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General Morphology, Classification, and Biology of Cerambycidae

Marcela L. Monné and Miguel A. Monné
Universidade Federal do Rio de Janeiro
Rio de Janeiro, Brasil

Qiao Wang
Massey University
Palmerston North, New Zealand

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1.1 Introduction

Cerambycidae Latreille, 1802, commonly known as longicorns, longhorns, longicorn beetles, longhorned beetles, longhorned borers, round-headed borers, timber beetles, or sawyer beetles, are among the most diverse and economically important families of Coleoptera. Taxonomic interest in the family has been fairly consistent for the past century, but the description of new taxa has accelerated in recent decades. The number of described cerambycid species in the world is about 36,300 in more than 5,300 genera (Tavakilian 2015). The adult body length ranges from less than 2 mm in *Cyrtinus pygmaeus* (Haldeman) (Linsley 1961) to greater than 170 mm in *Titanus giganteus* (L.) (Williams 2001). Cerambycids are widely distributed around the world—from sea level to 4,200 m above—wherever their host plants are found. Distribution and generic diversity of the world's cerambycid subfamilies and tribes are shown in Table 1.1.

The longicorn adults are free-living beetles that may or may not need to feed. They can live for a few days to a few months depending on whether they feed (Hanks 1999; Wang 2008). Cerambycids usually reproduce sexually but, in very rare cases—such as in some species of *Kurarus* Gressitt (Cerambycinae) (Goh 1977) and *Cortodera* Mulsant (Lepturinae) (Švácha and Lawrence 2014), they can reproduce parthenogenetically. Švácha and Lawrence (2014) suggested that at least in *Cortodera*, parthenogenesis probably is of recent origin because the female has a distinct spermatheca with a spermathecal gland. Mate location depends on the occurrence and status of larval hosts, adult food sources, and/or pheromones. Hanks (1999) predicted that the absence of feeding in the adult stage of many species is associated with the production of long-range pheromones, but the current knowledge shows that the use of volatile pheromones is widespread in cerambycids (see Chapter 5). The females lay their eggs on or near their hosts. The larvae of most cerambycid species feed on woody plants, but some select herbaceous hosts. The vast majority of species at the larval stage are living and feeding inside the plants although small minorities are free-living in soil and feed on plant roots.

Many cerambycid larvae are dead plant feeders and play a major role in recycling dead plants; others attack living plants of different health states, ranging from stressed to healthy plants. To date, there are about 200 cerambycid species worldwide that have some economic impact on agriculture, forestry, and horticulture, causing billions of dollars of damage in production losses, environmental disasters, and management costs. They may damage plants by direct feeding and/or transmission of plant diseases.

TABLE 1.1

Distribution and Generic Diversity of Cerambycid Subfamilies and Tribes

Subfamilies and Tribes	Biogeographic Regions	No. Genera
Cerambycinae Latreille, 1802	**All biogeographic regions**	**1,757**
Acangassuini Galileo & Martins, 2001	Neotropical	1
Achrysonini Lacordaire, 1868	All biogeographic regions	20
Agallissini Le Conte, 1873	Neotropical	3
Alanizini Di Iorio, 2003	Neotropical	1
Anaglyptini Lacordaire, 1868	All biogeographic regions	12
Aphanasiini Lacordaire, 1868	Afrotropical and Australian	6
Aphneopini Lacordaire, 1868	Australian	5
Auxesini Lepesme & Breuning, 1952	Afrotropical	8
Basipterini Fragoso, Monné & Campos Seabra, 1987	Neotropical	2
Bimiini Lacordaire, 1868	Australian and Neotropical	7
Bothriospilini Lane, 1950	Neotropical	11
Brachypteromatini Sama, 2008	Palaearctic	1
Callichromatini Swainson, 1840	All biogeographic regions	178
Callidiini Kirby, 1837	All biogeographic regions	38
Callidiopini Lacordaire, 1868	All biogeographic regions	62
Cerambycini Latreille, 1802	All biogeographic regions	99
Certallini Fairmaire, 1864	Palaearctic, Afrotropical, and Australian	9
Chlidonini Waterhouse, 1879	Afrotropical (Madagascar)	2
Cleomenini Lacordaire, 1868	Afrotropical and Oriental	23
Clytini Mulsant, 1839	All biogeographic regions	83
Compsocerini Thomson, 1864	All biogeographic regions	33
Coptommatini Lacordaire, 1869	Australian	1
Curiini LeConte, 1873	Neotropical	1
Deilini Fairmaire, 1864	Palaearctic and Australian	3
Dejanirini Lacordaire, 1868	Oriental	2
Diorini Lane, 1950	Neotropical	1
Distichocerini Pascoe, 1867	Australian	2
Dodecosini Aurivillius, 1912	Neotropical	4
Dryobiini Arnett, 1962	Nearctic and Neotropical	3
Eburiini Blanchard, 1845	Neotropical	23
Ectenessini Martins, 1998	Neotropical	12
Elaphidiini Thomson, 1864	Nearctic and Neotropical	91
Eligmodermini Lacordaire, 1868	Neotropical	5
Erlandiini Aurivillius, 1912	Neotropical	1
Eroschemini Lacordaire, 1868	Australian	2
Eumichthini Linsley, 1940	Nearctic	2
Gahaniini Quentin & Villiers, 1969	Afrotropical	1
Glaucytini Lacordaire, 1868	Oriental and Australian	18
Graciliini Mulsant, 1839	All biogeographic regions	22
Hesperophanini Mulsant, 1839	All biogeographic regions	85
Hesthesini Pascoe, 1867	Australian	1
Heteropsini Lacordaire, 1868	Neotropical and Australian	29
Hexoplini Martins, 2006	Neotropical	22
Holopleurini Chemsak & Linsley, 1974	Nearctic	1
Hyboderini Linsley, 1940	Nearctic and Neotropical	4
Hylotrupini Zagajkevich, 1991	Palaearctic	1
Ideratini Martins & Napp, 2009	Neotropical	1

(Continued)

TABLE 1.1 ***(Continued)***

Distribution and Generic Diversity of Cerambycid Subfamilies and Tribes

Subfamilies and Tribes	Biogeographic Regions	No. Genera
Lissonotini Swainson, 1840	Neotropical	1
Luscosmodicini Martins, 2003	Neotropical	1
Lygrini Sama, 2008	Afrotropical	1
Macronini Lacordaire, 1868	Australian	4
Megacoelini Quentin & Villiers, 1969	Afrotropical	2
Methiini Thomson, 1860	Oriental, Afrotropical, and Neotropical	19
Molorchini Gistel, 1848	All biogeographic regions	26
Mythodini Lacordaire, 1868	Oriental	4
Necydalopsini Lacordaire, 1868	Neotropical	12
Neocorini Martins, 2005	Neotropical	7
Neoibidionini Monné, 2012	Neotropical	55
Neostenini Lacordaire, 1868	Australian	4
Obriini Pascoe, 1871	All biogeographic regions	43
Ochyrini Pascoe, 1871	Australian	1
Oedenoderini Aurivillius, 1912	Afrotropical	1
Oemini Lacordaire, 1868	All biogeographic regions	101
Opsimini LeConte, 1873	Nearctic and Palaearctic	3
Oxycoleini Martins & Galileo, 2003	Neotropical	2
Paraholopterini Martins, 1997	Neotropical	1
Phalotini Lacordaire, 1868	Australian	4
Phlyctaenodini Lacordaire, 1868	Australian and Neotropical	17
Phoracanthini Newman, 1840	Australian	22
Phyllarthriini Lepesme & Breuning, 1956	Afrotropical	4
Piesarthriini McKeown, 1947	Australian	4
Piezocerini Lacordaire, 1868	Neotropical	19
Platyarthrini Bates, 1870	Neotropical	1
Plectogasterini Quentin & Villiers, 1969	Afrotropical	8
Plectromerini Nearns & Braham, 2008	Neotropical	1
Pleiarthrocerini Lane, 1950	Neotropical	1
Plesioclytini Wappes & Skelley, 2015	Nearctic	1
Proholopterini Monné, 2012	Neotropical	3
Protaxini Gahan, 1906	Oriental	1
Prothemini Lacordaire, 1868	Oriental	3
Psebiini Lacordaire, 1868	Afrotropical and Neotropical	24
Pseudocephalini Aurivillius, 1912	Australian and Neotropical	4
Pseudolepturini Thomson, 1861	Oriental	6
Psilomorphini Lacordaire, 1868	Australian	3
Pteroplatini Thomson, 1861	Afrotropical and Neotropical	10
Rhagiomorphini Newman, 1841	Australian	4
Rhinotragini Thomson, 1861	Neotropical	82
Rhopalophorini Blanchard, 1845	Nearctic, Neotropical, and Australian	29
Sestyrini Lacordaire, 1868	Oriental	2
Smodicini Lacordaire, 1868	Afrotropical, Nearctic, and Neotropical	8
Spintheriini Lacordaire, 1869	Australian	2
Stenhomalini Miroshnikov, 1989	Oriental	2
Stenoderini Pascoe, 1867	Australian and Oriental	10
Stenopterini Gistel, 1848	Palaearctic and Oriental	14
Strongylurini Lacordaire, 1868	Australian	6

(Continued)

TABLE 1.1 *(Continued)*

Distribution and Generic Diversity of Cerambycid Subfamilies and Tribes

Subfamilies and Tribes	Biogeographic Regions	No. Genera
Tessarommatini Lacordaire, 1868	Australian	1
Thraniini Gahan, 1906	Oriental	3
Thyrsiini Marinoni & Napp, 1984	Neotropical	1
Tillomorphini Lacordaire, 1868	Nearctic, Neotropical, Oriental, and Australian	31
Torneutini Thomson, 1861	Neotropical	16
Trachyderini Dupont, 1836	All biogeographic regions	154
Tragocerini Pascoe, 1867	Australian	1
Trichomesiini Aurivillius, 1912	Australian	1
Trigonarthrini Villiers, 1984	Afrotropical	2
Tropocalymmatini Lacordaire, 1868	Australian	1
Typhocesini Lacordaire, 1868	Australian	4
Unxiini Napp, 2007	Neotropical	8
Uracanthini Blanchard, 1853	Australian	6
Vesperellini Sama, 2008	Palaearctic	1
Xystrocerini Blanchard, 1845	Afrotropical and Australian	2
Dorcasominae Lacordaire, 1868	**Afrotropical, Oriental, and Palaearctic**	**95**
Apatophyseini Lacordaire, 1869	Afrotropical, Oriental, and Palaearctic	90
Dorcasomini Lacordaire, 1868	Afrotropical, Oriental, and Palaearctic	5
Lamiinae Latreille, 1825	**All biogeographic regions**	**2,964**
Acanthocinini Blanchard, 1845	All biogeographic regions	386
Acanthoderini Thomson, 1860	All biogeographic regions	66
Acmocerini Thomson, 1864	Afrotropical	6
Acridocephalini Dillon & Dillon, 1959	Afrotropical	1
Acrocinini Swainson, 1840	Neotropical	1
Aderpasini Breuning & Teocchi, 1978	Afrotropical	1
Aerenicini Lacordaire, 1872	Neotropical	26
Agapanthiini Mulsant, 1839	All biogeographic regions	84
Amphoecini Breuning, 1951	Australian	2
Ancitini Aurivillius, 1917	Australian	1
Ancylonotini Lacordaire, 1869	Afrotropical, Oriental, and Palaearctic	36
Anisocerini Thomson, 1860	Neotropical	26
Apomecynini Thomson, 1860	All biogeographic regions	240
Astathini Thomson, 1864	Australian, Afrotropical, Oriental, and Palaearctic	23
Batocerini Thomson, 1864	Australian, Oriental, and Palaearctic	10
Calliini Thomson, 1864	Neotropical	40
Ceroplesini Thomson, 1860	Afrotropical, Oriental, and Palaearctic	88
Cloniocerini Lacordaire, 1872	Afrotropical	1
Colobotheini Thomson, 1860	Neotropical	12
Compsosomatini Thomson, 1867	Neotropical	13
Cyrtinini Thomson, 1864	Australian and Neotropical	16
Desmiphorini Thomson, 1860	All biogeographic regions	319
Dorcadionini Swainson, 1840	Palaearctic and Oriental	14
Dorcaschematini Thomson, 1860	Oriental and Australian	9
Elytracanthinini Bousquet, 2009	Neotropical	1
Enicodini Thomson, 1864	Australian and Oriental	27
Eupromerini Galileo & Martins, 1995	Neotropical	5
Forsteriini Tippmann, 1960	Neotropical	16
Gnomini Thomson, 1860	Australian, Oriental, and Palaearctic	4

(Continued)

TABLE 1.1 ***(Continued)***

Distribution and Generic Diversity of Cerambycid Subfamilies and Tribes

Subfamilies and Tribes	Biogeographic Regions	No. Genera
Gyaritini Breuning, 1950	Australian and Oriental	14
Heliolini Breuning, 1951	Australian	1
Hemilophini Thomson, 1868	Neotropical and Nearctic	127
Homonoeini Thomson, 1864	Australian, Oriental, and Palaearctic	22
Hyborhabdini Aurivillius, 1911	Oriental	1
Lamiini Latreille, 1825	Afrotropical, Australian, Oriental, and Palaearctic	48
Laticraniini Lane, 1959	Neotropical	2
Mauesiini Lane, 1956	Neotropical	4
Megabasini Thomson, 1860	Neotropical	1
Mesosini Mulsant, 1839	All biogeographic regions	99
Microcymaturini Breuning & Teocchi, 1985	Afrotropical	3
Moneilemini Thomson, 1864	Nearctic and Neotropical	1
Monochamini Gistel, 1848	All biogeographic regions	263
Morimonellini Lobanov, Danilevsky & Murzin, 1981	Palaearctic	1
Morimopsini Lacordaire, 1869	All regions except Nearctic	47
Nyctimeniini Gressitt, 1951	Australian and Oriental	1
Obereini Thomson, 1864	All regions except Neotropical	3
Ocularini Breuning, 1950	Afrotropical	2
Onciderini Thomson, 1860	Neotropical and Nearctic	81
Oncideropsidini Aurivillius, 1922	Oriental	1
Onocephalini Thomson, 1860	Neotropical	3
Onychogleneini Aurivillius, 1923	Oriental	1
Parmenini Mulsant, 1839	All biogeographic regions	87
Petrognathini Blanchard, 1845	Afrotropical and Oriental	10
Phacellini Lacordaire, 1872	Neotropical	7
Phantasini Kolbe, 1897	Afrotropical	3
Phrynetini Thomson, 1864	Afrotropical, Oriental, and Palaearctic	14
Phymasternini Teocchi, 1989	Afrotropical	1
Phytoeciini Mulsant, 1839	All biogeographic regions	32
Pogonocherini Mulsant, 1839	All biogeographic regions	33
Polyrhaphidini Thomson, 1860	Afrotropical and Neotropical	2
Pretiliini Martins & Galileo, 1990	Neotropical	1
Proctocerini Aurivillius, 1922	Afrotropical	1
Prosopocerini Thomson, 1864	Afrotropical	18
Pteropliini Thomson, 1860	All biogeographic regions	256
Saperdini Mulsant, 1839	All regions except Neotropical	154
Stenobiini Breuning, 1950	Afrotropical	7
Sternotomini Thomson, 1860	Afrotropical	20
Tapeinini Thomson, 1857	Neotropical and Oriental	2
Tetraopini Thomson, 1860	Nearctic and Neotropical	3
Tetraulaxini Breuning & Teocchi, 1977	Afrotropical	2
Tetropini Portevin, 1927	Palaearctic	2
Theocrini Lacordaire, 1872	Afrotropical	8
Tmesisternini Blanchard, 1853	Australian and Oriental	12
Tragocephalini Thomson, 1857	Afrotropical	63
Xenicotelini Matsushita, 1933	Oriental	1
Xenofreini Aurivillius, 1923	Neotropical	3
Xenoleini Lacordaire, 1872	Australian, Oriental, and Palaearctic	3

(Continued)

TABLE 1.1 ***(Continued)***

Distribution and Generic Diversity of Cerambycid Subfamilies and Tribes

Subfamilies and Tribes	Biogeographic Regions	No. Genera
Xylorhizini Lacordaire, 1872	Afrotropical, Australian, Oriental, and Palaearctic	10
Zygocerini Thomson, 1864	Australian and Oriental	9
Lepturinae Latreille, 1802	**All biogeographic regions**	**210**
Desmocerini Blanchard, 1845	Nearctic	1
Encyclopini LeConte, 1873	Nearctic and Palaearctic	2
Lepturini Latreille, 1802	All biogeographic regions	140
Oxymirini Danilevsky, 1997	Palaearctic	1
Rhagiini Kirby, 1837	All biogeographic regions	53
Rhamnusiini Sama, 2009	Palaearctic and Oriental	2
Sachalinobiini Danilevsky, 2010	Nearctic and Palaearctic	1
Teledapini Pascoe, 1871	Oriental	3
Xylosteini Reitter, 1913	Palaearctic and Oriental	7
Necydalinae Latreille, 1825	**Nearctic, Palaearctic, and Oriental**	**2**
Necydalini Latreille, 1825	Nearctic, Palaearctic, and Oriental	2
Parandrinae Blanchard, 1845	**All biogeographic regions**	**19**
Erichsoniini Thomson, 1861	Neotropical	1
Parandrini Blanchard, 1845	All biogeographic regions	18
Prioninae Latreille, 1802	**All biogeographic regions**	**302**
Acanthophorini Thomson, 1864	Afrotropical	7
Aegosomatini Thomson, 1861	Afrotropical, Oriental, and Australian	20
Anacolini Thomson, 1857	Afrotropical, Oriental, and Neotropical	33
Cacoscelini Thomson, 1861	Afrotropical and Australian	5
Callipogonini Thomson, 1861	Afrotropical, Palaearctic, and Neotropical	17
Calocomini Galileo & Martins, 1993	Neotropical	1
Cantharocnemini Thomson, 1861	Afrotropical and Australian	6
Closterini, Lacordaire, 1868	Afrotropical, Australian, and Oriental	8
Ergatini Fairmaire, 1864	Afrotropical, Palaearctic, and Nearctic	5
Eurypodini Gahan, 1906	Palaearctic and Oriental	4
Hopliderini Thomson, 1864	Afrotropical	5
Macrodontiini Thomson, 1861	Neotropical	5
Macrotomini Thomson, 1861	All biogeographic regions	78
Mallaspini Thomson, 1861	Neotropical	10
Mallodonini Thomson, 1861	Afrotropical, Oriental, Nearctic, and Neotropical	10
Meroscelisini Thomson, 1861	Afrotropical, Australian, and Neotropical	21
Prionini Latreille, 1802	All biogeographic regions	50
Remphanini Lacordaire, 1868	Oriental	6
Solenopterini Lacordaire, 1868	Neotropical	7
Tereticini Lameere, 1913	Afrotropical and Australian	3
Vesperoctenini Vives, 2005	Neotropical	1
Spondylidinae Audinet-Serville, 1832	**All biogeographic regions**	**32**
Anisarthrini Mamaev & Danilevsky, 1973	Palaearctic	4
Asemini Thomson, 1861	All biogeographic regions	12
Atimiini LeConte, 1873	Nearctic, Neotropical, and Palaearctic	3
Saphanini Gistel 1848	Afrotropical and Nearctic	10
Spondylidini Audinet-Serville, 1832	Neotropical, Nearctic, and Palaearctic	3

With the increase of international trade in recent years, many cerambycid species have been intercepted; some have become established outside their natural distribution range, causing serious problems globally (Haack et al. 2010; see Chapter 13).

Linsley (1961, 1962a) and Wang (2008) summarize the general morphology and biology of the Cerambycidae. More recently, Švácha and Lawrence (2014) have made a very detailed treatment of the morphology and a general account of the ecology of the Cerambycidae. Ślipiński and Escalona (2013) gave a good introduction to the morphology and ecology of Australian cerambycids. In this chapter, we summarize the current knowledge about this family, including the definition and morphology, and a brief introduction to the taxonomy, distribution, and general biology at the subfamily level. We aim to provide readers with a fundamental knowledge of cerambycids as well as a guide for those who may wish to consult specific chapters in this book where detailed treatments of Cerambycid biology and pest management are discussed.

1.2 Definition and Morphology of the Family Cerambycidae

1.2.1 Definition

Traditionally, the family Cerambycidae had wider scope, including nine subfamilies: Anoplodermatinae, Aseminae, Cerambycinae, Lamiinae, Lepturinae, Parandrinae, Philinae, Prioninae, and Spondylidinae (Napp 1994). In the current classification system (Bouchard et al. 2011; Monné 2012; Švácha and Lawrence 2014), Oxypeltinae, Vesperinae, and Disteniinae are considered independent families. We use the new system in this book and discuss eight subfamilies: Cerambycinae, Dorcasominae, Lamiinae, Lepturinae, Necydalinae, Parandrinae, Prioninae, and Spondylidinae. Table 1.1 summarizes the distribution and generic diversity of cerambycid subfamilies and tribes.

1.2.2 General Morphology

The general morphology of Cerambycidae is extracted from Ślipiński and Escalona (2013) and Švácha and Lawrence (2014).

1.2.2.1 Adult

1.2.2.1.1 Diagnosis

General external morphology of cerambycid adults is illustrated in Figures 1.1 and 1.2. Antennae usually filiform, elongate, and 11-segmented, rarely serrate and >12-segmented, usually inserted on pronounced tubercles; eyes usually emarginate; prothorax without pleural sutures; tibia with two distinct tibial spurs; tarsi usually pseudotetramerous with fourth tarsomere usually minute and concealed by third tarsomere; elytra usually covering abdomen; hind wings with a spur on radio-medial crossvein; abdomen usually with five visible sternites, fifth sternite entire.

1.2.2.1.2 Description

1.2.2.1.2.1 Head The head is prognathous and more or less horizontal in the Parandrinae (Figures 1.3 and 1.4). It is produced anteriorly to form a short to moderately long muzzle in some Lepturinae (Figures 1.5 and 1.6), Dorcasominae, and Cerambycinae, inclined anteriorly in the Spondylidinae, and is vertical or retracted, with the genal line directed posteriorly, in the Lamiinae (Figure 1.7). The eyes are entire in the Parandrinae (Figure 1.3), most Lepturinae, and some Prioninae; feebly emarginate in the Spondylidinae (Figure 1.8) and most Prioninae (Figure 1.9); emarginate to entire in the Dorcasominae; and usually are deeply emarginate and reniform in the Cerambycinae (Figure 1.10) and Lamiinae (Figure 1.7); although occasionally they are divided—as in *Tetraopes* Schönherr—or lacking the upper lobe—as in *Tillomorpha* Blanchard. The facets of the eyes are large and coarse in the Parandrinae, most Prioninae, and some Asemini and Cerambycinae; usually, they are finer in the Lepturinae, Lamiinae, and more specialized Cerambycinae.

The antennae usually have 11 antennomeres (Figures 1.1 and 1.2) that are inserted near the base of the mandibles in the Parandrinae (Figure 1.3), Prioninae (Figure 1.9), and in some Spondylidinae;

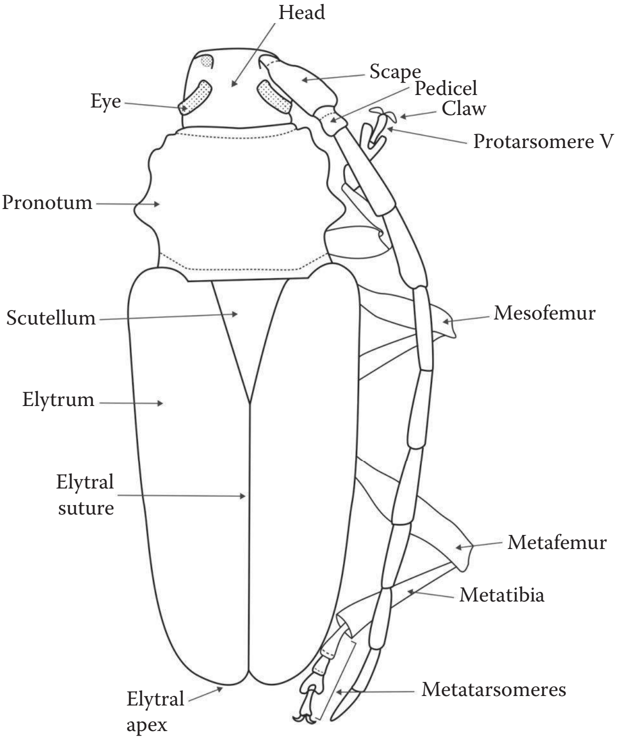

FIGURE 1.1 General morphology, dorsal view of *Trachyderes succinctus* (L.) (Cerambycinae).

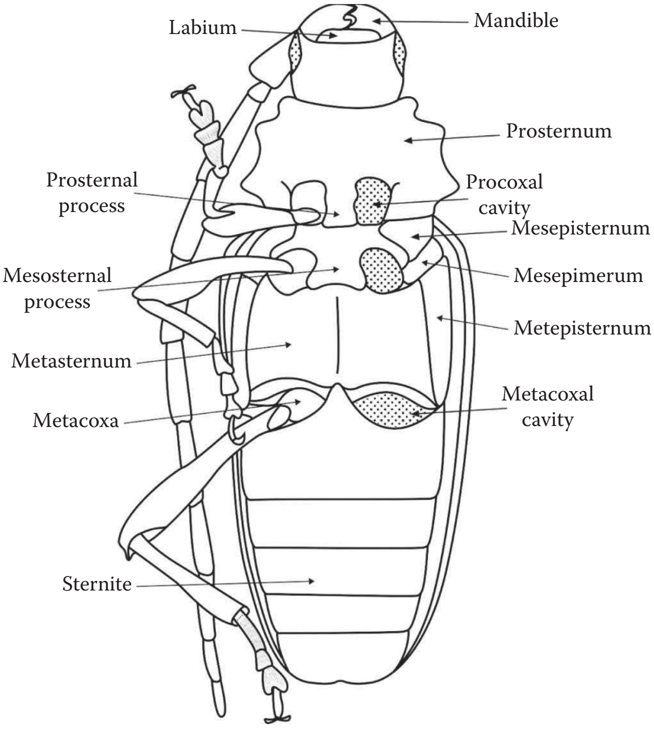

FIGURE 1.2 General morphology, ventral view of *Trachyderes succinctus* (L.) (Cerambycinae).

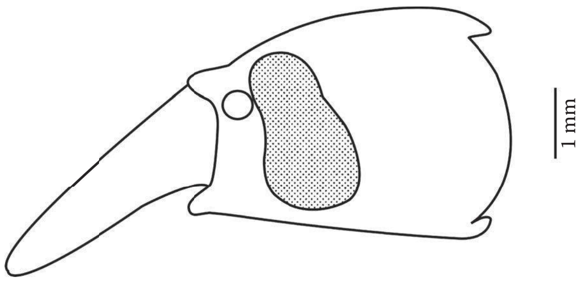

FIGURE 1.3 Head, lateral view of *Parandra (Parandra) glabra* (De Geer) (Parandrinae). (Reprinted with permission from C. J. B. Carvalho, editor. Napp, D. S., *Rev. Bras. Entomol.,* 38, 265–419, 1994.)

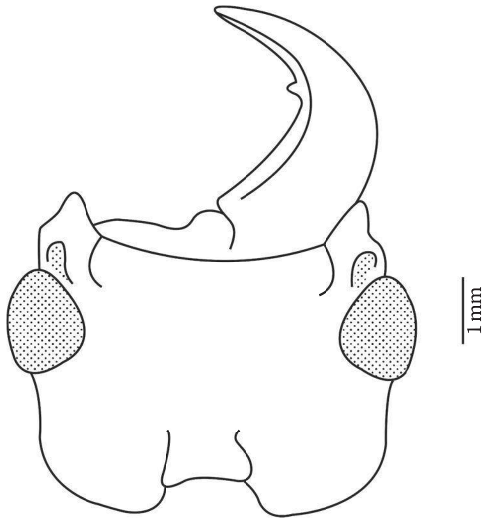

FIGURE 1.4 Head, dorsal view of *Parandra (Parandra) glabra* (De Geer) (Parandrinae). (Reprinted with permission from C. J. B. Carvalho, editor. Napp, D. S., *Rev. Bras. Entomol.*, 38, 265–419, 1994.)

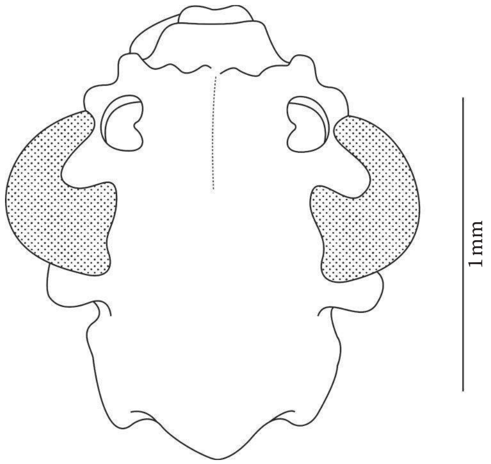

FIGURE 1.5 Head, dorsal view of *Leptura rubra* L. (Lepturinae). (Reprinted with permission from C. J. B. Carvalho, editor. Napp, D. S., *Rev. Bras. Entomol.,* 38, 265–419, 1994.)

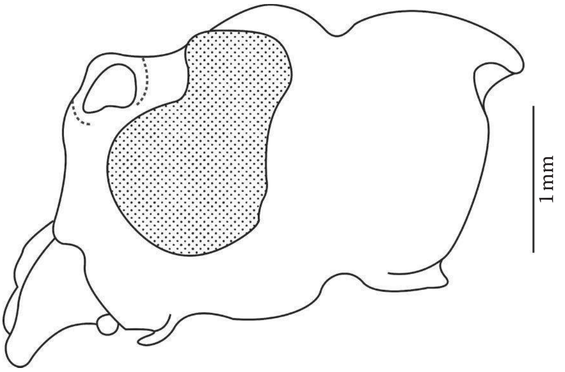

FIGURE 1.6 Head, lateral view of *Leptura rubra* L. (Lepturinae). (Reprinted with permission from C. J. B. Carvalho, editor. Napp, D. S., *Rev. Bras. Entomol.,* 38, 265–419, 1994.)

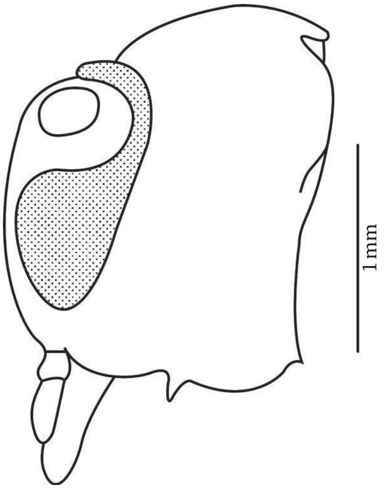

FIGURE 1.7 Head, lateral view of *Estola obscura* Thomson (Lamiinae). (Reprinted with permission from C. J. B. Carvalho, editor. Napp, D. S., *Rev. Bras. Entomol.,* 38, 265–419, 1994.)

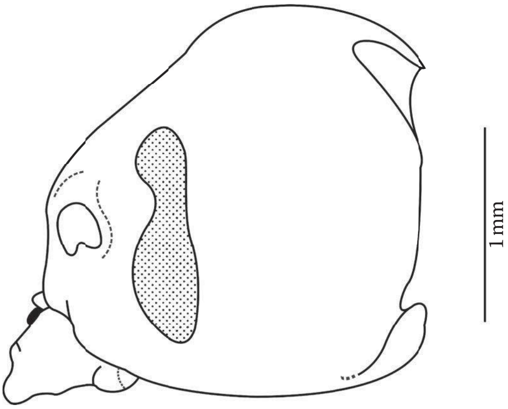

FIGURE 1.8 Head, lateral view of *Asemum striatum* (L.) (Spondylidinae). (Reprinted with permission from C. J. B. Carvalho, editor. Napp, D. S., *Rev. Bras. Entomol.,* 38, 265–419, 1994.)

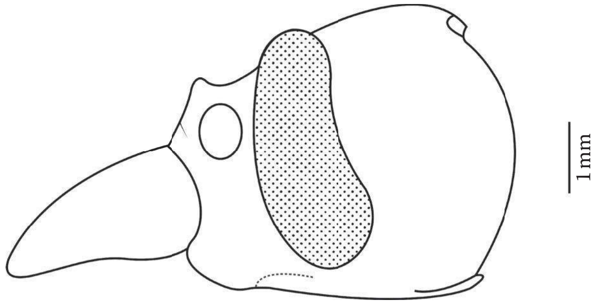

FIGURE 1.9 Head, lateral view of *Mallodon spinibarbis* (L.) (Prioninae). (Reprinted with permission from C. J. B. Carvalho, editor. Napp, D. S., *Rev. Bras. Entomol.*, 38, 265–419, 1994.)

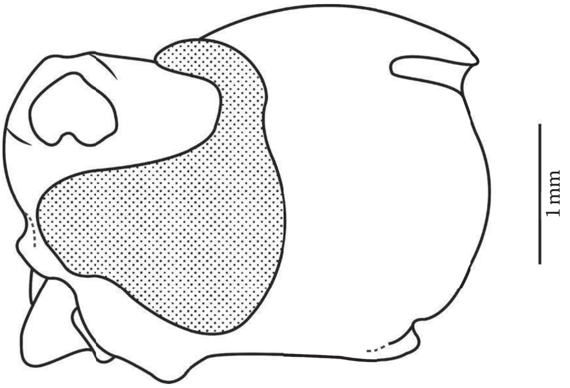

FIGURE 1.10 Head, lateral view of *Achryson surinamum* (L.) (Cerambycinae). (Reprinted with permission from C. J. B. Carvalho, editor. Napp, D. S., *Rev. Bras. Entomol.*, 38, 265–419, 1994.)

are near the eyes in the Asemini and Lepturinae (Figure 1.6); and are usually more or less embraced by the eyes in the Cerambycinae (Figure 1.10) and Lamiinae (Figure 1.7). In some diurnal Lamiinae (e.g., *Octotapnia* Galileo & Martins and *Pseudotapnia* Chemsak & Linsley) and Prioninae, the antennae may have fewer antennomeres. In some Lamiinae (e.g., *Paratenthras* Monné), the first three antennomeres are long, whereas the remaining flagella are reduced and sometimes moniliform. The number of antennomeres may be 12 in a number of unrelated groups and more than 12 in a few Cerambycinae and Prioninae (up to 30 in some species of *Prionus* Müller). The antennal structure is similar between sexes in the Parandrinae, Spondylidinae, and Lepturinae, and strikingly dissimilar in many Prioninae and in most Cerambycinae and Lamiinae. In the Parandrinae and Spondylidinae, differentiation of antennomeres is not well marked; the scape is short, the second antennomere is not greatly reduced in size, half as long as, or subequal to the third antennomere, and the segments that follow are subequal in length. In the remaining subfamilies, the scape is usually more elongate, the second segment is greatly reduced, and the following antennomeres are unequal in length—with the third usually greatly elongated and those that follow diminishing to the ultimate antennomere. The antennal segments are glabrous in the Parandrinae, Prioninae, and Spondylidinae, and are pubescent in other subfamilies.

The labrum is fused with the epistoma in the Parandrinae and Prioninae but free in other subfamilies. The mandibles are acute in all of the Cerambycidae; large and often toothed in the Parandrinae (Figure 1.4) and Prioninae (Figure 1.11); long, slender, and untoothed in the Spondylidinae; shorter in most other groups; and are provided with a dense fringe of hairs in the inner margin of the Dorcasominae and Lepturinae. The maxillae are typically bilobed; the inner lobe is obsolete in the Parandrinae (Figure 1.12) and Prioninae (Figure 1.13). The ultimate segment of the palpi (both

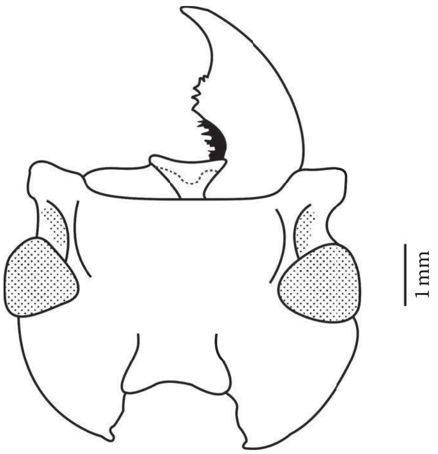

FIGURE 1.11 Head, dorsal view of *Mallodon spinibarbis* (L.) (Prioninae). (Reprinted with permission from C. J. B. Carvalho, editor. Napp, D. S., *Rev. Bras. Entomol.*, 38, 265–419, 1994.)

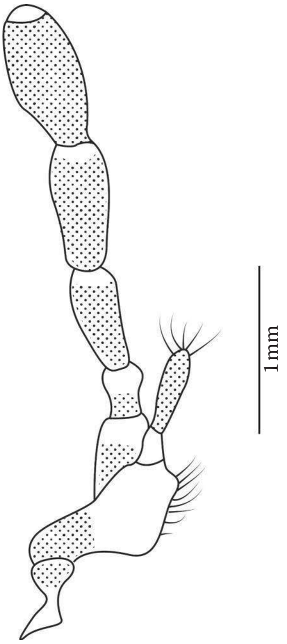

FIGURE 1.12 Maxilla, ventral view of *Parandra (Parandra) glabra* (De Geer) (Parandrinae). (Reprinted with permission from C. J. B. Carvalho, editor. Napp, D. S., *Rev. Bras. Entomol.*, 38, 265–419, 1994.)

maxillary and labial) is pointed at the apex in the Lamiinae (Figures 1.14 and 1.15) and truncated (Figures 1.16 through 1.19) in other subfamilies. The submentum projects between the bases of the maxillae in the Lepturinae; is short in many Cerambycinae; and is absent in the Parandrinae, Prioninae, and Spondylidinae. The mentum is distinctly transverse in the Parandrinae (Figure 1.20), Prioninae, and Spondylidinae, and trapezoidal in the Lepturinae, Cerambycinae (Figure 1.18), and Lamiinae (Figure 1.14). The ligula is corneous in the Parandrinae and Spondylidinae, and membranous or coriaceous in the Lepturinae, Cerambycinae (Figure 1.18) (except Oemini and Methini), and Lamiinae (Figure 1.14).

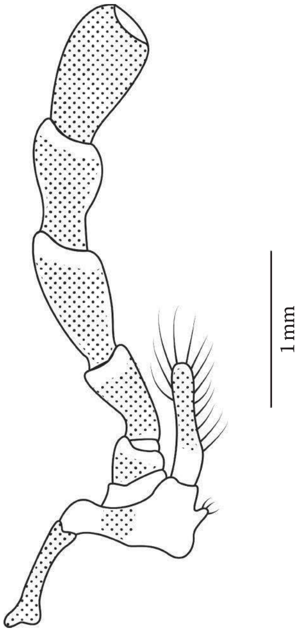

FIGURE 1.13 Maxilla, ventral view of *Mallodon spinibarbis* (L.) (Prioninae). (Reprinted with permission from C. J. B. Carvalho, editor. Napp, D. S., *Rev. Bras. Entomol.*, 38, 265–419, 1994.)

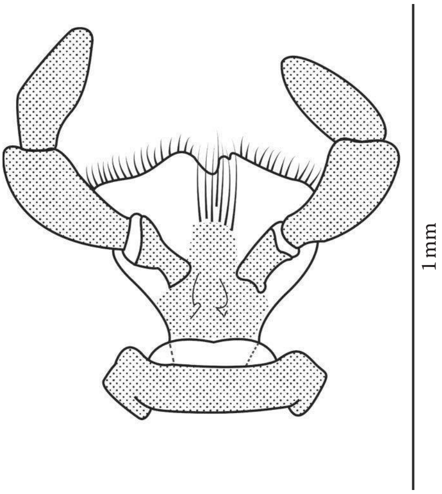

FIGURE 1.14 Labium, ventral view of *Estola obscura* Thomson (Lamiinae). (Reprinted with permission from C. J. B. Carvalho, editor. Napp, D. S., *Rev. Bras. Entomol.*, 38, 265–419, 1994.)

1.2.2.1.2.2 Thorax The prothorax bears lateral carinae in the Parandrinae (Figure 1.21) and Prioninae (Figures 1.22 and 1.23), which are lacking in other subfamilies (Figures 1.24 through 1.26). The procoxae are strongly transverse in the Parandrinae and Prioninae, less so in some Spondylidinae—such as Asemini, subconical in the rest Spondylidinae, conical in the Lepturinae, and usually rounded in the Cerambycinae and Lamiinae. The procoxal cavities are closed behind in some Parandrinae, in some Spondylidinae, and in most Lamiinae (Figure 1.26); wide open in the Prioninae (Figure 1.23), Asemini, and most Lepturinae (Figure 1.25); and open or closed in the Cerambycinae. The scutellum is visible, sometimes well developed (Figure 1.1) and usually is not abruptly elevated, anteriorly flat, or separated from

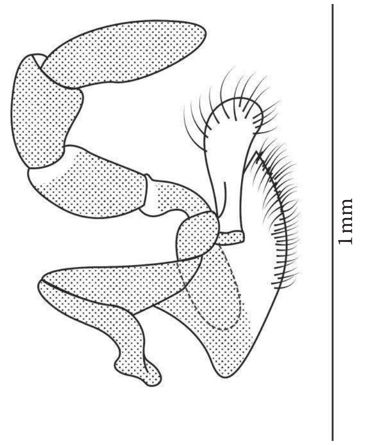

FIGURE 1.15 Maxilla, ventral view of *Estola obscura* Thomson (Lamiinae). (Reprinted with permission from C. J. B. Carvalho, editor. Napp, D. S., *Rev. Bras. Entomol.,* 38, 265–419, 1994.)

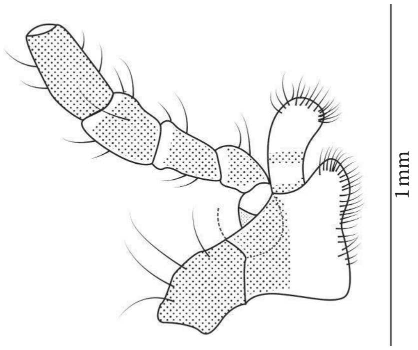

FIGURE 1.16 Maxilla, ventral view of *Asemum striatum* (L.) (Spondylidinae). (Reprinted with permission from C. J. B. Carvalho, editor. Napp, D. S., *Rev. Bras. Entomol.,* 38, 265–419, 1994.)

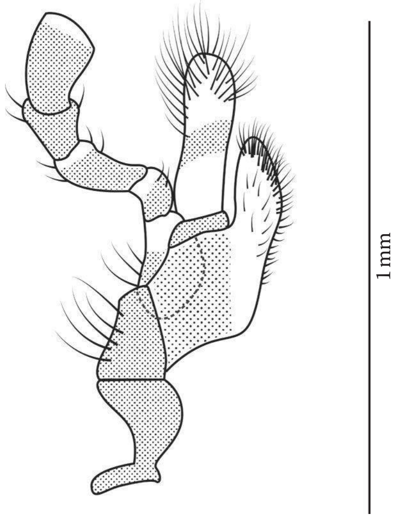

FIGURE 1.17 Maxilla, ventral view of *Necydalis major* L. (Necydalinae). (Reprinted with permission from C. J. B. Carvalho, editor. Napp, D. S., *Rev. Bras. Entomol.,* 38, 265–419, 1994.)

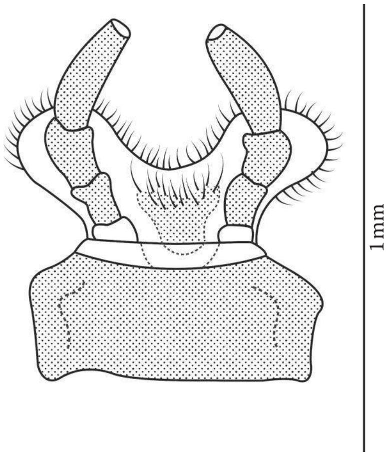

FIGURE 1.18 Labium, ventral view of *Rhopalophora collaris* (Germar) (Cerambycinae). (Reprinted with permission from C. J. B. Carvalho, editor. Napp, D. S., *Rev. Bras. Entomol.,* 38, 265–419, 1994.)

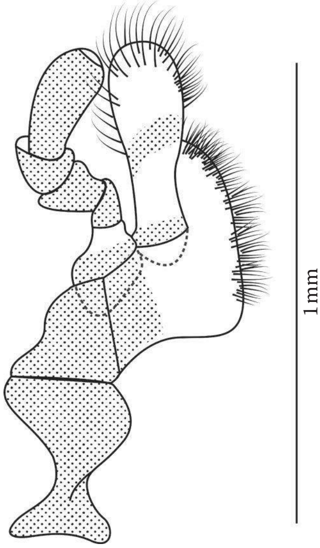

FIGURE 1.19 Maxilla, ventral view of *Trachyderes succinctus* (L.) (Cerambycinae). (Reprinted with permission from C. J. B. Carvalho, editor. Napp, D. S., *Rev. Bras. Entomol.,* 38, 265–419, 1994.)

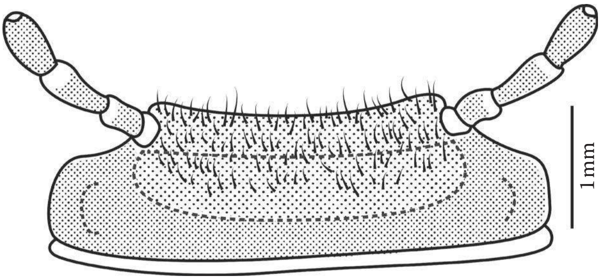

FIGURE 1.20 Labium, ventral view of *Parandra (Parandra) glabra* (De Geer) (Parandrinae). (Reprinted with permission from C. J. B. Carvalho, editor. Napp, D. S., *Rev. Bras. Entomol.,* 38, 265–419, 1994.)

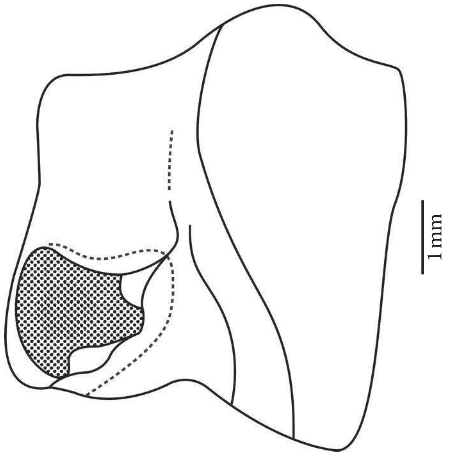

FIGURE 1.21 Prothorax, lateral view of *Parandra (Parandra) glabra* (De Geer) (Parandrinae). (Reprinted with permission from C. J. B. Carvalho, editor. Napp, D. S., *Rev. Bras. Entomol.,* 38, 265–419, 1994.)

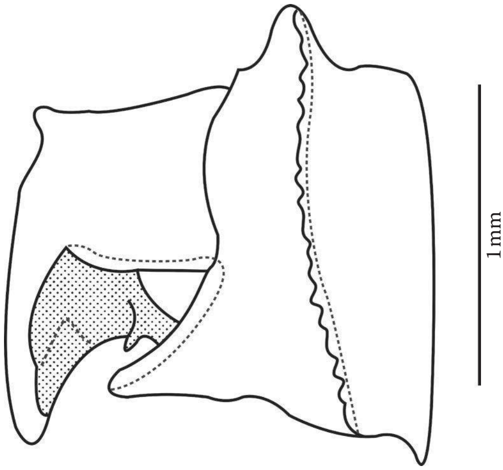

FIGURE 1.22 Prothorax, lateral view of *Mallodon spinibarbis* (L.) (Prioninae). (Reprinted with permission from C. J. B. Carvalho, editor. Napp, D. S., *Rev. Bras. Entomol.,* 38, 265–419, 1994.)

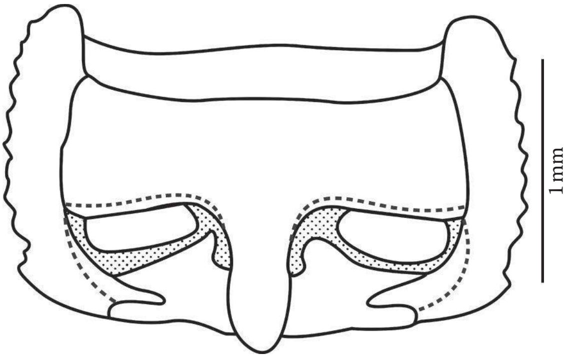

FIGURE 1.23 Prosternum, ventral view of *Mallodon spinibarbis* (L.) (Prioninae). (Reprinted with permission from C. J. B. Carvalho, editor. Napp, D. S., *Rev. Bras. Entomol.,* 38, 265–419, 1994.)

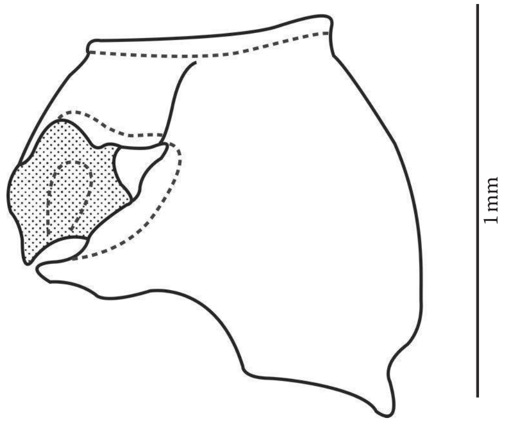

FIGURE 1.24 Prothorax, lateral view of *Leptura rubra* L. (Lepturinae). (Reprinted with permission from C. J. B. Carvalho, editor. Napp, D. S., *Rev. Bras. Entomol.,* 38, 265–419, 1994.)

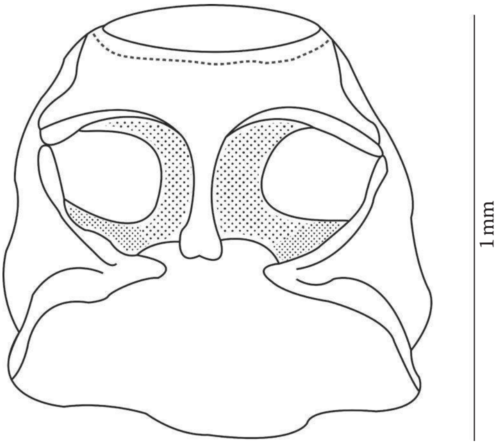

FIGURE 1.25 Prosternum, ventral view of *Leptura rubra* L. (Lepturinae). (Reprinted with permission from C. J. B. Carvalho, editor. Napp, D. S., *Rev. Bras. Entomol.,* 38, 265–419, 1994.)

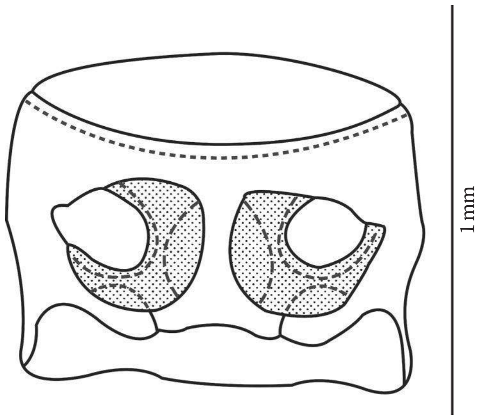

FIGURE 1.26 Prosternum, ventral view of *Adesmus hemispilus* Germar (Lamiinae). (Reprinted with permission from C. J. B. Carvalho, editor. Napp, D. S., *Rev. Bras. Entomol.,* 38, 265–419, 1994.)

mesoscutum by an impression. The mesonotum lacks a stridulatory plate in the Parandrinae (Figure 1.27), Prioninae, and some Spondylidinae; has a divided stridulatory plate in the Dorcasominae (if present), Asemini (Spondylidinae) (Figure 1.28), and Lepturinae (Figure 1.29), and an undivided stridulatory plate in the Necydalinae (Figure 1.30), Cerambycinae (Figure 1.31), and Lamiinae (Figure 1.32).

Legs mostly are cursorial (Figure 1.1) and usually moderately long in most longicorn beetles but can be very long in some species such as males of lamiine *Gerania* (Audinet-Serville); fore legs are enlarged in some (particularly males) Prioninae and Lamiinae and extremely long in the lamiine *Acrocinus* Illiger (fore femora in large males can be as long as body), where they reportedly are used for traversing tree branches; hind legs may be enlarged, such as metafemora in the male cerambycine *Utopia* Thomson, or plate-like tibial extensions in some Cerambycinae, but are never adapted for jumping. The tibia usually has two spurs at the terminal end (Figure 1.33). The legs exhibit an oblique groove along the inner side of the protibiae and a notch or groove on the outer face of the mesotibiae in the Lamiinae; these grooves and notches are lacking in other subfamilies. The tarsi are distinctly pentamerous without pubescent ventral

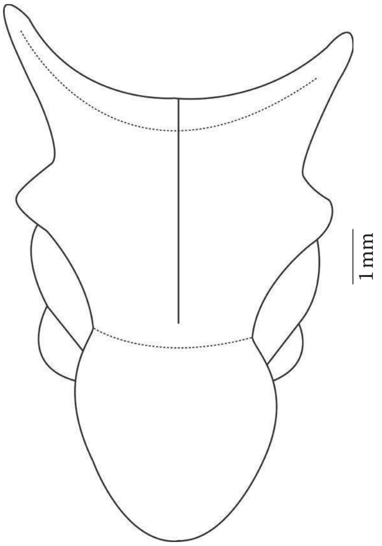

FIGURE 1.27 Mesonotum, dorsal view of *Parandra (Parandra) glabra* (De Geer) (Parandrinae). (Reprinted with permission from C. J. B. Carvalho, editor. Napp, D. S., *Rev. Bras. Entomol.*, 38, 265–419, 1994.)

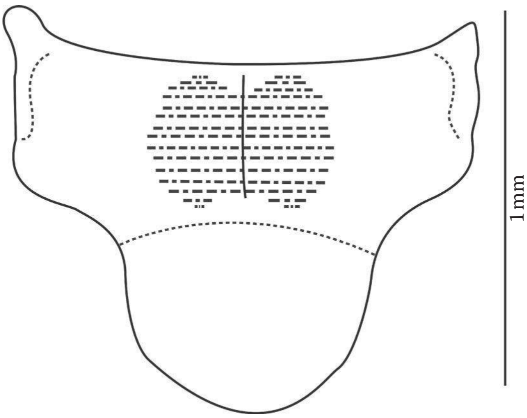

FIGURE 1.28 Mesonotum, dorsal view of *Asemum striatum* (L.) (Spondylidinae). (Reprinted with permission from C. J. B. Carvalho, editor. Napp, D. S., *Rev. Bras. Entomol.*, 38, 265–419, 1994.)

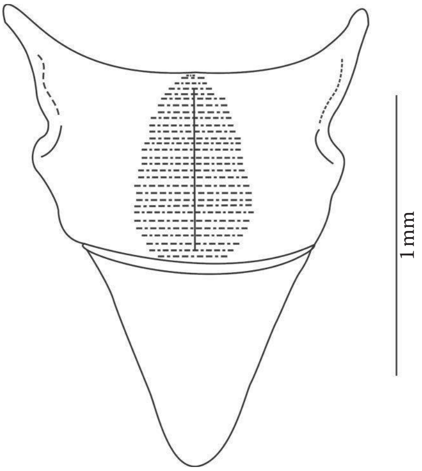

FIGURE 1.29 Mesonotum, dorsal view of *Leptura rubra* L. (Lepturinae). (Reprinted with permission from C. J. B. Carvalho, editor. Napp, D. S., *Rev. Bras. Entomol.,* 38, 265–419, 1994.)

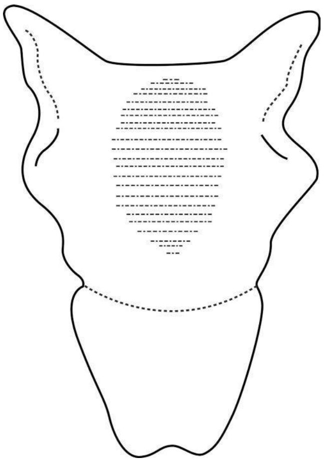

FIGURE 1.30 Mesonotum, dorsal view of *Necydalis major* L. (Necydalinae). (Reprinted with permission from C. J. B. Carvalho, editor. Napp, D. S., *Rev. Bras. Entomol.,* 38, 265–419, 1994.)

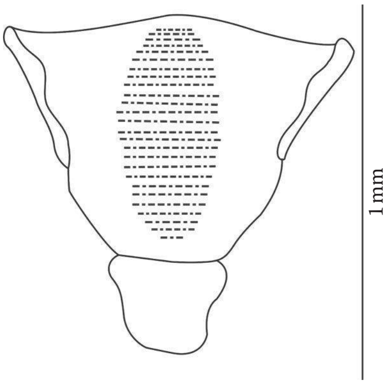

FIGURE 1.31 Mesonotum, dorsal view of *Rhopalophora collaris* (Germar) (Cerambycinae). (Reprinted with permission from C. J. B. Carvalho, editor. Napp, D. S., *Rev. Bras. Entomol.,* 38, 265–419, 1994.)

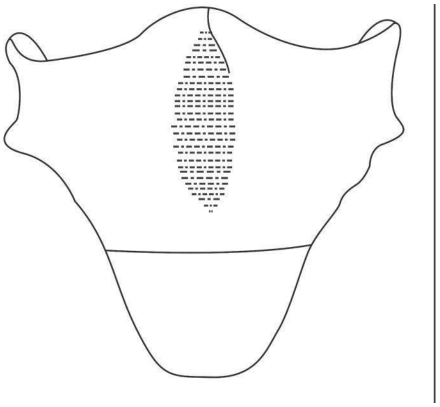

FIGURE 1.32 Mesonotum, dorsal view of *Adesmus hemispilus* Germar (Lamiinae). (Reprinted with permission from C. J. B. Carvalho, editor. Napp, D. S., *Rev. Bras. Entomol.,* 38, 265–419, 1994.)

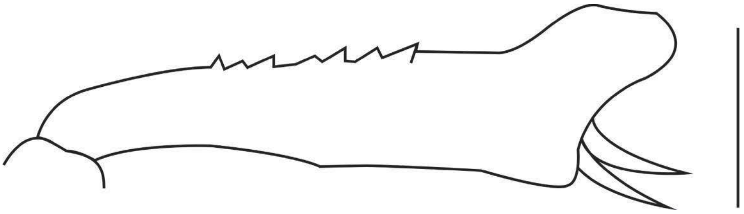

FIGURE 1.33 Protibia, lateral view of *Spondylis buprestoides* (L.) (Spondylidinae). (Reprinted with permission from C. J. B. Carvalho, editor. Napp, D. S., *Rev. Bras. Entomol.,* 38, 265–419, 1994.)

pads in the Parandrinae (Figure 1.34), although they are pseudotetramerous with ventral pads in the Prioninae, Lepturinae, Cerambycinae, Spondylidinae (Figure 1.35), and Lamiinae. The third tarsomere is simple in the Parandrinae but dilated in the remaining subfamilies (Figure 1.35). The tarsal claws are appendiculate or cleft in the most specialized Lamiinae but simple in all other subfamilies.

The hind wing usually has a moderately to very long apical field (though this is short in some very large forms, such as *Titanus* Audinet-Serville) with two more or less complete radial extensions converging and then diverging to form a scissor-like figure, with a dark sclerite apicad of radial cell and a subtriangular sclerite crossing r4. The radial cell often is well developed and more or less elongate (although sometimes it is short and broad or lacking basal limit). Cross-vein r3 is slightly to strongly oblique and sometimes is absent. The basal portion of radius posterior (RP) is long to very short and not surpassing r4. The medial field usually has four or five free veins (sometimes with three or, rarely, fewer) and always lacks medial fleck. The wedge cell is well developed in almost all Prioninae and some Lepturinae and Spondylidinae and is absent in all other subfamilies. If the elytra are shortened in macropterous forms, the hind wings are exposed (often giving the beetles a hymenopteran appearance) and their apex is then sometimes not folded (all Necydalinae, Figures 1.36 and 1.37). The hind wings are highly reduced or disappear in numerous Cerambycinae (such as males of *Torneutes* Reich), Lamiinae (usually both sexes) and Prioninae (more often only females), Lepturinae, and Spondylidinae (both sexes of *Michthisoma* LeConte); in some taxa, the beetles apparently are flightless even if wings are present.

1.2.2.1.2.3 Abdomen The abdomen usually has five free, visible ventrites (belonging to segments III–VII; sternites 1 and 2 form the posterointernal wall of metacoxal acetabula) (Figure 1.2), with the first usually not much longer than the second; rarely, it is almost as long as the remaining combined (females of the cerambycine Obriini). The intercoxal process is acute to broadly rounded or angulate—or absent, with the medial part of reduced sternum II visible between the hind coxae (Necydalinae and some slender wasp-mimicking

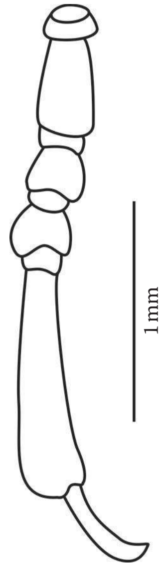

FIGURE 1.34 Metatarsus, lateral view of *Parandra (Parandra) glabra* (De Geer) (Parandrinae). (Reprinted with permission from C. J. B. Carvalho, editor. Napp, D. S., *Rev. Bras. Entomol.,* 38, 265–419, 1994.)

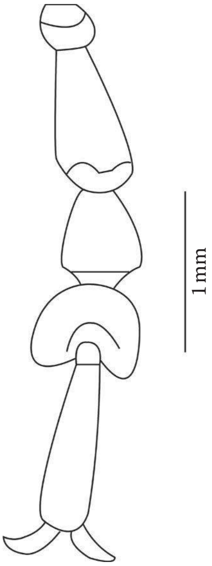

FIGURE 1.35 Metatarsus, dorsal view of *Spondylis buprestoides* (L.) (Spondylidinae). (Reprinted with permission from C. J. B. Carvalho, editor. Napp, D. S., *Rev. Bras. Entomol.,* 38, 265–419, 1994.)

Cerambycinae and the telescoped, with segment II forming a petiolus-like basal piece). The abdominal tergites 1–6 are semisclerotized. Functional spiracles are present on each side of abdominal segments I–VII (the first pair is very large, particularly in flying forms), and spiracles VIII are rudimentary and closed.

1.2.2.1.2.4 External Morphology of Terminalia Male terminalia (Figures 1.38 through 1.40) consist of three abdominal segments. The anterior edge of sternite VIII (Figure 1.38) usually bears a median strut (that is rudimentary or absent in some taxa); the anterior edge of sternite IX has spiculum gastrale; tergites IX and X are fused together and usually membranous. The anterior edge of tegmen (Figure 1.39)

FIGURE 1.36 *Necydalis major* L. (Necydalinae).

FIGURE 1.37 *Ulochaetes leoninus* LeConte (Necydalinae).

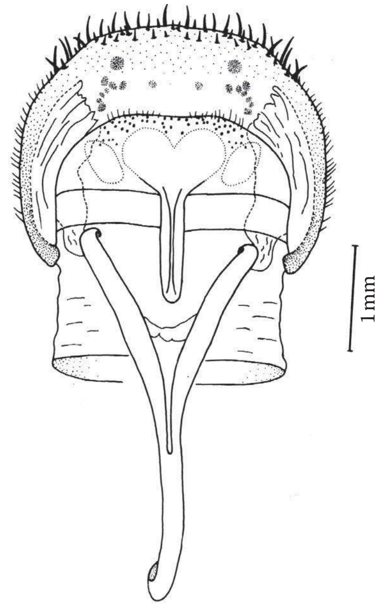

FIGURE 1.38 Male sternite VIII of *Hedypathes betulinus* (Klug) (Lamiinae). (Reprinted with permission from C. J. B. Carvalho, editor. Galileo, M. H. M., et al., *Rev. Bras. Entomol.,* 37, 705–715, 1993.)

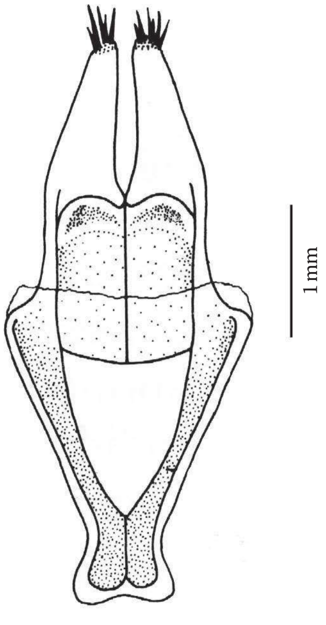

FIGURE 1.39 Tegmen of *Hedypathes betulinus* (Klug) (Lamiinae). (Reprinted with permission from C. J. B. Carvalho, editor. Galileo, M. H. M., et al., *Rev. Bras. Entomol.,* 37, 705–715, 1993.)

has a single or no strut; the parameres usually are fused to phallobase and free from one another, but they are more or less completely fused in some Cerambycinae (such as the Molorchini–Obriini complex—very short in some and nearly absent in the Neotropical Ectenessini). The aedeagus is cucujiform and symmetrical, but usually is rotated to one side in the abdominal cavity when at rest. Surrounding structures therefore may not be entirely symmetrical. The anterior edge of the aedeagus (Figure 1.40) almost

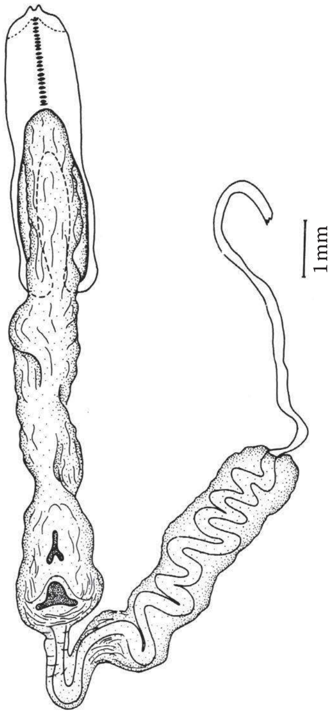

FIGURE 1.40 Aedeagus and internal sac of *Hedypathes betulinus* (Klug) (Lamiinae). (Reprinted with permission from C. J. B. Carvalho, editor. Galileo, M. H. M., et al., *Rev. Bras. Entomol.*, 37, 705–715, 1993.)

always has paired struts; the internal sac (endophallus) (Figure 1.40) may bear distinctive sclerotized structures such as asperities, paired or unpaired sclerites, or longitudinal sclerotized rods.

The terminalia of female cerambycids (Figures 1.41 and 1.42) follow the same structural plan as the male, with sclerites sequentially distributed along a more or less membranous tube, which is kept invaginated at rest. Segment VIII is entirely contained within the partially double-walled segment VII (where the first invagination occurs). Sternite VIII (Figure 1.41) bears a long ventral apodeme that is closely related with the ovipositor length among different taxa. Sternite and tergite VIII are mostly partly desclerotized and tend to fuse into a tube enclosing the "anus–ovipositor" complex, sometimes protruding from the abdomen, either "naked" or protected by posterior sternal and tergal projections of segment VII (e.g., some Acanthocinini of Lamiinae). The ovipositor (Figure 1.42) usually is long but secondarily shortened and modified—particularly in some Cerambycinae (such as Trachyderini) ovipositing on the host surface; the paraprocts are short without baculi (in all Lamiinae) and flexible with subapical styli; in some groups, the apex of the ovipositor is sclerotized with styli being lateral or laterodorsal and often reduced or virtually inbuilt in coxitis (this type occurs in several subfamilies depending on biology but is common in the Prioninae and universal in the Parandrinae). One or two pairs of glandular integumental invaginations often are present at the base of the ovipositor on both sides of anus.

1.2.2.1.2.5 Reproductive System Testes (Figure 1.43) consist of one to several pairs of testicular lobes, with each lobe having a number of radially arranged testicular follicles. The basal parts of vasa deferentia may be broadened into seminal vesicles. Usually, there are two pairs (or at least one pair) of accessory glands at or before the fusion of vasa deferentia. Ducts are more or less completely paired (mostly up to paired gonopores on the internal sac) in Lamiini and several related tribes of Lamiinae. Primary gonopore seldom projects into a long sclerotized flagellum.

Ovaries (Figure 1.44) are paired, each with a variable number (up to several tens) of ovarioles. There is a single more or less sclerotized spermatheca of simple shape (often an elongate, curved capsule bridged

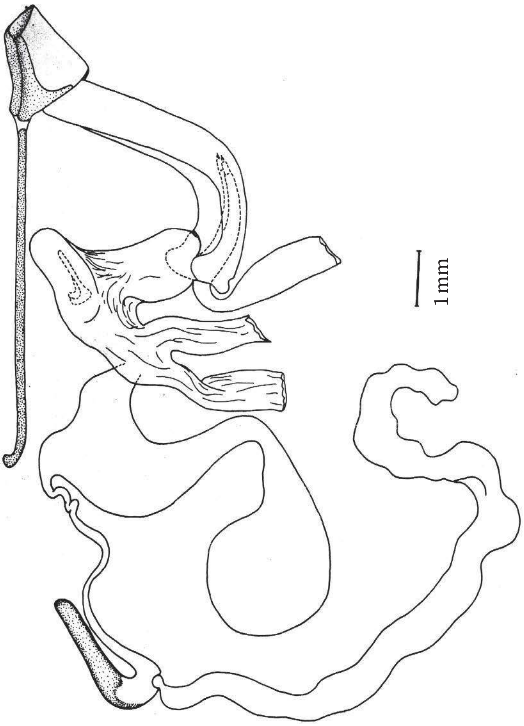

FIGURE 1.41 Female terminalia of *Hedypathes betulinus* (Klug) (Lamiinae). (Reprinted with permission from C. J. B. Carvalho, editor. Galileo, M. H. M., et al., *Rev. Bras. Entomol.,* 37, 705–715, 1993.)

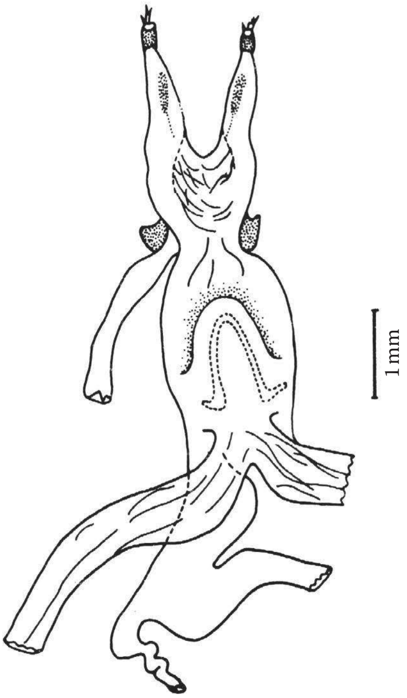

FIGURE 1.42 Ovipositor of *Hedypathes betulinus* (Klug) (Lamiinae). (Reprinted with permission from C. J. B. Carvalho, editor. Galileo, M. H. M., et al., *Rev. Bras. Entomol.,* 37, 705–715, 1993.)

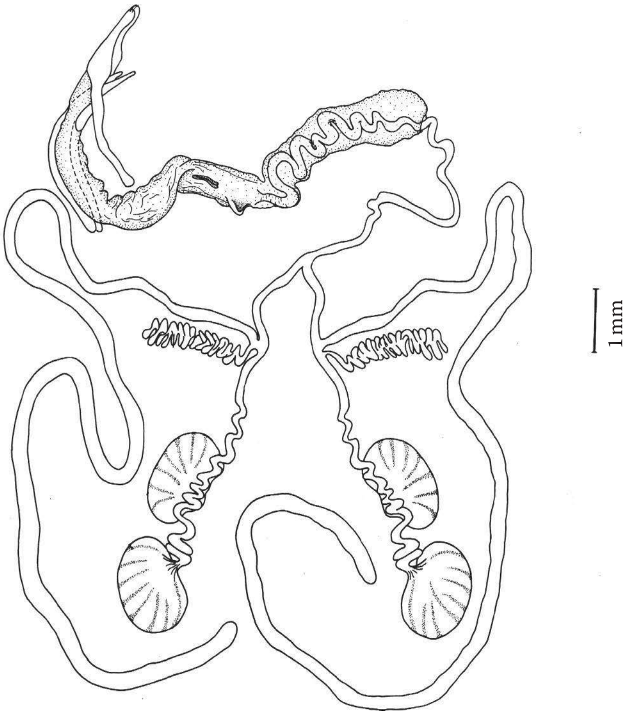

FIGURE 1.43 Male reproductive system of *Hedypathes betulinus* (Klug) (Lamiinae). (Reprinted with permission from C. J. B. Carvalho, editor. Galileo, M. H. M., et al., *Rev. Bras. Entomol.*, 37, 705–715, 1993.)

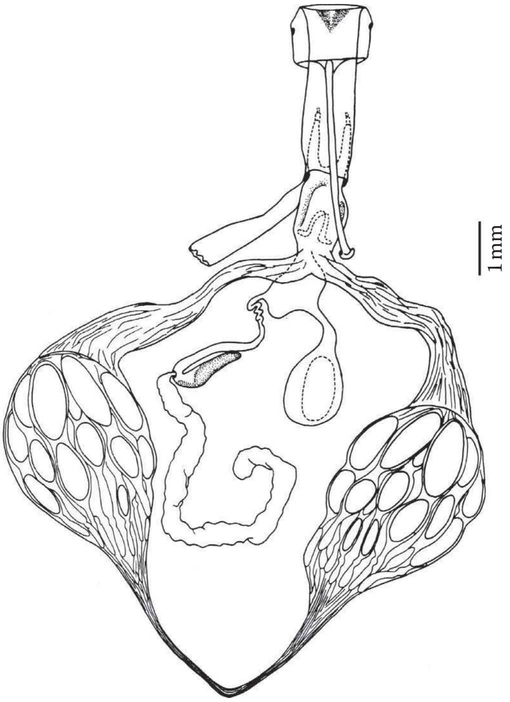

FIGURE 1.44 Female reproductive system of *Hedypathes betulinus* (Klug) (Lamiinae). (Reprinted with permission from C. J. B. Carvalho, editor. Galileo, M. H. M., et al., *Rev. Bras. Entomol.*, 37, 705–715, 1993.)

by spermathecal compressor) with a distinct, sometimes very large, spermathecal gland attached to it. A bursa copulatrix usually is present in the form of a soft diverticulum of various sizes and locations; the spermathecal duct arises on its base.

1.2.2.1.2.6 Digestive System The adult gut may be primitively rather reduced. In prionines and some cerambycines, the midgut is short and reduced with the posterior midgut being extremely reduced and thread-like (slightly less so in some floricolous Clytini of the Cerambycinae), suggesting adult aphagy. However, the gut is long and well developed in the Lamiinae whose adults feed extensively.

The digestive tube (Figure 1.45) usually does not have a distinct crop/proventriculus. The anterior midgut in some taxa (Necydalinae, Spondylidinae, and most Lepturinae) produces morphologically distinct mycetomes in the form of gut wall diverticula whose cells harbor intracellular yeast-like symbionts. The posterior midgut often bears numerous small, scattered evaginated crypts. Six cryptonephridial Malpighian tubules enter the gut separately in two clusters of three.

1.2.2.2 Immature Stages

The following morphological descriptions are based on Butovitsch (1939), Duffy (1953, 1957, 1960, 1968), Gardiner (1966), and Švácha and Lawrence (2014).

1.2.2.2.1 Eggs

The eggs (Figure 1.46) are elongate, ovoid, or fusiform and often have thin, flexible chorion so that their shape can adapt to the tight spaces in which they usually are laid. A female can lay a dozen to several hundred eggs in her lifetime. They usually hatch in a few days to a few weeks after oviposition, depending on species and climates. In some lamiine species, the larvae may overwinter within the chorion, particularly if the eggs are laid late in the season.

1.2.2.2.2 Larvae

The larvae are soft-bodied, eucephalic, oligopodous to apodous, prognathous, more or less elongate, and subcylindrical to dorsoventrally depressed (Figures 1.47 through 1.58). Their body shape and mechanics largely depend on hemolymph pressure.

The cranium (particularly its anterior part, which supports mouthparts, often called the "mouthframe") may be strongly sclerotized and pigmented, whereas the body generally is soft and white to yellow (Figures 1.51 through 1.54). In rare cases, the body can be grayish with some prothoracic regions and the abdominal end sclerotized and pigmented. The skin of the prothorax is not attached to the submentum. The ventral mouthparts are protracted; the mandibles (Figure 1.59) lack a molar tooth or other appendage; the labium bears a setose ligula, and gula and hypostoma are present. The abdomen, at least dorsally, has more or less retractile and often characteristically sculptured, protuberances called ambulatory ampullae, providing support in galleries; abdominal segments 1 to 6 or 7 have dorsal ampullae. The spiracular system is peripneustic, with one pair of functional spiracles on the mesothorax (Figure 1.60) and one pair on each of eight abdominal segments. The digestive system is similar to that of adults.

1.2.2.2.3 Pupae

The pupae (Figure 1.61a and b) are similar to adults in size, shape, and proportions of cephalic and thoracic appendages. Secondary sexual differences in adults generally are evident in the pupae. They are adecticous, exarate, and generally soft and pale (except for some special structures like spines or gin traps), with a strongly ventrally bent head so that mouthparts point caudally (except for some Prioninae). The body usually is waxy or milky white to testaceous, often with scattered setae or spinose areas or combinations of both.

The antennae extend at least as far as the mesothorax but generally to the abdominal segments, where they are nearly always curved downward beneath the body. The elytra are always glabrous (except Acanthocinini). The abdomen usually has nine movable segments, with the tenth (and occasionally

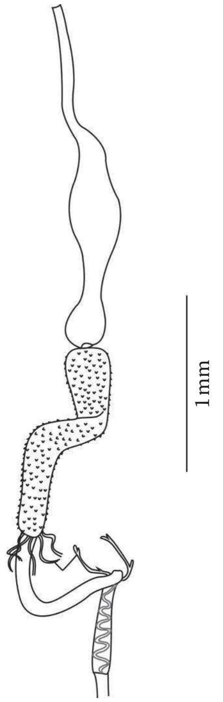

FIGURE 1.45 Digestive system of *Oxymerus luteus luteus* (Voet) (Cerambycinae). (Reprinted with permission from W. F. de Azevedo, Jr., editor. Moura, L. A., and A. F. Franceschini, *Biociências,* 2, 135–143, 1994.)

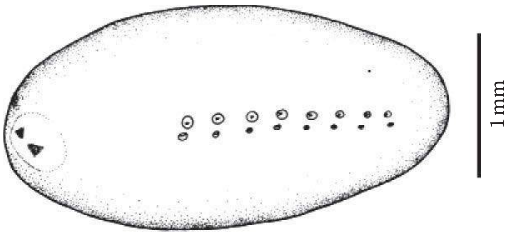

FIGURE 1.46 Egg of *Hedypathes betulinus* (Klug) (Lamiinae). (Reprinted with permission from C. J. B. Carvalho, editor. Galileo, M. H. M., et al., *Rev. Bras. Entomol.,* 37, 705–715, 1993.)

the ninth) being telescoped within the preceding segments. Abdominal segments 7 and 8 usually are more elongate than the preceding ones but sometimes considerably produced. The abdomen has five to seven pairs of functional spiracles. Segment 9 often ends in a vertical or horizontal spine or process or with a pair of incurved or outwardly curved urogomphi. Some prionines (tribes Callipogonini and Macrotomini) have paired paramedian gin-traps. The legs often have subapical setae on the femora and sometimes one or two setae on the tarsi.

1.3 Key to Subfamilies of the Family Cerambycidae

The key to adults is based on the work of Linsley (1962b), Ślipiński and Escalona (2013), and Švácha and Lawrence (2014). The key to larvae is based on Duffy (1953, 1957, 1960, 1968), Švácha and Danilevsky (1987, 1988, 1989), and Švácha and Lawrence (2014).

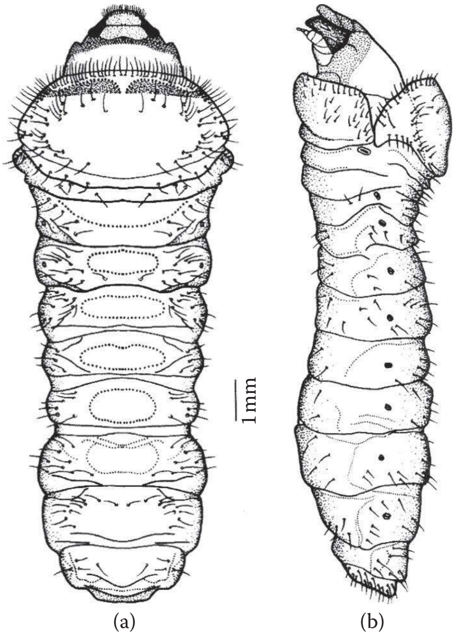

FIGURE 1.47 Larvae of *Acanthoderes (Psapharochrus) melanosticta* White (Lamiinae), dorsal view (a) and lateral view (b). (Reprinted with permission from C. J. B. Carvalho editor. Mermudes, J. R. M., and M. L. Monné, *Rev. Bras. Entomol.,* 45, 331–334, 2001.)

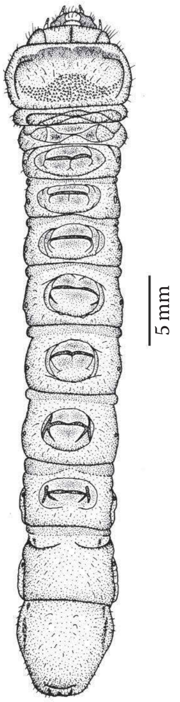

FIGURE 1.48 Larva of *Parandra* sp. (Parandrinae), dorsal view. (Reprinted from Costa, C., et al., *Larvas de Coleoptera do Brasil,* Museu de Zoologia, Universidade de São Paulo, São Paulo, 1988. With permission.)

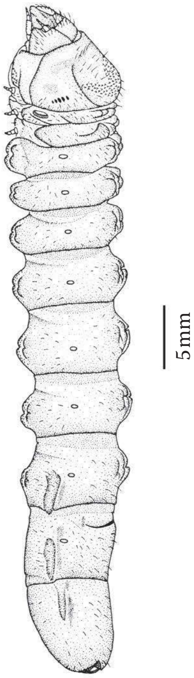

FIGURE 1.49 Larva of *Parandra* sp. (Parandrinae), lateral view. (Reprinted from Costa, C., et al., *Larvas de Coleoptera do Brasil,* Museu de Zoologia, Universidade de São Paulo, São Paulo, 1988. With permission.)

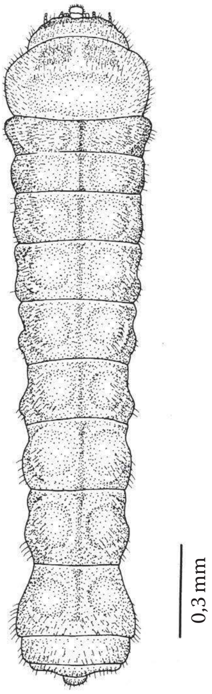

FIGURE 1.50 Larva of *Acyphoderes aurulenta* (Kirby) (Cerambycinae), dorsal view. (Reprinted from Costa, C., et al., *Larvas de Coleoptera do Brasil,* Museu de Zoologia, Universidade de São Paulo, São Paulo, 1988. With permission.)

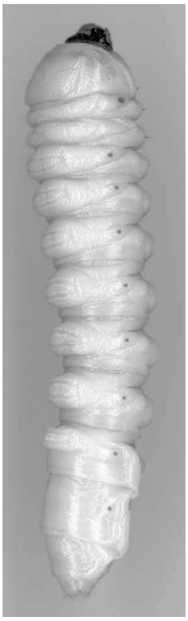

FIGURE 1.51 Larva of *Tsivoka simplicicollis* (Gahan) (Dorcasominae), laterodorsal view. (Reprinted with permission from Petr Švácha, owner. Švácha, P., and J. F. Lawrence, 2.1 Vesperidae Mulsant, 1839; 2.2 Oxypeltidae Lacordaire, 1868; 2.3 Disteniidae J. Thomson, 1861; 2.4 Cerambycidae Latreille, 1802, In *Handbook of zoology, Arthropoda: Insecta; Coleoptera, beetles, Volume 3: Morphology and systematics (Phytophaga)*, eds. R. A. B. Leschen and R. G. Beutel, Walter de Gruyter, Berlin, 2014, 16–177.)

FIGURE 1.52 Larva of *Tsivoka simplicicollis* (Gahan) (Dorcasominae), ventral view. (Reprinted with permission from Petr Švácha, owner. Švácha, P., and J. F. Lawrence, 2.1 Vesperidae Mulsant, 1839; 2.2 Oxypeltidae Lacordaire, 1868; 2.3 Disteniidae J. Thomson, 1861; 2.4 Cerambycidae Latreille, 1802, In *Handbook of zoology, Arthropoda: Insecta; Coleoptera, beetles, Volume 3: Morphology and systematics (Phytophaga)*, eds. R. A. B. Leschen and R. G. Beutel, Walter de Gruyter, Berlin, 2014, 16–177.)

FIGURE 1.53 Larva of *Judolia sexmaculata* (L.) (Lepturinae), ventral view. (Reprinted with permission from Petr Švácha, owner. Švácha, P., and J. F. Lawrence, 2.1 Vesperidae Mulsant, 1839; 2.2 Oxypeltidae Lacordaire, 1868; 2.3 Disteniidae J. Thomson, 1861; 2.4 Cerambycidae Latreille, 1802, In *Handbook of zoology, Arthropoda: Insecta; Coleoptera, beetles, Volume 3: Morphology and systematics (Phytophaga)*, eds. R. A. B. Leschen and R. G. Beutel, Walter de Gruyter, Berlin, 2014, 16–177.)

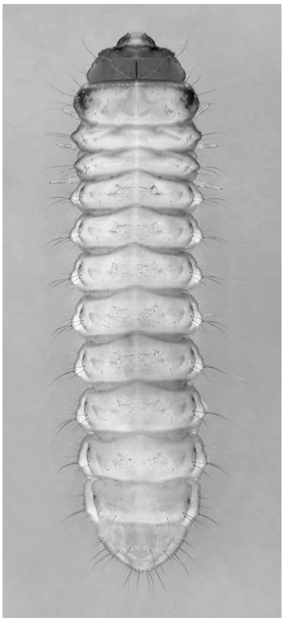

FIGURE 1.54 Larva of *Dinoptera collaris* (L.) (Lepturinae), dorsal view. (Reprinted with permission from Petr Švácha, owner. Švácha, P., and J. F. Lawrence, 2.1 Vesperidae Mulsant, 1839; 2.2 Oxypeltidae Lacordaire, 1868; 2.3 Disteniidae J. Thomson, 1861; 2.4 Cerambycidae Latreille, 1802, In *Handbook of zoology, Arthropoda: Insecta; Coleoptera, beetles, Volume 3: Morphology and systematics (Phytophaga)*, eds. R. A. B. Leschen and R. G. Beutel, Walter de Gruyter, Berlin, 2014, 16–177.)

FIGURE 1.55 Larva of *Prionus coriarius* (L.) (Prioninae), lateral view. (Reprinted with permission from Petr Švácha, owner. Švácha, P., and J. F. Lawrence, 2.1 Vesperidae Mulsant, 1839; 2.2 Oxypeltidae Lacordaire, 1868; 2.3 Disteniidae J. Thomson, 1861; 2.4 Cerambycidae Latreille, 1802, In *Handbook of zoology, Arthropoda: Insecta; Coleoptera, beetles, Volume 3: Morphology and systematics (Phytophaga)*, eds. R. A. B. Leschen and R. G. Beutel, Walter de Gruyter, Berlin, 2014, 16–177.)

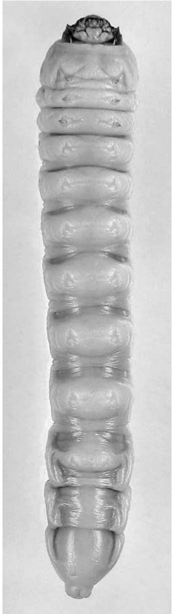

FIGURE 1.56 Larva of *Prionus coriarius* (L.) (Prioninae), ventral view. (Reprinted with permission from Petr Švácha, owner. Švácha, P., and J. F. Lawrence, 2.1 Vesperidae Mulsant, 1839; 2.2 Oxypeltidae Lacordaire, 1868; 2.3 Disteniidae J. Thomson, 1861; 2.4 Cerambycidae Latreille, 1802, In *Handbook of zoology, Arthropoda: Insecta; Coleoptera, beetles, Volume 3: Morphology and systematics (Phytophaga)*, eds. R. A. B. Leschen and R. G. Beutel, Walter de Gruyter, Berlin, 2014, 16–177.)

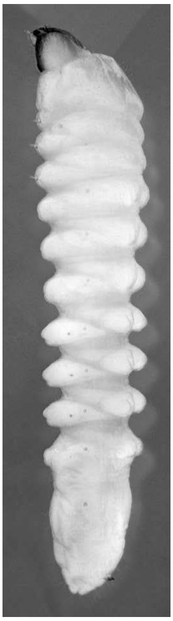

FIGURE 1.57 Larva of *Atimia okayamensis* Hayashi (Spondylidinae), lateral view. (Reprinted with permission from Petr Švácha, owner. Švácha, P., and J. F. Lawrence, 2.1 Vesperidae Mulsant, 1839; 2.2 Oxypeltidae Lacordaire, 1868; 2.3 Disteniidae J. Thomson, 1861; 2.4 Cerambycidae Latreille, 1802, In *Handbook of zoology, Arthropoda: Insecta; Coleoptera, beetles, Volume 3: Morphology and systematics (Phytophaga)*, eds. R. A. B. Leschen and R. G. Beutel, Walter de Gruyter, Berlin, 2014, 16–177.)

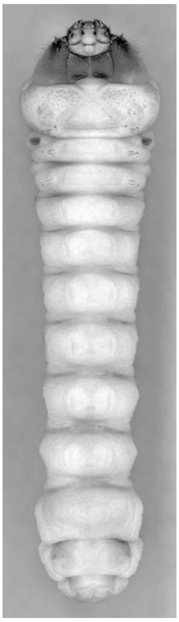

FIGURE 1.58 Larva of *Arhopalus rusticus* (L.) (Spondylidinae), ventral view. (Reprinted with permission from Petr Švácha, owner. Švácha, P., and J. F. Lawrence, 2.1 Vesperidae Mulsant, 1839; 2.2 Oxypeltidae Lacordaire, 1868; 2.3 Disteniidae J. Thomson, 1861; 2.4 Cerambycidae Latreille, 1802, In *Handbook of zoology, Arthropoda: Insecta; Coleoptera, beetles, Volume 3: Morphology and systematics (Phytophaga)*, eds. R. A. B. Leschen and R. G. Beutel, Walter de Gruyter, Berlin, 2014, 16–177.)

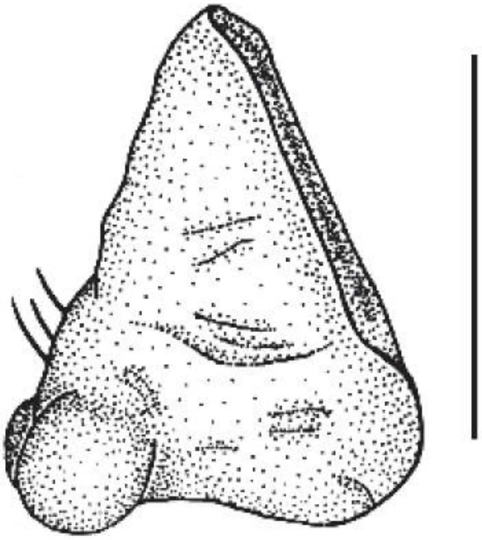

FIGURE 1.59 Mandible of the larva of *Acyphoderes aurulenta* (Kirby) (Cerambycinae), dorsal view. (Reprinted from Costa, C., et al., *Larvas de Coleoptera do Brasil,* Museu de Zoologia, Universidade de São Paulo, São Paulo, 1988. With permission.)

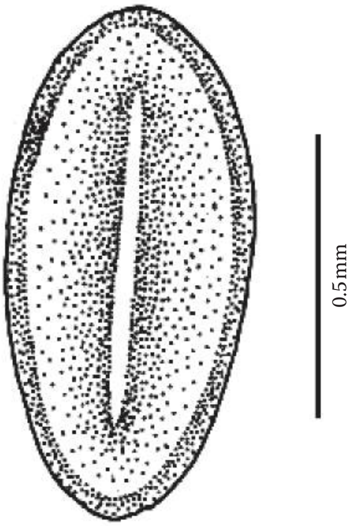

FIGURE 1.60 Thoracic spiracle of the larva of *Acyphoderes aurulenta* (Kirby) (Cerambycinae). (Reprinted from Costa, C., et al., *Larvas de Coleoptera do Brasil,* Museu de Zoologia, Universidade de São Paulo, São Paulo, 1988. With permission.)

1.3.1 Adults

1. Tarsi distinctly pentamerous (Figure 1.34); lateral pronotal carinae entire and simple (Figure 1.21) .... **Parandrinae**
   a. Tarsi pseudotetramerous (Figure 1.35); lateral pronotal carinae absent (Figure 1.24), or present, often dentate or spinose (Figures 1.22 and 1.23) 2

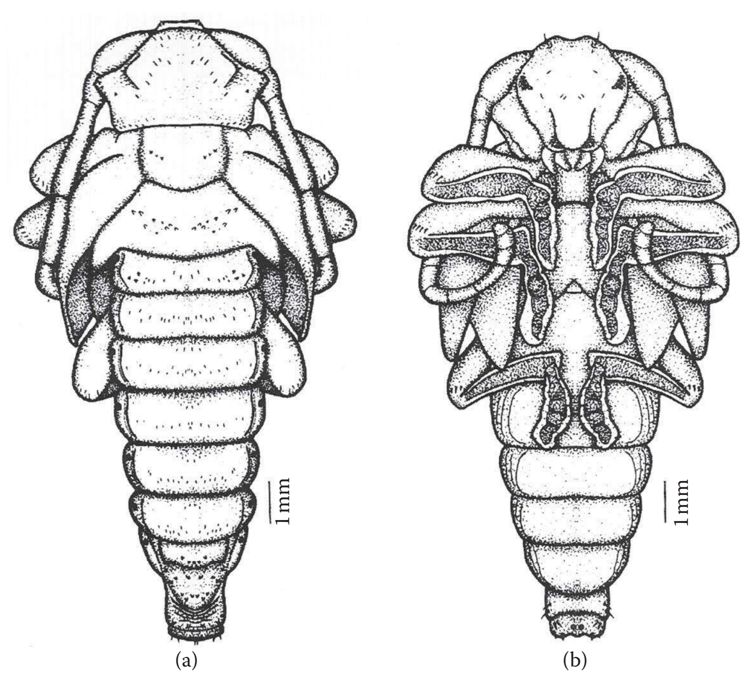

FIGURE 1.61 Pupae of *Acanthoderes (Psapharochrus) melanosticta* (White) (Lamiinae), dorsal view (a) and ventral view (b). (Reprinted with permission from C. J. B. Carvalho, editor. Mermudes, J. R. M., and M. L. Monné, *Rev. Bras. Entomol.*, 45, 331–334, 2001.)

2. Head vertical or retracted (Figure 1.7), genal margin always directed posteriorly; protibiae with mesial sinus; mesotibiae usually notched or grooved externally; last segment of maxillary palpi usually pointed at apex (Figures 1.14 and 1.15) .... **Lamiinae**
    a. Head usually prognathous or weakly deflexed (Figure 1.10), genal margin never directed posteriorly; protibiae without mesial sinus; mesotibiae never notched or grooved externally; last segment of maxillary palpi obtuse or truncate at apex (Figures 1.13 and 1.16 through 1.19) 3
3. Pronotum with elevated, often dentate or spinose lateral carinae (Figures 1.22 and 1.23); labrum fused with epistoma; inner lobe of maxillae obsolete (Figure 1.13); procoxae strongly transverse (Figure 1.23); mesoscutum without a striated stridulatory area .... **Prioninae**
    a. Pronotum without distinct lateral carinae; labrum free; inner lobe of maxillae usually well developed (Figures 1.16, 1.17, and 1.19); procoxae rarely transverse, usually rounded; mesoscutum with a finely striated stridulatory area (Figures 1.28 through 1.30) or without a stridulatory area 4
4. Mesoscutum without a median endocarina (Figure 1.30); elytra shortened, covering only the pterothorax, exposed hind wings with unfolded apex (Figures 1.36 and 1.37) ..... **Necydalinae**
    a. Mesoscutum with a median endocarina (Figures 1.28 and 1.29); elytra usually well developed, hind wings folded at apex 5
5. Head with region behind eyes usually having prominent temples followed by a constricted neck (Figures 1.5 and 1.6); procoxae conical, prominent, and strongly projecting below prosternal process .... **Lepturinae**
    a. Head may be gradually narrowing to abruptly constricted behind eyes, without prominent temples, followed by a constricted neck; procoxae of variable shape usually subglobular, seldom strongly projecting below prosternal process 6

6. Mandibula with incisor edge without fringe of hairs; hind wing with edge cell .... **Spondylidinae**
   a. Mandibula with incisor edge usually with fringe of long hairs; hind wing without edge cell 7
7. Mesonotum with an undivided stridulatory plate (Figure 1.31); notosternal suture rarely complete, usually indistinct or incomplete anteriorly or absent; empodium usually small or indistinct .... **Cerambycinae**
   a. Mesonotum with a divided stridulatory plate; notosternal suture may be relatively distinct and complete; empodium indistinct .... **Dorcasominae**

1.3.2 Larvae

1. Clypeus (Figure 1.62) very narrow, with only slender basal arms reaching to mandibular articulations; these arms may be more or less sclerotized and fused with epistomal margin. Mandibular apex and dorsal angle lacking; mandibles (Figure 1.59) short and apically rounded, spoon-like .... **Cerambycinae** (Figure 1.50)
   a. Clypeus more or less trapezoidal, filling entire space between dorsal mandibular articulations. Mandibles with distinct apex and more or less distinct dorsal angle 2
2. Legs absent, or present with only two minute segments visible under high magnification. Cardo extremely reduced, labiomaxillary base firmly attached to cranium along whole width; maxillae movable only from stipes .... **Lamiinae** (Figure 1.47a and b)
   a. Distinct four-segmented legs (Figure 1.65) present though may be strongly reduced and inconspicuous. Free movable cardo present 3
3. Main antennal sensillum flat, rarely convex, never conical 4
   a. Main antennal sensillum prominent and conical 5
4. Basal half of pronotum more or less roughly asperate. Labrum cordate (Figures 1.63 and 1.64), very long. Epistomal, frontal, and postcondylar carinae absent ..... **Parandrinae** (Figures 1.48 and 1.49)
   a. Body without coarse asperities. Labrum never as long as in *Parandra*. Distinct epistomal, frontal, and postcondylar carinae often present .... **Prioninae** (Figures 1.55 and 1.56)
5. Pretarsus without setae. Abdominal epipleurum protuberant on segments 7–9. Lateral furrows of pronotum long and distinct 6
   a. Pretarsus with distinct setae. Abdominal epipleurum protuberant on at least segments 6–9. Lateral furrows of pronotum rarely long and distinct 7
6. Large postnotal fold present. Urogomphi absent. Dorsal ampullae with one lateral impression on each side .... **Dorcasominae** (Figures 1.51 and 1.52)
   a. Postnotum absent. Urogomphi present or absent. Dorsal ampullae with two lateral impressions on each side .... **Spondylidinae** (Figures 1.57 and 1.58)
7. Dorsal ampullae with two broadly separate lateral impressions on each side (Figure 1.66) Prothoracic lateropresternum largely microspiculate .... **Necydalinae**
   a. Dorsal ampullae with one lateral impression. Prothoracic lateropresternum microspiculate at most along anterior margin .... **Lepturinae** (Figures 1.53 and 1.54)

1.4 Diagnosis, Biodiversity, Distribution, and Biology of Subfamilies

Phylogenetic relationships within the Cerambycidae are still highly controversial (e.g., Wang and Chiang 1991; Napp 1994; Švácha and Lawrence 2014). As a result, we order subfamilies alphabetically in this section. Morphological features of subfamilies mainly are extracted from Linsley (1962a, 1962b, 1963, 1964), Linsley and Chemsak (1972, 1984, 1995), Chemsak (1996), Ślipiński and Escalona (2013), and Švácha and Lawrence (2014).

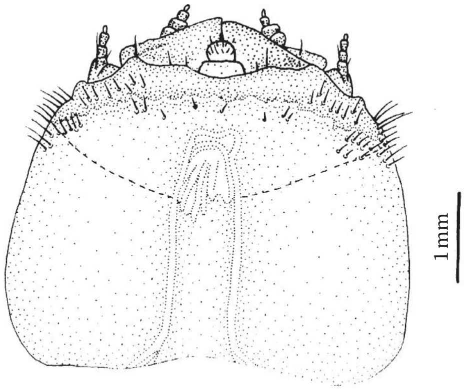

FIGURE 1.62 Head of the larva of *Acyphoderes aurulenta* (Kirby) (Cerambycinae), dorsal view. (Reprinted from Costa, C., et al., *Larvas de Coleoptera do Brasil,* Museu de Zoologia, Universidade de São Paulo, São Paulo, 1988. With permission.)

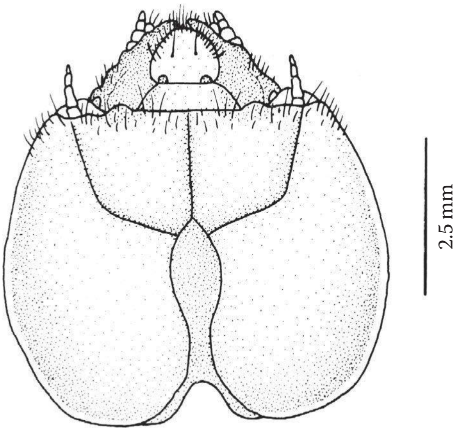

FIGURE 1.63 Head of the larva of *Parandra* sp. (Parandrinae), dorsal view. (Reprinted from Costa, C., et al., *Larvas de Coleoptera do Brasil,* Museu de Zoologia, Universidade de São Paulo, São Paulo, 1988. With permission.)

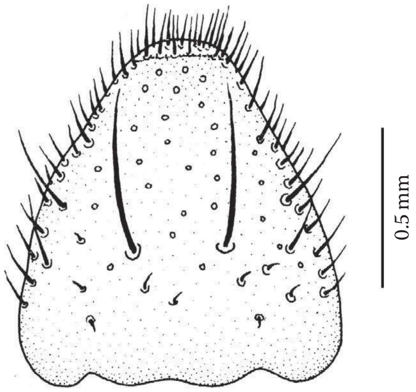

FIGURE 1.64 Labrum of the larva of *Parandra* sp. (Parandrinae), dorsal view. (Reprinted from Costa, C., et al., *Larvas de Coleoptera do Brasil,* Museu de Zoologia, Universidade de São Paulo, São Paulo, 1988. With permission.)

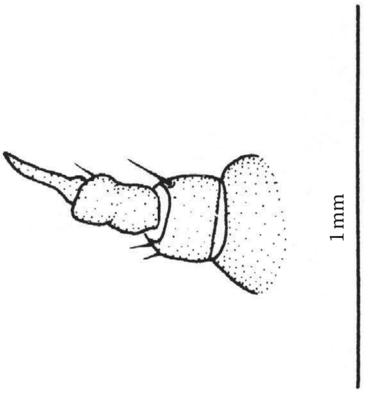

FIGURE 1.65 Proleg of the larva of *Parandra* sp. (Parandrinae), dorsal view. (Reprinted from Costa, C., et al., *Larvas de Coleoptera do Brasil*, Museu de Zoologia, Universidade de São Paulo, São Paulo, 1988. With permission.)

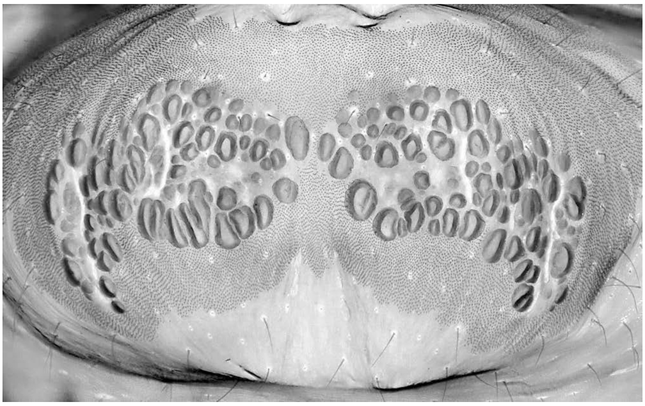

FIGURE 1.66 Larva of *Necydalis major* L. (Necydalinae), detail of ventral ambulatory ampulla 4. (Reprinted with permission from Petr Švácha, owner. Švácha, P., and J. F. Lawrence, 2.1 Vesperidae Mulsant, 1839; 2.2 Oxypeltidae Lacordaire, 1868; 2.3 Disteniidae J. Thomson, 1861; 2.4 Cerambycidae Latreille, 1802, In *Handbook of zoology, Arthropoda: Insecta; Coleoptera, beetles, Volume 3: Morphology and systematics (Phytophaga)*, eds. R. A. B. Leschen and R. G. Beutel, Walter de Gruyter, Berlin, 2014, 16–177.)

1.4.1 Subfamily Cerambycinae Latreille, 1802

1.4.1.1 Diagnosis

Small to large, elongate beetles (Figures 1.67 through 1.76). Head (Figure 1.10) subvertical, scarcely narrowed behind eyes; antennae inserted high on frons between eyes, usually very elongate, second antennomere short; eyes reniform, usually embracing antennal insertion; mandibles acute without molar plate; incisor edge with or without pubescent fringe; maxillae and labium variable, lacinia usually well developed (Figure 1.19); mentum usually trapezoidal (Figure 1.18); submentum sometimes produced between bases of maxillae as a short process. Pronotum without lateral margin; procoxae rarely prominent, usually rounded, cavities variable; notosternal suture rarely complete, usually indistinct or incomplete anteriorly, or absent; mesoscutum with a median endocarina; stridulatory plate, when present, undivided (Figure 1.31). Elytra usually not abbreviated; hind wings without closed cell in anal sector, radial cell closed. Legs moderately long; protibiae without mesial sinus; tarsi pseudotetramerous, padded beneath, third tarsomere dilated, bilobed concealing minute fourth tarsomere, empodium small or absent.

FIGURE 1.67 *Coccoderus sexmaculatus* Buquet (Cerambycinae).

FIGURE 1.68 *Compsibidion divisum* Martins (Cerambycinae).

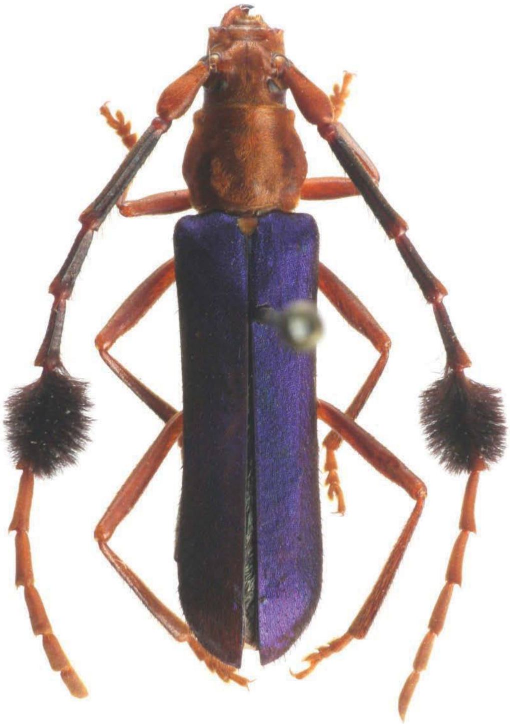

FIGURE 1.69 *Compsocerus deceptor* Napp (Cerambycinae).

FIGURE 1.70 *Disaulax hirsuticornis* (Kirby) (Cerambycinae).

FIGURE 1.71 *Lissonotus spadiceus* Dalman (Cerambycinae).

FIGURE 1.72 *Megacyllene (Megacyllene) patruelis* (Chevrolat) (Cerambycinae).

FIGURE 1.73 *Mionochroma chloe* (Gounelle) (Cerambycinae).

FIGURE 1.74 *Neoregostoma coccineum* (Gory) (Cerambycinae).

FIGURE 1.75 *Pronuba decora* Thomson (Cerambycinae).

FIGURE 1.76 *Psygmatocerus wagleri* Perty (Cerambycinae).

1.4.1.2 Comments

Due to the diversity of forms, the subfamily is one of the most difficult to define, with uncertain limits and relationships (Napp, 1994). Two groups of genera previously included in the Necydalinae are recognized as incertae sedis of Cerambycinae by Švácha and Lawrence (2014): (1) *Atelopteryx* Lacordaire, *Callisphyris* Newman, *Hephaestion* Newman, *Parahephaestion* Melzer, *Planopus* Bosq and *Stenorhopalus* Blanchard; and (2) *Cauarana* Lane, *Mendesina* Lane, *Rhathymoscelis* Thomson and *Hephaestioides* Zajciw.

1.4.1.3 Diversity and Distribution

This is the second largest subfamily in Cerambycidae, with 1,757 genera and more than 11,200 species in the world (Bouchard et al. 2011; Monné 2012; Tavakilian 2015) (Table 1.1). The Cerambycinae are widely distributed in all biogeographic regions. In the Australian, Nearctic, and southern Neotropical regions, the Cerambycinae are the most speciose subfamily compared to other subfamilies (e.g., Forchhammer and Wang 1987; Švácha and Lawrence 2014).

1.4.1.4 Biology

Adults are extremely diverse, from dark nocturnal forms to brightly colored mimetic diurnal species (Švácha and Lawrence 2014) (Figures 1.67 through 1.76). Linsley (1962b) has attempted to divide this subfamily into two groups based on adult activity patterns. Adults of many species from the Callidiopini, Gracilliini, Opsimini, Methiini, and so on are active during the night, for example, *Oemona hirta* (F.) (Wang et al. 1998). Some adults may be crepuscular (vespertine) such as *Nadezhdiella cantori* (Hope) (Wang et al. 2002), *Phoracantha semipunctata* (F.), and *P. recurva* Newman (Wang at el. 2008). Nocturnal or crepuscular adults may or may not need to feed depending on species. Adults of most species appear to be diurnal, such as species from the Aphneopini, Callidiini, Cleomenini, Clytini, Molorchini, and so forth. Many diurnally active adults visit flowers and feed on pollens and nectar, such as *Zorion guttigerum* Westwood (Wang 2002). Some cerambycine adults feed on tree foliage, such as *Lissonotus spadiceus* Dalman (Figure 1.71) (M. L. Monné, personal observation) and *Xylotrechus pyrrhoderus* Bates (Guo 1999); a few in Trachyderini feed on fruit. Adults can live for a week to a few months depending on whether they feed. Male-produced long-range sex and aggregation pheromones have been identified in many cerambycine species (see Chapter 5). Mating may occur on larval hosts or adult feeding sites (see Chapter 4). Depending on the nature of larval feeding biology, adults may be attracted to larval hosts of certain conditions for oviposition (Hanks 1999; see Chapter 3). They then lay their eggs on the surface of larval host plants or in crevices and wounds of bark or under loose bark. Each female can lay dozens to hundreds of eggs in her lifetime.

The distinctive cerambycine larval mouthparts are well suited for solid hosts; most larvae do not occur in soft rotten wood or in soil, and species feeding in soft herbs are rare (Švácha and Lawrence 2014). Although larvae of many species feed on dead (not rotten) plants, most species probably attack living plants that may be perfectly healthy, weakened, or stressed (Hanks 1999). The larval host range of cerambycine species can be from oligophagous to highly polyphagous across both angiosperms and gymnosperms (see Chapters 11 and 12). Larvae bore in branches and stems of host plants and sometimes enter roots, such as *O. hirta* (Wang et al. 1998). Mature larvae usually pupate in their host plants. The life cycle usually lasts one to four years. Many cerambycine species are important pests of trees and logs.

1.4.2 Subfamily Dorcasominae Lacordaire, 1868

1.4.2.1 Diagnosis

Small to moderately large, usually elongate beetles with tapering or subparallel elytra and often long cursorial legs; no strongly depressed forms. Head prognathous or distinctly rostrate, usually constricted immediately behind eyes but never with prominent temples followed by a constricted neck; antennal insertions of variable position but at least slightly away from mandibular condyle, antennal sockets usually facing laterally or laterodorsally; eyes moderate to very large, emarginate to entire; mandibles never enlarged, apex unidentate, inner margin usually with a distinct fringe of hairs; maxillae and labium well developed, lacinia distinct, submentum with a very short to long intermaxillary process, ligula usually large, membranous and emarginate or bilobed, terminal segments of both palps usually more or less truncate. Pronotum without lateral carina, often with a pair of lateral tubercles or spines; procoxal cavities closed internally and at least narrowly open posteriorly, prosternal process usually narrow but complete; notosternal suture may be relatively distinct and complete; mesonotum usually with a divided stridulatory plate; mesocoxal cavities open laterally. Elytra in some taxa strongly narrowed and separate or also shortened posteriorly, partly exposing hind wings yet almost always distinctly surpassing posterior pterothoracic margin; hind wing with radial cell closed proximally but without edge cell. Legs short to moderately long; procoxae transverse to subglobular, prominent, projecting at least slightly below prosternal process; tarsi pseudotetramerous and padded beneath, tarsomere 5 in males of some taxa remarkably broadened distally, claws free, divaricate to moderately divergent. Empodium indistinct.

1.4.2.2 Comments

Some authors treat this group of cerambycids as two separate subfamilies, Dorcasominae and Apatophyseinae, each with one tribe (e.g., Danilevsky 1979; Tavakilian 2015). However, most authors accept that these two subfamilies should be two tribes, Apatophyseini and Dorcasomini, under the subfamily Dorcasominae (e.g., Švácha and Danilevsky 1987, 1989; Özdikmen 2008; Švácha and Lawrence 2014; Adlbauer et al. 2015; Vives 2015). We adopt the latter opinion in this chapter.

1.4.2.3 Diversity and Distribution

There are about 340 described species in 95 genera and two tribes occurring in the Oriental, southern Palaearctic, and Afrotropical regions (Švácha and Lawrence 2014; Adlbauer et al. 2015; Tavakilian 2015; Vives 2015) (Table 1.1).

1.4.2.4 Biology

Similar to the Lepturinae, adults of many dorcasomine species are diurnal with some apatophyseine species being floricolous (Švácha and Lawrence 2014). Most adults may be nocturnally active and hide under the bark of trees or between dead logs and the ground. For example, the nocturnal *Apterotoxitiades vivesi* Adlbauer adults are found under one- to two-year-old pine logs lying on the ground adjacent to grassland (Adlbauer et al. 2015). It is not clear whether adults feed and how they reproduce. No long-range pheromones have been found.

Švácha and Lawrence (2014) summarized the known biology of this subfamily. Larvae of *Dorcasomus gigas* Aurivillius make wide galleries along the center of stems and branches of living trees and pupate in the host plant. Larvae of *Apatophysis* Chevrolat develop in dead or moribund underground parts of trees and shrubs and in dry, often treeless, habitats with large perennial herbs. Adlbauer et al. (2015) speculate that *A. vivesi* larvae may feed on grass roots. Undescribed larvae of many Madagascan and one South African (*Otteissa* Pascoe) genera were found in dead, often rotting, wood, mostly above the ground; but some species are subterranean (and larvae also tend to lose stemmata). They are found less frequently in relatively fresh dead branches where larvae usually feed subcortically; unidentified dorcasomine larvae were also found in the outer bark layer of large living broad-leaved trees. Mature larvae of nearly all known species leave the host material and pupate in soil. The life-cycle length is unknown for this subfamily.

1.4.3 Subfamily Lamiinae Latreille, 1825

1.4.3.1 Diagnosis

Small to large, elongate to robust beetles (Figures 1.77 through 1.91). Head (Figure 1.7) vertical in front or retracted and hypognathous, genal line directly posterior; antennae inserted high on frons between eyes;

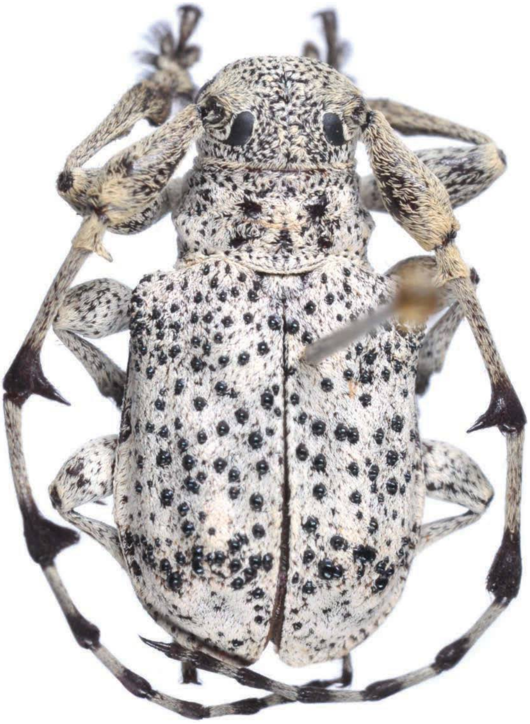

FIGURE 1.77 *Demophoo hammatus* (Chabrillac) (Lamiinae).

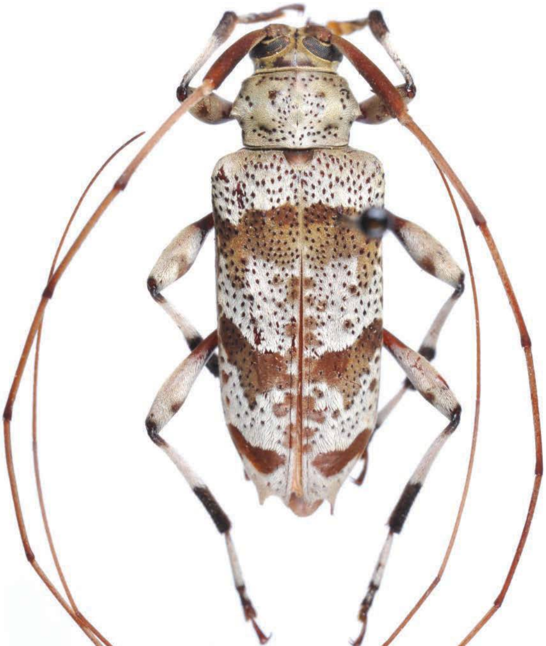

FIGURE 1.78 *Hamastatus conspectus* Monné (Lamiinae).

FIGURE 1.79 *Hydraschema fabulosa* Thomson (Lamiinae).

FIGURE 1.80 *Hylettus stigmosus* Monné (Lamiinae).

FIGURE 1.81 *Lycaneptia nigrobasalis* Tippmann (Lamiinae).

FIGURE 1.82 *Macronemus filicornis* (Thomson) (Lamiinae).

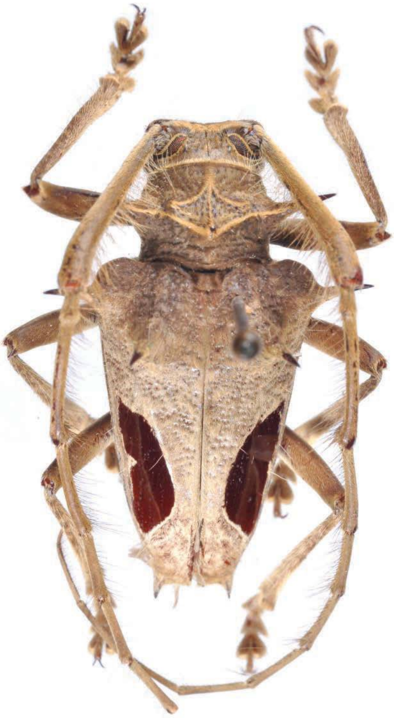

FIGURE 1.83 *Megabasis speculifera* (Kirby) (Lamiinae).

FIGURE 1.84 *Onychocerus albitarsis* Pascoe (Lamiinae).

FIGURE 1.85 *Pertyia sericea* (Perty) (Lamiinae).

FIGURE 1.86 *Melzerella lutzi* Lima (Lamiinae).

FIGURE 1.87 *Oncideres ulcerosa* (Germar) (Lamiinae).

FIGURE 1.88 *Onocephala obliquata* Lacordaire (Lamiinae).

FIGURE 1.89 *Psapharochrus luctuosus* (Bates) (Lamiinae).

FIGURE 1.90 *Scleronotus scabrosus* Thomson (Lamiinae).

FIGURE 1.91 *Trachysomus fragifer* (Kirby) (Lamiinae).

second antennomere small; eyes finely or coarsely faceted, emarginate, frequently divided; labrum free; mandibles acute without a molar plate and incisor edge without fringe of hairs; maxillae and labium well-developed; palpi with last segment pointed at apex (Figures 1.14 and 1.15); ligula membranous; mentum trapezoidal; gula usually with a short intermaxillary mentigerous process. Pronotum without a lateral margin; procoxae globose or subconical, cavities usually angulated externally (Figure 1.26); mesoscutum usually with a complete endocarina and an undivided stridulatory plate (Figure 1.32); mesocoxal cavities usually open to epimera. Legs usually short; protibiae with an oblique internal mesial sinus; mesotibiae usually with an oblique external sinus, tibial spurs short; tarsi pseudotetramerous, third tarsomere dilated, concealing the minute fourth tarsomere; tarsal claws divaricate, divergent, appendiculate, or bifid; empodium absent.

1.4.3.2 Comments

The subfamily Lamiinae had always been considered a very well-defined and monophyletic group (Napp 1994; Švácha and Lawrence 2014). Audinet-Serville (1832) was the first to propose a classification of the Cerambycidae, which included three “tribus”: Prioniens, Cerambycins, and Lamiares. Audinet-Serville (1834) divided Lamiares by the body form into “Déprimés” and “Convexes,” describing numerous genera and species. This classification generally was accepted in Europe by Bates (1861, 1862, 1863, 1864, 1865, 1866), Pascoe (1864–1869), and Thomson (1860, 1861, 1864).

LeConte and Horn (1883) recognized the Lamiinae by the prothorax not being margined, the palpi with the last joint cylindrical and pointed, and frequently the front tibiae obliquely sulcate on the inner side. They arranged the tribes represented in North America into nine series (including “Lamioides”) and several subdivisions.

Linsley and Chemsak (1984) were unable to resolve contradictions and inconsistencies in the recent usage of Lamiinae tribal classification, mainly in North America. The classification proposed by Linsley and Chemsak represents a compromise between that of LeConte and Horn and more recent work, thus retaining as many of the familiar names as possible of those currently in use by researchers of North American longicorn fauna.

1.4.3.3 Diversity and Distribution

This is the largest subfamily, with more than 21,000 species in 2,964 genera. It has representatives in all biogeographic regions and is particularly diverse in the tropics and subtropics (Table 1.1). Although the Lamiinae are the species-richest subfamily in most regions, they are outnumbered by the Cerambycinae in the Australian, Nearctic, and Neotropical regions (Forchhammer and Wang 1987).

1.4.3.4 Biology

A number of authors have summarized the general biology of the Lamiinae (e.g., Butovitsch 1939; Linsley 1961; Linsley and Chemsak 1984, 1995; Wang and Chiang 1991; Hanks 1999; Wang 2008; Ślipiński and Escalona 2013; Švácha and Lawrence 2014). Adults of most lamiine species probably are nocturnal or crepuscular in habit, based on evidence from morphological (such as coarsely faceted eyes) and biological studies. Many are diurnal, and a few are flower visitors. In almost all species of known biology, adults feed before sexual maturation; for example, many species feed for an average of seven days before mating (Hanks 1999). Most adults feed on leaves and stems of their larval hosts (Hanks 1999), such as *Paraglenea fortunei* Saunders (Wang et al. 1990), *Phytoecia rufiventris* Gautier (Wang et al. 1992), and *Glenea cantor* (F.) (Lu et al. 2011). Others feed on conifer needles and cones, such as *Acanthocinus* and *Monochamus* species, and a few on pollen, stamens, nectar, fungus, or fermented tree oozes (Butovitsch 1939). Due to the nature of adult feeding, active adult life span is relatively long, ranging from weeks to months. Flightlessness is not infrequent and obviously of multiple origin and apparently always occurs in both sexes. So far, only male-produced long-range aggregation pheromones have been identified for lamiines (see Chapter 5).

Lamiine adults usually prepare the oviposition sites in the bark of stems or branches using mandibles to cut slits where eggs are deposited. Some genera even girdle the plants before making oviposition slits. For example, the parent beetles of *Oncideres* Lepeletier and Serville and their relatives completely girdle twigs and branches and then lay eggs beyond the girdle, thus providing freshly killed tissue in which their larvae can develop (e.g., Linsley and Chemsak 1984; Cordeiro et al. 2010). Species from *Phytoecia* Dejean also girdle the twigs or shoots, but they lay eggs slightly below the girdled point, and neonate larvae bore away from the killed part of the twigs or shoots (e.g., Wang et al. 1992). Females never oviposit on barkless wood.

The larvae of most lamiines feed on living or recently dead plants, including both angiosperms and gymnosperms. Most are woodborers, such as *Anoplophora*, *Apriona*, and *Monochamus* species, and some are herbaceous plant feeders, such as *Dorcadion*, *Tetraopes*, and *Phytoecia* species. Most species feed on plant tissues above the ground level, and some consume those in the soil including roots. Lamiine larvae are very rarely found in strongly rotten wood (*Rhodopina* is an exception) and in dry, hard, long-dead wood, including seasoned construction timber. Most species probably have one generation a year although some need two years, and rarely three years, to complete a life cycle. Development may be very rapid for some tropical species; for example, *Steirastoma breve* (Sulzer) can complete four generations a year (Kliejunas et al. 2001) and *G. cantor* five generations a year (Lu et al. 2011). Except for terricolous larvae, pupation almost always occurs in the host. Many lamiine species are among the world's most important pests (see Chapters 11 and 12).

1.4.4 Subfamily Lepturinae Latreille, 1802

1.4.4.1 Diagnosis

Small to moderate, elongate, or robust beetles (Figures 1.92 and 1.93). Head oblique, rarely subvertical, gradually or suddenly narrowed behind the eyes (Figures 1.5 and 1.6); antennae inserted before or between the eyes, distinctly separated from bases of mandibles, moderately long, second antennomere short, transverse; eyes oval or emarginate, often entire, finely, or coarsely faceted; mandibles usually

FIGURE 1.92 *Euryptera unilineaticollis* Fuchs (Lepturinae).

FIGURE 1.93 *Strangalia melanura* (Redtenbacher) (Lepturinae).

flat, acute, usually with a molar tooth and a dense pubescence fringe; maxillae and labium well developed; palpi with last segment truncate at apex; ligula emarginate, frequently bilobed, membranous, or coriaceous; mentum flat, usually trapezoidal; gula produced between bases of maxillae as a distinct mentigerous process. Pronotum without lateral carinae (Figure 1.24); procoxae prominent, conical, cavities angulated externally, usually open posteriorly (Figure 1.25); mesoscutum usually with a complete median endocarina and a divided stridulatory plate (Figure 1.29); mesocoxal cavities open to epimera; metepisterna broad, usually narrowed posteriorly. Elytra usually narrowed posteriorly, rarely abbreviated, apices variable; posterior wings folded at apex, with or without a closed cell in the anal sector, radial cell closed. Legs slender; protibiae without a mesial sinus; tarsi pseudotetramerous, padded beneath (pads sometimes lacking on first tarsomere); claws divaricate to moderately divergent; empodium variable.

1.4.4.2 Comments

Audinet-Serville (1835) established the fourth "tribu" Lepturétes under the Cerambycidae with some characters that allow us to partially identify the subfamily: eyes rounded, scarcely reniforms; antennae inserted near the anterior margin of the eyes; head projected or suddenly constricted behind the eyes.

In their revision on North American Lepturinae, Linsley and Chemsak (1976) did not solve the taxonomic problems that had arisen since revisions by Swaine and Hopping (1928), Hopping (1937), and Hopping and Hopping (1947). The groupings are still not very clear because some groups are quite diverse in morphological and biological characters and their phylogenetic relationships are not solved.

1.4.4.3 Diversity and Distribution

The Lepturinae have more than 1,500 species in 210 genera and nine tribes in the world (Table 1.1). The subfamily is dominant in the Northern Hemisphere, particularly in the Holarctic, with a few species expanding to Afrotropical, Australian, Neotropical, and Oriental regions (Monné and Monné 2008; Švácha and Lawrence 2014).

1.4.4.4 Biology

Adults often are diurnally active flower visitors with head and mouthpart morphology of many taxa strongly adapted to pollen and nectar feeding (Linsley 1961; Linsley and Chemsak 1972; Gosling and Gosling 1976; Taki et al. 2013; Švácha and Lawrence 2014). They visit flowers of shrubs, trees, and even herbs depending on the availability (Gosling and Gosling 1976). Some species may feed on fungus spores (Linsley 1961). For example, pollens and fungus spores are found in guts of three Japanese *Rhagium* species (Kanda 1980). However, adults of most species from the Xylosteini appear to be nocturnally active (Linsley and Chemsak 1972). Some crepuscular or nocturnal adults may also visit flowers and feed on pollen. For example, pollen is found on the body of *Enoploderes sanguineum* Faldermann (Danilevsky and Miroshnikov 1981) and *Centrodera spurca* (LeConte) (Leech 1963). Adults live for a few weeks to a few months. Mating usually occurs on flowers. Although female-produced sex pheromones were evidenced earlier (Linsley 1961), they have not been identified until recently. For example, these have been identified for several species in the genera *Ortholeptura* Casey (Ray et al. 2011) and *Desmocerus* Serville (Ray et al. 2014). Millar and Hanks provide details about pheromones in this subfamily in Chapter 5. Females usually lay their eggs on or in the larval food material without special preparation of the oviposition site. However, females of some root feeders oviposit in soil or on the ground, and first instar larvae dig into the soil and search for the roots.

Linsley (1961) and Švácha and Lawrence (2014) summarized the biology of immature stages. Larvae of most species probably are dead wood feeders. Subcortical larval feeding and strongly flattened larval forms are widespread in Rhagiini but rare (Lepturini) or unknown in other tribes. Some dead wood feeders are associated with specific fungi; for example, *Pseudovadonia livida* (F.)

larvae tunnel in humus with mycelium of the fungus *Marasmius oreades* (Bolton) Fr. Larvae of *Encyclops* Newman and some *Pidonia* species bore in thick outer bark of living trees. In rare cases, larvae of some species from *Pseudogaurotina* Plavilstshikov and *Desmocerus* Serville feed within living tissues of woody plants. A few groups develop in or on the underground parts of living herbs, such as *Brachyta* Fairmaire, *Brachysomida* Casey, *Vadonia* Mulsant, many *Cortodera*, and some *Typocerus*; other *Cortodera* feed in wood fragments or conifer cones buried in humus. Larvae of many species may bore into the roots and, in specialized root feeders such as *Pachyta* Dejean, *Stenocorus* Geoffroy, and *Akimerus* Serville, the larvae start feeding in thinner distal roots and proceed toward the thicker proximal ones. Larvae of *Pidonia* Mulsant also are frequently subterranean, and related taxa (*Pseudosieversia* Pic, *Macropidonia* Pic) appear to be at least partly terricolous, feeding on the roots externally (Cherepanov 1979). Depending on the species, mature larvae may construct pupal chambers in the host plant or soil. The life cycle lasts from several months to several years.

1.4.5 Subfamily Necydalinae Latreille, 1825

1.4.5.1 Diagnosis

Small to moderate, usually elongate (Figures 1.36 and 1.37) but occasionally robust beetles. Head constricted behind eyes; frons large, vertical; antennae inserted high on frons; eyes finely faceted, deeply emarginate; mandibles small, robust, acute, densely fringed along inner margin; mentum short, transverse; ligula membranous, bilobed; palpi short. Pronotum with sides convex or tuberculate, constricted anteriorly and posteriorly; notosternal suture fine or incomplete; prosternum short, intercoxal process narrow; procoxae large, conical, nearly contiguous, cavities open to epimera; mesoscutum without median endocarina but with an undivided stridulatory plate (Figure 1.30); metepisterna broad, attenuated posteriorly. Elytra (Figures 1.36 and 1.37) short, scarcely longer than thorax, exposing abdomen, apices dehiscent; hind wings lying flat on abdomen, not folded at apex, without an anal cell. Legs slender; tibial spurs short; first metatarsomere without a pubescent sole. Empodium variable, in some cases distinct and multisetose. Abdomen with tergite corneous; sternites subequal in length, fifth sternite broadly emarginate in male.

1.4.5.2 Comments

The Necydalinae often have been classified as a tribe of the Lepturinae (Linsley 1940). Adult synapomorphies may include the mandibular molar plate, which is not known in other cerambycid subfamilies (but occurs in many Disteniidae and Oxypeltidae) and seems to be best developed in some derived floricolous Lepturinae (whereas it is less distinct in some presumed basal forms and in the Necydalinae).

1.4.5.3 Diversity and Distribution

This subfamily has about 70 species in two genera (Table 1.1): *Necydalis* L. and *Ulochaethes* LeConte. The former is distributed in the Nearctic, Palaearctic, and Oriental regions, although the latter is monotypic and only occurs in the western Nearctic. All other genera classified in the Necydalinae or Necydalini should be placed in the Cerambycinae (Švácha and Lawrence 2014).

1.4.5.4 Biology

Adults are predominantly diurnal and good fliers (Linsley 1940, 1961; Zolotov 2001). They mimic hymenopterans morphologically and behaviorally with *Necydalis* (Figure 1.36) resembling large wasps and *Ulochaetes* (Figure 1.37) similar to bumblebees (Linsley 1940, 1961; Švácha and Lawrence 2014). Some species of *Necydalis* visit flowers. Adults usually lay their eggs at the base of standing dead trees or stumps. Adults may feed on flowers or pollens but are relatively short-lived, probably less than a month (Linsley 1961).

Larvae of most species feed on the heartwood of dying or recently killed trees, with *Ulochaetes* attacking only conifers and most *Necydalis* mainly feeding on angiosperms and only some on conifers (Linsley 1961; Švácha and Lawrence 2014). *Ulochaetes* larvae bore in the base and roots of trees. Most *Necydalis* larvae may bore inside the trunk and stumps and occasionally in the roots. The life cycle normally lasts one year but, in some species, there may be two generations a year.

1.4.6 Subfamily Parandrinae Blanchard, 1845

1.4.6.1 Diagnosis

Moderate to large and usually robust beetles (Figure 1.94). Head (Figures 1.3 and 1.4) oblique to horizontal; antennae inserted in front of eyes, near base of mandibles, not extending beyond base of pronotum, similar in both sexes, glabrous, sensory areas deeply impressed; second antennomere at least one-half as long as third, remaining antennomeres subequal in length; eyes small, vertical, convex, feebly emarginate, coarsely faceted; labrum triangular fused with epistoma; mandibles dentate, molar tooth and pubescent fringe lacking; lobes of maxillae small, inner one obsolete (Figure 1.12); palpi with last segment truncate at apex; ligula very transverse, corneous; mentum transverse (Figure 1.20); submentum without intermaxillary process. Pronotum with an elevated, entire, and simple carina at each side (Figure 1.21); procoxae transverse; cavities open or closed posteriorly; mesoscutum without stridulatory plate (Figure 1.27); mesocoxal cavities open externally; metepisterna narrow, parallel-sided. Elytra parallel-sided, apices rounded; hind wings without closed cell in anal sector, radial cell open. Legs short; femora and tibiae compressed; procoxae without mesial sinus; tarsi (Figure 1.34) slender, five-segmented, without pubescent ventral pads, third tarsomere entire or feebly emarginate, not dilated, empodium small, slender, occasionally reduced or obsolete, usually uni- or bisetose.

FIGURE 1.94 *Erichsonia dentifrons* Westwood (Parandrinae).

1.4.6.2 Comments

Taxonomy of this small subfamily has been progressing rapidly in recent decades (Monné 2006; Švácha and Lawrence 2014). For example, there have been several revisions on the Afrotropical (Bouyer et al. 2012), Australian and Oriental (Santos-Silva et al. 2010; Komiya and Santos-Silva 2011), and Neotropical (Santos-Silva 2002, 2015) genera. Furthermore, Biffi and Fuhrmann (2013) gave a detailed treatment of the larvae and pupae of a Neotropical species, *Parandra longicollis* Thomson, generally discuss parandrine immature stages, and provide a key to parandrine larvae of the world.

1.4.6.3 Diversity and Distribution

Worldwide, the Parandrinae have about 120 species in 19 genera and two tribes (Table 1.1). The Erichsoniini contains only one genus and one species, *Erichsonia dentifrons* Westwood (Figure 1.94), and occurs only in Mexico and Central America. The Parandrini has representatives in all biogeographic regions, with six genera in the Oriental and Australian, five in the Neotropical, one in the Nearctic, one in Hawaii, one in the Palaearctic, one in the Afrotropical, and several species of uncertain generic position in the Afrotropical. Most parandrine species are distributed in warmer regions, and only a few occur in temperate zones.

1.4.6.4 Biology

The biology of the Parandrinae is still poorly understood. So far, nothing is known about the biology of the tribe Erichsoniini. Based on literature, Švácha and Lawrence (2014) summarized the general biology of the Parandrini. Adults are mostly nocturnal and hide in tree hollows, cracks, and under the loose bark during the day. Females lay eggs on the wood, with several generations often developing within the same dead wood. The life cycle usually lasts more than a year. For example, *Parandra brunnea* (F.) takes two to three years to complete growth and development (Gahan 1911). Lingafelter (1998) described mating behavioral interactions between sexes of a parandrine species, *P. (P.) glabra* (De Geer), for the first time. No pheromones have been found in this subfamily.

Larvae usually develop in dead moist logs, timber poles close to the ground surface, or in dead wood of living trees; sometimes they even develop in closed (healed over) hollows in which the adults may reproduce without leaving the tree (Linsley 1962a). Some species can feed on both dead and living plants. For example, the larvae of *P. brunnea* feed in the decayed heartwood and moist structural timber of many hardwood species and can also cause severe injury to living trees where the heartwood has been exposed (Gosling 1973). Most species are highly polyphagous, occasionally even attacking both gymnosperms and angiosperms with a preference for angiosperms (Linsley 1962a; Monné 2002). However, some southern species appear to be associated with, or at least frequently develop in, the gymnosperm tree genus *Araucaria* (Mecke et al. 2000; Mecke 2002). Mature larvae usually construct pupal cells inside the wood and pupate there.

1.4.7 Subfamily Prioninae Latreille, 1802

1.4.7.1 Diagnosis

Moderate to very large, usually robust beetles (Figures 1.95 and 1.96). Head (Figures 1.9 and 1.11) oblique or subvertical; antennae inserted near base of mandibles, variable in length but always surpassing base of pronotum, antennomeres glabrous, frequently produced or serrate in male; eyes large, usually coarsely faceted; labrum fused with epistoma; mandibles large, molar tooth and pubescent fringe lacking; maxillae with inner lobes obsolete (Figure 1.13); palpi with last segment truncate at apex; ligula transverse, corneous; mentum transverse; submentum without intermaxillary process. Pronotum with an elevated, often spinose or dentate, carina (Figures 1.22 and 1.23) at each side; cavities open behind; mesoscutum without a stridulatory plate; mesocoxal cavities usually open externally;

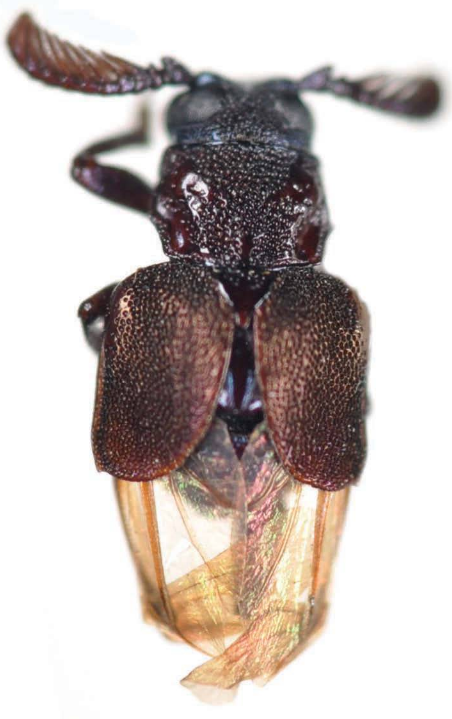

FIGURE 1.95 *Chariea birai* Monné and Monné (Prioninae).

FIGURE 1.96 *Poecilopyrodes pictus* (Perty) (Prioninae).

metepisterna variable. Elytra with variable apices; hind wings with a closed cell in anal and in radial sectors. Legs moderately robust; procoxae transverse; protibiae without mesial sinus; tarsi pseudotetramerous, padded beneath, third tarsomere dilated, concealing minute fourth tarsomere. Empodium from prominent and multisetose to indistinct.

1.4.7.2 Comments

Prioninae are remarkable by almost complete absence of very small forms—except the Neotropical genus *Chariea*. For example, *C. birai* Monné & Monné (Figure 1.95) is only 4.2 mm long, which is the smallest species of Prioninae (Monné and Monné 2015). This subfamily contains some of the largest known beetles (*Titanus*, *Xixuthrus*, and *Macrodontia* with specimens reaching 150–175 mm). Extreme sexual dimorphism in size, general form, antennal morphology, and color is common in some species, such as those in the tribe Anacolini.

1.4.7.3 Diversity and Distribution

About 1,100 species in 302 genera and 21 tribes have been described for this subfamily worldwide (Švácha and Lawrence 2014; Tavakilian 2015). The subfamily occurs in all biogeographic regions but predominantly in the tropical and subtropical regions (Table 1.1) such as the warmer areas of the Afrotropical, Australian, Oriental, and Neotropical. Relatively few species are distributed in temperate areas of the Nearctic and Palaearctic regions.

1.4.7.4 Biology

Švácha and Lawrence (2014) summarized some aspects of the general biology of this subfamily. Typically, adults are crepuscular or nocturnal and correspondingly sober, dull, or dark in color. In the few known diurnal species that exclusively occur in the tropics, adults can be brightly colored or metallic. Flightlessness or brachyptery is relatively common, particularly in dry regions; but except for some Neotropical long-legged "pedestrian" species, this usually is restricted to females. Some winged females apparently cannot fly until they lay a portion of their eggs. Adults usually do not feed, or at most feed on imbibed fluids. Most adults live for a few days, but some can survive for a few months. Mating usually occurs on the emergence day or the next. Long-range female-produced sex pheromones have been identified for *Prionus californicus* Motschulsky (Rodstein et al. 2011) and several *Tragosoma* species (Ray et al. 2012), all of which are from the Nearctic. Although female-produced sex pheromones are evidenced in a New Zealand species, *Prionoplus reticularis* White (Edwards 1961), these have never been identified. In Chapter 5, Millar and Hanks provide a detailed treatment of pheromones in this subfamily. Females lay eggs immediately or one day after mating; in many species, they can lay hundreds of eggs. For example, the female of the Oriental species *Dorysthenes granulosus* (Thomson) can lay up to 783 eggs in her lifetime (Zeng and Huang 1981).

Larvae of most species develop in dead plants, but those of some species feed on living plants. Dead plant feeders usually are highly polyphagous, while those that feed on living plants can be either polyphagous or oligophagous. In several tribes, such as Prionini and Cantharocnemini, larvae develop more or less exclusively underground, and some can even move through soil and feed on roots of trees or herbs externally and then internally. Some species can bore from the main roots to the stems up to 60 cm above the ground surface. Females of such species usually oviposit in soil near the host plants, for example, *P. californicus* (Linsley 1962a; Alston et al. 2014) and the Oriental species *D. hugelii* (Redtenbacher) (Duffy 1968; Sharma and Khajuria 2005; Singh et al. 2010) and *D. granulosus* (Zeng and Huang 1981). Mature larvae usually pupate in the pupal cells in soil. However, most prionines lay eggs directly on the hosts. For example, the females of the Afrotropical species *Macrotoma palmata* (F.) lay their eggs in the cracks and crevices in the bark of the trunks and main branches of healthy trees (Duffy 1957; Tawfik et al. 2014). The larvae bore into the bark and then into the wood. For example, *P. reticularis* bore inside logs, stumps, dead parts of living trees, and untreated sawn timber (Edwards 1961). Mature larvae pupate in the wood. However, the larvae of some trunk borer species may exit from the wood when mature and enter soil for pupation—for example, the Neotropical species *Macrodontia cervicornis* (L.) (Paprzycki 1942).

Almost all species of known biology from this subfamily take more than a year to complete their life cycles. For example, the growth and development of immature stages require three to five years in *P. californicus* (Linsley 1962a; Alston et al. 2014) and three to four years in *D. hugelii* (Duffy 1968) and *M. palmata* (Duffy 1957; Tawfik et al. 2014). A shorter life history has been recorded (about two years) in *D. granulosus* (Zeng and Huang 1981; Yu et al. 2012).

1.4.8 Subfamily Spondylidinae Audinet-Serville, 1832

1.4.8.1 Diagnosis

Moderate in size and elongate, sometimes robust in form (Figures 1.97 and 1.98). Head (Figure 1.8) large, oblique, may be constricted behind eyes but without prominent temples; mouthparts moderately to strongly oblique; frontoclypeal suture complete or somewhat obliterated medially, postclypeus strongly transverse to shortly triangular, protentorial pits mostly distinct, sublateral to dorsal/frontal; anteclypeus small, very short in Spondylidini; labrum separate but often short and transverse; antennal sockets broadly separate, relatively distant from mandibular condyle, and facing laterally in Anisarthrini, Saphanini, and Atimiini, closer to condyle and facing slightly anteriorly in Asemini and Spondylidini; eyes huge to very small, more or less emarginate, may be strongly constricted or completely divided; in the saphanine branch, eyes may be slightly protruding between mandibular articulation and antennal socket. Pronotum without elevated carina, sides entire; prosternal process present, procoxal cavities of variable shape (but lateral procoxa and trochantin at least partly exposed), closed internally, open or closed posteriorly; mesoscutum with a medial endocarina, and stridulatory plate (if present) divided (Figure 1.28); mesocoxal cavities open in most species or narrowly closed laterally in Atimiini. Elytra parallel-sided, apices rounded, unarmed; hind wings with edge cell. Legs short; femora and tibiae compressed; protibiae without mesial sinus, apex with a broad terminal lamella (Figure 1.33); tarsi pseudotetramerous (Figure 1.35), claws divaricate, empodium small and bisetose to indistinct; legs modified in Spondylidini (short and stout with slightly compressed dentate tibiae, somewhat reduced tarsal pads and enlarged fourth tarsomere).

FIGURE 1.97 *Asemum striatum* (L.) (Spondylidinae).

FIGURE 1.98 *Neospondylis mexicanus* (Bates) (Spondylidinae).

1.4.8.2 Comments

The relationships of the Spondylidinae with other subfamilies have been controversial. For example, the subfamily was considered more closely related with the Prioninae by Audinet-Serville (1832), although it was treated as a closer relative of the Anoplodermatinae by Thomson (1860). Based on larval morphology, Craighead (1923), Duffy (1960), and Švácha and Danilevsky (1987) included *Spondylis* in the Aseminae. In the current system, the tribes Asemini, Atimiini, and Spondylidini are included in the Spondylidinae.

1.4.8.3 Diversity and Distribution

The subfamily consists of about 160 species in 32 genera and 5 tribes and is distributed in all biogeographic regions (Table 1.1). However, Švácha and Lawrence (2014) listed only 20 genera. They show that the spondylidine branch (Spondylidini and Asemini) generally is Holarctic, with some Neotropical and Oriental representatives. Several *Arhopalus* species have been introduced to the Australian (Wang and Leschen 2003), Afrotropical (Adlbauer 2001), and Neotropical (López et al. 2008). In the saphanine branch, Anisarthrini primarily occur in the Palaearctic and Afrotropical, Saphanini mainly in the Palaearctic and Nearctic, and Atimiini in the Palaearctic, Nearctic, and Oriental.

1.4.8.4 Biology

Adults are predominantly crepuscular and nocturnal, usually somber-colored, nonfeeding and short-lived (Švácha and Lawrence 2014). Some species of *Tetropium* (tribe Asemini) are diurnal in habit and brightly colored. The Saphanini are mostly flightless; for example, *Saphanus* is macropterous, but at least females of some, if not all, populations do not fly and *Drymochares* and *Michthisoma* are micropterous. Male-produced long-range sex pheromones in *Tetropium fuscum* (F.) and *T. cinnamopterum* Kirb have been identified (Silk et al. 2007). Lemay et al. (2010) described calling behavior by *T. fuscum* males, during which time sex pheromones are released. After females are attracted to calling males, the latter use female-produced contact sex pheromones for sex recognition and mating (Silk et al. 2011). Details about pheromones in this subfamily are given in Chapter 5. Some *Arhopalus* species are attracted to newly burned pine forest for oviposition (Suckling et al. 2001).

Larvae from Saphanini and Anisarthrini usually feed on dead angiosperms, but those of most species from the remaining three tribes live on dead conifers. According to Švácha and Lawrence (2014), Asemini and Spondylidini adults usually do not oviposit on barkless wood. Larvae from *Tetropium* are completely subcortical, sometimes in freshly dead or live trees (Gosling 1973). Species of *Nothorhina* and *T. aquilonium* develop exclusively within the bark of large, standing, living trees (Heliövaara et al. 2004). Larvae of many Asemini feed on dead or stressed coniferous trees (Hanks 1999) and may bore into underground parts of the host trees. Many species from the Spondylidini are specialized root feeders, working from distal roots toward the tree base so that mature larvae may reach it and adults may emerge from stem or stump bases aboveground. Female *Spondylis* dig into the soil and oviposit directly on the root bark (Cherepanov 1979). All taxa pupate in the food material. The life cycle of this subfamily lasts one to several years, depending on species and climate.

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