora* Santos-Silva & Hovore (subgenus of *Elytrimitatrix*); *Hovorestenia* Santos-Silva; *Novantinoe* Santos-Silva & Hovore (*nom. nov. pro Antinoe* J. Thomson, preoccupied); *Myopsocometes* Santos-Silva & Tavakilian; *Oculipetilus* Santos-Silva & Hovore; *Paracometes* Villiers; *Villiersicometes* Santos-Silva (*nom. nov. pro Microcometes* Villiers, preoccupied).

Adults (Fig. 2.3.1 A–F, 2.3.2 A–C) with antennae longer or even much longer than body; long recumbent setae always present on (almost) all flagellomeres (in some cases indistinct on one or two apical segments, completely missing on flagellomere 1 in *Tengius*). Mandible with distinct mola and associated desclerotized region; apex scalpriform, broadly rounded, rarely (mainly *Nethinius*, Fig. 2.3.4 B) with simple sharp pointed apex. Male maxillary palps normal. Prothorax usually with lateral tubercles or spines, but sides convex and without tubercles in *Micronoemia*: figures in Adlbauer (2004) (placed in *Nethinius*) or Vives (2009). Prosternal process narrow but usually complete (rarely slightly expanded apically, very narrow and slightly shortened in *Nethinius*); procoxal cavities open externally; lateral procoxal projections and trochantins concealed. Mesocoxal cavities narrowly open to closed laterally. Wing rarely with wedge cell; *Clytomelegena* (Fig. 2.3.1 F, 2.3.2 C) and *Olemehlia* apterous. Legs simple (femora of some species with apical spine, Fig. 2.3.1 A), occasionally very long; lobe of tarsomere 3 deeply cleft.

Dynamostini Lacordaire, 1868. Name based on *Dynamostes audax* Pascoe from the Oriental Region (southern Himalayas): Nepal, northern India, and Yunnan (Lin *et al.* 2010). The genus, although formally unplaced, was apparently considered prionine by its author ("this most remarkable form has no very obvious affinity with any genus of Prionidae yet known": Pascoe 1857: 90). It was left as of uncertain taxonomic position by Thomson (1861: 379, in Cérambycites; 1864: 309, in Prionites). Lacordaire (1868) created a monogeneric tribe Dynamostides and placed it (together with Thaumasides and Spondylides) in "Légion I. Cérambycides aberrants" of his broad subfamily named Cérambycides. *Dynamostes* was moved to Disteniinae by Gahan (1906).

Adults of *Dynamostes* (Fig. 2.3.1 H, I, 2.3.2 E, F) are robust, relatively large (ca. 20 mm), parallel-sided, somewhat flattened. Color rusty brown to brown-black. Pronotum and elytra often with slightly darker median/sutural and lateral stripes. Antennae much shorter than body in both sexes; recumbent setae in grooves short and restricted to flagellomeres 2–8 (Fig. 2.3.3 E; rather indistinct, particularly on 2 and 8). Mandibular apex scalpriform; molar plate and associated desclerotized region poorly developed, but molar region prominent. Maxillary palps normal; last segment more or less truncate. Prothorax longer than broad, sides without tubercle or spine and coarsely longitudinally rugose. Prosternal process moderately broad and expanded apically; procoxal cavities externally closed (Fig. 2.3.2 E); lateral procoxal projections and trochantin concealed. Mesocoxal cavities closed laterally. Wing without wedge cell; the wing depicted by Villiers (1980: Fig. 65; examined by us) with a proximally open radial cell and only a distal disconnected rudiment of MP_4 may be aberrant as a closed radial cell and a complete bifurcate MP_{3+4} was present in both wings of another male. Legs moderately long, in males stronger and with hind legs more enlarged; hind tibia in males with two inner ridges ending as large teeth (Fig. 2.3.2 F); lobe of tarsomere 3 deeply cleft.

Santos-Silva & Martins (2004) added to this tribe the Neotropical *Aiurasyma potira* Martins & Galileo (Fig. 2.3.2 D; Colombia), originally described without tribal placement (Martins & Galileo 2001). This species shares with *Dynamostes* the pronotal sides without spine or tubercle and externally closed procoxal cavities. *Aiurasyma* is less robust and much smaller (length of the holotype male 7.9 mm), has longer antennae (about as long as body in males, much shorter in females), recumbent flagellar setae better developed and present on all flagellomeres (A. Santos-Silva, personal communication), coarsely punctate sides of the prothorax, and hind legs in males not distinctly enlarged and lacking tibial teeth. Known specimens of *Aiurasyma* are dark castaneous, with pale bases of the femora and more or less pale parts of the tibiae and elytral humeri, and a slight metallic tinge on the dark part of elytra.

Heteropalpini Villiers, 1961. Neotropical region, northern part of South America from French Guyana and northern Brazil to Colombia, Ecuador and Peru (P. Demez, personal communication). The two genera *Heteropalpus* Buquet and *Pseudocometes* Villiers (Fig. 2.3.1 G) comprise approximately three or four species. Only one male of *P. argutulus* (Buquet) was available, and no specimens were dissected for this work.

Adults with antennae longer than body in both sexes; all flagellomeres with long recumbent setae. Mandibular apex scalpriform; mola present. Male maxillary palps similar to those in Cyrtonopini; process longer and indistinctly annulate. Prothorax with lateral tubercles. Procoxal cavities open externally; prosternal process narrow but complete; lateral procoxal projections and trochantins concealed. Mesocoxal cavities narrowly open (*Heteropalpus*: A. Santos-Silva, personal communication) or closed laterally. Wing without wedge cell. Legs simple; lobe of tarsomere 3 deeply cleft.

Cyrtonopini Gressitt, 1940. The only genus *Cyrtonops* White (syn. *Cladopalpus* Lansberge) comprises eleven species (the status of some of them is uncertain) in the Oriental region, reaching Taiwan, Borneo, Sumatra and Java. The genus was treated as a member of Prionidae by its author (White 1853: 32) who described and depicted a female; in a footnote, he briefly mentioned the peculiar maxillary palp of one available male specimen, considering it a malformation (and thus possibly allowing the subsequent description of *Cladopalpus*). *Cyrtonops* was poorly known to Thomson (1861: 284, 381, 1864: 309) and Lacordaire (1868: 162) who both based its placement in their Prionitae or Prionides, respectively, on White's original description and figure. The genus was placed in Disteniinae by Gahan (1906).

Adults (Fig. 2.3.1 J, K) robust, yellow-brown to black; abdomen and parts of legs may be pale; rarely elytra with blue metallic luster (Bornean *C. metallicus* Hüdepohl). Antennae shorter than body, without long recumbent flagellar setae. Mandible without molar plate; apex bilobed to bidentate. Male maxillary palps as in Fig. 2.3.3 F. Prothorax short and with lateral spines. Procoxal cavities open externally; prosternal process short and partly hidden between prominent contiguous procoxae, their lateral projections and trochantins partly exposed. Mesocoxal cavities open laterally. Wing without wedge cell; AP_3 may be surrounded by distinct sclerotization (Fig. 2.3.4 E). Legs moderately long, strongly developed; hind legs in males usually enlarged and with dentate inner margins of femur and tibia; pro- and mesotibial cleaning devices virtually absent (more or less distinct in remaining three tribes; corresponds with presence or absence of long recumbent flagellar setae); tarsi broad and lobe of tarsomere 3 only moderately emarginate, not deeply cleft.

Acknowledgments

We are grateful to X. Zhu (Shanghai, China) for biological information on *Dynamostes audax*; to G. Biffi (Museum of Zoology, University of São Paulo), I. Jeniš (Náklo, Czech Republic), N. P. Lord (Department of Biology, University of New Mexico, Albuquerque) and E. H. Nearns (National Museum of Natural History, Washington, DC), for permission to use their photographs; to J. Hájek (Department of Entomology, National Museum, Prague), Meiying Lin (Institute of Zoology, Chinese Academy of Sciences, Beijing), S. W. Lingafelter (Systematic Entomology Laboratory, National Museum of Natural History, Washington, DC) and N. Ohbayashi (Miura, Japan) for loan or gift of specimens; to A. Santos-Silva (Museum of Zoology, University of São Paulo) for information on the morphology of *Aiurasyma potira* and valuable comments on the manuscript; to P. Demez (Ica, Peru) for information on the occurrence of Heteropalpini in Peru. P. Svacha acknowledges support from the Institute of Entomology (RVO:60077344).

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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 mimetism. 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 inquilines 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 cerambycoids, in which presumed basal forms are often large and/or lack a suitable type of mouthparts. Widespread floricoly 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 floricoly 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, floricolous 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: Nearns & 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: Krahmer 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 Vesperidae (*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 (Krahmer 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, *fide* 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.

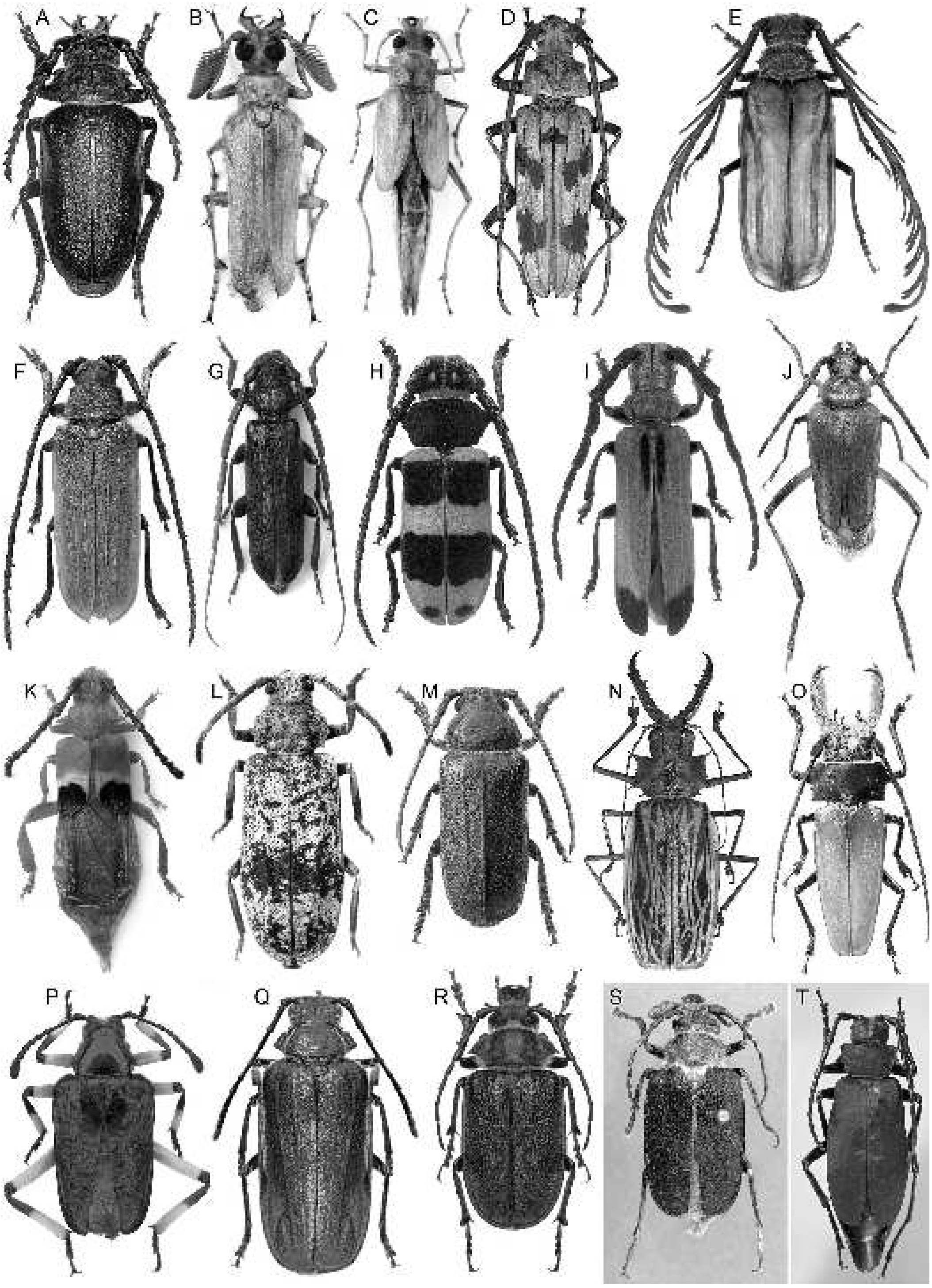


Fig. 2.4.1 Adults of Prioninae, dorsal view (data about size or sex not available for some specimens in plates 2.4.1 to 2.4.9). A, *Prionus coriarius* (Linnaeus), male, size unknown; B, *Microarthron komaroffi* (Dohrn), male, 22 mm; C, *M. komaroffi*, female, 32 mm; D, *Baralipton maculosum* J. Thomson, 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, *Macrodontia 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, *Meroscelisus 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. Nearns.)

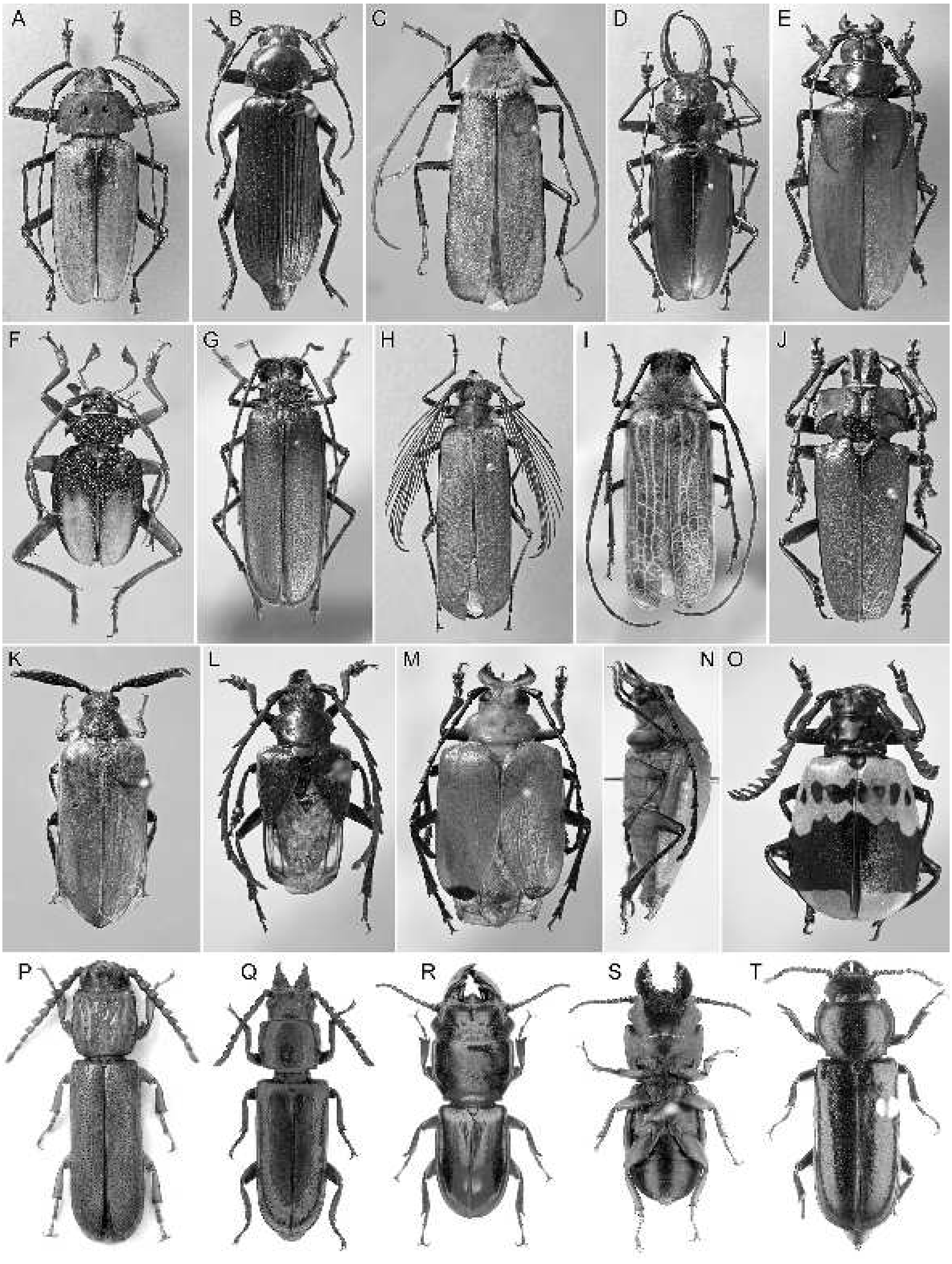


Fig. 2.4.2 Adults of Prioninae (A–N), Parandrinae (P–T) and uncertain subfamily position (O), dorsal view except for N and S; size unknown for A–O. A, *Xixuthrus domingoensis* Fisher, male; B, *Apocaulus foveiceps* (Harold), female; C, *Erioderus pallens* (Fabricius), male; D, *Stenodontes exsertus* (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. Nearns; P © I. Jeniš; R © CSIRO, Canberra; S, T © A. Santos-Silva.)

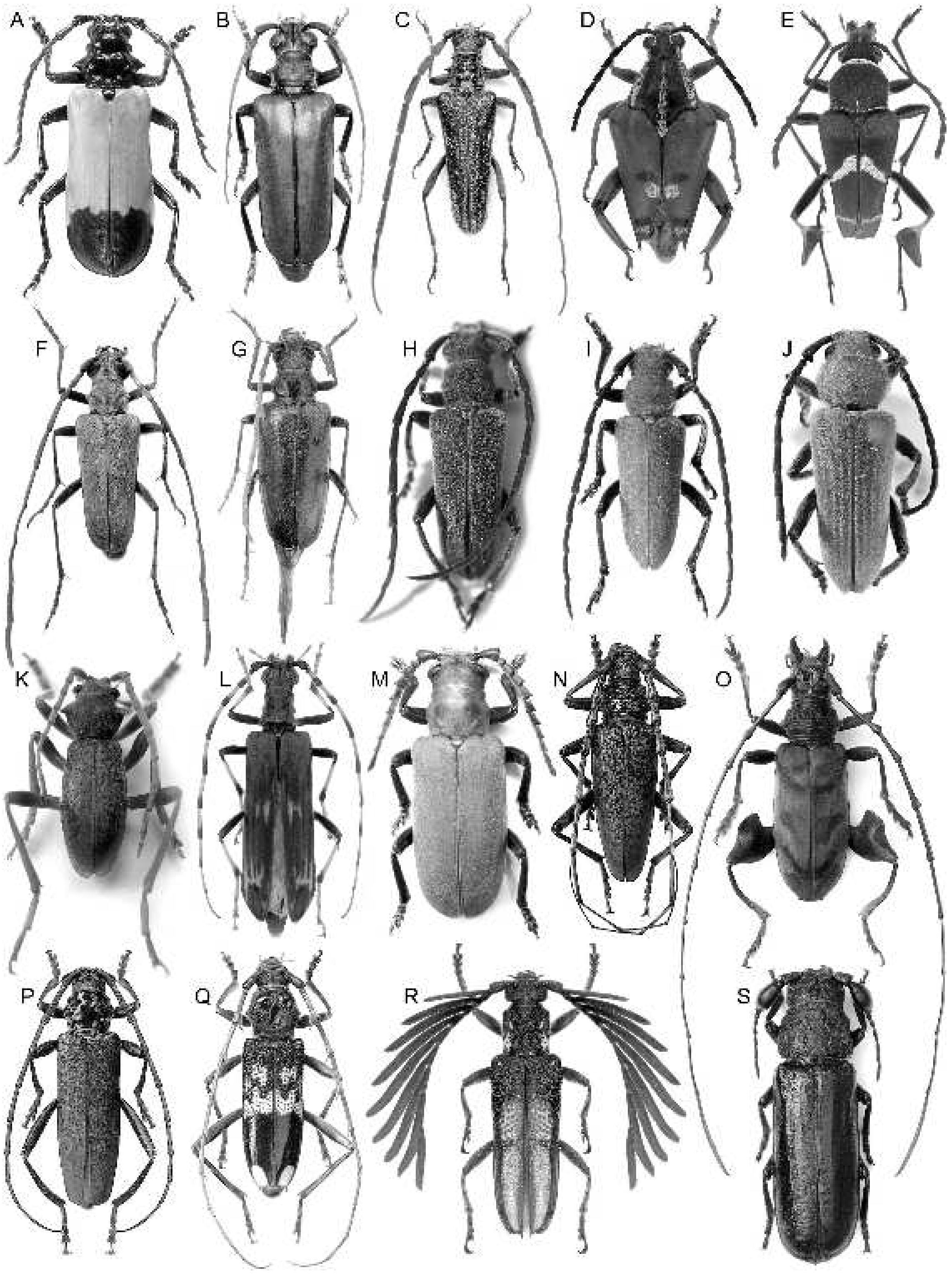


Fig. 2.4.3 Adults of Dorcasominae (A–L and possibly M) and Cerambycinae (N–S), dorsal view. A, *Dorcasomus delegorguei* Guérin-Méneville, male, 26 mm; B, *Xanthopiodus* sp., male, 28 mm; C, *Capetoxotus rugosus* Tippmann [possibly a junior synonym of *Aristogitus cylindricus* (J. Thomson)], male, 18 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.)

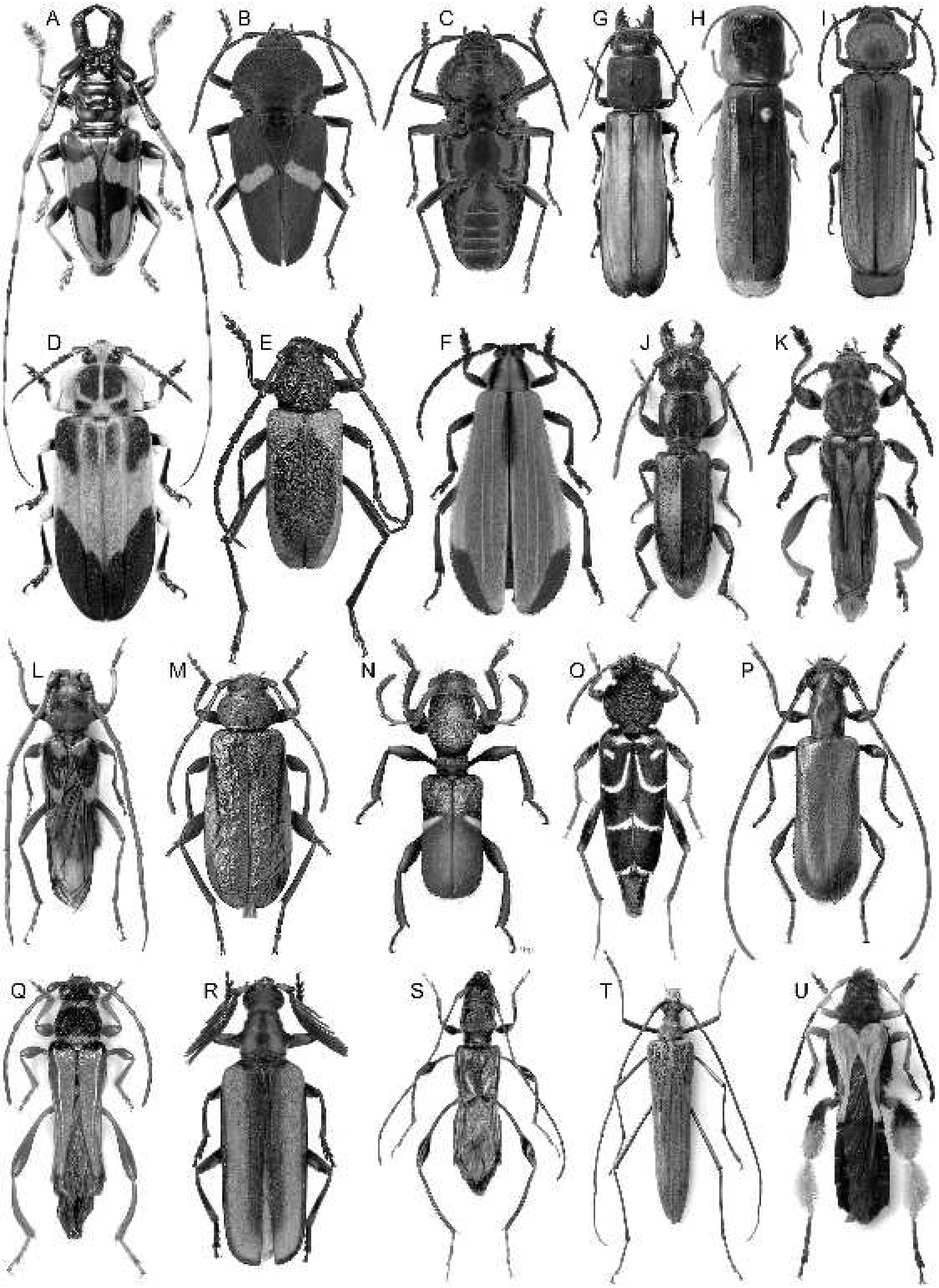


Fig. 2.4.4 Adults of Cerambycinae, dorsal view except for C. A, *Trachyderes mandibularis* (Dupont), male, 34 mm; B, *Megaderus stigma* (Linnaeus), female, 20 mm; C, same, ventral view; D, *Allocerus spencei* (Kirby), male, 27 mm; E, *Purpuricenus kaehleri* (Linnaeus), female, size unknown; F, *Amphidesmus 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, *Acyphoderes 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, *Callisphyris 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.)

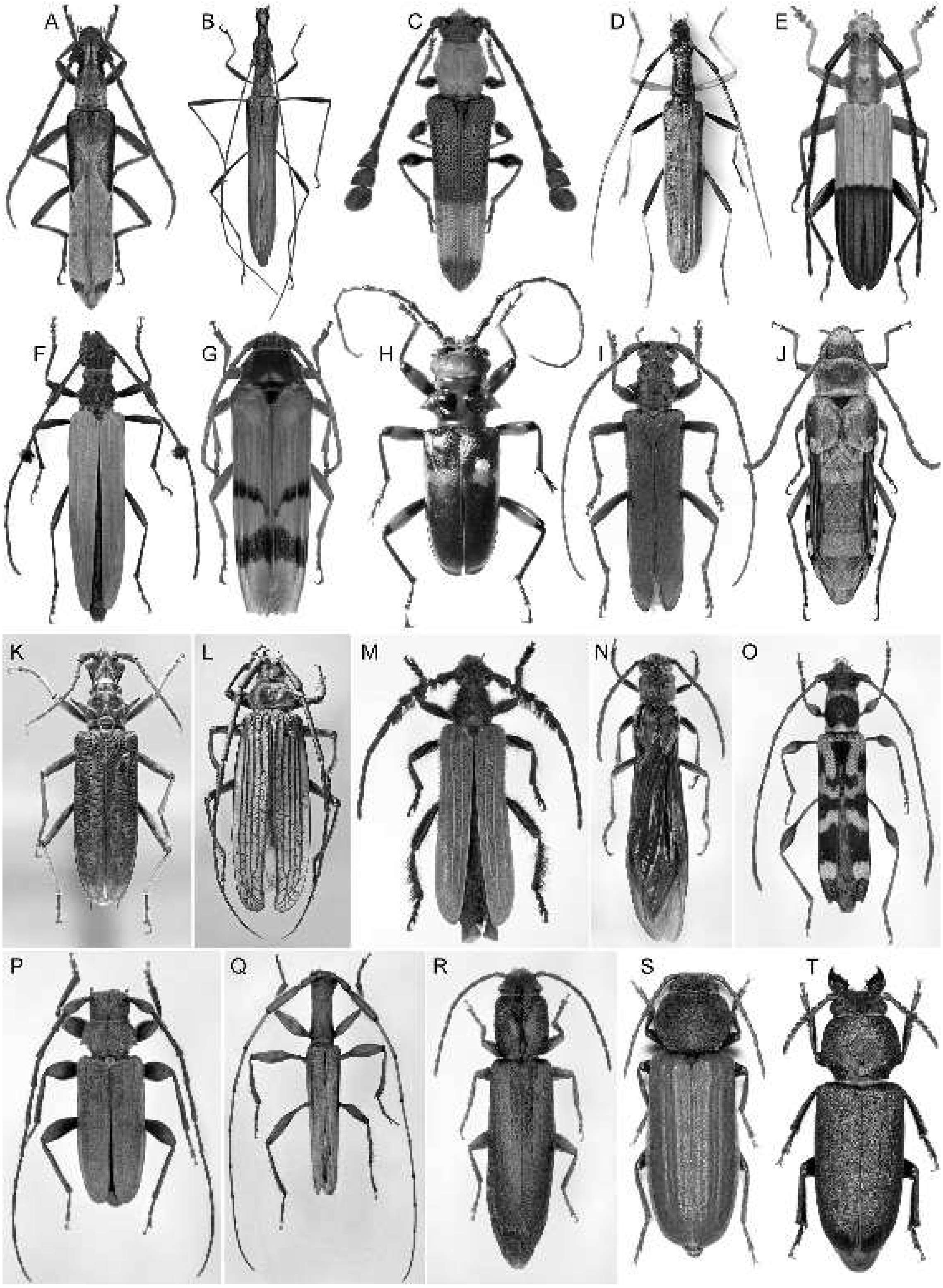


Fig. 2.4.5 Adults of Cerambycinae (A–Q) and Spondylidinae (R–T), dorsal view. A, *Uracanthus triangularis* Hope, female, 23 mm; B, *Rhinophthalmus* sp., sex unknown, 17 mm; C, *Telocera wollastoni* White, male, 7 mm; D, *Stenopotes pallidus* Pascoe, female, 19 mm; E, *Stenoderus ostricilla* Newman, sex uncertain, 12 mm; F, *Tritocosmia* sp., female, 19.5 mm; G, *Tragocerus spencii* Hope, female, 27 mm; H, *Australodon nearnsi* Escalona & Ślipiński, 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-Méneville, 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. Nearns; S © M. Hoskovec.)

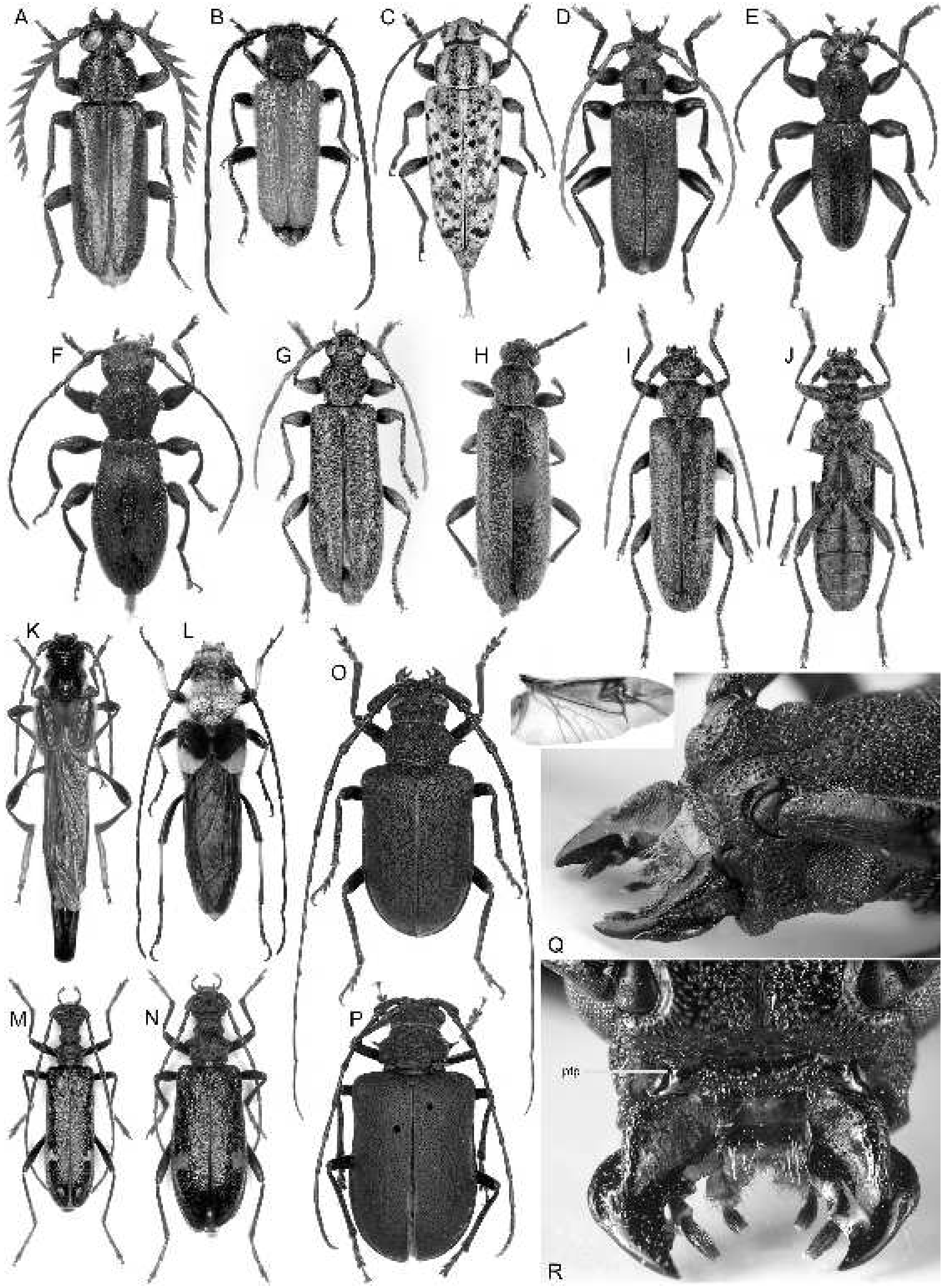


Fig. 2.4.6 Adults of Spondylidinae (A–J), Necydalinae (K, L), and Lepturinae (M–R), dorsal view except for J, Q, and R. A, *Pectoctenus scalabrii* Fairmaire, male, 9 mm; B, *Anisarthron barbipes* (Schrank), male, 8 mm; C, *Atimia huachucae* Champlain & Knull, female, 15 mm (excluding ovipositor); D, *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; Ginzel 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 Acanthocinini 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", indicating 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

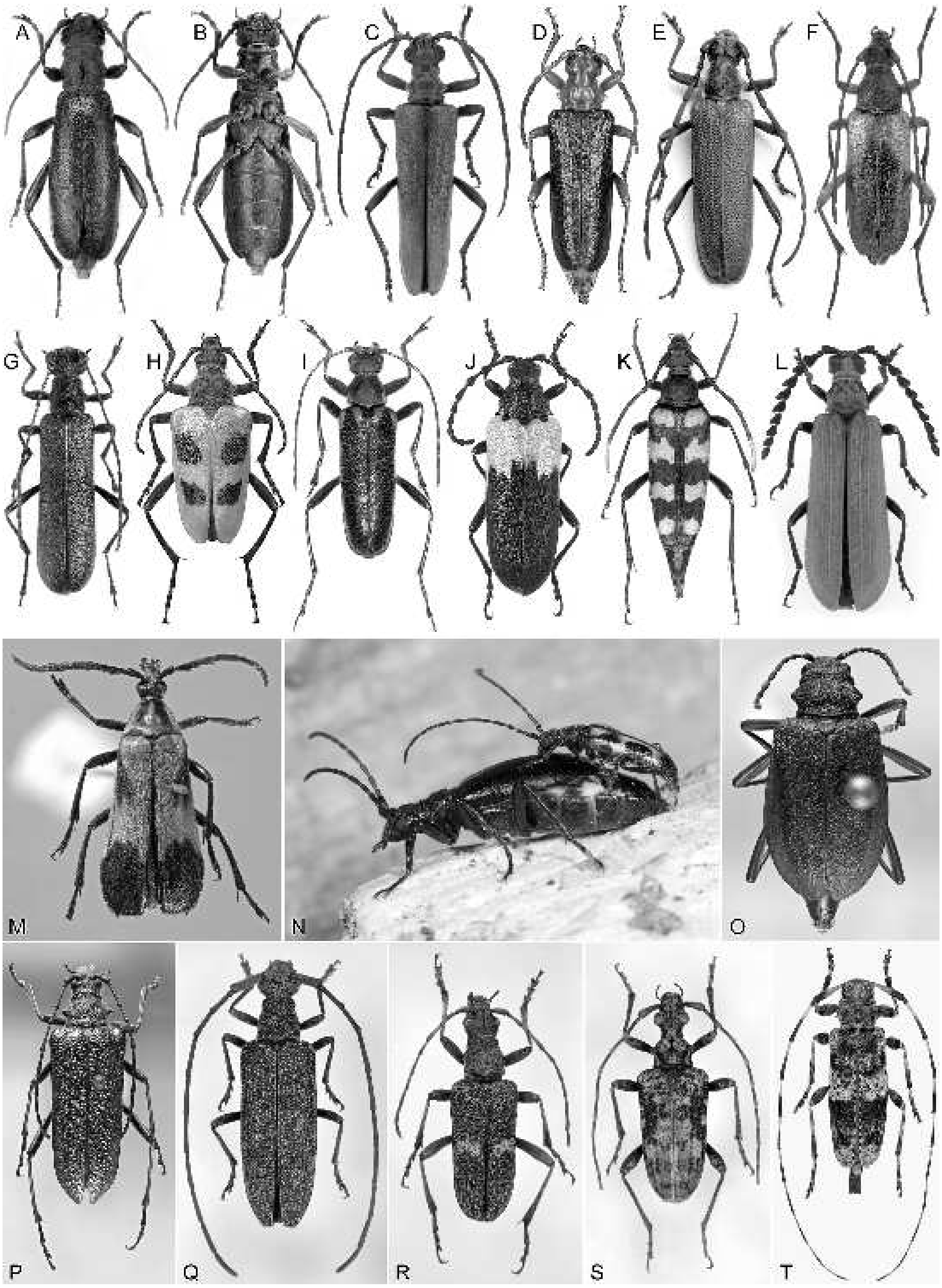


Fig. 2.4.7 Adults of Lepturinae (A–S) and Lamiinae (T), dorsal view except for B and N. A, *Teledapus celsicola* Holzschuh, female, 18 mm; B, same, ventral view; C, *Centrodera decolorata* (Harris), male, 21 mm; D, *Rhamnusium bicolor* (Schrank), female, 21 mm; E, *Enoploderes sanguineum* Faldermann, 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, *Apiocephalus 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. Nearns; N © W. Bi.)

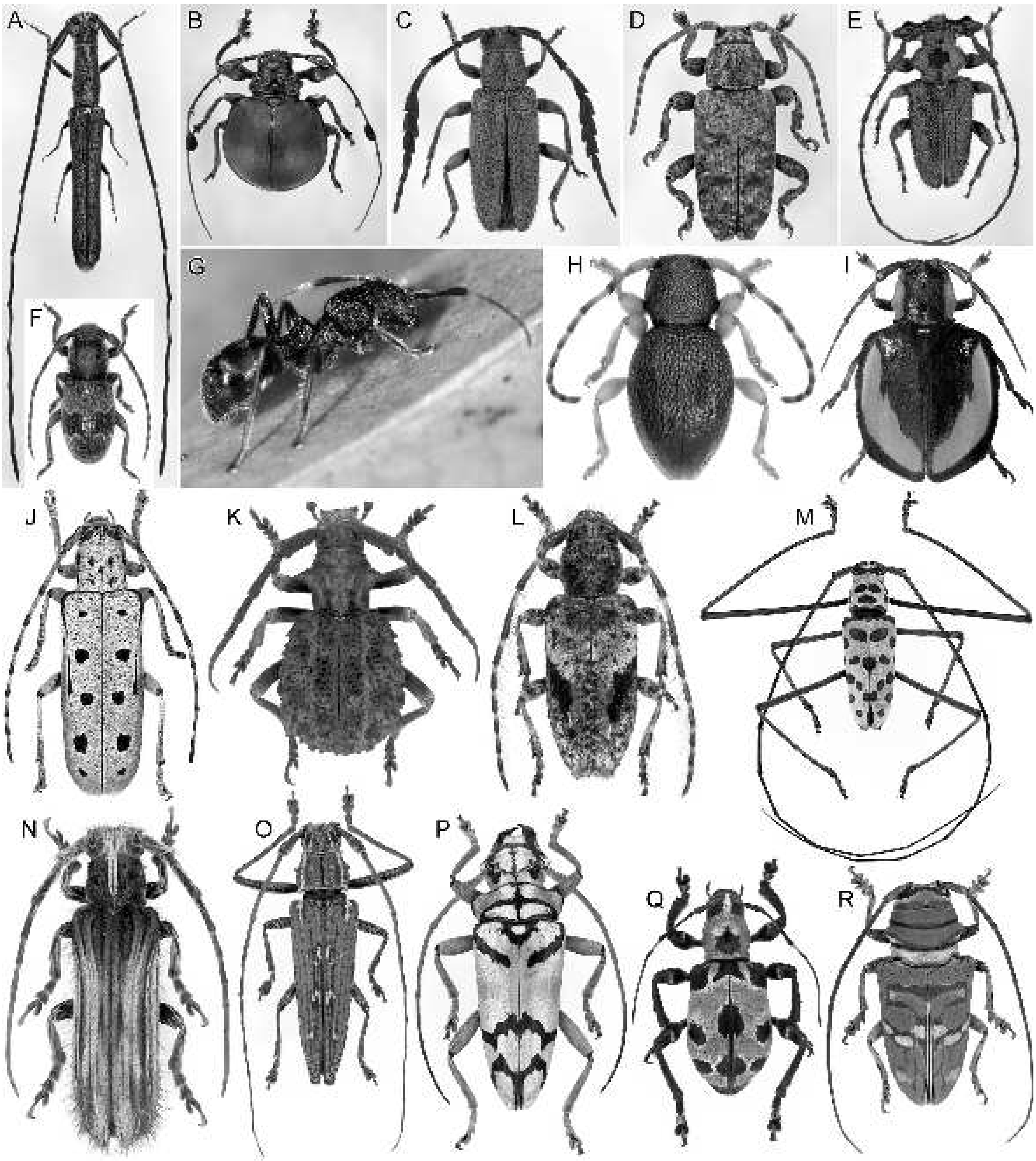


Fig. 2.4.8 Adults of Lamiinae, dorsal view except for G. A, *Anauxesis* sp., male, 12 mm; B, *Cyclopeplus batesi* J. Thomson, male, 10 mm; C, *Hemicladus dejeani* Buquet, female, 7 mm; D, *Enaretta* sp., male, 10 mm; E, *Tapeina ?melzeri* Zajciw, male, 9.5 mm; F, *Parmena balteus* (Linnaeus), ?female, 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, *Homonoea albosignata* Breuning, male, 28 mm; P, *Tmesisternus rafaelae* 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 *Psacothea 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 Rhagiini, 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 (Beeson & 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-β-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-β-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-β-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 *Psacothea 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 laboratory-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-deterring 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 *Sphallotrichus* Fragoso 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 elongate 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 *Psacothea 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" (uneclosed 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°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; Rożek *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 Tenebrionoidea), 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, Bethylidae 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 subfamiles contribute species that harm living or freshly dead plants. Some species have considerable invasive potential, as demonstrated recently by some *Anoplophora* (Lamiinae) (Lingafelter & Hoebeke 2002; Carter *et al*. 2009, 2010; Hu *et al*. 2009; Haack *et al*. 2010), but outbreaks of native species 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 lamiines 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; Tatarinova *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;

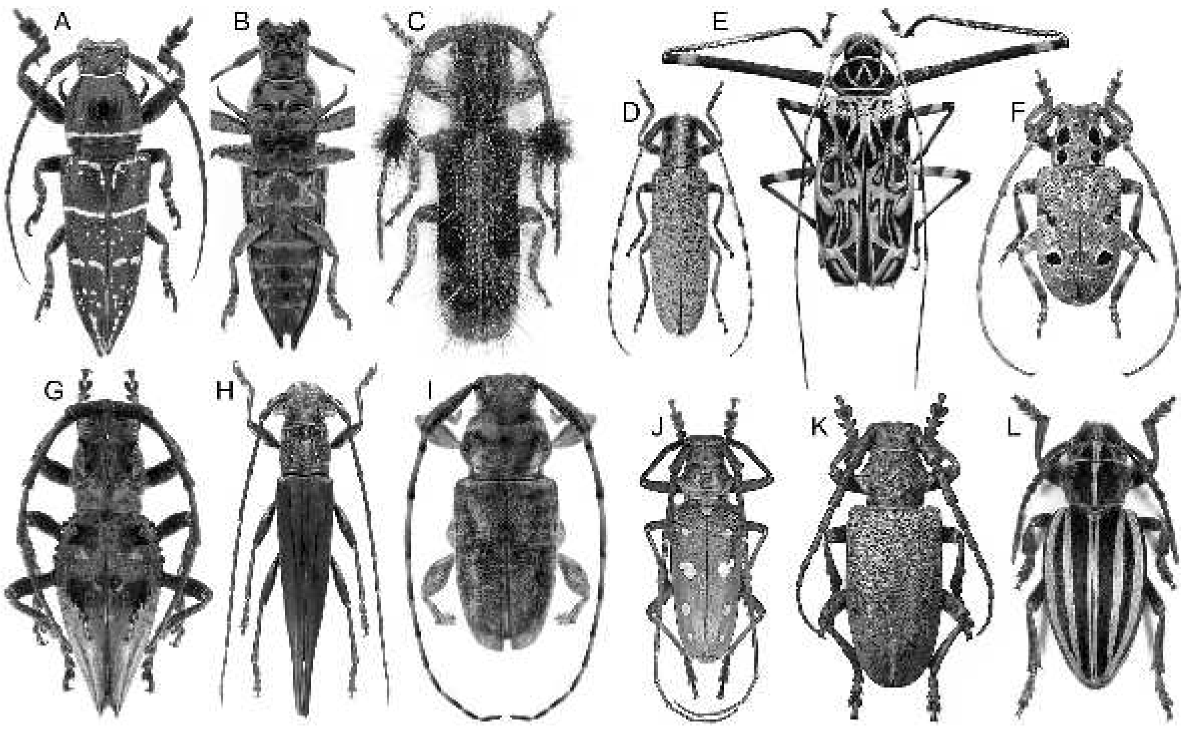


Fig. 2.4.9 Adults of Lamiinae, dorsal view except for B. A, *Xiphotheata saundersii* Pascoe, male, 25.5 mm; B, same, ventral view; C, *Apodasya pilosa* Pascoe, male, 9.5 mm; D, *Agapanthia villosoviridescens* (De Geer), female, size unknown; E, *Acrocinus longimanus* (Linnaeus), male (complete antennae 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 scopolii* (Herbst), female, size unknown. (D, F, J, K © S. Ziarko; E © V. Seichert; G–I © CSIRO, Canberra; L © M. Hoskovec.)

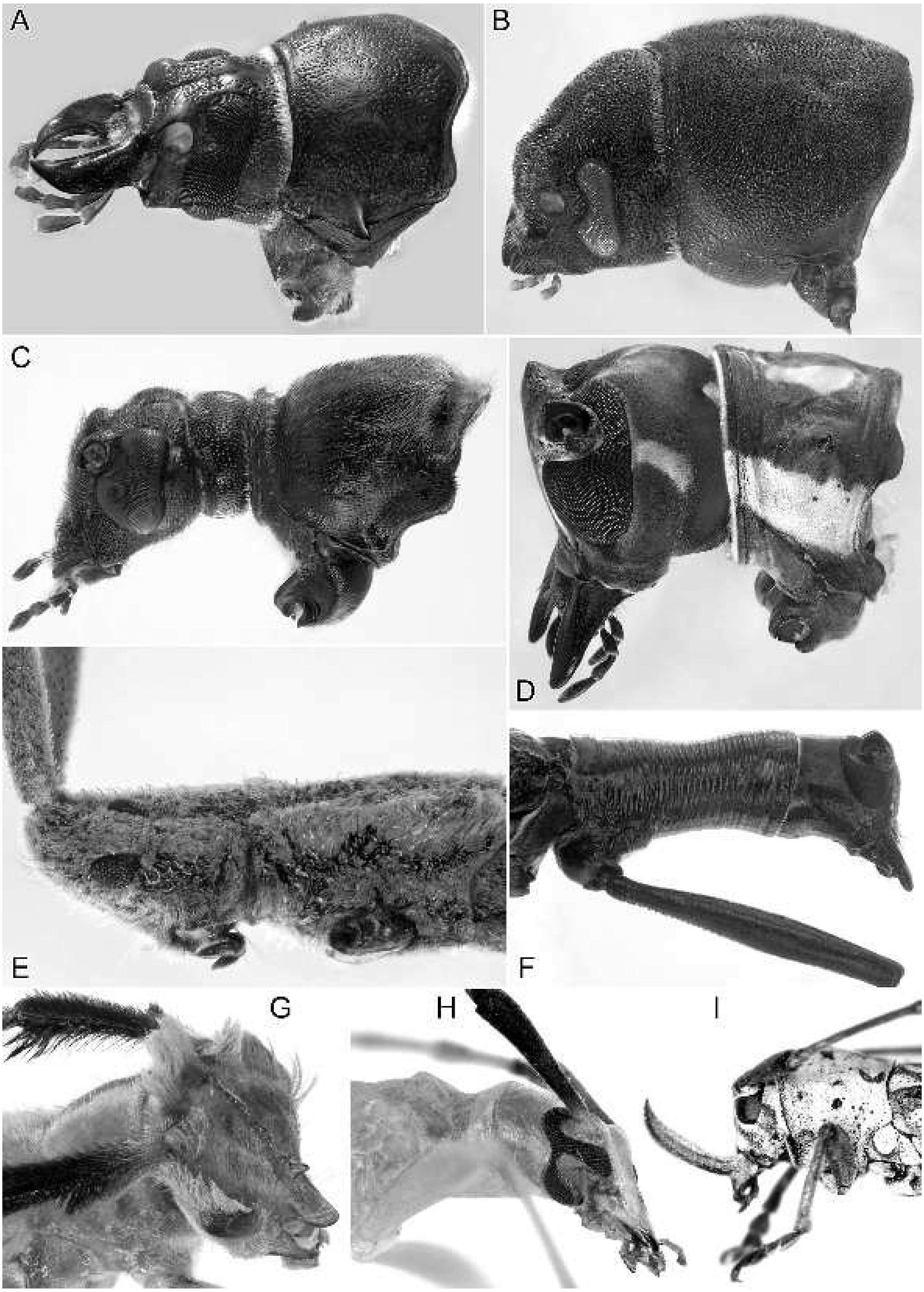


Fig. 2.4.10 Adults, head and prothorax lateral or laterodorsal. A, *Prionus coriarius* (Prioninae), female; B, *Asemum striatum* (Spondylidinae), female; C, *Leptura quadrifasciata* (Lepturinae), male; D, *Batocera victoriana* J. Thomson (Lamiinae), female; E, *Tetraglenes hirticornis* (Fabricius) (Lamiinae), male; F, *Gnoma luzonica* Erichson (Lamiinae), male; G, *Momisis melanura* Gahan (Lamiinae), male (dentate median frontal line and strongly projecting post-clypeus); 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 retinular 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 floricoly; 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 *Sceleocantha 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

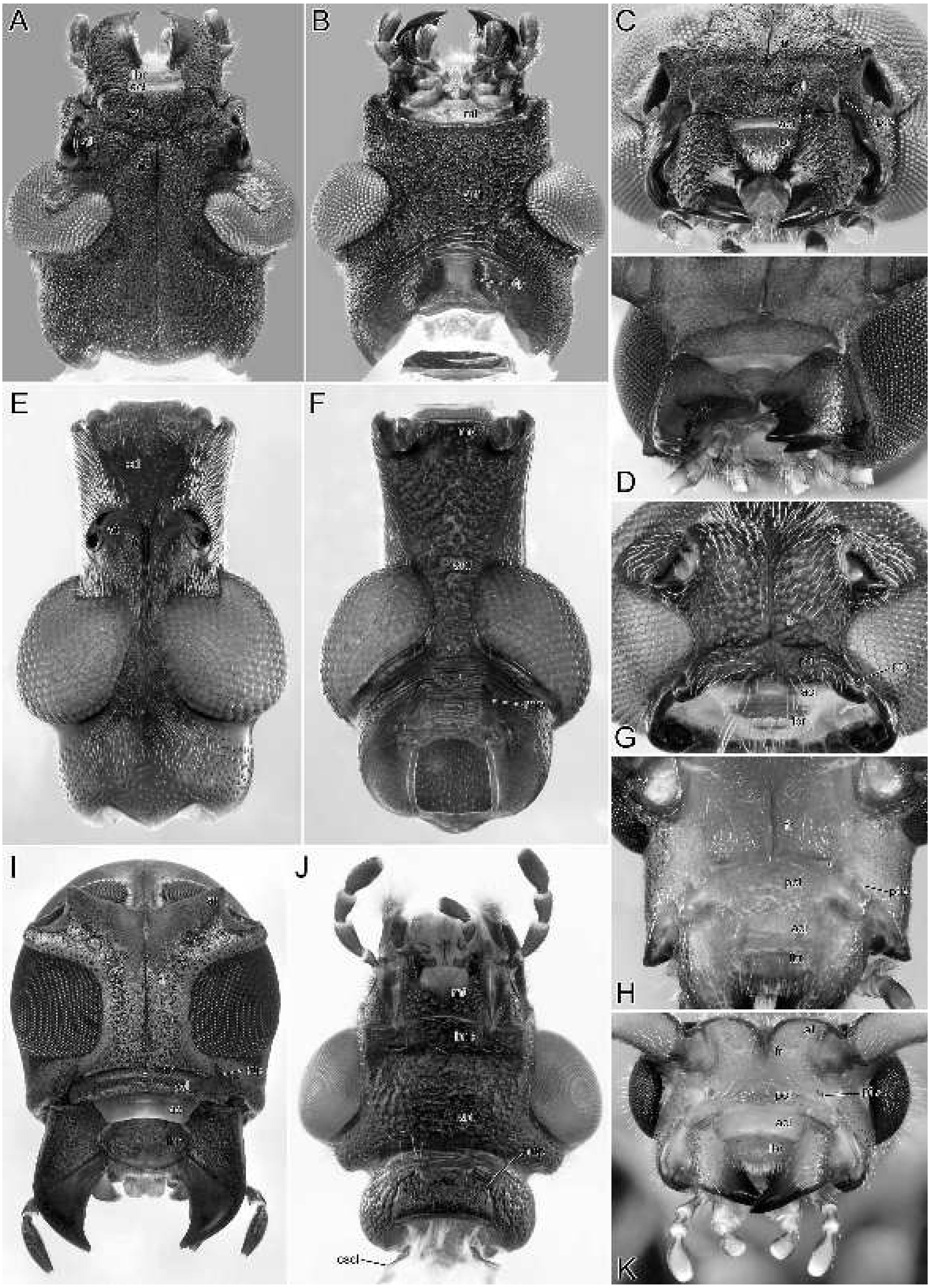


Fig. 2.4.11 Adult head structures, Prioninae (A–D), Dorcasominae (E, F), Cerambycinae (G, H), Lamiinae (I), and Lepturinae (J, K). A, *Aegosoma scabricorne* (Scopoli), female, head, dorsal view; B, same, ventral view; C, same, anterior view; D, *Delocheilus prionoides* J. Thomson, female, head, anterolateral 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.

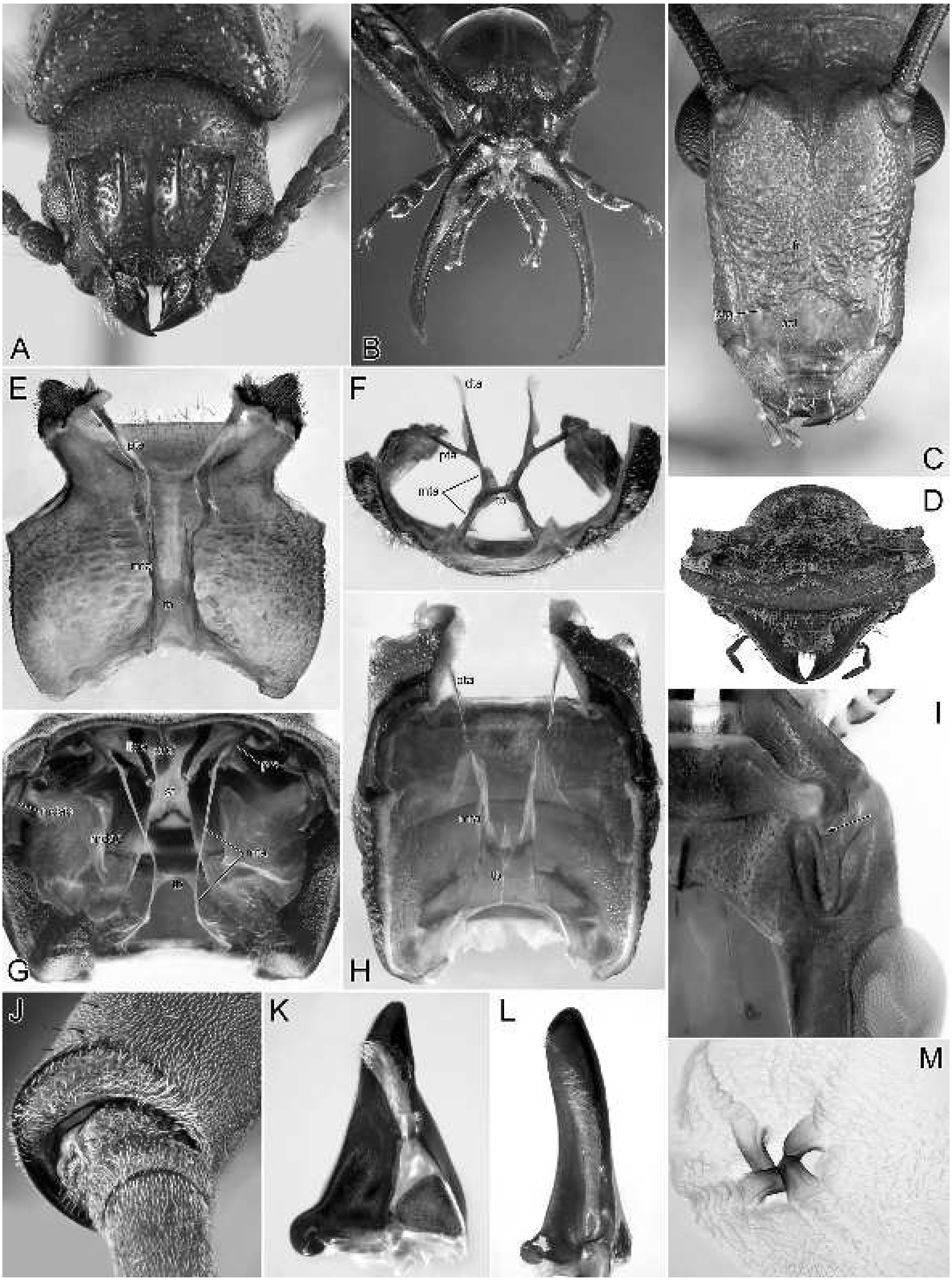


Fig. 2.4.12 Adult structures of Parandrinae (A), Prioninae (B), Cerambycinae (C, E, H, I), Lamiinae (D, G, J, M), Lepturinae (F, K), and Dorcasominae (L). A, *Erichsonia dentifrons* Westwood, female, head, anterodorsal view; B, *Dorysthenes walkeri* (Waterhouse), head, anterior view; C, *Macrones rufus* 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, *Peblephaeus 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.

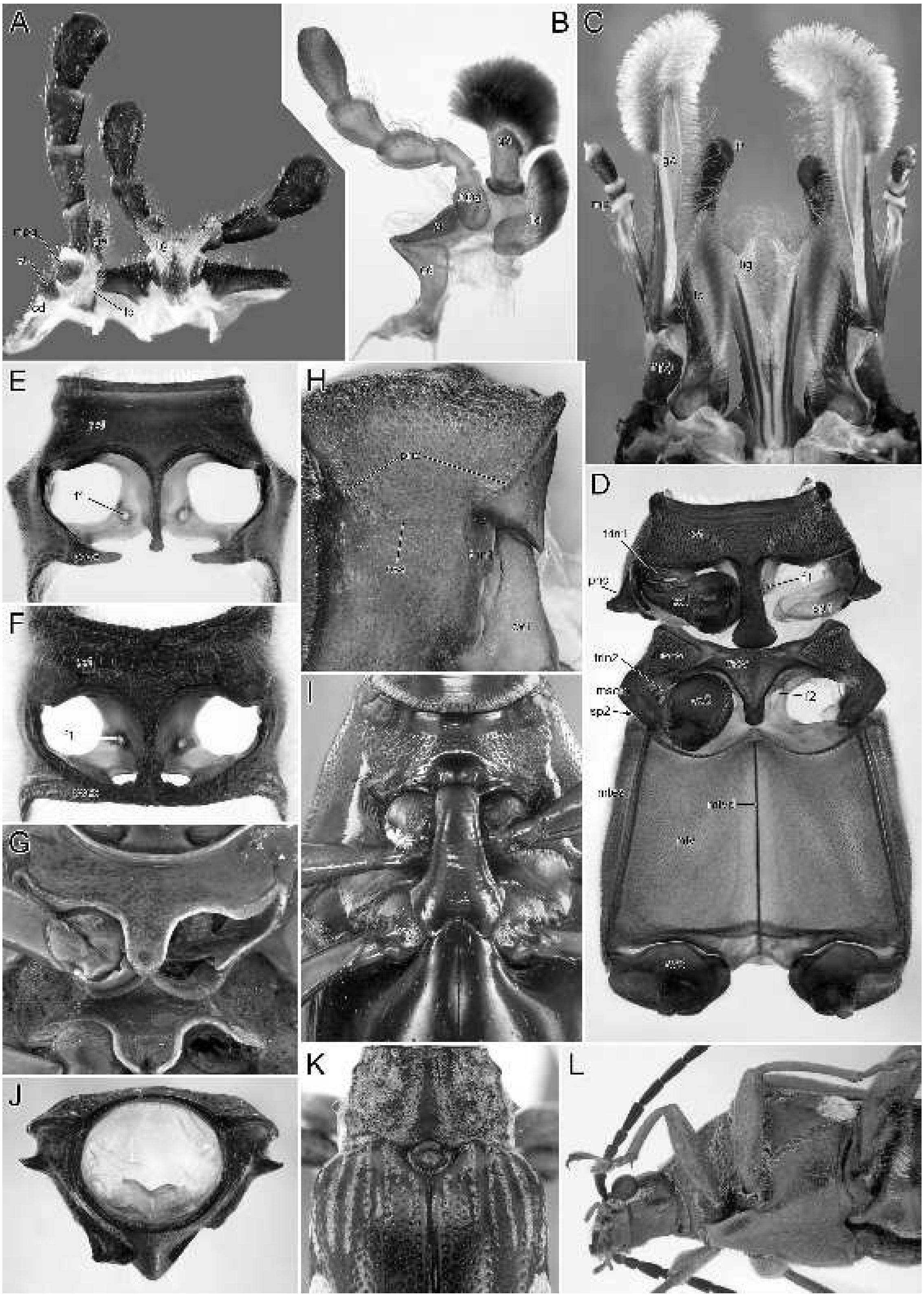


Fig. 2.4.13 Adult structures of Prioninae (A, B, D, H), Cerambycinae (C, I), Dorcasominae (E, L), Necydalinae (F), Lamiinae (J, K), and of uncertain subfamily (G). A, *Mallodon* sp., female, left maxilla and labium, dorsal view; B, *Hoplideres aquilus* Coquerel, female, left maxilla, dorsal view; C, *Pachyteria dimidiata* Westwood, male, specialized maxillolabial 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 mesoventer, 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, metaventrite; mtvd, metaventral discrimen; nss, prothoracic notosternal suture; pnc, lateral pronotal carina; pocx, postcoxal process (of protergal 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 groundplan 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)

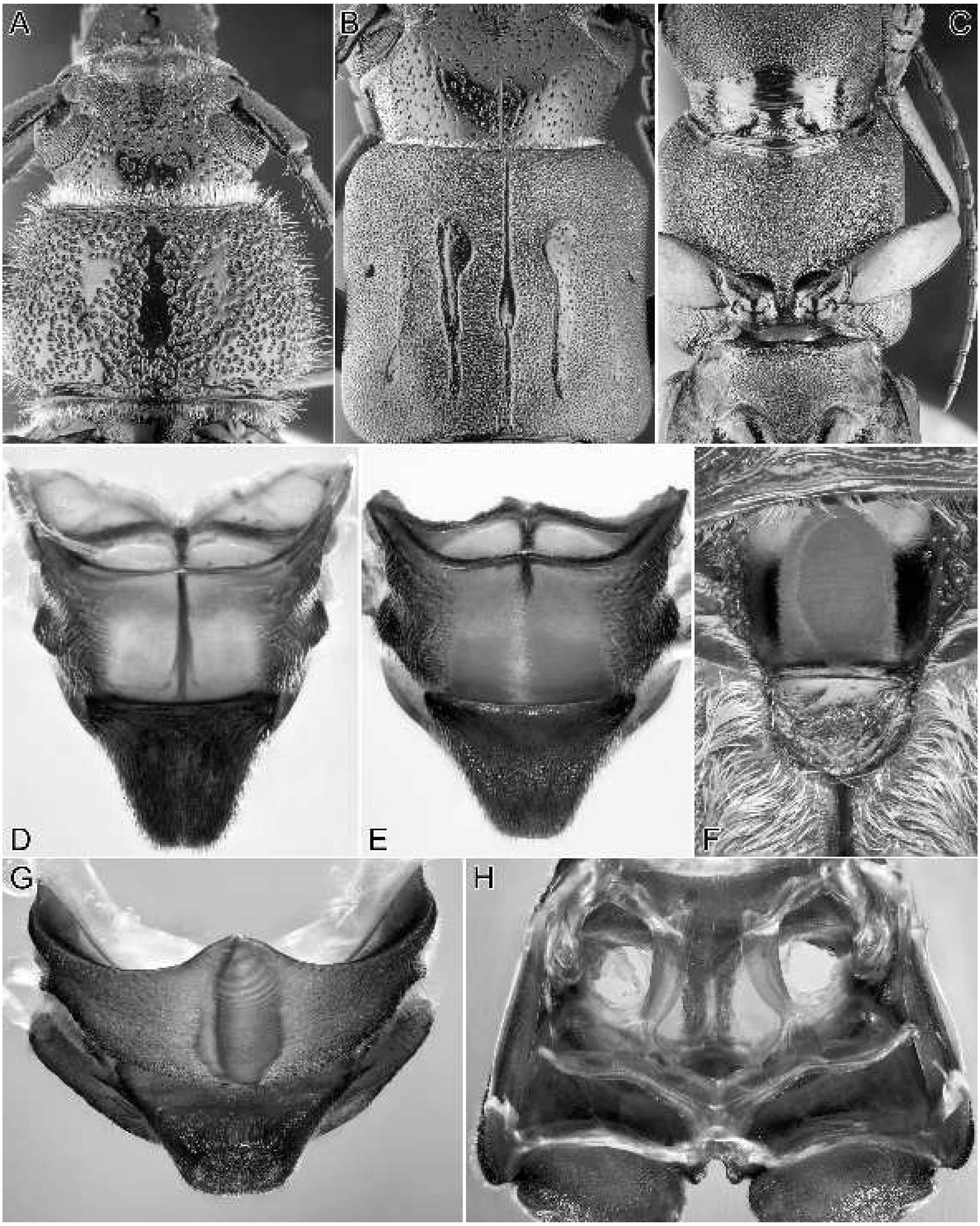


Fig. 2.4.14 Adults of Cerambycinae (A–C, F), Dorcasominae (D, E), and Lamiinae (G, H). A, *Torneutes pallidipennis* Reich, female, head and prothorax, dorsal view; B, *T. pallidipennis*, male, head and prothorax, dorsal view; C, same, head, pro- and mesothorax, ventral view (probably glandular fields 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 *Michthisoma* LeConte of Saphanini); very rarely only males are brachypterous (*Storeyandra* Santos-Silva, Heffern & 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 Obriini of Cerambycinae), without postcoxal lines. Intercoxal 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

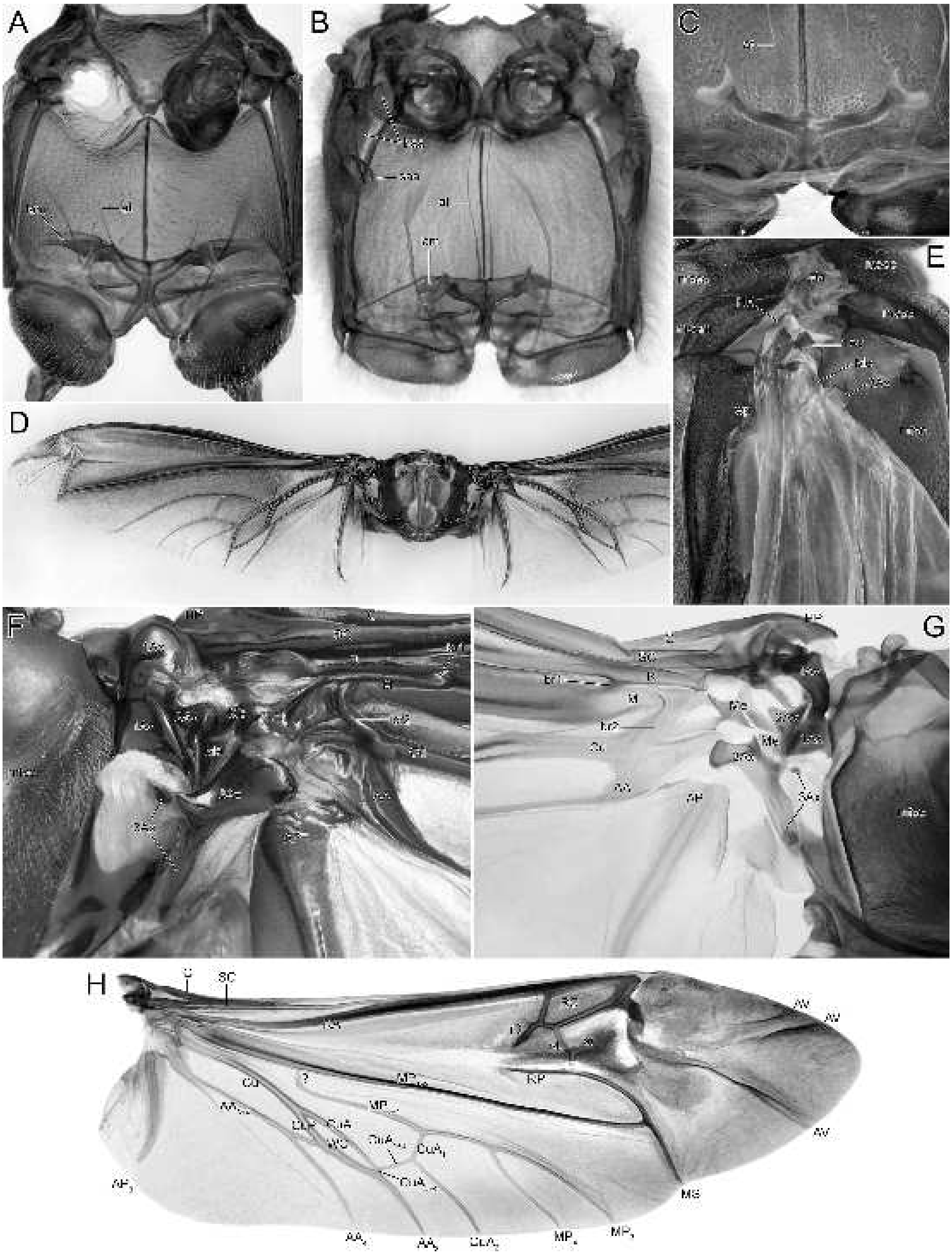


Fig. 2.4.15 Adults of Cerambycinae (A), Prioninae (B–D, F), and Lepturinae (E, G, H). A, *Callidium violaceum* (Linnaeus), male, pterothoracic venter with endoskeleton, dorsal view (metendosternite with large laminae and broadly separate anterior tendons); B, *Closterus grandidieri* Lameere, male, same (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 Kukalová-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}).

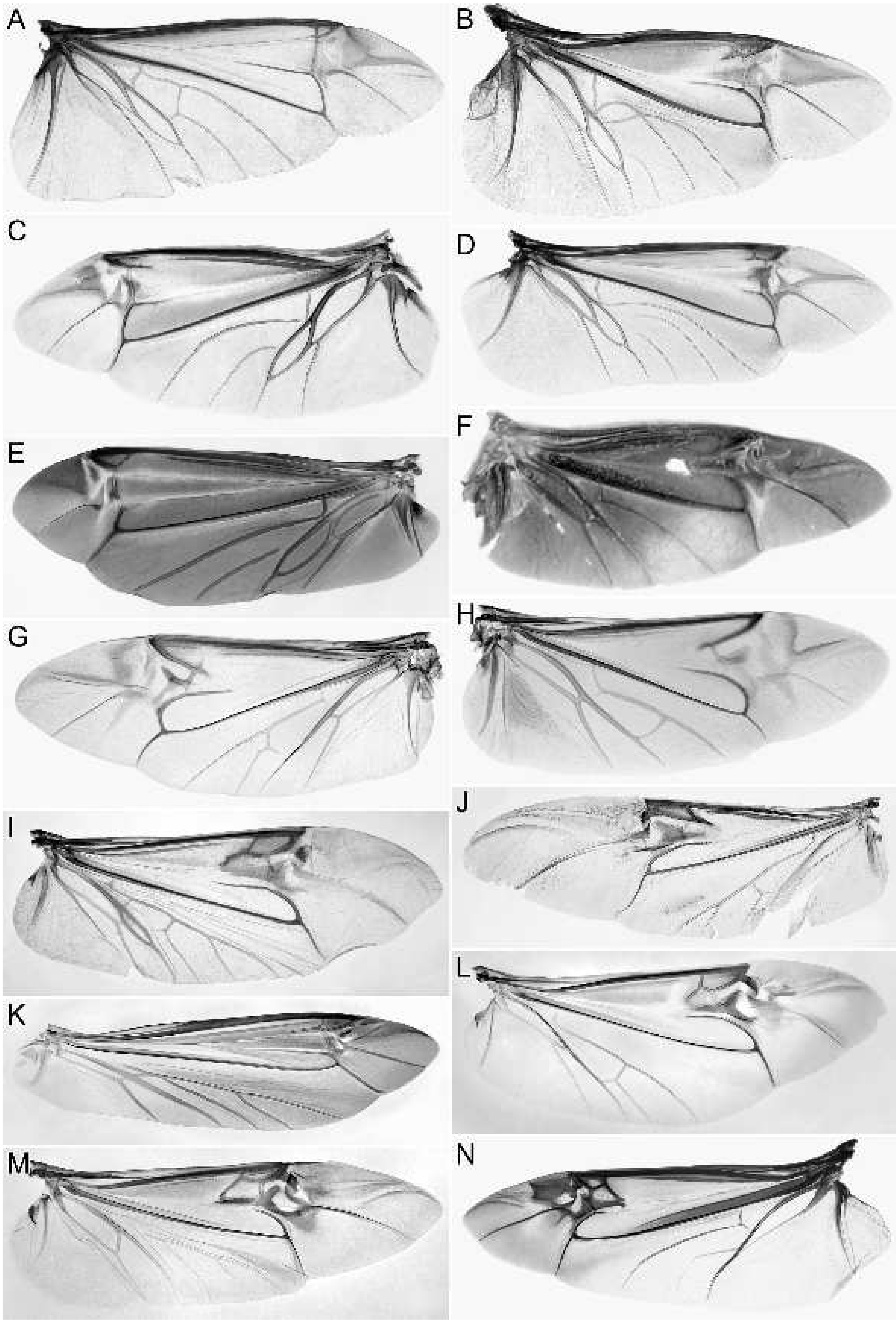


Fig. 2.4.16 Hind wings of Prioninae (A–E), Parandrinae (G, H), Spondylidinae (I, J), Necydalinae (K), Lepturinae (L), Lamiinae (M, N), and of uncertain subfamily (F). A, *Tithoes maculatus* (Fabricius), male; B, *Sceleocantha* sp., male; C, *Prionus coriarius*, male; D, *Hoplideres aquilus*, female; 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.

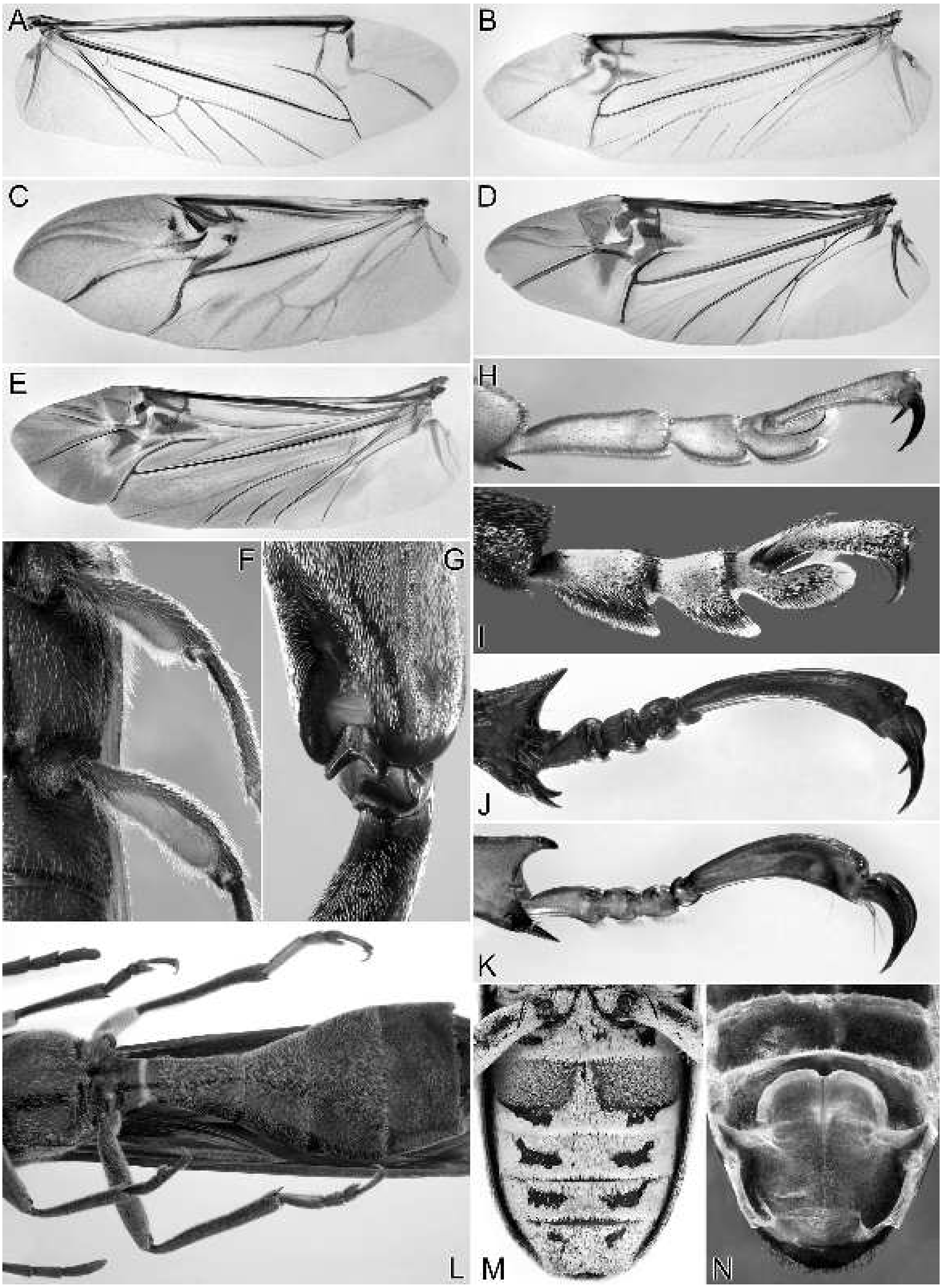


Fig. 2.4.17 Adults. A–E, hind wings of Cerambycinae (A–D) and Dorcasominae (E): A, *Stenopotes pallidus*, male; B, *Phlyctaenodes pustulosus*, male; C, *Opsimus quadrilineatus*, male; D, *Sphinteria gratiosa*, male; E, *Tsivoka simplicicollis*, male; F, *Anisarthron barbipes* (Spondylidinae), male, left 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).

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 Astathini (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; Penteado-Dias 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; Ślipiński & 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

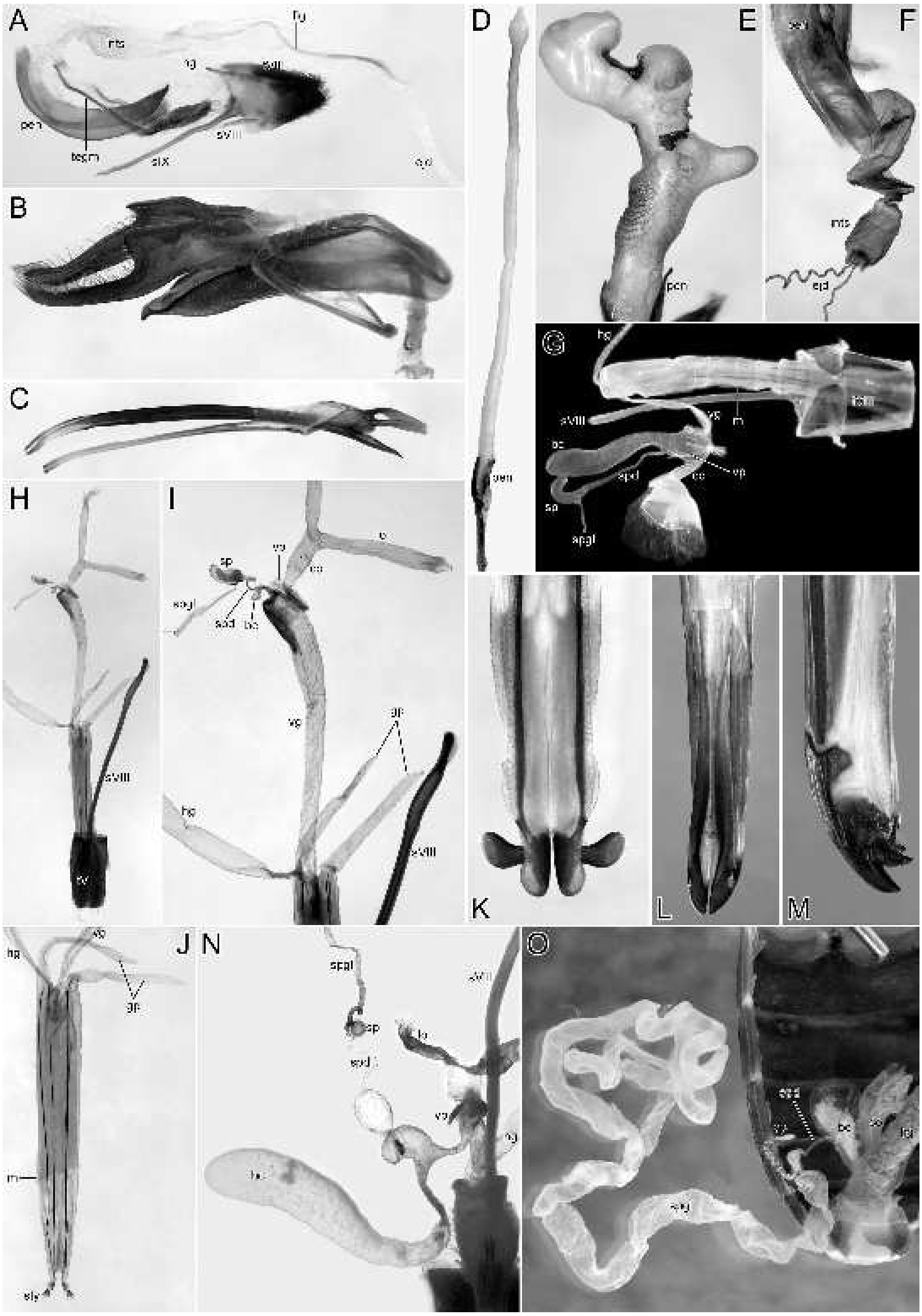


Fig. 2.4.18 Adult terminalia and internal genital structures, Lepturinae (A, B, H–J), Dorcasominae (C), Prioninae (D, G, K, L), Cerambycinae (E), Lamiinae (F, N, O), and Parandrinae (M). A, *Leptura aurulenta* Fabricius, male, terminal abdominal sclerites and genitalia, ventral view; B, *Oxymirus cursor*, male, penis and tegmen, right laterodorsal view; C, *Sagridola maculosa* (Guérin-Méneville), 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, *Phantasis 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.

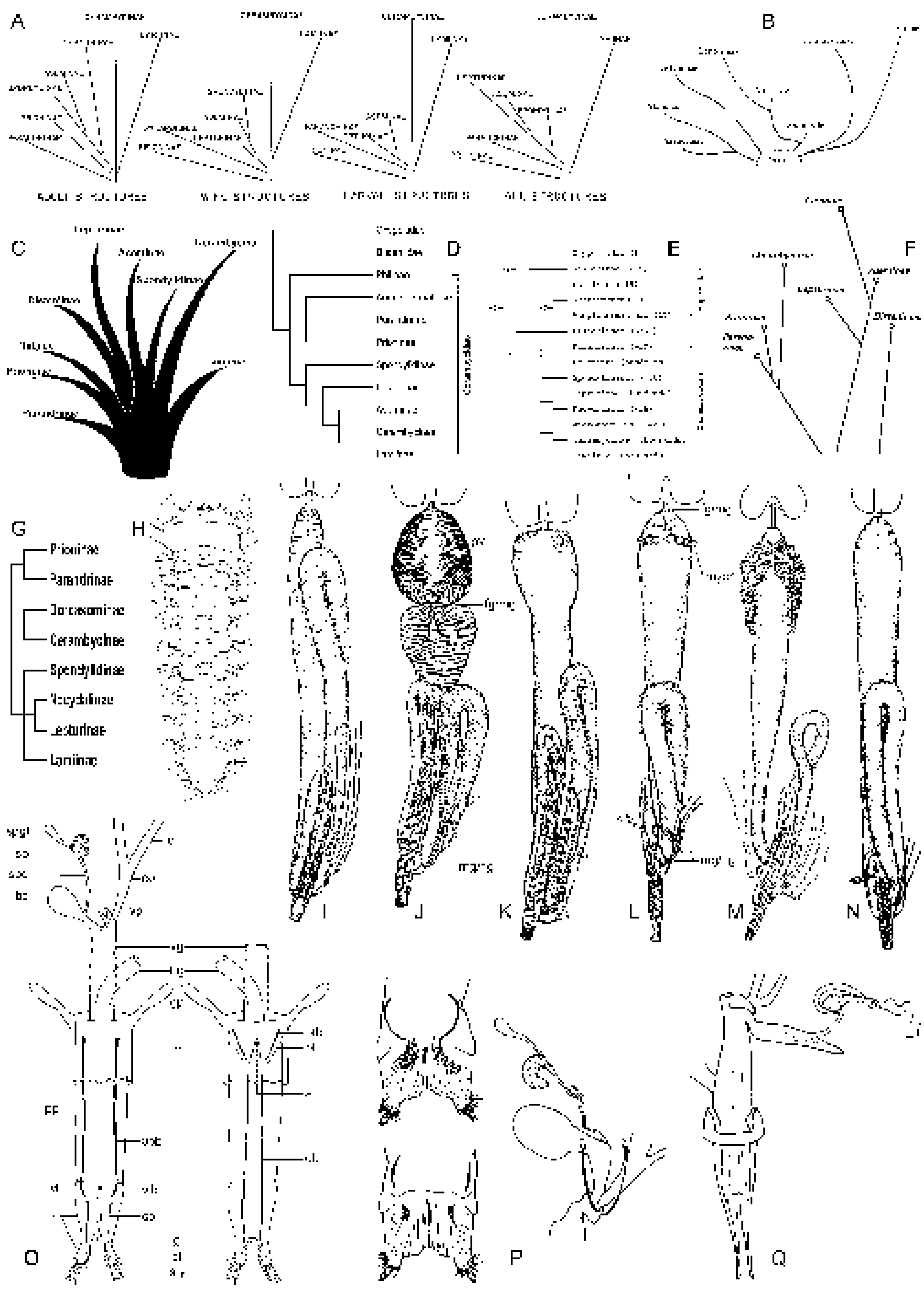


Fig. 2.4.19 A–F, cerambycoid relationships proposed by various authors: A, Linsley (1961) (based on various structures); B, Nakamura (1981); C, Villiers (1978); D, Napp (1994) (reconstructed from text and approved by the author); E, Svacha *et al.* (1997); F, Danilevsky (1979 a); G, preliminary incompletely 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 oviposior, 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 duplicature (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

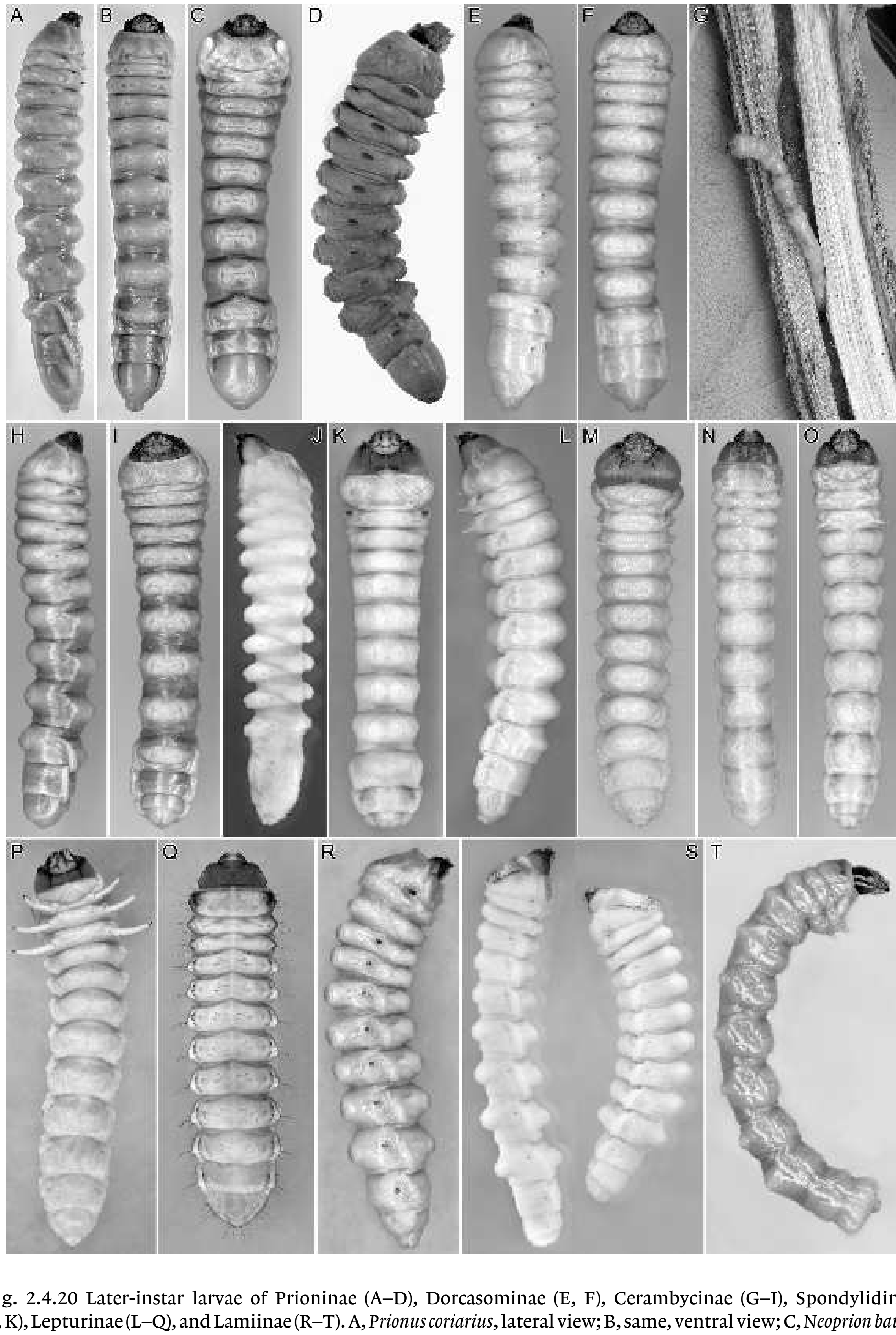


Fig. 2.4.20 Later-instar larvae of Prioninae (A–D), Dorcasominae (E, F), Cerambycinae (G–I), Spondylidinae (J, K), Lepturinae (L–Q), and Lamiinae (R–T). A, *Prionus coriarius*, lateral view; B, same, ventral view; C, *Neoprion batesi* (Gahan), ventral view; D, *Macrodontia cervicornis* (Linnaeus), lateral 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.

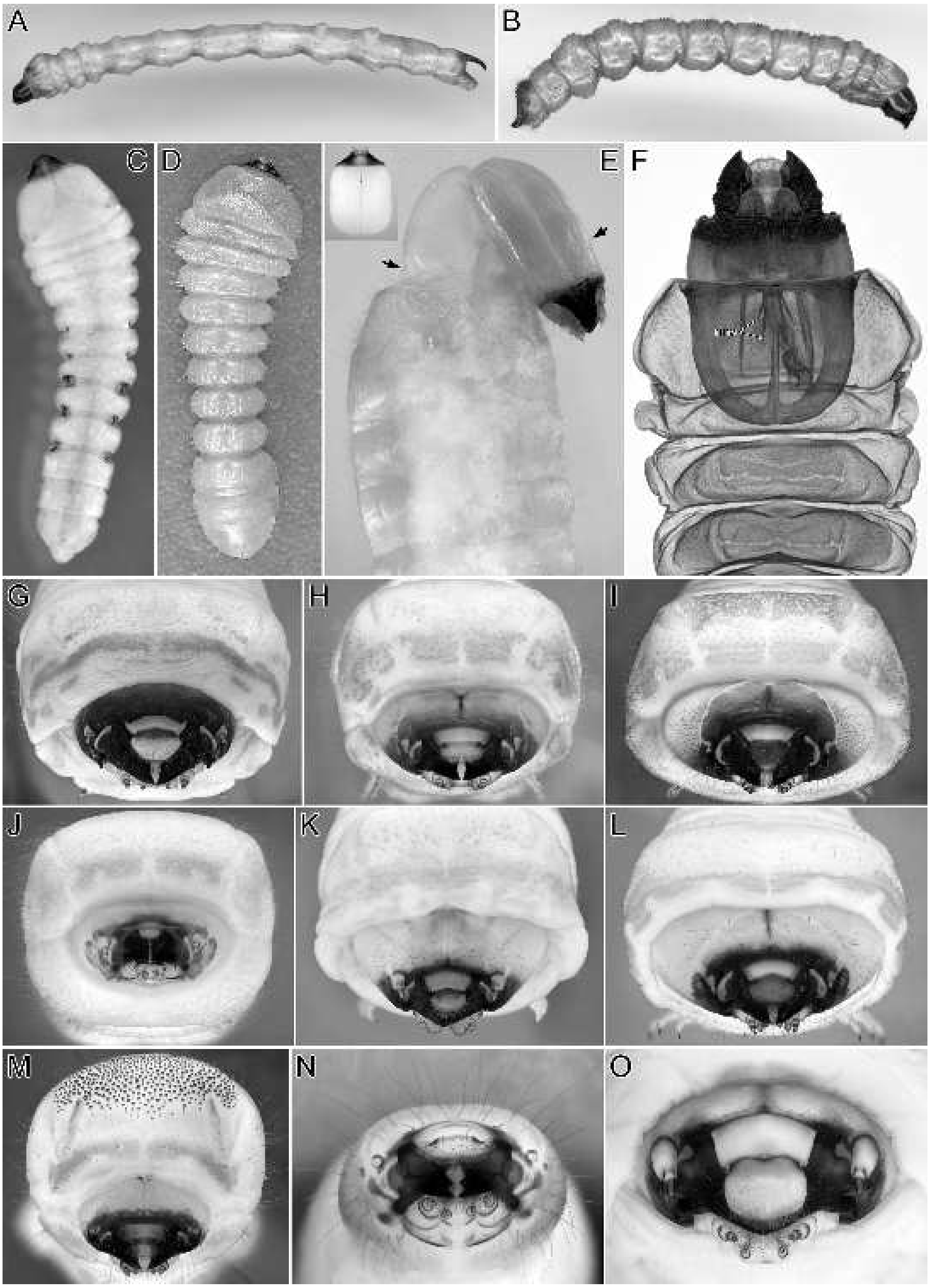


Fig. 2.4.21 Larvae. A–F, later-instar larvae of Lamiinae: A, *Aerenicopsis mendosa* Martins & Galileo, lateral view; B, unidentified larva from Barro Colorado (Panama) labelled as "*Parysatis* or *Esthlogena*" (former genus is now a synonym of *Ataxia* Haldeman), lateral view; C, *Pseudhoplomelas elegans* (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.

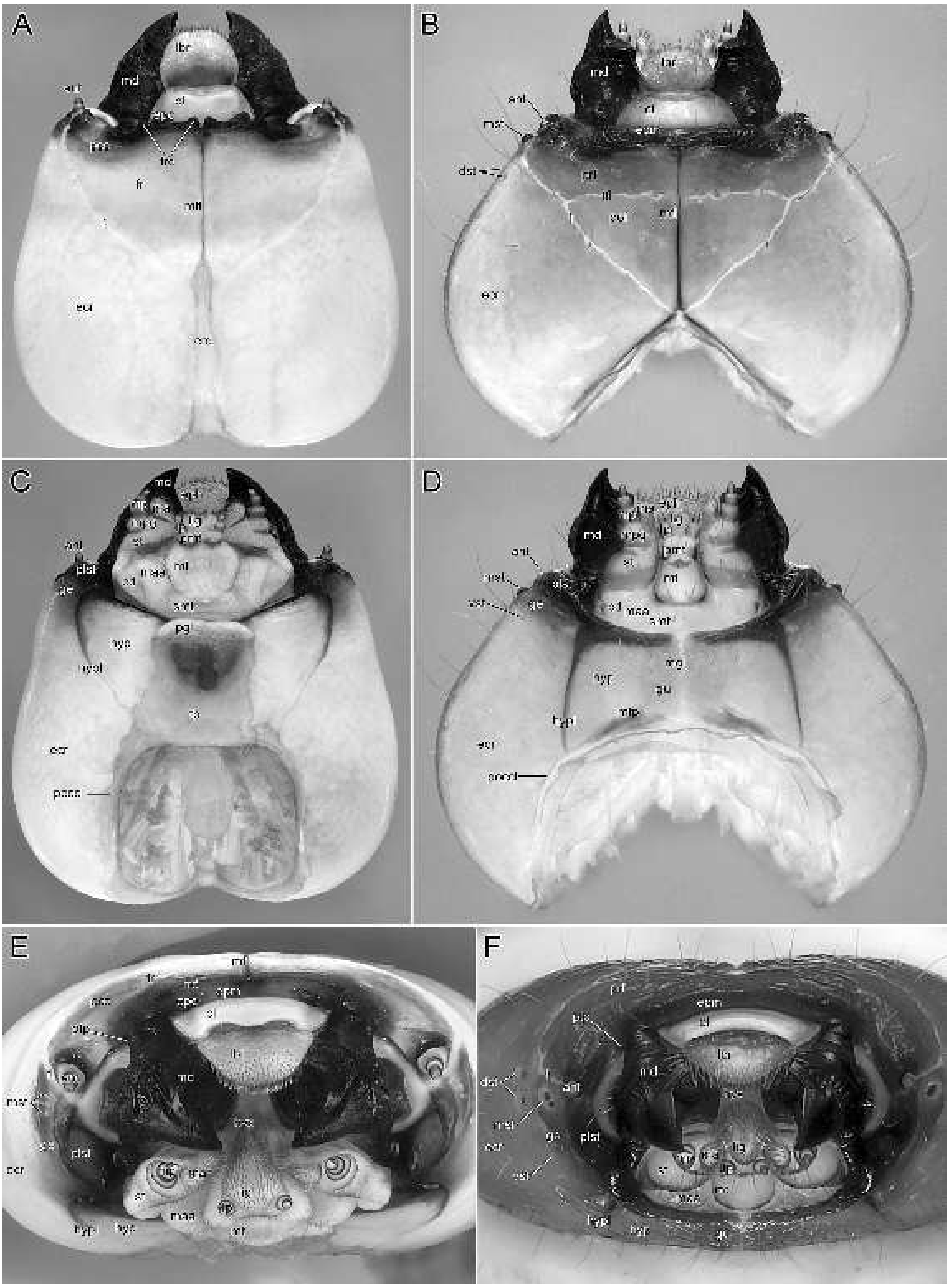


Fig. 2.4.22 Larval head, terminology, *Aegosoma scabricorne* (Prioninae; A, C, E) and *Oxymirus cursor* (Lepturinae; B, D, F) in dorsal (A, B), ventral (C, D), and anterior (E, F) view. ant, antenna; cd, cardo; cl, clypeus (in cerambycids actually anteclypeus); crd, dorsomedian cranial duplicature; dst, 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; hypl, 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; tfl, transfrontal line; vst, ventral stemma.

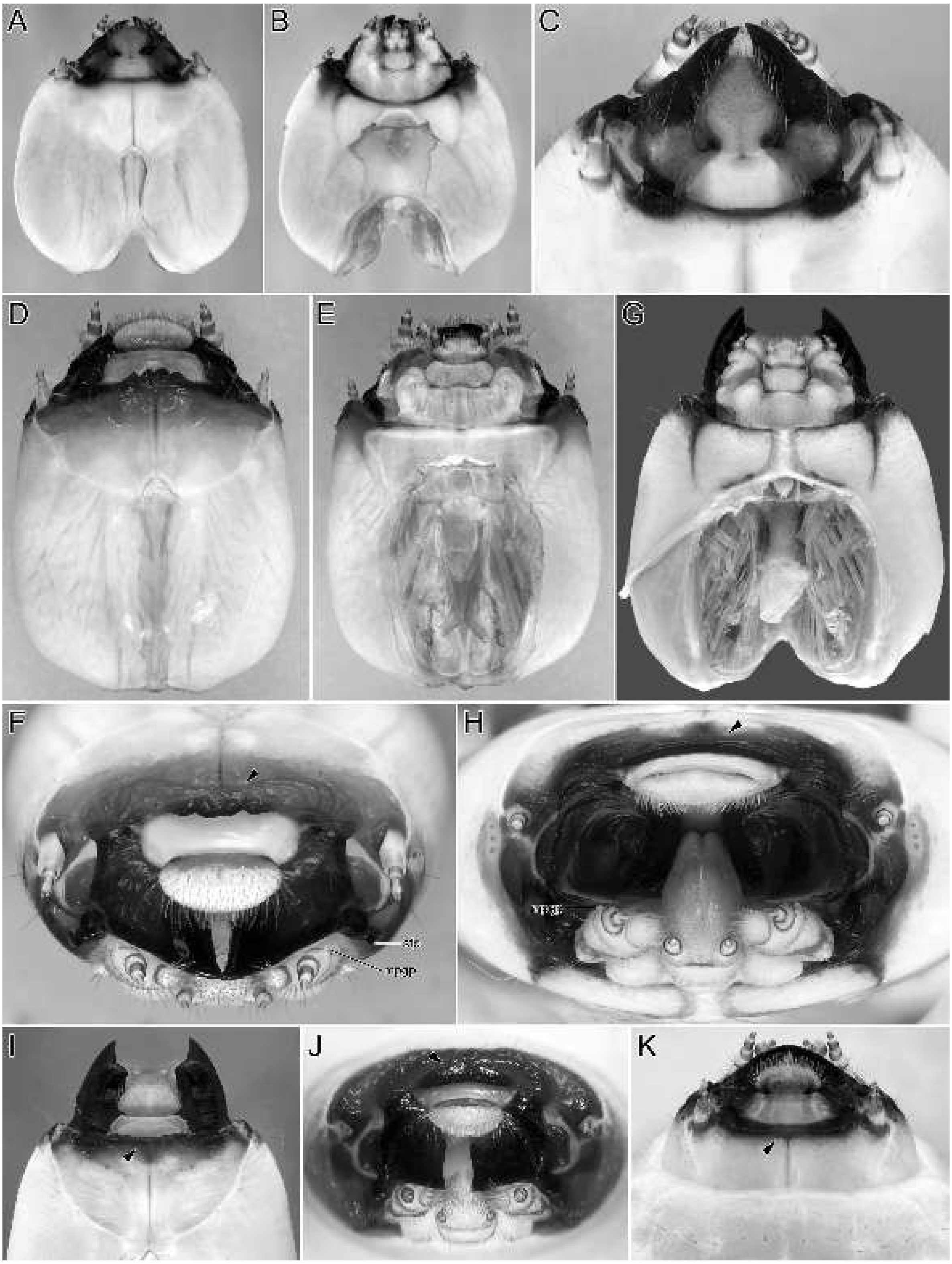


Fig. 2.4.23 Larval head of Parandrinae (A–C) and Dorcasominae (D–K). A, *Neandra brunnea* (Fabricius), head, dorsal view; B, same, ventral view; C, same, anterior head, anterodorsal view; D, *Artelida crinipes* J. Thomson, head, dorsal view; E, same, ventral view; F, same, anterior head, anterodorsal 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. mpgp, 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).

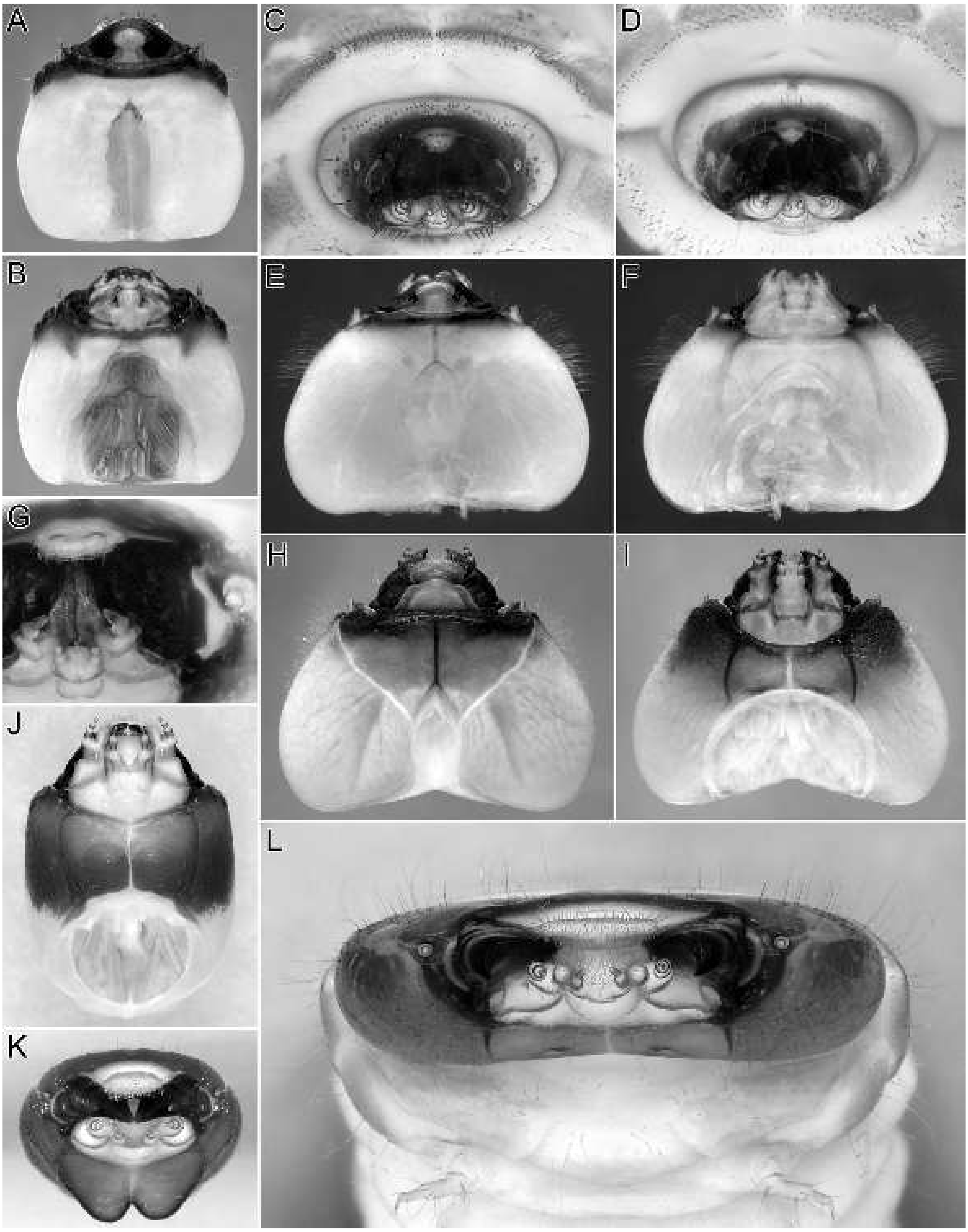


Fig. 2.4.24 Larval head of Cerambycinae (A–G), Spondylidinae (H, I), Lamiinae (J, K), and Lepturinae (L). A, *Xylotrechus antilope* (Schoenherr), head, dorsal view; B, same, ventral view; C, *Holopterus chilensis*, head, anterior view; D, *Callisphyris macropus*, same; E, *Opsimus quadrilineatus*, head, 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.

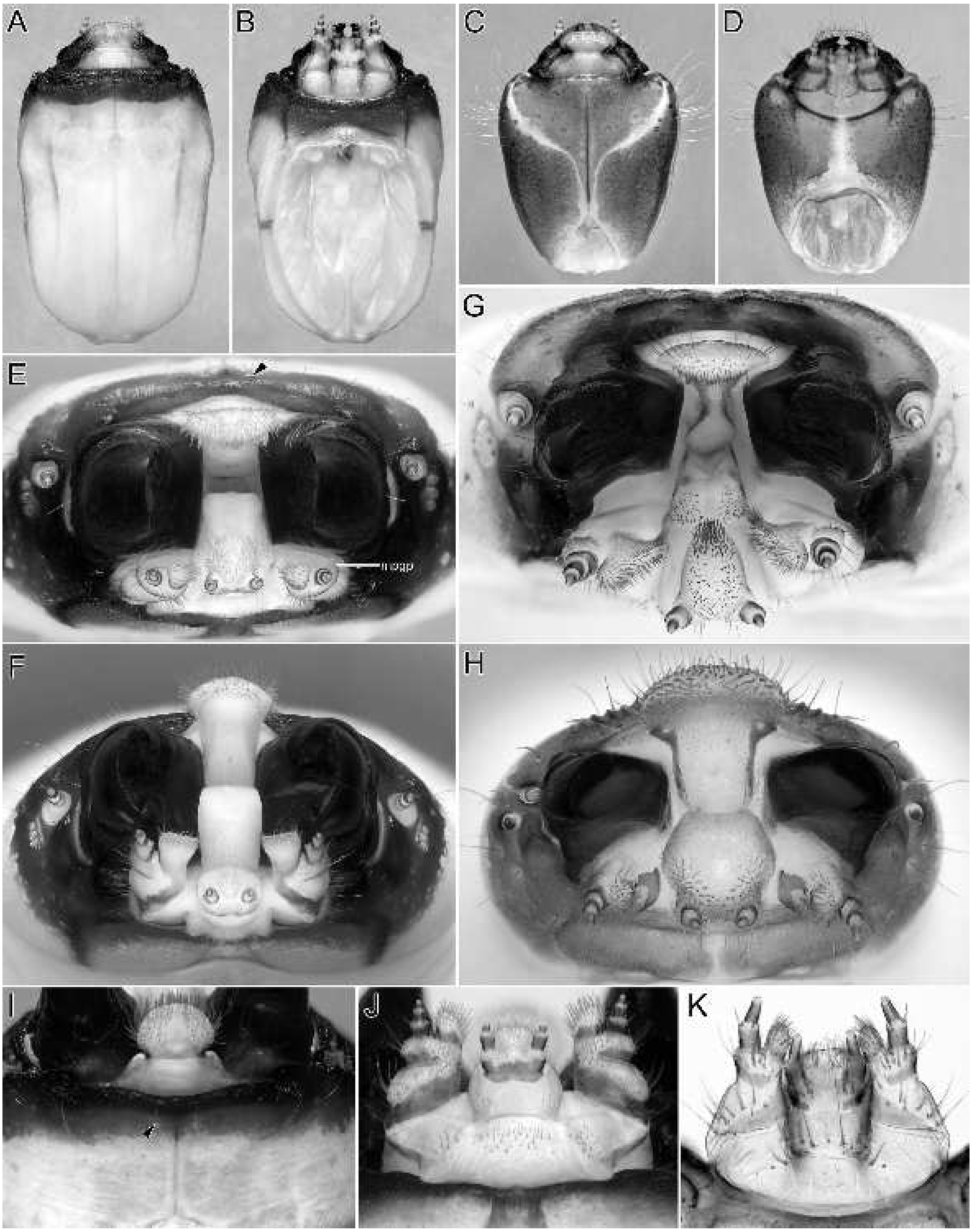


Fig. 2.4.25 Larval head and mouth parts of Lamiinae (A–D, H, K), Cerambycinae (E, F, I, J), and Prioninae (G). A, *Epiglenea comes* Bates, head, dorsal view; B, same, ventral view; C, *Agapanthia villosoviridescens*, head, dorsal view; D, same, ventral view; E, *Cerambyx cerdo*, head, anterior view; 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, *Oplosia 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. mpgp, 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 monomerous 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

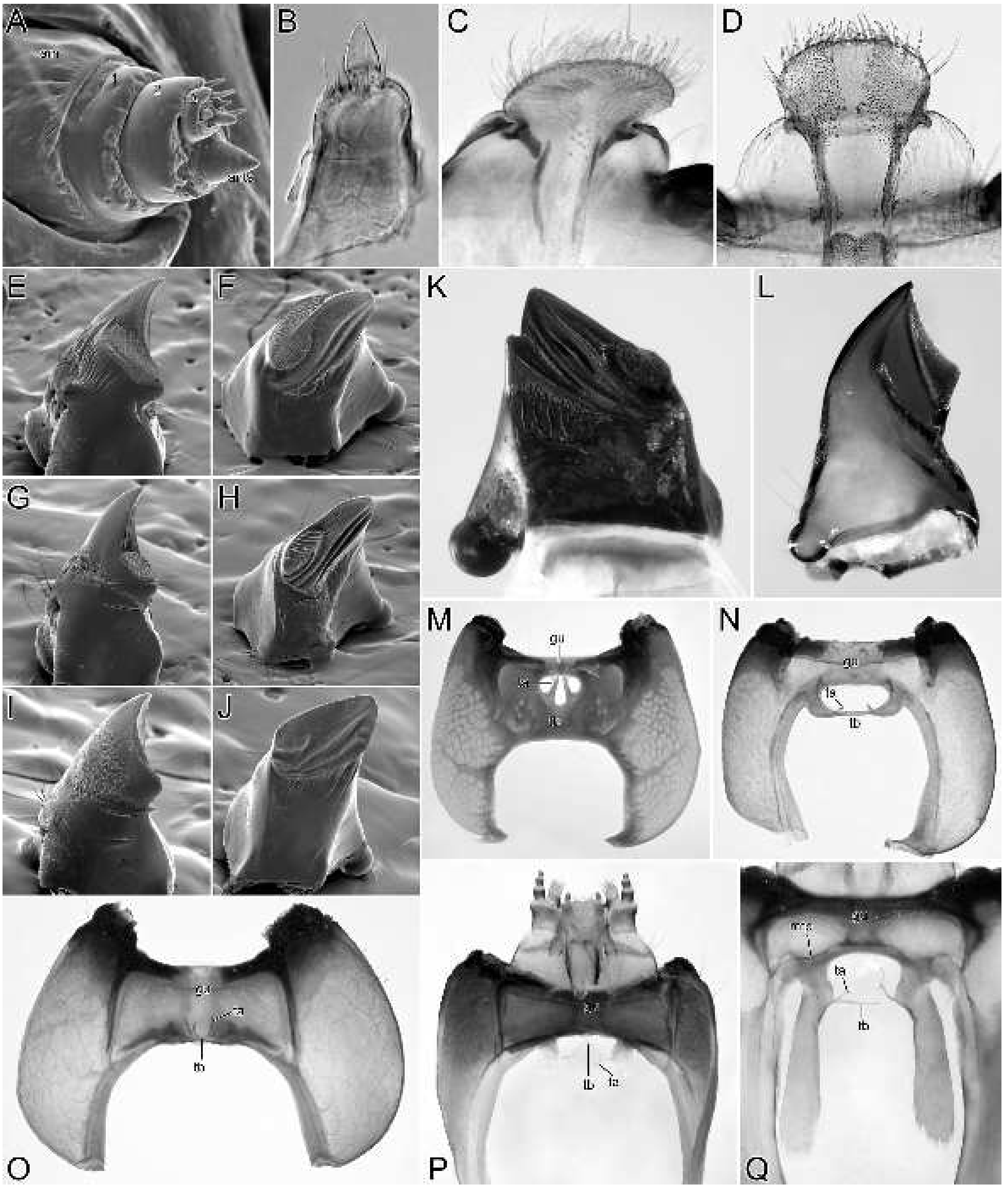


Fig. 2.4.26 Larval structures of Lamiinae (A–D, L, P, Q), Prioninae (E, F, K, M), Lepturinae (G, H, O), Spondylidinae (I, J) and Dorcasominae (N). A, *Monochamus sutor* (Linnaeus), right antenna, dorsolateral view (SEM, modified from Svacha 2001); B, *Pogonocherus hispidus*, right antenna, lateral view; 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.

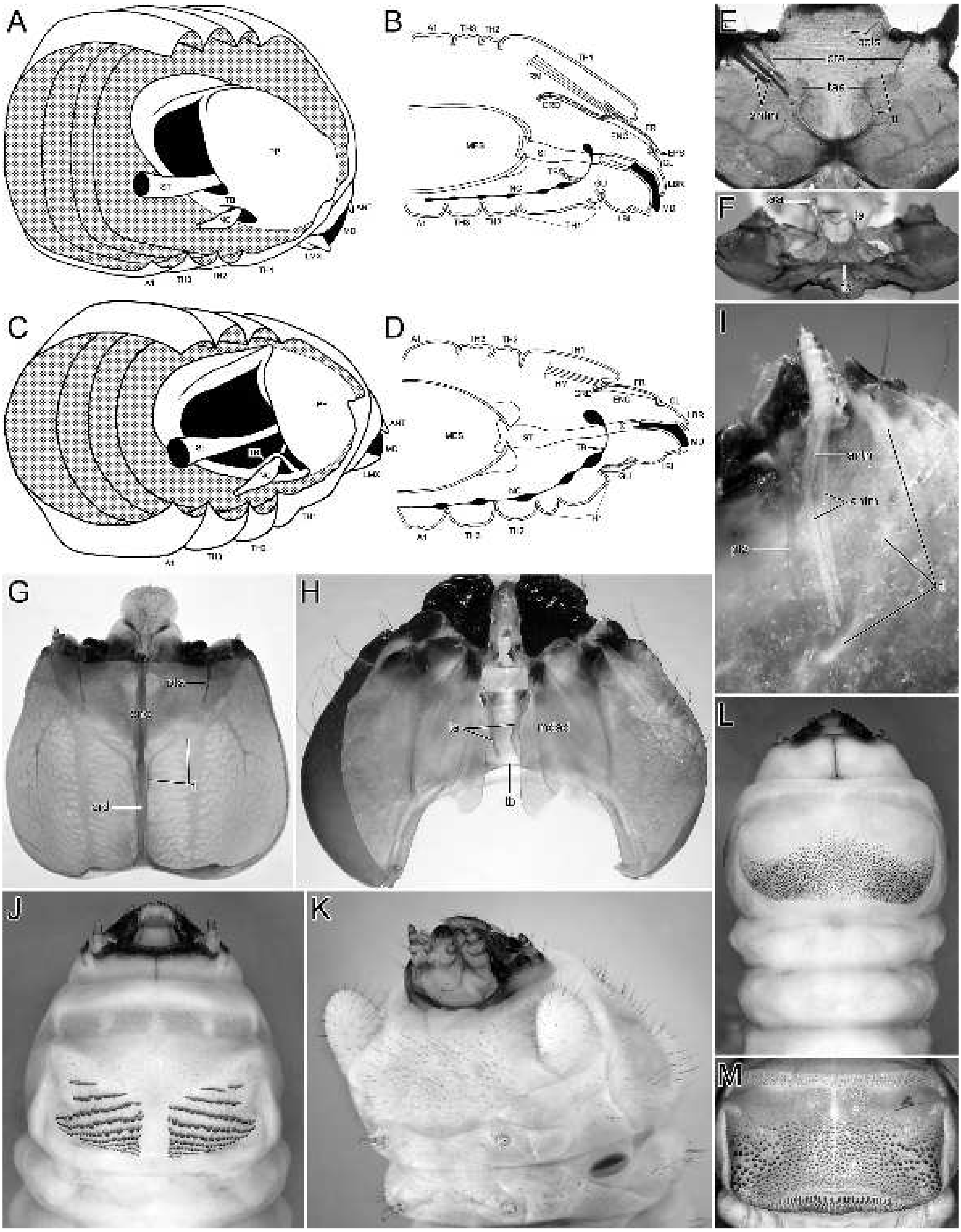


Fig. 2.4.27 Larval structures. A, C, Prioninae and Lepturinae, respectively, head, thorax and first abdominal segment, posterolateral view, diagrammatic (right lateral part of body wall removed to show relative position of some internal structures, more or less deeply retracted head inserted in membranous 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 maxillolabial 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

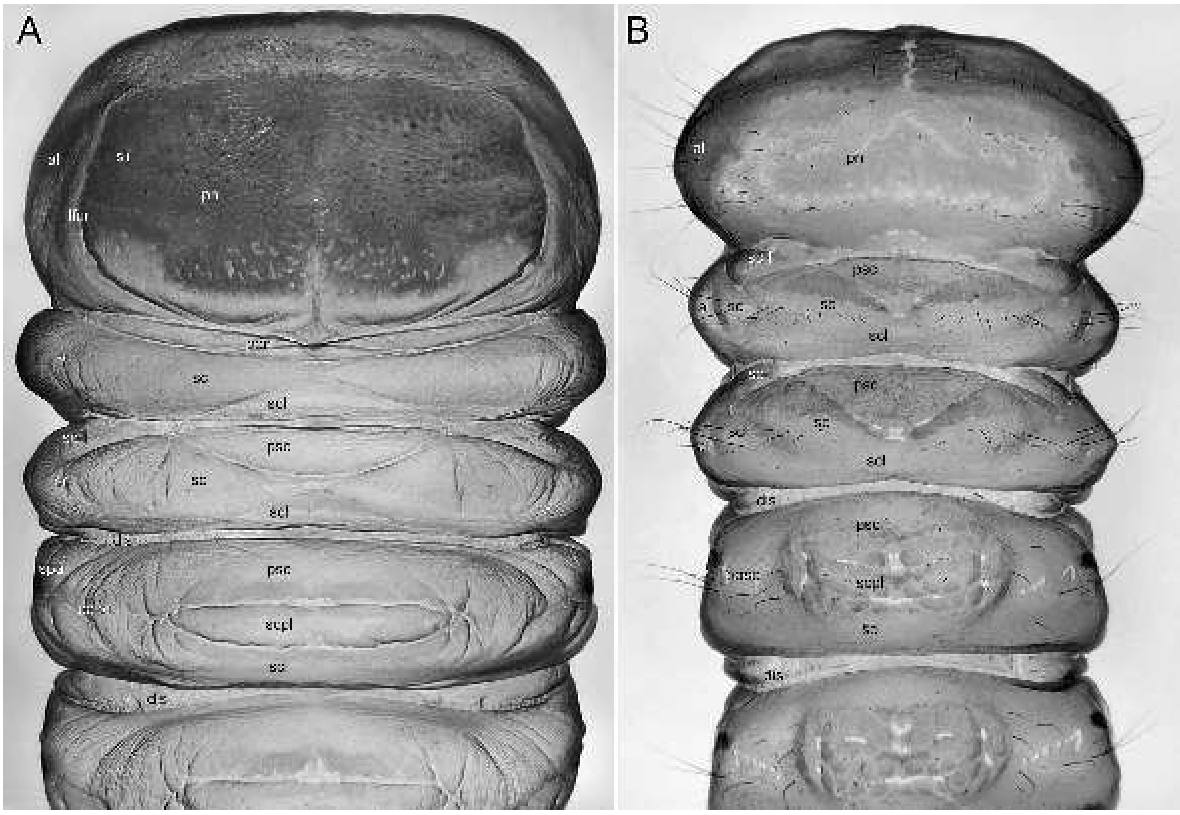
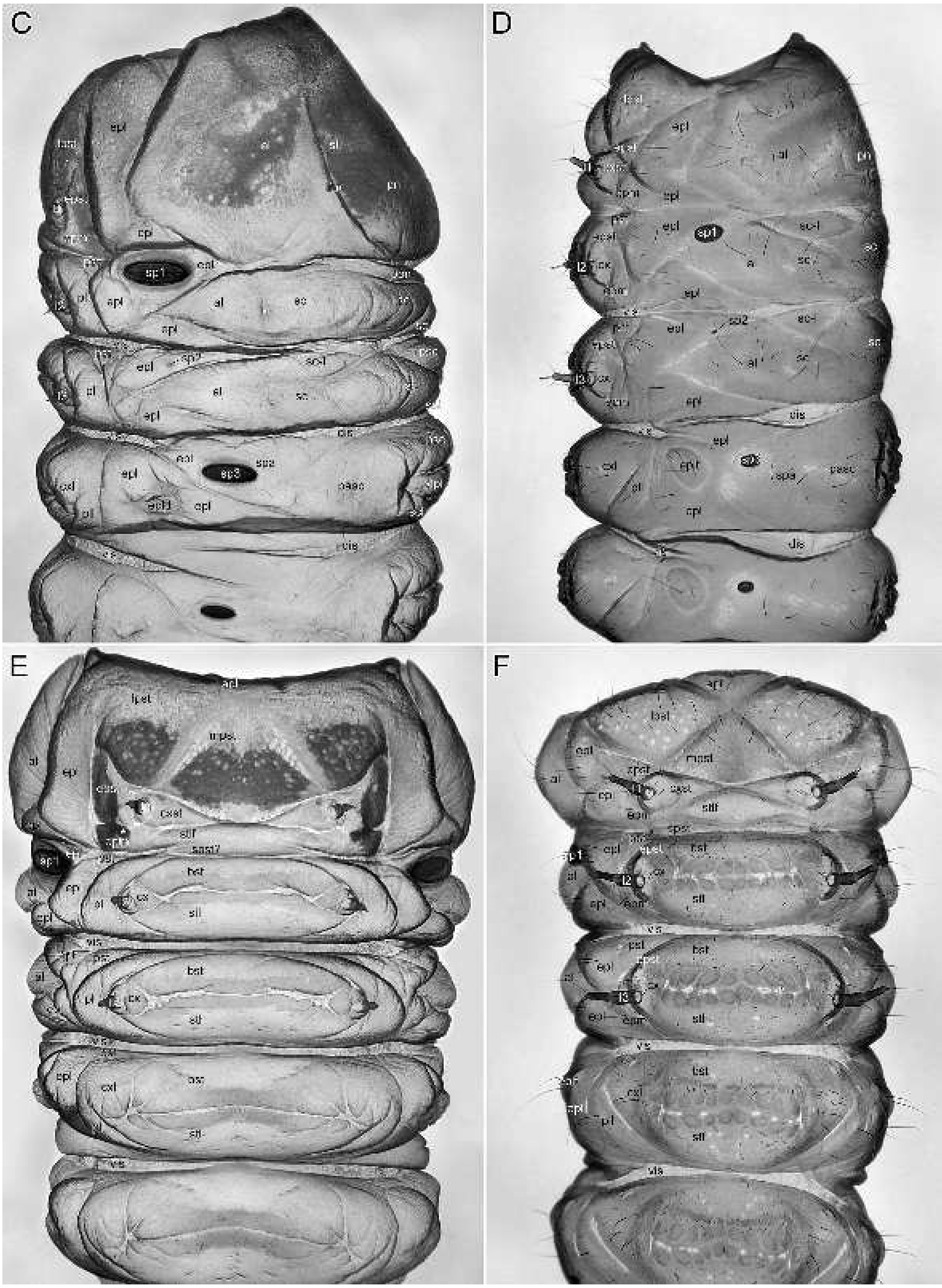


Fig. 2.4.28 (continued on opposite page) Larval thorax and abdomen, terminology, *Aegosoma scabricorne* (Prioninae; A, C, E) and *Oxymirus cursor* (Lepturinae; B, D, F) in dorsal (A, B), lateral (C, D), and ventral (E, F) views. al, alar lobe; apl, anterior presternal lobe; bst, basisternum; cx, coxa; 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 (Lepturinae 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

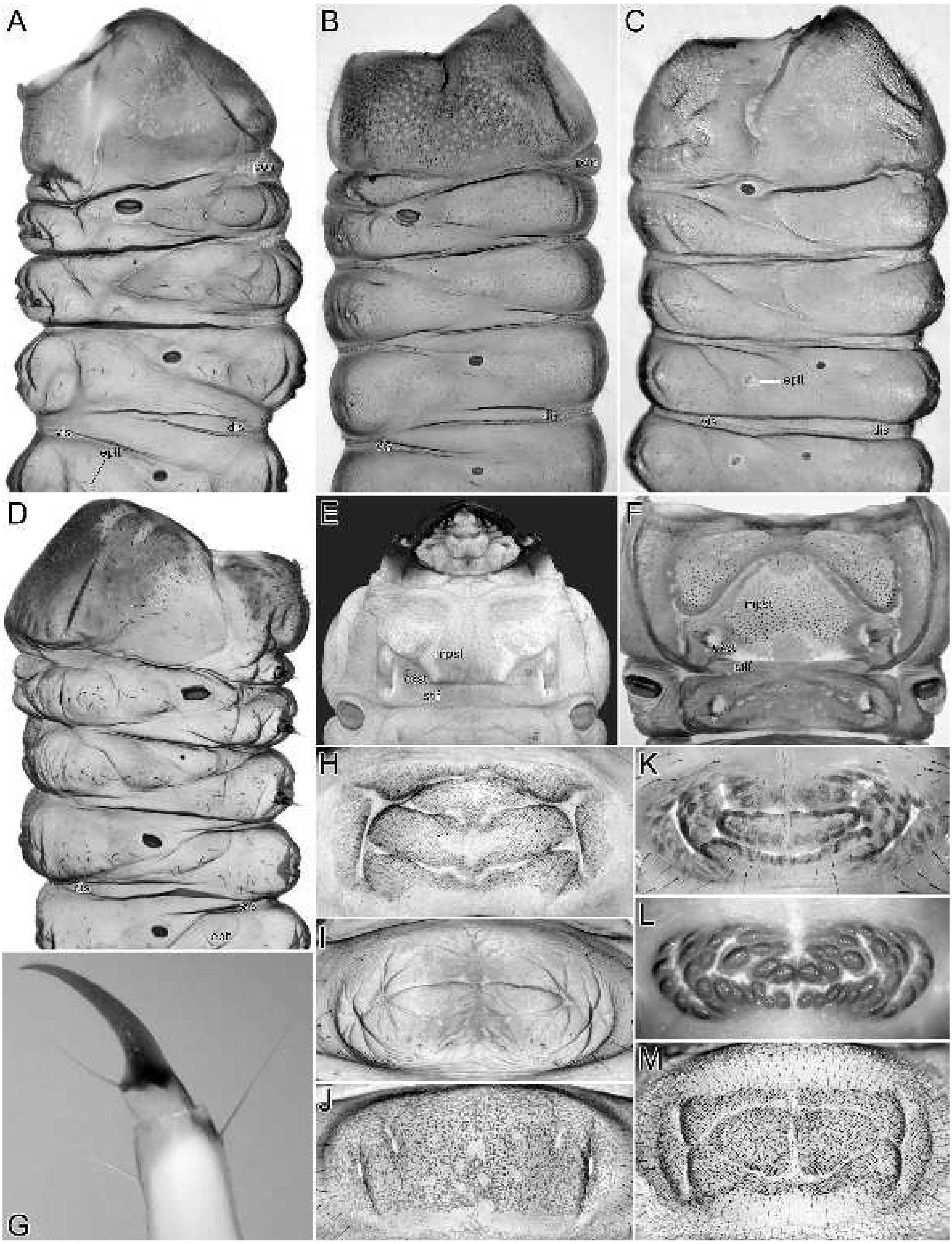


Fig. 2.4.29 Larvae. A–D, thorax and abdominal segments I and II, cleared cuticle stained with Chlorazol Black E, lateral view: A, *Artelida crinipes* (Dorcasominae); B, *Plagionotus* sp. (Cerambycinae); C, *Exocentrus adspersus* (Lamiinae); D, *Saphanus piceus* (Spondylidinae); E, *Rhaesus serricollis* (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 ambulatory 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 macroasperities, 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 anteroventrally 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 *Apiocephalus* (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 scutoscutellar 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

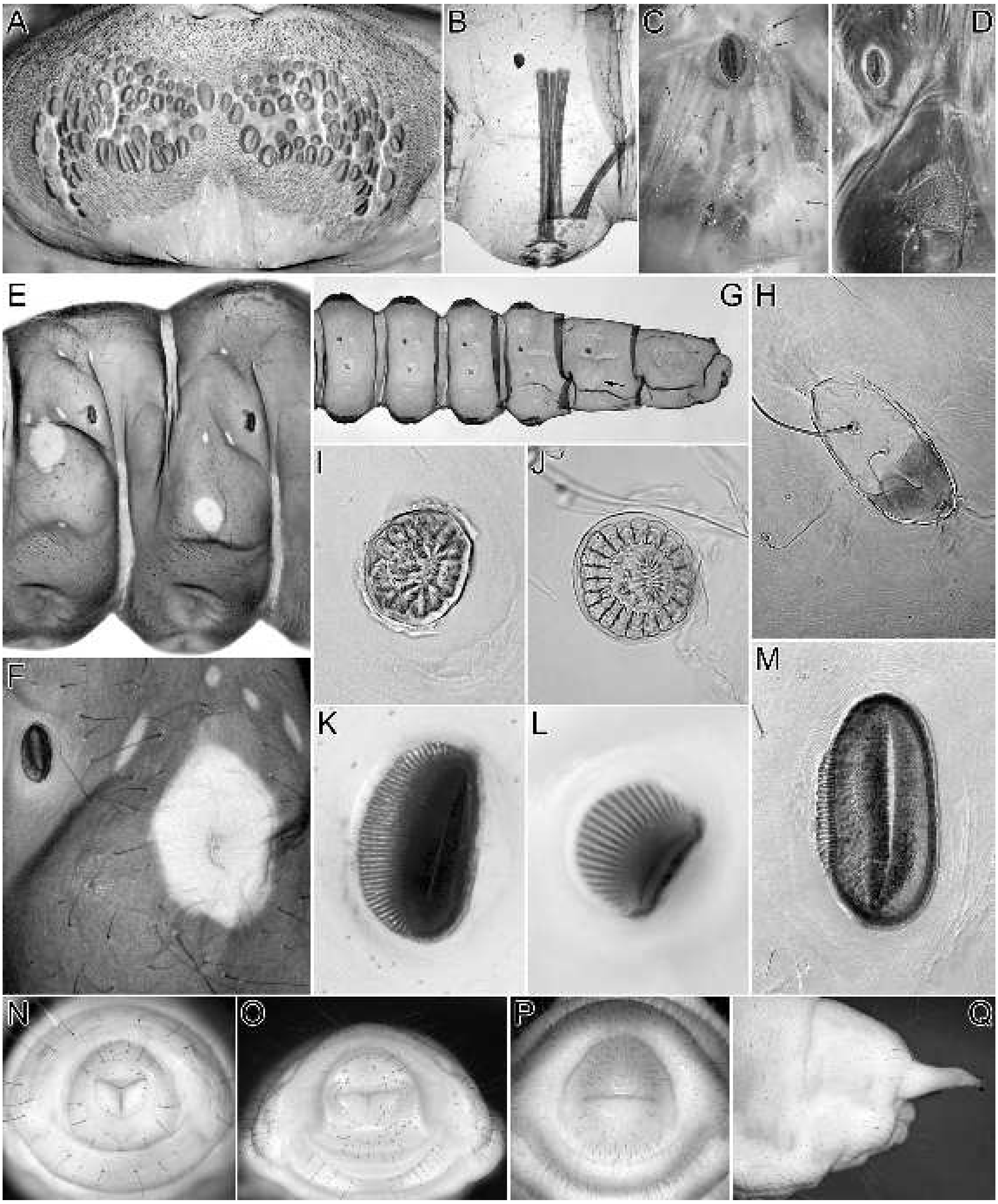


Fig. 2.4.30 Larval structures of Necydalinae (A, B), Lamiinae (C, G–J, N–P), Prioninae (D), Cerambycinae (E, F, K, L), Parandrinae (M), and Lepturinae (Q); A, D, E–H, cleared cuticular preparations stained with Chlorazol Black E. A, *Necydalis major*, ventral ambulatory ampulla 4 (showing two pairs of 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, *Callisphyris 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 *Apiocephalus* 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; Penteado-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 *Mallodon* 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 *Aegosoma* 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 Asemini 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

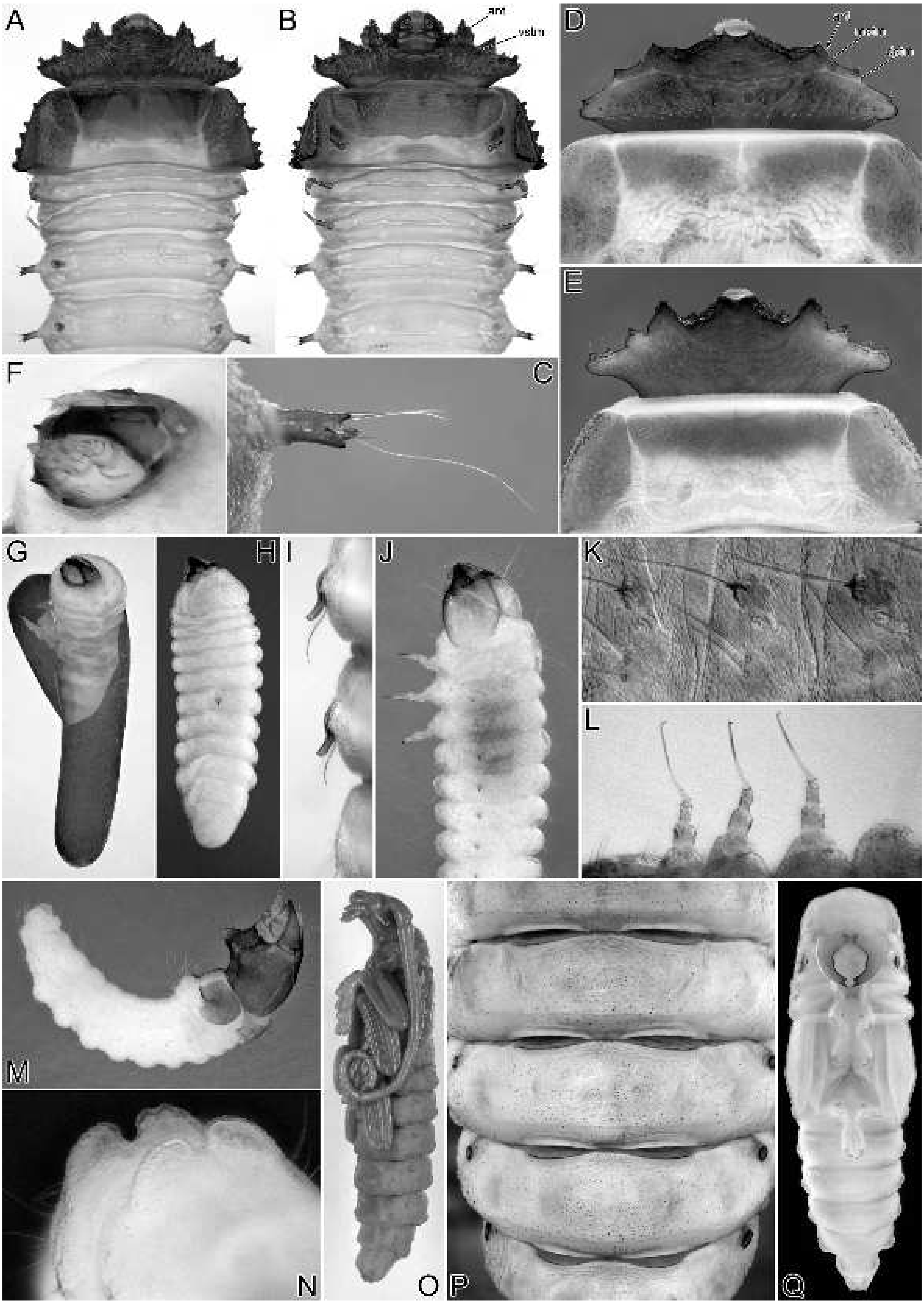


Fig. 2.4.31 A–E, aberrant larvae of the *Capnolymma-Apiocephalus* group of Lepturinae: A, *Capnolymma* sp. (Chiang Mai, Thailand), head, thorax and abdominal segments I and II of a cleared larva, dorsal view; B, same, ventral view; C, same larva, right epipleural process on abdominal segment VII bearing 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, *Mallodon* 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 subspherical 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 Asemini (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 Necydalinae, 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 nonprominent. 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

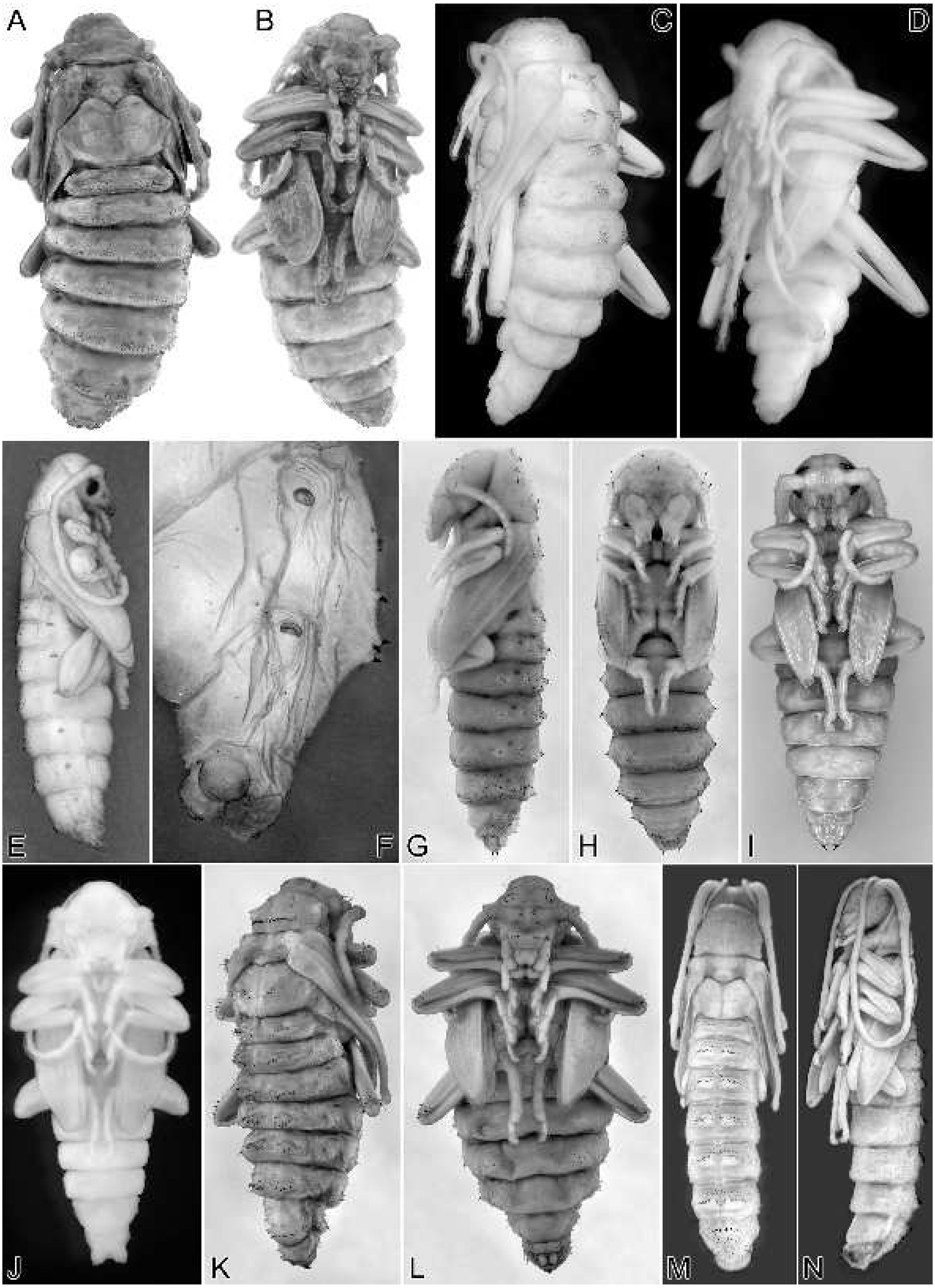


Fig. 2.4.32 Pupae of Dorcasominae (A–D), Cerambycinae (E, F); Spondylidinae (G–J), Lepturinae (K, L), and Lamiinae (M, N). A, *Dorcasomus gigas*, female, 38 mm, dorsal view; B, same, ventral view; C, *Tsivoka simplicicollis*, female, 19.5 mm, laterodorsal view; D, same, lateroventral view; E, *Pyrrhidium 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 cerambycoid 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 cerambycoid 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 cerambycoid 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 *Hypocephalus* 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 cerambycoid 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. Cerambycoid larvae (with the possibly secondary exception of *Vesperus*) lack an exposed coronal stem, which is present in some taxa of the chrysomelid assemblage.

Cerambycoid 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, nonphylogenetic 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 19th-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 (parallelled 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* + *Anoploderma* 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. *Anoploderma* + *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. *Anoploderma* + *Parandra* were characterized by the similar wing venation lacking the wedge cell, the male falciform mandibles (not in all Anoplodermatinae and Parandrinae and present in numerous Prioninae), and by the pentamerous tarsi (pseudotetramerous in males of some Anoplodermatinae). 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 defining 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 Sýkorová (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 crambycoids. 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 (Palaearctic, 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 *Apterocaulus* 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 *Macrodontia* 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*, *Toxeutes* 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*, *Prionoplus*, *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 r4, 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_{3+4} and CuA_2) and no CuA_1, or sometimes also CuA_2 missing; however, some taxa have CuA_1 (*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 pseudotetramerous 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 Aegosomatini); female abdominal segment VIII may be long and tubular and projecting from abdomen (some Aegosomatini). 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), *Sarmydus* 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 *Spinimegopis cingalensis* (White) (Gardner 1931 a, as *Megopis*) 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 *Eurypoda 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* Geoffroy (Duffy 1953), *Psephactus* (Oka 1977) or *Prinobius* Mulsant, but very large on segments III and IV in *Mallodon* (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 cerambycoid 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 r4, 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_{3+4} always unbranched; CuA_2 (if present) always connected basally with MP_{3+4} (i.e., CuA_1 present), in *Erichsonia* and more or less completely in some Parandrini also connected with the region of former wedge cell (i.e., CuA_{1+2} present); in some Parandrini, CuA_2 or the entire CuA_{1+2} 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_4 and AP_3 (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 (parallelled 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. morettoi* (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), *Papuandra* 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 parandrines among other on the absence of a distinct pretarsal empodium, but it is indistinct also in some Parandrini.

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 broadleaved 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; *Apterotoxitiades* 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_{3+4} unbranched, CuA_2 present to absent; higher number of veins may occur as individual variation); CuA_2, if present, mostly disconnected from CuA base (i.e., CuA_{1+2} absent or basally broadly interrupted) and sometimes also from MP_{3+4} (CuA_1 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 *Dorcasomus* (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 (*Dorcasomus*, 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 (*Dorcasomus*, 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 *Dorcasomus*; hypostoma and gula moderately long, usually glabrous. Metatentorial arms in Apatophyseini 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 *Dorcasomus* (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 *Dorcasomus* (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 lepturine 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. tenuisseni* 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*).

Palaearctic 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 *Trypogeus*, 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 *Apiocephalus*, *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 Pseudocephalini 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, *Gnathopraxithea 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 r4, latter crossvein with spur distinct to absent; wedge cell invariably absent, medial field usually with four or three regular free veins, seldom five, CuA_2, if present, usually remains connected with MP_{3+4} (CuA_1 present) but mostly disconnected from CuA stem (CuA_{1+2} 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 Necydalinae 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, Necydalinae 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* Frivaldsky) and Afrotropical (*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 ferus* (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	*Alocerus* Mulsant	2	0	0
	Schurmannia Sama	1	0	0
	Pectoctenus Fairmaire	3(2?)	0	0
	Anisarthron Dejean	2	0	0
Saphanini	*Saphanus* Audinet-Serville	2	0	0
	Drymochares Mulsant	3	0	0
	Michthisoma LeConte	0	0	1
Atimiini	*Oxypleurus* Mulsant	1(2?)	0	0
	Proatimia Gressitt	1	0	0
	Paratimia Haldeman	0	0	1
	Atimia Haldeman	6	0	7
Asemini	*Asemum* Eschscholtz	5	1	5
	Megasemum Kraatz	1	0	1
	Arhopalus Audinet-Serville	14	1	6
	Cephalallus Sharp	3	0	0
	Tetropium Kirby	13	0	13
	Nothorhina Redtenbacher	2	0	0
Spondylidini	*Spondylis* Fabricius	1	0	0
	Neospondylis Sama	0	0	2
	Scaphinus 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 r4; spur of r4 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_2 either connected with both neighboring veins (CuA_{1+2} and CuA_1 present), or CuA_{1+2} 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 spondylidine (Asemini + Spondylidini, the latter often an ingroup of the former) and saphanine (Anisarthrini + Saphanini + Atimiini). Within the branches, tribes are not well-defined (in particular the Anisarthrini and Asemini may be paraphyletic). The spondylidine 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 saphanine 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 1-2-2 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 spondylidine 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. chiloensis* 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 r4, latter sometimes with short spur; wedge cell absent; medial field mostly with five or four free veins; CuA_{1+2} branching off far proximally (about level of attachment of AA_3) and fused with MP_{3+4} (a separate CuA_1 is therefore absent); base of MP_{3+4} weakened to absent proximally to CuA_{1+2} 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 r4; only three free veins in medial region as MP_{3+4} is unbranched (but long basally, not reduced as in Necydalinae) and entire CuA_{1+2} 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 (*Apiocephalus 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 tunelling 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 Oxymirini. 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). Floricoly 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, *fide* Butovitsch 1939). However, floricoly or pollinophagy may occur (and remain unknown) in crepuscular or nocturnal species, 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; gulamentum 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_4 absent or reduced to basal stub; e.g., *Evodinus* LeConte, *Brachyta*, *Capnolymma*, *Apiocephalus*, some members of the *Acmaeops*-complex, *Centrodera sublineata* LeConte); CuA_{1+2} complete or only narrowly interrupted at base; CuA_1 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 (*Enoploderes*, *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 (*Enoploderes*) 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 *Apiocephalus* 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 *Apiocephalus* 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 facetted 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 (*Rhamnusium*, *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 Encyclopini, 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), *Caraphia 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_3 and MP_4, CuA_{1+2} only narrowly interrupted at base), pretentorial pits are very large, pre- and metatentorial 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
Necydalis	NEI	NEI	NEI	NEE	NEE	NEI	NEE	NEE	NEE	NEE	NEE
(Pseudo)Xylosteus	LEP		XYL	XYL		LEP	XYL			XYL	XYL
Leptorhabdium	LEP		XYL	XYL		LEP	XYL			XYL	XYL
Centrodera decolorata	LEP			XYL		LEP					RHA
Teledapus										XYL	
Oxymirus		RHA	RHA	OXY			OXY	STE		OXY	
Anthophylax	LEP			OXY		LEP					RHA
Rhamnusium		RHA	RHA	RHM			RHM	RHA		RHM	
Enoploderes	LEP			RHM	RHA	LEP	ENO			RHA	ENC
Sachalinobia	LEP	RHA		SAC	RHA	LEP			XYL	SAC	SAC
Xenoleptura				SAC						LEP	
Caraphia					LEP				XYL	LEP	
Centrodera spurca	LEP			RHA		LEP					RHA
Rhagium	LEP	RHA	RHA	RHA	RHA	LEP	RHA	RHA	RHA	RHA	RHA
Stenocorus	LEP	RHA	RHA	RHA	RHA	LEP	RHA	STE	STE	RHA	RHA
Pachyta	LEP	RHA	RHA	RHA	RHA	LEP	RHA	STE	STE	RHA	RHA
Evodinus	LEP	RHA	RHA	RHA	RHA	LEP	RHA	STE	STE	RHA	RHA
Gaurotes sensu lato	LEP	RHA	RHA	RHA	RHA	LEP	RHA	STE	STE	RHA	RHA
Acmaeops	LEP	RHA	RHA	RHA	RHA	LEP	RHA	STE	STE	RHA	RHA
Desmocerus	DES			RHA		DES					DES
Encyclops	LEP	XYL		RHA	RHA	LEP			STE	ENC	ENC
Pidonia	LEP	RHA	RHA	RHA	RHA	LEP	RHA		STE	RHA	RHA
Cortodera	LEP	LEP	LEP	RHA		LEP	LEP	LEP		RHA	RHA
Grammoptera	LEP	LEP	LEP	RHA		LEP	LEP	LEP	STE	LEP	LEP
Pedostrangalia		LEP	LEP	LEP	LEP		LEP	LEP	LEP	LEP	
Etorofus	LEP	LEP	LEP	LEP	LEP	LEP	LEP	LEP	LEP	LEP	LEP
Lepturobosca	LEP	LEP	LEP	LEP	LEP	LEP	LEP	LEP	LEP	LEP	LEP
Judolia	LEP	LEP	LEP	LEP	LEP	LEP	LEP	LEP	LEP	LEP	LEP
Anastrangalia	LEP	LEP	LEP	LEP	LEP	LEP	LEP	LEP	LEP	LEP	LEP
Stictoleptura	LEP	LEP	LEP	LEP	LEP	LEP	LEP	LEP	LEP	LEP	LEP
Leptura	LEP	LEP	LEP	LEP	LEP	LEP	LEP	LEP	LEP	LEP	LEP
Strangalia	LEP	LEP	LEP	LEP	LEP	LEP	LEP	LEP	LEP	LEP	LEP

Some genera were included under different names (*Enoploderes* = *Pyrotrichus*; *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, Encyclopini; ENO, Enoploderini (*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, Homonoeini, 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 usually simple, never pectinate or flabellate; very rarely several flagellomeres broad and flattened but then this concerns both sexes (*Hemicladus* 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 r4; spur on latter crossvein short to absent; wedge cell absent; medial field in plesiomorphic situations with five free veins reaching wing margin; CuA_{1+2} stem absent (probably missing in the groundplan) and CuA_2 only connected with MP_{3+4} (i.e., CuA_1 present), which thus appears to have three branches (Fig. 2.4.16 M); the common MP_{3+4} 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 disproportionally 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, Tetropini and Astathini, Dorcaschematini, or a cluster of tribes around Lamiini but excluding some Monochamini: *Mecynippus* Bates, *Psacothea* 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 mediopresternal 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 *Falsohomaemota* 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).

Acknowledgments

For providing material, information, or commenting upon drafts of this chapter we are grateful to K. Adlbauer (Graz, Austria), J. E. Barriga (Curicó, Chile), Amy Berkov (Department of Biology, The City University, and Division of Invertebrate Zoology, American Museum of Natural History, New York), M. L. Danilevsky (A. N. Severtsov Institute of Ecology and Evolution, Russian Academy of Sciences, Moscow), Stephanie Haddad (Department of Biological Sciences, University of Memphis), J. Hájek (Department of Entomology, National Museum, Prague), C. Holzschuh (Villach, Austria), R. Iwata (Department of Forest Science and Resources, Nihon University, Tokyo), D. Kasatkin (Centre of Plant Quarantine, Rostovon-Don, Russia), S. Laplante (Agriculture and Agri-Food, Ottawa), Meiying Lin (Institute of Zoology, Chinese Academy of Sciences, Beijing), S. W. Lingafelter (Systematic Entomology Laboratory, National Museum of Natural History, Washington, DC), U. R. Martins (Museum of Zoology, University of São Paulo), M. A. Monné (National Museum, Federal University of Rio de Janeiro), G. Monteith (Queensland Museum, Brisbane), K. Murakami (Tokushima, Japan), D. S. Napp (Federal University of Paraná, Curitiba), E. H. Nearns (National Museum of Natural History, Washington, DC), N. Ohbayashi (Miura, Japan), the late P. Pokluda (South Bohemian University, Ceske Budejovice), G. Sama (Cesena, Italy), A. Santos-Silva (Museum of Zoology, University of São Paulo), S. A. Ślipiński and H. Escalona (CSIRO, Canberra), E. Vives (Terrassa, Spain). For providing photographs of adults we are grateful to K. Adlbauer, W. Bi (Shanghai, China), G. Biffi (Museum of Zoology, University of São Paulo), Lynette Clennell (Durban, RSA.), M. L. Danilevsky, M. Hoskovec (Institute of Organic Chemistry and Biochemistry, Czech Academy of Sciences, Prague), I. Jeniš (Náklo, Czech Republic), D. Kasatkin, J. Kurzawa

(Tomaszow Mazowiecki, Poland), S. W. Lingafelter, N. P. Lord (Department of Biology, University of New Mexico, Albuquerque), E. H. Nearns, G. Sama, A, Santos-Silva, V. Seichert (Prague, Czech Republic), E. Vives, S. Ziarko (Poturzyn, Poland), CSIRO, Canberra (photographs by Cate Lemann, S. A. Ślipiński, and H. Escalona), Museum Victoria, Melbourne (K. Walker), the Natural History Museum, London (M. V. L. Barclay), and the Queensland Museum, Brisbane (photograph by J. Wright). Copyright for those photographs remains with their providers. All other photographs © P. Svacha who acknowledges support from the Institute of Entomology (RVO:60077344).

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