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## Arthropoda: Insecta

Editors Niels P. Kristensen & Rolf G. Beutel

**DE GRUYTER**

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(Volume Editors)

# **Coleoptera, Beetles**

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Morphology and Systematics  
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*Scientific Editors*

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## 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 sanzii* 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

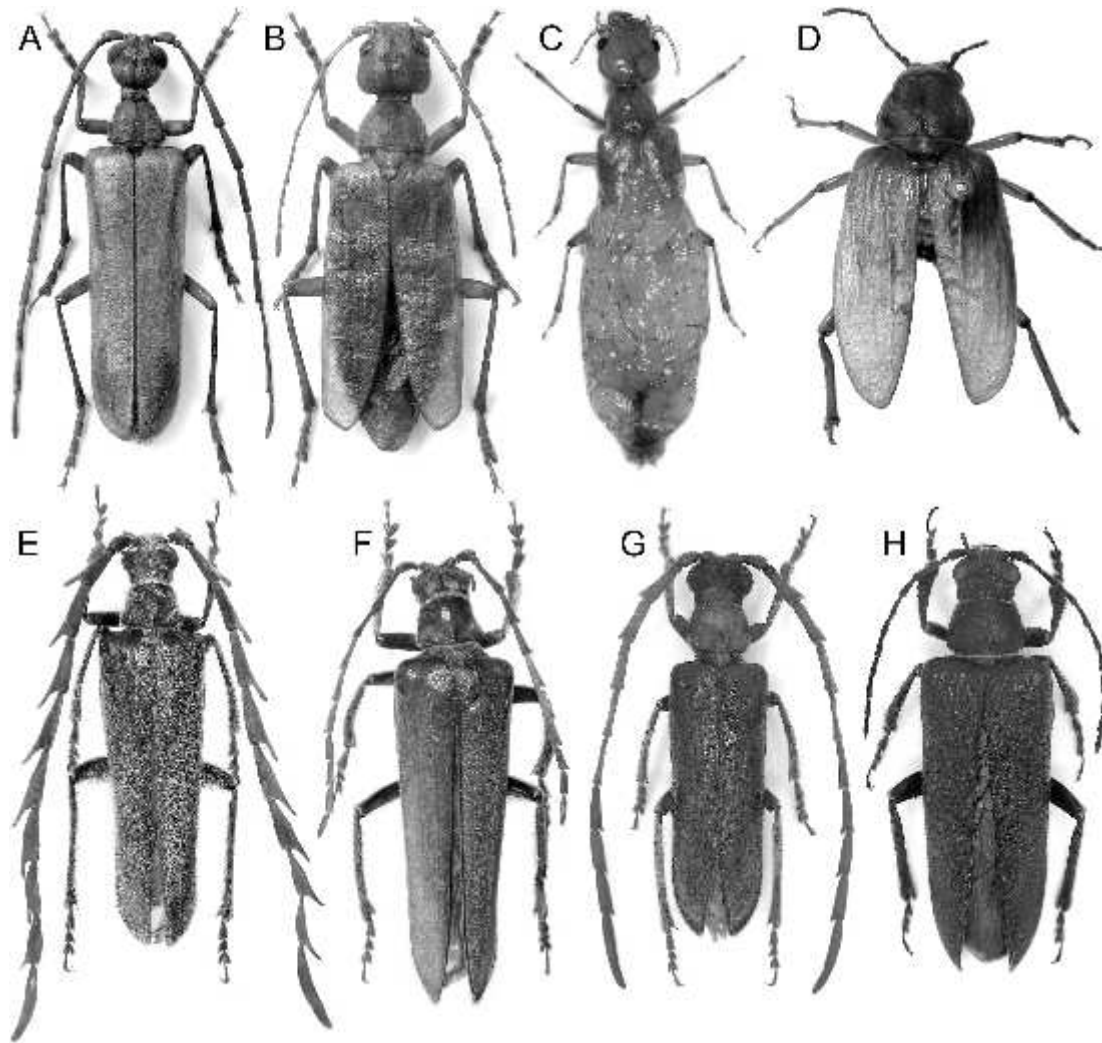


Fig. 2.1.1 Adults of Vesperinae (A–C) and Philinae (D–H), dorsal view. A, *Vesperus strepens* (Fabricius), male, 21 mm (© I. Jeniš); B, *V. strepens*, female, 23 mm (© I. Jeniš); C, *V. jertensis* Bercedo & Bahillo, female with incomplete antennae, 17.5 mm (from Calvo Sánchez 2008, © F. Calvo Sánchez); D, *Heterophilus* sp., one of two known females (from Lin & Bi 2011, © Meiyong Lin); E, *Spiniphilus spinicornis* Lin & Bi, male, 26 mm (from Lin & Bi 2011, © Meiyong Lin); F, *S. spinicornis*, female, 37 mm (from Lin & Bi 2011, © Meiyong 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 X<sub>y</sub> 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 XY<sub>1</sub>Y<sub>2</sub> 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 faceted; 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 post-clypeal projection in some Anoplodermatinae. Various 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 prosthema 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.

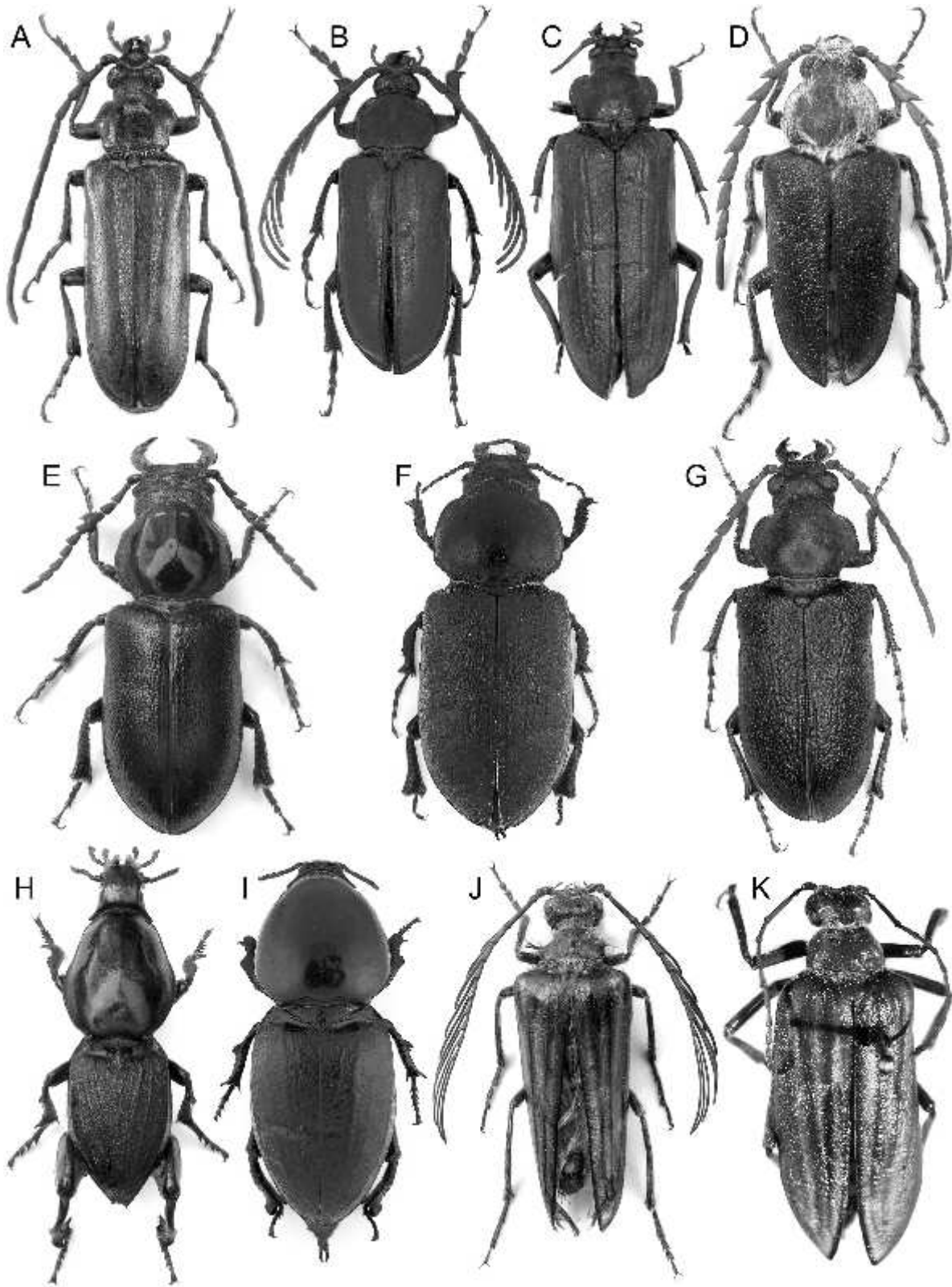


Fig. 2.1.2 Adults of Anoplodermatinae (A–I) and Vesperoctenini (J, K), dorsal view. A, *Mysteria minuta* Dias, male, 15.5 mm; B, *Pseudopathocerus humboldti* (Lameere), male, 21 mm; C, *Pathocerus wagneri* Waterhouse, damaged female, 49 mm; D, *Sypilus orbignyi* Guérin-Méneville, male, 19 mm (© I. Jeniš); 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).

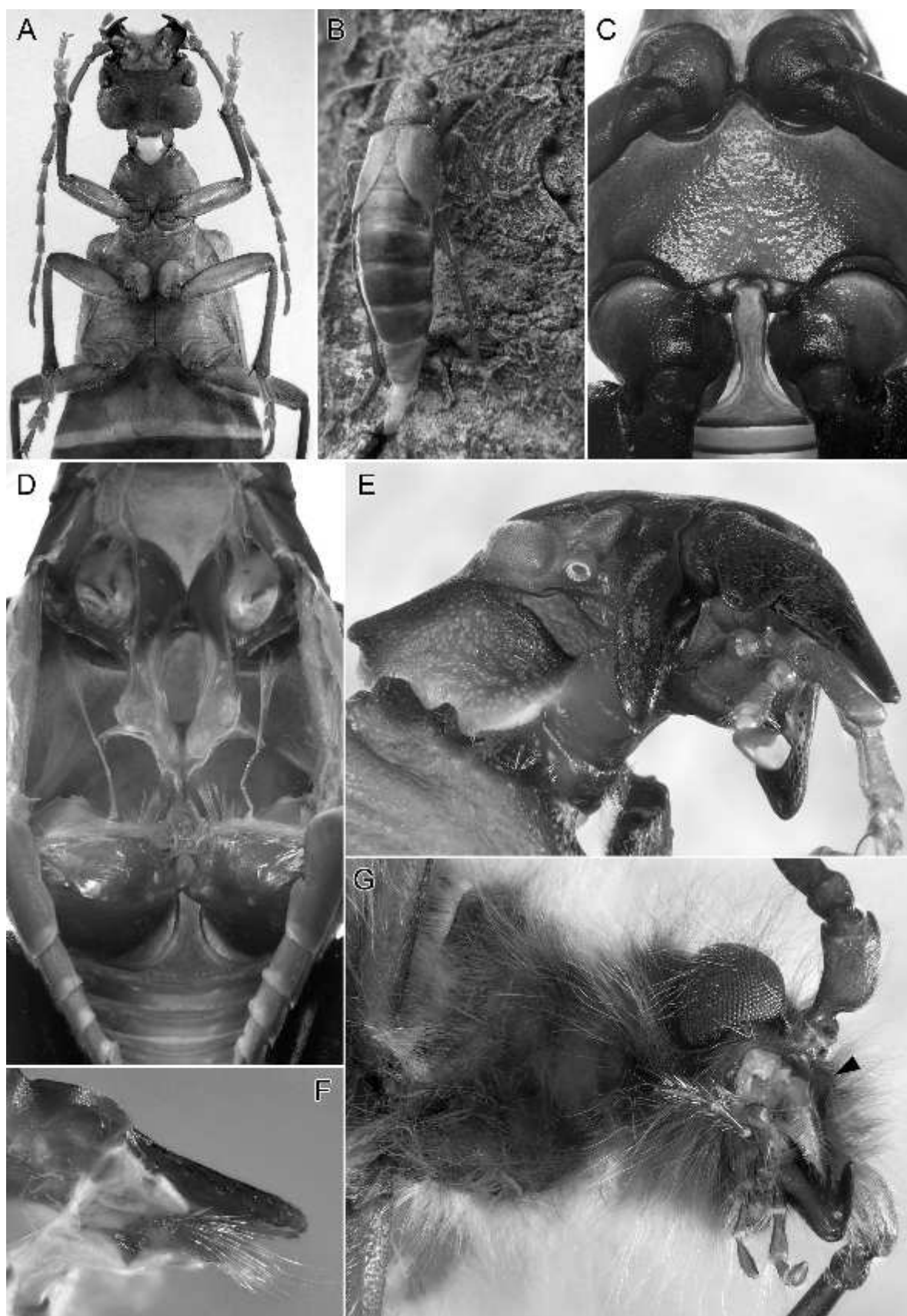


Fig. 2.1.3 A, *Vesperus strepens*, female, ventral view; B, *Mantitheus pekinensis* Fairmaire, female ovipositing in bark of a fruit tree (© E. Kučera); C, *Hypocephalus armatus*, male, pterothorax and base of abdomen, ventral view; D, *H. armatus*, male, pterothoracic endoskeleton, dorsal view; E, *H. 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).



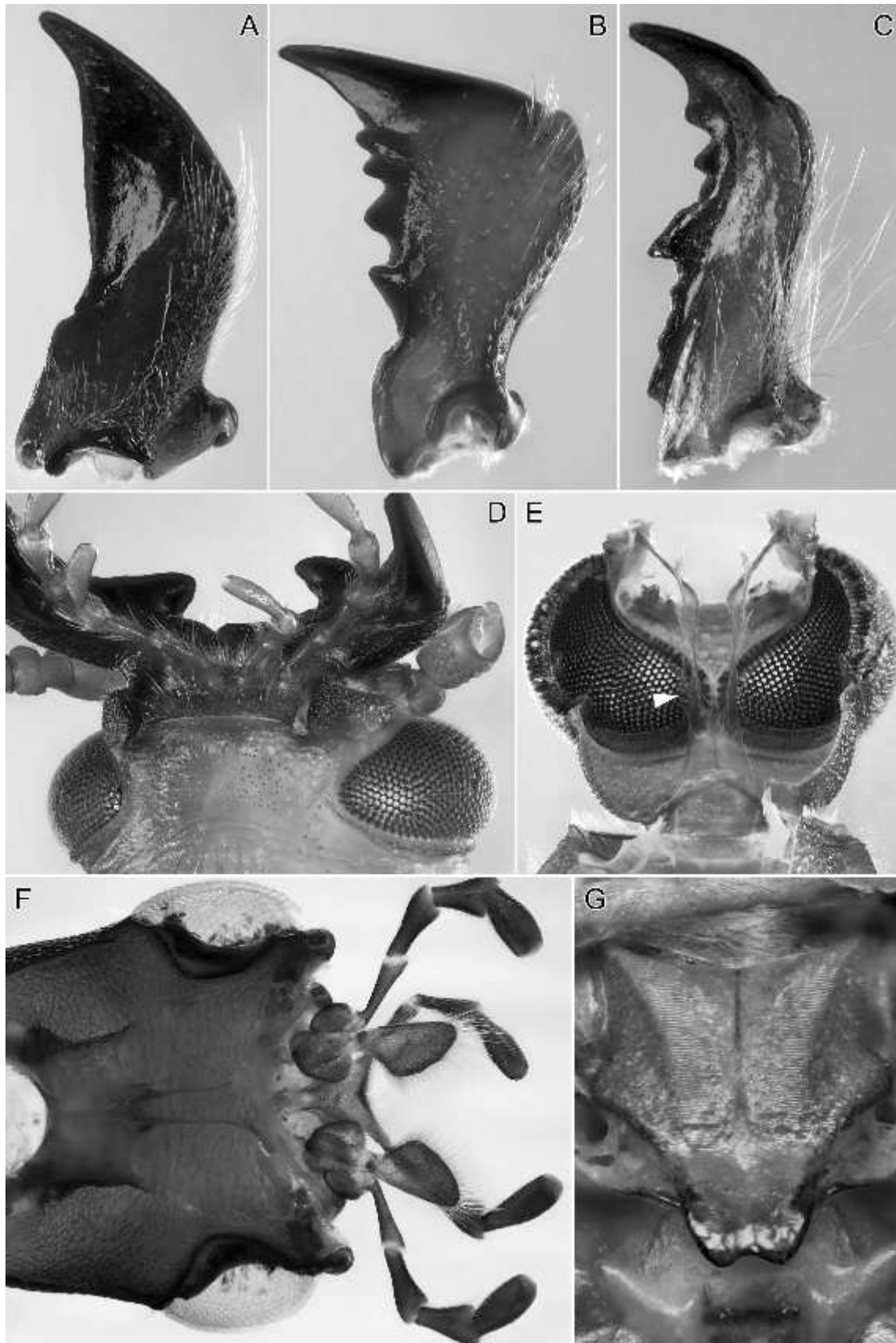


Fig. 2.1.4 A, *Philus antennatus*, female, right mandible, dorsal view; B, *Pseudopathocerus humboldti*, male, right mandible, dorsal view; C, *Vesproctenus flohri*, male, right mandible, dorsal view; D, *Anoploderma breueri*, male, anterior head, lateroventral view; E, *Pathocerus wagneri*, male, ventral 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 conicollis 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<sub>3+4</sub> or reduced MP<sub>3</sub>); 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*

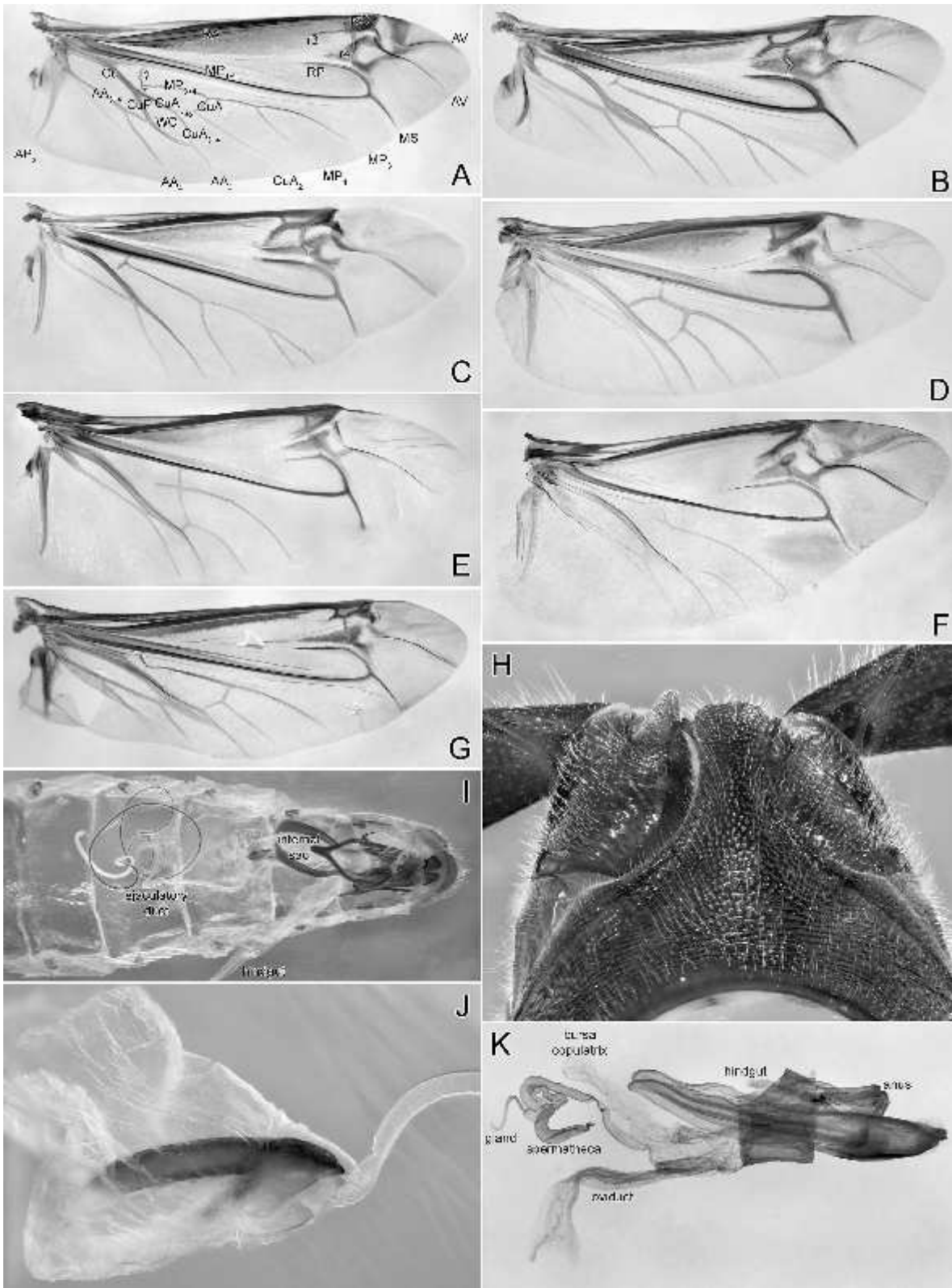


Fig. 2.1.5 A–G, right wing: A, *Philus pallescens* Bates, female; B, *Vesperus conicicollis hispalensis*, male; C, *V. strepens*, male; D, *Mysteria minuta*, male; E, *Pathocerus wagneri*, male; F, *Migdolus fryanus*, male; G, *Vesperoctenus flohri*, male; H, *Philus antennatus*, female, procoxae and 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<sub>3+4</sub>-cu; ?, a vein of uncertain homology (either a crossvein or base of MP<sub>3+4</sub>).

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

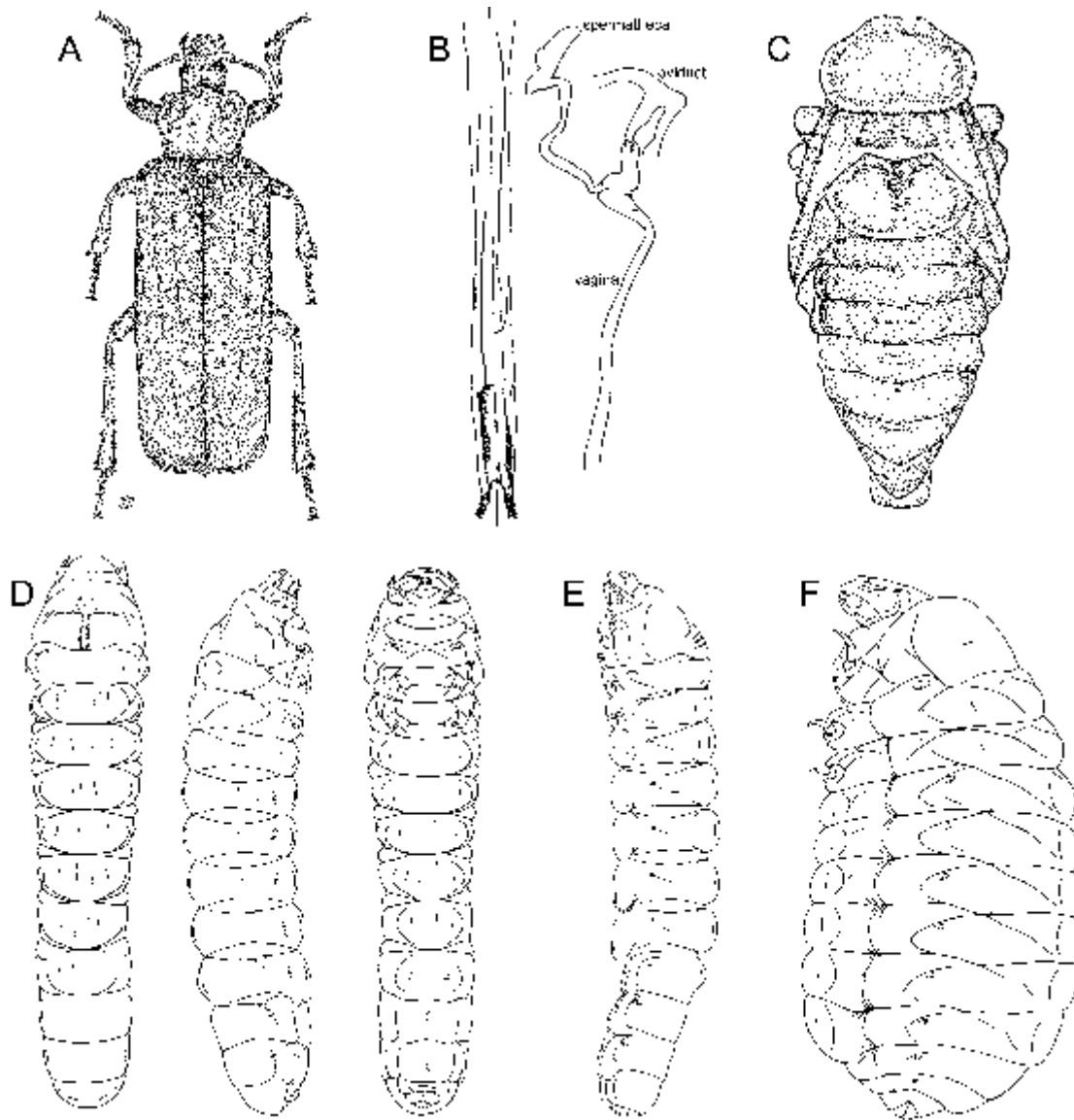


Fig. 2.1.6 A, *Mysteria darwini* (Lameere), female, dorsal view, 37 mm (from Dias 2004); B, *Vesperus strepens*, female, ovipositor (left half ventral view, right half dorsal view) and internal genitalia (from Saito 1990); C, *Migdolus fryanus*, pupa, dorsal view (from Costa *et al.* 1988); D, *Philus 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 prosthema; 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

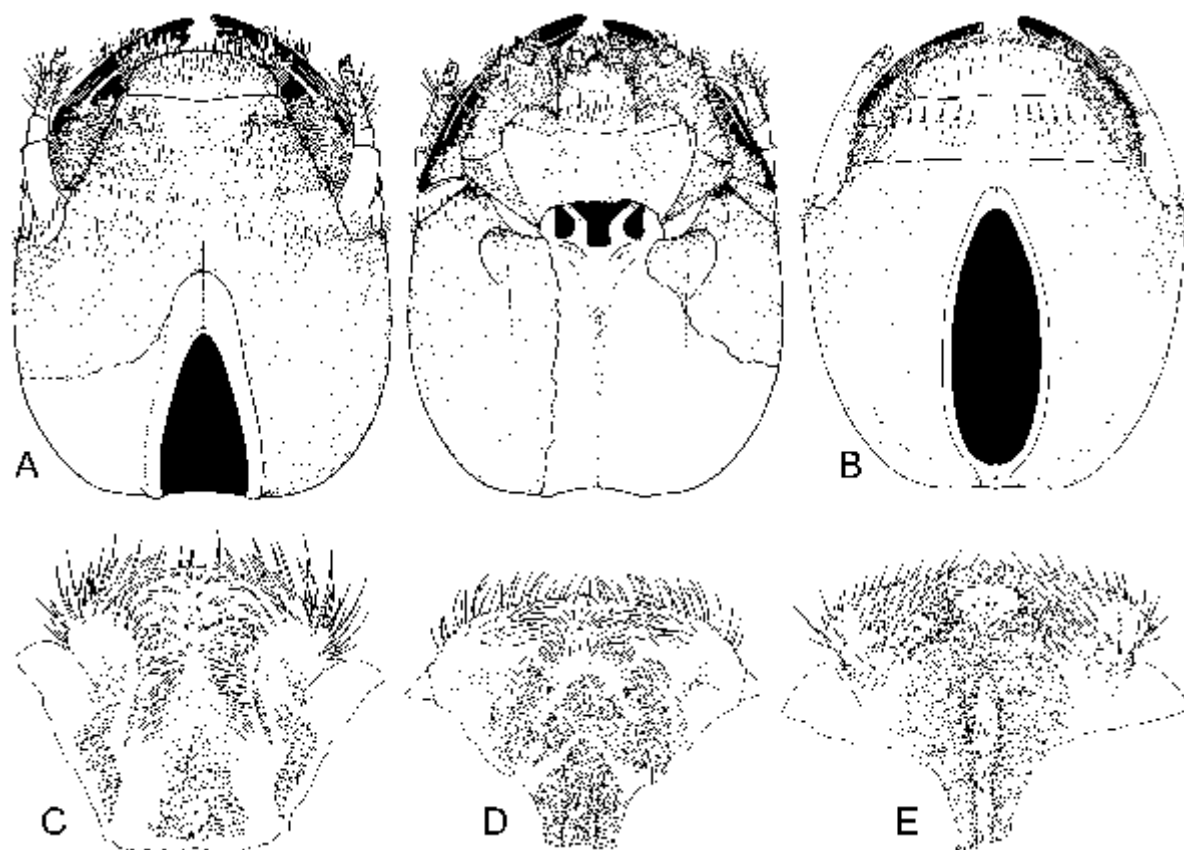


Fig. 2.1.7 Larvae. A, *Philus antennatus*, head, dorsal (left) and ventral view (right); B, *Migdolus fryanus*, head, dorsal view; C, *Vesperus luridus* (Rossi), epipharynx; D, *Philus antennatus*, epipharynx; E, *Migdolus fryanus*, epipharynx (all figures from Svacha *et al.* 1997).

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



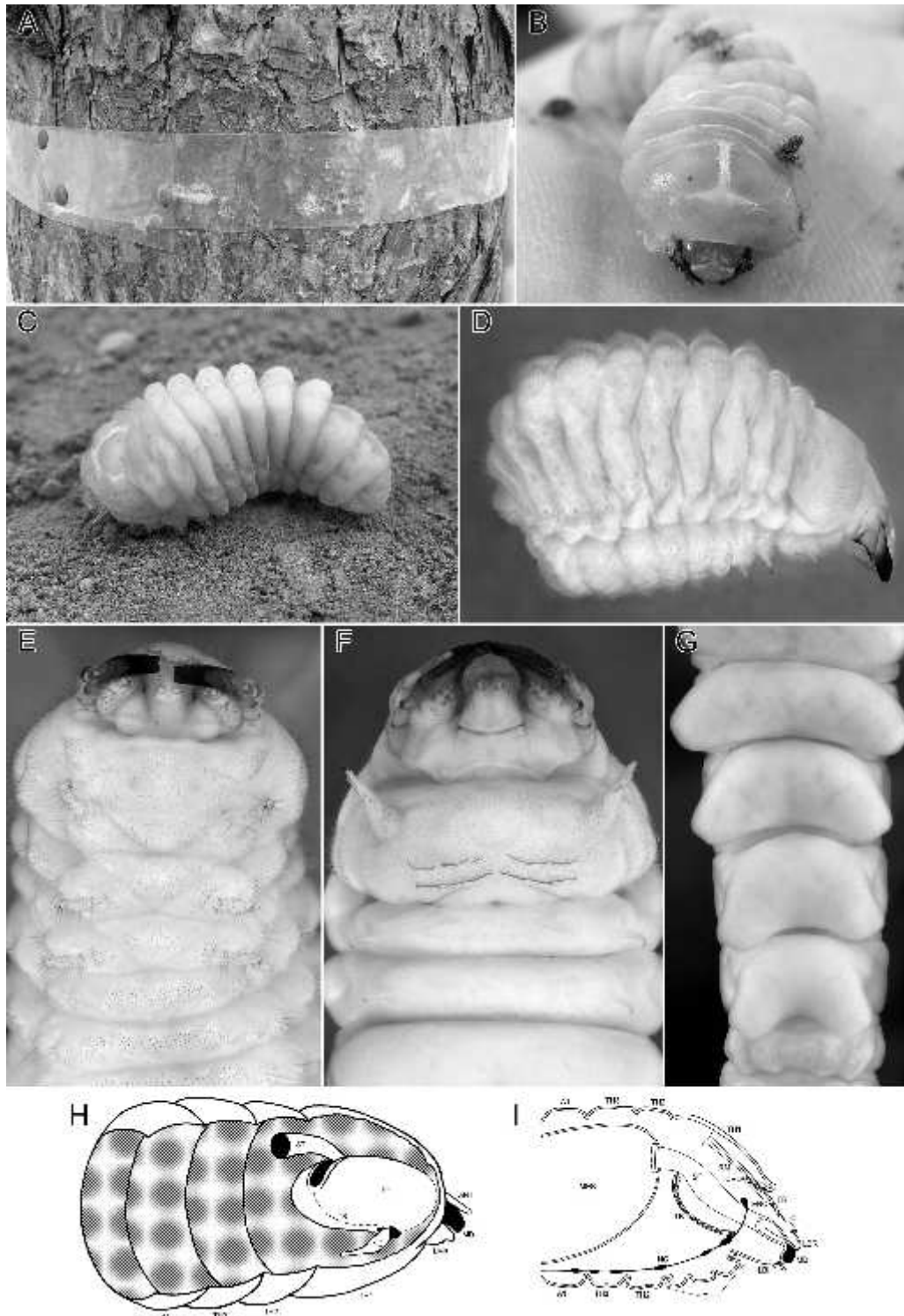


Fig. 2.1.8 A, *Mantispeckia pekinensis*, hatched egg batches under protective plastic band on a pine tree in Beijing Botanical Garden (© W. Bi); B–I, larvae: B and C, *M. pekinensis*, living specimen, anterior (B) and lateral view (C) (© W. Bi); D, *Vesperus sanzii* Reitter, lateral view; E, *V. sanzii*, 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.

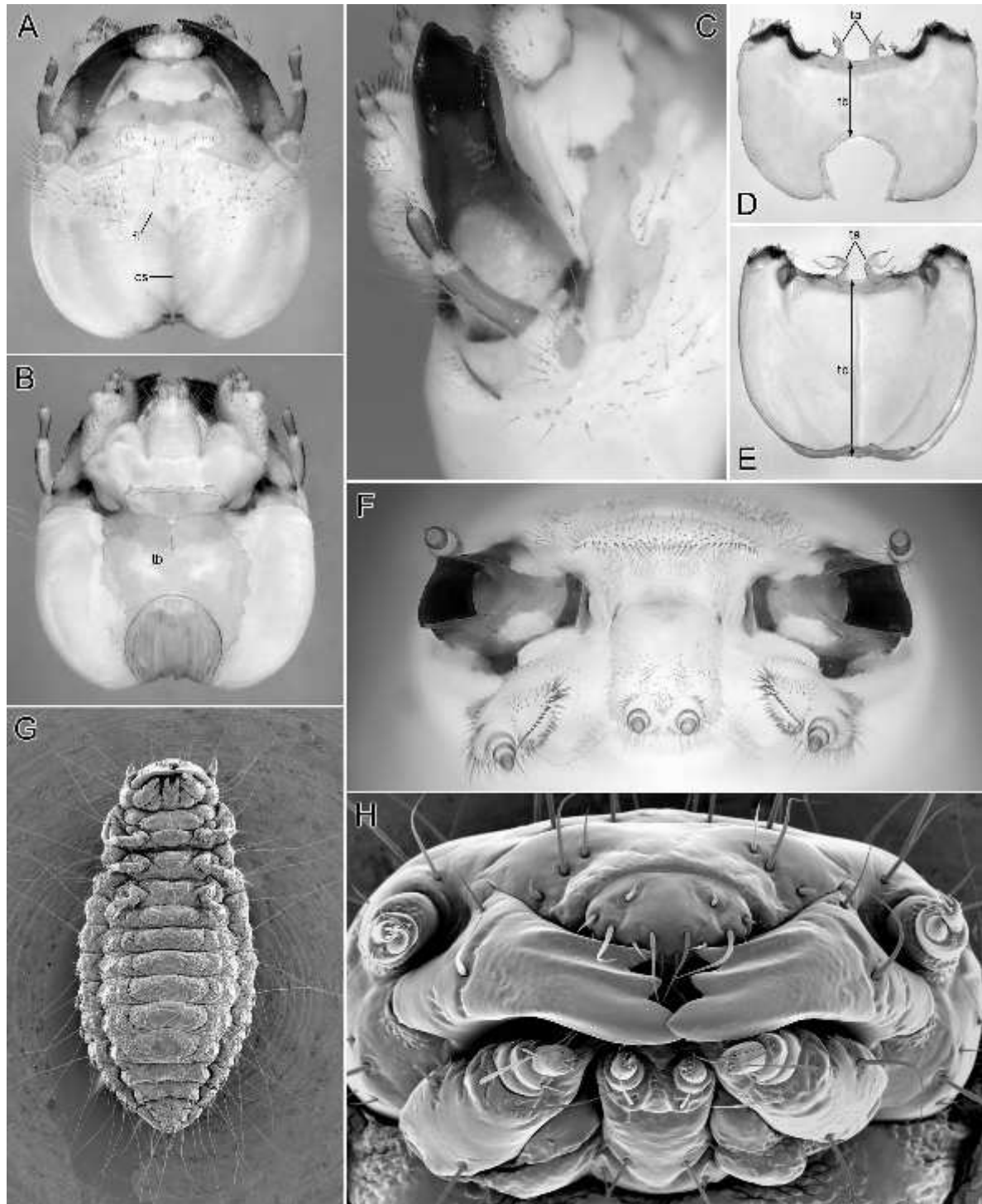


Fig. 2.1.9 Larvae. A, *Vesperus sanzii*, head, dorsal view; B, *V. sanzii*, head, ventral view; C, *V. sanzii*, head, anterolateral view; D, *V. luridus*, ventral half of cranium, dorsal view (tentorial arms on anterior margin of tentorial bridge cut to short stubs); E, *Migdolus fryanus*, dttto.; F, *Mantiitheus 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



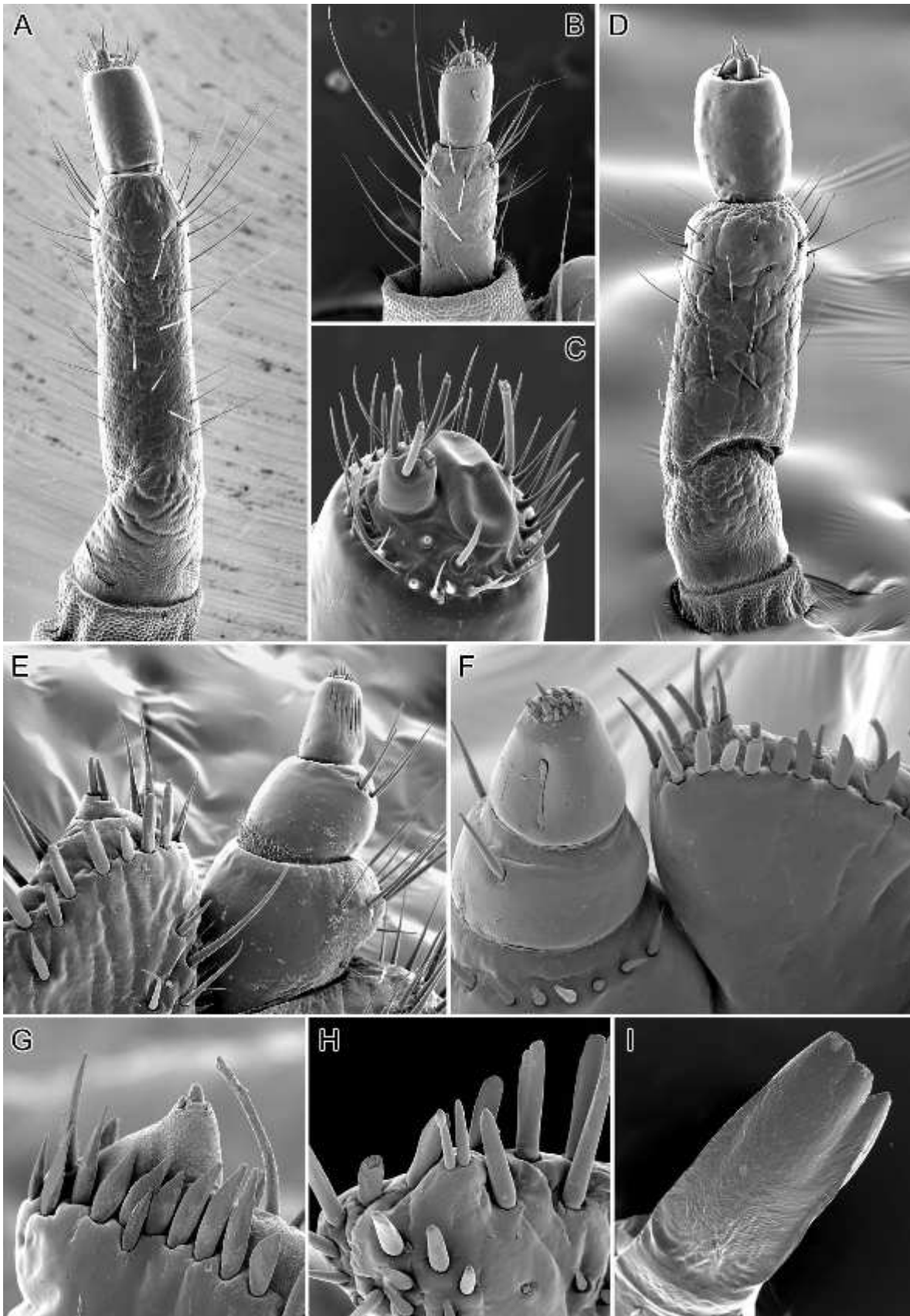


Fig. 2.1.10 Larvae, SEM. A, *Philus antennatus*, right antenna fully protracted, dorsal view; B, *P. antennatus*, left antenna half-retracted, dorsal view; C, *P. antennatus*, same specimen as in A, antennal apex, anterolateral view; D, *Heterophilus punctulatus* Chiang, Chen & Zhang, left antenna fully 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).

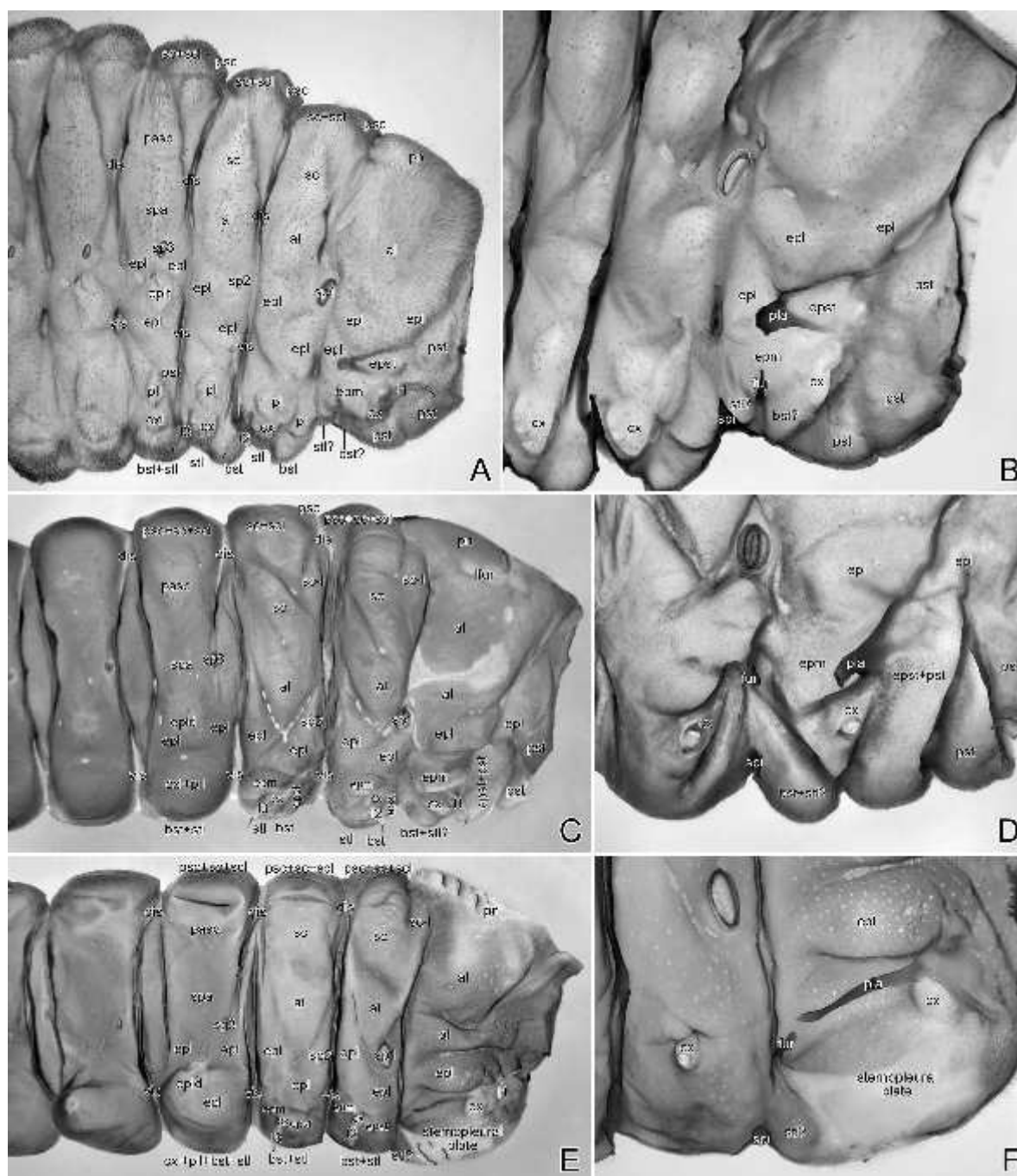


Fig. 2.1.11 Larvae, anterior part of body, cleaned cuticle stained with Chlorazol Black E. A, *Vesperus luridus*, right half of thorax and abdominal segments I and II, lateral view; B, *V. luridus*, left half of thorax, mesal view; C, *Philus antennatus*, right half of thorax and abdominal segments I 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; 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 sanzii* 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 zantennatus* 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 sanzii*, 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 cerambycid 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

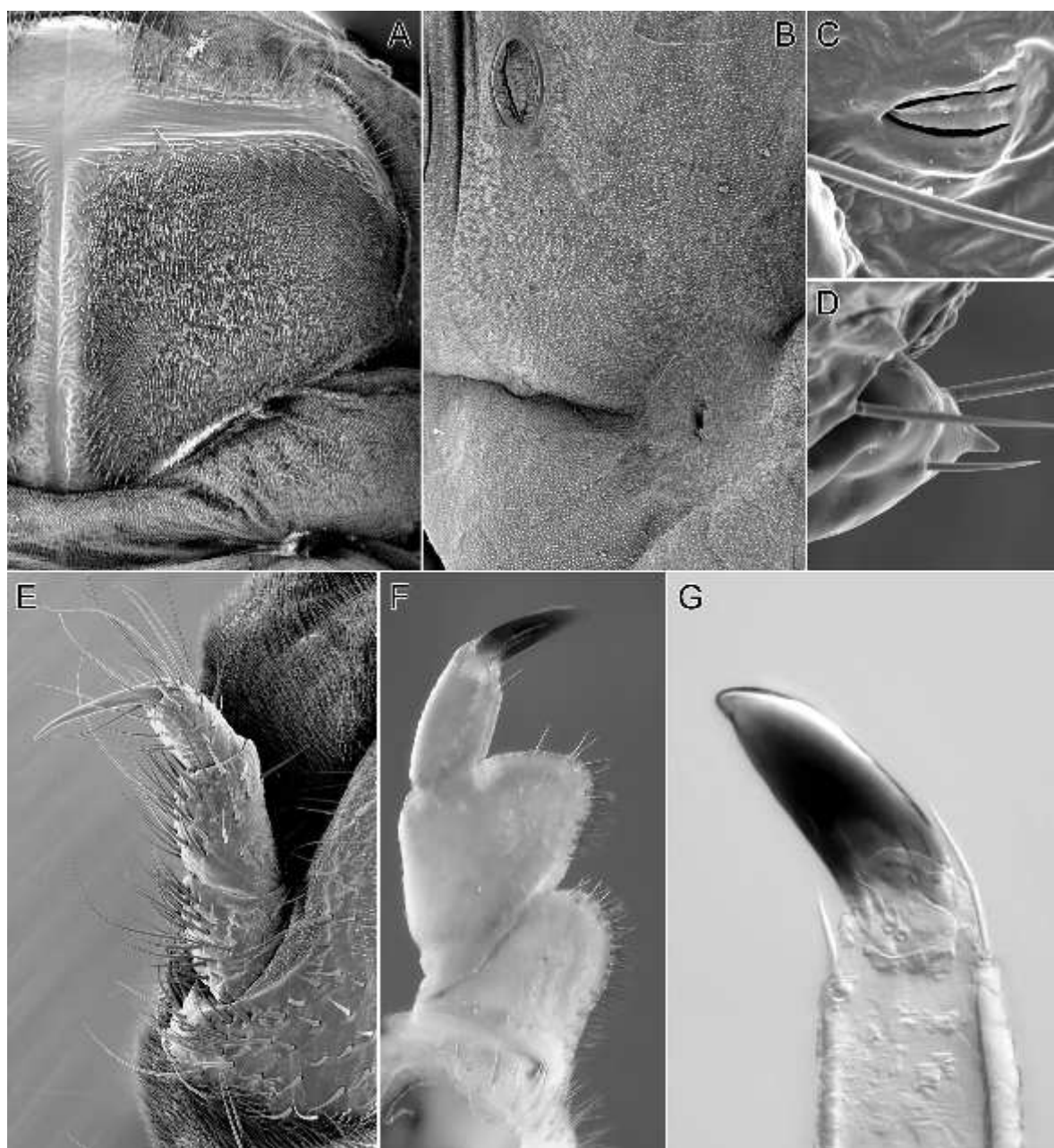


Fig. 2.1.12 Larvae. A, *Philus antennatus*, right half of pro- and mesonotum (SEM); B, *Heterophilus punctulatus*, left lateral part of abdominal segment I with spiracle and epipleural disc (SEM); C, *Vesperus luridus*, first instar, left abdominal spiracle VI (SEM); D, *V. luridus*, first instar, left 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; gumentum not forming intermaxillary process; and tentorial bridge broad and roof-like. Alternatively, in Lacordaire's (1869) classification, the Vesperides and Apatophysides composed the cohort "Cerambycides vrais souterrains", and *Vesperus* was thus far from Lepturinae, which were placed in Section B of "Cerambycides 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).



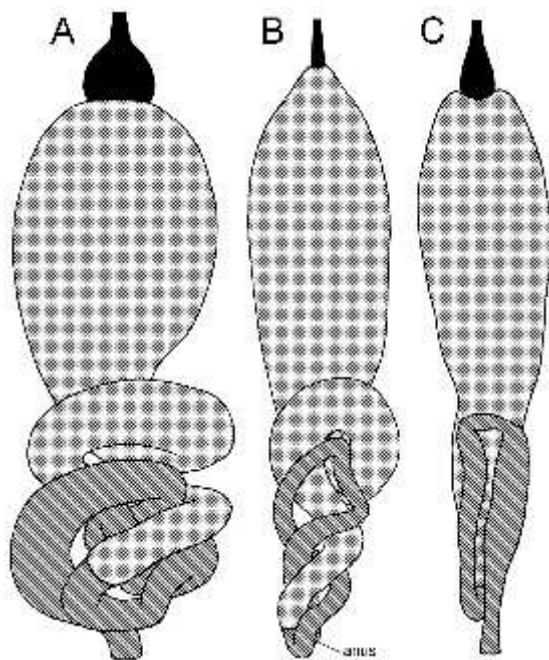


Fig. 2.1.13 Gross morphology of larval gut, diagrammatic, dorsal view. A, *Vesperus luridus*; B, *Philus antennatus*; C, *Migdolus fryanus*. Foregut black, midgut stippled, hindgut crosshatched (from Svacha *et al.* 1997).

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 Cerambycitrae: Spondylitae containing, besides Spondylitae verae (now Spondylidinae: Spondylidini), and Anoplodermiteae, also Torneutitae (now Torneutini of Cerambycinae), Erichsonitae (now a tribe of Parandrinae), and Cantharocnemitae (now in Prioninae). *Hypocephalus* was

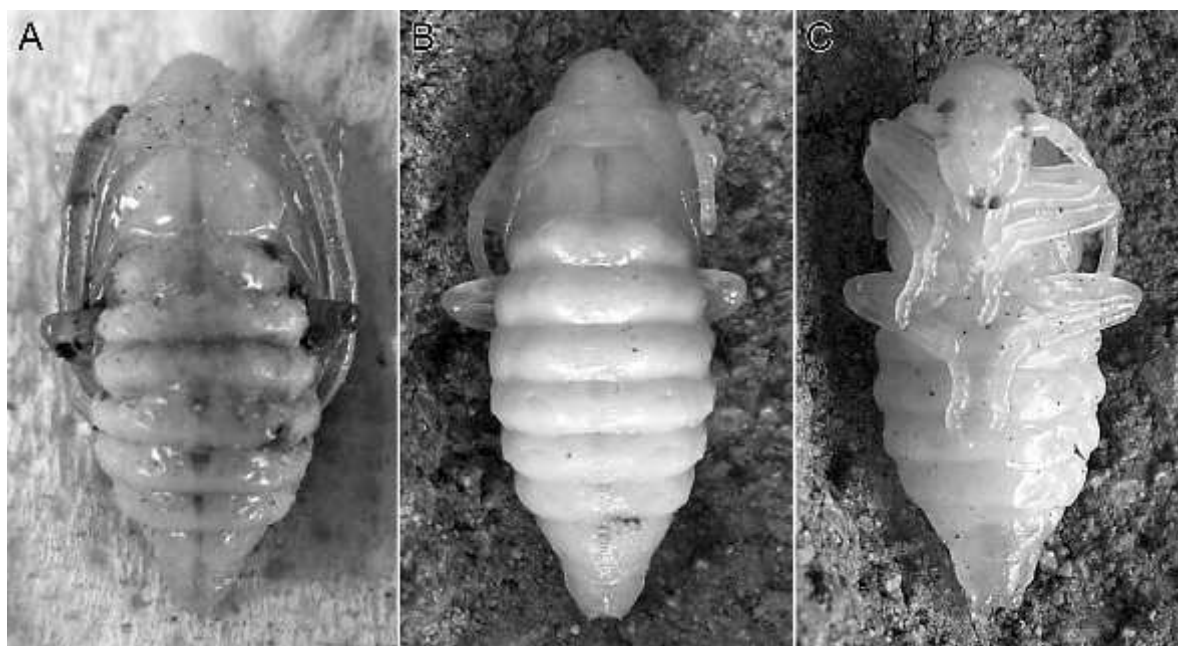


Fig. 2.1.14 *Vesperus sanzii*, pupa (© F. Calvo Sánchez). A, male, dorsal view; B, slightly malformed female, dorsal view; C, same, ventral view.

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 chrysoloids 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 gulum 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 chrysoloid 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 Anoplodermatinae (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 cerambycid 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 occurring 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 synapomorphy 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 cerambycid 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 1891). 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<sub>1+2</sub> and MP<sub>3+4</sub> 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<sub>1+2</sub> and MP<sub>3+4</sub> 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 sanzii* 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. sanzii* collected from the soil pupal chambers was not significantly different. Females of *V. xatarti* produce a long-range pheromone. Males of

*V. sanzii* 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. sanzii* 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. sanzii* 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. sanzii*), oviposit in cavities in the soil, among roots, or in grass sods. *Vesperus sanzii* 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. sanzii*, 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. sanzii*, 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 smoothed 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 faceted, 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<sub>1</sub> present but CuA<sub>1+2</sub> may be absent and MP<sub>3+4</sub> then appears to have three branches; connection between MP<sub>1+2</sub> and MP<sub>3+4</sub> 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. sanzti*) 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. Pre-sternal 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* occurring 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 cogongrass (*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 faceted 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. Meiyang 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 faceted (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<sub>3+4</sub> with only one branch); wedge cell absent; CuA<sub>1+2</sub> and CuA<sub>1</sub> present or the former or both more or less reduced (*Migdolus*); connection between MP<sub>1+2</sub> and MP<sub>3+4</sub> shifted distally and relatively close to (occasionally directly adjacent to) CuA<sub>1</sub>; fine medial fleck present in some

Anoplodermatini (Fig. 2.1.5 F). Legs moderately long and relatively unmodified in *Mysteriini* and *Cherrocricus*, 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 faceted, 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 maxillo-labial 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 *Cherrocarius* 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 faceted. 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-Ménéville with three species, *Migdolus* Westwood with ten species, *Paramigdolus* Dias with *P. tetropioides* (Fairmaire), and *Sypilus* Guérin-Ménéville 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 species 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 faceted, 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 interfaccial 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<sub>3+4</sub> with only one branch) and with narrow yet distinct wedge cell; CuA<sub>1+2</sub> present, CuA<sub>1</sub> present or (Fig. 7 in Vives 2001) absent; connection between MP<sub>1+2</sub> and MP<sub>3+4</sub> 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.

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## Literature

- Araujo, R. L. (1954): Revisão da bibliografia e notas à ecologia de *Hypocephalus armatus* Desm., 1832 (Coleoptera, Hypocephalidae). – *Revista Brasileira de Entomologia* 2: 175–192.
- Aurivillius, C. (1912): *Coleopterorum Catalogus. Pars 39. Cerambycidae: Cerambycinae*. 574 pp. W. Junk, Berlin.
- Bates, H. W. (1891): New longicorn Coleoptera, chiefly from Mexico. – *Entomologist's Monthly Magazine* 27: 158–161.
- Bento, J. M. S., Albino, F. E., Della Lucia, T. M. C. & Vilela, E. F. (1992): Field trapping of *Migdolus fryanus* Westwood (Coleoptera: Cerambycidae) using natural sex pheromone. – *Journal of Chemical Ecology* 18 (2): 245–251.
- Bento, J. M. S., Della Lucia, T. M. C. & Frighetto, R. T. S. (1993): Male response to natural sex pheromone of *Migdolus fryanus* Westwood (Coleoptera: Cerambycidae) females as affected by daily climatic factors. – *Journal of Chemical Ecology* 19 (10): 2347–2351.
- Bento, J. M. S., Vilela, E. F., Della Lucia, T. M. C., Leal, W. S. & Novaretti, W. R. T. (1995): *Migdolus: Biologia, Comportamento e Controle*. iv + 58 pp. By the authors, Salvador (Bahia).
- Bezark, L. G. & Monné, M. A. (2013): *Checklist of the Oxytelidae, Vesperidae, Disteniidae and Cerambycidae (Coleoptera) of the Western Hemisphere, 2013 Edition (Updated through 31 December 2012)*. 484 pp. Available at: <http://plant.cdfa.ca.gov/byciddb/documents.html>.
- Boppe, P. (1921): Coleoptera Longicornia Fam. Cerambycidae Subfam. Disteniinae – Lepturinae. 121 pp., 8 pls. In Wytzman, P. (ed.) *Genera Insectorum Fascicule 178*. L. Desmet-Verteneuil, Brussels.
- Botelho, P. S. M. & Degaspari, N. (1980): Some bionomic data and recommendations for the control of *Migdolus fonsecae* (Coleoptera, Cerambycidae [sic]) in sugarcane in Brazil. – *Entomology Newsletter of the International Society of Sugarcane Technology* 9: 7–8.
- Bouchard, P., Bousquet, Y., Davies, A. E., Alonso-Zarazaga, M. A., Lawrence, J. F., Lyal, C. H. C., Newton, A. F., Reid, C. A. M., Schmitt, M., Slipiński, S. A. & Smith, A. B. T. (2011): Family-group names in Coleoptera (Insecta). – *ZooKeys* 88: 1–972.
- Bousquet, Y., Heffern, D. J., Bouchard, P. & Nearn, E. (2009): Catalogue of family-group names in Cerambycidae (Coleoptera). – *Zootaxa* 2321: 1–80.
- Boyer, F. D., Malosse, C., Zagatti, P. & Einhorn, J. (1997): Identification and synthesis of vesperal, the female sex pheromone of the longhorn beetle *Vesperus xatarti*. – *Bulletin de la Société Chimique de France* 134: 757–764.
- Butovitsch, V. (1939): Zur Kenntnis der Paarung, Eiablage und Ernährung der Cerambyciden. – *Entomologisk Tidskrift* 60: 206–258.
- Calvo Sánchez, F. (2007): *Vesperus sanzii* Reitter, 1895 (Coleoptera, Cerambycidae): Estudio de su biología, etología y distribución geográfica (Península Ibérica). – *Boletín de la Sociedad Entomológica Aragonesa* 40: 267–280.
- (2008): Descripción de la hembra de *Vesperus jertensis* Bercedo Páramo & Bahillo de la Puebla, 1999 (Coleoptera: Cerambycidae). – *Boletín de la Sociedad Entomológica Aragonesa* 43: 117–120.
- Chiang [Jiang], S.-N. & Chen, L. (1996): Description of two species of philine larvae (Coleoptera: Cerambycoidea) from China. – *Entomotaxonomia* 18: 113–118.
- Chiang [Jiang], S.-N., Chen, B. & Zhang, R. (1996): Two new species of the genus *Heterophilus* (Coleoptera: Cerambycoidea) from China. – *Entomotaxonomia* 18: 109–112 (in Chinese with English descriptions).
- Costa, C., Vanin, S. A. & Casari-Chen, S. A. (1988): *Larvas de Coleoptera do Brasil*. viii + 282 pp. Museu de Zoologia, Universidade de São Paulo, São Paulo.
- Crowson, R. A. (1955): *The Natural Classification of the Families of Coleoptera*. 187 pp. Nathaniel Lloyd, London.
- (1967): The natural classification of the families of Coleoptera. Addenda et corrigenda. – *Entomologist's Monthly Magazine* 103: 209–214.
- (1981): *The Biology of the Coleoptera*. xii + 802 pp. Academic Press, London.
- Di Iorio, O. R. (2004). Cerambycidae. Pp. 17–79 in Cordo, H. A., Logarzo, G., Braun, K. & Di Iorio, O. R. (eds.) *Catálogo de Insectos Fitófagos de la Argentina y sus Plantas Asociadas*. Sociedad Entomológica Argentina, Buenos Aires.
- Dias, M. M. (1984): Revisão da subfamília Anoplodermatinae. Parte I. Tribo Anoplodermatini. Genero *Migdolus* Westwood, 1863 (Coleoptera, Cerambycidae). – *Revista Brasileira de Entomologia* 28 (4): 507–535.
- (1986): Revisão da subfamília Anoplodermatinae. Parte II. Tribo Anoplodermatini. Generos: *Acanthomigdolus* Bruch, 1941, *Paramigdolus*, gen. n., *Anoploderma* Guérin-Méneville, 1840, *Sypilus* Guérin-Méneville, 1849 (Coleoptera, Cerambycidae). – *Revista Brasileira de Entomologia* 30 (1): 115–139.
- (1987): Revisão da subfamília Anoplodermatinae. Parte III. Tribo Anoplodermatini. Generos: *Cherrocarius* Berg, 1898, *Hypocephalus* Desmarest, 1832 (Coleoptera, Cerambycidae). – *Revista Brasileira de Entomologia* 31 (1): 101–112.
- (1988): Revisão da subfamília Anoplodermatinae. Parte IV. Tribo Mysteriini. Generos: *Mysteria* Thomson, 1860, *Pathocerus* Waterhouse, 1901, *Pseudopathocerus*, gen. n. (Coleoptera, Cerambycidae). – *Revista Brasileira de Entomologia* 32 (2): 139–160.
- (2004): Novas ocorrências e descrição da fêmea de *Mysteria darwini* (Lameere) (Coleoptera, Vesperidae, Anoplodermatinae). – *Revista Brasileira de Entomologia* 48 (1): 141–143.
- Duffy, E. A. J. (1953): *A Monograph of the Immature Stages of British and Imported Timber Beetles (Cerambycidae)*. 350 pp., 8 pls. British Museum (Natural History), London.

- (1957): *A Monograph of the Immature Stages of African Timber Beetles (Cerambycidae)*. 338 pp., 10 pls. British Museum (Natural History), London.
- (1960): *A Monograph of the Immature Stages of Neotropical Timber Beetles (Cerambycidae)*. 327 pp., 13 pls. British Museum (Natural History), London.
- (1968): *A Monograph of the Immature Stages of Oriental Timber Beetles (Cerambycidae)*. 434 pp., 18 pls. British Museum (Natural History), London.
- Dutrillaux, A.-M., Moulin, S. & Dutrillaux, B. (2007): Présence d'un caryotype très original à 53–54 chromosomes chez *Vesperus xatarti* Mulsant 1839 (Coleoptera: Cerambycidae: Vesperinae). – *Annales de la Société Entomologique de France* (N. S.) 43 (1): 81–85.
- Fonseca, J. P. da (1959): *Migdolus morretesi* Lane (Coleoptero Anoplodermidae) uma bróca eventual da cana de açúcar e do eucalipto. – *Arquivos do Instituto Biológico* (São Paulo) 25 [1958]: 29–40, 4 pls.
- Fonseca-Gessner, A. A. (1990): *Estudo Comparativo da Morfologia e da Histologia do Tubo Digestivo das Larvas de Cerambycidae (Coleoptera) e sua Importância na Classificação*. v + 115 pp. Unpublished thesis, Universidade Estadual Paulista “Júlio de Mesquita Filho”, Rio Claro.
- Gahan, C. J. (1895): *Vesperoctenus*, Bates, and its systematic position. – *Entomologist's Monthly Magazine* 31: 22–24.
- (1906): *Coleoptera. Volume 1. (Cerambycidae). The Fauna of British India, Including Ceylon and Burma*. xviii + 329 pp. Taylor and Francis, London.
- Gounelle, E. (1905): Contribution à l'étude des moeurs d'*Hypocephalus armatus* (Col.). – *Annales de la Société Entomologique de France* 74: 105–108.
- Gressitt, J. L. (1951): Longicorn beetles of China. 667 pp., 22 pls. In Lepesme, P. (ed.) *Longicornia – Études et Notes sur les Longicornes. Volume II*. P. Lechevalier, Paris.
- Gressitt, J. L. & Rondon, J. A. (1970): Cerambycids of Laos (Disteniidae, Prioninae, Philinae, Aseminae, Lepturinae, Cerambycinae). – *Pacific Insects Monographs* 24: 1–314.
- Horn, G. H. (1894): The Coleoptera of Baja California. – *Proceedings of the California Academy of Sciences* (Series 2) 4: 302–449, pls. VII and VIII.
- (1895): *Vesperoctenus flohri* Bates. – *Entomological News* 6: 114–115.
- Hovore, F. T. (1988): Additions to the cerambycid beetle fauna of Baja California, Mexico: Records and descriptions (Coleoptera: Cerambycidae). – *Wasmann Journal of Biology* 46 (1–2): 1–29.
- Hüdepohl, K.-E. (1990): The longhorn beetles of the Philippines Part II. – *Entomofauna* (Ansfelden) 11 (3/1): 45–72.
- Lacordaire, J. T. (1868): *Histoire Naturelle des Insectes. Genera des Coléoptères. Volume 8*. 552 pp., pls. 81–91. Librairie Encyclopédique de Roret, Paris [dated 1869].
- (1869): *Histoire naturelle des Insectes. Genera des Coléoptères. Vol. 9 Part 1*. Pp. 1–409, pls. 92–100. Librairie Encyclopédique de Roret, Paris.
- Lameere, A. (1902): Révision des Prionides. Deuxième mémoire. Anoplodermines. – *Annales de la Société Entomologique de Belgique* 46: 191–225.
- (1913): *Coleopterorum Catalogus Pars 52. Cerambycidae: Prioninae*. 108 pp. W. Junk, Berlin.
- (1919): Coleoptera Longicornia Fam. Cerambycidae Subfam. Prioninae. 189 pp. In Wytzman, P. (ed.) *Genera Insectorum. Fascicule 172*. L. Desmet-Verteneuil, Bruxelles.
- Lane, F. (1937): Esboço monográfico des Anoplodermeos. – *Revista do Museu Paulista* 23: 153–223.
- Leal, W. S., Bento, J. M. S., Vilela, E. F. & Della Lucia, T. M. C. (1994): Female sex pheromone of the longhorn beetle *Migdolus fryanus* Westwood: N-(2'S)-methylbutanoyl 2-methylbutylamine. – *Experientia* 50 (9): 853–856.
- LeConte, J. L. (1876): On the affinities of *Hypocephalus*. – *Transactions of the American Entomological Society* 5: 209–218.
- Lin, M. & Bi, W. (2011): A new genus and species of the subfamily Philinae (Coleoptera: Vesperidae). – *Zootaxa* 2777: 54–60.
- Lin, M. Y., Chen, S. K. & Chang, H. Y. (2004): Morphological and ecological studies of *Philus antennatus*. – *Plant Protection Bulletin* (Taipei) 46: 177–180.
- Linsley, E. G. (1961): The Cerambycidae of North America. Part I. Introduction. – *University of California Publications in Entomology* 18: i–vi + 1–97, pls. 1–35.
- (1962): The Cerambycidae of North America, Part II. Taxonomy and classification of the Parandrinae, Prioninae, Spondylinae, and Aseminae. – *University of California Publications in Entomology* 19: i–vi + 1–102, pl. 1.
- Löbl, I. & Smetana, A. (eds.) (2010): *Catalogue of Palaearctic Coleoptera. Volume 6. Chrysomeloidea*. 924 pp. Apollo Books, Stenstrup.
- Machado, L. A. & Habib, M. (2006): *Migdolus fryanus* (Westwood, 1863) (Coleoptera: Vesperidae): Praga da cultura de cana-de-açúcar. – *Arquivos do Instituto Biológico* (São Paulo) 73 (3): 375–381.
- Machado, L. A., Habib, M., Leite, L. G., Calegari, L. C., Goulart, R. M. & Tavares, F. M. (2005): Patogenicidade de nematóides entomopatogênicos a ovos e larvas de *Migdolus fryanus* (Westwood, 1863) (Coleoptera: Vesperidae). – *Arquivos do Instituto Biológico* (São Paulo) 72 (2): 221–226.
- Machado, L. A., Habib, M., Leite, L. G. & Mendes, J. M. (2006 a): Estudos ecológicos e comportamentais de *Migdolus fryanus* (Westwood, 1863) (Coleoptera: Vesperidae), em cultura de cana-de-açúcar, em quatro municípios do Estado de São Paulo. – *Arquivos do Instituto Biológico* (São Paulo) 73 (2): 227–233.
- Machado, L. A., Habib, M., Leite, L. G. & Carregari, L. C. (2006 b): Aspectos biológicos e morfológicos de *Migdolus fryanus* (Westwood, 1863) (Coleoptera: Vesperidae). – *Arquivos do Instituto Biológico* (São Paulo) 73 (4): 447–454.
- Mesa, A. & Martins, V. G. (1992): The chromosomes of *Migdolus* [sic] *fryanus* Westwood, 1863 (Coleoptera, Cerambycidae, Anoplodermatinae). – *Revista Brasileira de Genética* 15 (1): 205–208.
- Mitchell, B. K., Whitehead, A. T. & Backus, E. (1979): Ultrastructure of the lateral and medial galeal sensilla of the larva of the red turnip beetle, *Entomosce-*

- lis americana* Brown (Coleoptera: Chrysomelidae). – *International Journal of Insect Morphology and Embryology* 8: 289–295.
- Monné, M. A. (2002): Catalogue of the Neotropical Cerambycidae (Coleoptera) with known host plant – Part V: Subfamilies Prioninae, Parandrinae, Oxypeltinae, Anoplodermatinae, Aseminae and Lepurinae. – *Publicações Avulsas do Museu Nacional* (Rio de Janeiro) 96: 3–70.
- Mulsant, E. (1839): *Histoire Naturelle des Coléoptères de France. Longicornes*. xi + 304 pp., 3 pls. Maisson, Paris.
- Napp, D. S. (1994): Phylogenetic relationships among the subfamilies of Cerambycidae (Coleoptera – Chrysomeloidea). – *Revista Brasileira de Entomologia* 38: 265–419.
- Penteado-Dias, A. M. (1984): Estudo comparativo do cordão nervoso nos Cerambycidae (Coleoptera). – *Revista Brasileira de Entomologia* 28 (3): 223–243.
- Peslier, S. & Mazel, R. (2009): Données éthologiques et notes sur la répartition de quelques espèces du genre *Vesperus* Dejean, 1821 (Coleoptera, Cerambycidae, Vesperinae). – *Revue de l'Association Roussillonaise d'Entomologie* 18 (2): 49–53.
- Prosen, A. F. (1960): Notas sobre la familia Anoplodermatidae (Coleoptera, Cerambycoidea). – *Anales del Instituto de Medicina Regional* (Tucumán) 5 (2): 87–100.
- Pu, F.-J. (1988): Coleoptera: Cerambycidae. Pp. 293–304 in Huang, F.-S., Wang, P.-Y., Yin, W.-Y., Yu, P.-Y., Lee, T.-S., Yang, C.-K. & Wang, X.-J. (eds.) *Insects of Mt. Namjagbarwa Region of Xizang*. Science Press, Beijing (in Chinese with English summary).
- Reid, C. A. M. (1995): A cladistic analysis of subfamilial relationships in the Chrysomelidae sensu lato (Chrysomeloidea). Pp. 559–631 in Pakaluk, J. & Ślipiński, S. A. (eds.) *Biology, Phylogeny, and Classification of Coleoptera: Papers Celebrating the 80th Birthday of Roy A. Crowson*. Vol. 2. Muzeum i Instytut Zoologii PAN, Warszawa.
- Saito, A. (1990): Female reproductive organs of cerambycid beetles from Japan and the neighboring areas. I. Philini through Atimiini. – *Elytra* (Tokyo) 18 (2): 231–260.
- Santos-Silva, A., Heffern, D. & Matsuda, K. (2010): Revision of Hawaiian, Australasian, Oriental, and Japanese Parandrinae (Coleoptera, Cerambycidae). – *Insecta Mundi* 130: 1–120.
- Schiødte, J. C. (1864): Danmarks Cerambyces. – *Naturhistorisk Tidsskrift* (Ser. III) 2 (3): 483–576, pl. XX (in Danish and Latin).
- Schomann, H. (1937): Die Symbiose der Bockkäfer. – *Zeitschrift für Morphologie und Ökologie der Tiere* 32: 542–612.
- Sechi, D. (2012): Osservazioni sulla biologia di *Vesperus macropterus* (Coleoptera, Cerambycidae). – *Fragmenta Entomologica* 43 (1): 75–87.
- Sharp, D. (1884): Some observations on *Hypocephalus armatus*. – *Annales de la Société Entomologique de Belgique* 28: cvii–cxii.
- Svacha, P. & Danilevsky, M. L. (1987): Cerambycid larvae of Europe and Soviet Union (Coleoptera, Cerambycoidea). Part I. – *Acta Universitatis Carolinae (Biologica)* 30 [1986]: 1–176.
- Svacha, P., Wang, J.-J. & Chen, S.-C. (1997): Larval morphology and biology of *Philus antennatus* and *Heterophilus punctulatus*, and systematic position of the Philinae (Coleoptera: Cerambycidae and Vesperidae). – *Annales de la Société Entomologique de France* (N. S.) 33: 323–369.
- Thomson, J. (1860–1861): *Essai d'une Classification de la Famille des Cérambycides et Matériaux pour Servir à une Monographie de cette Famille*. Pp. i–xvi + 1–128 [1860], 129–396 + 3 pls. [1861]. By the author, Paris.
- (1864–1865): *Systema Cerambycidarum ou Exposé de Tous les Genres Compris dans la Famille des Cérambycides et Familles Limitrophes*. Pp. 1–352 [Livres 1–3, 1864], 353–578 [Livre 4, 1865]. H. Dessain, Liège.
- Verdugo-Páez, A. (2009): Descripción de *Vesperus barre-dai* (Coleoptera, Cerambycidae, Vesperinae), nueva especie de cerambycido de la Península Ibérica. – *Boletín de la Sociedad Andaluza de Entomología* 16: 21–32.
- Villiers, A. (1978): *Cerambycidae. Faune des Coléoptères de France I*. xxvii + 607 pp. P. Lechevalier, Paris.
- Vives, E. (2001): The systematic position of *Vesperoctenus flohri* Bates, 1891 and the taxonomic status of the Vesperidae (Coleoptera). – *Occasional Papers of the Consortium Coleopterorum* 4 (1): 35–44.
- (2005): Revision du genre *Vesperus* Dejean 1821 (Coleoptera: Cerambycidae). – *Annales de la Société Entomologique de France* 40 (3–4): 437–457.
- Wilcken, C. F., Orlato, C. & Ottati, A. L. T. (2005): Ocorrência de *Migdolus fryanus* (Coleoptera: Cerambycidae) em plantios de *Pinus caribaea* var. *hondurensis*. – *Revista Árvore* 29 (1): 171–173.
- Wu, W.-W. & Chiang [Jiang], S.-N. (2000): A taxonomic study of the male genitalia of some philid beetles with one new species in China (Coleoptera: Cerambycoidea). – *Acta Entomologica Sinica* 43 (1): 78–87 (in Chinese with English abstract).
- Yin, X.-M. (1994): Morphological observation of the immature and adult stages of the philid longicorn beetle (*Philus antennatus*) (Coleoptera: Cerambycidae). – *Journal of Southwest Agricultural University* 16: 265–269 (in Chinese with English abstract).

## 2.2 Oxypeltidae Lacordaire, 1868

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**Distribution.** Two genera (*Oxypeltus* Blanchard in Gay and *Cheloderus* Gray in Griffith) with three species (*Oxypeltus quadrispinosus* Blanchard in Gay, *Cheloderus childreni* Gray in Griffith and *C. penai* Kuschel; Cerda 1972, 1986) occur in central and southern Chile (*Oxypeltus* reaching Magallanes province) and in adjacent southwestern Argentina (all three species in Neuquén province, *Oxypeltus* also in Chubut), within the South American range of the tree genus *Nothofagus* (Nothofagaceae). Although the two species of *Cheloderus* are broadly sympatric, *C. penai* (the most restricted of the three