# Chapter 2
# General Overview of Saproxylic Coleoptera

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**Abstract** A broad survey of saproxylic beetles (Coleoptera) from literature and personal observations was conducted, and extensive references were included to serve as a single resource on the topic. Results are summarized in a table featuring all beetle families and subfamilies with saproxylicity indicated for both adults and larvae (where known), along with information on diversity, distribution, habits, habitat, and other relevant notes. A discussion about the prevalence of and evolutionary origins of beetles in relation to the saproxylic habitat, as well as the variety of saproxylic beetle habits by microhabitat, is provided. This initial attempt at an overview of the entire order shows that 122 (about 65%) of the 187 presently recognized beetle families have at least one saproxylic member. However, the state of knowledge of most saproxylic beetle groups is extremely fragmentary, particularly in regard to larval stages and their feeding habits.

## 2.1 Introduction to Beetles

There are nearly 400,000 described species of beetles, which comprise 40% of all described insect species (Zhang 2011). In fact, one in every four *animal* species (from jellyfish to Javan rhinos) is a beetle. The dominance of this group in terrestrial ecosystems can hardly be overstated—and the dead wood habitat is no exception in this regard. The largest (see Acorn 2006), longest-lived, and geologically oldest beetles are saproxylic. Of the roster of saproxylic insect pests in forests, beetles

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dominate in terms of sheer number of species and, arguably, economic losses (Furniss and Carolin 1977; Solomon 1995).

Beetles (order Coleoptera) fall within the Endopterygota (Holometabola) and therefore undergo so-called complete metamorphosis, passing through anatomically and behaviorally disparate larval, pupal, and adult stages. This temporal division of labor—in which the primary directive of the larval stage is to eat and grow and the function of the adult is to disperse and reproduce, often in a habitat quite different from the larva—is thought to be a key innovation within the insect tree of life. Indeed, although the Endopterygota contains less than half of the 29 extant insect orders, it contains over 80% of described insect species [numbers derived from Zhang (2011)]. When considering saproxylicity among beetle species, the disparate nature of life stages is a key discussion topic, since a frequent strategy among beetles is to have a saproxylic larva and a non-saproxylic adult (see Table 2.1).

The anatomy of beetles is peculiar among insects, making them one of the most distinctive major orders. The most salient feature of beetles is the presence of elytra, mesothoracic wings modified and corneous and not generally used for flight, which most often completely cover the dorsal portions of the meso-metathorax (including flight wings) and abdomen (but can be significantly shortened in some families) and usually meet in a straight line middorsally. Hardened elytra confer obvious protection against would-be attackers. As adults, beetles are often heavily armored throughout and exhibit an ability to retract appendages in defense of predators or to assist in the ability to squeeze into tight spaces. These adaptations are also related to protection from pathogens and from water loss in arid habitats (Lawrence and Newton 1982; Grimaldi and Engel 2005). The general anatomical direction of beetles has been one of fusion and increased sclerotization; however, there are many notable exceptions (e.g., Staphylinidae and many Elateroidea).

## 2.2 Early Evolution of Beetles in Dead Wood

Perhaps no major order of insects typifies the saproxylic habit more than beetles. Of the "big four" holometabolous insect groups, beetles express the highest diversity in dead wood habitat in terms of both number of taxa present as well as microhabitat diversity. They are probably the only order of Endopterygota that can attribute their evolutionary origins and unique morphology to the dead wood habitat (Hamilton 1978).

During their initial period of diversification, taking place prior to the Early Permian, beetles experienced major anatomical modifications. Most obvious among these was the hardening of the forewings into protective elytra. Other adaptations included dorsoventral flattening of the body, migration of the antennal insertions laterally (lower) on the head, non-projection of the coxae, rotation of the mouthparts into a prognathous aspect, reduction of the mesothorax and its fusion with the metathorax (with concomitant loss of mesothoracic flight muscles), and fusion of the hind coxae with the metathorax (see Grimaldi and Engel (2005) for a good overview).

Based on Lubkin and Engel (2005), the two Early Permian "beetle" families are Tshekardocoleidae (from Tshekarda, Russia) and Oborocoleidae (from Obora, Czech Republic); even though the latter are older (268 Ma), they are only known from scattered elytra. Tshekardocoleidae are conclusively placed as beetles based on mesothoracic structure (Kukalová 1969). Late Permian beetle families include Permocupedidae, Asiocoleidae, Rhombocoleidae, and Schizocoleidae. Before *Permocoleus* (Lubkin and Engel 2005), no Permian beetles were known from North American deposits. These families, collectively referred to as Protocoleoptera (sensu Lawrence and Ślipiński 2013: 4), are distinguished from one another based on the morphology of the elytra. All possess varying degrees of apparent sclerotization of the elytra as visualized through the relative area proportion of "window punctures" (presumably the original wing membrane) versus the principal and interstitial veins separating them.

Recently, however, the fossil beetle *Coleopsis archaica* (Kirejtshuk et al. 2014) has come to light from the earliest Permian of Germany (ca. 295 Ma), which was classified in the Tshekardocoleidae; additionally, the authors synonymized Uralocoleidae and Moravocoleidae with this family. This fossil in part led Toussaint et al. (2017) to re-calibrate and re-date the beetle tree of life dataset of McKenna et al. (2015), shifting the origin of Coleoptera about 80 million years older to approximately 333 Ma (95% CI: 349 to 317 Ma)—a Late Carboniferous origin for the order. An excellent summary of the fossil history of beetles can be found in Lawrence and Ślipiński (2013: 4–8).

Whether the morphological changes outlined above developed in association with saproxylicity is not known with certainty, though present-day forms adapted to this habitat possess these features in particular. The Permian experienced a rapid rise in the dominance of the gymnosperms, while tree lycopods typical of the Carboniferous went extinct, probably in connection with Northern Hemisphere desertification and Southern Hemisphere glaciation (Shear and Kukalová-Peck 1990). Ponomarenko (2003) concluded that the beetle ancestral habit was "xylomycetophagy," with xylophagy and rhizophagy not appearing until later (Jurassic) times. At the very least, evolution of these Protocoleoptera preadapted beetles to a saproxylic lifestyle, allowing them to squeeze into bark crevices without damaging flight wings and other appendages [although Permian Protocoleoptera tended to have more complete wing venation, suggesting that folding mechanisms had not yet developed; see Crowson (1975)]. Additionally, fossils of trees whose bark was probably prone to sloughing were present in the same deposits as these early beetles (Crowson 1981). Unfortunately there are no known fossils of beetle larvae or wood borings in these deposits, so this evidence remains strictly circumstantial. Since larvae lack the same dispersal abilities as adults and are generally tied to their habitats more intimately, form is generally much more closely tied to habits in this life stage. Consequently, larval evidence would go a long way toward informing the habits of the world's first beetles. However, Crowson (1981: 660) believed, based on the presumed groundplan of larval beetle mouthparts, that the first beetle larva was more likely to have been a mold-feeding type than a wood-boring type. Even so, this potentially places the protocoleopteran larvae on or around decaying wood. Although most of the Permian forms are currently grouped into the extinct suborder Protocoleoptera, they are quite similar morphologically to many members of the extant order Archostemata, which contains almost exclusively saproxylic members today.

One report of Carboniferous wood-boring activity by Cichan and Taylor (1982) is suggestive of early beetles in a (presumably aerial) root of a gymnosperm and consists of 0.3–0.6 mm-diameter burrows with accompanying frass. However, it is not until Triassic fossils that we have unambiguous evidence of wood-inhabiting activity in beetles. The remarkable published findings of Walker (1938) based on numerous examples of fossilized wood of *Araucarioxylon arizonicum* Knowlton (Araucariaceae) in the Petrified Forest of Arizona exhibit a wide range of boring patterns, whose similarity to modern boring behavior of Buprestidae and Scolytinae (Curculionidae) was noted. Tapanila and Roberts (2012) later reported ichnofossils of pupation in wood that probably represented early beetles from similar deposits (Late Triassic Chinle Formation of southern Utah). Based on the foregoing evidence, both fossil and ichnofossil, it seems likely that saproxylic beetles have existed since at least the Permian, for nearly 300 million years.

## 2.3 Habits and Habitats of Saproxylic Beetles

Saproxylic beetles can be conceptually divided up along a variety of axes, including but not limited to (1) taxonomic, (2) feeding type, (3) succession, and (4) microhabitat. Division along the taxonomic axis is accomplished in Table 2.1. As the study of saproxylic beetles progresses, in the future it would be perhaps more biologically useful to divide up these taxa along the feeding type axis—categories might be, e.g., mycophagy, myxomycophagy, xylophagy, predatory, saprophagy, and parasitoids. However, given the incomplete nature of this knowledge at present and the difficulty of ascertaining such information through detailed life history studies and careful labwork, we can only indicate these feeding types where known. An additional axis related to feeding types is succession, in a sense treating the dead log as a forensic entomologist treats a dead body; categorizing beetles as early, middle, and late (veteris) in relation to the death of the tree; and recognizing important differences related to “carcass” size, position, geography, tree species, and macrohabitat. For the discussion below we divide up saproxylic beetles into categories based on microhabitat, for this can be directly and unambiguously observed in the field. The flow of categories below progresses (roughly) from the interior of a dead log to the periphery of dead-wood-dependent habitats, with a discussion of aquatic dead-wood habitats appearing at the end. For a lengthy discussion of the European saproxylic beetle fauna by habitat, see Merkl (2016).

### 2.3.1 Wood-Inhabiting Taxa

This subcategory is typified by classic wood-boring taxa, which tend to sport strong, stout mandibles in whichever stage actively tunnels through wood. Larvae that are borers are more prevalent than adults and tend to be more or less cylindrical and have a poorly sclerotized cuticle, and the head capsule tends to be retracted into the thorax. Some adults, however, are wood-boring and include Bostrichidae, Ptinidae, and Curculionidae (Lawrence and Ślipiński 2013). Beetles in the first two groups are often pests of wood inside houses (Lewis and Seybold 2010). Other groups include certain Curculionidae (Platypodinae and Scolytinae: Xyleborini), Cerambycidae, Passalidae, Buprestidae, Lymexylidae, Ptinidae, and Bostrichidae. For a more detailed discussion of the ambrosia beetles (Curculionidae: Platypodinae and certain Scolytinae), see Sect. 2.3.7.

Cerambycidae, which contain an enormous number of wood-borers ("round-headed borers"), whose adults do not tunnel through wood, typically start as larvae by boring subcortically and then bore directly into sapwood and heartwood as they develop (Evans 1975). Buprestidae larvae ("flat-headed borers") often have similar habits, boring through wood just under the cambium before plunging into the wood toward the center of the log to finish larval development and to pupate.

As woody debris reaches an advanced stage of decay, it plays host to a distinct fauna. Especially rotten wood is known to be a classic habitat for scarabaeoid grubs, particularly of the families Lucanidae, Passalidae, and Scarabaeidae (chiefly the subfamilies Cetoniinae and Dynastinae), a fact well-known among enthusiasts of those groups, while larvae of Callirhipidae are typical of white-rotted wood in an advanced decay stage (Lawrence and Ślipiński 2013). However, Ferro et al. (2012a) demonstrated a distinct fauna of smaller beetles within the final decay stage of hardwood logs in an eastern North American forest (Ferro 2018, see Chap. 22). For an in-depth discussion of the habits of Passalidae and Lucanidae, see Ulyshen (2018) and Huang (2018) (Chaps. 3 and 4, respectively).

Some beetles seem to be typical of red-colored rotten wood. Notable examples include *Micromalthus debilis* LeConte (Micromalthidae); *Schizophilus subrufus* (Randall) of the Eucnemidae (Otto and Young 1998); members of the small family Prostomidae, which prefer wood with a mud- or clay-like consistency (Lawrence 1991; Klimaszewski and Watt 1997; Lawrence and Ślipiński 2013); the Nearctic *Priognathus monilicornis* (Randall) (Pythidae) (Pollock 2002a); and certain terrestrial larvae of Scirtidae from the Southern Hemisphere (Lawrence and Ślipiński 2013).

### 2.3.2 Subcortical Taxa, Including Phloem Feeders

The subcortical group is dominated, both in terms of number of species and abundance, by the "bark beetles" of the subfamily Scolytinae (Curculionidae). An extremely wide variety of other beetle groups, however, are typical of this habitat. Cucujidae, Laemophloeidae, and Silvanidae, collectively known as "flat bark beetles," contain adults and larvae often highly flattened and specialized for living under bark. Their habits are not entirely clear, but many are at least facultative predators and are probably opportunistic scavengers or saprophages. Predatory beetles typical of this habitat, and often associated with Scolytinae, are the Histeridae, Trogossitidae (Trogossitinae), Carabidae (Bembidiini: Tachyina), Synteliidae, Chaetosomatidae, Thanerocleridae, Cleridae, Brentidae, larvae of Brachypsectridae, Cantharidae, Lampyridae, Rhadalidae, adults of Elateridae, Bothrideridae, and certain Zopheridae (Colydiinae). Parasitoid beetles include Bothrideridae and Passandridae. Other taxa present in this microhabitat, probably feeding upon fungal mycelium, are Biphyllidae, Cerylonidae, Cryptophagidae, Endomychidae, Teredidae, Carabidae (Rhysodinae), Euxestidae, Jacobsoniidae, Eupsilobiidae, Boridae, Pythidae, Pyrochroidae, Salpingidae, Monotomidae, Myraboliidae, Nitidulidae, Curculionidae (Cossoninae), larvae of Synchroidae, Mycteridae, and Scraptiidae.

Since microclimates on even a single log can differ greatly (Evans 1975: 159, from Geiger 1950: 235, also Chauvin 1967), their beetle faunas correspondingly differ. The wet, waterlogged parts of the wood-bark interface have a distinctive beetle fauna, apparently most diverse in the Southern Hemisphere, which may contain Hydrophilidae (especially Cylominae) and larvae of Scirtidae (M. Fikáček, pers. com.; MLG, pers. obs.).

### *2.3.3 Dead Wood Surface (Including Contact with Substrate)*

A large number of beetles find optimum shelter under dead logs, since they provide a relatively stable microclimate along the ground surface, with much lower thermal conductivity than rocks and with high moisture retention properties. In addition to those beetles obligately associated with wood-rotting fungi (which often reach their peak toward the more moist underside), adult and larval beetles typical of this habitat include in particular Carabidae, Leiodidae (Camiarinae), Staphylinidae, Tenebrionidae, and Zopheridae.

A large number of adult beetles occur on the surface of dead wood at night; some of these are predacious (e.g., Carabidae), but many of these graze on lichens and microfungi and may include certain Tenebrionidae (especially Stenochiinae), Cerambycidae, Erotylidae, and Chalcodryidae. Adults of Buprestidae are also typical of this habitat but are mostly diurnal. Some larvae of Cryptocephalinae (Chrysomelidae) graze the outer layer of dead twigs (Chamorro 2014). Among predacious Carabidae, remarkable larval examples include tiger beetles of the genera *Collyris*, *Ctenostoma*, *Therates*, and some *Tricondyla*, which occupy tunnels opening to the bark surface, from which they hunt prey nocturnally (Balduf 1935; Trautner and Schawaller 1996; Pearson and Vogler 2001; excellent illustrations of burrows in Zikan 1929).

An interesting community of beetles is also associated with wounded parts of living trees (sap flows and slime fluxes), a microhabitat often infected with bacteria, yeasts, and other microfungi. Members of the family Nosodendridae are perhaps the most strikingly adapted beetles in this peculiar habitat, the larvae possessing mostly dorsal spiracles, with the last pair being located at the apex of an elongated terminal abdominal segment, allowing the larvae to be totally immersed in the slime flux (Crowson 1981; Leschen and Beutel 2010b). The larvae also possess a rough dorsal surface which allows debris to adhere and causes the larvae to virtually disappear in their habitat. Other taxa typical in the sap flow or slime flux microhabitat include *Peltastica* (Derodontidae; Leschen and Beutel 2010a), Sphaeritidae (Newton 2016a), some Histeridae (Kovarik and Caterino 2016), adult Lucanidae (Scholtz and Grebennikov 2016), *Euderia* (Bostrichidae; Klimaszewski and Watt 1997), and many Nitidulidae (Jelínek et al. 2010).

Tree holes (or tree hollows) with an accumulation of woody debris and other organic matter represent unique environments with a distinct community. These habitats are covered in detail by Micó (2018, see Chap. 21). Coleoptera species in these habitats are dominated by certain Histeridae, Ptiliidae, Staphylinidae (especially Pselaphinae), Hybosoridae, Scarabaeidae, Elateridae (larval), Ciidae, Tenebrionidae, and Curculionidae (Park et al. 1950; Park and Auerbach 1954; pers. obs.).

### *2.3.4 Wood-Rotting Fungal Bodies and Slime Molds*

Inhabiting fungal fruiting bodies on a dead wood substrate is one of the largest single categories of saproxylicity in beetles, and many beetle families possess this habit (Crowson 1981; Lawrence 1989). Perhaps most typical of this habit are the families Staphylinidae (especially subfamilies Aleocharinae, Oxyporinae, and Tachyporinae) and Erotylidae. Significant numbers or percentages of Tetratomidae, Tenebrionidae, Zopheridae, Ciidae, Ptiliidae, Anthribidae, Nitidulidae, Endomychidae, Anamorphidae, Latridiidae, Discolomatidae, Endecatomidae, Phloiophilidae, Mycetophagidae, Hobartiidae, Cryptophagidae, Lamingtoniidae, and Leiodidae also occur in this habitat. Gilled mushrooms (Agaricales) and polypore-style basidiomycetes harbor the greatest number of beetles, though significant associations occur in other wood-inhabiting fungi (including Ascomycetes, see Crowson 1984) as well. Certain members of *Derodontus* (Derodontidae) are partial to the "tooth fungi" (Hydnaceae) (Leschen 1994) and members of *Litochropus* (Phalacridae) inhabit and consume the woody galls of *Daldinia* (Ascomycota: Xylariales) (Gimmel 2013). Lawrence (1977) reported on a broad collection of beetles from *Hypoxylon* on dead oak and discussed this habitat in detail. For an excellent summary of mycophagy among Coleoptera, see Lawrence (1989).

Inhabitants of myxomycetes (slime molds), which are most often associated with woody debris, include certain Leiodidae (particularly Leiodinae: Agathidiini) (Newton 1984), certain Carabidae, Staphylinidae, Clambidae, Eucinetidae, Cerylonidae, and Latridiidae (Forrester and McHugh 2010). Perhaps most intimately tied to this habitat are members of the family Sphindidae, whose members are known to feed and develop only in myxomycetes, both as larvae and adults.

### 2.3.5 Other Woody Plant Parts

Other woody or corky plant tissues (cones, galls, woody carps, etc.) are inhabited by a variety of small beetles, including a number of Scolytinae and Ptinidae. Scolytines often found in fallen woody carps include *Araptus* and *Hypothenemus* species; species of *Conophthorus* develop in cones of *Pinus*; one species of *Spermophthorus* has been reported from a gall (Wood 1982). Members of one spondylidine cerambycid genus, *Paratimia*, develop in pine cones (Svacha and Lawrence 2014b). As for Ptinidae, species of *Ernobius* can be found inhabiting cones of conifers (Ruckes 1957), while *Ozognathus* larvae inhabit oak galls (Philips and Bell 2010). Ommatidae are suspected of developing in underground roots, though this has not been confirmed (Hörnschemeyer and Beutel 2016). Root-feeding larvae in woody plants are typical of many Scarabaeidae, Elateridae, Cerambycidae and Curculionidae (Evans 1975), and certain termitophilous beetles are associated with termites whose nests occupy such roots (e.g., *Anorus* of the Dascillidae; Lawrence 2016b).

### 2.3.6 Aquatic Saproxylic Habitats

#### 2.3.6.1 Waterlogged and Submerged Woody Debris

Several families of beetles are typical of wood submerged in lentic or lotic environments, including Amphizoidae (adults and larvae), Lutrochidae (adults and larvae), Cneoglossidae (larvae only), some Elmidae (adults and larvae), some Dryopidae (adults only), some Hydraenidae (adults only), some Psephenidae (larvae only), and some Eulichadidae (larvae only; Ivie 2016). Larvae of certain Lutrochidae and Elmidae may even burrow into submerged wood (Valente-Neto and Fonseca-Gessner 2011). Waterlogged wood may harbor larvae of Oedemeridae and larvae of some Ptilodactylidae (Ptilodactylinae) (Lawrence and Ślipiński 2013: 237). Many larvae of Scirtidae also forage on submerged wood (Lawrence 2016a). Larvae of Oedemeridae may inhabit intermittently buried pieces of driftwood (Kriska 2002); the so-called wharf borer, *Nacerdes melanura* (Linnaeus), even inhabits wood pilings and other structural timber inundated by seawater and has the potential to be a minor pest (Arnett 1951). As indicated by Dudley and Anderson (1982), wood-degrading activity of aquatic beetles is relatively minor, at least in temperate regions.

#### 2.3.6.2 Water Trapped in Tree and Log Holes

These peculiar habitats play host to a few aquatic Coleoptera, primarily including larvae of Scirtidae and adults and larvae of Dytiscidae. A summary of beetles recorded from container habitats (including water in saproxylic environments) was provided by Kitching (2000, Table A.13). Scirtidae larvae are actively moving detritus feeders mostly present among debris in the hole but also crawling inverted just under the water surface (Lawrence 2016a). Dytiscidae are predacious, primarily on other invertebrates, as both adults and larvae, and are active swimmers through the water column. A few genera of this family are present in phytotelmata broadly, including tree and log holes, and the fauna of these habitats is distinctive (Miller and Bergsten 2016); however, most of these are probably not restricted to particular types of phytotelmata. A remarkable southeast Asian species of Nitidulidae, *Amphicrossus japonicus* Reitter, is an aquatic predator of mosquito larvae in injured bamboo culms and stumps that have filled with water. Adults seize mosquito larvae with their front legs (Kovac et al. 2007).

## *2.3.7 Ambrosia Beetles*

### 2.3.7.1 Saproxylic Beetle Agriculture

Three major groups of beetles may be referred to as “ambrosia beetles”: Lymexylidae; Curculionidae, Scolytinae (various tribes); and Curculionidae, Platypodinae. The nature of the ambrosia habit in Lymexylidae is not nearly as developed as in the curculionid lineages, but they were probably the first group to evolve such habits (Wheeler 1986). In this family, it is pouches in the female genitalia that act as mycangia, transporting fungal inoculum to the site of egg laying. The fungus (which belongs to Ascoidaceae), while containing nutrients consumed by the larvae, probably serves to condition the wood for tunneling by the larvae (Wheeler 1986).

Unlike their relatives that create two-dimensional superficial galleries under bark, most ambrosia beetles in Scolytinae and Platypodinae bore directly into wood, across the grain, where the larvae feed not on the wood itself but exclusively on fungi cultivated in the tunnels by the adults. These specialized fungi (primarily Ophiostomales and Microascales) are delivered using mycangia, which are cuticular invaginations on the beetle cuticle that transport fungal inoculum. Three types of mycangia are known in Xyleborini: mandibular, mesothoracic, and elytral (Cognato et al. 2011) (for a discussion of the distribution of mycangia among beetles, see Grebennikov and Leschen 2010). As the fungi grow, they form a dark carpet of conidia that are then fed upon by the larvae (Jordal and Cognato 2012). Not only are the beetles totally dependent on the fungus for food, but they apparently also cannot complete development without the presence of certain fungal steroids (Jordal and Cognato 2012).

About 2000 species of Scolytinae have evolved to use these cultivated fungi as a primary food source, apparently at least ten separate times, represented by the following lineages: Corthylini, Corthylina (460 spp.); Scolytini, *Camptocerus* (30 spp.); Bothrosternini, *Bothrosternus* and *Eupagiocerus* (16 spp.); Xyleborini (1300 spp.); Xyloterini (24 spp.); Scolytoplatypodini (32 spp.); Hyorrhynchini

(15 spp.); Premnobiini (25 spp.); and one species each of *Hypothenemus* (Cryphalini) and *Scolytodes* (Hexacolini) (Jordal and Cognato 2012). Xyleborini are the most widespread and dominant group and comprise about 30 genera and 1300 species that are concentrated in tropical regions but contain a number of temperate species as well (Cognato et al. 2011; Jordal and Cognato 2012). The habit of fungus cultivation among Scolytinae is apparently less than 50 million years old, with Xyleborini developing this trait only about 20 million years ago. This is corroborated by both a dated phylogenetic hypothesis (Jordal and Cognato 2012) and lack of presence of Xyleborini in Dominican amber which, however, does contain inclusions of Corthylina and Platypodinae (Bright and Poinar 1994).

The Platypodinae ("pinhole borers"), the other main beetle group with advanced fungus-cultivating habits, is probably the oldest such group of insects, estimated at around 80 ma or older (Jordal 2015), and presumably the habit evolved only once within the group. All except two of the about 1400 described species are ambrosia beetles, and they occur primarily in tropical areas (Jordal 2015). However, unlike the Xyleborini, all Platypodinae are monogamous and not haplodiploid and do not engage in parthenogenesis. The only known eusocial beetle is the Australian platypodine species *Austroplatypus incompertus* (Schedl) (Kent and Simpson 1992).

Ambrosia beetles have a number of advantages through their specialized habits. The beetles are able to attack a wide variety of tree hosts since their fungi have wide tolerances, a particular advantage in hyper-diverse tropical regions. In addition, the Xyleborini have evolved haplodiploidy, with the flightless dwarf (haploid) males from unfertilized eggs being rarely produced, and matings occurring primarily between siblings. The fact that a colony can be started by a single female allows them to colonize rapidly and efficiently (Cognato et al. 2011). Because they tend to be so widespread and abundant and among the first colonizers of newly created saproxylic habitats, ambrosia beetle populations in wood generally bring with them or otherwise attract a veritable ecosystem of associates, including mutualists, predators, and commensals. Interestingly, ambrosia beetles are much less likely to kill healthy host trees than certain scolytine bark beetle counterparts which spread so-called blue-staining pathogenic fungi (Evans 1975; Crowson 1981; see above), with a few exceptions, such as Fusarium dieback associated with shot-hole borers (*Euwallacea* spp.).

## *2.3.8 Notable Unique Structures, Adaptations, and Mysteries*

### 2.3.8.1 Unique Structures

One extraordinary adaptation of a few saproxylic beetles that deserves mention is the possession of infrared-sensitive pits on the adult cuticle. These structures are located in the thoracic sclerites or abdomen and apparently serve as detectors for beetles seeking to oviposit in fire-killed wood. The structures are known to occur in two phylogenetically distant families: Buprestidae [represented by *Melanophila* (s.str.)

and *Merimna atrata* (Gory and Laporte)] and Acanthocnemidae (containing only *Acanthocnemus nigricans* Hope). In *Melanophila* (s.str.), each of a pair of pits is located on the metaventrite, adjacent to the mesocoxal cavity. Each pit contains a number of spherical sensillae (Evans 1966). In *Merimna atrata*, these organs are similar, but 1–3 pairs occur laterally on abdominal ventrites 2–4 (Mainz et al. 2004). In *Acanthocnemus nigricans*, each of a pair of pits is located along the notosternal suture of the prothorax (anterior to procoxae) and is made up of a flat disc overlying a small airspace. A large number of sensillae are located on the surface of the disc, and the type of infrared receptor is quite different from that of the buprestids (Kreiss et al. 2005).

Larvae of the family Eucnemidae are unique among Coleoptera for several structures: (1) non-opposing mandibles that curve outward rather than inward (also possessed by some Elateridae: Cardiophorinae), (2) microtrichial patches on most body segments, and (3) areoles (median oval shiny structures) on most body segments (Muona and Teräväinen 2008). All of these structures appear to be adaptations for squeezing through hard, often fluid-filled wood. When the mandibular muscles contract, the mandibular apices move away from each other (Van Horn 1909). The microtrichial patches serve as cuticular anchors as the legless larva creeps forward using waves of internal fluid pressure, while the areoles apparently drain excess water from the larva (Muona and Teräväinen 2008).

As a group, beetles are well-known for their tendency to evolve elaborate weaponry as adults, usually horns or other cuticular projections, especially among males. Interestingly, this occurs primarily in saproxylic taxa, especially those specializing on well-decayed wood, sap flows, or wood-decaying fungi, though it also occurs in taxa associated with other habitats (e.g., dung). Saproxylic taxa possessing this trait include Scarabaeidae (several subfamilies), Lucanidae, Staphylinidae (Piestinae), Ptinidae, Ciidae, and Tenebrionidae. One explanation for this phenomenon is that habitats that are highly localized and defendable (e.g., those listed above), in combination with unrestricted terrain for fighting, such as the surface of a log or tree trunk, provide selection pressure to evolve fight-performance-related structures (see Emlen (2008) for an extensive discussion).

#### 2.3.8.2 Parasitoids

There are not many parasitoids among beetles, but two saproxylic families are exclusively ectoparasitoid as larvae, Bothrideridae and Passandridae, the former being parasitic on larvae and pupae of wood-boring beetles, as well as Hymenoptera, Xiphydriidae and Apidae (*Xylocopa*). Passandridae are also parasites of various wood-boring beetles (especially Phytophaga) and larval Hymenoptera. The most advanced forms, however, are represented by the endoparasitoid larvae of Ripiphoridae, of which members of two of the five subfamilies (Hemirhipidiinae and Pelecotominae) are known to attack wood-boring beetle larvae, particularly of the families Ptinidae and Cerambycidae (Lawrence et al. 2010b).

As pointed out by Crowson (1981: 555), the dividing line between predators and parasitoids is a blurry one, particularly in saproxylic forms. Brentidae and Zopheridae contain some species inhabiting brood burrows of Scolytinae; Cleridae (e.g., *Orthopleura*) contain more-or-less parasitic forms on wood-boring beetle larvae (Crowson 1981: 555). Intermediate forms between predators and parasitoids exist among members of the zopherid genus *Colydium*, which are often present with *Platypus*, and *Aulonium* which is associated with *Scolytus* (Crowson 1981: 556). Adults of *Lasconotus* (Zopheridae) often have a concave dorsal surface, presumably to assist in squeezing past obstacles among the burrows of Scolytinae (MLG, pers. obs.).

#### 2.3.8.3 Sociality

Eusociality and even subsociality are quite rare among beetles, but it is notable that these traits are only known to occur in saproxylic species. The most widespread and well-known among these taxa are within the Passalidae (Ulyshen 2018, see Chap. 3). Less well-known subsocial species are the passalid-looking members of the genus *Phrenapates* (Tenebrionidae: Phrenapatinae) (Lawrence and Ślipiński 2013). As mentioned previously, the only known eusocial beetle is *Austroplatypus incompertus* (Schedl) (Curculionidae: Platypodinae), which lives in galleries in the heartwood of *Eucalyptus* trees in southeastern Australia (Kent and Simpson 1992).

#### 2.3.8.4 A Mystery

The family Trictenotomidae contains some of the largest adult beetles in the world, which are among the most popular collectors' items in Coleoptera. There are two genera (*Autocrates* and *Trictenotoma*) that occur in southern and eastern Asia. However, the presumed saproxylic larva has apparently only been found once, in Java in association with "débris of pupae and imagines" of *Trictenotoma childreni* Gray. This remarkable larva measured 12 cm long (Gahan 1908). Unfortunately the whereabouts of this specimen are currently unknown, and additional collecting efforts have so far not been fruitful (M. Barclay, pers. com.). For further notes on the life history of Trictenotomidae, see Pollock and Telnov (2010).

## 2.4 Overview of Saproxylic Beetles (Table 2.1)

While a few families of saproxylic beetles are dominant on the research radar of most dead wood entomologists, one of the primary purposes of this chapter, Table 2.1 in particular, is to highlight some lesser-known but biologically or numerically significant groups. Well-known groups with large numbers of well-studied species include Carabidae, Scarabaeoidea, Buprestidae, Elateridae, Bostrichidae, Cleridae,

**Table 2.1** Annotated checklist of all world beetle families and subfamilies [modified from Beutel and Leschen (2016a)], with saproxylic groups indicated

| # | Taxon | Sap[a] | #Spp[b] | % S[c] | Regions[d] | Adult found[e] | A food[f] | Larva found[e] | L food[f] | Notes |
|---|---|---|---|---|---|---|---|---|---|---|
| | **Suborder Archostemata (4)** | | | | | | | | | All known L assoc with fungus-infected wood |
| 1 | **Ommatidae** | X | 6 | Most | Aus, SAm | Away | Unk | In WD | Sapro | Habits very poorly known, but apparently saproxylic |
| | Tetraphalerinae | X | 2 | Most | SAm | Away | Unk | In WD | Sapro | May live on roots or stems of shrubs; L unk (Hörnschemeyer and Beutel 2016) |
| | Ommatinae | X | 4 | Most | Aus | Away | Unk | In WD | Sapro | L assoc with dead wood or tree roots; only one presumed L known (Hörnschemeyer and Beutel 2016) |
| 2 | **Crowsoniellidae** | | | | | | | | | L and habits unk |
| 3 | **Micromalthidae** | X | 1 | All | NW, adv WW | In WD | Sapro | In WD | Sapro | Entire life cycle takes place in red rotten wood (Pollock and Normark 2002) |
| 4 | **Cupedidae** | X | 31 | All | WW exc Eur | In WD; away | Poll | In WD | Sapro | Subcortical; all known L feed on fungus-infected wood; pupation takes place in wood (Snyder 1956; Neboiss 1968) |
| | Priacminae | X | 3 | All | NW | In WD; away | Unk | In WD | Sapro | L habits unstudied, certainly saproxylic |
| | Cupedinae | X | 28 | All | WW exc Eur | In WD; away | Poll | In WD | Sapro | Subcortical; all known L feed on fungus-infected wood; pupation takes place in wood (Snyder 1956; Neboiss 1968) |
| | **Suborder Myxophaga (4)** | | | | | | | | | |

(continued)

**Table 2.1** (continued)

| # | Taxon | Sap[a] | #Spp[b] | % S[c] | Regions[d] | Adult found[e] | A food[f] | Larva found[e] | L food[f] | Notes |
|---|---|---|---|---|---|---|---|---|---|---|
| 5 | **Lepiceridae** | | | | | | | | | Aquatic, grazers |
| 6 | **Torridincolidae** | | | | | | | | | Aquatic, algae grazers |
| 7 | **Hydroscaphidae** | | | | | | | | | Aquatic, algae grazers |
| 8 | **Sphaeriusidae** | | | | | | | | | Aquatic, algae grazers |
| | **Suborder Adephaga (10)** | | | | | | | | | |
| 9 | **Gyrinidae** | | | | | | | | | Aquatic, pred |
| | *Non-saproxylic subfamilies*: Gyrininae, Heterogyrinae, Spanglerogyrinae | | | | | | | | | |
| 10 | **Haliplidae** | | | | | | | | | Aquatic omnivores |
| 11 | **Trachypachidae** | | | | | | | | | Ground dwelling, probably pred |
| 12 | **Meruidae** | | | | | | | | | Aquatic in rock seepages |
| 13 | **Noteridae** | | | | | | | | | Aquatic omnivores |
| | *Non-saproxylic subfamilies*: Noterinae, Notomicrinae | | | | | | | | | |
| 14 | **Amphizoidae** | X | 5 | Most | Hol | On WD | Pred | On WD | Pred | A and L cling to aquatic woody debris (Dettner 2016; MLG, pers. obs.) |
| 15 | **Aspidytidae** | | | | | | | | | Aquatic, pred |
| 16 | **Hygrobiidae** | | | | | | | | | Aquatic, pred |
| 17 | **Dytiscidae** | X | 4300 | Few | WW | Water-filled tree holes | Sapro, pred | Water-filled tree holes | Sapro, pred | A few spp. occur in water-filled tree holes |
| | Laccophilinae | X | 200 | Few | WW | Water-filled tree holes | Pred | Water-filled tree holes | Pred | Data from Miller and Bergsten (2016) |

| | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | Copelatinae | X | 700 | Few | WW | Water-filled tree holes | Pred | Water-filled tree holes | Pred | Data from Miller and Bergsten (2016) |
| | Hydroporinae | X | 2200 | Few | WW | Water-filled tree holes | Pred | Water-filled tree holes | Pred | Data from Miller and Bergsten (2016) |
| | *Non-saproxylic subfamilies*: Agabinae, Colymbetinae, Coptotominae, Dytiscinae, Hydrodytinae, Lancetinae, Matinae | | | | | | | | | |
| 18 | **Carabidae** | X | 40,000 | Few | WW | In WD | Pred | In WD | Pred | Subcortical, many spp. may seek shelter under bark, few are consistently there |
| | Paussinae | X | 750 | Some | WW | In WD | Pred | In WD | Pred | L and A found under bark, in rotting wood, or on trees at night (Moore 2008); L may construct galleries in wood (Moore and Di Giulio 2006) |
| | Cicindelinae | X | 2000 | Few | WW | Away | Pred | In WD | Pred | Rarely L in rotten wood (Arndt et al. 2016); L of some found in tunnels in bark (Zikan 1929; Balduf 1935; Trautner and Schawaller 1996; Pearson and Vogler 2001) |
| | Carabinae | X | 1300 | Few | WW | In WD | Pred | Away | Pred | A of especially *Scaphinotus* can be found under bark or in rotten wood or tree hollows or under driftwood (Erwin 2007) |
| | Rhysodinae | X | 170 | All | WW | In WD | Myxo, myco | In WD | Myxo, myco | Subcortical; A and L found in logs, stumps, or roots, probably feed on slime molds (Beutel 2016) |
| | Psydrinae | X | 6 | Some | Nea, Aus, Africa, w Pal | In WD | Pred | Unk | Unk | *Psydrus piceus* found under bark of large coniferous trees (Bousquet 2012) |

(continued)

**Table 2.1** (continued)

| # | Taxon | Sap[a] | #Spp[b] | % S[c] | Regions[d] | Adult found[e] | A food[f] | Larva found[e] | L food[f] | Notes |
|---|---|---|---|---|---|---|---|---|---|---|
| | Siagoninae | X | 100 | Most | Africa, Pal, SAm | In WD | Pred | ? | Unk | Subcortical, esp *Cymbionotum*, *Siagona*, *Enceladus* |
| | Trechinae | X | 4000 | Few | WW | In WD | Pred | ? | Unk | Subcortical, esp certain Tachyina (*Tachys* and relatives) |
| | Pseudomorphinae | X | 500 | Most | Aus, Or | In WD | Pred | In ant or termite nests in soil or canopy | Unk | A subcortical (Arndt et al. 2016) |
| | Harpalinae | X | 20,000 | Some | WW | In WD | Pred | In WD | | A subcortical, esp Morionini, Platynini, and many Pterostichini (MLG, pers. obs.) |
| | *Non-saproxylic subfamilies*: Apotominae, Brachininae, Broscinae, Cicindinae, Clivininae, Elaphrinae, Gehringiinae, Hiletinae, Loricerinae, Melaeninae, Migadopinae, Moriomorphinae, Nebriinae, Nototylinae, Omophroninae, Promecognathinae, Scaritinae | | | | | | | | | |
| | **Suborder Polyphaga** | | | | | | | | | |
| | **?Series ?Superfamily (1)** | | | | | | | | | |
| 19 | **Jurodidae** | | | | | | | | | L and habits unk |
| | **Series Scirtiformia** | | | | | | | | | |
| | **Superfamily Scirtoidea (4)** | | | | | | | | | |
| 20 | **Decliniidae** | | | | | | | | | A apparently poll, L unk |
| 21 | **Eucinetidae** | X | 40 | All | WW | In WD | Myxo, myco | In WD | Myxo, myco | A and L in rotting wood; at least some myxo and myco (Leschen 2016a) |
| 22 | **Clambidae** | X | 150 | Some | WW | In WD | Myco, myxo | In, on WD | Myco, myxo | A and L fungus feeding in various habitats (Leschen 2016b) |

| | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | Calyptomerinae | X | 4 | All | Hol (adv Aus, Afr) | On WD | Myco | In, on WD | Myco | A of *Calyptomerus* found on dead/dying spruce in New Mexico (Hinson and Buss 2014) |
| | Acalyptomerinae | X | 4 | Some | Neo, Afr, Or | In, on WD | Myco | In, on WD | Myco | A collected from rotten palm litter, under log, and from *Auricularia* mushrooms (Endrödy-Younga 1998) |
| | Clambinae | X | 130 | Some | WW | On WD | Myco, myxo | In, on WD | Myco, myxo | A of *Sphaerothorax* found on tree stumps, in heap of *Eucalyptus* branches, in cut bamboo (Klimaszewski and Watt 1997) |
| 23 | **Scirtidae** | X | 800 | few | WW | Away | Pred, non | Water-filled tree holes | Sapro | Some L in tree and log holes (Kitching 2000), pupation of some in upper dryer parts of tree holes; L of other aquatic spp. forage on submerged wood (Lawrence 2016a) |
| | Scirtinae | X | 800 | few | WW | Away | Pred, non | Water-filled tree holes | Sapro | Some L in tree and log holes, pupation of some in upper dryer parts of tree holes; L of other aquatic spp. forage on submerged wood (Lawrence 2016a); other L terrestrial in wood (Ruta et al. 2017) |
| | *Non-saproxylic subfamilies*: Nipponocyphoninae, Stenocyphoninae | | | | | | | | | |
| | **Series Derodontiformia** | | | | | | | | | |
| | **Superfamily Derodontoidea (1)** | | | | | | | | | |
| 24 | **Derodontidae** | X | 37 | Some | Hol, STem | On fungi, sap flows | Myco | On fungi, sap flows | Myco | A few spp. assoc with woody debris |

(continued)

**Table 2.1** (continued)

| # | Taxon | Sap[a] | #Spp[b] | % S[c] | Regions[d] | Adult found[e] | A food[f] | Larva found[e] | L food[f] | Notes |
|---|---|---|---|---|---|---|---|---|---|---|
| | Peltasticinae | X | 2 | All | Hol | At sap flows | Myco | At sap flows | Myco | *Peltastica* A and L feed on fungi and suspended nutrients in ferm sap (Leschen and Beutel 2010a) |
| | Derodontinae | X | 14 | Some | Hol, STem | On fungi | Myco | On fungi | Myco | Some *Derodontus* A and L on wood-dec fungi (Leschen 1994; Leschen and Beutel 2010a) |
| | *Non-saproxylic subfamily*: Laricobiinae (pred on Adelgidae or on sooty molds on living trees) | | | | | | | | | |
| | **?Series ?Superfamily (1)** | | | | | | | | | |
| 25 | **Jacobsoniidae** | X | 20 | Most | WW | In WD | Sapro | in WD | Sapro | *Saphophagus* subcortical (Lawrence and Leschen 2010a; MLG, pers. obs.), other gen may be found in rotten wood (Lawrence and Leschen 2010a) |
| | **Series Staphyliniformia** | | | | | | | | | |
| | **Superfamily Hydrophiloidea (9)** | | | | | | | | | |
| 26 | **Helophoridae** | | | | | | | | | Aquatic omnivores |
| 27 | **Epimetopidae** | | | | | | | | | Aquatic omnivores |
| 28 | **Georissidae** | | | | | | | | | Aquatic omnivores |
| 29 | **Hydrochidae** | | | | | | | | | Aquatic omnivores |
| 30 | **Spercheidae** | | | | | | | | | Aquatic omnivores |
| 31 | **Hydrophilidae** | X | 2932 | Few | WW | In WD | Sapro | In WD | Sapro | Most spp. aquatic; terrestrial forms assoc with rotting material; in tree holes in southern Aus (Kitching 2000) |

| | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | Cylominae | X | 48 | Few | Aus, Neo, Afr | In WD | Sapro | In WD | Sapro | Some spp. occur in dec logs (M. Fikáček, pers. com.; MLG, pers. obs.) |
| | Sphaeridiinae | X | 950 | Few | WW | In WD | Sapro | In WD | Sapro | Smetana (1978) recorded *Cercyon assecla* Smetana, *Cryptopleurum subtile* Sharp, and *Cryptopleurum minutum* (Fabricius) from “fresh wood-cuttings soaked with sap”; Costa et al. (1988) recorded *Dactylosternum subrotundatum* (Fabricius) from well-rotted and wet fallen logs; some *Cercyon* assoc with beach driftwood |
| | *Non-saproxylic subfamilies*: Acidocerinae, Chaetarthriinae, Enochrinae, Hydrophilinae | | | | | | | | | |
| 32 | **Sphaeritidae** | X | 5 | Few | Hol | On WD | Pred | On WD | Pred | A and L from sap flows of dying/dead trees and stumps (Newton 2016a) |
| 33 | **Synteliidae** | X | 9 | Most | E Asia, CAm | In WD | Pred | In WD | Pred | Subcortical in dec logs, some at sap flows, others in moist interior of dec columnar cacti; pred on diptera; pupate under bark (Newton 2016b) |
| 34 | **Histeridae** | X | 3900 | Some | WW | In WD | Pred | In WD | Pred | Subcortical, some in tree holes or wood boring beetle tunnels, fungal spore feeders in older dead trees and rotting wood, or assoc with bracket and polypore fungi |
| | Niponiinae | X | 21 | All | Pal, Or | In WD | Pred | In WD | Pred | In wood-boring beetle tunnels (Kovarik and Caterino 2016) |
| | Chlamydopsinae | X | 180 | Few | Or, Aus | In WD | Pred | ? | Unk | One sp. known from termite nest in Aus (Kovarik and Caterino 2016) |
| | Onthophilinae | X | 80 | Some | WW | In WD | Pred, myco | In WD | Pred | One *Onthophilus* known from ferm sap, *Epiechinus* myco in rotten wood (Kovarik and Caterino 2016) |

(continued)

**Table 2.1** (continued)

| # | Taxon | Sap[a] | #Spp[b] | % S[c] | Regions[d] | Adult found[e] | A food[f] | Larva found[e] | L food[f] | Notes |
|---|---|---|---|---|---|---|---|---|---|---|
| | Dendrophilinae | X | 460 | Some | WW | In WD | Pred, myco | In WD | Pred | Many under bark of fresh wood (esp. Paromalini), a few in tree holes (*Bacanius*, *Dendrophilus*), some in bark beetle galleries (*Paromalus*), in rotten wood (*Bacanius*, *Cyclobacanius*) (Kovarik and Caterino 2016) |
| | Abraeinae | X | 440 | Most | WW | In WD | Pred, myco | In WD | Pred | Some in tree holes (*Abraeus*, *Chaetabraeus*), some in bark beetle tunnels (Plegaderini, Teretriini), some in rotten wood (*Aeletes*, *Acritus*) (Kovarik and Caterino 2016) |
| | Trypeticinae | X | 110 | All | Afr, Or, Aus | In WD | Pred | In WD | Pred | Many in bark beetle tunnels, one *Pygocoelis* in rotten wood (Kovarik and Caterino 2016) |
| | Trypanaeinae | X | 75 | All | Neo | In WD | Pred | In WD | Pred | In wood-boring beetle tunnels (Kovarik and Caterino 2016) |
| | Saprininae | X | 620 | Few | WW | In WD | Pred | In WD | Pred | *Gnathoncus* in tree holes, some coastal *Hypocaccus* under driftwood (Kovarik and Caterino 2016) |
| | Tribalinae | X | 215 | Few | WW | In WD | Pred, myco | In WD | Pred | *Epierus* in wood-boring beetle tunnels and in rotten wood, *Tribalus* and *Parepierus* in rotten wood (Kovarik and Caterino 2016) |
| | Histerinae | X | 1950 | Some | WW | In WD | Pred, myco | In WD | Pred | Many under bark of fresh wood (esp. Hololeptini), some in tree holes, some at sap fluxes, some in bark beetle tunnels, some in rotten wood (Kovarik and Caterino 2016) |

| | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | Haeteriinae | X | 330 | Few | WW | In WD | Pred | In WD | Pred | Some assoc with wood-inhabiting ants and termites (Kovarik and Caterino 2016) |
| | **Superfamily Staphylinoidea (6)** | | | | | | | | | |
| 35 | **Hydraenidae** | X | 1300 | Few | WW | On WD | Sapro? | Away | Unk | Aquatic A of *Hydraena vandykei* saproxylic (Dudley and Anderson 1982) |
| | Hydraeninae | X | 1000 | Few | WW | On WD | Sapro? | Away | Unk | Aquatic A of *Hydraena vandykei* saproxylic (Dudley and Anderson 1982) |
| | *Non-saproxylic subfamilies*: Ochthebiinae, Orchymontiinae, Prosthetopinae | | | | | | | | | |
| 36 | **Ptiliidae** | X | 600 | Some | WW | In WD | Myco | In WD | Myco | Some A in rotten wood, polypore fungi (Hall 2016) |
| | Ptiliinae | X | 400 | Some | WW | In WD | Myco | In WD | Myco | Tree-related niches, tree holes, rotting logs, etc., also wood-related habitats near social insects |
| | Nanosellinae | X | 100 | Most | WW | In fungi | Myco | In fungi | Myco | Usu assoc with polypore fungi (Newton 1984) |
| | *Non-saproxylic subfamilies*: Acrotrichinae (primarily leaf litter, ant refuse piles), Cephaloplectinae (myrmecophiles) | | | | | | | | | |
| 37 | **Agyrtidae** | X | 61 | Some | WW exc Aus, Afr | In WD | Myco, sapro | In WD | Myco, sapro | Several spp. assoc with woody debris (Newton 2016c) |
| | Agyrtinae | X | 25 | Some | Hol, Or | In WD | Myco, sapro | In WD | Myco, sapro | *Ipelates latus* A assoc with dec logs and fungi (Newton 2016c) |
| | *Non-saproxylic subfamilies*: Necrophilinae, Pterolomatinae | | | | | | | | | |
| 38 | **Leiodidae** | X | 3460 | Some | WW | In WD | Myco, sapro, myxo | In WD | Myco, sapro, myxo | Maj sapro and myco inhabitants of the forest floor including dead logs |
| | Camiarinae | X | 90 | Some | STem | On WD | Myxo, myco | On WD | Myxo, myco | *Neopelatops* is myxo (Lawrence and Ślipiński 2013) |

(continued)

**Table 2.1** (continued)

| # | Taxon | Sap[a] | #Spp[b] | % S[c] | Regions[d] | Adult found[e] | A food[f] | Larva found[e] | L food[f] | Notes |
|---|---|---|---|---|---|---|---|---|---|---|
| | Catopocerinae | X | 50 | Some | Hol, STem | In WD | Myco | In WD | Myco | Present in highly decomposed wood (Ferro et al. 2012a) |
| | Leiodinae | X | 1780 | Some | WW | On WD | Myco, myxo, Sapro | In, on WD | Myco, myxo, Sapro | Some are myxo, others are assoc with gilled, fleshy [wood-rotting] fungi (Peck and Newton 2017) |
| | Cholevinae | X | 2040 | Few | WW | In WD | Sapro | In WD | Sapro | Generally assoc with dec matter, some members found in rotten wood (Ferro et al. 2012a) |
| | *Non-saproxylic subfamilies*: Coloninae (saprophages and mold feeders), Platypsyllinae (assoc with mammal nests and fur) | | | | | | | | | |
| 39 | **Silphidae** | | | | | | | | | Carrion; sometimes incidental on rotten wood-rotting fungal fruiting bodies (Newton 1984) |
| | *Non-saproxylic subfamilies*: Nicrophorinae, Silphinae | | | | | | | | | |
| 40 | **Staphylinidae** | X | 62,000 | Some | WW | In, on WD; away | Myco, sapro, pred | In, on WD | Myco, sapro, pred | Enormous diversity of habits and habitats, even within individual subfamilies (Thayer 2016) |
| | Glypholomatinae | X | 8 | Some | STem | In WD | Myco, sapro | In WD | Myco | Assoc with "logs" (Thayer 2016) |
| | Microsilphinae | X | 4 | Some | STem | In, on WD | Myco | Unk | Myco? | Assoc with "logs"; L poorly known (Thayer 2016) |
| | Omaliinae | X | 1400 | Some | WW | In, on WD; away | Myco, sapro, Pred | In WD | Myco | Assoc with "logs," fungi, and fermenting plant material (Thayer 2016); several genera reported as subcortical (Newton et al. 2000) |
| | Empelinae | X | 1 | All | Nea | On WD | Myco | Unk | Unk | A on gilled fungi on aged cedar (MLF, pers. obs.) |

| | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | Proteininae | X | 190 | Some | WW | On WD | Myco, sapro, Pred | In WD | Myco, sapro | Assoc with "logs," fungi, and fermenting plant material (Thayer 2016); some under bark, in rotten wood (Newton et al. 2000) |
| | Micropeplinae | X | 80 | Some | Hol, Neo, Afr, Or | In, on WD | Myco | In, on WD | Myco | Assoc with "logs" (Thayer 2016) |
| | Dasycerinae | X | 17 | Most | Hol, Or | In, on WD | Myco | Away | Myco | Assoc with fungi or dec wood; L in litter (Wheeler 1984) |
| | Pselaphinae | X | 10,000 | Some | WW | In, on WD | Pred | In WD | Pred | Assoc with "logs" (Thayer 2016); maj of gen in leaf litter but many reported from rotten wood, tree holes or under bark (Newton et al. 2000) |
| | Phloeocharinae | X | 5 | Some | Hol, Neo, STem | In WD | Pred | In WD | Pred | Assoc with "logs" (Thayer 2016); A and L of *Charhyphus* found together under bark (Newton et al. 2000) |
| | Olisthaerinae | X | 2 | All | Hol | In WD | Pred | In WD | Pred | Assoc with "logs" (Thayer 2016); under bark of dead conifers (Newton et al. 2000) |
| | Tachyporinae | X | 1520 | Some | WW | In, on WD | Myco, sapro, pred | In WD | Myco | Assoc with "logs" (Thayer 2016); a few gen under bark of dead trees, in wood-rotting fungal fruiting bodies, wood debris (Newton et al. 2000) |
| | Trichophyinae | X | 16 | Few | Hol, Neo, Or | ? | Myco, pred | ? | Myco | Assoc with "logs" (Thayer 2016); A and L only reported from forest litter in Ashe and Newton (1993) |

(continued)

**Table 2.1** (continued)

| # | Taxon | Sap[a] | #Spp[b] | % S[c] | Regions[d] | Adult found[e] | A food[f] | Larva found[e] | L food[f] | Notes |
|---|---|---|---|---|---|---|---|---|---|---|
| | Habrocerinae | X | 22 | Some | WW | In WD | Myco, sapro, pred | In WD | Myco, sapro | Assoc with "logs" (Thayer 2016); in litter, wood debris and fungi (Newton et al. 2000) |
| | Aleocharinae | X | 13,000 | Some | WW | In, on WD | Myco, sapro, pred | In WD | Myco, sapro, pred | Assoc with "logs" (Thayer 2016); many gen under bark, a few assoc with termites, fallen logs or wood-dec fungal fruiting bodies (Newton et al. 2000) |
| | Trigonurinae | X | 10 | All | Hol, Or | In WD | Sapro | In WD | Sapro | Assoc with "logs" (Thayer 2016); A and L under bark, especially of conifer logs (Newton et al. 2000) |
| | Apateticinae | X | 25 | Some | Pal, Or | ? | Sapro | ? | Sapro | Assoc with "logs" (Thayer 2016) |
| | Scaphidiinae | X | 1450 | Most | WW | In, on WD | Myco, sapro, Myxo | In, on WD | Myco, sapro, myxo | Assoc with "logs" (Thayer 2016); *Baeocera* myxo, other genera on logs with polypores or other mushrooms (Newton et al. 2000) |
| | Piestinae | X | 110 | Most | Hol, Neo, STem | In WD | Myco, sapro | In WD | Myco, sapro | Assoc with "logs" (Thayer 2016); maj under bark of dec trees (Newton et al. 2000) |
| | Osoriinae | X | 2100 | Most | WW | In WD | Myco, sapro, pred | In WD | Myco, sapro, pred | Assoc with "logs" (Thayer 2016); maj under bark or in rotting wood, others in soil (Newton et al. 2000) |
| | Oxytelinae | X | 2000 | Few | WW | In WD | Myco, sapro, pred | In WD | Myco, sapro, pred | Assoc with "logs," fungi, and fermenting plant material (Thayer 2016); maj assoc with wet rotting material and riparian areas, but a few, e.g., *Syntomium*, assoc with rotting logs (Newton et al. 2000) |

| | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | Oxyporinae | X | 122 | Most | Hol, Neo, Or | On WD | Myco | On WD | Myco | Obligate associates of fleshy mush-rooms as A and L, most of which are produced by wood-rotting fungi (Hanley and Goodrich 1995) |
| | Megalopsidiinae | X | 165 | Most | WW | In, on WD | Pred | In, on WD | Pred? | Assoc with "logs" (Thayer 2016); usu found in association with dec trees and fungusy logs, biology, and L poorly known (Newton et al. 2000) |
| | Scydmaeninae | X | 4600 | Some | WW | In WD | Pred | In WD | Pred | Some assoc with rotting wood (Jałoszyński 2016) |
| | Steninae | X | 2250 | Few | WW | In, on WD | Pred | In, on WD | Pred | Assoc with "logs" (Thayer 2016); may be found on or in forest debris (Newton et al. 2000) |
| | Euaesthetinae | X | 760 | Few | WW | In WD | Pred | In WD | Pred | Assoc with "logs" (Thayer 2016); maj assoc with forest leaf litter (Newton et al. 2000) |
| | Pseudopsinae | X | 55 | Few | WW exc Aus, Afr | In WD | Pred | In WD | Pred? | Assoc with "logs," fungi, and fermenting plant material (Thayer 2016); maj in litter or riparian, a few *Pseudopsis* in fungi (Newton et al. 2000) |
| | Paederinae | X | 6100 | Some | WW | In, on WD | Pred | In, on WD | Pred | Assoc with "logs," fungi, and fermenting plant material (Thayer 2016); many in forest litter, some on fungus or under bark (Newton et al. 2000) |
| | Staphylininae | X | 6900 | Some | WW | In, on WD | Pred | In, on WD | Pred | Assoc with "logs," fungi, and fermenting plant material (Thayer 2016); many in dec matter, some under bark, in log litter, tree holes or on fungi (Newton et al. 2000) |

(continued)

**Table 2.1** (continued)

| # | Taxon | Sap[a] | #Spp[b] | % S[c] | Regions[d] | Adult found[e] | A food[f] | Larva found[e] | L food[f] | Notes |
|---|---|---|---|---|---|---|---|---|---|---|
| | *Non-saproxylic subfamilies*: Neophoninae (L poorly known), Protopselaphinae (habits poorly known, L unk), Solieriinae (habits and L unk), Leptotyphlinae (deep soil and leaf litter inhabitants) | | | | | | | | | |
| | **Series Scarabaeiformia** | | | | | | | | | |
| | **Superfamily Scarabaeoidea (12)** | | | | | | | | | The ancestor of this superfamily was probably assoc with dead wood (Beutel and Leschen 2016a) |
| 41 | **Pleocomidae** | | | | | | | | | L are root feeders |
| 42 | **Geotrupidae** | | | | | | | | | L eat dung, humus, fungi |
| | *Non-saproxylic subfamilies*: Bolboceratinae, Geotrupinae, Taurocerastinae | | | | | | | | | |
| 43 | **Belohinidae** | | | | | | | | | L and habits unk |
| 44 | **Passalidae** | X | 680 | All | WW | In WD | Sapro | In WD | Sapro | A and L spend entire life cycle in dead wood (Scholtz and Grebennikov 2016) |
| | Aulacocyclinae | X | ? | All | Or, Aus | In WD | Sapro | In WD | Sapro | Ulyshen (2018) |
| | Passalinae | X | ? | All | WW | In WD | Sapro | In WD | Sapro | Ulyshen (2018) |
| 45 | **Trogidae** | | | | | | | | | A and L feed on carrion |
| 46 | **Glaresidae** | | | | | | | | | Habits and L unk |
| 47 | **Diphyllostomatidae** | | | | | | | | | Habits and L unk |
| 48 | **Lucanidae** | X | 1250 | All | WW | On WD; away | Phyto, non | In WD | Sapro | Most L develop in CWD, A feed at sap flows and flowers (Scholtz and Grebennikov 2016) |
| | Aesalinae | X | ? | All | Hol, Neo, Or | On WD; away | Phyto, non | In WD | Sapro | See Huang (2018) |

| | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | Nicaginae | X | ? | All | Hol | On WD; away | Phyto, non | In WD | Sapro | See Huang (2018) |
| | Ceratognathinae | X | ? | All | Neo, Or, Aus | On WD; away | Phyto, non | In WD | Sapro | See Huang (2018) |
| | Syndesinae | X | ? | All | WW exc Afr | On WD; away | Phyto, non | In WD | Sapro | See Huang (2018) |
| | Lampriminae | X | ? | All | Neo, Aus | On WD; away | Phyto, non | In WD | Sapro | See Huang (2018) |
| | Lucaninae | X | ? | Most | WW | On WD; away | Phyto, non | In WD | Sapro | All except South African genus *Colophron* develop in dead wood (Scholtz and Grebennikov 2016) |
| 49 | **Ochodaeidae** | | | | | | | | | Poorly known; possibly underground fungus feeders |
| | *Non-saproxylic subfamilies*: Chaetocanthinae, Ochodaeinae | | | | | | | | | |
| 50 | **Hybosoridae** | X | 600 | Some | WW | In, on WD; away | Sapro, pred, Myco | In WD | Sapro, myco, Pred | A and L feed on carrion and decomposing plant material, some may be predatory |
| | Ceratocanthinae | X | 366 | Most | WW exc Eur | In, on WD | Myco | In WD | Myco | A and L found in rotten wood, adult mouthparts indicate fungal feeding (Scholtz and Grebennikov 2016) |
| | *Non-saproxylic subfamilies*: Anaidinae, Dynamopodinae (habits and L unk), Hybosorinae, Liparochrinae, Pachyplectrinae | | | | | | | | | |
| 51 | **Glaphyridae** | | | | | | | | | L feed on detritus, A visit flowers |
| 52 | **Scarabaeidae** | X | 27,000 | Some | WW | In WD, away | Sapro, phyto, poll, nec | In WD | Sapro | Extremely diverse habits |

(continued)

**Table 2.1** (continued)

| # | Taxon | Sap[a] | #Spp[b] | % S[c] | Regions[d] | Adult found[e] | A food[f] | Larva found[e] | L food[f] | Notes |
|---|---|---|---|---|---|---|---|---|---|---|
| | Aphodiinae | X | 3300 | Few | WW | In WD | Sapro | ? | Sapro? | Aulonocnemini under bark (Lawrence et al. 1999a) |
| | Orphninae | X | 200 | Few | WW exc Aus, Nea | Away | Sapro | In WD | Sapro | L of *Aegidium cribratum* under rotting logs (Scholtz and Grebennikov 2016) |
| | Dynastinae | X | 1500 | Some | WW | Away | Phyto | In WD | Sapro | Some L are borers (Scholtz and Grebennikov 2016) |
| | Cetoniinae | X | 3270 | Few | WW | Away | Poll, nec | In WD | Sapro | Valgini L develop in rotting wood (Scholtz and Grebennikov 2016) |
| | Euchirinae | X | 12 | All | Asia | Away | Phyto | In WD | Sapro | L in rotten wood (Scholtz and Grebennikov 2016) |
| | *Non-saproxylic subfamilies*: Aclopinae (habits and L unk), Allidiostomatinae (habits and L unk), Phaenomeridinae (habits and L unk), Melolonthinae (A and L phytophagous), Rutelinae (A and L phytophagous), Scarabaeinae (dung beetles) | | | | | | | | | |
| | **?Series ?Superfamily (1)** | | | | | | | | | |
| 53 | **Nosodendridae** | X | 50 | All | WW | On WD | Sapro, myco | On WD | Sapro, myco | A and L at slime flux from tree wounds (Leschen and Beutel 2010b) |
| | **Series Elateriformia** | | | | | | | | | |
| | **Superfamily Dascilloidea (2)** | | | | | | | | | |
| 54 | **Dascillidae** | X | 80 | Few | NHem | In WD | Unk | In WD | Unk | Root-feeding, some may be assoc with termites (Lawrence 2016b) |
| | Karumiinae | X | 20 | Some | WW | In WD | Unk | ? | Unk | Flightless female *Anorus* was found in a dead root of *Acacia greggii* in AZ (Lawrence 2016b) |

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|---|---|---|---|---|---|---|---|---|---|---|
| | *Non-saproxylic subfamily*: Dascillinae | | | | | | | | | |
| 55 | **Rhipiceridae** | | | | | | | | | L are parasites of Cicadidae |
| | **Superfamily Buprestoidea (2)** | | | | | | | | | |
| 56 | **Schizopodidae** | | | | | | | | | External root feeders |
| 57 | **Buprestidae** | X | 14,600 | Most | WW | Away | Phyto, poll, nec | In WD | Sapro | Maj of L are wood-borers, feeding on inner bark and outer wood of roots, trunks, and branches (Lawrence 1991) |
| | Polycestinae | X | 1250 | Most | WW | Away | Poll, nec | In WD | Sapro | Many wood borers |
| | Galbellinae | X | 85 | All | Afr, Or, Pal | Away | Unk | In WD | Sapro | L in twigs and wood of *Acacia* and *Phillyrea* (Volkovitsh and Bílý 2001) |
| | Chrysochroinae | X | 2700 | Most | WW | Away | Phyto, poll, nec | In WD | Sapro | Many wood borers |
| | Buprestinae | X | 3300 | Most | WW | Away | Phyto, poll, nec | In WD | Sapro | Many wood borers |
| | Agrilinae | X | 7120 | Most | WW | Away | Phyto, poll, nec | In WD | Sapro | Many wood borers; a significant number (>2000 spp.) are leaf miners (Evans et al. 2015) |
| | *Non-saproxylic subfamily*: Julodinae (external root feeders) | | | | | | | | | |
| | **Superfamily Byrrhoidea (12)** | | | | | | | | | |
| 58 | **Byrrhidae** | | | | | | | | | A and L phytophagous on mosses and other plants |

(continued)

**Table 2.1** (continued)

| # | Taxon | Sap[a] | #Spp[b] | % S[c] | Regions[d] | Adult found[e] | A food[f] | Larva found[e] | L food[f] | Notes |
|---|---|---|---|---|---|---|---|---|---|---|
| | *Non-saproxylic subfamilies*: Amphicyrtinae, Byrrhinae, Syncalyptinae | | | | | | | | | |
| 59 | **Elmidae** | X | 1500 | Few | WW | On WD | Sapro | In, on WD | Sapro | Aquatic, some A and L assoc with woody debris |
| | Larainae | X | 160 | Most | WW | On WD | Sapro | In, on WD | Sapro | *Potamophilus* dwell on submerged wood; *Lara avara* L feed on dec wood; both probably get nutrients from algae, microbes, and dec wood (Kodada et al. 2016a) |
| | Elminae | X | 1350 | Few | WW | On WD | Sapro | In, on WD | Sapro | *Graphelmis* and some *Macronychus* are strictly assoc with wood (Kodada et al. 2016a); *Stegoelmis* bore into wood as L (Valente-Neto and Fonseca-Gessner 2011) |
| 60 | **Dryopidae** | X | 280 | Few | WW | On WD | Sapro | In WD | Sapro | Generally eat dec plant matter; A (aquatic) and L (mostly terrestrial) live on and under dead wood, some *Dryops* larvae observed to chew on dead wood (Kodada et al. 2016b) |
| 61 | **Lutrochidae** | X | 15 | all | NW | On WD | sapro | In WD | Sapro | Aquatic, A and L on wood; *Lutrochus germari* bore into wood as L (Valente-Neto and Fonseca-Gessner 2011) |
| 62 | **Limnichidae** | | | | | | | | | Poorly known, L may eat algae |
| | *Non-saproxylic subfamilies*: Cephalobyrrhinae, Hyphalinae, Limnichinae, Thaumastodinae | | | | | | | | | |
| 63 | **Heteroceridae** | | | | | | | | | A and L in wet sand |

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|---|---|---|---|---|---|---|---|---|---|---|
| | *Non-saproxylic subfamilies*: Elythomerinae, Heterocerinae | | | | | | | | | |
| 64 | **Psephenidae** | X | 272 | Few | WW | Away | Non | On WD | Sapro | Some L are xylophagous on submerged logs, some pupate in dead wood (Lee et al. 2016) |
| | Psephenoidinae | X | 30 | Some | Afr, Or, Pal | Away | Non | On WD | Sapro | *Xylopsephenoides* L xylophagous on submerged logs (Lee et al. 2016) |
| | Eubrianacinae | X | 50 | Some | Hol, Afr, Or | Away | Non | On WD | Sapro | *Jaechanax* and *Mubrianax* L xylophagous on submerged logs (Lee et al. 2016) |
| | *Non-saproxylic subfamilies*: Afroeubriinae (on stones in water), Eubriinae (generally on stones in water, though some may pupate in holes and crevices in dead logs), Psepheninae (generally on stones in water) | | | | | | | | | |
| 65 | **Cneoglossidae** | X | 8 | All | Neo | Away | Unk | In WD | Sapro | Apparently aquatic L have emerged from submerged rotting brushwood (Costa et al. 2016) |
| 66 | **Ptilodactylidae** | X | 500 | Some | WW | Away | Myco | In WD | Sapro | Some L in wet or submerged rotten wood (Lawrence 2016c) |
| | Anchytarsinae | X | ? | ? | ? | ? | ? | ? | ? | L live in or on submerged wood (Ivie 2002) |
| | Ptilodactylinae | X | ? | ? | ? | ? | ? | ? | ? | L from moist leaf litter and rotten logs (Ivie 2002) |
| | *Non-saproxylic subfamilies*: Aploglossinae (L and habits unk), Araeopidiinae [L at margins of streams (Ivie 2002)], Cladotominae [L with known habits assoc with gravel, mud, or rock faces (Lawrence 2016c)], Podabrocephalinae (L and habits unk) | | | | | | | | | |
| 67 | **Chelonariidae** | X | 300 | Some | Ptrop | Away | Unk | In WD | Unk | Possibly assoc with ants or termites; L sometimes found under bark (Beutel and Leschen 2016b) |
| 68 | **Eulichadidae** | X | 22 | Few | Nea, Or | Away | Unk | On WD | Sapro | L aquatic, feeding mostly on rotting detritus and roots; gut of one *Eulichas* contained wood particles (Ivie 2016) |
| 69 | **Callirhipidae** | X | 16 | Most | WW | In, on WD; away | Unk | In WD | Sapro | L are borers, primarily in wood with white rot fungi (Lawrence 2016d) |

(continued)

**Table 2.1** (continued)

| # | Taxon | Sap[a] | #Spp[b] | % S[c] | Regions[d] | Adult found[e] | A food[f] | Larva found[e] | L food[f] | Notes |
|---|---|---|---|---|---|---|---|---|---|---|
| | **Superfamily Elateroidea (17)** | | | | | | | | | |
| 70 | **Artematopodidae** | | | | | | | | | Probably moss-feeding |
| | *Non-saproxylic subfamilies*: Allopogoniinae, Artematopodinae, Electribiinae | | | | | | | | | |
| 71 | **Rhinorhipidae** | | | | | | | | | Habits poorly known, L possibly in soil |
| 72 | **Brachypsectridae** | X | 6 | All | Hol, Or, Aus, WI | Away | Non? | In WD | Pred | L and rarely A subcortical (Neck 1993; Costa et al. 2010a; Petrzelkova et al. 2017) |
| 73 | **Cerophytidae** | X | 21 | Some | Hol, Neo | Away | Phyto? | In WD | Sapro | L from wood infested with brown rot (Costa et al. 2010b) |
| 74 | **Eucnemidae** | X | 1500 | Most | WW | On WD | Non? | In WD | Sapro | L wedge their way through wood, and probably have extra-oral digestion (Muona 2010) |
| | Pseudomeninae | X | 2 | All | Nea, Aus | In WD | Unk | In WD | Sapro | L of *Schizophyllus* in oak in red rotten stage (Otto and Young 1998) |
| | Palaeoxeninae | X | 1 | All | Nea | In WD | Unk | In WD | Sapro | In stumps of incense cedar (Muona 2000) |
| | Anischiinae | X | 6 | Most | Neo, Ausas | On WD | Unk | In WD | Unk | On wood-dec fungi, rotten wood, and dead branches (Lawrence et al. 2007); presumed L in rotten wood (Lawrence et al. 2007) |
| | Melasinae | X | ? | Most | ? | In WD | Unk | In WD | Sapro | Maj in dead logs (Muona 1993) |
| | Eucneminae | X | ? | Most | ? | In WD | Unk | In WD | Sapro | Maj in dead logs (Muona 1993) |
| | Macraulacinae | X | ? | Most | ? | In WD | Unk | In WD | Sapro | Maj in dead logs (Muona 1993) |

| | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | *Non-saproxylic subfamilies*: Perothopinae [L develop in soil (Muona 2010)], Phyllocerinae [L develop in soil (Muona 1993, 2000, 2010)], Phlegoninae [biology unk (Muona 1993)] | | | | | | | | | |
| 75 | **Throscidae** | X | 150 | Some | WW | Away | Unk | In WD | Sapro | Some L in soft rotten wood, in logs (Muona et al. 2010); L and A may be extraordinarily abundant in fresh WD (Ferro et al. 2012b) |
| 76 | **Elateridae** | X | 10,000 | Some | WW | Away | Phyto | In WD | Sapro, pred | Diverse habits, but all L liquid feeders (Costa et al. 2010c) |
| | Cebrioninae | X | ? | Few | WW exc Aus | In WD | Phyto | Away | Unk | A *Euthysanius* found under pine bark (Evans and Hogue 2006); otherwise L in soil (Lawrence et al. 1999a) |
| | Agrypninae | X | 2500 | Some | WW | Away | Phyto | In WD | Sapro, pred | Some Tetralobini live in termite nests in wood (Costa et al. 2010c); some gen in wood, under bark (Becker and Dogger 1991) |
| | Thylacosterninae | X | 45 | Most | Neo, Afr, Ausas | Away | Phyto | In WD | Sapro, pred | In wood logs (Vahtera et al. 2009) |
| | Lissominae | X | 150 | Some | WW | In WD | Phyto | In WD | Sapro, pred | A of *Drapetes* under loose bark, L saproxylic under loose bark or within dec wood (Johnson 2015) |
| | Semiotinae | X | 92 | Some | Neo | Away | Phyto | In WD | Pred | L usu in moist, sappy areas under bark (Lawrence et al. 1999b) |
| | Pityobiinae | X | 20 | All | Nea, Neo, STem | Away | Phyto | In WD | Pred | Some gen in wood, under bark (Becker and Dogger 1991); L pred in rotten wood (Costa et al. 2010c) |
| | Dendrometrinae | X | 1500 | Some | WW | Away | Phyto | In WD | Pred, phyto | Some gen in wood, under bark (Becker and Dogger 1991; Lawrence et al. 1999a) |
| | Elaterinae | X | 3500 | Most | WW | Away | Phyto, nec | In WD | Pred | Some gen in wood, under bark (Becker and Dogger 1991) |
| | Cardiophorinae | X | 800 | Few | WW | Away | Phyto | In WD | Pred | L in soil or rotten wood (Costa et al. 2010c) |

(continued)

**Table 2.1** (continued)

| # | Taxon | Sap[a] | #Spp[b] | % S[c] | Regions[d] | Adult found[e] | A food[f] | Larva found[e] | L food[f] | Notes |
|---|---|---|---|---|---|---|---|---|---|---|
| | *Non-saproxylic subfamilies*: Campyloxeninae (habits and L unk), Hemiopinae [L unk (Costa et al. 2010c)], Eudicronychinae [L unk (Costa et al. 2010c)], Morostomatinae (habits and L unk), Negastriinae (L in leaf litter and soil, often riparian), Oestodinae (habits and L unk), Oxynopterinae (habits and L unk), Parablacinae (habits and L unk), Physodactylinae [L unk (Costa et al. 2010c)], Subprotelaterinae (habits and L unk) | | | | | | | | | |
| 77 | **Plastoceridae** | | | | | | | | | L and habits unk |
| 78 | **Omalisidae** | | | | | | | | | Pred on millipedes |
| 79 | **Iberobaeniidae** | | | | | | | | | A collected from pitfall traps and sweeping vegetation (Kundrata et al. 2017) |
| 80 | **Lycidae** | X | 4600 | Some | WW | Away | Nec, non | In, on WD | Sapro | L in dead wood in various stages, less often in forest litter and soil (Bocak and Matsuda 2003); not pred but feed on soft or fluid material assoc with rotting wood (Lawrence 1991) |
| | Dictyopterinae | X | ? | Some | Hol, Ausas | Away | Nec, non | In, on WD | Sapro | A of *Dictyoptera* found overwintering under pine bark (Bocak and Bocakova 2008); L presumably saproxylic |
| | Lyropaeinae | X | ? | Some | Or | Away | Nec, non | In, on WD | Sapro | L of *Platerodrilus* is known to be saproxylic (Bocak and Matsuda 2003; as *Duliticola*) |
| | Lycinae | X | ? | Most | WW | Away | Nec, non | In, on WD | Sapro | Maj are probably saproxylic (Bocak and Matsuda 2003) |
| | *Non-saproxylic subfamilies*: Ateliinae (L unk), Dexorinae (L unk), Libnetinae (L unk) | | | | | | | | | |
| 81 | **Telegeusidae** | | | | | | | | | Habits, females, and L unk |
| 82 | **Phengodidae** | | | | | | | | | L pred on millipedes |

| | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | *Non-saproxylic subfamilies*: Mastinocerinae, Penicilliphorinae, Phengodinae | | | | | | | | | |
| 83 | **Rhagophthalmidae** | | | | | | | | | L predacious in soil and litter |
| 84 | **Lampyridae** | X | 2000 | Few | WW | Away | Pred | In, on WD | Pred | L may be found "in rotten logs" (Branham 2010) |
| | Lampyrinae | X | 1000 | Few | WW exc Aus | Away | Pred | In, on WD | Pred | *Ellychnia* and *Lucidota* L inhabit rotting logs (Lloyd 2002) |
| | *Non-saproxylic subfamilies*: Luciolinae (L aquatic or subaquatic), Ototretinae (L in leaf litter and soil), Photurinae (L general pred of snails and soft-bodied insects on surface of soil), Psilocladinae, Pterotinae (L in leaf litter and soil) | | | | | | | | | |
| 85 | **Omethidae** | | | | | | | | | L unk |
| | *Non-saproxylic subfamilies*: Driloniinae, Matheteinae, Omethinae | | | | | | | | | |
| 86 | **Cantharidae** | X | 5083 | Some | WW | Away | Poll, nec, pred | In, on WD | Pred | Some L may be subcortical, on dec wood debris (Ramsdale 2010); possibly not obligate |
| | Saproxylic habits by subfamily unk: Cantharinae, Chauliognathinae, Dysmorphocerinae, Malthininae, Silinae | | | | | | | | | |
| | **Series Elateriformia: ?family (1)** | | | | | | | | | |
| | Cydistinae | | | | | | | | | L unk |
| | **Series Bostrichiformia** | | | | | | | | | |
| | **Superfamily Bostrichoidea (4)** | | | | | | | | | |
| 87 | **Dermestidae** | X | 1000 | Few | WW | Away | Poll, nec, sapro | In WD | Sapro | A, L occasionally in dry woody debris (Lawrence and Ślipiński 2010) |
| | Orphilinae | X | 10 | Most | WW | Away | Poll, nec | In WD | Sapro, myco | *Orphilus* and possibly *Orphilodes* L assoc with dead wood (Lawrence and Ślipiński 2005, 2010a) |
| | *Non-saproxylic subfamilies*: Attageninae, Dermestinae, Megatominae, Thorictinae, Trinodinae | | | | | | | | | |
| 88 | **Endecatomidae** | X | 4 | All | Hol | In, on fungi | Myco | In, on fungi | Myco | A and L bore into polypores and other wood-dec fungi on dead wood (Lawrence 2010a) |

(continued)

**Table 2.1** (continued)

| # | Taxon | Sap[a] | #Spp[b] | % S[c] | Regions[d] | Adult found[e] | A food[f] | Larva found[e] | L food[f] | Notes |
|---|---|---|---|---|---|---|---|---|---|---|
| 89 | **Bostrichidae** | X | 570 | All | WW | In WD | Sapro, phyto | In WD | Sapro | Most A and L wood borers (Liu et al. 2008; Lawrence 2010b); some in cones |
| | Dysidinae | X | 2 | All | Or, Neo | In WD | Sapro | In WD | Sapro | A have been found in dead soft-wood board (Lawrence et al. 1999b) |
| | Polycaoninae | X | 28 | All | Or, NW | In WD | Sapro, phyto | In WD | Sapro | *Polycaon* and *Melalgus* may attack living tissue (Lawrence 2010b); former may attack dead trunks or branches of *Eucalyptus* (Liu et al. 2008) |
| | Bostrichinae | X | 450 | All | WW | In WD | Sapro, phyto | In WD | Sapro | Maj bore into dying or dead trees (Lawrence et al. 1999b); *Dinapate* attacks living trees |
| | Psoinae | X | 13 | All | Hol, Afr, Or | In WD | Sapro, phyto | In WD | Sapro | *Psoa* attacks shrubs (Tilden 1953) |
| | Dinoderinae | X | 50 | Most | WW exc Aus | In WD | Sapro | In WD | Sapro | Non-wood-feeding grain borers belong to this group; others wood-boring, including *Stephanopachys* in conifers (Liu et al. 2008) |
| | Lyctinae | X | 32 | All | WW | In WD | Sapro | In WD | Sapro | Primary group of powder-post beetles, includes pests of furniture and cane (Lawrence 2010b) |
| | Euderiinae | X | 1 | All | NZ | Away | Sapro | In WD | Sapro | L from moist or sappy bark of dead or injured trees (Klimaszewski and Watt 1997) |
| 90 | **Ptinidae (=Anobiidae)** | X | 2200 | Most | WW | In, on WD; away | Sapro | In WD | Sapro | A and L found in dry woody debris (Philips and Bell 2010) |

| | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | Eucradinae | X | 70 | All | Hol, Afr, Or | In, on WD | Sapro | In WD | Sapro | Wood borers, L tunnel between bark and wood of mainly dead hardwoods (Arango and Young 2012) |
| | Ptininae | X | 650 | Some | WW | In, on WD | Sapro | In WD | Sapro | Most members feed on accumulated dried plant or animal material, but some members are wood borers (Philips 2002); *Ptinus fur* reported from cones of conifers (Arango and Young 2012) |
| | Dryophilinae | X | 75 | All | WW | In, on WD | Sapro | In WD | Sapro | Wood borers (Philips 2002) |
| | Ernobiinae | X | 150 | All | WW exc Aus | In, on WD | Sapro | In WD | Sapro | Bore beneath bark or into wood; some in cones of conifers (Arango and Young 2012) |
| | Anobiinae | X | 400 | Most | WW | In, on WD | Sapro | In WD | Sapro | Most are wood-boring, some are stored product pests (Arango and Young 2012) |
| | Ptilininae | X | 65 | All | WW exc Aus | In, on WD | Sapro | In WD | Sapro | *Ptilinus* are wood-feeding (Arango and Young 2012) |
| | Xyletininae | X | 370 | Most | WW | In, on WD | Sapro | In WD | Sapro | L of most bore into dead wood (Arango and Young 2012) |
| | Dorcatominae | X | 670 | Some | WW | In, on WD | Sapro, myco | In WD | Sapro, myco | L in woody (sometimes wood-dec) fungi, wood, branches twigs, vines, as well as puffballs and other mushrooms (Arango and Young 2012) |
| | Mesocoelopodinae | X | 370 | Some | WW | In, on WD | Sapro | In WD | Sapro | L habitats varied, including seeds, wood, branches, vines, galls, bark, kelp (Arango and Young 2012) |

(continued)

**Table 2.1** (continued)

| # | Taxon | Sap[a] | #Spp[b] | % S[c] | Regions[d] | Adult found[e] | A food[f] | Larva found[e] | L food[f] | Notes |
|---|---|---|---|---|---|---|---|---|---|---|
| | *Non-saproxylic subfamily*: Alvarenganiellinae (L and habits unk) | | | | | | | | | |
| | **Series Cucujiformia** | | | | | | | | | |
| | **Superfamily Coccinelloidea (15)** | | | | | | | | | |
| 91 | **Bothrideridae** | X | 270 | All | WW | In WD | Unk | In WD | Ecpar | L ecto of L and pupae of wood-boring Coleoptera and Hymenoptera (Ślipiński et al. 2010b) |
| 92 | **Murmidiidae** | X | 12 | Some | WW | In WD | Myco | In WD | Myco | Under bark, often of trees infested by fungi; otherwise in dec vegetation (Ślipiński 1990) |
| 93 | **Discolomatidae** | X | 400 | Some | Ptrop | In, on WD and fungi | Myco, sapro | In, on WD and fungi | Myco, sapro | Habits and L poorly known |
| | Aphanocephalinae | X | 90 | Some | Neo, Ausas, Sey | On WD | Myco | on WD | Myco | A of *Aphanocephalus* from fungi, including wood-dec polypores (Cline and Ślipiński 2010) |
| | Discolomatinae | X | 40 | Some | Neo, Afr | On WD | Myco | Unk | Unk | A of *Discoloma* from old twigs encrusted with lichens and various subcortical fungi (Cline and Ślipiński 2010) |
| | *Non-saproxylic subfamilies*: Cephalophaninae, Notiophyginae, Pondonatinae (only myrmecophilous?) | | | | | | | | | |
| 94 | **Teredidae** | X | 120 | Some | WW | In, on WD | Myco | In, on WD | Myco, pred | Habits various |
| | Teredinae | X | 20 | All | WW | In, on WD | Myco | In, on WD | Myco | L myco, some on Xylariaceae, some inhabit tunnels and galleries of Ptinidae, Cerambycidae, Curculionidae (Ślipiński et al. 2010b) |

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|---|---|---|---|---|---|---|---|---|---|---|
| | *Non-saproxylic subfamily*: Anommatinae (L and A in dec vegetation, L habits unk) | | | | | | | | | |
| 95 | **Euxestidae** | X | 62 | Most | WW | In WD | Myco | In WD | Myco | Subcortical, often early stage of dec, but can be late |
| 96 | **Cerylonidae** | X | 410 | Most | WW | In WD | Myco | In WD | Myco, myxo | Subcortical, often early stage of dec, but can be late |
| | Ostomopsinae | X | 2 | All | Neo, Ausas, Sey | In WD | Myco | ? | Unk | A assoc with rotten palm wood, under bark, or extracted from leaf/ log litter (Ślipiński 1990) |
| | Loebliorylоninae | X | 9 | Some | Or | In WD | Myco | ? | Unk | In leaf litter and rotten wood (Ślipiński 1990); L unk |
| | Ceryloninae | X | 400 | Most | WW | In WD | Myco | In WD | Myco, myxo | Habits various: A and L under bark, in rotten wood, leaf litter, probably feeding on wood juices, hyphae, and myxo (Ślipiński 1990) |
| 97 | **Latridiidae** | X | 760 | Some | WW | In, on WD | Myco | In, on WD | Myco | Generally myco and occasionally with woody debris, including fallen branches; L habits very poorly known (Hartley and McHugh 2010); in dec trunks and stumps, wood mold, cut branches, bracket fungi, among other habitats (Klimaszewski and Watt 1997) |
| | Latridiinae | X | 258 | Some | WW | In, on WD | Myco | In, on WD | Myco | Some members assoc with woody debris; habits poorly known |
| | Corticariinae | X | 502 | Some | WW | In, on WD | Myco | In, on WD | Myco | Some members assoc with woody debris (Plewa et al. 2017); habits poorly known |
| 98 | **Akalyptoischiidae** | | | | | | | | | Myco in leaf litter |
| 99 | **Alexiidae** | X | 50 | Some | w Pal | In, on WD and fungi | Myco | In, on WD and fungi | Myco | Subcortical, on mushrooms (Ślipiński and Tomaszewska 2010) |

(continued)

**Table 2.1** (continued)

| # | Taxon | Sap[a] | #Spp[b] | % S[c] | Regions[d] | Adult found[e] | A food[f] | Larva found[e] | L food[f] | Notes |
|---|---|---|---|---|---|---|---|---|---|---|
| 100 | **Anamorphidae** | X | 170 | Some | WW | In, on WD and fungi | Myco | In, on WD and fungi | Myco | Many on wood-dec fungal fruiting bodies (Shockley et al. 2009) |
| 101 | **Corylophidae** | X | 300 | Some | WW | In, on WD and fungi | Myco | In, on WD and fungi | Myco | Generally myco on internal and external wood-dec fungi |
| | Periptyctinae | X | 6 | Some | Aus | On WD | Myco | On WD | Myco | *Pakalukodes* from logs (Ślipiński et al. 2009) |
| | Corylophinae | X | 300 | Some | WW | On WD | Myco | On WD | Myco | Many under bark (Ślipiński et al. 2010c) |
| 102 | **Endomychidae** | X | 1585 | Most | WW | In, on WD and fungi | Myco | In, on WD and fungi | Myco | Generally subcortical or on fungal fruiting bodies |
| | Pleganophorinae | X | 24 | Most | WW | On WD | Myco | On WD | Myco | *Trochoideus* on wood-dec Auriculariaceae fungi (Shockley et al. 2009) |
| | Leiestinae | X | 15 | Most | Hol | In, on WD | Myco | In, on WD | Myco | Many on wood-dec fungal fruiting bodies (Shockley et al. 2009) |
| | Xenomycetinae | X | 2 | All | Nea | On WD | Myco | On WD | Myco | L of *Xenomycetes rivesi* only known from softwood-dec *Paxillus atrotomentosus* (Johnson 1986) |
| | Danascelinae | X | 2 | All | Nea, Pakistan | In WD | Myco | Unk | Unk | One A of *Hadromychus chandleri* collected "sifting conifer log" (Bousquet and Leschen 2002); L unk |

| | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | Stenotarsinae | X | 458 | Some | WW | In, on WD | Myco | In, on WD | Myco | Some on wood-dec fungal fruiting bodies (Shockley et al. 2009) |
| | Endomychinae | X | 94 | Most | Hol, Or | In, on WD | Myco | In, on WD | Myco | Many on wood-dec fungal fruiting bodies (Shockley et al. 2009) |
| | Epipocinae | X | 166 | Some | Neo, Nea | In, on WD | Myco | In, on WD | Myco | Some on wood-dec fungal fruiting bodies (Shockley et al. 2009) |
| | Lycoperdininae | X | 713 | Most | WW | In, on WD | Myco | In, on WD | Myco | Many on wood-dec fungal fruiting bodies (Shockley et al. 2009) |
| | *Non-saproxylic subfamily*: Merophysiinae | | | | | | | | | |
| 103 | **Mycetaeidae** | X | 7 | Few | WW exc Aus | In, on WD | Myco | In, on WD | Myco | General myco, presence in woody debris possibly incidental |
| 104 | **Eupsilobiidae** | X | 16 | Some | NW, s Afr | In, on WD and fungi | Myco | In, on WD and fungi | Myco | Many are social insect inquilines (Shockley et al. 2009) |
| 105 | **Coccinellidae** | | | | | | | | | Mostly pred, occasionally phyto or poll, myco |
| | *Non-saproxylic subfamilies*: Coccinellinae, Microweiseinae | | | | | | | | | |
| | **Superfamily Tenebrionoidea (29)** | | | | | | | | | |
| 106 | **Lymexylidae** | X | 65 | All | WW | In, on WD | Unk | In WD | Sapro, myco | L develop in fungal-infected wood and are wood borers; A *Elateroides dermestoides* inoculate wood with fungi for L to consume (Lawrence 2010c) |
| | Hylecoetinae | X | 5 | All | Hol, Or | In, on WD | Unk | In WD | Sapro, myco | A may be found under bark, on wood surfaces or in rotten wood; L wood borers (Lawrence 2010c) |
| | Lymexylinae | X | 4 | All | Pal | In, on WD | Unk | In WD | Sapro, myco | A may be found under bark, on wood surfaces or in rotten wood; L wood borers (Lawrence 2010c) |

(continued)

**Table 2.1** (continued)

| # | Taxon | Sap[a] | #Spp[b] | % S[c] | Regions[d] | Adult found[e] | A food[f] | Larva found[e] | L food[f] | Notes |
|---|---|---|---|---|---|---|---|---|---|---|
| | Melittommatinae | X | 25 | All | WW | In, on WD | Unk | In WD | Sapro, myco | A may be found under bark, on wood surfaces or in rotten wood; L wood borers (Lawrence 2010c) |
| | Atractocerinae | X | 30 | All | Ptrop, Pal | Away | Unk | In WD | Sapro, myco | A active fliers; L wood borers (Lawrence 2010c) |
| 107 | **Mycetophagidae** | X | 130 | Few | WW | In, on WD | Myco, sapro | In, on WD | Myco, sapro | A and L in wood-dec fungi |
| | Esarcinae | X | 10 | Some | Pal | On WD | Myco | On WD | Myco | At least one *Esarcus* on Xylariaceae fruiting bodies (Lawrence 1991) |
| | Mycetophaginae | X | 125 | Most | WW | In, on WD | Myco, sapro | In, on WD | Myco, sapro | Maj feed on wood-dec fungi; some on ferns or stored products (Lawrence 1991) |
| | *Non-saproxylic subfamily*: Bergininae (pred, poll, or assoc with leaf litter and palms) | | | | | | | | | |
| 108 | **Archeocrypticidae** | X | 50 | Some | WW | In, on WD | Myco, sapro | In, on WD | Myco, sapro | Some Aus members on wood-dec polypores (Lawrence 2010d) |
| 109 | **Pterogeniidae** | X | 24 | Some | Asia | In, on fungi | Myco | In, on fungi | Myco | A and L of some gen in wood-dec polypores (Lawrence 2010e) |
| 110 | **Ciidae** | X | 640 | All | WW | In, on fungi | Myco | In, on fungi | Myco | A and L of all spp. in or on wood-dec fungi (Lawrence and Lopes-Andrade 2010) |
| | Sphindociinae | X | 1 | All | Nea | In WD, fungi | Myco | In WD, fungi | Myco | L bore into dry rotten wood at base of fruiting body of *Antrodia albida* (Lawrence and Lopes-Andrade 2010) |
| | Ciinae | X | 640 | All | WW | In, on fungi | Myco | In, on fungi | Myco | A and L of all spp. in or on wood-dec fungi (Lawrence and Lopes-Andrade 2010) |

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|---|---|---|---|---|---|---|---|---|---|---|
| 111 | **Tetratomidae** | X | 150 | All | WW | In, on fungi | Myco | In fungi | Myco | Usu assoc with fruiting bodies of various wood-dec fungi, L feed internally (Lawrence and Leschen 2010f) |
| | Tetratominae | X | 22 | All | Hol | In, on fungi | Myco | In fungi | Myco | Usu assoc with fruiting bodies of various wood-dec fungi, L feed internally (Lawrence and Leschen 2010f) |
| | Piseninae | X | 9 | All | Hol, Or, s SAm | In, on fungi | Myco | In fungi | Myco | Usu assoc with fruiting bodies of various wood-dec fungi, L feed internally (Lawrence and Leschen 2010f) |
| | Penthinae | X | 13 | All | Hol, Or | In, on fungi | Myco | In fungi | Myco | Usu assoc with fruiting bodies of various wood-dec fungi, L feed internally (Lawrence and Leschen 2010f) |
| | Hallomeninae | X | 17 | All | Hol | In, on fungi | Myco | In fungi | Myco | L assoc with various wood-dec fungi, especially polypores (Lawrence 1991) |
| | Eustrophinae | X | 86 | All | WW exc Aus | In, on fungi | Myco | In fungi | Myco | Found in a wide variety of bracket fungi (Lawrence 1991) |
| 112 | **Melandryidae** | X | 420 | All | WW | In, on WD | Myco | In WD | Myco | L of maj inhabit dead wood of varying consistency (Lawrence 1991); maj are wood borers |
| | Melandryinae | X | 400 | All | WW | In, on WD | Myco | In WD | Myco | L of maj inhabit dead wood (Lawrence 1991) |
| | Osphyinae | X | 35 | All | Hol, Neo, Or | Away | Unk | In WD | Myco | L inhabit dead wood (Lawrence 1991) |
| 113 | **Mordellidae** | X | 1500 | Most | WW | Away | Poll, myco | In, on WD and fungi | Myco, sapro | L primarily in dead wood and rotten stems, some in polypores (Lawrence and Ślipiński 2010c) |

(continued)

**Table 2.1** (continued)

| # | Taxon | Sap[a] | #Spp[b] | % S[c] | Regions[d] | Adult found[e] | A food[f] | Larva found[e] | L food[f] | Notes |
|---|---|---|---|---|---|---|---|---|---|---|
| | Mordellinae | X | 1500 | Most | WW | Away | Poll, myco | In, on WD | Myco, sapro | L primarily in dead wood and rotten stems, some in polypores (Lawrence and Ślipiński 2010c) |
| | *Non-saproxylic subfamily*: Ctenidiinae (L and habits unk) | | | | | | | | | |
| 114 | **Ripiphoridae** | X | 400 | Some | WW | Away | Poll, non | In WD | Enpar | Endo on other insects, including wood-boring beetle larvae |
| | Pelecotominae | X | 15 | All | WW | Away | Unk | In WD | Enpar | Hosts are wood-boring beetle L (Lawrence et al. 2010b) |
| | Hemirhipidiinae | X | 9 | All | Ausas | Away | Unk | In WD | Enpar | Hosts are wood-boring beetle L (Lawrence et al. 2010b) |
| | *Non-saproxylic subfamilies*: Ptilophorinae (L and habits unk), Ripidiinae (endo of Blattodea), Ripiphorinae (endo of Hymenoptera) | | | | | | | | | |
| 115 | **Zopheridae** | X | 1700 | All | WW | In, on WD | Myco, pred | In, on WD | Myco, pred | Maj assoc with dead wood, on which L feed (Ślipiński and Lawrence 2010a) |
| | Colydiinae | X | 1000 | All | WW | In, on WD | Myco, pred | In, on WD | Myco, pred | Usu feed on dead plant material and assoc with rotten logs; some groups pred on scolytines (Ślipiński and Lawrence 2010a) |
| | Zopherinae | X | 700 | All | WW | In, on WD | Myco | In, on WD | Myco | Assoc with various fungi and dec plant material (Ślipiński and Lawrence 2010a) |
| 116 | **Ulodidae** | X | 40 | All | STem | In, on WD and fungi | Myco | In, on WD and fungi | Myco | Maj assoc with dead wood and wood-dec fungi (Leschen and Ślipiński 2010) |
| 117 | **Promecheilidae** | | | | | | | | | Probably feed on mosses and lichens |

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|---|---|---|---|---|---|---|---|---|---|---|
| 118 | **Chalcodryidae** | X | 6 | Some | NZ | On WD | Unk | In, on WD | Lichens? | L reported from "refuge galleries" in dead twigs and branches, A and L on moss/lichen-covered branches (Lawrence and Leschen 2010g) |
| 119 | **Tenebrionidae** | X | 20,000 | Most | WW | In, on WD | Myco, sapro, pred | In, on WD | Myco, sapro, pred | Large family with a wide variety of life histories; may be subcortical, on fungi, in rotten wood, or in bark beetle tunnels |
| | Zolodininae | X | 2 | All | NZ, Tasmania | In, on WD | Unk | In WD | Sapro | L under bark of logs and in rotten wood (Matthews et al. 2010) |
| | Lagriinae | X | ?3000 | Most | WW | In, on WD | Unk | In WD | Sapro | Maj in leaf litter and dead plant material; some Adeliini and Lupropini L feed internally in dead wood (Matthews et al. 2010) |
| | Nilioninae | X | 40 | All | Neo | On WD | Myco | On WD | Myco | L and A gregarious on fungus-infested branches (Matthews et al. 2010) |
| | Phrenapatinae | X | 175 | All | WW | In WD | Sapro | In WD | Sapro | All A and L live in and feed on rotten wood (Matthews et al. 2010) |
| | Tenebrioninae | X | ?4000 | Most | WW | In, on WD | Sapro, myco | In WD | Sapro, myco | Many feed as L in rotting wood (Matthews et al. 2010); includes former family Trachelostenidae, whose A have been collected under tight-fitting bark (Lawrence and Ślipiński 2010d) |
| | Alleculinae | X | ?2000 | Most | WW | On WD; away | Unk | In WD | Sapro | L either live in rotten wood or soil (Matthews et al. 2010) |
| | Diaperinae | X | ?1500 | Some | WW | In, on WD | Sapro, myco | In WD | Sapro, myco | Many subcortical or in dead wood as A and L, some A external feeders on fungi (Matthews et al. 2010) |

(continued)

**Table 2.1** (continued)

| # | Taxon | Sap[a] | #Spp[b] | % S[c] | Regions[d] | Adult found[e] | A food[f] | Larva found[e] | L food[f] | Notes |
|---|---|---|---|---|---|---|---|---|---|---|
| | Stenochiinae | X | ?2500 | All | WW | On WD; away | Sapro | In WD | Sapro | A on wood surfaces at night, L feed in rotting wood (Matthews et al. 2010) |
| | *Non-saproxylic subfamily*: Pimeliinae (ground-dwelling scavengers) | | | | | | | | | |
| 120 | **Prostomidae** | X | 29 | All | WW exc Neo | In, on WD | Myco | In WD | Myco | In soft, mud-like substrate in reddish rotten wood of large diameter logs (Seago and Beutel 2010) |
| 121 | **Synchroidae** | X | 9 | All | Hol, SE Asia | On WD | Unk | In WD | Myco | L feed on rotten cambium of deciduous trees (Ślipiński and Lawrence 2010b) |
| 122 | **Stenotrachelidae** | X | 21 | All | Hol | Away | Poll, non | In WD | Myco | L reported from well-rotted, brown rot, "lucanid stage of decomposition" wood (Lawrence and Ślipiński 2010e) |
| | Stenotrachelinae | X | 6 | All | Hol | Away | Poll, non | In WD | Myco | L of *Stenotrachelus aeneus* under bark or in wood of dead angiosperm trees (Lawrence and Ślipiński 2010e) |
| | Nematoplinae | X | 4 | All | Hol | Away | Poll, non | In WD | Myco | L of *Nematoplus semenovi* typical of wood in "lucanid stage" of decomposition (Lawrence and Ślipiński 2010e) |
| | Cephaloinae | X | 9 | All | Hol | Away | Poll, non | In WD | Myco | L of *Cephaloon* collected from old brown-rot-infected conifer logs (Lawrence and Ślipiński 2010e) |
| | Stoliinae | X | 2 | All | Pal | Away | Poll, non | Unk | Unk | L and habits unk; presumed saproxylic |

| | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| 123 | **Oedemeridae** | X | 1500 | Most | WW | On WD; away | Poll, nec | In WD | Sapro, phyto, myco? | L in moist rotting wood, including driftwood |
| | Calopodinae | X | 35 | Most | Hol, Neo, Or | Away | Poll, nec | In WD | Sapro, phyto | L *Calopus* known to damage living trees (Lawrence and Ślipiński 2010f) |
| | Oedemerinae | X | 1500 | Most | WW | On WD; away | Poll, nec | In WD | Sapro, phyto, myco? | L in dec wood, including logs, stumps, roots, driftwood, structural timber (Lawrence and Ślipiński 2010f) |
| | *Non-saproxylic subfamily*: Polypriinae (L and habits unk) | | | | | | | | | |
| 124 | **Meloidae** | | | | | | | | | A phyto, L pred; *Eletica wahlbergi* oviposits under bark; L of *Eletica* and *Iselma* (Eleticinae) possibly saproxylic pred (Bologna et al. 2010) |
| | *Non-saproxylic subfamilies*: Eleticinae (see note above), Meloinae, Nemognathinae, Tetraonychinae | | | | | | | | | |
| 125 | **Mycteridae** | X | 170 | Some | WW | On WD; away | Poll, nec | In WD | Myco | Poorly known, but L appear to be subcortical, myco |
| | Mycterinae | X | 16 | All | Hol, Afr, Or | Away | Poll, nec | In WD | Unk | *Mycterus curculioides* L found under dead pine bark (Pollock 2010a) |
| | Eurypinae | X | 120 | Most | WW | On WD; away | Unk | In WD | Myco | Maj of L under bark; *Stilpnonotus postsignatus* in tunnels perpendicular to long axis of logs (Pollock 2010a) |
| | *Non-saproxylic subfamily*: Hemipeplinae (L and A assoc with grasses and unopened palm fronds) | | | | | | | | | |
| 126 | **Boridae** | X | 4 | All | Hol, Aus | In, on WD | Unk | In WD | Unk | L subcortical in conifers, especially fire-killed trees (Pollock 2010b) |

(continued)

**Table 2.1** (continued)

| # | Taxon | Sap[a] | #Spp[b] | % S[c] | Regions[d] | Adult found[e] | A food[f] | Larva found[e] | L food[f] | Notes |
|---|---|---|---|---|---|---|---|---|---|---|
| | Borinae | X | 3 | All | Hol | In, on WD | Unk | In WD | Unk | L subcortical in conifers, especially fire-killed trees (Pollock 2010b) |
| | *Non-saproxylic subfamily*: Synercticinae (L and habits unk) | | | | | | | | | |
| 127 | **Trictenotomidae** | X | 14 | Unk | Se Pal | On WD | Unk | Unk | Unk | A collected on WD, subcortically, and on tree fungi; L poorly known (Pollock and Telnov 2010) |
| 128 | **Pythidae** | X | 22 | Most | WW exc Afr | Away | Unk | In WD | Myco | Subcortical, one sp. in red rotten wood of conifers (Pollock 2010c) |
| 129 | **Pyrochroidae** | X | 200 | Most | WW | Away | Unk | In WD | Myco | L subcortical |
| | Tydessinae | X | 2 | All | Hol | Away | Poll? | In WD | Myco | L under bark of various hardwoods (Young and Pollock 2010) |
| | Pilipalpinae | X | 37 | All | SHem | In WD; away | Unk | In WD | Myco | L under bark of dead trees (Young and Pollock 2010) |
| | Pyrochroinae | X | 100 | All | Hol, Or | Away | Unk | In WD | Myco | L mostly subcortical, some within dec wood (Young and Pollock 2010) |
| | *Non-saproxylic subfamilies*: Agnathinae (L from dry, dec vegetation and dung), Pedilinae (most L unk, but known spp. in soil and dec vegetation) | | | | | | | | | |
| 130 | **Salpingidae** | X | 350 | Most | WW | In, on WD; away | Unk | In WD | Myco, sapro, pred | L often subcortical, some assoc with scolytines (Lawrence et al. 2010c) |
| | Othniinae | X | 50 | All | WW | Away | Unk | In WD | Unk | L collected under pine bark (Pollock 2002b) |
| | Prostominiinae | X | 30 | Most | Ptrop | On WD | Unk | In WD | Myco, sapro | Usu under bark; some in rotten leaf axils of tree ferns or palms (Lawrence et al. 2010c) |

| | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | Inopeplinae | X | 75 | All | WW | In, on WD | Unk | In WD | Unk | L and A usu under bark (Lawrence et al. 2010c) |
| | Salpinginae | X | 150 | Most | WW | In, on WD; away | Unk | In WD | Myco, sapro, pred | L in dec logs, branches or twigs; some assoc with scolytines (Lawrence et al. 2010c); a few phyto |
| | *Non-saproxylic subfamilies*: Aegialitinae (A and L under intertidal rocks), Agleninae (A and L from manure and dec vegetation), Dacoderinae (under stones, myrmecophiles) | | | | | | | | | |
| 131 | **Anthicidae** | X | 3000 | Few | WW | On WD; away | Myco, sapro, pred | In WD | Myco, sapro, pred | Some L have been reported from beneath bark of dead trees (Chandler 2010) |
| | Lemodinae | X | 40 | Most | Aus | On WD | Unk | In WD | Myco | A and L of *Lemodes* assoc with rotten logs (Telnov 2007); *Trichananca* L found under bark (Lawrence et al. 1999a) |
| | *Non-saproxylic subfamilies*: Anthicinae [maj of L in moist soil or organic debris (Chandler 2010)], Copobaeninae (L and habits unk), Eurygeniinae (L have been collected from a cranberry bog), Macratriinae (presumed L collected in forest litter), Notoxinae (some may bore into tubers), Steropinae (L and habits unk), Tomoderinae (L collected in forest litter) | | | | | | | | | |
| 132 | **Aderidae** | X | 1000 | Most | WW | Away | Unk | In WD | Sapro | L usu occur in rotten wood, leaf litter, or under bark; L *Megaxenus* assoc with termites (Lawrence and Ślipiński 2010g) |
| 133 | **Scraptiidae** | X | 400 | Some | WW | Away | Poll | In WD | Myco?, pred? | L usu subcortical in dead trees, some in leaf litter (Lawrence and Ślipiński 2010h) |
| | Scraptiinae | X | 100 | Most | WW | Away | Poll | In WD | Myco?, pred? | L usu subcortical; some in litter, with ants or in moldy hay (Lawrence and Ślipiński 2010h) |
| | *Non-saproxylic subfamily*: Anaspidinae (only known L habits are feeding on lichens on a rock (Lawrence and Ślipiński 2010h); possibly not saproxylic) | | | | | | | | | |
| 134 | **Ischaliidae** | X | 37 | Most | Asia, NAm | Away | Unk | In WD | Myco | L of *Ischalia vancouverensis* feed on fungal mycelium assoc with dec stumps or logs (Lawrence et al. 2010d) |

(continued)

**Table 2.1** (continued)

| # | Taxon | Sap[a] | #Spp[b] | % S[c] | Regions[d] | Adult found[e] | A food[f] | Larva found[e] | L food[f] | Notes |
|---|---|---|---|---|---|---|---|---|---|---|
| | **Superfamily Tenebrionoidea: ?family (3)** | | | | | | | | | |
| | Lagrioidinae | X | 5 | Most | Aus, NZ, s SAm | On WD | Unk | Away | Sapro | A may be found under logs or driftwood (Lawrence et al. 2010d; MLG, pers. obs.), but L feed on rotting vegetation |
| | *Rhizonium antiquum* | X | 1 | All | NZ | In WD | Unk | In WD | Unk | A and L in dead fronds of tree ferns and dec wood (Lawrence et al. 2010d; MLG, pers. obs.) |
| | *Non-saproxylic subfamily*: Afreminae (L, females and habits unk) | | | | | | | | | |
| | **Superfamily Cleroidea (14)** | | | | | | | | | |
| 135 | **Byturidae** | | | | | | | | | A and L fruit and poll |
| | *Non-saproxylic subfamilies*: Byturinae, Platydascillinae | | | | | | | | | |
| 136 | **Biphyllidae** | X | 200 | Most | WW | In, on WD | Myco | In, on WD | Myco | Maj under bark of dead trees or fallen branches (Cline and Shockley 2010) |
| 137 | **Phloiophilidae** | X | 1 | All | Eur | On fungi | Myco | On fungi | Myco | A and L eat basidiomycete fungi, L also on dead *Quercus* branches (Lawrence and Leschen 2010b) |
| 138 | **Trogossitidae** | X | 634 | Most | WW | In, on WD | Myco, pred | In, on WD and fungi | Myco, pred | Maj assoc with dead wood, either pred or myco |
| | Peltinae | X | 33 | Most | WW exc Afr | In, on WD | Myco | On fungi | Myco | L mostly in dec wood or on fungi, A under bark or on fungi (Kolibáč and Leschen 2010a) |
| | Lophocaterinae | X | 117 | Most | WW | In, on WD; away | Myco, poll | In WD | Myco, pred | Some in leaf litter or on flowers or stored products, but maj under bark or in dec wood (Kolibáč and Leschen 2010a) |

| | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | Trogossitinae | X | 484 | Most | WW | In, on WD | Pred | In WD | Pred, myco | Maj subcortical as A and L, some in rotten wood or in galleries of wood-boring insects (Kolibáč and Leschen 2010a) |
| 139 | **Acanthocnemidae** | X | 1 | All | Aus (adv WW) | On WD | Unk | Unk | Sapro? | A attracted to burning dead wood, probably pyrophilous (Lawrence and Leschen 2010c) |
| 140 | **Chaetosomatidae** | X | 12 | All | NZ, Mad | In, on WD | Unk | In WD | Sapro | L and A in woody debris, including tunnels of wood-boring beetles and moths (Leschen 2010) |
| 141 | **Metaxinidae** | | | | | | | | | In sooty mold on living trees, L pred |
| 142 | **Thanerocleridae** | X | 30 | All | WW | In, on WD | Pred | In, on WD | Pred | Pred on wood-boring or myco beetles (Kolibáč and Leschen 2010b) |
| 143 | **Cleridae** | X | 3400 | Some | WW | On WD | Pred, poll | In WD | Sapro, pred | Many pred on wood-boring beetles |
| | Tillinae | X | 600 | Some | WW exc SAm | On WD; away | Pred | In WD | Pred | At least some L are xylophilous pred in tunnels of wood-boring insects (Foster and Lawrence 1991a) |
| | Korynetinae | X | 700 | Some | WW | On WD; away | Pred | In WD | Pred | At least some L are xylophilous pred in tunnels of wood-boring insects (Foster and Lawrence 1991a) |
| | Hydnocerinae | X | 600 | Some | WW exc Eur | On WD; away | Pred, poll | In WD | Pred | At least some *Phyllobaenus* in woody habitats (Foster and Lawrence 1991a) |
| | Clerinae | X | 1500 | Most | WW | On WD | Pred | In WD | Pred, poll | Maj of A pred on wood-boring insects on trunks and branches; L within galleries (Kolibáč 2010) |
| | *Non-saproxylic subfamily*: Epiclininae (poll as A; L unk) | | | | | | | | | |
| 144 | **Phycosecidae** | | | | | | | | | A and L scavengers in marine littoral zones |

(continued)

**Table 2.1** (continued)

| # | Taxon | Sap[a] | #Spp[b] | % S[c] | Regions[d] | Adult found[e] | A food[f] | Larva found[e] | L food[f] | Notes |
|---|---|---|---|---|---|---|---|---|---|---|
| 145 | **Prionoceridae** | X | 158 | Few | Pal, Or, Afr, Aus | Away | Poll | In WD | Sapro?, pred? | *Idgia* L may be found under bark (Lawrence and Leschen 2010d) |
| 146 | **Mauroniscidae** | | | | | | | | | Habits poorly known, L unk |
| 147 | **Rhadalidae** | X | 250 | Some | WW | Away | Poll, pred | In WD | Pred | L of *Rhadalus* known from rotting yucca stems (Foster and Lawrence 2010); L of *Aplocnemus* under bark, pred; *Trichoceble* L may develop in pine and fir cones (Kolibáč et al. 2005) |
| 148 | **Melyridae** | X | 6000 | Few | WW | Away | Poll, pred | In WD | Sapro, phyto, pred, myco | L mostly pred, with many occurring in dec wood |
| | Dasytinae | X | 1300 | Some | WW | Away | Poll, pred | In WD | Sapro, phyto, pred, myco | L in rotting stems or wood, under bark, in cerambycid galleries, in polypore fungi or cones (Kolibáč et al. 2005) |
| | Malachiinae | X | 4000 | Some | WW | Away | Poll, pred | In WD | Pred | *Anthocomus*, *Hypebaeus*, and *Malachius* L found under bark (Foster and Lawrence 1991b) |
| | *Non-saproxylic subfamily*: Melyrinae (known L soil-inhabiting, feeding on seeds; A poll) | | | | | | | | | |
| | **Superfamily Cucujoidea (25)** | | | | | | | | | |
| 149 | **Boganiidae** | | | | | | | | | A and L poll |
| | *Non-saproxylic subfamilies*: Boganiinae, Paracucujinae | | | | | | | | | |
| 150 | **Helotidae** | X | 100 | Most | Pal, Or, Afr | On WD | Ferm sap | In, on WD | Ferm sap | A and L assoc with sap flows from trees damaged by wood-boring insects (Lawrence et al. 2010a) |

| | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| 151 | **Protocucujidae** | | | | | | | | | A and L probably living on vegetation or in leaf litter |
| 152 | **Sphindidae** | X | 64 | All | WW | In, on slime mold | Myxo | In, on slime mold | Myxo | A and L of all known members myxo (Forrester and McHugh 2010) |
| | Sphindinae | X | 58 | All | WW | In, on slime mold | Myxo | In, on slime mold | Myxo | A and L of all known members myxo |
| | Protosphindinae | X | 2 | All | Chile | In, on slime mold | Myxo | In, on slime mold | Myxo | A and L of all known members myxo |
| | Odontosphindinae | X | 3 | All | Hol | In, on slime mold | Myxo | In, on slime mold | Myxo | A and L of all known members myxo |
| | Sphindiphorinae | X | 1 | All | Afr | In, on slime mold | Myxo | In, on slime mold | Myxo | A and L of all known members myxo |
| 153 | **Cybocephalidae** | | | | | | | | | Pred of sternorrhynchine Hemiptera |
| 154 | **Monotomidae** | X | 240 | Most | WW | In, on WD | Myco, pred | In, on WD | Myco, pred | Generally myco, many under bark or in bark beetle galleries (Bousquet 2010) |
| | Rhizophaginae | X | 50 | Most | Hol, Or | In, on WD | Myco, pred | In, on WD | Myco, pred | Some *Rhizophagus* pred on scolytines (Bousquet 2010) |
| | Monotominae | X | 190 | Most | WW | In, on WD | Myco, pred | In, on WD | Myco, pred | Several gen reported from under bark of dead trees (Bousquet 2010) |
| 155 | **Erotylidae** | X | 3500 | Most | WW | In, on WD and fungi | Myco, sapro | In, on WD and fungi | Myco, sapro | Maj myco or sapro, but one major lineage (Languriinae) primarily phyto |

(continued)

**Table 2.1** (continued)

| # | Taxon | Sap[a] | #Spp[b] | % S[c] | Regions[d] | Adult found[e] | A food[f] | Larva found[e] | L food[f] | Notes |
|---|---|---|---|---|---|---|---|---|---|---|
| | Xenoscelinae | X | 10 | Some | WW exc Nea | In, on WD | Unk | In, on WD | Unk | *Zavaljus*, *Protoloberus*, and perhaps *Xenoscelis* assoc with dead wood (Leschen 2003) |
| | Cryptophilinae | X | 33 | Some | WW | In WD | Myco, sapro | In WD | Myco, sapro | Some members found under bark; some Toramini on Xylariaceae (Leschen 2003) |
| | Erotylinae | X | 2563 | Most | WW | In, on WD and fungi | Myco, sapro | In, on WD and fungi | Myco, sapro | Most members assoc with wood-dec fungi (Leschen 2003) |
| | *Non-saproxylic subfamilies*: Languriinae (maj phyto on living tissues, some in leaf litter), Loberinae (assoc with leaf litter, rotting and live vegetation), Pharaxonothinae (on cycad cones, rotting vegetation or assoc with stored products) | | | | | | | | | |
| 156 | **Hobartiidae** | X | 6 | All | Aus, SAm | In, on WD and fungi | Myco | In, on WD and fungi | Myco | A and L from fungus-infested logs, often on soft fruiting bodies of basidiomycetes (Tomaszewska and Ślipiński 2010) |
| 157 | **Cryptophagidae** | X | 600 | Most | WW | In, on WD and fungi | Myco | In, on WD and fungi | Myco | Mostly myco |
| | Cryptophaginae | X | 400 | Some | WW | In, on WD and fungi | Myco, poll | In, on WD | Myco | Many spp. on wood-rotting macrofungi (Leschen 1996) |
| | Atomariinae | X | 200 | Some | WW | In, on WD and fungi | Myco | In, on WD and fungi | Myco | Some spp. of *Atomaria* assoc with wood-rotting macrofungi (Leschen 1996) |

| | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| 158 | **Agapythidae** | | | | | | | | | In sooty mold on living trees, myco |
| 159 | **Priasilphidae** | X | 11 | Some | Aus, Chile, NZ | In, on WD | Myco | In, on WD | Myco | Have been collected in dec wood (Leschen and Lawrence 2010) |
| 160 | **Phloeostichidae** | X | 6 | Most | Pal, s SAm, Aus | In, on WD | Myco | In, on WD | Myco | A and L often found under bark of dead trees (Lawrence and Ślipiński 2010b) |
| 161 | **Silvanidae** | X | 500 | Most | WW | In, on WD | Myco | In, on WD | Myco | Mostly subcortical and myco (Thomas and Leschen 2010a) |
| | Brontinae | X | 300 | Most | WW | In, on WD | Myco | In, on WD | Myco | Mostly subcortical and myco (Thomas and Leschen 2010a) |
| | Silvaninae | X | 200 | Most | WW | In, on WD | Myco | In, on WD | Myco | Mostly subcortical and myco (Thomas and Leschen 2010a) |
| 162 | **Cucujidae** | X | 48 | All | WW exc Afr | In WD | Unk | In WD | Pred | L and A under bark of dead trees (Thomas and Leschen 2010b) |
| 163 | **Myraboliidae** | X | 13 | All | Aus | In WD | Unk | In WD | Unk | A and putative L found under bark of living *Eucalyptus* (Ślipiński et al. 2010a) |
| 164 | **Cavognathidae** | | | | | | | | | Assoc with bird nests |
| 165 | **Lamingtoniidae** | X | 3 | All | Aus | On fungi | Myco | On fungi | Myco | A and L in wood-rotting basidio-mycete fungi (Lawrence and Leschen 2010e) |
| 166 | **Passandridae** | X | 109 | All | WW | In WD | Unk | In WD | Ecpar | Ecto on wood-boring insect L and pupae (Burckhardt and Ślipiński 2010) |
| 167 | **Phalacridae** | X | 635 | Few | WW | In WD | Myco | In WD | Myco | Generally myco, mostly on mold-forming fungi; others poll (Gimmel 2013) |

(continued)

**Table 2.1** (continued)

| # | Taxon | Sap[a] | #Spp[b] | % S[c] | Regions[d] | Adult found[e] | A food[f] | Larva found[e] | L food[f] | Notes |
|---|---|---|---|---|---|---|---|---|---|---|
| | Phalacrinae | X | 615 | Few | WW | In WD | Myco | In WD | Myco | *Litochrus* L reported from rotten wood or bark, *Litochropus* A and L from wood-rotting *Daldinia* galls (Steiner 1984; Gimmel 2013) |
| | *Non-saproxylic subfamily*: Phaenocephalinae (assoc with hanging dead leaves or leaf litter). | | | | | | | | | |
| 168 | **Laemophloeidae** | X | 470 | Most | WW | In WD | Myco, pred | In WD | Myco, pred | Maj feed on subcortical fungi, though some pred on bark beetles in their burrows (Thomas and Leschen 2010c) |
| 169 | **Tasmosalpingidae** | | | | | | | | | Presumptive L fogged from bark of a living tree |
| 170 | **Cyclaxyridae** | | | | | | | | | In sooty mold on living trees, myco |
| 171 | **Smicripidae** | | | | | | | | | A assoc with palm flowers, L in litter |
| 172 | **Kateretidae** | | | | | | | | | L and A develop and feed in flowers |
| 173 | **Nitidulidae** | X | 4500 | Some | WW | In, on WD; away | Myco | In, on WD and fungi | Myco | Some A assoc with dead wood, either under bark or in wood-boring insect tunnels, others in fleshy fungi, some at tree wounds and ferm sap (Jelínek et al. 2010) |
| | Calonecrinae | X | 3 | All | Or | In, on WD | Myco | In, on WD | Myco | At tree wounds and ferm sap (Jelínek et al. 2010) |
| | Cryptarchinae | X | 300 | Most | WW | In, on WD | Myco | In, on WD | Myco | Often at tree wounds and ferm sap (Jelínek et al. 2010) |
| | Prometopiinae | X | ?30 | ? | ? | ? | ? | ? | ? | At least some at tree wounds and ferm sap (Jelínek et al. 2010) |
| | Epuraeinae | X | 350 | Some | Hol | In WD | Myco | In WD | Myco | Some subcortical (Jelínek et al. 2010) |

| | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | Carpophilinae | X | 500 | Some | Hol | In WD | Myco | In WD | Myco | Some subcortical (Jelínek et al. 2010) |
| | Amphicrossinae | X | 41 | Some | Hol | In WD | Myco, pred | In WD | Myco | One spp. aquatic and pred in bamboo culms and stumps (Kovac et al. 2007) |
| | Nitidulinae | X | 1000 | Most | WW | In, on WD | Myco | In, on WD | Myco | Maj in fleshy fungi, some assoc with tree wounds and ferm sap; some subcortical (Jelínek et al. 2010) |
| | Cillaeinae | X | 450 | Some | Ptrop | In, on WD | Myco | In, on WD | Myco | *Colopterus* at tree wounds and ferm sap; some subcortical (Jelínek et al. 2010) |
| | *Non-saproxylic subfamilies*: Maynipeplinae (habits and L unk), Meligethinae [primarily anthophiles and phyto (Jelínek et al. 2010)] | | | | | | | | | |
| | **Superfamily Chrysomeloidea (7)** | | | | | | | | | |
| 174 | **Oxypeltidae** | | | | | | | | | L develop in living *Nothofagus* |
| 175 | **Vesperidae** | | | | | | | | | L feed on living roots |
| | *Non-saproxylic subfamilies*: Anoplodermatinae, Philinae, Vesperinae | | | | | | | | | |
| 176 | **Disteniidae** | X | 300 | Most | WW exc Aus | Away | Nec, non | In WD | Unk | L subcortical and in sapwood of dead and dying trees and shrubs (Svacha and Lawrence 2014a) |
| 177 | **Cerambycidae** | X | 35,000 | Most | WW | In, on WD; away | Phyto, nec, non | In WD | Sapro, phyto | Maj of L in dead or dying wood; some L root feeders in soil, in living trees; one leaf miner (Svacha and Lawrence 2014b) |
| | Prioninae | X | 1000 | All | WW | Away | Non (most) | In WD | Sapro | Dead wood, occasionally dead parts of living trees, but not subcortical (Svacha and Lawrence 2014b) |

(continued)

**Table 2.1** (continued)

| # | Taxon | Sap[a] | #Spp[b] | % S[c] | Regions[d] | Adult found[e] | A food[f] | Larva found[e] | L food[f] | Notes |
|---|---|---|---|---|---|---|---|---|---|---|
| | Parandrinae | X | 119 | All | WW | In, on WD | Non | In WD | Sapro | Dead moist logs, dead wood of living trees; sometimes L mature in healed over tree hollows and resultant A reproduce without leaving the tree (Svacha and Lawrence 2014b) |
| | Spondylidinae | X | 100 | Most | WW (adv Aus) | Away | Non | In WD | Sapro, phyto | Maj of L are dead wood feeders, some within dead wood of living trees, few root feeders (Svacha and Lawrence 2014b) |
| | Lepturinae | X | 1500 | Most | WW exc Aus | Away | Poll (most) | In WD | Sapro, phyto | L in moist rotting wood, some subcortical, some in living tree, some root feeders (Svacha and Lawrence 2014b) |
| | Necydalinae | X | 73 | All | Hol, Or | Away | Poll (most) | In WD | Sapro, phyto | L in dead wood, occasionally in living trees (Svacha and Lawrence 2014b) |
| | Dorcasominae | X | 300 | Most | Or, Pal, Afr | Away | Poll (most) | In WD | Sapro, phyto | Some L in living host, most in dead wood, some subcortical, some in herbs or underground (Svacha and Lawrence 2014b) |
| | Cerambycinae | X | 11,000 | Most | WW | Away | Poll, non | In WD | Sapro | L do NOT occur in soft rotten wood, only firm dead wood; rarely subcortical (Svacha and Lawrence 2014b) |
| | Lamiinae | X | 20,000 | Most | WW | Away | Phyto, sapro, myco | In WD | Sapro, phyto | Typically develop in fresh or living hosts; spp. in dead wood require moist wood and fungi, rarely in strongly rotten wood (Svacha and Lawrence 2014b) |

| | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| 178 | **Megalopodidae** | | | | | | | | | Exclusively phyt |
| | *Non-saproxylic subfamilies*: Megalopodinae, Palophaginae, Zeugophorinae | | | | | | | | | |
| 179 | **Orsodacnidae** | | | | | | | | | Exclusively phyto |
| | *Non-saproxylic subfamilies*: Aulacoscelidinae, Orsodacninae | | | | | | | | | |
| 180 | **Chrysomelidae** | X | 35,000 | Few | WW | Away | Phyto, poll | On WD; away | Sapro, phyto | Very few spp. are not exclusively phyto |
| | Cryptocephalinae | X | 5300 | Few | WW | Away | Phyto, poll | On WD | Sapro | Some L are general sapro, occasionally eating outer layer of dead twigs (Chamorro 2014) |
| | *Non-saproxylic subfamilies*: Bruchinae (L develop in seeds), Cassidinae (exclusively phyto), Chrysomelinae (exclusively phyto), Criocerinae (exclusively phyto), Donaciinae (exclusively phyto), Eumolpinae (exclusively phyto), Galerucinae (exclusively phyto), Lamprosomatinae (L feed on bark of living trees), Sagrinae (exclusively phyto), Spilopyrinae (exclusively phyto, with some feeding on bark), Synetinae (exclusively phyto) | | | | | | | | | |
| | **Superfamily Curculionoidea (7)** | | | | | | | | | |
| 181 | **Nemonychidae** | | | | | | | | | Exclusively phyto as L, poll as A |
| | *Non-saproxylic subfamilies*: Cimberidinae, Nemonychinae, Rhinorhynchinae | | | | | | | | | |
| 182 | **Anthribidae** | X | 3861 | Most | WW | In, on WD and fungi | Myco, sapro, phyto | In, on WD and fungi | Myco, sapro, pred | Most myco, some phyto (Mermudes and Leschen 2014) |
| | Anthribinae | X | 3148 | Most | WW | In, on WD and fungi | Myco, sapro, phyto | In, on WD and fungi | Myco, sapro, pred | Maj of spp. develop in bark or wood of trees affected by fungi (Mermudes and Leschen 2014) |
| | Choraginae | X | 630 | Most | WW | In, on WD and fungi | Myco | In, on WD and fungi | Myco | Maj of spp. myco as A and L, developing in fungus-infested wood (Mermudes and Leschen 2014) |

(continued)

**Table 2.1** (continued)

| # | Taxon | Sap[a] | #Spp[b] | % S[c] | Regions[d] | Adult found[e] | A food[f] | Larva found[e] | L food[f] | Notes |
|---|---|---|---|---|---|---|---|---|---|---|
| | *Non-saproxylic subfamily*: Urodontinae (exclusively phyto) | | | | | | | | | |
| 183 | **Belidae** | X | 350 | Some | WW exc Eur | Away | Unk | In WD | Sapro, phyto | Most in reproductive structures of plants; some subcortical in fresh dead, dying branches (Marvaldi and Ferrer 2014) |
| | Belinae | X | 145 | Most | SHem | Away | Unk | In WD | Sapro, phyto | Borers in stems and branches of shrubs and trees (Marvaldi and Ferrer 2014) |
| | Oxycoryninae | X | 200 | Some | WW exc Pal | Away | Unk | In WD | Sapro, phyto | Usu develop in plant reproductive organs, but some (especially Aglycyderini) develop in stems or bark (Marvaldi and Ferrer 2014) |
| 184 | **Caridae** | | | | | | | | | Exclusively phyto |
| 185 | **Attelabidae** | X | 2500 | Few | WW | Away | Phyto | In WD | Sapro | Maj are phyto, some feed in dead twigs (Riedel 2014) |
| | Rhynchitinae | X | 1700 | Few | WW | Away | Phyto | In WD | Sapro | L of 3 spp. of *Lasiorhynchites* feed in young, dead twigs of trees (Riedel 2014) |
| | *Non-saproxylic subfamily*: Attelabinae | | | | | | | | | |
| 186 | **Brentidae** | X | 4400 | Some | WW | In, on WD; away | Sapro, pred | In WD | Sapro, pred, myco | Maj are phyto |
| | Brentinae | X | 1760 | Most | WW | In, on WD; away | Sapro, pred | In WD | Sapro, pred, myco | L are wood borers; some develop within Scolytinae and Platypodinae burrows (Sforzi et al. 2014) |

| | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | *Non-saproxylic subfamilies*: Apioninae (all are phyto), Eurhynchinae (L develop in living branches), Ithycerinae (L develop on cambium and phloem of tree roots), Microcerinae (L develop on herbaceous roots), Nanophyinae (all are phyto) | | | | | | | | | |
| 187 | **Curculionidae** | X | 51,000 | Few | WW | In, on WD; away | Myco, sapro, phyto | In WD | Myco, sapro, phyto | Most are phyto |
| | Dryophthorinae | X | 1200 | Some | WW | In WD | Sapro | In WD | Sapro | In dec and dying stems of cycads (*Phacecorynes* spp) and in dec and rotten wood (Anderson and Marvaldi 2014) |
| | Platypodinae | X | 1400 | All | WW | In WD | Myco | In WD | Myco | Nearly all spp. cultivate and consume fungi in tunnels in sapwood and heartwood (Jordal 2014c) |
| | Brachycerinae | X | 1350 | Few | WW | In WD | Unk | Unk | Unk | A few gen in Myrtonymini and Raymondionymini found in rotting wood, less than 20 spp. (Oberprieler 2014a) |
| | Cyclominae | X | 1550 | Few | WW | Away | Unk | In WD | Sapro | A few spp. of Aterpini with L that bore into dead wood (Oberprieler 2014b) |
| | Molytinae | X | 8700 | Some | WW | In, on WD; away | Sapro | In WD | Sapro | Some from dead wood, including subcortical, some wood borers, some twig or root borers, some on driftwood, some in old dead bamboo, some sap feeders (Lyal 2014a) |
| | Conoderinae | X | 7571 | Some | WW | Away | Myco, sapro | In WD | Myco, sapro | Many spp. borers in dead wood; *Phaenomerus* occupy platypodine tunnels (Prena et al. 2014) |
| | Cossoninae | X | 1700 | Most | WW | In, on WD | Sapro | In WD | Myco, sapro | Many L develop in fresh or rotten wood (Jordal 2014a) |

(continued)

**Table 2.1** (continued)

| # | Taxon | Sap[a] | #Spp[b] | % S[c] | Regions[d] | Adult found[e] | A food[f] | Larva found[e] | L food[f] | Notes |
|---|---|---|---|---|---|---|---|---|---|---|
| | Scolytinae | X | 6000 | Most | WW | In, on WD | Myco, sapro | In WD | Myco, sapro | Most A and L bore into dying wood; about 300 spp. don't use traditional food sources, only a few dozen attack living trees (Jordal 2014b) |
| | Mesoptiliinae | X | 200 | Most | WW | Away | Unk | In WD | Sapro | L in living or dead wood of twigs and branches, in or under bark (Lyal 2014b) |
| | *Non-saproxylic subfamilies*: Curculioninae (all are phyto), Entiminae (L phyto, living freely in soil; A feed on leaves and flowers) | | | | | | | | | |

[a]Sap, saproxylic
[b]World tally of species; numbers are approximate in most cases
[c]% S, estimate of the percent of taxa that are saproxylic, based on our interpretation of the literature: all, 90–100%; most, 50–90%; some, 10–50%; few, <10%
[d]Distribution of the group, without regard to saproxylicity; *adv* adventive, *Afr* Afrotropical, *Aus* Australia, *Ausas* Australasia, *CAm* Central America, *Eur* Europe, *exc* except, *Hol* Holarctic, *Mad* Madagascar, *NAm* North America, *Nea* Nearctic, *Neo* Neotropical, *NG* New Guinea, *NHem* Northern Hemisphere, *NW* New World, *NZ* New Zealand, *Or* Oriental, *OW* Old World, *Pal* Palearctic, *Ptrop* pantropical, *s*, southern, *se*, southeastern, *Sey* Seychelles, *SAm* South America, *SHem* Southern Hemisphere, *STem* Southern Temperate, *w* western, *WI* West Indies, *WW* Worldwide
[e]*Away* away from woody debris, *WD* woody debris
[f]Feeding habits, not limited to saproxylic taxa: *ecpar*, ectoparasitoid; *enpar* endoparasitoid, *ferm sap* fermenting sap flows, *myco* mycophagous, *myxo* myxomycophagous, *nec* nectar, *non* non-feeding, *phyto* phytophagous, *poll* pollen-feeding, *pred* predacious, *sapro* saprophagous, *unk* unknown
Other abbreviations: *A* adult(s), *L* larva(e), *assoc* associated, *dec* decayed/ing, *gen*, genus/genera, *maj* majority, *sp./spp.* species, *usu* usually

Cerambycidae, and Curculionidae. In our view, the most significant poorly studied groups in saproxylic habitats are the Leiodidae, Staphylinidae, Eucnemidae, Ptinidae, Trogossitidae, Laemophloeidae, Silvanidae, Erotylidae, Mordellidae, Melandryidae, Ciidae, Zopheridae, and Tenebrionidae.

Our working definition of saproxylic for this chapter is *any species that would no longer be present in a community if dead and dying woody material were no longer available (including dead and dying wood in live trees)*. This definition is similar to that of Alexander (2008) in that it includes such habitats as sap flows and slime fluxes. For this chapter, we elected to favor a more inclusive definition of saproxylic habitats when deciding about apparently borderline cases. The reason for this was to highlight taxa that have not been traditionally included in discussions of saproxylic organisms in the interest of a more complete survey of beetles associated with woody material. We feel we have provided ample information about the specific habits and habitats of such organisms (where known) so that researchers employing a more restricted definition will be able to unambiguously include or exclude taxa belonging to particular guilds according to whichever scheme is being followed. Additionally, we hope that this more inclusive approach helps encourage future researchers to investigate the true habits and habitat requirements of such nontraditional and otherwise overlooked taxa, particularly where their specific habits and habitats are currently unknown.

As suggested above, the state of knowledge of the habits and habitats of some beetle groups is exceedingly poor, so these numbers are certainly underestimates, though vast numbers of undescribed species are known to occur among both saproxylic and non-saproxylic Coleoptera. Saproxylicity among Coleoptera broadly is a vast and largely unexplored research area, and we encourage other researchers and observers to assist in refining our table of saproxylic beetles. As the core of this contribution, we have included a list of all beetle families and subfamilies, regardless of saproxylicity, in order to (1) facilitate the visualization of errors, omissions, or potential current discoveries, as well as (2) to appreciate the proportion of higher-level diversity with saproxylic members (Table 2.1). It should be clear based on the foregoing that lack of indication of saproxylic habits in the table should not be taken as a positive assertion that the group contains no saproxylic members—immature stages are still undescribed for most described species of beetles (see, e.g., Acorn 2006) and even among described immatures, habits are incompletely known. For groups with saproxylic members, we indicate approximate world species totals, an estimate of the percentage of members saproxylic, world distribution of the group, and more specific habits and habitats where known (by us) through literature surveys, personal observations, and communication with other workers. The primary sources of information for this table were the three volumes of the Handbook of Zoology, Coleoptera volumes {Volume 1: Beutel and Leschen (2005) [updated version: Beutel and Leschen (2016a)]; Volume 2: Leschen et al. (2010); Volume 3: Leschen and Beutel (2014)}, the two volumes of American Beetles [Volume 1: Arnett and Thomas (2000); Volume 2: Arnett et al. (2002)], the Coleoptera chapter of immature insects (Lawrence 1991), references contained within these sources, and a smattering of other sources cited in the text and "Notes" section of Table 2.1. Since the two active stages of beetles, larvae and adults, often have dramatically different habits or habitats, we created two different columns and indicate habits and habitats for both, even in the case of larval- or adult-only saproxylic taxa. Entries concerning habits and feeding types refer to the group as a whole and not just to saproxylic members. We hope this will be a helpful tool for those investigating the presence of particular saproxylic taxa, since indirect surveys can be a viable alternative to directly sampling saproxylic habitats.

The classification used here recognizes 187 beetle families, of which 122, or about 65%, contain at least one known saproxylic member (Table 2.1). Saproxylic beetles are represented in three of the four suborders of beetles—only Myxophaga lacks known saproxylic members. Our current state of knowledge indicates that there are 32 beetle families in which all or virtually all species (90–100%) would be considered saproxylic, 31 families in which most species (50–90%) are saproxylic, 35 families with some species (10–50%) that are saproxylic, 22 with a few (<10%) saproxylic species, and one family (Trictenotomidae) for which no estimate can be given. Adults of saproxylic species are found within woody debris in about 61 families, on woody debris or fungi in 64 families, and away from woody debris in 43 families (categories overlapping, not cumulative). Where known, adults are mostly (in descending order) mycophagous, saprophagous, and predacious, with a few that are phytophagous, non-feeding, pollen-feeding, nectar-feeding, sap-feeding, or myxomycophagous. Adult feeding is unknown for about 27 families. Larvae of saproxylic species are found within dead wood for about 100 families and on dead wood or fungi in about 49 families. Where known, larvae are mostly mycophagous, saprophagous, or predacious with a very few myxomycophagous, phytophagous, sap-feeding, or parasitic. Larval feeding is unknown for about seven saproxylic families.

## 2.5 Conclusion

The primary purposes of this chapter were twofold: firstly, to assemble what is known concerning the higher beetle taxa associated with the saproxylic habitat and provide a broad summary thereof. While we did not attempt an exhaustive review of the topic, we hope that the information and resources provided in this chapter provide sufficient ordnance to successfully storm the landscape of this topic and further interrogate particular saproxylic beetle groups.

Secondly, this chapter provides a map of sorts to parts of the saproxylic beetle landscape, highlighting those that are unknown, veiled, and beyond the wall of ignorance. Table 2.1 is bespotted with the term "unk" (i.e., unknown, 153 times!), to us evoking the spots that cover the fawn of a white-tailed deer—immature, gangly, and unsure of itself and the world. Our knowledge of saproxylic beetles is in much the same state, a long way from maturity. The reader is provided with a thin guide that we hope will be useful when marshalling resources and directing excursions into that mysterious realm. Every "unk" is an opportunity for future students of the topic to help piece together the complex tapestry of saproxylic beetle natural history.

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