Handbook of Zoology
Arthropoda: Insecta

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

Handbook of Zoology

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Arthropoda: Insecta

Editors Niels P. Kristensen & Rolf G. Beutel

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(Volume Editors)

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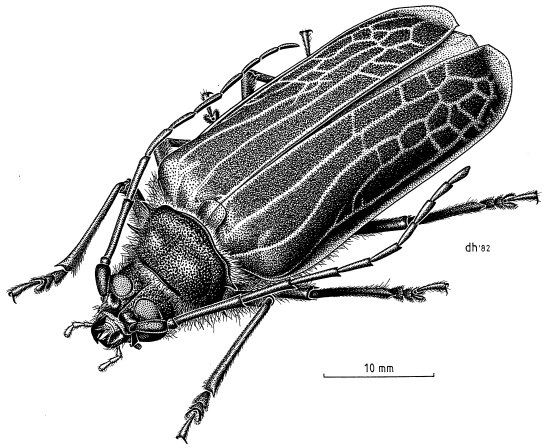
Editors' preface

You hold in your hands Volume III of the *Handbook of Zoology*, which covers the Phytophaga, a poorly documented monster group containing an incredibly high number of species, especially the weevils, which includes 6,000 scolytines (which all look alike to us!). The third part of the *Coleoptera Handbook of Zoology* series brings together the first major modern world treatments of weevils and the intensely sought after Cerambycidae.

While biology is experiencing a downturn in taxonomic training, natural history remains a draw for most new biology students and young savvy systematists are expanding integrative taxonomy to include the new technologies while having a knack for the nuances of taxonomic nomenclature and homology assessment. There are also universities and museums that remain supportive of taxonomy, and there are the hardworking amateurs who continue to describe species and document the diversity of the beetle world wide: We hope that the completed Coleoptera volumes will serve the biological community well and will be a resource for future systematics projects, large or small.

Our editorial collaboration that started in 2000 ends here and plans for Volume IV (morphology, natural history, and evolution) have been deferred, left for the next generation. We thank all of the authors for their hard work and contributions to Volume III of the *Handbook*: from those who were timely and patient to those who were late and cantankerous with their submissions. We are especially indebted to John Lawrence for his tireless commitment to the entire volume and his help with the chrysomeloid chapters and Rolf Oberprieler who assisted with the weevil chapters: without the help of John and Rolf Oberprieler this Volume III would have been more difficult if not impossible to complete. We also thank the De Gruyter staff who have helped over years, including Stephanie Dawson, who was there at the beginning of the Coleoptera volumes, and Julia Lauterbach who has helped significantly with Volume III.

Richard A. B. Leschen
Rolf G. Beutel



Prionoplus reticularis White (Cerambycidae: Cerambycinae) is the largest beetle species in New Zealand. Referred to as the Huhu beetle, the larvae are edible and develop in dead wood. Adults are nocturnal and it is one of the few New Zealand species that come to lights. Illustration by Des Helmore (© Landcare Research).

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1 Molecular phylogenetics and evolution of Coleoptera

Duane D. McKenna

Introduction. Here I review the current status of beetle molecular phylogenetics with a focus on higher-level (supra-familial) relationships, progress since the last treatment of this subject by Vogler (2005) and current and future directions. Further, I briefly discuss recent advances in our understanding of timing and patterns of ecological and taxonomic diversification in beetles, including prospects for resolving the apparent conundrum of "inordinate fondness" (e.g., Hutchinson 1959; Farrell 1998). Unless otherwise stated, the supra-familial classification used follows Lawrence *et al.* (2010 b).

Subordinal-level relationships. Caterino *et al.* (2005) sampled 18S rDNA (18S) sequences from 110 species of beetles, including representatives of all four suborders (Table 1.1), with an emphasis on Staphyliniformia and Scarabaeiformia (Scarabaeoidea) (85 exemplars). Analyses under Bayesian inference (BI) and maximum likelihood (ML) inference recovered Adephaga and Polyphaga as sister groups, and Archostemata (one exemplar) alone or in combination with Myxophaga as the closest relative of the other suborders. However, parsimony analysis recovered Myxophaga in a position sister to Polyphaga. Hughes *et al.* (2006) used 66 expressed sequence tags (ESTs; matrix 28.6% complete; Table 1.1) to reconstruct beetle phylogeny from 20 exemplars. When trees were rooted with Archostemata (one exemplar), Myxophaga (one exemplar) and Polyphaga were recovered as sister groups, these together sister to Adephaga. Supertree analyses placed the single myxophagan within Polyphaga.

Hunt *et al.* (2007) published both the first extensively taxon-sampled multigene molecular phylogeny and the first molecular timetree for beetles. Their study included nearly complete 18S sequences from 1880 taxa and sequences from mitochondrial 16S rDNA (16S) and cytochrome oxidase I (*COI*) for nearly half of those (Table 1.1). In phylogenetic trees resulting from both parsimony and BI analyses, Adephaga and Polyphaga were sister groups, and Archostemata (one exemplar) was recovered within Myxophaga. Hunt & Vogler (2008), in analyses of 18S sequences from 1161 beetles, recovered Myxophaga plus Archostemata, and Adephaga and Polyphaga as sister groups (Table 1.1).

Wild & Maddison (2008) evaluated the phylogenetic performance of nine nuclear genes sequenced from 31 beetles in 18 genera representing all suborders except Myxophaga (Table 1.1). BI and parsimony analyses of the combined data recovered Archostemata and Adephaga as sister groups, and these together sister to Polyphaga. Although ostensibly focused on Adephaga, this was the first higher-level molecular phylogenetic study of beetles to include extensive data from nuclear protein-coding (NPC) genes. McKenna & Farrell (2009) analyzed nearly complete 18S sequences from 955 beetle genera, including representatives of all four suborders. Analysis under ML inference recovered Adephaga and Polyphaga as sister groups. Archostemata was derived from within Myxophaga. Maddison *et al.* (2009) used sequences from 18S and 28S rDNA (28S) and the NPC gene wingless to reconstruct the phylogeny of Adephaga. In addition to 60 adephagan terminals, they sampled 17 beetles representing the other three suborders, including more Archostemata (four genera in two families) than in any other molecular phylogenetic study to date. Analysis of the combined data under BI recovered Archostemata and Myxophaga as sister groups, and also Adephaga and Polyphaga.

Song *et al.* (2010) is the most extensively taxon-sampled study of mitochondrial (mt) genomes to date focused on reconstructing higher level relationships in beetles. Their MP "reference phylogeny"[1], based on amino acid sequences of mitochondrial protein-coding (MPC) genes from 24 taxa representing all four suborders, recovered Myxophaga (one exemplar) sister to Adephaga, and these together sister to Polyphaga. Archostemata (one exemplar) was sister to all other beetles. Several other recent investigators have also used mt genomes to study beetle phylogeny and evolution (e.g., Sheffield *et al.* 2008, 2009; Cameron *et al.* 2009; Kim *et al.* 2009; Pons *et al.* 2010; Song *et al.* 2010; Timmermans & Vogler 2012). Pons *et al.* (2010) notably estimated nucleotide substitution rates for the full set of beetle MPC genes based on analyses of 15 exemplar mt genomes.

Series, superfamily, and other higher-level relationships. DNA sequence data are available for a large proportion of extant species in the suborders Archostemata and Myxophaga. However, except for available sequences of 18S and

[1] Considered by the authors to be the least likely to violate phylogenetic assumptions.

Table 1.1 Summary of taxon and gene sampling for molecular phylogenetic studies sampling 20 or more species of Coleoptera and focused on a sufficiently high taxonomic level to permit at least partial evaluation of subordinal relationships.

Author(s)	Adephaga	Archostemata	Myxophaga	Polyphaga	Taxonomic focus	Gene(s)
Howland & Hewitt 1995	8	0	0	29	Coleoptera	Cytochrome oxidase I
Shull *et al.* 2001	37	*Distocupes*	2	6	Adephaga	18S
Whiting 2002	13	*Distocupes*	2	31	Holometabola	18S
Caterino *et al.* 2002	9	*Distocupes*	3	12	Coleoptera	18S
Caterino *et al.* 2005	6	*Distocupes*	3	100 (85)	Staphyliniformia Scarabaeiformia	18S
Vogler 2005	220	*Distocupes*	2	575	Coleoptera	18S
Hughes *et al.* 2006	3 genera, 5 species	*Micromalthus*	*Sphaerius*	15	Coleoptera	ESTs (66 RP genes)
Hunt *et al.* 2007	233	*Distocupes*	9	1637	Coleoptera	18S, 16S, Cytochrome oxidase I
Hunt & Vogler 2008	224	*Distocupes*	7	1161	Coleoptera	18S
Wild & Maddison 2008	21 (10 *Bembidion*)	3	0	3	N/A	28S Arginine kinase Alpha-spectrin Carbamoylphosphate synthase domain Enolase Phosphoenolpyruvate carboxykinase RNA polymerase II Topoisomerase I Wingless
Maddison *et al.* 2009	60	4	3	10	Adephaga	18S, 28S, Wingless
McKenna & Farrell 2009	175	2	4	774	Coleoptera	18S
Song *et al.* 2010	3	1	1	19	Coleoptera	mt genomes

28S rDNA, these data are generally not broadly compatible, i.e., relatively few taxa have been sequenced for the same genes or gene regions, limiting insight into the internal relationships of these suborders.

Adephaga have been the focus of several extensively taxon-sampled molecular phylogenetic studies (e.g., Maddison *et al*. 1999; Shull *et al*. 2001; Caterino *et al*. 2002; Ribera *et al*. 2002; Maddison *et al*. 2009) and have also been extensively sampled in several recent studies focused at the ordinal level (e.g., Vogler 2005; Hunt *et al*. 2007; Hunt & Vogler 2008; McKenna & Farrell 2009). Nonetheless, only two of these studies used data from multiple genes (Hunt *et al*. 2007; Maddison *et al*. 2009), and only Maddison *et al*. (2009) included data from a NPC gene (wingless). The results of some analyses reported in the aforementioned studies are consistent with the reciprocal monophyly of the aquatic Hydradephaga (Amphizoidae, Aspidytidae, Dytiscidae, Gyrinidae, Haliplidae, Hygrobiidae, Meruidae and Noteridae) and terrestrial Geadephaga (Carabidae, Cicindelidae, Paussidae, Rhysodidae and Trachypachidae) (e.g., Shull *et al*. 2001; Ribera *et al*. 2002; Vogler 2005; Hunt *et al*. 2007; Hunt & Vogler 2008; McKenna & Farrell 2009). However, Maddison *et al*. (2009), employing data from the nuclear genes 18S, 28S and wingless recovered only limited support for the monophyly of Hydradephaga and recovered evidence that Geadephaga (strongly supported as monophyletic and including Trachypachidae) may be derived from hydradephagan ancestors. Wild & Maddison (2008) intriguingly recovered strong support for the monophyly of Hydradephaga and Geadephaga in a combined analysis of data from nine genes; however, their study was focused on determining the phylogenetic utility of nuclear genes in beetles and not on reconstructing the phylogeny of Adephaga (they sampled 23 adephagan terminals in twelve genera). Their taxon sample therefore lacked many key taxa needed to evaluate the monophyly and interrelationships of higher-level taxa within Adephaga.

Of the five traditionally recognized series of superfamilies within Polyphaga, only the monophyly of Scarabaeiformia and Cucujiformia received strong support in Hunt *et al*. (2007) (which remains the only comprehensive sample of beetle superfamilies published to date that includes information about nodal support). Recent studies, e.g., Caterino *et al*. (2005); Vogler (2005); Hunt *et al*. (2007); Hunt & Vogler (2008) and McKenna & Farrell (2009), recover Derodontidae (Derodontoidea) in close but uncertain relation to Scirtoidea [which forms a paraphyletic grade in Bocakova *et al*. (2007), Hunt *et al*. (2007), and McKenna & Farrell (2009)], sister to the remaining Polyphaga. Derodontoidea is traditionally placed in series Bostrichiformia, and Scirtoidea in series Elateriformia (e.g., Lawrence & Newton 1982, 1995). Nosodendridae, which are placed in series Derodontiformia (Derodontoidea) by Lawrence *et al*. (2010 a) and Bouchard *et al*. (2011), are close relatives of Elateriformia in Hunt *et al*. (2007) and McKenna & Farrell (2009). Molecular data therefore suggest that series Scirtiformia (Scirtoidea) of recent classifications (Lawrence *et al*. 2010 b; Bouchard *et al*. 2011) is paraphyletic and that series Derodontiformia of recent classifications (Lawrence *et al*. 2010 a, Bouchard *et al*. 2011) is polyphyletic.

The phylogenetic placement of Scarabaeiformia relative to Staphyliniformia and the placement of Scarabaeiformia and Staphylinformia among early divergent Polyphaga remain unclear. Korte *et al*. (2004) and Caterino *et al*. (2005) recovered relatively little well-supported resolution at higher taxonomic levels in Staphyliniformia and recovered evidence for the placement of Scarabaeiformia within Staphyliniformia (as did Hunt *et al*. 2007). Staphyliniformia was recovered as a paraphyletic grade in Hunt *et al*. (2007) and McKenna & Farrell (2009). Bernhard *et al*. (2009) recovered strong support for many internal relationships within Hydrophiloidea (22 exemplars) in a combined analysis of data from 18S, 28S, 12S, 16S, *COI*, cytochrome oxidase II (*COII*) and morphology under BI. Other analytical methods recovered relatively little well-supported resolution, and analyses of molecular data alone were not reported. Bernhard *et al*. (2006) published a molecular phylogeny for Hydrophilidae based on a subset of these data. Smith *et al*. (2006) reported the results of preliminary analyses of 28S and 18S DNA sequence data for over 600 terminals of Scarabaeoidea (exact number unclear) and outgroups (13 species in as many genera of Hydrophilidae).

Relationships among the superfamilies of Elateriformia (Buprestoidea, Byrrhoidea, Dascilloidea, and Elateroidea) were relatively well supported in analyses of the combined 18S and 28S data set of Bocakova *et al.* (2007). However, Byrrhoidea was polyphyletic. Byrrhoidea was also polyphyletic in Hunt *et al.* (2007) and in analyses of gene order and nucleotide sequences from the mt genome data set of Timmermans & Vogler (2012).

The monophyly of Cucujiformia appears to be well supported by molecular data (e.g., Hunt *et al*. 2007; Marvaldi *et al*. 2009). However, interrelationships among the cucujiform superfamilies remain unsettled and lack consistently strong nodal support in analyses to date. The most extensively studied cucujiform superfamilies (with regard to molecular data) are the sister groups Chrysomeloidea and Curculionoidea, together sometimes called the "Phytophaga" (e.g., Farrell 1998; Marvaldi *et al*. 2002; Farrell & Sequeira 2004; Gomez-Zurita *et al*. 2007; Hundsdoerfer *et al*. 2009; Marvaldi *et al*. 2009; McKenna *et al*. 2009; McKenna 2011 a). The reciprocal monophyly of Chrysomeloidea and Curculionoidea has been recovered in several molecular phylogenetic studies (Farrell 1998; Farrell & Sequeira 2004; Marvaldi *et al*. 2008; McKenna *et al*. 2009).

Cucujoidea and Tenebrionoidea remain among the least well-known superfamilies of Polyphaga based on DNA sequence data. Parsimony and BI analyses of the combined 18S and 28S data set of Robertson *et al*. (2008) and other recent data sets (e.g., Vogler 2005; Hunt *et al*. 2007; Buder *et al*. 2008; Marvaldi *et al*. 2008; McKenna & Farrell 2009) lend further support to the long-assumed paraphyly of Cucujoidea (e.g., Crowson 1955; Vogler & Caterino 2003; Robertson *et al*. 2004; Leschen *et al*. 2005) and confirm monophyly of the cerylonid series of cucujoid families. The phylogenetic placement of superfamily Lymexyloidea, while uncertain, appears to be within early-divergent Tenebrionoidea (e.g., Hunt *et al*. 2007; McKenna & Farrell 2009). The placement of Cleroidea among the other cucujiform superfamilies remains unsettled (Hunt *et al*. 2007; Buder *et al*. 2008).

Strepsiptera and the sister group to beetles. A number of recent molecular phylogenetic studies (e.g., Wiegmann *et al*. 2009 a, b; Longhorn *et al*. 2010; McKenna & Farrell 2010; Ishiwata *et al*. 2011) have shown that Strepsiptera belong to the supra-ordinal group Neuropteroidea, which otherwise contains beetles and Neuropterida. However, several alternative hypotheses for the phylogenetic placement of Strepsiptera within Neuropteroidea were suggested or supported by these studies: (a) as the sister group to beetles (forming the supra-ordinal group "Coleopterida"); (b) as the sister group to Neuropterida; or (c) within beetles, most likely derived from within Polyphaga.

A recent study of 13 insect genomes (Niehuis *et al*. 2012) showed that Strepsiptera [represented by *Mengenilla moldrzyki* Pohl *et al*. (Mengenillidae)] are not a subordinate group of beetles (represented by *Priacma serrata* (LeConte) (Cupedidae) and *Tribolium castaneum* (Herbst) (Tenebrionidae), which together span the basal split in Coleoptera) and that molecular and morphological data combined are consistent only with a sister group relationship between Strepsiptera and beetles, notably ruling out the possibility that Strepsiptera is a subordinate group of beetles. However, genome sequences from a neuropterid, which could verify this conclusion independent of morphological data, have so far been lacking. Therefore, it remains possible (though unlikely, based on morphological data) that instead of the sister group to beetles, Strepsiptera is the sister group to Neuropterida, as in the seven-gene phylogeny of McKenna & Farrell (2010)[2], or Strepsiptera is the sister group to beetles plus Neuropterida.

To address these remaining possibilities using genomic data, I added unpublished sequences of 2549 genes (7,400,736 aligned nucleotide positions) from the genome of the neuropterid *Chauliodes pectinicornis* (Linnaeus) (Megaloptera: Corydalidae: Chauliodinae)[3] to the 13-genome data set of Niehuis *et al*. (2012). Phylogenetic analyses of the resulting DNA sequence data from 14 insect genomes recovered a single maximally supported phylogenetic tree (100% ML bootstrap support, 1.00 Bayesian posterior probability support for all nodes) in which both Coleopterida (Strepsiptera + Coleoptera) and Neuropteroidea (Neuropterida + Coleopterida) were monophyletic. These findings are fully consistent with Niehuis *et al*. (2012).

Gene sampling. 18S was a staple gene for higher-level molecular phylogenetic studies of beetles at the time of publication of Vogler (2005), and is still in wide use today, particularly in projects focused on relationships at or above the family level. Most studies focused on higher-level relationships in beetles still sequence nearly the entire 18S gene, excluding short pieces on either end. Until recently, 28S was not widely used in higher-level molecular phylogenetic studies of beetles. However, this is changing (e.g., see Wild & Maddison 2008; Maddison *et al.* 2009), and 28S is now being sequenced as part of most ongoing higher-level molecular phylogenetic studies of beetles, including the Beetle Tree of Life Project[4]. 28S continues to be important in relatively lower-level studies of beetles.

A relatively small number of other genes have been used in recent studies focused on relationships at or above the level of individual superfamilies of beetles. These include *COI* (e.g., Hunt *et al*. 2007; Bernhard *et al*. 2009); *COII* (Bernhard *et al*. 2009) 16S (Hunt *et al*. 2007; Bernhard *et al*. 2009; Hundsdoerfer *et al*. 2009); 12S (Bernhard *et al*. 2009) and the NPC genes wingless (Wild & Maddison 2008; Maddison *et al*. 2009); elongation factor 1-alpha (McKenna *et al*. 2009) and arginine kinase (*AK*) (Wild & Maddison 2008; McKenna *et al*. 2009). Wild & Maddison (2008) evaluated the phylogenetic performance of nine nuclear genes (alpha-spectrin, *AK*, carbamoylphosphate synthase domain (*CAD*), enolase, phosphoenolpyruvate carboxykinase (*PEPCK*), RNA polymerase II (*RNA Pol II*), topoisomerase I,

[2] This placement lacked strong nodal support and was not recovered in the nine-gene phylogeny published in the same paper.

[3] The *C. pectinicornis* genome was sequenced and assembled by D.M. Additional information about *C. pectinicornis* genome sequencing and assembly, orthology prediction and phylogenetic analyses are available from D.M.

[4] The Beetle Tree of Life (BToL) project, funded by the United States National Science Foundation's "Assembling the Tree of Life" program, seeks to develop a phylogenetic hypothesis for beetle suborders, superfamilies, families and most subfamilies, based on nuclear and mt DNA sequences and morphological data.

wingless and 28S), at various taxonomic levels across beetles. These genes were chosen from a total of 25 NPC genes screened for this purpose. Other than 28S, *AK*, and wingless, these genes have not otherwise been used in published higher-level studies of beetle phylogeny (Table 1.1). Hughes *et al*. (2006) used 66 ESTs to reconstruct the phylogeny of beetles. Mitochondrial genomes have been used by multiple investigators to reconstruct the higher-level phylogeny of beetles or the phylogeny of supra-familial groups within beetles (Sheffield *et al*. 2008, 2009; Cameron *et al*. 2009; Kim *et al*. 2009; Pons *et al*. 2010; Song *et al*. 2010; Timmermans & Vogler 2012) and are available for all four suborders. However, the analysis of data from mt genomes has proven challenging, e.g., due to systematic bias contributed by base compositional heterogeneity and among-site rate variation (see Song *et al*. 2010).

The identification of genes useful for reconstructing beetle phylogeny has been much aided by the genome of *Tribolium castaneum* (family Tenebrionidae). An additional beetle genome, Dendroctonus ponderosae Hopkins (Curculionidae), was recently published (Keeling *et al*. 2013). At the time of this writing there are therefore only two published annotated beetle genomes (*Tribolium* Genome Sequencing Consortium 2008). A subset of the contigs from a standard draft genome (without annotation) for the archostematan *Priacma serrata* were recently published by Niehuis *et al*. (2012), along with aligned DNA sequence matrices for 4485 1:1 orthologs from 13 endopterygote insect genomes (including *Priacma serrata* and *Tribolium castaneum*). otional beetle genomes (and transcriptomes) are in progress or will soon be published, e.g., as part of the 5000 Insect Genomes Project (i5k) and 1000 Insect Transcriptome Evolution Project (1KITE). When available, these genomic resources will further facilitate the tasks of identifying genes for use in molecular phylogenetic studies of beetles, and designing primers for amplification of genes of interest via polymerase chain reaction, and related approaches.

Taxon sampling. Most studies focused on reconstructing the phylogeny of beetles using DNA sequence data have included a diversity of Adephaga and Polyphaga. However, Archostemata have not been well sampled in most studies to date. The 18S sequence of *Distocupes* Neboiss, first published by Shull *et al*. (2001), served as the only representative for the suborder Archostemata in studies of beetle molecular phylogeny (e.g., Caterino *et al*. 2002, 2005; Vogler 2005) until the publication of Hughes *et al*. (2006) (Table 1.1), which included EST data from *Micromalthus debilis* LeConte. Even in the extensively taxon-sampled study of Hunt *et al*. (2007), Archostemata was represented only by the aforementioned 18S sequence of *Distocupes* sp.; no 16S or COI sequences were included for Archostemata. Wild & Maddison (2008) sequenced up to nine nuclear genes from the archostematans *Priacma serrata*, *Prolixocupes lobiceps* (LeConte) and *Tenomerga cinerea* (Say). This remains the most extensive gene sample of Archostemata to date, outside of mt genomes. Sheffield *et al*. (2008) analyzed mt genomes from 13 beetles, including the archostematan *Tetraphalerus bruchi* Heller *et al*. (Ommatidae) (also used in several later studies by these and other authors). McKenna & Farrell (2009) analyzed nearly complete 18S sequences from 955 genera of beetles, but Archostemata were represented only by the aforementioned *Distocupes* and by a then-new sequence for *Prolixocupes lobiceps*. Maddison *et al*. (2009) analyzed 18S and 28S sequences from four genera representing two families of Archostemata (*Cupes capitatus* Fabricius, *Micromalthus debilis, Priacma serrata* and *Tenomerga cinerea*). Their taxon sample included more representatives of Archostemata than any other molecular phylogenetic study to date. Nuclear rDNA sequences are so far only available for representatives of two (Cupedidae and Micromalthidae) of the five extant families of Archostemata.

Hydroscapha natans LeConte is the only myxophagan for which DNA sequence data are available from NPC genes (elongation factor 1-alpha, *RNA Pol II*, and *CAD*; McKenna & Farrell 2010). Published DNA sequence data for Myxophaga is otherwise limited to the genes 16S, 18S, 28S and the mt genome. Shull *et al*. (2001) sampled 18S from the myxophagans *Hydroscapha natans* and *Torridincola rhodesica* Steffan. Caterino *et al*. (2002) used the Shull *et al*. (2001) 18S sequences for *Torridincola* Steffan and *Hydroscapha* LeConte, and a "new" 18S sequence from *Sphaerius* sp. (as *Microsporus* sp.) Caterino *et al*. (2005) sampled the aforementioned 18S sequences from *Hydroscapha* and *Torridincola*, and a "new" 18S sequence was added from *Delevea bertrandi* Reichardt. *Microsporus* sp. was not included in their study. The phylogeny of Vogler (2005) included two terminals for Myxophaga (it is not clear which species were sampled). Hughes *et al*. (2006) sampled ESTs from *Sphaerius* sp. Hunt *et al*. (2007) sampled nine Myxophaga in three families, the most extensive sample of Myxophaga included in a molecular phylogenetic study to date. Hunt & Vogler (2008) sampled seven species of Myxophaga. Sheffield *et al*. (2008) analyzed mt genomes from 13 beetles, including the myxophagan *Sphaerius* sp. (also used in several later studies by these and other authors). Maddison *et al*. (2009) sampled *Hydroscapha natans, Sphaerius* sp. and *Torridincola rhodesiaca*. However, these were sequenced only for 18S and 28S (data from wingless were included for other taxa, but not for Myxophaga). McKenna & Farrell (2009) included 18S sequences from GenBank for four myxophagans. Pons *et al*. (2010) sampled mt genomes from *Hydroscapha granulum* Motschulsky and *Sphaerius* sp.

Inferring causes and consequences of "Inordinate Fondness". Hunt *et al*. (2007) published the first molecular timetree for beetles based on a

340-taxon subset of their 1880-taxon tree. Seven fossil-age constraints were used to calibrate the tree and date internal nodes. Based on this and other analyses, they concluded that the success of beetles is "explained neither by exceptional net diversification rates nor by a predominant role of herbivory and the Cretaceous rise of angiosperms". Alternatively, they proposed that the apparent success of beetles is due to low extinction rates and "sustained diversification in a variety of niches" (Hunt *et al*. 2007). McKenna & Farrell (2009) published the most extensively taxon-sampled molecular timetree for beetles to date (955 genera in 134 families). Six fossils and each of two alternative maximum constraints on the age of Endopterygota were used to calibrate the tree and date internal nodes. The split between the clade composed of Myxophaga and Archostemata and the clade composed of the sister groups Adephaga and Polyphaga was estimated to have occurred ~269–265 Ma (mean 266.8 Ma). By comparison, Hunt *et al*. (2007) fixed the age of this split at 285 Ma. McKenna & Farrell (2009) estimated that the Adephaga–Polyphaga split occurred ~269–265 Ma (mean 266.4 Ma), slightly later than Hunt *et al*. (2007), who estimated this split to have occurred ~277 Ma. McKenna & Farrell (2009) did not evaluate divergence times below the subordinal level, nor the role of angiosperms in beetle diversification, due to the lack of well-supported resolution at lower taxonomic levels. Molecular chronograms focused on individual series or superfamilies of beetles and, calibrated with temporal information to produce a timetree, are so far available only for the cucujiform superfamilies Chrysomeloidea (Farrell 1998; Gómez-Zurita *et al*. 2007) and Curculionoidea (Farrell 1998; McKenna *et al*. 2009).

Conclusions and current and future directions. Most molecular studies of higher-level relationships in beetles have relied largely or solely on data from 18S (Table 1.1) and recover topologies, under at least some analytical conditions, with Adephaga and Polyphaga as sister groups and Archostemata alone or in combination with Myxophaga as the sister group of all other beetles (Fig. 1.1) (McKenna 2011 b). Despite the relative consistency of subordinal relationships recovered in these studies, most fail to recover extensive compatible and well-supported resolution, particularly at the series and superfamily levels in Polyphaga[5]. Consequently, molecular phylogenies for beetles that are based largely or solely on 18S should be viewed as tentative, pending reinforcement from analyses of data from additional genes, particularly NPC genes. The recent nine-gene phylogeny of Wild & Maddison (2008) and the six-gene phylogeny of McKenna *et al*. (2009), although focused on specific major groups of beetles, recovered considerable well-supported resolution, a feature lacking from many other extensively taxon-sampled but lesser gene-sampled studies. A similar or even more extensive gene sample will likely be required to resolve relationships in and among other higher-level groups of beetles.

Phylogenomic approaches (other than the study of mt genomes) may ultimately be required to unambiguously resolve certain higher-level relationships in beetles. Although there remain significant hurdles to such work, this is an area where there will continue to be much growth over the next few years. Most current phylogenomic studies involving beetles are RNA-based. Although such approaches can readily contribute deep gene sampling, they have (as one of several drawbacks) the requirement of specially preserved tissue for RNA. DNA-based approaches that do not require the sequencing and de novo assembly of entire genomes (e.g., partial exome capture) are on the horizon and will likely see dramatic growth once suitable resources are developed for their application to studies of beetles. Along with genomic

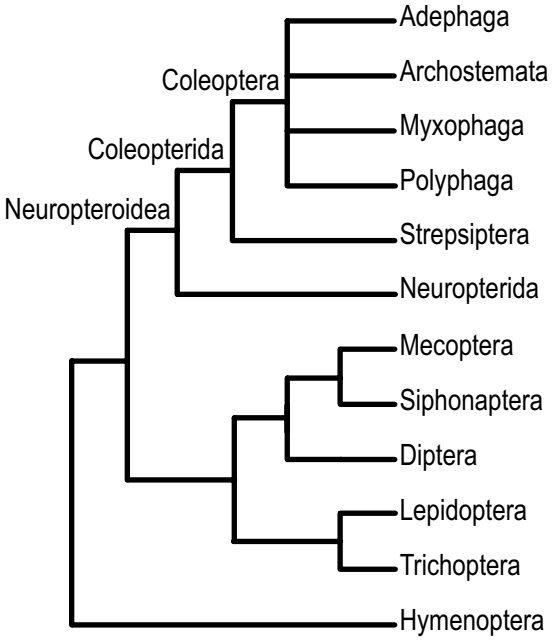

Fig. 1.1 Proposed phylogenetic placement of Coleoptera in the context of Endopterygota based on Wiegmann *et al*. (2009 a, b); McKenna & Farrell (2010); Niehuis *et al*. (2012) and McKenna (herein). The subordinal relationships of beetles are shown here as unresolved. While Adephaga and Polyphaga are recovered as sister groups in most published analyses of DNA sequence data (primarily 18S rDNA), some recent studies, e.g., Wild & Maddison (2008); McKenna & Farrell (2010); Pons *et al*. (2010) and Song *et al*. (2010), recover other arrangements.

[5] Note, although these studies sampled sufficient taxa to inform our understanding of higher-level relationships in beetles, not all of them were concerned with relationships within Polyphaga, or even across all Coleoptera.

data sets will come opportunities to expand data collection for beetles beyond that traditionally obtained from nucleotide or amino acid sequences themselves, e.g., to include information on gene content, order and structure (e.g., see Niehuis *et al*. 2012).

On account of the current lack of strong nodal support for the interrelationships and internal relationships of most supra-familial groups of beetles, it is difficult to justify detailed evaluation of the timing and causes of ecological and taxonomic diversification for most groups, let alone across the entire order. Future studies focused on obtaining compatible data from additional molecular markers for a broad cross-section of beetle taxa (especially including more Archostemata), employing appropriate and statistically rigorous methods for estimating beetle phylogeny and divergence times and taking advantage of the extensive morphological data set of Lawrence *et al*. (2011), will undoubtedly contribute further and more robust insights into beetle phylogeny and evolution, including factors contributing to the apparent extraordinary success of the order Coleoptera.

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Literature

Bernhard, D., Schmidt, C., Korte, A., Fritzsch, G. & Beutel, R. G. (2006): From terrestrial to aquatic habitats and back again – molecular insights into the evolution and phylogeny of Hydrophiloidea (Coleoptera) using multigene analyses. – *Zoologica Scripta* 35: 597–306.

Bernhard, D., Ribera, I., Komarek, A. & Beutel, R. G. (2009): Phylogenetic analysis of Hydrophiloidea (Coleoptera: Polyphaga) based on molecular data and morphological characters of adults and immature stages. – *Insect Systematics & Evolution* 40: 3–41.

Bocakova, M., Bocak, L., Hunt, T., Teravainen, M. & Vogler, A. P. (2007): Molecular phylogenetics of Elateriformia (Coleoptera): evolution of bioluminescence and neoteny. – *Cladistics* 23: 477–496.

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., Ślipiński, S. A. & Smith, A. B. T. (2011): Family-group names in Coleoptera (Insecta). – *ZooKeys* 88: 1–972.

Buder, G., Grossmann, C., Hundsdoerfer, A. & Klass, K. D. (2008): A contribution to the phylogeny of the Ciidae and its relationships with other cucujoid and tenebrionoid beetles (Coleoptera: Cucujiformia). – *Arthropod Systematics and Phylogeny* 66 (2): 165–190.

Cameron, S. L., Sullivan, J., Song, H., Miller, K. B. & Whiting, M. F. (2009): A mitochondrial genome phylogeny of the Neuropterida (lace-wings, alderflies and snakeflies) and their relationship to the other holometabolous insect orders. – *Zoologica Scripta* 38: 575–590.

Caterino, M. S., Cho, S. & Sperling, F. A. H. (2000): The current state of insect molecular systematics: a thriving tower of Babel. – *Annual Review of Entomology* 45: 1–54.

Caterino, M. S., Shull, V. L., Hammond, P. M. & Vogler, A. P. (2002): Basal relationships of Coleoptera inferred from 18S rDNA sequences. – *Zoologica Scripta* 31: 41–49.

Caterino, M. S., Hunt, T. & Vogler, A. P. (2005): On the constitution and phylogeny of Staphyliniformia (Insecta: Coleoptera). – *Molecular Phylogenetics and Evolution* 34: 655–672.

Crowson, R. A. (1955): *The Natural Classification of the Families of Coleoptera*. Nathaniel Lloyd, London.

Farrell, B. D. (1998): "Inordinate fondness" explained: Why are there so many beetles? – *Science* 281: 555–559.

Farrell, B. D. & Sequeira, A. S. (2004): Evolutionary rates in the adaptive radiation of beetles on plants. – *Evolution* 58: 1984–2001.

Gómez-Zurita, J., Hunt, T., Kopliku, F. & Vogler, A. P. (2007): Recalibrated tree of Leaf Beetles (Chrysomelidae) indicates independent diversification of angiosperms and their insect herbivores. – *PLoS ONE* 2: e360.

Howland, D. E. & Hewitt, G. M. (1995): Phylogeny of Coleoptera based on mitochondrial cytochrome oxidase I sequence data. – *Insect Molecular Biology* 4: 203–215.

Hughes, J., Longhorn, S. J., Papadopoulou, A., Theodorides, K., de Riva, A., Mejia-Chang, M., Foster, P. G. & Vogler, A. P. (2006): Dense taxonomic EST sampling and its applications for molecular systematics of the Coleoptera (beetles). – *Molecular Biology and Evolution* 23: 268–278.

Hundsdoerfer, A. K., Rheinheimer, J. & Wink, M. (2009): Towards the phylogeny of the Curculionoidea (Coleoptera): reconstructions from mitochondrial and nuclear ribosomal DNA sequences. – *Zoologischer Anzeiger* 248: 9–31.

Hunt, T., Bergsten, J., Levkanicova, Z., Papadopoulou, A., John, O. S., Wild, R., Hammond, P. M., Ahrens, D., Balke, M., Caterino, M. S., Gómez–Zurita, J., Ribera, I., Barraclough, T. G., Bocakova, M., Bocak, L. & Vogler, A. P. (2007): A

comprehensive phylogeny of beetles reveals the evolutionary origins of a superradiation. – *Science* 318: 1913–1916.

Hunt, T. & Vogler, A. P. (2008): A protocol for large-scale rRNA sequence analysis: towards a detailed phylogeny of Coleoptera. – *Molecular Phylogenetics and Evolution* 47: 289–301.

Hutchinson, G. E. (1959): Homage to Santa Rosalia, or Why are there so many kinds of animals? – *The American Naturalist* 93: 145–159.

Ishiwata, K., Sasaki, G., Ogawa, J., Miyata, T. & Su, Z. (2011): Phylogenetic relationships among insect orders based on three nuclear protein-coding gene sequences. – *Molecular Phylogenetics and Evolution* 58: 169–180.

Keeling, C. I., Yuen, M. M. S., Liao, N. Y., Docking, T. R., Chan, S. K., Taylor, G. A., Palmquist, D. L., Jackman, S. D., Nguyen, A., Li, M., Henderson, H., Janes, J. K., Zhao, Y., Pandoh, P., Moore, R., Sperling, F. A. H., Huber, D. P. W., Birol, I., Jones, S. J. M. & Bohlmann, J. (2013): Draft genome of the mountain pine beetle, Dendroctonus ponderosae Hopkins, a major forest pest. – *Genome Biology* 14: R27.

Kim, K. G., Hong, M. Y., Kim, M. J., Im, H. H., Kim, M. I., Bae, C. H., Seo, S. J., Lee, S. H. & Kim, I. (2009): Complete mitochondrial genome sequence of the yellow-spotted long-horned beetle Psacothea hilaris (Coleoptera: Cerambycidae) and phylogenetic analysis among coleopteran insects. – *Molecules and Cells* 27: 429–441.

Korte, A., Ribera, I., Beutel, R. G. & Bernhard, D. (2004): Interrelationships of Staphyliniform groups inferred from 18S and 28S rDNA sequences, with special emphasis on Hydrophiloidea (Coleoptera, Staphyliniformia). – *Journal of Zoological Systematics and Evolutionary Research* 42: 281–288.

Lawrence, J. F. & Newton, A. F. Jr. (1982): Evolution and classification of beetles. – *Annual Review of Ecology and Systematics* 13: 261–290.

– (1995): Families and subfamilies of Coleoptera (with selected genera, notes, references and data on family-group names). Pp. 779–1006 *in* Pakaluk, J. & Ślipiński, S. A. (eds.) *Biology, Phylogeny, and Classification of Coleoptera: Papers Celebrating the 80th Birthday of Roy A. Crowson.* Muzeum I Instytut Zoologii Polska Akademia Nauk, Warsaw.

Lawrence, J. F., Beutel, R. G., Leschen, R. A. B. (2010 a): Chapter 5. Derodontiformia: Introduction, Phylogeny. pp. 179–180. In: Leschen, R. A. B., Beutel, R. G. & Lawrence, J. F. (eds.). *Handbook of Zoology, Coleoptera Volume 2: Morphology and Systematics (Elateroidea, Bostrichformia, Cucujiformia partim).* Walter de Gruyter, Berlin.

Lawrence, J. F., Beutel, R. G., Leschen, R. A. B., Ślipiński, S. A. (2010 b): Chapter 1. Changes in classification and list of families. pp. 1–7. In: Leschen, R. A. B., Beutel, R. G. & Lawrence, J. F. (eds.). *Handbook of Zoology, Coleoptera Volume 2: Morphology and Systematics (Elateroidea, Bostrichformia, Cucujiformia partim).* Walter de Gruyter, Berlin.

Lawrence, J. F., Ślipiński, S. A., Seago, A. E., Thayer, M. K., Newton, A. F. & Marvaldi, A. E. (2011): Phylogeny of the Coleoptera based on morphological characters of adults and larvae. – *Annales Zoologici* 61: 1–271.

Leschen, R. A. B., Lawrence, J. F. & Ślipiński, S. A. (2005): Classification of basal Cucujoidea (Coleoptera: Polyphaga): cladistic analysis, keys and review of new families. – *Invertebrate Systematics* 19: 17–73.

Longhorn, S. J., Pohl, H. W. & Vogler, A. P. (2010): Ribosomal protein genes of holometabolan insects reject the Halteria, instead revealing a close affinity of Strepsiptera with Coleoptera. – *Molecular Phylogenetics and Evolution* 55: 846–59.

Maddison, D. R., Baker, M. D. & Ober, K. A. (1999): Phylogeny of carabid beetles as inferred from 18S ribosomal DNA. – *Systematic Entomology* 24: 103–138.

Maddison, D. R., Moore, W., Baker, M. D., Ellis, T. M., Ober, K. A., Cannone, J. J. & Gutell, R. R. (2009): Monophyly of terrestrial adephagan beetles as indicated by three nuclear genes (Coleoptera: Carabidae and Trachypachidae). – *Zoologica Scripta* 38: 43–62.

Marvaldi, A. E., Sequeira, A. S., O'Brien, C. W. & Farrell, B. D. (2002): Molecular and morphological phylogenetics of weevils (Coleoptera, Curculionoidea): do niche shifts accompany diversification? – *Systematic Biology* 51: 761–785.

Marvaldi, A. E., Duckett, C. N., Kjer, K. M. & Gillespie, J. J. (2009): Structural alignment of 18S and 28S rDNA sequences provides insights into phylogeny of Phytophaga (Coleoptera: Curculionoidea and Chrysomeloidea). – *Zoologica Scripta* 38: 63–77.

McKenna, D. D. (2011 a). Temporal lags and overlap in the diversification of weevils and flowering plants: recent advances and prospects for additional resolution. – *American Entomologist* 57: 54–55.

– (2011 b). Towards a temporal framework for "Inordinate Fondness": Reconstructing the macroevolutionary history of beetles (Coleoptera). – *Entomologica Americana* 117: 28–36.

McKenna, D. D. & Farrell, B. D. (2009): Beetles (Coleoptera). Pp. 278–289 *in* Hedges, S. B. & Kumar, S. (eds.) *The Timetree of Life.* Oxford University Press, Oxford, UK.

– (2010): 9-genes reinforce the phylogeny of Holometabola and yield alternate views on the phylogenetic placement of Strepsiptera. *PLoS ONE* 5: e11887.

McKenna, D. D., Sequeira, A. S., Marvaldi, A. E. & Farrell, B. D. (2009): Temporal lags and overlap in the diversification of weevils and flowering plants. *Proceedings of the National Academy of Sciences USA* 106: 7083–7088.

Niehuis, O., Hartig, G., Grath, S., Pohl, H., Lehmann, J., Tafer, H., Donath, A., Krauss, V., Eisenhardt, C., Hertel, J., Petersen, M., Mayer, C., Meusemann, K., Peters, R., Stadler, P., Beutel, R., Bornberg-Bauer, E., McKenna, D. D. & Misof, B. (2012): Genomic and morphological evidence converge to resolve the enigma of Strepsiptera. – *Current Biology* 22: 1309–13.

Pons, J., Ribera, I., Bertranpetit, J. & Balke, M. (2010): Nucleotide substitution rates for the full set of mitochondrial protein-coding genes in Coleoptera. – *Molecular Phylogenetics and Evolution* 56: 796–807.

Ribera, I., Hogan, J. E. & Vogler, A. P. (2002): Phylogeny of hydradephagan water beetles inferred from 18S rDNA sequences. – *Molecular Phylogenetics and Evolution* 23: 43–62.

Robertson, J. A., McHugh, J. V. & Whiting, M. F. (2004): A molecular phylogenetic analysis of the leasing fungus beetles (Coleoptera: Erotylidae): evolution of colour patterns, gregariousness and mycophagy. – *Systematic Entomology* 29: 173–187.

Robertson, J. A., Whiting, M. F. & McHugh, J. V. (2008): Searching for natural lineages within the Cerylonid Series (Coleoptera: Cucujoidea). – *Molecular Phylogenetics and Evolution* 46 (1): 193–205.

Sheffield, N. C., Song, H., Cameron, S. L. & Whiting, M. F. (2008): A comparative analysis of mitochondrial genomes in Coleoptera (Arthropoda: Insecta) and genome descriptions of six new beetles. – *Molecular Biology and Evolution* 25: 2499–2509.

– (2009): Nonstationary evolution and compositional heterogeneity in beetle mitochondrial phylogenomics. – *Systematic Biology* 58: 381–394.

Shull, V. L., Vogler, A. P., Baker, M. D., Maddison, D. R. & Hammond, P. M. (2001): Sequence alignment of 18S ribosomal RNA and the basal relationships of Adephagan beetles: evidence for monophyly of aquatic families and the placement of Trachypachidae. – *Systematic Biology* 50: 945–969.

Smith, A. B. T., Hawks, D. C., & Heraty, J. M. (2006): *An Overview of the Classification and Evolution of the Major Scarab Beetle Clades (Coleoptera: Scarabaeoidea) Based on Preliminary Molecular Analyses. Papers in Entomology, Paper 121*. University of Nebraska State Museum, Lincoln. Available at: http://digitalcommons.unl.edu/entomologypapers/121.

Song, H., Sheffield, N. C., Cameron, S. L., Miller, K. B. & Whiting, M. F. (2010): When the phylogenetic assumptions are violated: the effect of base compositional heterogeneity and among-site rate variation in beetle mitochondrial phylogenomics. – *Systematic Entomology* 35: 429–448.

Timmermans, M. J. T. N. & Vogler, A. P. (2012): Phylogenetically informative rearrangements in mitochondrial genomes of Coleoptera, and monophyly of aquatic elateriform beetles (Dryopoidea). – *Molecular Phylogenetics and Evolution* 63: 299–304.

Tribolium Genome Sequencing Consortium (2008): The genome of the model beetle and pest – *Tribolium castaneum. Nature* 452: 949–955.

Vogler, A. P. & Caterino, M. S. (2003): The basal relationships of Coleoptera based on 18S rRNA sequences. – *Entomologische Abhandlungen* 61: 159–160.

Vogler, A. (2005): Molecular systematics of Coleoptera: what has been achieved so far? Pp. 17–22 in Beutel, R. G. & Leschen, R. A. B. (eds.) *Handbook of Zoology, Vol. IV Arthropoda: Insecta. Part 38. Coleoptera, Vol. 1: Morphology and Systematics (Archostemata, Adephaga, Myxophaga, Polyphaga (partim).* DeGruyter, Berlin.

Whiting, M. F. (2002): Phylogeny of the holometabolous insect orders: molecular evidence. – *Zoologica Scripta* 31: 3–17.

Wiegmann, B. M., Kim, J. & Trautwein, M. D. (2009 a): Holometabolous Insects (Holometabola). Pp. 260 – 263 in Hedges, B., & Kumar, S. (eds.) *The Timetree of Life*. Oxford University Press, Oxford, UK.

Wiegmann, B. M., Trautwein, M. D., Kim, J., Cassel, B. K., Bertone, M., Winterton, S. L. & Yeates, D. K. (2009 b): Single-copy nuclear genes resolve the phylogeny of the holometabolous insects. – *BMC Biology* 7: 34.

Wild, A. L. & Maddison, D. R. (2008): Evaluating nuclear protein-coding genes for phylogenetic utility in the Coleoptera. – *Molecular Phylogenetics and Evolution* 48: 877–891.

2 Chrysomeloidea Latreille, 1802

Chris A. M. Reid

Introduction. The megadiverse leaf, seed and longhorned beetles (Chrysomelidae, Megalopodidae, Orsodacnidae, Cerambycidae, Vesperidae, Oxypeltidae, Disteniidae) consist of large and often brightly colored species that are well-represented in collections. Their taxonomy has been puzzling for a long time, and their classification has been the source of considerable dispute. In the last 15 years, some consensus has been achieved through the application of modern analytical methods to both morphological and molecular data.

Early Classification. In the first half of the 20th century, three major assemblages of Chrysomeloidea were commonly recognized, usually as the families Chrysomelidae, Bruchidae and Cerambycidae (Crowson 1955). Occasionally this has been reduced to two, Chrysomelidae and Cerambycidae (by dropping one rank in Böving & Craighead 1931), or all subfamilies were given family rank in separate superfamilies. [See Crowson 1955; Seeno & Wilcox 1982; Svacha & Danilevsky 1987; Reid 1995 a, Schmitt 1996; Svacha *et al*. 1997 (background history) and Bouchard *et al*. 2011 (validity of family rank names).]

Roy Crowson was the first to seriously challenge this triumvirate, combining evidence from larvae (Böving & Craghead 1931), his own studies on the metendosternite (Crowson 1938, 1944) and new anatomical research (Crowson 1955). He showed that Bruchidae belong within Chrysomelidae *sensu lato*, or with Sagrinae, Donaciinae and Criocerinae in a separate family. He also noted the similarity of Megalopodinae *sensu lato* to Cerambycidae and the "primitiveness" of Orsodacninae, but failed to appreciate the distinctiveness of Aulacoscelidinae. Crowson discussed possible division of the Cerambycidae but considered that there were "too many intermediate forms" (Crowson 1955).

Crowson's early work on chrysomeloids strongly influenced Monrós (1960: Fig. 1 A), who identified three separate lineages, Cerambycidae, "legion Chrysomelae" and "legion Alticae". Bruchidae were given family rank but were recognized as an offshoot within "Chrysomelae", sister to Sagrinae. This work was overlooked. Instead, misinterpretation of Crowson's early comments about the "primitiveness" of Sagrinae (at that time including all of the most morphologically plesiomorphic taxa in Chrysomelidae; Crowson 1946) led to classifications placing Sagrinae as the ancestors of all, or most other, Chrysomelidae (Jolivet 1959, 1988; Medvedev 1971).

Crowson developed theories about the evolution of Chrysomelidae in a series of collaborative studies (Kasap & Crowson 1976, 1979, 1980, 1985; Mann & Crowson 1981, 1983 a–c, 1984). However, this body of work was published without any resolution of the various conflicting phylogenies and probably for that reason was largely ignored by chrysomelid and cerambycid workers (e.g., Seeno & Wilcox 1982). One interpretation of these studies was presented by Crowson (1981), with the recognition of five families in Chrysomeloidea: Disteniidae, Cerambycidae, Megalopodidae, Bruchidae (including three former chrysomelid subfamilies) and Chrysomelidae, but without formal justification.

Modern Period. The classification of Cerambycidae was revised in a thorough study of larval morphology based on most of the critical taxa (Svacha & Danilevsky 1987). This work provided justification for separation of four families from the old Cerambycidae (e.g., of Crowson 1955), the Anoplodermatidae, Disteniidae, Oxypeltidae and Vesperidae, as well as the recognition of eight subfamilies of Cerambycidae.

Discovery of the larva of a genus related to the enigmatic *Cucujopsis* Crowson led the curculionoid specialists Kuschel & May (1990) to erect a new subfamily, Palophaginae, and make a detailed assessment of the "primitive" chrysomeloids. They separated both Megalopodidae (with three subfamilies, including Palophaginae) and Orsodacnidae (with two subfamilies, treated by Crowson as Chrysomelidae) from Chrysomelidae, based on a number of characters. Furthermore, they reunited Bruchidae and Chrysomelidae but did not treat these groups further, and overlooked the work of Svacha & Danilevsky (1987) on cerambycids.

By the early 1990s, Chrysomeloidea included four families, Cerambycidae, Megalopodidae, Orsodacnidae and Chrysomelidae (Kuschel & May 1990). There had been no formal cladistic analysis of the relationships of these groups or their constituent subfamilies (the most useful unit for phylogenetic study in the group). This was provided by Reid's (1995 a) study of 29 family rank taxa and 71 characters culled from literature. The character set was selected to resolve relationships within Chrysomelidae, so the study included an incomplete sample of "cerambycoids" (only Disteniidae, Anoplodermatidae, Vesperidae and four subfamilies of Cerambycidae) and did not allow the testing of some traditional subfamilies, which were treated as single terminal taxa: Hispinae = Cassidinae +

Hispinae (separately non-monophyletic; Crowson 1955; Borowiec 1995); Galerucinae = Alticinae + Galerucinae (separately non-monophyletic; Böving & Craighead 1931; Crowson 1981; Reid 1992); Cryptocephalinae = Clytrinae + Cryptocephalinae + Chlamisinae (probably monophyletic, but poorly distinguished and treated as part of one subfamily by Crowson 1955, 1981; Reid 2000). To circumvent the problem of scoring characters in enormously variable taxa (e.g., up to 12,000 species in Galerucinae), "most plesiomorphic" states were assigned based on outgroup comparison prior to analysis. Three significant larval forms were unknown and not scored (Aulacoscelidinae, Megascelidini, Spilopyrini). The cladistic analysis revealed considerable conflict between adult and larval characters and low resolution of the data set without a priori weighting. However, there was strong support for a three-family division suggested by Kuschel & May (1990), Megalopodidae, Orsodacnidae and Chrysomelidae, with some support for their separation from a monophyletic cerambycoid group. Bruchinae were resolved as sister to Sagrinae, Lamprosomatinae sister to Cryptocephalinae and Chrysomelinae usually grouped with Galerucinae. The position of several taxa, including Synetini, was unclear. The results suggested that the evolution of Chrysomelidae began with leaf feeding adults and larvae on angiosperms, with subsequent radiations on dicots and through cryptic soil inhabiting larvae. However, the absence of data for three larval types significantly compromised this analysis and errors were made in scoring (Reid 1995 b). The data set published by Reid (1995 a) was independently re-analysed by Schmitt (1996), with similar results but different conclusions due to a much more conservative approach to taxonomy. The morphological analyses by Reid (1995 a) were later revised (Reid 2000) using descriptions of the previously unknown larvae of Aulacoscelidinae (Cox & Windsor 1999), Megascelidini (Cox 1998) and Spilopyrini (Jerez & Ibarra-Vidal 1992), and treating only Chrysomeloidea in a narrow sense (excluding cerambycoids). The new data confirmed the systematic positions of Aulacoscelidinae (with Orsodacninae) and Megascelidini (in Eumolpinae) but suggested that Spilopyrini be elevated to subfamily rank, as sister of at least two other subfamilies. As before, relationships were only weakly resolved, but Bruchinae + Sagrinae and Lamprosomatinae + Cryptocephalinae were confirmed and there was some support for Galerucinae + Chrysomelinae and Synetini + Eumolpinae.

Meanwhile, the discovery of the larva of the cerambycoid Philinae had allowed Svacha *et al.* (1997) to revisit the classification of cerambycids. Using both adult and larval characters, the families and subfamilies, Oxypeltidae, Vesperidae (including former Anoplodermatidae), Disteniidae and Cerambycidae (with eight subfamilies) were revised, with results that have been widely accepted (Bouchard *et al.* 2011; Monné 2012). The present state of cerambycid classification is discussed in the following cerambycoid chapters, and the remainder of this chapter deals with the remaining chrysomeloids.

Analyses of molecular data sets began in the 1990s with the first application to Chrysomelidae based on eleven species, each representing a different family-group taxa, and a short sequence of *12S mtDNA* (Hsiao 1994). This pioneering study provided support for combining Chlamisinae and Clytrinae under Cryptocephalinae. Farrell (1998) produced the first large scale molecular study of chrysomelid relationships, coding *18S rRNA* for 115 species of Phytophaga, including most chrysomelid subfamilies. Though criticized (Reid 2000; Chaboo 2007; Franz & Engel 2010), the results supported the three family structure, Megalopod-idae, Orsodacnidae and Chrysomelidae, the latter including Bruchinae.

The monophyly of each of the subgroups Galerucinae and Alticinae was tested by Lingafelter & Konstantinov (1999), who recovered a monophyletic Alticinae that rendered the Galerucinae paraphyletic. However, their conclusion was a misinterpretation, as *Orthaltica* Crotch was considered an alticine despite not having a metafemoral spring (Reid 1992). The monophyly of each of the taxa Cassidinae and Hispinae was tested by Chaboo (2007), who showed conclusively that neither was monophyletic as traditionally understood, but that an expanded Cassidini was monophyletic within paraphyletic "Hispinae". The oldest name for this combined subfamily is Cassidinae (Chen 1940).

In the last 15 years there have been many molecular studies of the Chrysomeloidea, some of them in conjunction with morphological data, generally focusing on either family-rank classifications or internal relationships within the subfamilies. Farrell's (1998) *18S* data set was re-analyzed with the addition of a small number of taxa (77 species in total from chrysomeloid families) by Farrell & Sequiera (2004) and combined with morphological data from Reid (1995 a, 2000) and Svacha *et al.* (1997). Their analysis of molecular data indicated that Orsodacninae was contained within Cerambycidae, distantly related to Aulacoscelidinae. Orsodacninae were omitted from the preferred phylogenetic scenario based on both character sets (Farrell & Sequiera 2004: Fig. 4), with other relationships similar to Reid (2000), where Megalopodidae and Aulacoscelidinae were isolated from Chrysomelidae. Sagrinae + Bruchinae were monophyletic; the sagroid subfamilies (Sagrinae + Bruchinae, Donaciinae and Criocerinae) were paraphyletic; Cassidinae were sister to the non-sagroids; Spilopyrinae were sister to Eumolpinae, Lamprosomatinae and Cryptocephalinae; the two latter were sister taxa; Synetini were placed with Eumolpinae; Chrysomelinae and Galerucinae were sister taxa.

Also using *18S* combined with morphological data from Reid (1995 a, 2000), Duckett *et al.* (2004) scored 113 species in 20 chrysomeloid subfamilies.

This study omitted Sagrinae and Spilopyrinae and was biased towards Galerucinae, with 43% of terminal taxa belonging to this subfamily. They used the tertiary structure of *18S rRNA* and the relationships for Megalopodidae, Orsodacnidae and Chrysomelidae were as shown in Reid (1995 a). A monophyletic group of Bruchinae, Donaciinae and Criocerinae was sister to remaining Chrysomelidae in all analyses. Their preferred option, by weighted parsimony analysis, resolved Megascelidini in Eumolpinae, Synetini separated from Eumolpinae as sister to (Lamprosomatinae + Cryptocephalinae) and a clade [Cassidinae + (Chrysomelinae + Galerucinae)]. This study suggested that host-plant shifts to dicots preceded species radiations in the Chrysomelidae.

More recently there has been a series of studies using multiple gene sequences. Gomez-Zurita and co-workers have pioneered the multigene approach in Chrysomelidae, using *16S rRNA*, *18S rRNA* and *28S rRNA* (Gomez-Zuirita *et al*. 2007, 2008) and *18S rRNA*, *16S rRNA* and *CO1* (Hunt *et al*. 2007). Four subfamilies, Palophaginae, Zeugophorinae, Sagrinae and Lamprosomatinae, were not sampled by Gomez-Zurita *et al*. (2007, 2008). The results of each study differed but can be summarized as follows: Megalopodidae and Orsodacnidae were mixed with cerambycoids, which were polyphyletic; a sagrine clade included Bruchinae, Donaciinae and Criocerinae (but not in Hunt *et al*. 2007) and was sister to the remaining Chrysomelidae; Chrysomelinae were paraphyletic with respect to Galerucinae; Spilopyrinae were sister to paraphyletic Eumolpinae, Cassidinae and Cryptocephalinae; the position of Synetini was unresolved.

Marvaldi *et al*. (2009) modeled the tertiary structure of the *18S* and *28S rRNA* molecules in Phytophaga to obtain alignments. Their study included only 23 species of chrysomelids, and most subfamilies were not resolved as monophyletic.

The largest and most comprehensive morphological study of Coleoptera to date, by Lawrence *et al*. (2011), was designed to test higher order relationships so included only six subfamilies of Chrysomelidae. It corroborated the monophyly of Chrysomelidae (including Bruchinae), the monophyly of cerambycoids and the isolated positions of Megalopodidae and Orsodacnidae.

Franz & Engel (2010) have critically reviewed molecular studies in Phytophaga, including Chrysomeloidea, and provided guidelines for future studies. They recommended the study of relationships within smaller taxa such as subfamilies. Important recent phylogenetic studies of single chrysomelid subfamilies are as follows (more detailed discussions are presented in the subfamily chapters).

Bruchinae: a combination of nine different molecular analyses of bruchine taxa was presented by Kergoat *et al*. (2008), rejecting the traditional arrangement of tribes.

Cassidinae: based on morphological data, Chaboo (2007) showed conclusively that neither traditional "Hispinae" nor "Cassidinae" are monophyletic, although the latter could be rendered monophyletic by inclusion of a few hispine taxa.

Chrysomelinae: Gomez-Zurita *et al*. (2007, 2008) recently suggested the non-monophyly of the subfamily, but this has not been supported in a study of Galerucinae, including many chrysomeline taxa (Ge *et al*. 2012). Jurado-Rivera *et al*. (2009) combined *CO1* and *EF-1a* genes to study the relationships of 81 species and their hostplants, the results of which contradicted the traditional classification of Daccordi (1996).

Donaciinae: Kölsch & Pedersen (2008) used t CO1 and *EF-1a* genes to provide a well-resolved phylogeny to examine host-plant relationships.

Eumolpinae: Gomez-Zurita *et al*. (2005) combined *16S rRNA*, *18S rRNA* and *28S rRNA* and morphological characters for 57 species of Eumolpinae, Spilopyrinae, Megascelidini and Synetini. The results suggested isolated positions for Spilopyrinae and Synetinae and the inclusion of Megascelidini.

Galerucinae: non-monophyly of alticines and galerucines was suggested by two molecular studies, using *28S-D2 rRNA* (Kim *et al*. 2003), and *18S rDNA* (Duckett *et al*. 2004). A multigene analysis of *rrnl mtDNA*, *cox1 mtDNA*, *LSU rRNA* and *SSU rRNAn* genes with a large taxon sample (Ge *et al*. 2012) has convincingly shown non-monophyly of both groups.

Lamprosomatinae: a morphological study by Chamorro & Konstantinov (2011) resolved the placement of Sphaerocharitini in Lamprosomatinae (some authors had suggested that Sphaerocharitini should be elevated to subfamily status, e.g., Kasap & Crowson 1976).

Summary

There is clear evidence from morphological (e.g., Reid 2000) and molecular studies (e.g., Gomez-Zurita *et al*. 2008) for the following relationships: Megalopodidae (including Zeugophorinae) and Orsodacnidae (including Aulacoscelidinae) do not belong within Chrysomelidae; there is a sagrine clade consisting of Donaciinae, Criocerinae, Bruchinae and Sagrinae; Bruchinae and Sagrinae are sister taxa; Galerucinae and Chrysomelinae are sister taxa; Galerucinae include the traditional alticines and neither of the traditional "Galerucinae" or "Alticinae" are monophyletic; Cassidinae include the traditional hispines and neither of the traditional "Cassidinae" or "Hispinae" are monophyletic; Lamprosomatinae and Cryptocephalinae are sister taxa; Spilopyrinae are sister to more than

one subfamily; Eumolpinae include Magascelidini. In contrast, the relationship of Cassidinae to other subfamilies remains uncertain, whereas the position of Synetini is not clear from morphological or molecular data, which suggests possible status as a separate subfamily, Synetinae.

Literature

Borowiec, L. (1995): Tribal classification of the cassidoid Hispinae (Coleoptera: Chrysomelidae). Pp. 541–558 *in* Pakaluk, J. & Ślipiński, S. A. (eds) *Biology, Phylogeny and Classification of Coleoptera. Papers Celebrating the 80th Birthday of Roy A. Crowson*. Muzeum i Instytut Zoologii PAN, Warszawa.

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., Ślipiński, S. A. & Smith, A. B. T. (2011): Family group names in Coleoptera (Insecta). – *ZooKeys* 88: 1–972.

Böving, A. G. & Craighead, F. C. (1931): *An Illustrated Synopsis of the Principal Larval Forms of the Order Coleoptera*. Pp. viii + 351 pp. Brooklyn Entomological Society, New York.

Chaboo, C. S. (2007): Biology and phylogeny of the Cassidinae Gyllenhal *sensu lato* (tortoise and leaf-mining beetles) (Coleoptera: Chrysomelidae). – *Bulletin of the American Museum of Natural History*. 305: 1–250.

Chamorro, M. L. & Konstantinov, A. S. (2011): Cachiporrini, a remarkable new tribe of Lamprosomatinae (Coleoptera, Chrysomelidae) from South America. – *ZooKeys* 78: 43–59.

Chen, S. (1940): Attempt at a new classification of the leaf beetles. – *Sinensia* 11 (5–6): 451–481.

Cox, M. L. (1998): The first-instar larva of *Megascelis puella* Lacordaire (Coleoptera: Chrysomelidae: Megascelinae) and its value in the placement of the Megascelinae. – *Journal of Natural History* 32: 387–403.

Cox, M. L. & Windsor, D. M. (1999): The first instar larva of *Aulacoscelis appendiculata* n. sp. (Coleoptera: Chrysomelidae: Aulacoscelinae) and its value in the placement of the Aulacoscelinae. – *Journal of Natural History* 33: 1049–1087.

Crowson, R. A. (1938): The metendosternite in Coleoptera: a comparative study. – *Transactions of the Royal Entomological Society, London* 87: 379–416.

– (1944): Further studies on the metendosternite in Coleoptera. – *Transactions of the Royal Entomological Society, London* 94: 273–310.

– (1946): A revision of the genera of the chrysomelid group Sagrinae (Coleoptera). – *Transactions of the Royal Entomological Society, London* 94: 273–310.

– (1955): *The Natural Classification of the Families of Coleoptera*. Nathaniel Lloyd, London. 187 pp.

– (1970): *Classification and Biology*. 350 pp Heinemann Educational Books, London.

– (1981): *The Biology of the Coleoptera*. xii + 802 pp Academic Press, London.

Daccordi, M. (1996): Notes on the distribution of the Chrysomelinae and their possible origin. Pp. 399–412 *in* Jolivet, P. H. & Cox, M. L. (eds) *Chrysomelidae Biology, Vol. 1: The Classification, Phylogeny and Genetics*. SPB Academic Publishing, Amsterdam.

Duckett, C. N., Gillespie, J. J. & Kjer, K. M. (2004): Relationships among the subfamilies of Chrysomelidae inferred from small subunit ribosomal DNA and morphology, with special emphasis on the relationship among the flea beetles and the Galerucinae. pp. 3–18 *in* Jolivet, P. H. A., Santiago-Blay, J. A. & Schmitt, M. (eds.) *New Developments in the Biology of Chrysomelidae*. SPB Academic Publishing, The Hague.

Farrell, B. D. (1998): Inordinate fondness explained: why are there so many beetles? – *Science* 281: 555–559.

Farrell, B. D. & Sequeira, A. S. (2004): Evolutionary rates in the adaptive radiation of beetles on plants. – *Evolution* 58: 1984–2001.

Franz, N. M. & Engel, M. S. (2010): Can higher level phylogenies of weevils explain their evolutionary success? A critical review. – *Systematic Entomology* 35: 597–606.

Ge, D., Chesters, D., Gomez-Zurita, J., Zhang, L., Yang, X. & Vogler, A. P. (2011): Anti predator defence drives parallel morphological evolution in flea beetles. – *Proceedings of the Royal Society Biological Sciences Series B* 278: 2133–2141.

Gomez-Zurita, J., Hunt, T., Kopliku, F. & Vogler, A. P. (2007): Recalibrated tree of leaf beetles indicates independent diversification of angiosperms and their insect herbivores. – *PLoS One* 2: 1–8.

Gomez-Zurita, J., Hunt, T. & Vogler, A. P. (2008): Multilocus ribosomal RNA phylogeny of the leaf beetles (Chrysomelidae). – *Cladistics* 24: 34–50.

Gomez-Zurita, J., Jolivet, P. & Vogler, A. P. (2005): Molecular systematics of Eumolpinae and the relationships with Spilopyrinae (Coleopetra, Chrysomelidae). – *Molecular Phylogenetics and Evolution* 34: 584–600.

Hennig, (1966): *Phylogenetic Systematics*. 263 pp. University of Illinois Press, Urbana.

Hsiao, T. H. (1994): Molecular techniques for studying systematics and phylogeny of Chrysomelidae. pp. 237–248 *in* Jolivet, P. H., Cox, M. L. & Petitpierre, E. (eds.) *Novel Aspects of the Biology of Chrysomelidae*. Kluwer Academic Publishing, Dordrecht.

Hunt, T., Bergsten, J., Levkanicova, Z., Papadopoulou, A., St John, O., Wild, R., Hammond, P. M., Ahrens, D., Balke, M., Caterino, M. S., Gomez-Zurita, J., Ribera, I., Barraclough, T. G., Bocakova, M., Bocak, L. & Vogler, A. P. (2007): A comprehensive phylogeny of beetles reveals the evolutionary origins of a superradiation. – *Science* 318: 1913–1916.

Jerez, V. & Ibarra-Vidal, H. (1992): Morfología y bionomía de *Hornius grandis* (Phil. y Phil. 1864). (Chrysomelidae, Eumolpinae). – *Bolletin de la Sociedad Biologica de Concepción* 63: 93–100.

Jolivet, P. H. (1959): Recherches sur l'aile des Chrysomeloidea (Coleoptera). Deuxieme partie. – *Mémoires de l'Institut royale des Sciences naturelles de Belgique* 2 (58): 1–152.

– (1988): Food habits and food selection of Chyrysomelidae. Bionomic and evolutionary perspectives. pp. 1–24 *in* Jolivet, P. H., Petitpierre, T. H. & Hsiao, T. H.

(eds.) *Biology of Chrysomelidae*. Kluwer Academic Publishing, Dordrecht.

Jurado-Rivera, J. A., Vogler, A. P., Reid, C. A. M., Petitpierre, E. & Gomez-Zurita, J. (2009): DNA barcoding insect-host plant associations. – *Proceedings of the Royal Society Biological Sciences Series B* 276 (1657): 639–648.

Kasap, H. & Crowson, R. A. (1976): On systematic relations of *Oomorphus concolor* (Sturm) (Col., Chrysomelidae), with descriptions of its larva and of an aberrant cryptocephaline larva from Australia. – *Journal of Natural History* 10 (1): 99–112.

– (1979): The male reproductive organs of Bruchidae and Chrysomelidae (Coleoptera). – *Turkiye Bitki Koruma Dergisi* 3 (4): 199–216.

– (1980): The female reproductive organs of Bruchidae and Chrysomelidae (Coleoptera). – *Turkiye Bitki Koruma Dergisi* 4 (2): 85–102.

– (1985): The studies on the ovipositors and eighth abdominal segments of some species of Bruchidae and Chrysomelidae (Coleoptera). – *Turkiye Bitki Koruma Dergisi* 9 (3): 131–145.

Kergoat, G., Delobel, A., Le Ru, B. & Silvain, J.-F. (2008): Seed beetles in the age of the molecule: recent advances on systematics and host-plant association patterns, pp. 59–86 *in* Jolivet, P., Santiago-Blay, J. & Schmitt, M. (eds) *Research on Chrysomelidae, Volume 1*. Brill, Leiden.

Kim, S., Kjer, K. M. & Duckett, C. N. (2003): Comparison between molecular and morphological-based phylogenies of galerucine/alticine leaf beetles. (Coleoptera: Chrysomelidae). – *Insect Systematics and Evolution* 34: 53–64.

Kolsch, G. & Pedersen, B. V. (2008): Molecular phylogeny of reed beetles (Col., Chrysomelidae, Donaciinae): the signature of ecological specialization and geographical isolation. – *Molecular Phylogenetics and Evolution* 48: 936–952.

Kuschel, G. (1995): A phylogenetic classification of Curculionoidea to families and subfamilies. – *Memoirs of the Entomological Society of Washington* 14: 5–33.

Kuschel, G. & May, B. M. (1990): Palophaginae: a new subfamily for leaf-beetles, feeding as adult and larva on araucarian pollen in Australia (Coleoptera: Megalopodidae). – *Invertebrate Taxonomy* 3: 697–719.

Lawrence, J. F., Ślipiński, A., Seago, A., Thayer, M. K., Newton, A. F. & Marvaldi, A. E. (2011): Phylogeny of the Coleoptera based on morphological characters of adults and larvae. – *Annales Zoologici* 61 (1): 1–217.

Lingafelter, S. W. & Konstantinov, A. S. (1999): The monophyly and relative rank of alticine and galerucine leaf-beetles: a cladistic analysis using adult morphological characters (Coleoptera: Chrysomelidae). – *Entomologica Scandinavica* (4) 30: 397–416.

Mann, J. S. & Crowson, R. A. (1981): The systematic positions of *Orsodacne* Latr. and *Syneta* Lac. (Coleoptera Chrysomelidae), in relation to characters of larvae, internal anatomy and tarsal vestiture. – *Journal of Natural History* 15: 727–749.

– (1983 a): On the occurrence of mid-gut caeca, and organs of symbiont transmission, in leaf-beetles (Coleoptera: Chrysomelidae). – *Coleopterists Bulletin* 37 (1): 1–15.

– (1983 b): On the internal male reprouctive organs and their taxonomic significance in the leaf beetles. – *Entomologia Generalis* 9 (1–2): 75–99.

– (1983 c): Phylogenetic significances of the ventral nerve cord in the Chrysomeloidea (Coleoptera, Phytophaga). – *Systematic Entomology* 8: 103–119.

– (1984): On the digitiform sensilla of adult leaf beetles (Coleoptera: Chrysomelidae). – *Entomologia Generalis* 9 (3): 121–133.

Marvaldi, A. E., Duckett, C. N., Kjer, K. M. & Gillespie, J. J. (2009): Structural alignment of 18s and 28s rDNA sequences provides insights into phylogeny of Phytophaga (Coleoptera: Curculionoidea and Chrysomeloidea). – *Zoologica Scripta* 38: 63–77.

Medvedev, L. N. (1971): The ways of evolution and the phylogeny of Chrysomelidae (Coleoptera). – *Proceedings of the 13th International Congress of Entomology.* Moscow (1968) 1: 271.

Monné, M. A. (2012): Catalogue of the type-species of the genera of the Cerambycidae, Disteniidae, Oxypeltidae and Vesperidae (Coleoptera) of the Neotropical Region. – *Zootaxa* 3213: 1–183.

Monrós, F. (1960): Los generos de Chrysomelidae (Coleoptera). – *Opera lilloana* 3 [1959]: 5–337, pls 1–3.

Reid, C. A. M. (1992): The leaf-beetle genus *Microdonacia* Blackburn (Coleoptera: Chrysomelidae: Galerucinae): revision and systematic placement. – *Systematic Entomology* 17: 359–387.

– (1995 a): 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*. Muzeum i Instytut Zoologii PAN, Warszawa.

– (1995 b): Errors noted, changes needed. – *Chrysomela* 30: 4.

– (2000): Spilopyrinae Chapuis: a new subfamily in the Chrysomelidae and its systematic placement (Coleoptera). – *Invertebrate Taxonomy* 14: 837–862.

Schmitt, M. (1996): The phylogenetic system of the Chrysomelidae – history of ideas and present state of knowledge. Pp. 57–96 *in* Jolivet, P. H. A. & Cox, M. L. (eds) *Chrysomelidae Biology, Volume 1. The Classification, Phylogeny and Genetics*. SPB Academic Publishing, Amsterdam.

Seeno, T. N. & Wilcox, J. A. (1982): Leaf beetle genera (Coleoptera, Chrysomelidae). – *Entomography* 1: 1–221.

Svacha, P. & Danilevsky, M. L. (1987): Cerambycoid larvae of Europe and Soviet Union (Coleoptera, Cerambycoidea). Part 1. – *Acta Universitatis Carolinae, Biologica* 30 [1986]: 1–176.

Svacha, P., Wang, J. & Chen, S. (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* 33 (3): 323–369.

2.1 Vesperidae Mulsant, 1839

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

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

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

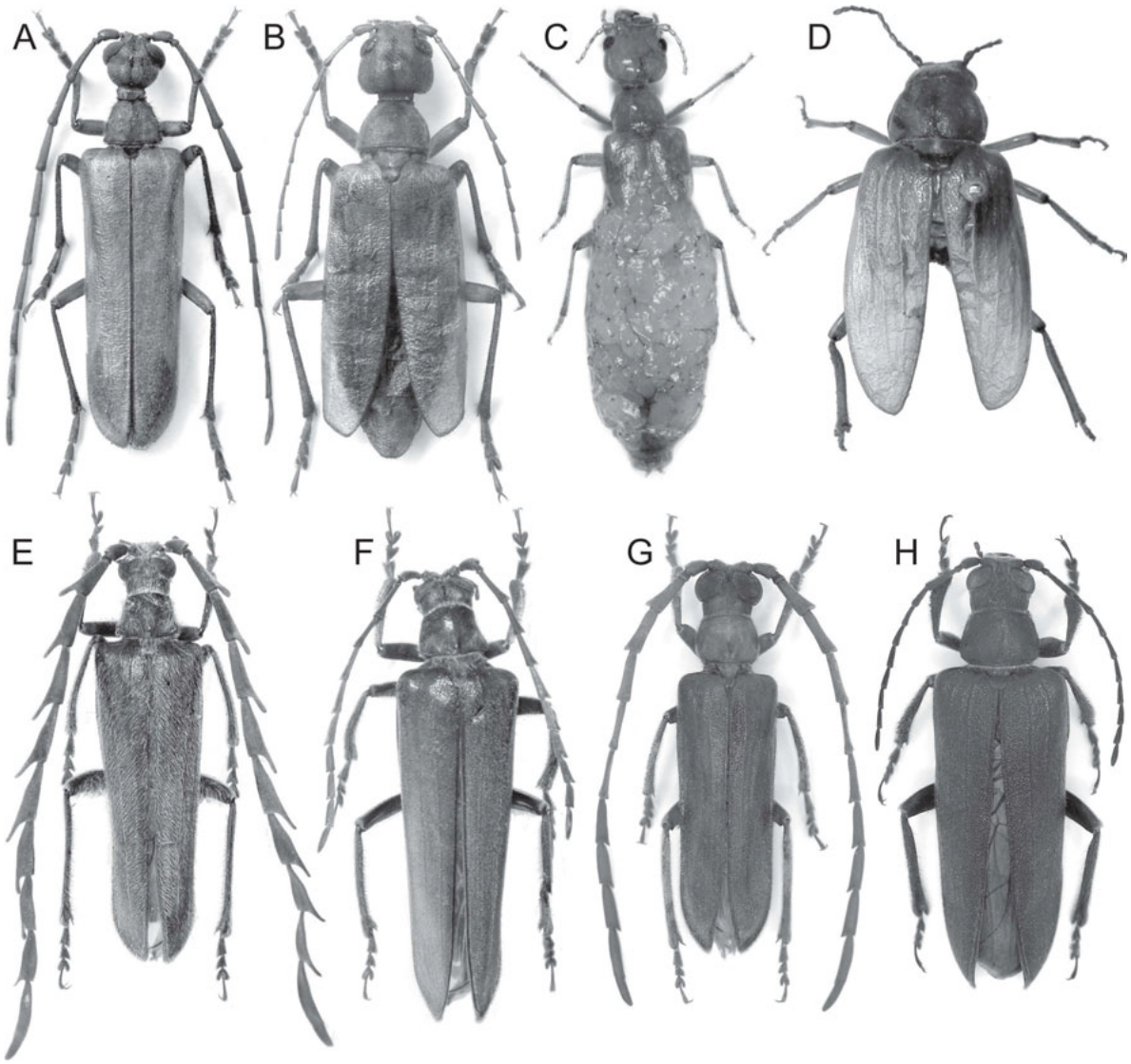

Fig. 2.1.1 Adults of Vesperinae (A–C) and Philinae (D–H), dorsal view. A, *Vesperus strepens* (Fabricius), male, 21 mm (© I. Jeniš); B, *V. strepens*, female, 23 mm (© I. Jeniš); C, *V. jertensis* Bercedo & Bahillo, female with incomplete antennae, 17.5 mm (from Calvo Sánchez 2008, © F. Calvo Sánchez);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

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

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

Recorded enemies are usually unspecific. Flying males of *Vesperus* are apparently attacked by bats, as Peslier & Mazel (2009) observed numerous living males lying on the ground with missing abdomens and mutilated thoraces. Night-active ants and,

less frequently, scorpions and solifuges were the main predators of the flightless females of *V. sanzi* Reitter (Calvo Sánchez 2007), and various spiders (including orb-web builders in the case of males) captured *V. macropterus* (Sechi 2011). *Philus* adults were preyed upon by birds, and specimens were seen naturally infested by the entomopathogenic fungus *Beauveria bassiana* (Svacha *et al.* 1997). Adults of *Migdolus* (mostly the active free-living males) may be parasitized by flies of the family Sarcophagidae (Botelho & Degaspari 1980). Terricolous immature stages of *Philus* and *Migdolus* are susceptible to infection by parasitic nematodes (Svacha *et al.* 1997; Machado *et al.* 2005).

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

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

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

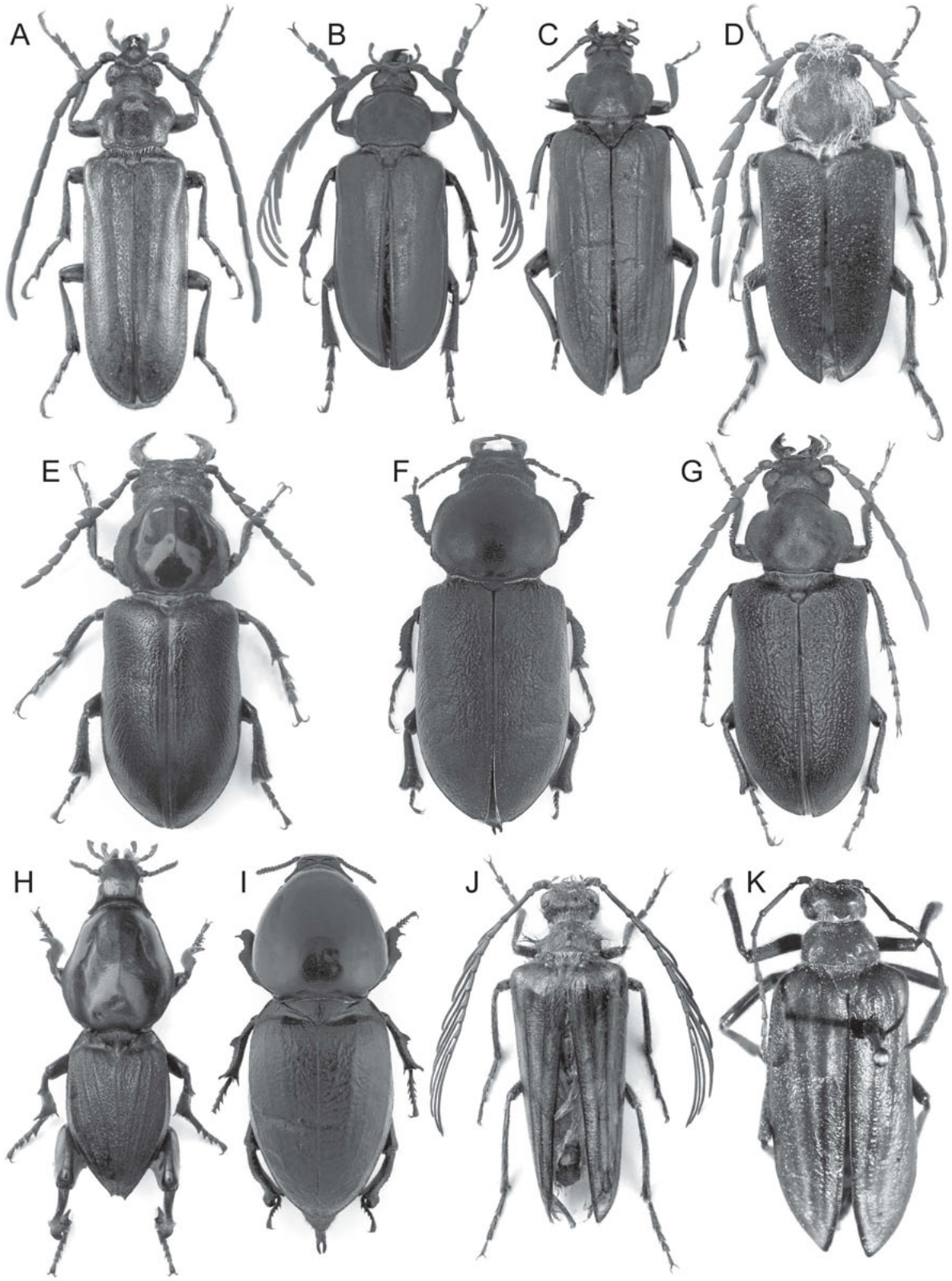

Fig. 2.1.2 Adults of Anoplodermatinae (A–I) and Vesperoctenini (J, K), dorsal view. A, *Mysteria minuta* Dias, male, 15.5 mm; B, *Pseudopathocerus humboldti* (Lameere), male, 21 mm; C, *Pathocerus wagneri* Waterhouse, damaged female, 49 mm; D, *Sypilus orbignyi* Guérin-Méneville, male, 19 mm (© I. Jeniš);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

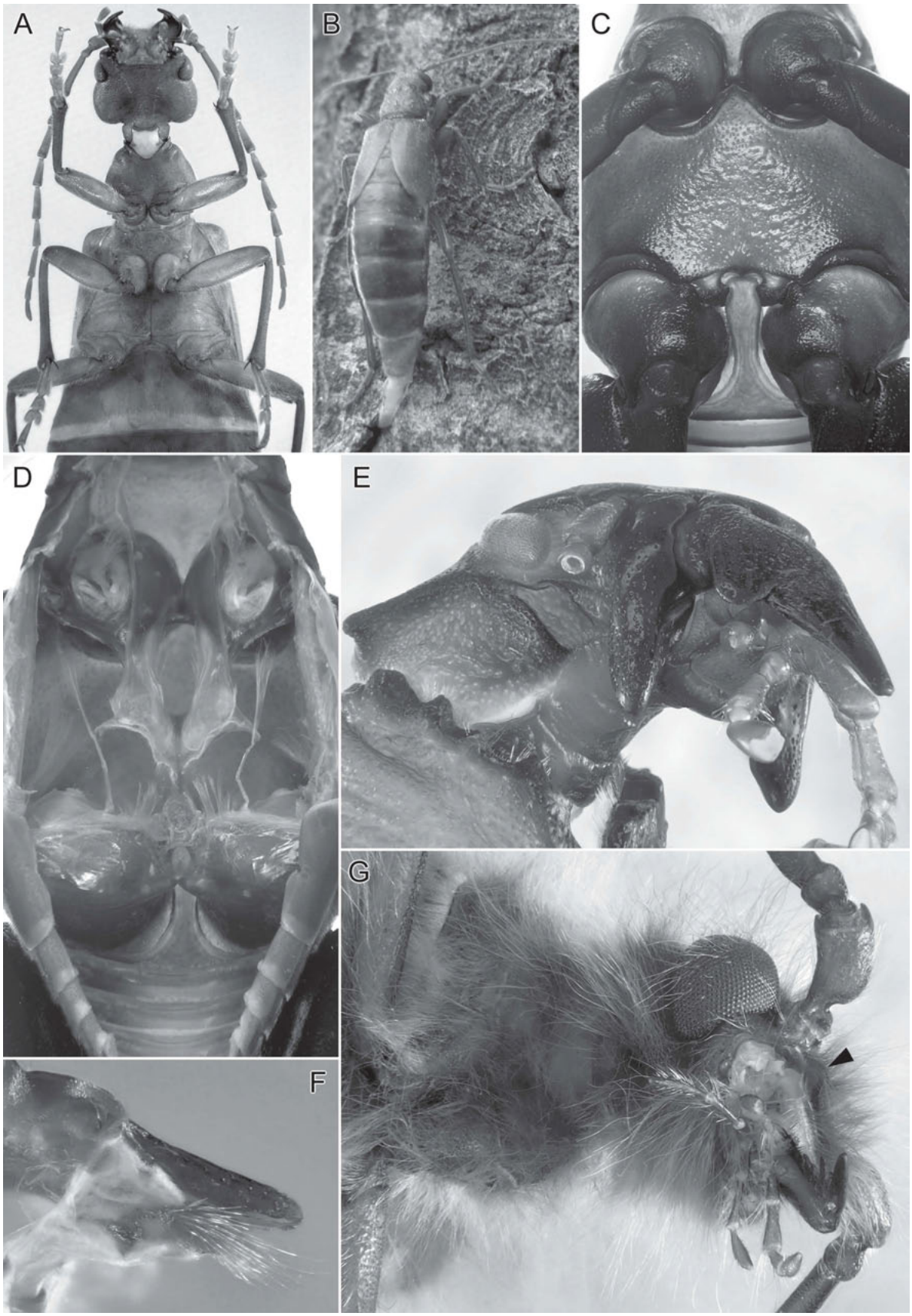

Fig. 2.1.3 A, *Vesperus strepens*, female, ventral view; B, *Mantitheus pekinensis* Fairmaire, female ovipositing in bark of a fruit tree (© E. Kučera); C, *Hypocephalus armatus*, male, pterothorax and base of abdomen, ventral view; D, *H. armatus*, male, pterothoracic endoskeleton, dorsal view; E, *H.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

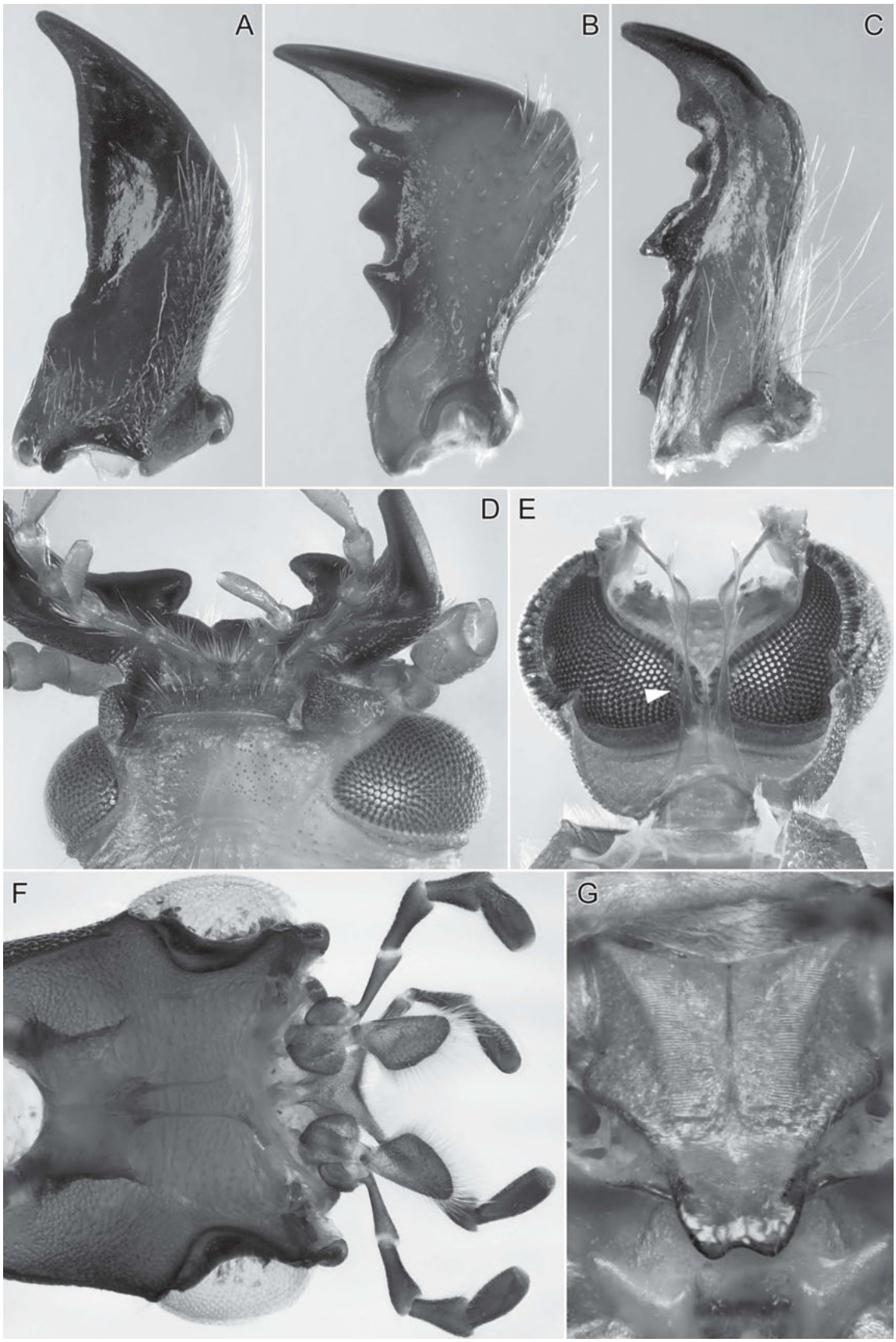

Fig. 2.1.4 A, *Philus antennatus*, female, right mandible, dorsal view; B, *Pseudopathocerus humboldti*, male, right mandible, dorsal view; C, *Vesperoctenus flohri*, male, right mandible, dorsal view; D, *Anoploderma breueri*, male, anterior head, lateroventral view; E, *Pathocerus wagneri*, male, ventral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

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

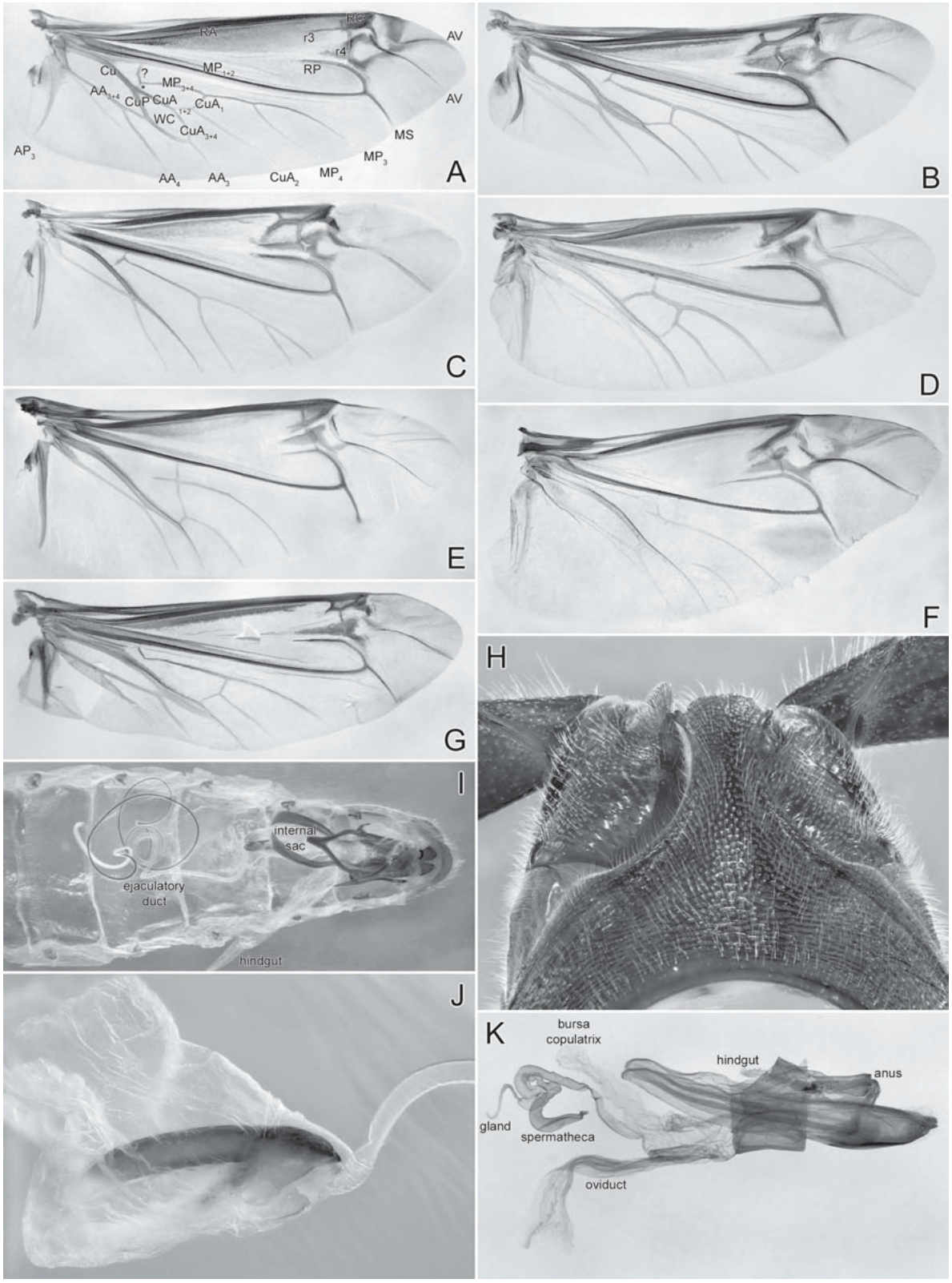

Fig. 2.1.5 A–G, right wing: A, *Philus pallescens* Bates, female; B, *Vesperus conicicollis hispalensis*, male; C, *V. strepens*, male; D, *Mysteria minuta*, male; E, *Pathocerus wagneri*, male; F, *Migdolus fryanus*, male; G, *Vesperoctenus flohri*, male; H, *Philus antennatus*, female, procoxae and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

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

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

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

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

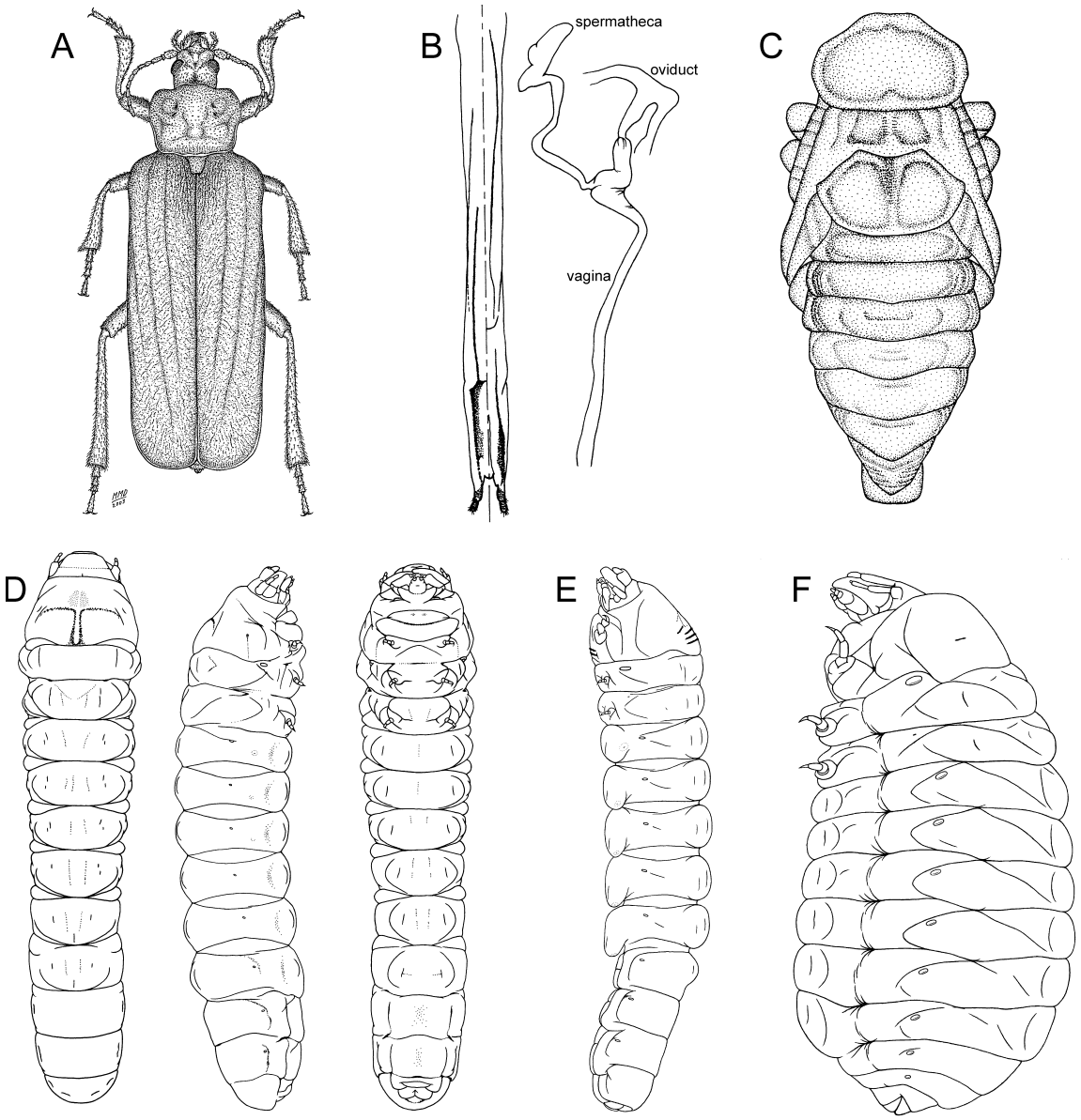

Fig. 2.1.6 A, *Mysteria darwini* (Lameere), female, dorsal view, 37 mm (from Dias 2004); B, *Vesperus strepens*, female, ovipositor (left half ventral view, right half dorsal view) and internal genitalia (from Saito 1990); C, *Migdolus fryanus*, pupa, dorsal view (from Costa *et al*. 1988); D, *Philus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

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

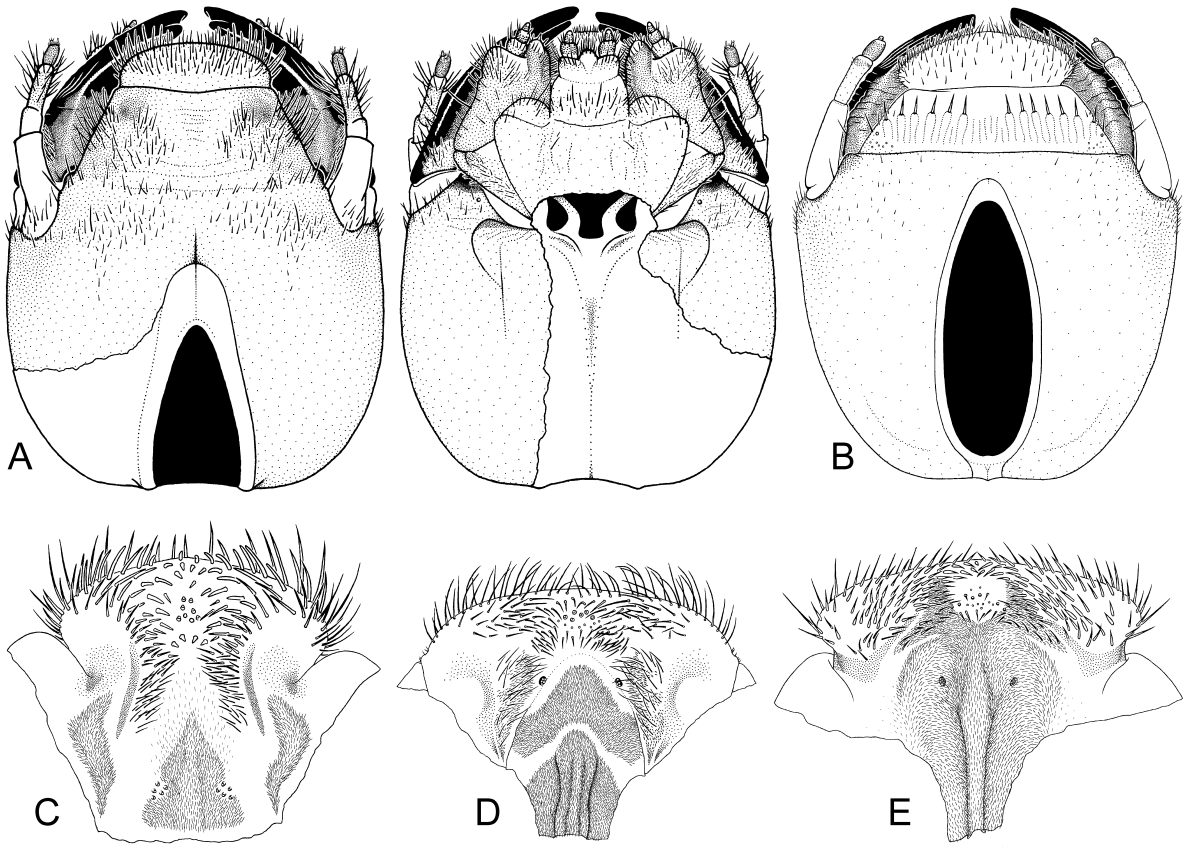

Fig. 2.1.7 Larvae. A, *Philus antennatus*, head, dorsal (left) and ventral view (right); B, *Migdolus fryanus*, head, dorsal view; C, *Vesperus luridus* (Rossi), epipharynx; D, *Philus antennatus*, epipharynx; E, *Migdolus fryanus*, epipharynx (all figures from Svacha *et al*. 1997).

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

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

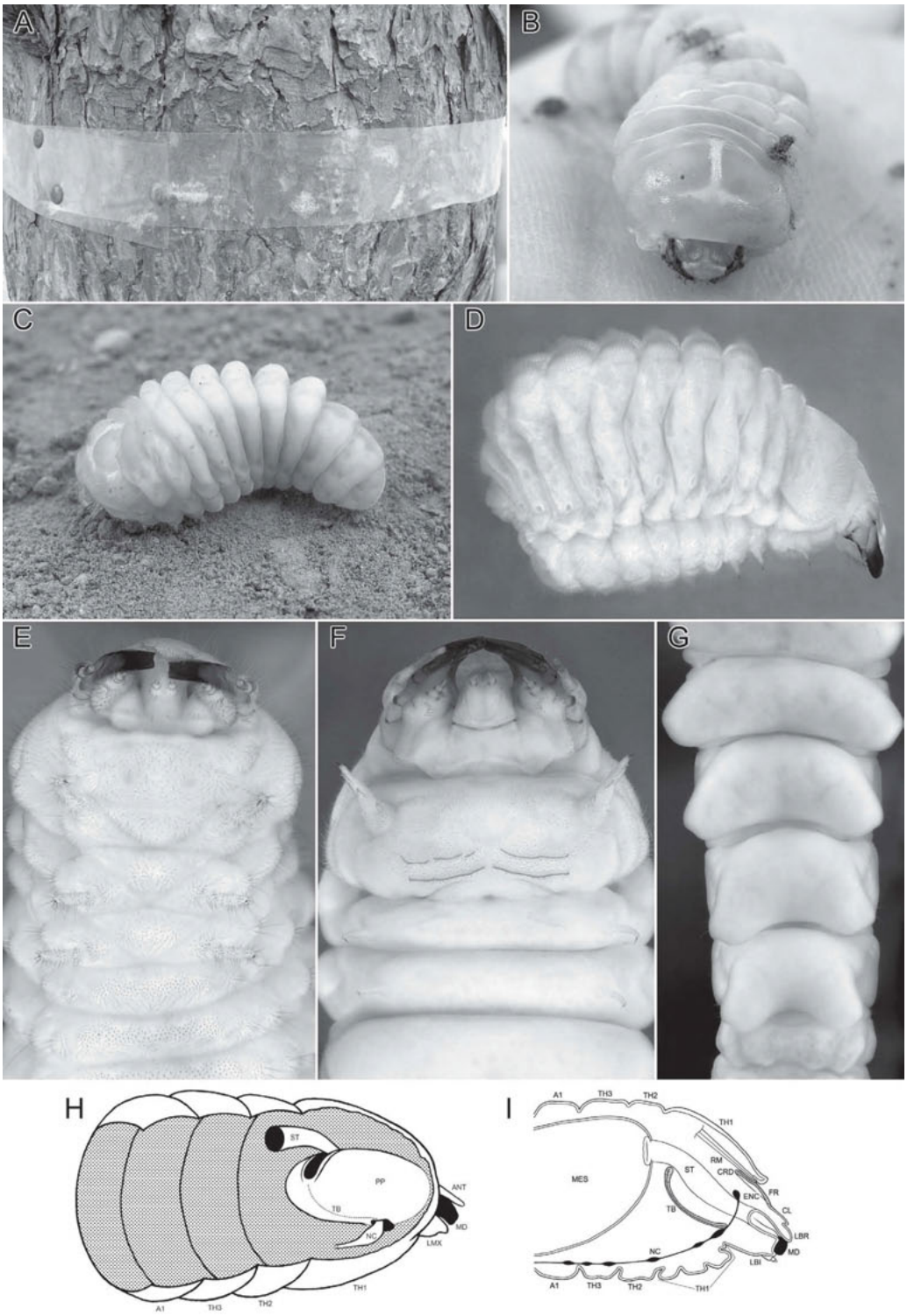

Fig. 2.1.8 A, *Mantitheus pekinensis*, hatched egg batches under protective plastic band on a pine tree in Beijing Botanical Garden (© W. Bi); B–I, larvae: B and C, *M. pekinensis*, living specimen, anterior (B) and lateral view (C) (© W. Bi); D, *Vesperus sanzi* Reitter, lateral view; E, *V. sanzi*,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

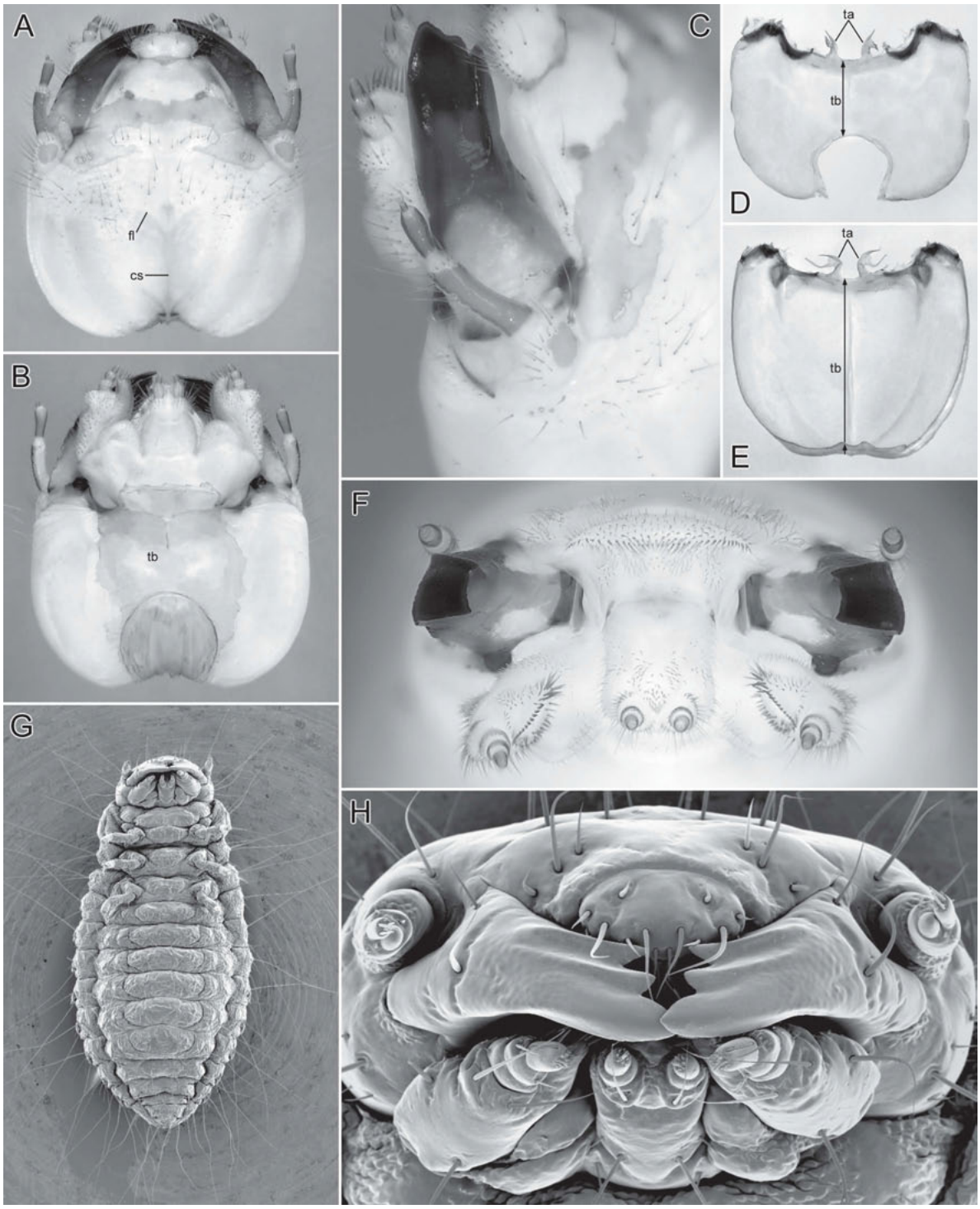

Fig. 2.1.9 Larvae. A, *Vesperus sanzi*, head, dorsal view; B, *V. sanzi*, head, ventral view; C, *V. sanzi*, head, anterolateral view; D, *V. luridus*, ventral half of cranium, dorsal view (tentorial arms on anterior margin of tentorial bridge cut to short stubs); E, *Migdolus fryanus*, dtto.; F, *Mantitheus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

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

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

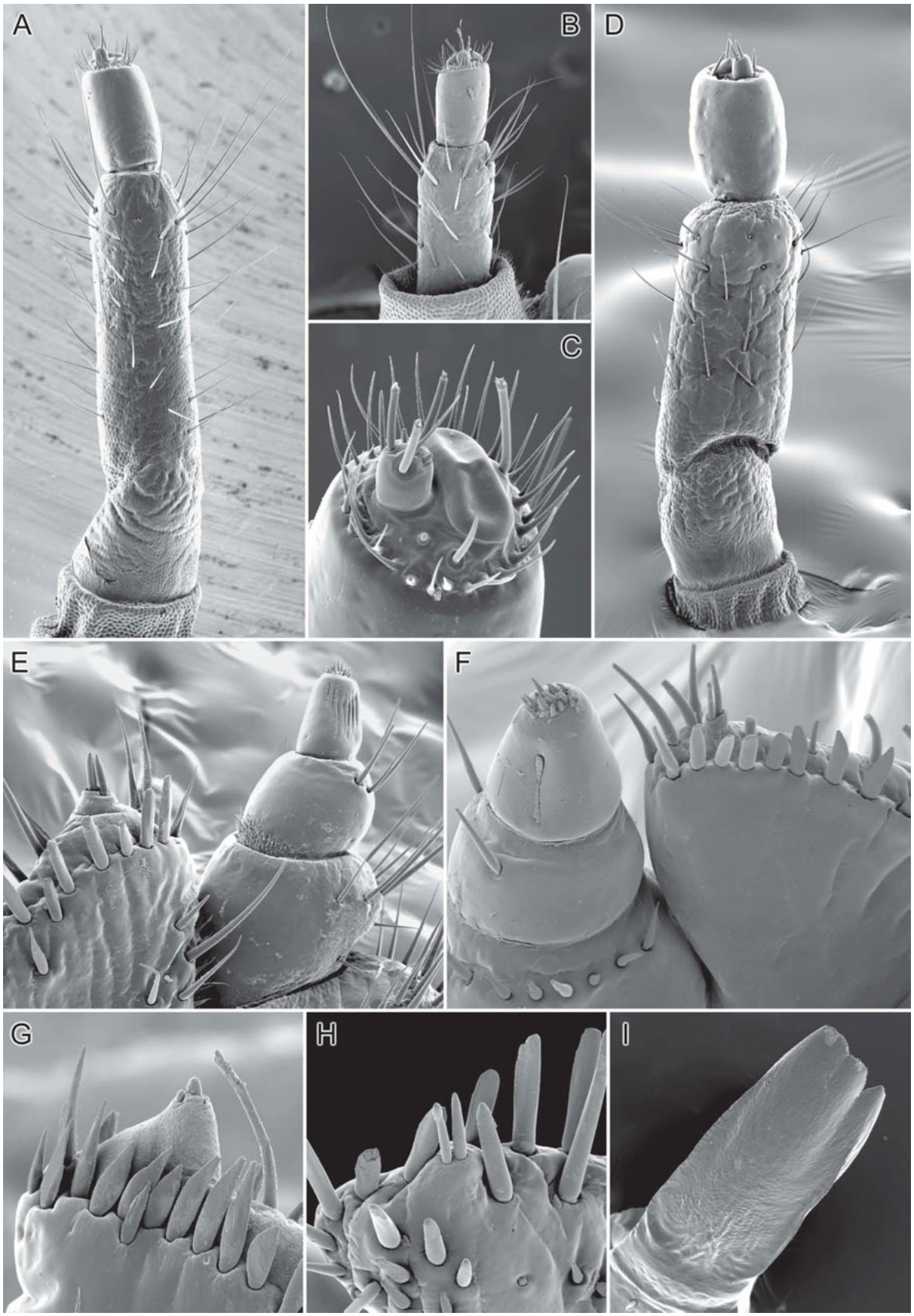

Fig. 2.1.10 Larvae, SEM. A, *Philus antennatus*, right antenna fully protracted, dorsal view; B, *P. antennatus*, left antenna half-retracted, dorsal view; C, *P. antennatus*, same specimen as in A, antennal apex, anterolateral view; D, *Heterophilus punctulatus* Chiang, Chen & Zhang, left antenna fully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

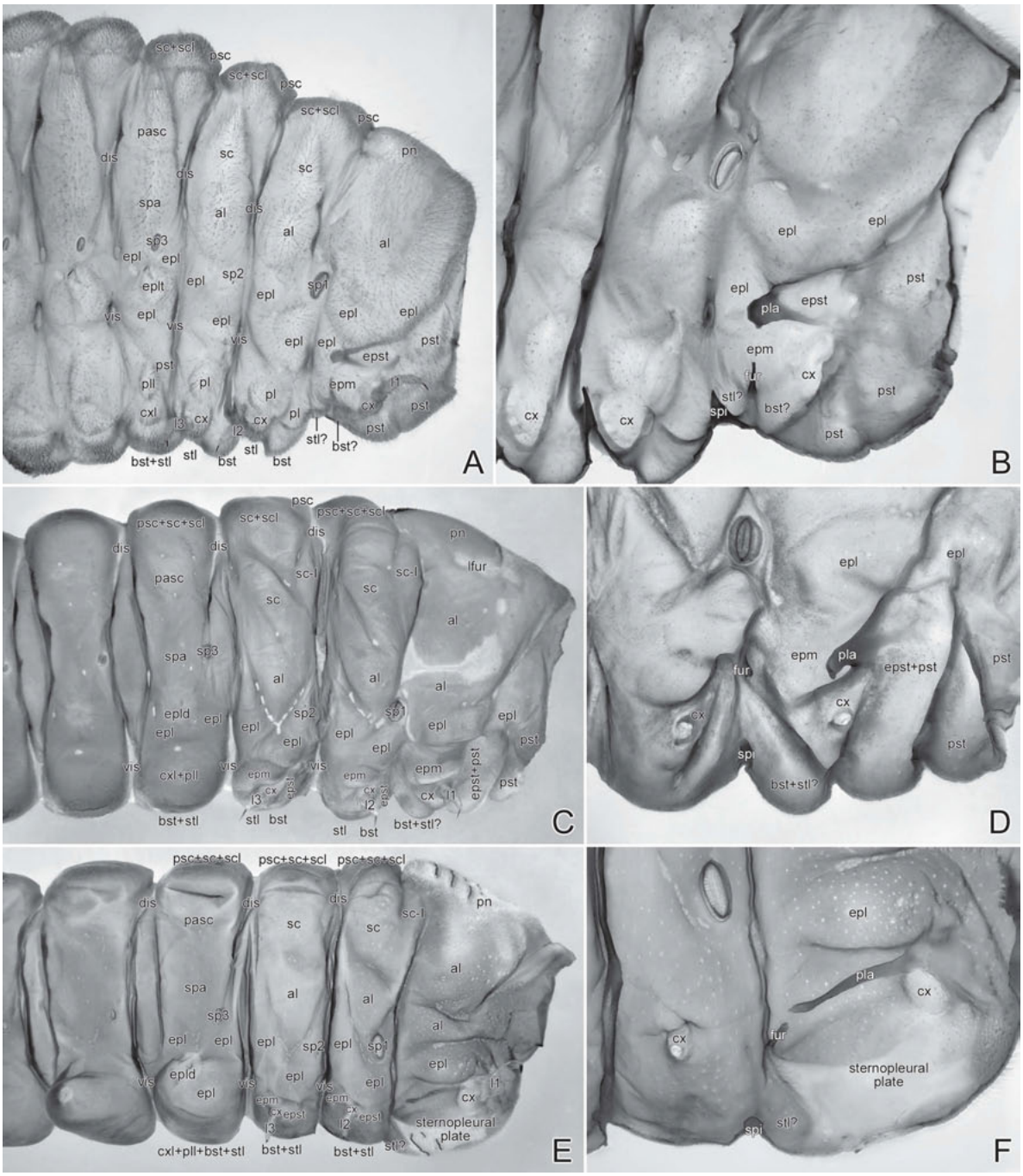

Fig. 2.1.11 Larvae, anterior part of body, cleaned cuticle stained with Chlorazol Black E. A, *Vesperus luridus*, right half of thorax and abdominal segments I and II, lateral view; B, *V. luridus*, left half of thorax, mesal view; C, *Philus antennatus*, right half of thorax and abdominal segments I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

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

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

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

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

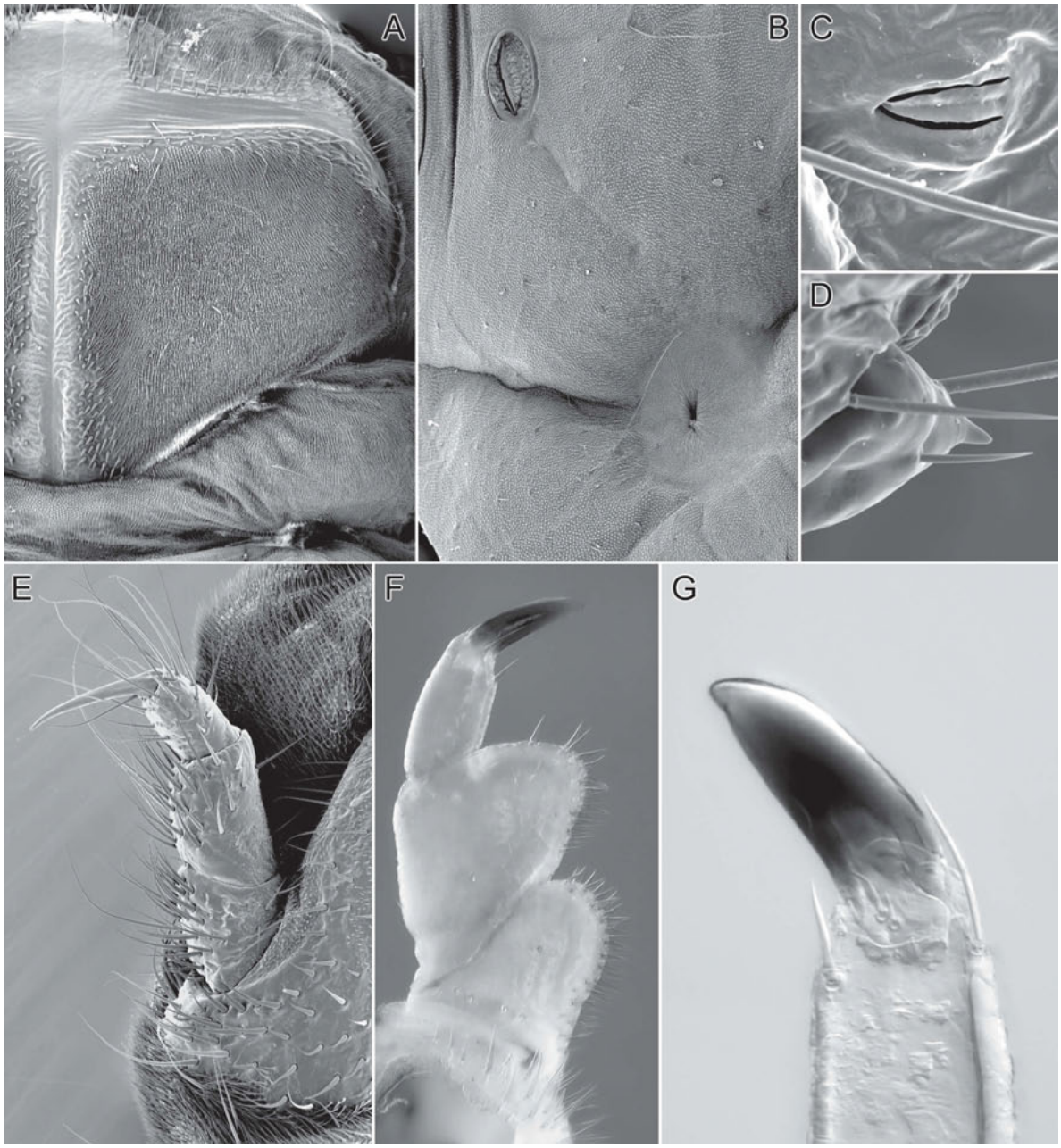

Fig. 2.1.12 Larvae. A, *Philus antennatus*, right half of pro- and mesonotum (SEM); B, *Heterophilus punctulatus*, left lateral part of abdominal segment I with spiracle and epipleural disc (SEM); C, *Vesperus luridus*, first instar, left abdominal spiracle VI (SEM); D, *V. luridus*, first instar, left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

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

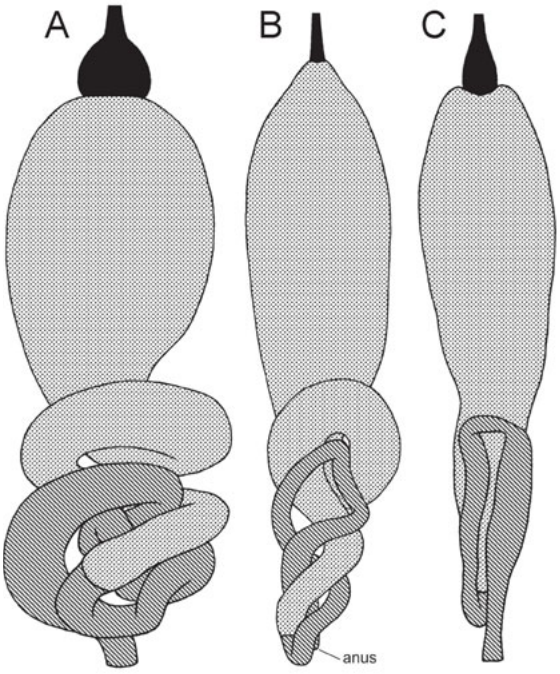

Fig. 2.1.13 Gross morphology of larval gut, diagrammatic, dorsal view. A, *Vesperus luridus*; B, *Philus antennatus*; C, *Migdolus fryanus*. Foregut black, midgut stippled, hindgut crosshatched (from Svacha *et al*. 1997).

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

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

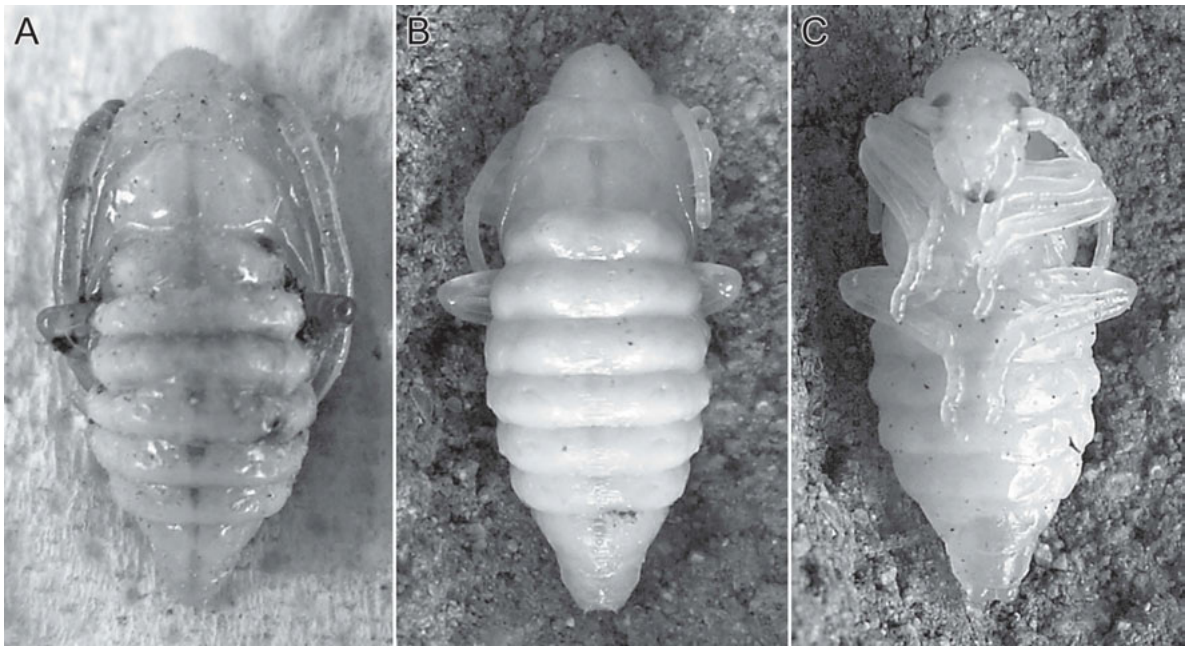

Fig. 2.1.14 *Vesperus sanzi*, pupa (© F. Calvo Sánchez). A, male, dorsal view; B, slightly malformed female, dorsal view; C, same, ventral view.

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

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

Svacha *in* Svacha & Danilevsky (1987) redescribed larvae of *Vesperus* and *Migdolus* (larvae of the Philinae were unknown) and accepted Vesperidae and Anoplodermatidae (together with Oxypeltidae and Disteniidae) as separate families because he did not find any common larval characters beyond the plesiomorphic lack of the gula (whose presence defined his Cerambycidae *s.str.*). Saito (1990) studied female genitalia of *Vesperus*, *Philus* and *Mantitheus*. She accepted the separate family Vesperidae and included the Philinae (as a tribe Philini) based on the very similar and very unusual (probably apomorphic) female genitalia with extremely long proctiger and desclerotized spermatheca. Larvae of Philinae were described by Yin (1994) and redescribed by Svacha (in Svacha *et al.* 1997), who accepted Saito's placement of Philinae (treated by him as a subfamily) in Vesperidae and added also the Anoplodermatinae, using the similarities of the newly discovered philine larvae to both *Vesperus* and *Migdolus*, thus creating the family Vesperidae as accepted here. As Svacha defined Vesperidae mainly based on larval characters, he preliminarily placed *Vesperoctenus* (larvae unknown) in Vesperidae as a genus *incertae sedis*, possibly related to Anoplodermatinae (see below). Definition of Vesperidae

on adult characters is very difficult as Philinae have retained an extensive set of plesiomorphies probably close to the chrysomeloid ground plan. The undoubtedly apomorphic absence of a sclerotized spermatheca in Vesperinae and Philinae is not shared by the Anoplodermatinae (present data). The tendency for flightless females (Vesperinae, Anoplodermatinae, Vesperoctenini, some Philinae; see Svacha *et al*. 1997) is not universal because at least some females of *Philus* can fly (C. Chen and Y. Lin, personal communication for two species of *Philus* occurring in Taiwan) and female flightlessness is shared by the Oxypeltidae. Vesperid larvae differ fundamentally from those of all other cerambycoid groups, but many of their features may be plesiomorphic. The following presumed larval apomorphies were used by Svacha (in Svacha *et al*. 1997) to define Vesperidae: "Very long antennae [concerns later instars, antennae are shorter in first instars]; twin malar sensory organ [see comments below]; spiracles in later instars without marginal chambers; terricolous habits (probably including *Vesperoctenus*). Perhaps also long digging mandibles and later instar larvae with stemmata inconspicuous or absent". The "malar organ" (Fig. 2.1.10 E–H) comprises two sensilla widespread (possibly universally present) in cerambycoids and other Chrysomeloidea (and occuring also in other beetle groups). They are homologous to the "lateral and medial galeal sensilla" described in chrysomelids (e.g., Mitchell *et al.* 1979); at least one of these sensilla was identified as a contact chemoreceptor (whereas the surrounding sensilla are generally mechanoreceptive setae). In Vesperidae, the two sensilla are placed on a more or less prominent common tubercle. However, an inconspicuous tubercle bearing these sensilla has been since observed also in some Cerambycidae.

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

The tribe Vesperoctenini was erected by Vives (2005) for the enigmatic Mexican genus *Vesperoctenus* containing a single species, *V. flohri*. The genus differs from all other Vesperidae by the apomorphic 12-segmented antennae in both sexes (in the other groups the terminal flagellomere may be appendiculate but never divided). The original description (Bates 1891) did not assign the genus to any particular cerambycid group but proposed relationships to the Old World *Vesperus*. *Vesperoctenus* was therefore later placed with the cerambycid subfamily Lepturinae or equivalents, with similar problems as in the case of *Vesperus* (see above). Svacha (in Svacha *et al.* 1997) considered the genus as a taxon *incertae sedis* in the newly defined Vesperidae, based mainly on the presumed subterranean root-feeding larval habits and the derived 2-2-1 formula of tibial spurs shared with most Anoplodermatinae (Dias 1984–1988; further reduced in some females and both sexes of *Hypocephalus*), but unknown in Vesperinae (2-2-2) or Philinae (2-2-2 or 1-2-2); Napp (1994) is incorrect in stating that *Philus* has only one spur on the hind tibia. Oxypeltidae and Disteniidae also have two spurs on all tibiae, and the 2-2-1 formula is very uncommon in Cerambycidae. Reviewing *Vesperoctenus*, Vives (2001) questioned the concept of the family Vesperidae in the present sense (indeed its monophyly is by no means well supported, see above and in Cerambycidae) and used another set of characters to advocate a relationship of *Vesperoctenus* to *Vesperus* as proposed in the original description (Bates 1981). Similarities to *Vesperus* (possible apomorphies marked by "A", characters shared also with the Philinae marked by "Ph") include the constricted neck (A), a mentum not expanded and not covering the maxillary base (Ph), the lack of an

intermaxillary process (A?, Ph), well-developed broad dorsal tentorial arms (verification needed; Ph), a pronotum without a lateral carina (A?), procoxal cavities externally open (Ph), procoxae projecting above very narrow prosternal process (A?; polarity uncertain, see discussion of secondary procoxal articulation above), mesocoxal cavities not sharply defined posteriorly (A?, Ph), wings with wedge cell (Ph; present in Philinae and some Vesperinae, universally absent in Anoplodermatinae) and with the connection between MP_{1+2} and MP_{3+4} not shifted distally (Ph), the presence of metendosternal laminae (Ph), and possibly an unmodified ovipositor with terminal styli (more data needed; Ph). It will be of interest whether females share the apomorphic absence of a sclerotized spermatheca as is the case in Vesperinae and Philinae. Although it can be deduced from the previous list that *Vesperoctenus* lacks many of the anoplodermatine apomorphies, such as the broad plate-like mentum covering the maxillary base, procoxal cavities closed externally; wing without wedge cell and with the connection between MP_{1+2} and MP_{3+4} shifted distally, the absence of metendosternal laminae, and possibly the modified sclerotized ovipositor, it displays some similarities to all or some Anoplodermatinae. This includes a postclypeus projecting above the anteclypeus (A), mandibles with a dentate incisor edge and a small external projection (A?), a medial field of the hind wing with only four free veins (A), a 2-2-1 tibial spur pattern (A), and possibly also the extremely setose body and pectinate antennae of males (A?; one or both occur in some Anoplodermatinae, but pectinate antennae also occur in males of the philine genus *Spiniphilus*). Thus, relationships of *Vesperoctenus* also remain obscure. However, the placement of Vesperoctenini (but not any other of the present subgroups of Vesperidae) in the cerambycid subfamily Prioninae (Bousquet *et al.* 2009; Bouchard *et al.* 2011; accepted in Bezark & Monné 2013) is entirely unsupported.

Vesperinae Mulsant, 1839

Biology and Ecology. Based mainly on the summary in Vives (2005), a very detailed account of the biology of *Vesperus sanzi* Reitter (one of the smaller species developing predominantly in grasslands; Calvo Sánchez 2007), and data for *V. macropterus* (Sechi 2011). Adults are crepuscular and nocturnal, with males and occasionally also females attracted to light; males usually fly during the hours immediately after sunset. Females are flightless but not subterranean, although they are mostly hidden during the day and not frequently encountered, whereas males may be abundantly collected during the flight period. In contrast to this, the number of males and females of *V. sanzi* collected from the soil pupal chambers was not significantly different. Females of *V. xatarti* produce a long-range pheromone. Males of *V. sanzi* often perch on grass stems or other higher plants with the head upward and antennae outstretched, apparently trying to detect the female pheromone. They were also observed patrolling on the ground in areas of female emergence, occasionally violently pulling out the emerging female and immediately attempting to copulate. Males may battle for mates. Females of *V. sanzi* were not seen to climb on plants or other elevated objects. Copulation lasted several minutes and could occur repeatedly with the same female. Unmated males and females of *V. sanzi* lived for about 4 and 8 days, respectively, but both sexes died within a day or two after copulation or oviposition. Females of *V. macropterus* apparently lay all eggs during one night and die soon after, and males may be even more ephemeral. The period of adult activity differs among species, those occurring at low altitudes may be active in winter. Some species lay eggs in or on various objects above ground level, such as stones or tree bark (Butovitsch 1939). Oviposition in dry inflorescences of dead herbs up to 1.5 m tall was observed in *V. macropterus*; in suitable plants, the newly-emerged larvae at least partly bored down through the soft pith of the plant stem, thus avoiding exposure before entering soil. The macropterous females cannot fly but may use the well-developed elytra and wings to "parachute" from the dry plants (e.g., when disturbed). Other species, particularly those developing in grasslands (such as *V. sanzi*), oviposit in cavities in the soil, among roots, or in grass sods. *Vesperus sanzi* often oviposits in its own emergence galleries. Eggs are mostly laid in batches and covered and held together by a sticky substance (not in *V. macropterus*). One female lays over 100 and usually several hundred eggs (the ovipositor may become non-functional before all eggs are laid). In *V. sanzi,* in which adults are active in summer, the egg incubation period in the laboratory was 25–28 days, but egg hatching is delayed in species with winter activity. Rain might be a stimulus for egg hatching in *V. macropterus*, presumably to avoid desiccation of the minute first instar larvae and to facilitate entering the otherwise dry hard soil. The egg chorion is split longitudinally in *V. sanzi*, probably by the lateral egg bursters (see larval morphology and Fig. 2.1.12 D), and larvae leave the egg through that lateral split. The first instars (Fig. 2.1.9 G; see also Vives 2005) differ distinctly from the later stages: they are slightly more slender and elongate, their terminal abdominal segments are less retracted (*cf.* Fig. 2.1.7 F and 2.1.8 D), the setae are arranged more sparsely (some of them are very long) and the antennae are shorter. However, these differences are comparable to those between first and later instars in many other species. Mayet's old figure of first instar larva reprinted in Duffy (1953, 1957) is very inaccurate, undoubtedly depicting a strongly inflated specimen, and suggestions of considerable larval differences

amounting to hypermetamorphosis are incorrect. First instars search for suitable roots in soil. In *V. sanzi* they are able to survive for over a month without food. At least *V. strepens* (Fabricius) and *V. luridus* (Rossi) are apparently very broadly polyphagous on various trees and herbs (Vives 2005). *Vesperus sanzi* developing in grasslands feeds on roots of herbs of several families. Some species are pests in vineyards. Larval development takes several years. Larvae of *V. sanzi* actively feed in spring and early autumn, with periods of inactivity during the hot dry summer and winter when the larvae are dormant in soil chambers at depths of up to 50 cm. In the laboratory, larvae moulted at least twice a year (after each dormant period) and were estimated to undergo at least a total of ten moults during a life cycle of 5 years. Pupation occurs in soil. In June, the mature larva of *V. sanzi* descends from a superficial layer to depths of 10–20 cm where it constructs an ellipsoid oblique pupal chamber with smoothened walls. The descending larval gallery remains largely empty and serves for the emergence of adults (which have no fossorial adaptations). The pupal stage of *V. sanzi* lasts 18–20 days, with adults emerging in August.

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

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

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

Sternum III is usually the first visible, but intercoxal process may be reduced particularly in females, where sternum II may be more or less visible between (Fig. 2.1.3 A) and, in extreme cases, also behind the broadly separated coxae. Male terminalia with distinct paired parameres; gonopore without spiculum; ejaculatory duct usually with long internal sclerotized rod; latter missing

in *V. conicicollis* and according to Vives (2005), who refers to this structure as a flagellum, also in *V. bolivari* Oliveira, *V. fuentei* Pic, *V. serranoi* Zuzarte, and probably *V. macropterus* (treated by Vives as a subspecies of *V. conicicollis*). Female genitalia (Saito 1990) similar to Philinae: ovipositor long, flexible, with very long proctiger and distinct apical styli; small "intersegmental pouches" (but without symbionts) were found in an unidentified species of *Vesperus* by Schomann (1937); sclerotized spermatheca absent; vagina bearing only one petiolate membranous sac (Fig. 2.1.6 B) interpreted by Saito as a desclerotized spermatheca without gland.

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

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

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

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

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

Philinae J. Thomson, 1861

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

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

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

Prothorax narrower than base of elytra, at most moderately tapering anteriorly, about as long as broad to distinctly transverse (females of *Heterophilus*). Lateral pronotal carina oblique but not touching procoxal sockets, usually incomplete anteriorly (complete in females of *Heterophilus*), virtually absent in some males; pronotal disc may bear a pair of tubercles in anterior half. Procoxae prominent but not surpassing elevated prosternal process; somewhat broadened top of prosternal process with secondary coxal articulation (Fig. 2.1.5 H), consequently procoxa rotating along single axis; procoxal sockets open externally; internal closure present but very narrow and fine. Mesoscutum with median endocarina (may be incomplete posteriorly, apparently absent in *Heterophilus* but material not available), in some taxa bearing a more or less distinctly striate stridulatory file; scutellar shield small, subtriangular to broadly bilobed. Elytra covering abdomen or (females of *Heterophilus* and *Mantitheus*) more or less shortened and dehiscent. Mesocoxal sockets very narrowly separated, not sharply defined posteriorly. Mesocoxae slightly conical and projecting, may be contiguous when mesometaventral junction is reduced. Mesometaventral junction very

narrow or its metathoracic component reduced and mesoventral process ending freely between coxae. Exposed metanepisternum subtriangular, tapering posteriorly. Metaventrite with discrimen incomplete anteriorly (only short posterior rudiments in some taxa). Metacoxae contiguous to narrowly separated in macropterous specimens, more broadly separated in females with reduced wings. Metendosternite with laminae. Females in *Heterophilus* strongly brachypterous, micropterous in *Mantitheus*; wing in macropterous specimens with very complete venation (Fig. 2.1.5 A) except for males of *Heterophilus* and *Mantitheus* having unbranched MP_{3+4} and the latter also lacking CuA_{1+2} (Lin & Bi 2011); apical field with two distinct veins; radial cell closed; r3 short or absent, r4 attached on radial cell and with at most rudimentary spur; connection between MP_{1+2} and MP_{3+4} not shifted distally; medial fleck absent; wedge cell large. Legs moderately long, without distinct fossorial modifications (although outer side of tibiae dentate in some cases); tibial ends not remarkably expanded, without thick setal fringes along apical edge; tibial spurs 2-2-2 (*Spiniphilus*, *Mantitheus*, *Philus globulicollis*) or 1-2-2 (*Philus*, *Doesus*, *Heterophilus*); tarsi pseudotetramerous and tarsomeres 1–3 padded (apparently slightly reduced in females of *Heterophilus*); plurisetose empodium present.

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

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

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

Prothorax broadest posteriorly. Pronotum without sclerotized ridges, expanded backward in middle, thus slightly constricting mesonotum; with distinct median furrow and anterior transverse zone slightly sclerotized; lined with short setae and devoid of microtrichia (Fig. 2.1.12 A); lateral furrows delimiting pronotum present, incomplete anteriorly. Alar lobes with strengthened oblique internal ledge (Fig. 2.1.11 C). Presternal region

with two transverse areas, posterior one including also episterna; anterior transverse area with pair of broad flat depressions. Coxae flat and poorly defined medially. Posterior sternal region with recurved impressed line, its lateral extremities pointing toward very strongly reduced furcal pits located very near to posterior prothoracic margin. Sternal endoskeleton (furca and spina) reduced (small internal tubercles); propleural apodeme well-developed, slender, arising at lateral coxal extremity and reaching obliquely posteromedially across much of coxal width (Fig. 2.1.11 D). Mesonotum almost undivided. Metanotum with more or less distinctly separated triangular prescutum. Scutum-I distinct on both pterothoracic segments. Alar lobes not remarkably protuberant, deeply wedged into epipleural region. Mesothoracic spiracle very slightly protruding into prothorax. Pterothoracic coxae flat, poorly defined posteriorly, extended and angular anterolaterally, almost touching epipleural region (pleural sulcus very short). Epimeron posterolateral to coxa, distinctly protuberant; episternum anterior to coxa; both pleural divisions not distinctly separated from adjacent sternal parts. Transsternal line incomplete medially. Pterothoracic endoskeleton absent. Distal parts of legs (Fig. 2.1.12 E) short, much shorter than half of basal distance between trochanters, devoid of microtrichia; fore legs not distinctly enlarged or modified; pretarsus slender, with needle-shaped claw and one medial seta at base.

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

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

Anoplodermatinae Guérin-Méneville, 1840

Biology and Ecology. Very little biological information is available for Mysteriini. Adults are nocturnal and attracted to light (Dias 1988; S. Lingafelter, personal communication for *Pathocerus*). *Acacia cavenia* (Mimosaceae) was listed as a host for *Pathocerus wagneri* Waterhouse by Duffy 1960 (record attributed to F. Monrós and questioned by Di Iorio 2004). What little is known about *Hypocephalus armatus* Desmarest (placed either in Anoplodermatini or in a separate tribe Hypocephalini) comes mainly from Gounelle (1905) and was reviewed by Araujo (1954) and Duffy (1960). Both sexes are apterous, with fossorial habits. The species' occurrence is very localized but where it occurs, it may not be rare. Emergence usually starts in December after beginning of rainfall. Adults are found crawling or hidden under various objects in largely open areas with some deciduous scrub but devoid of trees or continuous vegetation cover, on clay and sandy soils with quartz fragments. As in all anoplodermatines, females are rarely encountered and probably remain in the soil for most of their life. At least the males are not strictly nocturnal. Larvae are unknown but are very likely subterranean. Of Anoplodermatini, the biology is known for *Migdolus fryanus* (the only anoplodermatine with known larval development) damaging sugar cane and some other cultured plants in Brazil (a summary with references can be found in Machado & Habib 2006; see also Bento *et al.* 1993, 1995; Botelho & Degaspari 1980 (*M. fonsecai* Lane, misspelled by the authors as *fonsecae*, is a synonym of *M. fryanus*); Fonseca 1959 (misidentified as *M. morretesi* Lane); Machado *et al.* 2006 a, b). Emerged males are short-lived (3–9 days in the laboratory), whereas active females live up to 38 days. The flight period is a week long, and timing differs depending upon region (October to March, usually following rainfall). Males are diurnal and

fly and search for females mainly during forenoon. Females remain in their soil burrows, coming to the surface only for copulation, and attract males with a long-range sex pheromone (males often gather at the burrow entrance before the female appears on the surface). Copulation lasts 5–30 seconds. Females oviposit underground. In the laboratory a single female can lay up to approximately 50 elongate-oval, relatively large eggs (length up to 5 mm). The incubation period was 17–25 days. Larvae live in soil at depths up to 5 m, depending on the season of the year, and feed externally on plant roots; they are extremely polyphagous and were found damaging such taxonomically diverse plants as *Pinus*, *Eucalyptus* and *Saccharum*. Pupation occurs in soil at a considerable depth (typically 3–4 m) and adults remain in their pupal cells for some time before emergence (freshly moulted adults collected from soil have enlarged abdomens with fat reserves and can be kept alive in the laboratory for up to 4 months). Development period is from 1 to 3 years. Larvae reared in laboratory on semisynthetic diet for 2 years attained lengths of 4–5 cm and underwent 6–7 moults without reaching the pupal stage. Very little is known about other genera of Anoplodermatini, except that at least some of them are nocturnal and males fly to light (*Anoploderma breueri*: S. Lingafelter, personal communication).

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

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

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

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

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

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

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

Prothorax (Fig. 2.1.11 E) broadest posteriorly; large areas very densely setose and without microtrichia. Pronotum fused with alar lobes (lateral furrows absent), expanded posteromedially, thus slightly constricting mesonotum; in posterior half with several transverse sclerotized ridges interrupted by median line; lateral part of alar lobe

forming separate fold above epipleural region. Prothoracic venter strongly modified and difficult to homologize, most parts (presternum, episternum, epimeron, basisternum) fused into large plate anteriorly bearing ventral part of the membranous collar surrounding head and in basal half with several transverse sclerotized ridges (Fig. 2.1.8 F); fore legs strongly shifted anterolaterally to anterior angles of that plate, virtually touching epipleural region, thus strongly reducing pleural sulcus; procoxa round, sharply defined, densely setose. Posterior prosternal margin with separate bilobed laterally tapering area (?sternellum) bearing short but distinct furcal rudiments at lateral extremities and a median spina on posterior margin; pleural apodeme narrow, rod-like but very long, originating at anterior procoxal margin and almost reaching furcal arms (Fig. 2.1.11 F). Mesonotum almost undivided. Metanotum with indistinct X-shaped lines and with scutum I indistinct. Alar lobes not protuberant. Mesothoracic spiracle not protruding into prothorax; spiracle-bearing epipleural triangle tends to fuse with alar lobe. Coxae small, flat, close to epipleural region (i.e., pleural sulcus short); otherwise all pleural and sternal regions more or less fused into one transverse fold. Small mesothoracic spina present. Fore legs (Fig. 2.1.12 F) enlarged, directed obliquely anteriorly; trochanter and femur large, with produced carinate inner side bearing row of short stout setae; pretarsal claw flattened; middle and hind legs much smaller, unmodified, with sparse fine setae and needle-shaped claw; pretarsus of all legs with two minute adjacent setae at base, one usually much smaller and hardly visible (Fig. 2.1.12 G; overlooked in Svacha & Danilevsky 1987; described in Costa *et al.* 1988).

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

Taxonomy. The group was revised by Dias (1984–1988; female of *Mysteria* described by Dias 2004) and contains ten genera and 37 species placed by Dias in two tribes as follows: Mysteriini Prosen, 1960 (Fig. 2.1.2 A–C, 2.1.6 A). Males slender, parallel-sided and slightly flattened (less so in *Pseudopathocerus*). Head prognathous. Eyes coarsely facetted, in males very large, approaching or touching each other dorsally and particularly ventrally, constricting the gula (Fig. 2.1.4 E). Antenna in males serrate or (*Pathocerus* and *Pseudopathocerus*) pectinate including first flagellomere. Postclypeus with a flattened conical projection covering small anteclypeus and labrum (Fig. 2.1.3 F). Mandibles broad and flat, not sickle-shaped; apical part abruptly curved mesad; usually with several incisor teeth and an external protuberance or process (Fig. 2.1.4 B). Functional mouth and maxillolabial complex narrow. Pronotum narrower than elytra, subcordate, with sharp prominent lateral carina. Legs moderately long, in males cursorial or (*Pseudopathocerus*) slightly strengthened; tibial spurs 2-2-1 in both sexes; mid tarsi not distinctly longer than hind tarsi. Immatures unknown. Three genera and seven species: *Mysteria* Thomson with five species, *Pathocerus* Waterhouse with *P. wagneri* Waterhouse, and *Pseudopathocerus* Dias with *P. humboldti* (Lameere). Anoplodermatini Guérin-Méneville, 1840 (Fig. 2.1.2 D–G). Seven genera with 20 species. The monospecific *Cherrocrius* and *Hypocephalus* are treated separately below. The remaining five genera form a relatively coherent group: body stout, convex; males of *Sypilus* with extremely long dense yellowish pubescence (Fig. 2.1.2 D; often abraded on pronotum) except for glabrous elytra. Head broad to very broad, strongly oblique to subvertical (but relatively extensively movable vertically). Eyes always well separated, in some cases relatively finely facetted. Labrum transverse and visible or (*Anoploderma*) hidden in dorsal view under sclerotized flat projecting clypeus, but postclypeus never forms a conical projection; in *Sypilus*, labrum apparently both partly hidden by and fused to clypeus. Antennae in males serrate, slightly pectinate in *Sypilus* but first flagellomere strongly reduced and without process. Mandibles more slender and sickle-shaped, with only one incisor tooth either at midlength (*Migdolus*; Fig. 2.1.2 E, F) or close to base and more or less blocking mouth when mandibles are closed (remaining four genera; Fig. 2.1.2 G, 2.1.4 D); outer process small or absent. Functional mouth and maxillolabial base (particularly mentum) broad. Pronotum larger than in Mysteriini, convex, occasionally almost as broad as base of elytra; lateral carina relatively blunt in some cases. Legs shorter and stouter, with more or less distinct fossorial modifications; tibial spurs 2-2-1 in males, 2-2-0 or (*Sypilus*) 1-1-0 in known

females; mid tarsi more or less distinctly longer than others (very slightly so in *Sypilus*). Larvae known only of *Migdolus*. Genera: *Acanthomigdolus* Bruch with *A. quadricollis* (Bates), *Anoploderma* Guérin-Méneville with three species, *Migdolus* Westwood with ten species, *Paramigdolus* Dias with *P. tetropioides* (Fairmaire), and *Sypilus* Guérin-Méneville with three species. *Cherrocrius bruchi* Berg (based on Dias 1987). Males differ from those of the five genera treated above by the bicolored appearance with the body black-brown (with very long dark pubescence) and the elytra yellow-brown (and glabrous as in all Anoplodermatinae), by a narrower head, flat and straight mandibles (more similar in shape to those of Mysteriini except for the absence of distinct incisor teeth) and exposed and triangular labrum, antenna distinctly pectinate including a well-developed first flagellomere, slender legs with only slight modifications (tibial apices with flat teeth and outer side of fore tibia slightly dentate), and mid tarsi not distinctly longer than the hind tarsi. Immatures unknown. Prosen (1960) created a subfamily Cherrocriinae for this genus in his Anoplodermatidae (some South American authors accepted cerambycoids as a superfamily containing a number of families more or less corresponding to subfamilies of other authors). *Hypocephalus armatus* Desmarest (Fig. 2.1.2 H, I). This extremely specialized spe cies of rich taxonomic history (see systematic discussion of the family Vesperidae) was placed in Anoplodermatini by Dias (1987), but it is often singled out in a separate tribe, Hypocephalini Blanchard, 1845 (recently for instance in Bousquet *et al.* 2009 and Bezark & Monné 2013), as it makes any group in which it would be classified almost impossible to characterize. Body length 33–50 mm or more (size depends on position of head). Cylindrical, strongly sclerotized; black to black-brown, with very restricted and short pubescence. Head (Fig. 2.1.3 E) of unique shape and extensively movable vertically, may be flexed on prosternum (apparently a defensive position protecting large ventral membranous area between head and prosternum) or lifted to an almost prognathous position (Sharp 1902), although mouthparts even then point obliquely ventrally due to cranium being abruptly bent down in anterior half. Eyes small, oval, lateral, finely facetted, far from anterior cranial margin and placed above deep excavations. Antennal sockets without tubercles, lateral, slightly separated from mandibular articulation. Frontoclypeal region smooth; frontoclypeal sulcus obliterated; pretentorial pits small, lateral, connected by sulcus with antennal sockets; anteclypeus small and abruptly deflexed. Labrum separate, long (about twice as long as broad in males), almost perpendicular between mandibular bases. Antennae 11-segmented, extremely short, even in male shorter than head. Mandibles straight, vertical, parallel and of limited mobility (not working against each other); sharply pointed and with lateral projection; vestiture of setae reduced to several small patches. Gena bearing large (males) or small (females) ventral conical projections. Galea well-developed. Mentum strongly transverse but scarcely covering bases of maxillae; ligula reduced but with anterolateral projections. Tentorial bridge broad and roof-like; pre- and metatentorial arms connected at an angle due to ventrally curved anterior cranium. Pronotum extremely large, as broad as elytra and in males also as long; prosternum before coxae very long and emarginate anteriorly to accommodate head when flexed ventrally; emargination with series of round notches, particularly distinct in males. Procoxae project above prosternal process, not articulating on it. Mesoscutum externally with smooth median line but without internal endocarina, largely exposed except when prothorax raised and its posterior margin covering both mesoscutum and flat elytral bases. Scutellar shield minute. Elytra locked together at suture, subparallel and then converging, in males each with an acute tip. Hind wings absent. Metanepisternum fused without traces with metaventrite which lacks a discrimen (Fig. 2.1.3 C). Pterothoracic endoskeleton extremely hypertrophied and modified; mesofurca with two posteriorly directed very broad flaps dorsally attached on extremely broad metendosternal branches arising from very high laterally compressed metendosternal shaft (Fig. 2.1.3 D). All legs strongly fossorial; hind legs extremely hypertrophied in males; tibial spurs 2-2-0 in both sexes; hind tibia with densely pubescent terminal area; tarsi pentamerous, mid tarsi distinctly longer than others; empodium present, usually multisetose. Abdomen small; intercoxal process in male very long, slightly expanded apically and locked on both sides by processes of metaventrite (Fig. 2.1.3 C); in female shorter, broader and less distinctly locked. Males with strut on sternum VIII vestigial; ejaculatory duct with thick internal sclerotized tube. Female not dissected. Immatures unknown.

Incertae Sedis: Vesperoctenini Vives, 2005

Biology and Ecology. The single species of *Vesperoctenus* Bates, *Vesperoctenus flohri*, occurs exclusively in Mexico and is seldom collected. Very little is known about its biology (Vives 2001). Males (Fig. 2.1.2 J) are winged. Females (Fig. 2.1.2 K), which are much rarer in collections, are brachypterous but without distinct fossorial adaptations. Adults are nocturnal and attracted to light. The larval development is presumably subterranean. In the original description Bates (1891) writes: "Mr. Flohr informs me that the specimens were taken by Mr. Becker at night, by spreading a white sheet on the ground and lighting a fire, which attracts them; they come out of the ground after the manner of the *Cebrios* and *Scaptoleni*. Their habits are, no doubt, similar to those of the *Vesperi*, which

are subterranean in their early stages". The species occurs in sparse oak and mixed groves usually above 1000 m and up to at least 2000 m altitude. Adults (obviously males) were also beaten from branches of *Quercus devia* in Baja California (Hovore 1988).

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

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

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

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

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

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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 Oxypeltidae, 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* Wytsman, 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, Cerambicidae [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. & Nearns, 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 sanzi* 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: *Cherrocrius* 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 (Coleóptero 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 a 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* Wytsman, P. (ed.) *Genera Insectorum. Fascicule 172*. L. Desmet-Verteneuil, Bruxelles.
Lane, F. (1937): Esboço monographico des Anoplodermideos. – *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 *Mygdolus* [sic] *fryanus* Westwood, 1863 (Coleoptera, Cerambycidae, Anoplodermatinae). – *Revista Brasileira de Genetica* 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 Lepturinae. – *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. Maison, 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 Roussillonnaise d'Entomologie* 18 (2): 49–53.

Prosen, A. F. (1960): Notas sobre la família 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): Cerambycoid 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 a 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 Cerambycides 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 barredai* (Coleoptera, Cerambycidae, Vesperinae), nueva especie de cerambícido 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

Petr Svacha and John F. Lawrence

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

species occurring in Ñuble and Biobío to Osorno provinces in Chile, and Neuquén province in Argentina) prefers higher altitudes. The nearly flightless females and high host specificity would imply great vulnerability of this relict group without known relatives to forest fragmentation.

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

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

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

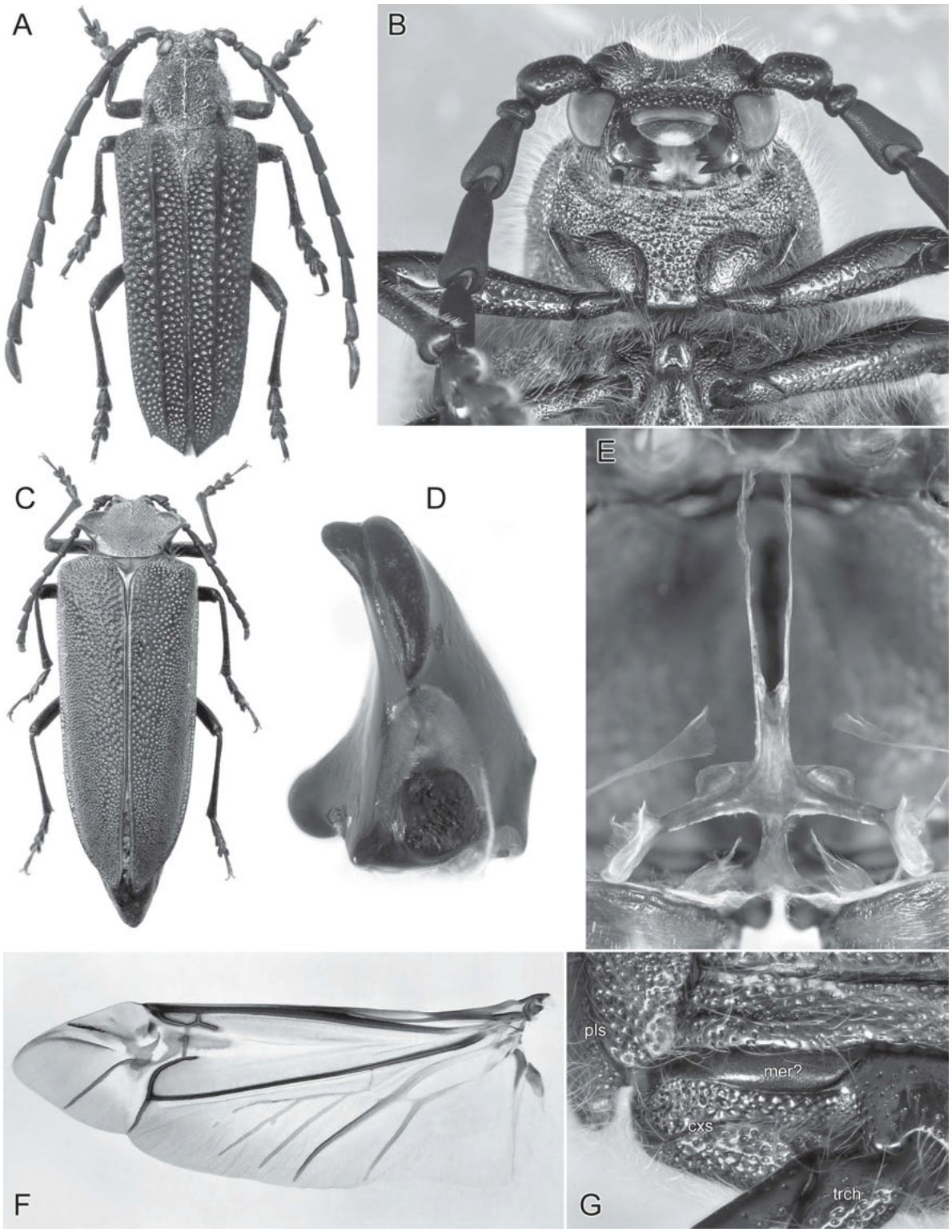

Fig. 2.2.1 Adults. A, *Oxypeltus quadrispinosus* Blanchard in Gay, male, dorsal view, 17 mm (© I. Jeniš); B, *O. quadrispinosus*, male, head and anterior thorax, ventral view; C, *Cheloderus childreni* Gray in Griffith, female, dorsal view, 41 mm (© I. Jeniš); D, *C. childreni*, male, right mandible,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

hairs; molar plate well-developed, subcircular and coarsely rugose; anteriorly largely enclosed by membranous region bearing dense microtrichia but not projecting into a prostheca. Maxilla with distinct, densely setose galea and lacinia, the latter shorter and without uncus. Labial ligula membranous,

bilobed, moderately large. Maxillary palp tetramerous, labial palp trimerous, both short and with fusiform terminal segments. Subgenal ridges absent. Metatentorial slits widely separate. Gular sutures more or less distinct along entire gular length; gula fused with submentum, which projects slightly between maxillary bases. Tentorial bridge intermediate, firm but not broad and roof-like; pre- and metatentorium connected; dorsal tentorial arms present. Cervical sclerites very large.

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

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

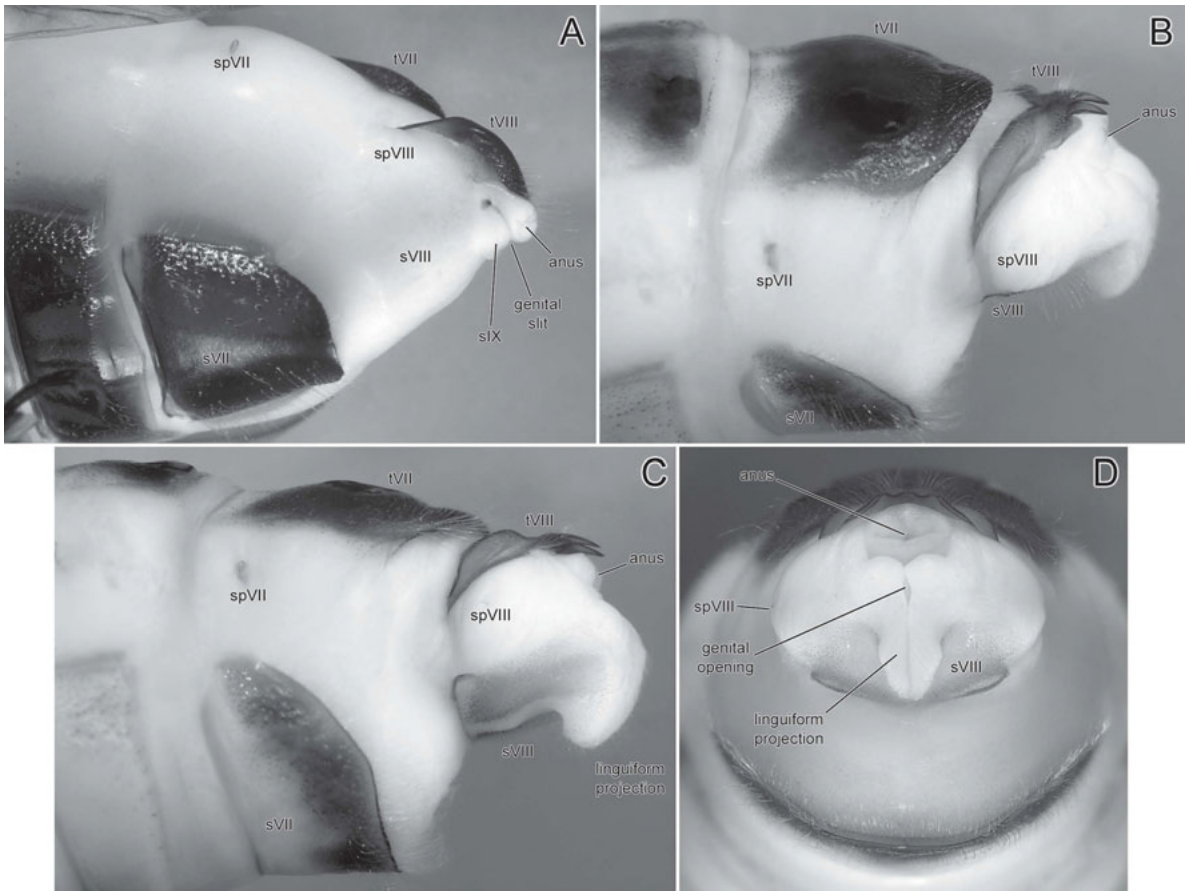

Fig. 2.2.2 *Oxypeltus quadrispinosus*, abdominal end of freshly moulted adults before the fat reserves are resorbed and membranes infolded. A, male, lateroventral view; B–D, female: B, laterodorsal view; C, lateroventral view; D, caudal view. s, sternum; sp, spiracle (vestigial on segment VIII); t, tergum.

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

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

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

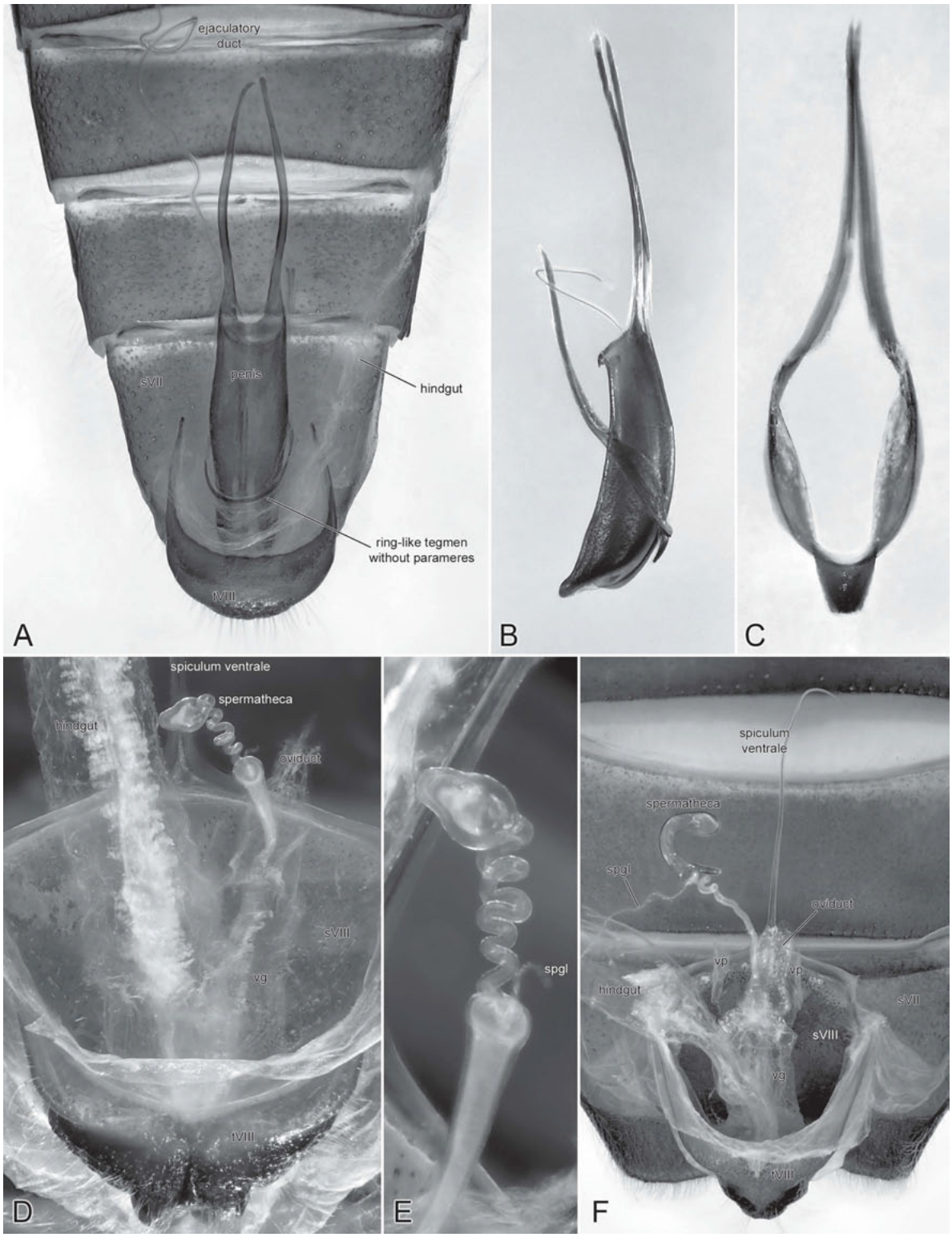

Fig. 2.2.3 Genitalia. A, *Oxypeltus quadrispinosus*, male, end of abdomen, dorsal view (terga removed except for VIII); B, *Cheloderus childreni*, penis (with part of ejaculatory duct) and tegmen, left lateral view (membranes removed); C, *C. childreni*, tegmen, dorsal view; D, *O. quadrispinosus*, female,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

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

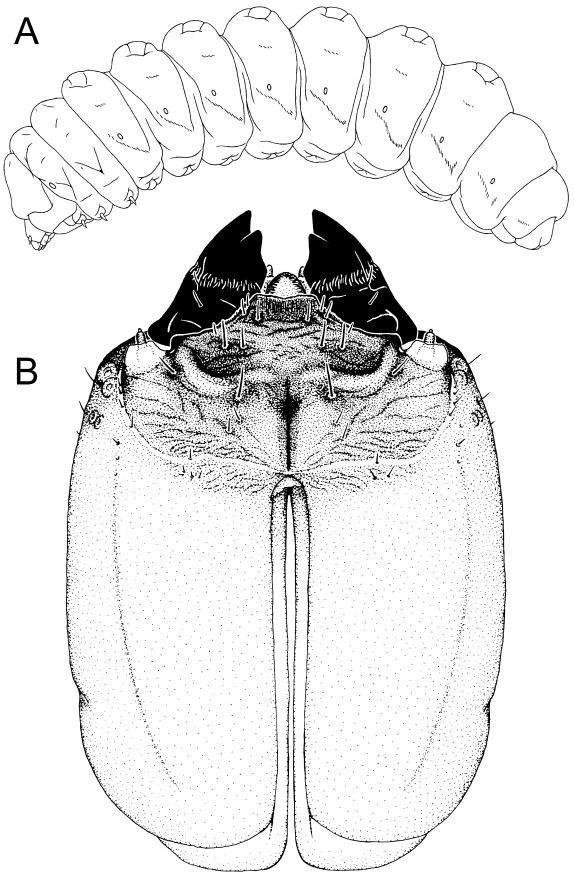

Fig. 2.2.4 Larvae. A, *Oxypeltus quadrispinosus*, larval habitus, left lateral view (from Svacha *et al*. 1997); B, *Cheloderus childreni*, head, dorsal view (from Svacha & Danilevsky 1987).

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

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

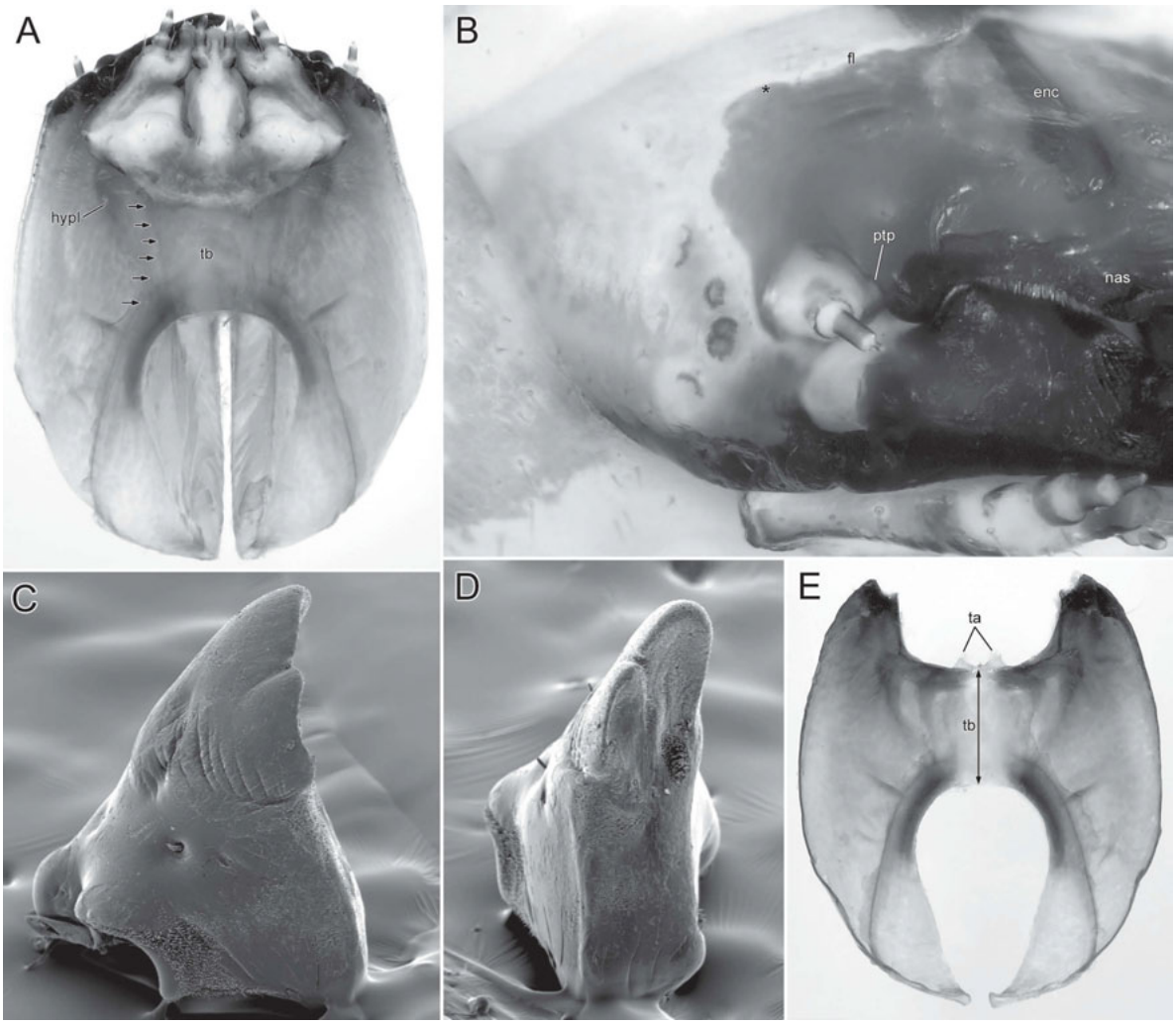

Fig. 2.2.5 *Oxypeltus quadrispinosus*, larva. A, head, ventral view; B, head, anterolateral view; C, left mandible, dorsal view; D, same, mesal view (C and D from Svacha *et al*. 1997); E, ventral half of cranium, dorsal view. enc, median frontal endocarina; fl, right frontal line; hypl, hypostomal lines;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

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

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

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

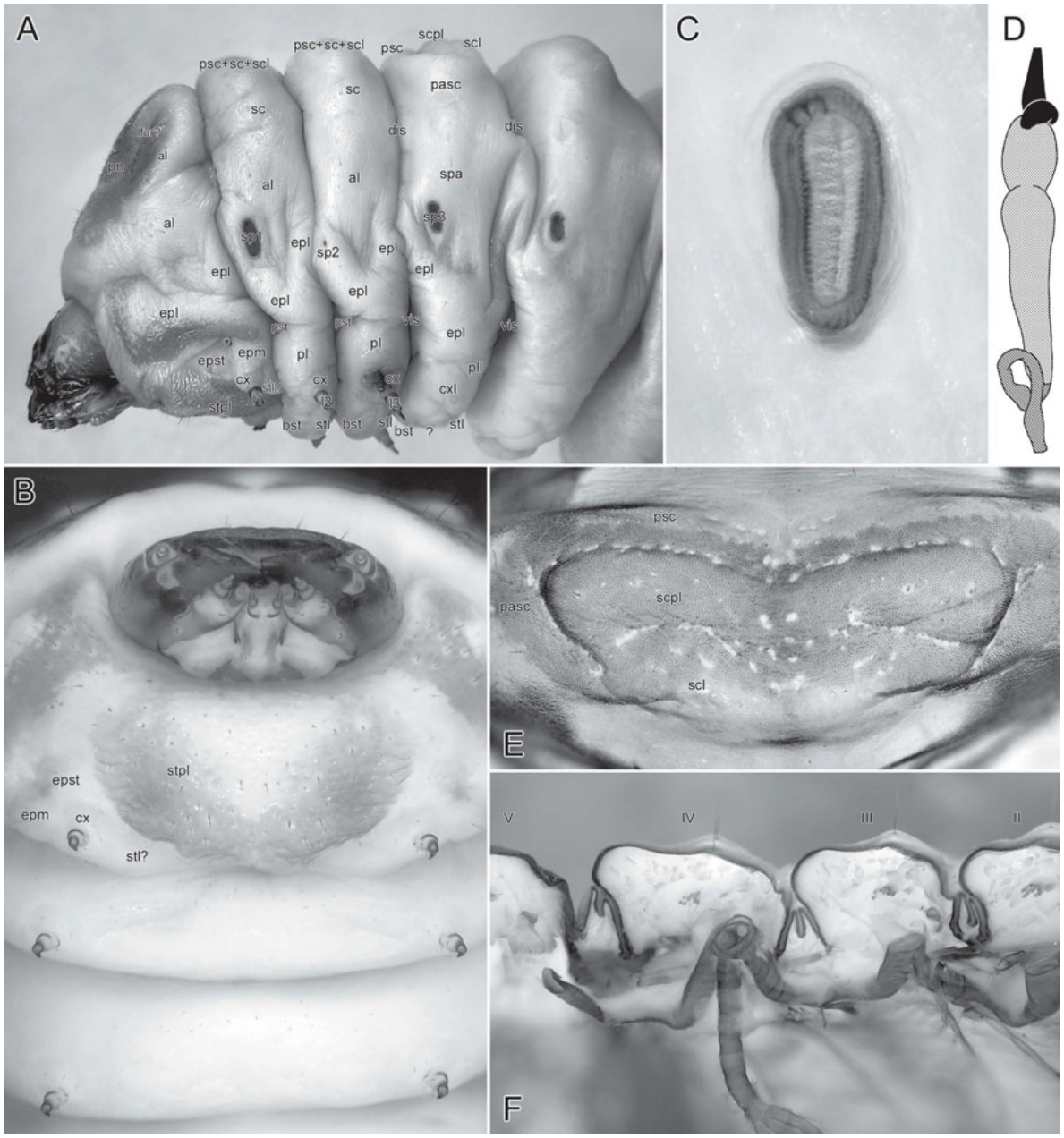

Fig. 2.2.6 Larvae. A, *Cheloderus childreni*, head, thorax and first two abdominal segments, left lateral view; B, *Oxypeltus quadrispinosus*, head and thorax, ventral view; C, *O. quadrispinosus*, 7th right abdominal spiracle; D, *O. quadrispinosus*, gross morphology of larval gut, diagrammatic, dorsal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

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