Evolution and Diversity of Bark and Ambrosia Beetles

Chapter · July 2015

DOI: 10.1016/B978-0-12-417156-5.00003-4

Lawrence Kirkendall
University of Bergen
92 PUBLICATIONS **1,691** CITATIONS
SEE PROFILE

Peter H W Biedermann
University of Wuerzburg
60 PUBLICATIONS **717** CITATIONS
SEE PROFILE

Chapter 3

Evolution and Diversity of Bark and Ambrosia Beetles

Lawrence R. Kirkendall[1], Peter H.W. Biedermann[2], and Bjarte H. Jordal[3]

[1] Department of Biology, University of Bergen, Bergen, Norway [2] Research Group Insect Symbiosis, Max Planck Institute for Chemical Ecology, Jena, Germany [3] University Museum of Bergen, University of Bergen, Bergen, Norway

1. INTRODUCTION

> *"No other family of beetles shows such interesting habits as do the members of the family Ipidae."*
>
> —Milton W. Blackman, 1928

Most wood-boring insect species only tunnel in wood as larvae. Their adults are free-flying insects that must move about the landscape to encounter mates, find food, and locate oviposition sites; in so doing, they face a myriad of invertebrate and vertebrate predators, and must deal with the vagaries of wind, temperature, and precipitation. A few beetles, however, have evolved to spend nearly their entire adult lives inside woody tissues. Bark beetles (Scolytinae) and pinhole borers (Platypodinae)—which we will refer to collectively as bark and ambrosia beetles—are weevils that have lost their snouts and that spend most of their adult existence ensconced in dead wood (occasionally, in other plant tissues), and by many measures, they are the most successful lineages to do so. In this chapter, we will document and discuss the striking variability in biology of these weevils.

Wood is important to humans in many ways, and bark and ambrosia beetles are abundant in forests and plantations, so it is not surprising that there is a long history of interest in these relatively small and nondescript insects. Carl Linnaeus, the father of modern taxonomy and one of the founders of ecology, described five species of Scolytinae, including four of the most common European species, which he described in 1758 (*Trypodendron domesticum*, *Tomicus piniperda*, *Polygraphus poligraphus*, *Ips typographus*, and *Pityogenes chalcographus*) (Linnaeus, 1758). There are Scolytinae and Platypodinae in the beetle collections of the fathers of evolutionary theory, Charles Darwin and Alfred Russel Wallace, and the latter even published on them (Wallace, 1860). It is only in the first half of the 20th century though that we first began to be aware of the wealth of details of their fascinating but cryptic lives.

1.1 Topics and Taxonomic Coverage

We will focus on the evolution and ecology of feeding and breeding biology, especially mating systems and social behavior. Much of this variation is little known outside of a small circle of specialists, as the vast majority of basic and applied research in Scolytinae and Platypodinae is focused on a handful of serious forest and agricultural pests that have considerable economic and ecological impact. Though well deserving of research, these taxa are not representative of bark and ambrosia beetle biology as a whole. We will not cover population ecology or pheromone biology, as these topics are much more widely known and have been thoroughly addressed in many research and review articles, in this book (Chapters 1, 4, and 5), as well as in other books, e.g., Chararas (1962), Berryman (1982), Mitton and Sturgeon (1982), Speight and Wainhouse (1989), Lieutier *et al.* (2004), and Paine (2006). We will also let others review in detail the growing and fascinating topic of relationships with fungi and other symbionts (but see Section 3; Chapter 6).

There are currently 247 genera of recognized Scolytinae (see Appendix), most of which breed predominantly or entirely in angiosperms (Figure 3.1); 86% of these genera are represented in the tropics or subtropics, and 59% are restricted to these warmer regions (Chapter 2). In terms of numbers of species, 79% (four of five) are found primarily in tropical or subtropical ecosystems. Less than 1% of the ca. 6000 Scolytinae species regularly kill healthy standing trees, and from the existing literature it seems unlikely that more than 5 to 10% occasionally do so (but see Section 3.9).

Books dealing with the biology of Scolytinae (or of Scolytinae plus Platypodinae) often reflect biases towards species breeding in temperate conifer forests or vectoring pathogens with significant impact on urban or ornamental broadleaf trees (e.g., Chararas, 1962; Mitton and Sturgeon, 1982; Lieutier *et al.*, 2004). It is hoped that this

Bark Beetles. http://dx.doi.org/10.1016/B978-0-12-417156-5.00003-4

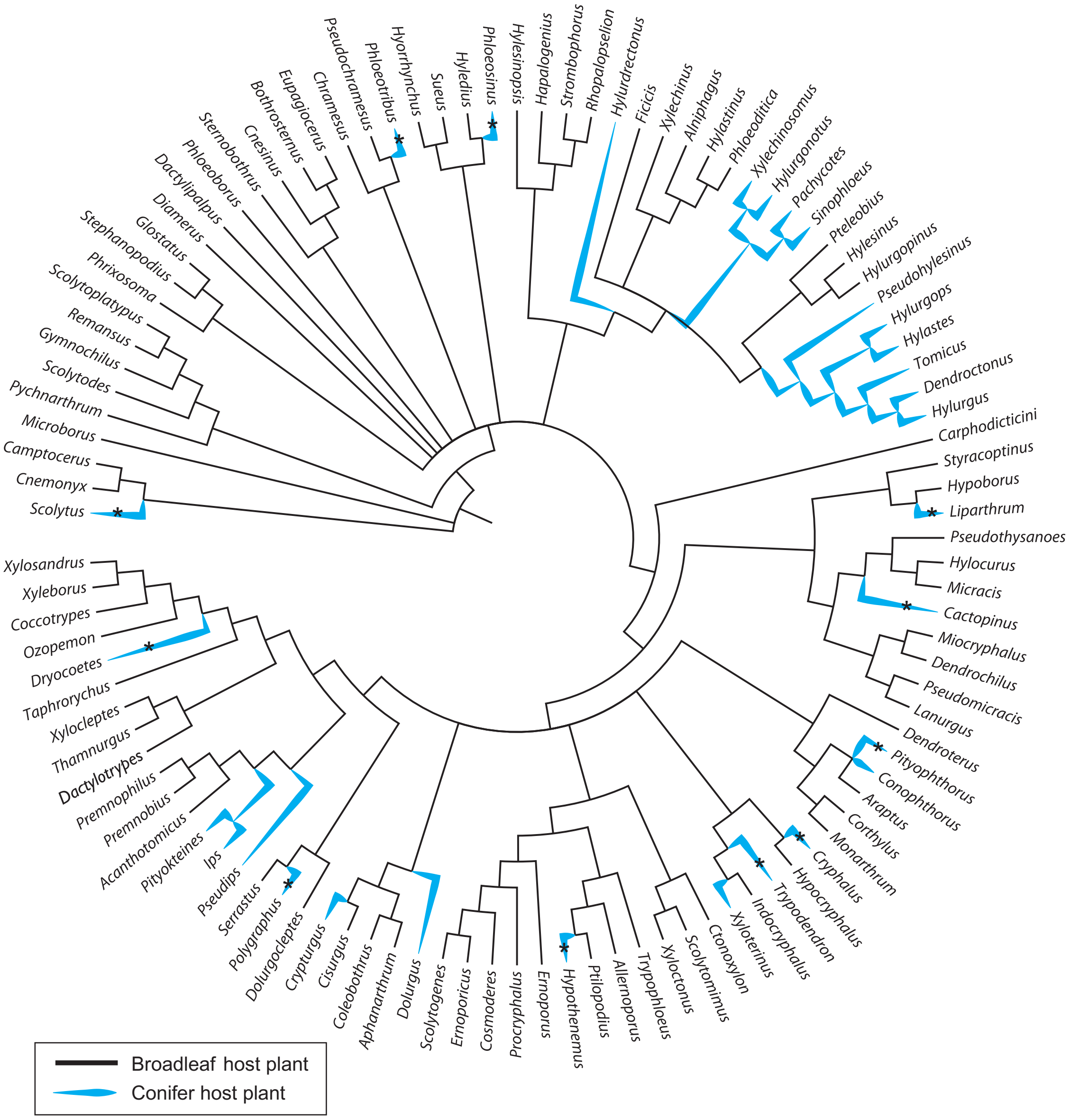

FIGURE 3.1 **Phylogenetic tree of Scolytinae indicating associations with broadleaf and conifer host plants.** The tree used here and in Figures 3.4 and 3.7 summarizes phylogenetic results based on molecular data with unresolved relationships resolved in part based on morphological evidence (Normark *et al*., 1999; Farrell *et al*., 2001; Jordal *et al*., 2008, 2011; Jordal and Cognato, 2012).

chapter can help to redress this imbalance (see also Chapters 1, 11, and 12).

For less (in)famous bark and ambrosia beetles, information on ecology and behavior can be gleaned from regional or global faunal works by, for example, Thomas Atkinson and colleagues (see references), Roger Beaver (see references), Cyril Beeson (1941), Maulsby Blackman (Blackman, 1922; Blackman and Stage, 1918, 1924), Francis George Browne (1961), Willard Joseph Chamberlin (1939, 1958), Constantin Chararas (1962), L. G. E. Kalshoven (1959, 1960b), Akira Nobuchi (1972), Karl E. Schedl (1961, 1962a, b), James Malcolm Swaine (1918), and Stephen L. Wood (1982, 2007). Besides the sources of natural history information mentioned above, there are recent, more quantitative treatments of bark and ambrosia beetle ecology, biogeography, and phylogeography: ecological aspects of bark and ambrosia beetle biodiversity (Ødegaard, 2000, 2006; Ødegaard *et al*., 2000, 2005; Hulcr *et al*., 2007, 2008a, b; Novotny *et al*., 2007, 2010); island biogeography (Kirkendall, 1993; Jordal *et al*., 2001); and phylogeography (Cognato *et al*., 1999; Jordal *et al*., 2006; Maroja *et al*., 2007; Cai *et al*., 2008; Schrey *et al*., 2011; Garrick *et al*., 2013; Jordal and Kambestad, 2014).

Only a few aspects of bark beetle evolutionary biology have been reviewed for Scolytinae (or Scolytinae and Platypodinae) as a group: mating systems (Kirkendall, 1983); inbreeding and other sources of biased sex ratios (Kirkendall, 1993); the evolution of social behavior (Kirkendall *et al.*, 1997); and the evolutionary history of bark beetles and pinholes borers (Jordal *et al.*, 2011; Jordal, 2014a, b, c; Chapter 2).

1.2 Why We include Platypodinae

We have chosen to include Platypodinae ("pinhole borers") in our chapter (as Hulcr *et al.* did in Chapter 2), primarily with respect to mating and social behavior. The extreme morphological similarity of Platypodinae to Scolytinae has bedeviled systematists for decades, and highlights the importance of convergent evolution in wood-tunneling beetles (Figure 3.2). Pinhole borers were long treated by entomologists as a separate family, closely related to "Scolytidae." More recently, phylogenies based on molecular and morphological characters strongly suggest that this group, too, is a highly derived group of weevils, but the Platypodinae may not even be closely related to Scolytinae (reviewed in Chapter 2, but also see McKenna *et al.* (2009), Jordal *et al.* (2011), McKenna (2011), Haran *et al.* (2013), and Gillett *et al.* (2014)).

Virtually all broadly oriented bark beetle specialists have worked with both groups (and usually primarily or exclusively these two), which until recently were considered to be two very closely related but separate families, Platypodidae (ca. 1400 species) and Scolytidae (ca. 6000 species). Platypodine biology seems to only be known to Scolytinae researchers and a few generally oriented forest entomologists: we are not aware of the existence of any specialists who restrict their focus to Platypodinae. It has become common practice to include both Scolytinae and Platypodinae in taxonomic, faunistic and ecological works, and until fairly recently to refer to them jointly as "Scolytoidea" (Hubbard, 1897; Blackman, 1922; Beal and Massey, 1945; Pfeffer, 1955, 1995; Schedl, 1962b, 1974; Chamberlin, 1939, 1958; Kalshoven, 1960a, b; Browne, 1961; Nunberg, 1963; Nobuchi, 1969; Bright and Stark, 1973; Beaver and Browne, 1975; Kirkendall, 1983; Atkinson and Equihua-Martínez, 1985a; Wood and Bright, 1987, 1992 and subsequent supplements; Beaver, 1989; Atkinson and Peck, 1994; Kirkendall *et al.*, 1997). Scolytine and platypodine ambrosia beetles are frequently collected together in dead and dying trees. Platypodinae are strikingly similar to monogynous scolytine ambrosia beetles in gross morphology, tunnel system architecture, use of chemical and acoustic signals, mating behavior, social behavior, and relationships with symbiotic fungi. All but the most basal platypodines are monogynous ambrosia beetles with extensive parental care; one species, *Austroplatypus incompertus* (Schedl), is notable for being eusocial (Kirkendall *et al.*, 1997).

2. WHAT ARE BARK AND AMBROSIA BEETLES?

2.1 Phylogenetics

Why tunnel? Foraging in the green is a dangerous place. Being exposed to parasitoids and predators—and occasionally extreme competition from hyperdiverse insect communities—as well as to wind, rain, and occasional extreme temperatures can generate a selective advantage for a complete life cycle inside dead plant tissues. Although less nutritious, such resources are less hostile in terms of physical and chemical defenses mustered by live plants.

In fact, life under bark has evolved multiple times in weevils (McKenna *et al.*, 2009; Jordal *et al.*, 2011; Haran *et al.*, 2013; Gillett *et al.*, 2014) (Figure 3.2). Most, or

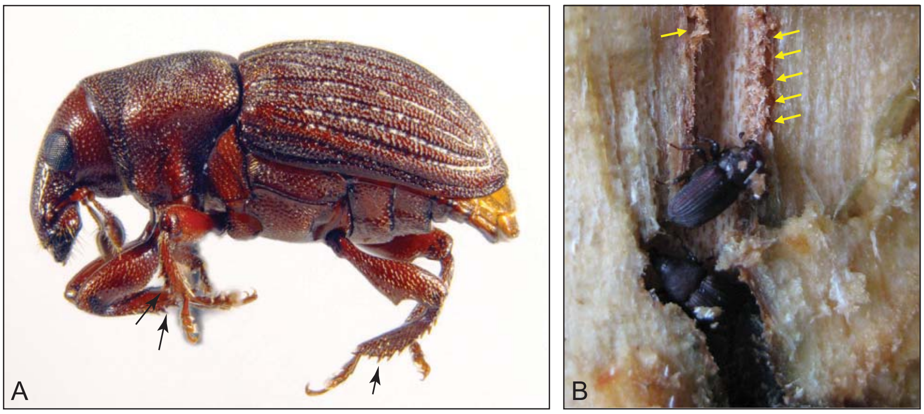

FIGURE 3.2 **Convergence in wood-boring weevils: the genus *Homoeometamelus* (subfamily Baridinae or Conoderinae, tribe Menemachini).** (A) Lateral view; note the lateral socketed teeth on all tibiae (arrows), of the same type as in many Scolytinae. (B) Mating niche with longitudinal egg tunnel; arrows point to eggs laid in niches.

perhaps all, wood-boring groups are old, originating at least some 90–120 millions of years ago (Ma). The oldest scolytine fossil is known from Lebanese amber that dates back to Mid-Cretaceous some 120 Ma (Kirejtshuk *et al*., 2009). This is about the same age as the oldest known Curculionidae known from the Santana formation in Brazil (116 Ma) (Santos *et al*., 2011). The Lebanese amber fossil *Cylindrobrotus pectinatus* Kirejtshuk, Azar, Beaver, Mandelshtam and Nel is not closely related to any extant or fossil lineage of Scolytinae, but has all defining morphological characters of a bark beetle. Another fossil (100 Ma) from Burmese amber belongs to the current genus *Microborus*, which may indicate that Scolytinae was well established as a dominant group already at that time (Cognato and Grimaldi, 2009).

Platypodinae has a less documented fossil record, but is represented by tesserocerine and platypodine inclusions in Mexican, Dominican, Sicilian, and Rovno ambers (Schedl, 1972; Bright and Poinar, 1994). This group is much older, however, and two fossils from Burmese amber indicate possible tesserocerine affinity (Cognato and Grimaldi, pers. commun.), in accordance with molecular age estimates (McKenna *et al*., 2009; Jordal *et al*., 2011).

The exact phylogenetic position of Scolytinae is uncertain, but it is now well documented that this group originated at the same time as modern phytophagous curculionids (McKenna *et al*., 2009; Jordal *et al*., 2011; Haran *et al*., 2013; Gillett *et al*., 2014). Soon after the split between the broad-nosed weevils and most other groups of advanced weevils, Scolytinae makes up a consistently monophyletic group closely related to typical long-nosed weevils such as Molytinae, Cryptorrhynchinae, Baridinae, Curculioninae, and Cossoninae. They may not be closely related to Platypodinae, which seem more closely related to Dryophthorinae than to Scolytinae (McKenna *et al*., 2009; Gillett *et al*., 2014).

It seems certain that the wood-boring habit evolved from external feeding on green leaves. Herbivorous Scolytinae exist today, but none of these are basal lineages in the phylogenetic tree of bark and ambrosia beetles. The closest match is the Scolytini genus *Camptocerus*, where adults feed on green leaves before tunneling into the bark to breed (Smith and Cognato, 2011). With rare exceptions, Scolytinae are restricted to denser, drier plant tissues such as those in stems and branches of trees and shrubs. Few taxa can deal with the typically soft, very moist tissues associated with herbaceous plants. Even most species categorized as "herbiphagous" breed in the dense supportive tissues of stems or leaf petioles, not in leaves.

2.2 General Morphology

Bark and ambrosia beetles are highly adapted morphologically and ecologically to this unusual lifestyle and to the special challenges of constructing and living nearly their entire adult lives in tunnels. The adaptation to a life in concealed niches in dead lignified plant material apparently followed a distinct selection regime with consequences for morphological change. The change in diet from green leaves to bark, wood or fungi has modified both the external chewing appendages as well as the internal digestive system. Boring in bark and wood also dramatically changed their reproductive biology due to control of valuable resources in the form of durable, protective tunnels. Control of access to the tunnel by the opposite sex has therefore led to a variety of behavioral and morphological changes in the context of optimal mate choice. Maintenance and protection of tunnels has furthermore led to changes in morphology to optimize movement in the tunnel, shoveling of frass, and the blocking of the entrance hole.

Life in tunnels and caves places obvious restrictions on body shapes, since protuberant body parts would limit movement and flexibility. Adult beetles that bore into wood are generally cylindrical, as are bark and ambrosia beetles (Haack and Slansky, 1987). In addition, all bark and ambrosia beetles have large, flattened eyes and short antennae that can be folded into the body. A unique feature involves vertically enlarged eyes, which extend from the vertex to the gula, sometimes slightly or even completely divided where the antennal scape attaches and folds back. It is not known if eye enlargement has evolved due to a life in near darkness, but we note that certain weevil groups, which do not tunnel as adults (such as many conoderines), also have large, flat, contiguous eyes.

Excavation of tunnels requires a considerable biting force, and scolytines and platypodines have larger mandibles than most other weevils. Mandibles are short and thick, and have strong muscles attached (Schedl, 1931). The chewing procedure varies depending on whether the woody tissue is ingested for food or simply chopped up to be removed, as in most ambrosia beetles. These bore new tunnels by cutting with their mandibles during back and forth movements of the head and rotation of the whole body within the tunnel. By contrast, when feeding, they crop the enlarged nutritious spores ("ambrosial growth") of their fungi by horizontal movements of the maxillae (which have comb-like hairs or structures at the end) and swallowing movements of the labrum. Effective chewing of wood bits is enabled by a flexible rotating head with strong muscle attachments.

Wood-boring beetles are generally well equipped with cuticular structures that aid in pushing and scraping, such as various spines and socketed denticles on the tibiae (penultimate leg segment) (Swaine, 1918). While a terminal tibial spine (uncus) is commonly seen across the weevils, many scolytines have additional socketed denticles along the lateral edge of the tibiae. These denticles are typically evolved from ordinary hair-like setae, and their socketed origin is clearly visible (Wood, 1978), although they are sometimes reinforced and overgrown by cuticle (Jordal, 1998). It is unclear how important such denticles are for wood-boring beetles given that several groups are lacking denticles, such as *Scolytus* and close relatives, most wood-boring cossonines, and in Platypodinae, the latter instead have developed sharp ridges and rugae on their protibiae (Strohmeyer, 1918). On the other hand, we do see similarly developed denticles in unrelated wood-boring groups such as Amorphoceriini (Molytinae), Araucariini (Cossoninae), Campyloscelini (Baridinae), and in certain bostrichid wood borers as well as for digging insects in general (e.g., scarabs) (Figure 3.2).

Some scolytines are cleptoinquilines, and take over ready-made nests of ambrosia beetles, killing or ejecting the original tenants in the process. These species have developed dramatic features such as a sharply prolonged anterior pronotum and various elaborately sculpted sharp elongations of the declivity; the former often takes the form of a pointed hood with or without a terminal hook (Figure 3.3F). Nest parasitism is most common among corthylines in the genera *Tricolus* and *Amphicranus* and

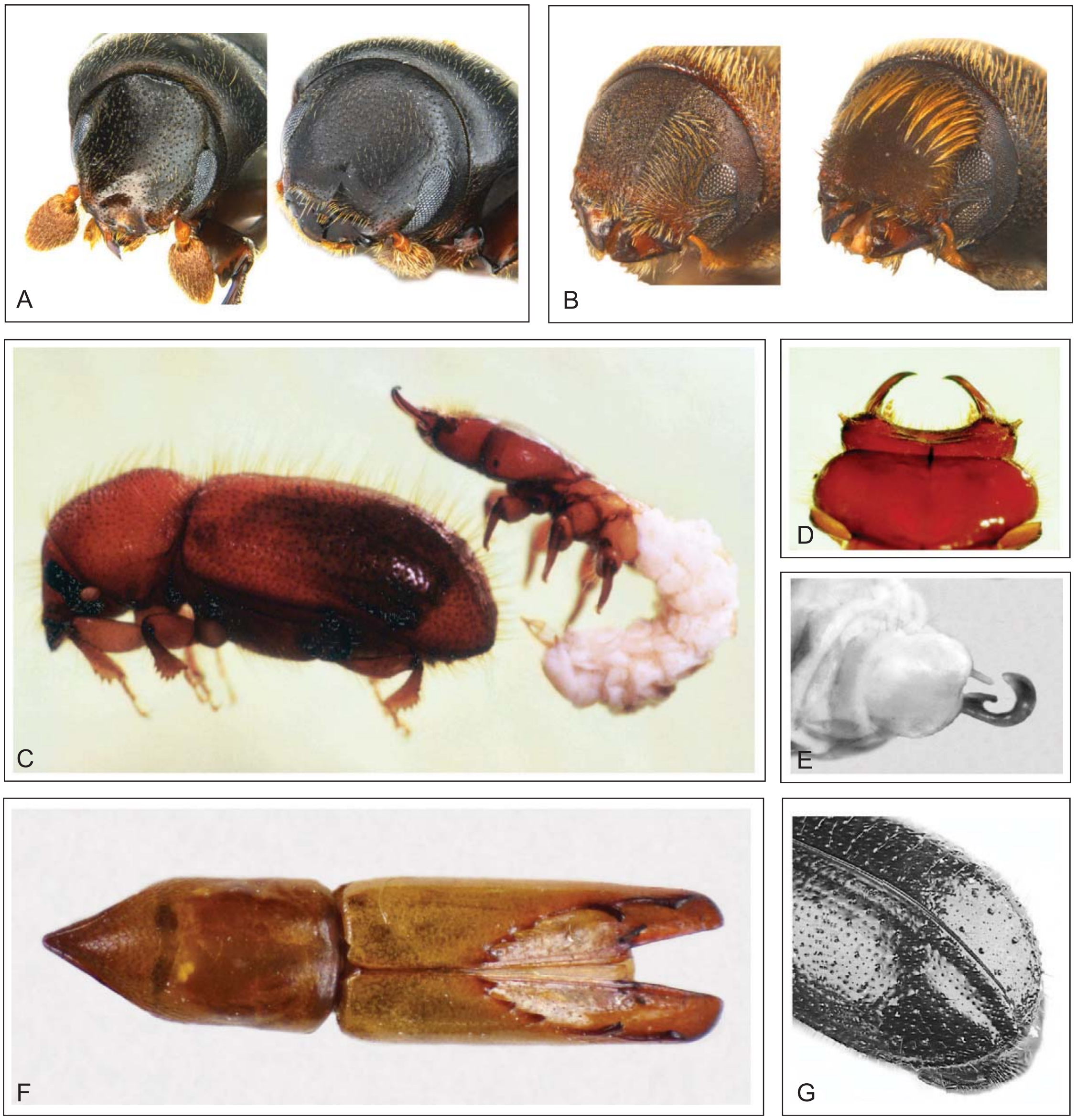

FIGURE 3.3 **Morphology of Scolytinae.** (A, B) Sexual dimorphism, here represented by different shapes of the frons. (A) Male and female *Scolytoplatypus rugosus* Jordal. (B) Male and female *Phrixosoma concavifrons* Jordal. (C–E) Extreme sexual dimorphism in an inbreeding bark beetle. (C) Male (left) and female (right) siblings of *Ozopemon uniseriatus* Eggers. (D) Head features of the male. (E) The male is fully developed and reproductively mature, note the aedeagus. (F, G) Examples of declivity variation. (F) *Amphicranus fastigiatus* Blandford, holotype. (G) *Tomicus piniperda* (L.).

in the xyleborine genus *Sampsonius*. As with declivital teeth and spines in Scolytinae and Platypodinae (Hubbard, 1897; Hamilton, 1979), it is likely that acute developments on the front and back end of the cleptoinquilines are used in fighting and tunnel defense. Other weevil groups also take over ambrosia beetle tunnels, for instance in Brentidae (Kleine, 1931; Beeson, 1941; Roberts, 1969; Sforzi and Bartolozzi, 2004) and in the baridine subtribe Campyloscelina (Schedl, 1972; Thompson, 1996), and these show strikingly similar morphological adaptations.

Life in tunnels has led to multiple origins of fungus farming, including 10 times or more in Scolytinae and once in Platypodinae (Jordal and Cognato, 2012). Shifting from consuming woody to fungal tissues (which are softer and require less chewing) selects for changes in mouthpart and digestive tract morphologies. While phloem-feeding bark beetles have their maxillary laciniae fringed by coarse bristle-like setae, those feeding solely on fungal mycelium and conidia have very fine hair-like setae (Jordal, 2001). We see the same trend in the proventriculus that is situated in the alimentary tract in the prothorax and which functions like the gizzard of birds (Nobuchi, 1969). The normal condition for a bark beetle is to have a strongly sclerotized proventriculus with a large anterior plate containing nodules, teeth or transverse ridges. All ambrosia beetles have their anterior plate strongly reduced or totally absent. Remnants of the anterior plate are most evident in some of the most recently evolved lineages of ambrosia beetles such as Xyleborini and Premnobiina (Ipini), each roughly 20 million years old (Jordal and Cognato, 2012; Cognato, 2013). In each of these groups, the anterior plate is clearly visible, but very short and less sclerotized.

Finally, access to a tunnel for food and reproduction is limited in the sense that the tunnel-initiating individual can control access. This has consequences for mate recognition and mate choice, and for how late arrivals such as nest parasites and predators are rejected. The largest variation in morphological traits is therefore not surprisingly seen in body parts associated with tunnel blocking (discussed further in Section 2.3). Morphological adaptations to blocking the entrance to gallery systems are primarily seen in the declivity. Many taxa have evolved various teeth, knobs, and ridges on the declivity. Though there are few observations and no experiments on the function of these, Hubbard (1897) and Hamilton (1979) have hypothesized that especially the sharp teeth often seen on the borders or apex of the declivity function as weapons of defense against potential rivals and natural enemies. The overall shape of the declivity is likely also an adaptation to burrow blocking, particularly in species with flat or convex declivities, as the back end of the beetle ideally should fit the curvature of the outer bark surface as seamlessly as possible. This hypothesis could be tested by comparing the degree of curvature of the declivity (for the blocking sex) with the surface curvature of preferred host material, where one would expect to find flatter declivities in species regularly breeding in large diameter trunks and more strongly curved declivities in species with strong preferences for twig and small branches or thin stems.

Alternatively, in some taxa, the ventral aspect of the abdomen may be partly or entirely involved in forming the hind end of the beetle. In such cases, the apex rises more or less sharply, involving all or just the last few sternites depending on the group. The venter is only weakly raised in *Xyloctonus* and certain cryphalines, but rises steeply from the second ventrite in *Scolytus* and close relatives. In the latter group, the venter completely takes over the role of the declivity, in forming the hind end, which blocks the entrance. Development of the venter in this manner is extreme in the Platypodinae genera *Doliopygus* and *Mesoplatypus* (Strohmeyer, 1918; Schedl, 1972).

A cryptic lifestyle makes coloration less important for wood-boring beetles compared to those living in the outside world. Very few groups show any coloration beyond shades of brown; the color of mature adults ranges from dark yellow to reddish brown to black. The only significant exception to this pattern is found in three species of *Camptocerus*, a genus closely related to *Scolytus* (Smith and Cognato, 2010, 2011). The metallic green to bronze shine is unique to these species (see Fig. 2.7 in Chapter 2). Although the function of the metallic shine is completely unknown, it is interesting that species in this genus are also unique in spending extended periods aggregating and feeding on green leaves, before moving into wood (Smith and Cognato, 2010, 2011).

Scolytinae beetle bodies are usually 2–3 times as long as wide and fairly parallel sided; they vary in size from ca. 0.5 mm to a little over a centimeter in length, and most species fall in the range 1 to 4 mm long. There is no strong correlation between diameter of breeding material and body size: one finds small species that prefer larger trunks, and medium to large species that breed in branches or even twigs. Platypodines are more slender and on average longer, and they are more frequently confined to trunks and medium to large branches than are scolytines. Browne (1961) has speculated that there may be an evolutionary trend towards small body size, driven by selection for escaping predators that use tunnel entrances to get into gallery systems, especially with respect to ambrosia beetles. This intriguing hypothesis has yet to be tested comparatively. Scolytinae as a group are the smallest of the major groups of wood-boring insects, and platypodines are among the smallest (Haack and Slansky, 1987).

Within species-specific limits, body size of wood-boring beetles such as scolytines and platypodines is generally determined by the quality and amount of food consumed by larvae (Andersen and Nilssen, 1983; Kirkendall, 1983; Haack and Slansky, 1987; Kajimura and Hijii, 1994). Resource quality, in turn, is affected strongly by factors such as how fresh or old the breeding material is, remnants of defensive chemicals, and presence of fungi and microorganisms, while quantity is affected by factors such as inner bark thickness (for phloeophagous species), tunnel length (for ambrosia beetles), and density of competing larvae of the same or different species. Body size is important in natural selection (fecundity, survivorship), and sexual selection (fighting, mate choice), and affects features such as survival in cold temperatures (e.g., *Dendroctonus*; Safranyik, 1976), attractant pheromone production (Anderbrandt *et al*., 1985), and anti-aggregation pheromone production (Pureswaran and Borden, 2003).

2.3 Sexual Dimorphism

Sexual selection is a powerful evolutionary force (Darwin, 1859; Shuster and Wade, 2003), and has surely been a prime factor in the evolution of sex differences in bark and ambrosia beetles. Dimorphic features are especially common in the frons (Figure 3.3) and declivity, and often in the underside of the abdomen (venter). This is to be expected, since characters involved in mating behavior (primary and secondary sexual characters) often evolve more rapidly than other morphological features (Civetta and Singh, 1999), and the frons, declivity, and venter are directly involved in mating behavior. As is often the case, the features exhibiting sexual dimorphism are frequently the best characters for separating closely related species, and are presumably used by the beetles themselves in species recognition as well as mate recognition.

Courtship in both Scolytinae and Platypodinae involves primarily tactile, chemical, and acoustic stimuli. Typically, the courting sex rubs or bumps the frons against the declivity or venter of the first arriving sex. There is evidence for specific types of setae in these body regions that match between the different sexes of a species, such as in *Scolytus* (Page and Willis, 1983). Species in many outbreeding bark and ambrosia beetle genera are therefore diagnosable mainly based on extravagant sculpturing or ornamentation (such as long setae) seen in only one of the sexes, commonly of the frons (Figure 3.3). Very generally, the frons of the courting sex is frequently flat or concave, while that of the colonizing sex is convex, and frequently the frons of the courting sex has longer or denser setae (S. L. Wood, 1982). In species with a dimorphic frons, individuals of the courted sex from closely related species might be identical in frons features, while frons characters are diagnostic in the courting sex. If there is noticeable sexual dimorphism in features of the declivity, such as degree of concavity or presence and size of teeth or spines, these characters are most developed in the courted (pioneering) sex. However, both frons and declivity can be monomorphic or nearly so; it is not clear why some species are distinctly sexually dimorphic and others not so.

Characters other than the frons and declivity can be sexually dimorphic as well. Some of these, such as modifications of the antennae, or of the shape or setation of the last ventral abdominal segment, are certainly associated with acquiring mates or with copulation, but others (such as modifications of legs or pronota) may be adaptations to differences in sex roles (including differences in which sex carries symbiotic fungi). The basal antennal segments may differ in shape and setae pattern. For example, individuals of the courting sex (females) in most Micracidini have dense, long setae on the antennal scape, which are not present in the pioneering sex (males); a similar antennal scape dimorphism occurs in *Chramesus* and some *Camptocerus*, but in these genera it is males who court and who bear the long setae on the scape (S. L. Wood, 1982). In *Camptocerus noel* Smith and Cognato, it has been confirmed that the setal brush on the scape is used quite actively in courtship (Smith and Cognato, 2011). In many corthyline ambrosia beetles, the antennal club is enlarged (extremely so in *Corthylus*) and may be different in shape in females (the courting sex). The pronotum is differently shaped in *Trypodendron* (S. L. Wood, 1982), and in some groups (such as *Phloeoborus*, *Scolytoplatypus*, some *Cryphalus*, and some *Scolytodes*) the sexes differ in surface sculpture of the pronotum. The sexes of *Scolytoplatypus* differ dramatically in the protibiae and procoxae (segments of the first pair of legs). The protibiae of females have a rougher surface and more strongly developed teeth (Beaver and Gebhardt, 2006; Jordal, 2013), characters that we speculate might be an adaptation to fungus farming in these ambrosia beetles.

An additional difference between the sexes (occasionally the only one) is body size. Although the pattern has yet to be investigated systematically, it is clear from the average measurements in taxonomic treatments (such as S. L. Wood, 1982, 2007; Jordal, 1998) that, where size differences exist, it is the pioneering sex that is the larger. This is generally associated with mating system, females being the larger sex in monogynous species and males in harem polygynous species (see also Foelker and Hofstetter, 2014). This pattern for size dimorphism in outbreeding species may arise from differences in selection on the two sexes. Females are generally larger in insects, including weevils, probably because of fecundity selection on females being stronger than any selection for large size in males. However, in harem polygynous species, there is likely both intrasexual and intersexual selection for large male size (males being the pioneering sex, and the sex with greater variance in reproductive success), and in these cases this seems to be stronger than fecundity selection on conspecific females.

Sexual selection is presumably weak or absent in extreme inbreeders, where many species frequently or regularly have only one male per brood. Interspecific differences in the frons of females from related species are weak or nonexistent. Declivital differences do exist for females of related inbreeding species, especially in xyleborines, but overall interspecific differences in groups of related inbreeders seem to be much less than those found in groups of related outbreeders.

Sexual dimorphism in extreme inbreeders takes a very different form than that for outbreeding species, and is consistent with patterns found in other regularly inbreeding arthropods (Hamilton, 1967). Males of regularly inbreeding Scolytinae are rare, and are usually smaller (considerably smaller in many species), are less sclerotized, and are differently shaped; they have reduced eyes (Vega *et al.*, 2014) and males cannot fly because the second pair of wings is vestigial. Curiously, there are some striking exceptions. In certain unusually large species of Xyleborini (such as the *Xyleborus princeps* group of species), males are very similar to females in both size and shape. *Cyclorhipidion* males are about the same size as females, but have the pronotum more elongated. *Dendroctonus micans* (Kugelann) and its sister species *D. punctuatus* LeConte are unique among inbreeding Scolytinae in their lack of significant sexual dimorphism; in these species, males are very similar to females in size, and can in fact fly (see Section 4.2). At the other extreme is *Ozopemon*, a genus of haplodiploid, phloeophagous inbreeding scolytines that comprise one of only two examples in Coleoptera of larviform males (Jordal *et al.*, 2002). Sexual dimorphism is so extreme in *Ozopemon* (Figure 3.3C–E) that for about 50 years the rarely collected larva-like males were thought by some leading beetle experts to belong to the family Histeridae (Crowson, 1974).

One rare form of dimorphism in Scolytinae involves the development of horn-like structures on the anterior (rather than posterior) part of the body. Long horns are a particularly striking feature of many *Cactopinus* species, where they originate from the lower part of the frons. Various forms of nodules or carinae are found on the frons of a variety of scolytines, but the large size of these horns is a unique feature for this genus. A few other genera have small spines originating from the mandibles of the courting sex, such as in male *Triotemnus* (Knížek, 2010) and other dryocoetines, female *Styphlosoma* (S. L. Wood, 1982), female *Araptus araguensis* Wood, *Phelloterus* females (Wood, 2007), or female *Diapus* in Platypodinae. At least for *Diapus*, the mandibular teeth are dehiscent and only used during courtship to pull out the pioneering male (Beaver, 2000). Mandibles are greatly enlarged in the courting sex in *Gnatholeptus* females and *Phelloterus* females (Wood, 2007). The role in courtship behavior of these mandibular adaptations is not known.

Dimorphism is also frequently expressed on the declivity of the elytra. The blocking sex can have more strongly developed or a larger number of spines, teeth, or setae, and can have the declivity more flattened or concave than in the other sex. Such differences are so pronounced in, for example, the ambrosia beetle genera *Amphicranus* and *Gnathotrupes* that specialists have occasionally initially assigned males and females to different species or even different genera. However, it should be emphasized that sexual dimorphism of the declivity in many genera is very mild or nonexistent; in our experience, interspecific differences in the declivity are more frequent than intersexual differences, and are a great aid in separating closely related species. Hypothesized functions of features of bark and ambrosia beetle declivities have never been seriously analyzed or studied experimentally, which is unfortunate given the extraordinary variation that can be found within both Scolytinae and Platypodinae.

The various shapes of spines and tubercles on declivities may well serve several purposes, the most obvious possibilities being mate recognition and effective shoveling of frass. Though we can find few mentions of the idea in the literature (as mentioned above, Hubbard, 1897 and Hamilton, 1979), specialists often speculate in conversations that the sharp projections and borders seen in many platypodines and scolytines may be stabbing or cutting weapons useful against conspecific usurpers and natural enemies trying to gain entrance to the gallery system. Hubbard describes finding fragments of “vanquished” males in the tunnel systems of *Euplatypus compositus* (Say), an abundant North American platypodine ambrosia beetle. He writes (p. 14):

> *The female is frequently accompanied by several males, and as they are savage fighters, fierce sexual contests take place, as a result of which the galleries are often strewn with the fragments of the vanquished. The projecting spines at the end of the wing-cases are very effective weapons in these fights. With their aid a beetle attacked in the rear can make a good defense and frequently by a lucky stroke is able to dislocate the outstretched neck of his enemy.*

We mentioned earlier that there are taxa in which the venter takes over part or all of the role of forming the hind end of burrow-blocking bark and ambrosia beetles. Sexual dimorphism in the venter of *Scolytus*, and many platypodine genera, takes the form of differences in spines and setae, exactly as with sexual dimorphism of declivities.

3. EVOLUTIONARY ECOLOGY OF FEEDING

Scolytinae and Platypodinae are components of what are increasingly being termed “saproxylic” beetle communities—species associated with dead wood and associated structures (such as woody fungi) (Ausmus, 1977; Swift, 1977; Ahnlund, 1996; Hammond *et al.*, 2001; Ulyshen *et al.*, 2004; Ødegaard, 2004; Tykarski, 2006; Lachat *et al.*, 2006, 2012; Zanzot *et al.*, 2010). Host trees are usually dead or severely weakened, and their colonization by these beetles, which often carry with them a complex community of fungi, bacteria, yeasts, and mites, initiates the breakdown of plant tissues and recycling of nutrients.

Actually, bark and ambrosia beetles breed in a wide variety of plant tissues. The feeding behavior of Scolytinae and Platypodinae has traditionally been broken down into categories based, first, on whether the larvae feed directly on plant tissues or on cultivated fungus, and second, for the direct plant feeders, on the tissues consumed by developing larvae. Since adults feed within their breeding material, the substances consumed by larvae are normally adult food as well (larvae in some ambrosia beetles feed on fungus-infested wood, whereas adults only feed on fungal tissues, but they here are both regarded as feeding on farmed fungi; see Section 5.3). We adopt the categories that have been standard for over five decades (Table 3.1). However, as Beaver (1986) emphasizes, "[the beetles] do not cooperate very readily in tidy classifications" (quoting Browne, 1961). Though most species can easily be placed in one of these categories, some feeding habits are hard to classify, and our classifications in some cases could be disputed. In this section, we will briefly describe the larval feeding modes of bark and ambrosia beetles, with a focus on more unusual habits, which are less well known than phloem feeding or fungus tending.

As pointed out by many authors, many or most Scolytinae (and all Platypodinae) are associated in one way or

TABLE 3.1 **Traditional Classification of Larval Feeding Modes of Scolytinae and Platypodinae (Schedl, 1958; S. L. Wood, 1982, 1986, 2007). The Examples Given are not Exhaustive; for more Details, see Appendix**

Larval Feeding Mode	Examples (see Appendix for complete list)	Feeding
Herbiphagy	*Hylastinus obscures* (Marsham) (where invasive), clover roots; *Thamnurgus euphorbiae* (Kuster), stems of *Euphorbia*; *Xylocleptes bispinus* (Duftschmid) in *Clematis*; *Coccotrypes rhizophorae* Eggers, mangrove propagules; petiole-breeding *Scolytodes* species.	Feeding on fresh or dry fleshy plant tissues, including stems of herbaceous plants, leaf petioles, cactus "leaves," grass stems, mangrove viviparous propagules.
Spermatophagy	Most *Coccotrypes*; *Conophthorus*, developing gymnosperm cones; *Araptus*, clade in legume seeds; *Pagiocerus frontalis* (F.), Lauraceae and *Zea* seeds; *Hypothenemus obscures* (F.), macadamia seeds, etc.; *Hypothenemus hampei* (Ferrari), developing *Coffea* fruits; *Dactylotrypes*, palm seeds.	Feeding in large hard seeds and the encompassing fruit tissues.
Mycophagy	*Trischidias* and *Lymantor decipiens* (LeConte), ascomycete fruiting bodies in dry twigs or bark.	Feeding in free-living (not cultivated) fungi (but see Harrington, 2005).
Myelophagy	*Pityophthorus* (some); *Araptus* (some); Bothrosternini (non-xylomycetophagous species); *Cryptocarenus*; *Micracisella*; *Hypothenemus* (a few); *Chramesus* (a few); *Scolytodes* (a few); *Dendrocranulus*, curcubit vines.	Feeding in pith of twigs, small branches or small stems, including small vines (e.g., *Dendrocranulus* in cucurbit vines).
Phloeophagy	Most Scolytinae, no Platypodinae: *Dendroctonus*, *Ips*, *Tomicus*, most *Scolytus*, most *Pityophthorus*, etc.	Feeding in phloem tissues (inner bark), though some larvae engrave outer sapwood; may or may not be regularly associated with fungi which increase nutritional value of the substrate.
Xylomycetophagy (ambrosia beetles)	Platypodinae; Xyleborini; Scolytoplatypodinae; Xyloterini; Hyorrhynchini; Corthylini-Corthylina; *Camptocerus*; *Hypothenemus* (a few); *Premnobius*; *Scolytodes unipunctatus* (Blandford).	Feeding on "farmed" ectosymbiotic fungi growing in wood; larvae of some species also ingest wood. Schedl's (1958) original definition: "larvae. . .feeding. . .upon the mycelia of fungi cultivated on the walls of their tunnels."
Xylophagy	*Dactylipalpus*; *Hylocurus*, *Micracis*, *Thysanoes*; *Chramesus xylophagus* Wood; *Dendrosinus*; *Phloeoborus*; some *Lymantor*, *Scolytodes multistriatus* (Marsham).	Feeding in xylem tissues (sapwood, never heartwood) but not cultivating symbiotic fungus.

another with fungi and other microorganisms (Six, 2013). Phloeophagous bark beetle-vectored fungi have long been known to be important in overcoming host defenses of live trees, but their role in nutrition is only now being puzzled out for a few model species. As more is learned about the roles microorganisms play, we will be able to make finer distinctions in feeding categories: one could separate out species of *Ips* and *Dendroctonus* that feed in phloem enriched with symbiotic beetle-borne fungi as "phloeomycophagous," for example (Six, 2012), and distinguish between ambrosia beetles whose larvae feed purely on fungus and those that also consume wood (Roeper, 1995; Hulcr *et al*., 2007; Chapter 2). These distinctions make sense biologically and reflect different morphological, physiological, and behavioral adaptations, but the usefulness of such fine distinctions will remain limited until we have investigated a broad selection of species. Oversimplified as it is, our categorization of larval feeding habits does have considerable heuristic value and has been essential in documenting and explaining major ecological and evolutionary trends in these two subfamilies (Beaver, 1979a; Kirkendall, 1983, 1993; Atkinson and Equihua-Martínez, 1986a).

Larval feeding habits have consequences for patterns of host usage. Generally, species breeding in live trees tend to be relatively host specific, sometimes very narrowly so (Section 3.9). Phloeophagous and herbiphagous species are more host specific than species breeding in wood, pith, seeds, or as ambrosia beetles (Beaver, 1979a; Atkinson and Equihua-Martínez, 1986b; Hulcr *et al*., 2007).

Larval feeding habits also have consequences for fecundity, and thus for suites of interrelated life history traits. Plant tissues are generally a poor resource from the point of view of nutritional quality, being much lower in nitrogen than beetle bodies (White, 1993; Ayres *et al*., 2000). Fresh and particularly living phloem is a better resource than older, dead inner bark (Kirkendall, 1983; Reid and Robb, 1999). Inner bark and seeds are much higher in nitrogen than wood or pith. However, ambrosia fungi and some fungi associated with phloem feeders (Section 3.1) are rich in nitrogen (French and Roeper, 1975; Ayres *et al*., 2000); ambrosia fungi concentrate nitrogen, and have much higher amounts than the wood itself (French and Roeper, 1975). That pith, wood, and woody leafstalks are unusually poor in nutrition is reflected in the fact that scolytines breeding in these substrates have considerably lower fecundity than those breeding in inner bark or seeds (Kirkendall, 1983, 1984; Jordal and Kirkendall, 1998).

For detailed insight into the ecology of bark and ambrosia beetle feeding see general resources such as the works in our reference list by Beeson, Blackman, Browne, Kalshoven, Schedl, or Wood, review papers by Kirkendall (1983, 1993; Kirkendall *et al*., 1997) and Beaver (1977, 1979a, b) and the research papers by, for example, Atkinson and collaborators (Mexico, S. E. US), Blackman (eastern US), Beaver (worldwide), Cognato and collaborators (Hulcr, Smith, and others) (worldwide), and, for fungus farming in particular, by Hulcr, Cognato, Jordal and collaborators Six, and Harrington.

3.1 Phloeophagy (Breeding in Inner Bark)

Of woody tissues, inner bark is the richest, especially in nitrogen (Cowling and Merrill, 1966; Kirkendall, 1983), so it is no surprise that the most primitive Scolytinae breed in dead inner bark of trunks and branches (Figures 3.4 and 3.5), or that phloem feeding is the most widespread larval feeding mode. Roughly half of all Scolytinae genera are wholly or partly phloeophagous, and 20 of 26 tribes have at least some phloeophagous species in them (Table 3.2; Figure 3.4). Only phloeophagous species are known from Hylastini, Phloeotribini, and Polygraphini, and several other tribes are primarily phloeophagous (Appendix).

3.1.1 Phloeophagous with Some Consumption of Wood

In certain phloeophagous species in hardwoods, older larvae (often the final instar) tunnel in the outermost sapwood, and pupate in the wood. Thus, late-stage larvae of *Scolytus muticus* Say, which breeds in *Celtis* (hackberry), burrow "for some distance" in the sapwood, ". . .and if they are at all numerous soon reduce the outer part of the wood and bark to a mere shell" (Blackman, 1922). *Triotemnus pseudolepineyi* Knížek larvae consume all phloem and sapwood, when breeding in branches of the shrub *Bupleurum spinosum* Gouan (Apiaceae) in Morocco (Knížek, 2010). Other examples include *Chramesus hicoriae* LeConte (Blackman and Stage, 1924); *Phloeosinus sequoia* (Hopkins) (De Leon, 1952); *Strombophorus ericius* (Schaufuss) (Browne, 1963); and species of *Hylurgonotus* and *Xylechinosomus* breeding in *Araucaria* (Rühm, 1981; Jordal and Kirkendall, pers. observ.).

Sapwood is roughly an order of magnitude lower in nitrogen than inner bark and more heavily lignified (Cowling and Merill, 1966; Haack and Slansky, 1987); therefore, phloeophagous larvae should avoid feeding on it, if possible. It is possible that fungi nutritionally improve the wood quality for beetles, but this has not been studied. One possible hypothesis for "late-stage xylophagy" is that in thin-barked hosts, larvae simply are forced to consume wood as they get larger (Browne, 1963); in many species, bark beetle larvae are small enough to be able to feed entirely in inner bark, but in others, the amount of wood consumed will be inversely proportional to the diameter of the breeding material. A second hypothesis is that burrowing into the wood makes it more difficult for parasitoid

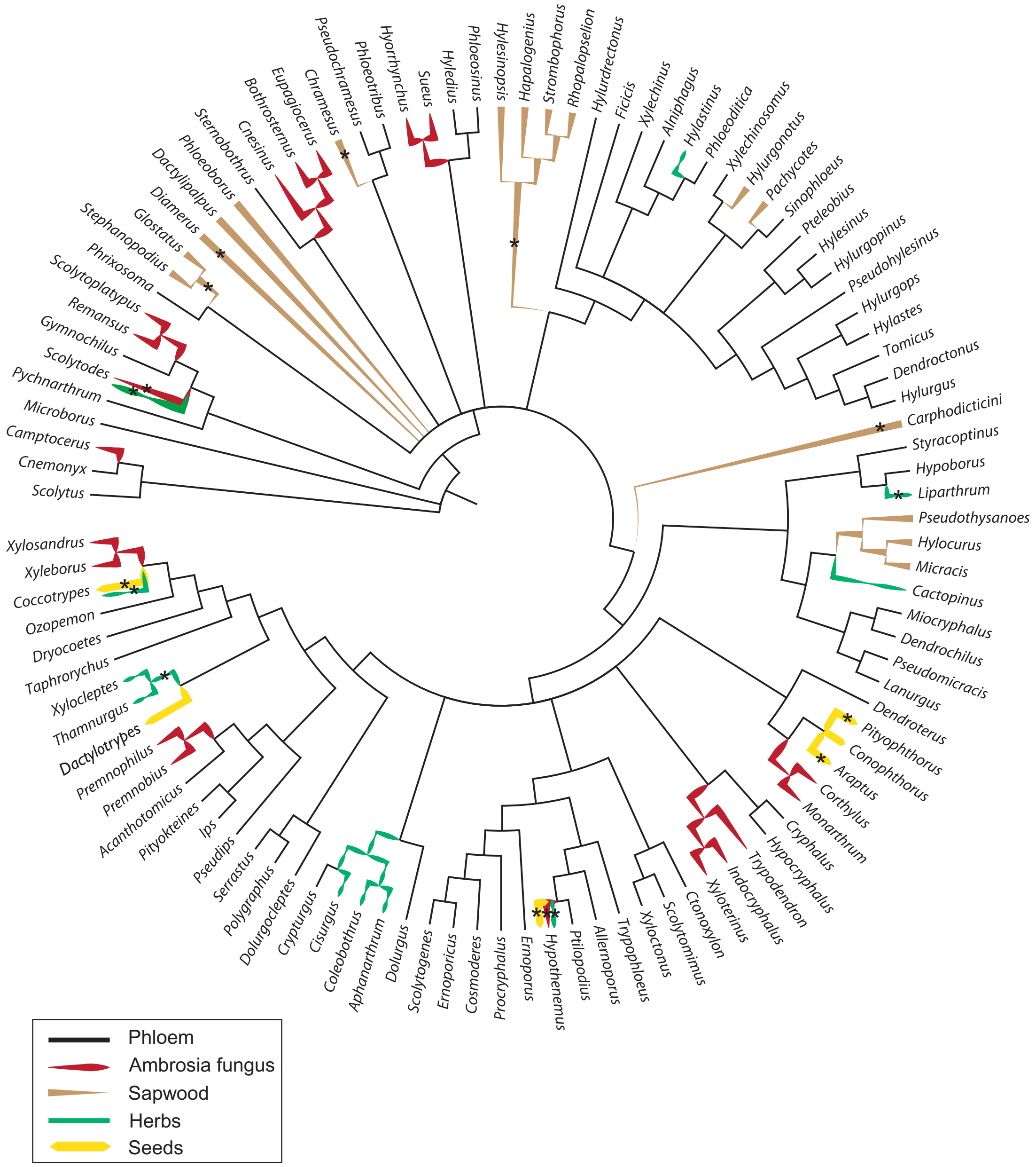

FIGURE 3.4 **Phylogenetic tree of Scolytinae with feeding modes indicated (see inset legend).** Stars indicate genera or lineages (if on a node) in which the feeding mode is rare (one or just a few species).

wasps to locate and parasitize larvae. Additionally, wood might be less strongly infested by potentially harmful microbial pathogens than more nutrient-rich phloem. Many bark beetles pupate in the sapwood, in some cases tunneling directly inwards to do so; this likely is an adaptation to reducing parasitism. Testing the second hypothesis is self-evident; a test for the first hypothesis would be to compare resultant body size of offspring that do not feed on sapwood as larvae (larval tunnels do not engrave the wood) with those that do consume much sapwood as larvae (their tunnels clearly etching the wood).

3.1.2 Feeding on Phloem Nutritionally Improved by Fungi

Insects breeding in dead woody tissues will always have constant interactions with a variety of mites, nematodes, fungi, and bacteria (Hamilton, 1978). Bark and ambrosia beetles are an optimal vehicle for transport of mites, nematodes, fungi, and bacteria from old host material to new, and many hitch rides on them (Stone, 1990; Paine *et al.*, 1997; Six, 2003, 2012; Harrington, 2005; Cardoza *et al.*, 2006a; Hofstetter *et al.*, 2006; Knee *et al.*, 2013;

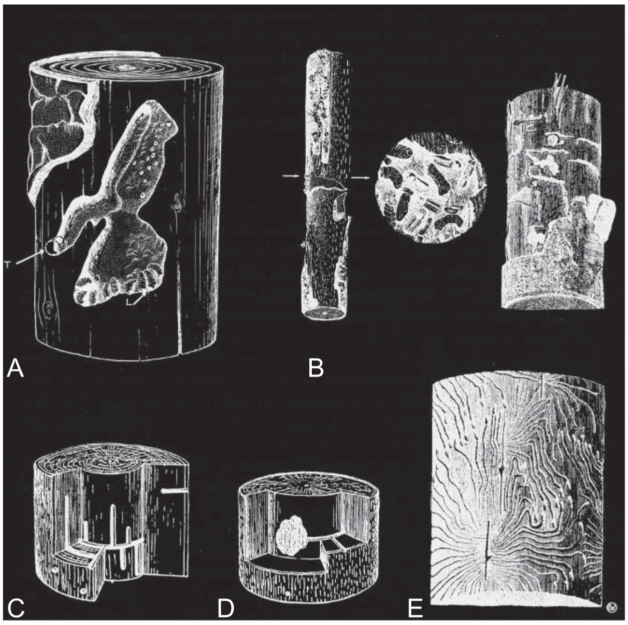

FIGURE 3.5 **Variation in gallery systems made by bark and ambrosia beetles.** (A, B, E) Engravings in phloem. (A, B) Cave-type galleries of inbreeding polygynous species with communal larval feeding for *Dendroctonus micans* (Kugelann) (from Chararas, 1962) and in *Hypothenemus colae* (Schedl) (from Schedl, 1961b). (C, D) Ambrosia beetle tunnel systems in sapwood for fungus cultivation for inbreeding polygynous *Xyleborus dispar* (F.) and *Xyleborinus saxeseni* (Ratzeburg) (from Balachowsky, 1949). (E) Monogynous egg tunnels of *Kissophagus granulatus* Lepesme in *Ficus* (from Schedl, 1959).

Shimizu *et al.*, 2013; Susoy and Herrmann, 2014; Chapter 6). Some small organisms perform useful functions from the beetle's point of view, and many bark and ambrosia beetles have morphological adaptations that increase the likelihood of successful transport of helpful symbionts. In particular, a wide variety of species have developed external crevices, pits, simple pockets, or complex invaginations somewhere on the body, for transporting fungi (and perhaps other microorganisms) (Beaver, 1988; Harrington, 2005; Six, 2012); these structures are often bordered by setae, which help in combing fungal spores into the receptacle. Most species with such structures are ambrosia beetles (discussed below and in Section 5.1), but some breed in inner bark and feed on phloem they have inoculated with fungi they have introduced. There are also phloeophagous species with consistent associations with fungi but which have no special structures for transporting them, including *D. pseudotsugae* Hopkins, *D. rufipennis* Kirby, *Ips avulsus* (Eichhoff), and *Tomicus minor* (Hartig) (Beaver, 1988).

Many species even have structures for transporting fungi from host to host in more or less sophisticated cuticular invaginations or pits known as mycetangia (Francke-Grosmann, 1956a) or mycangia (Batra, 1963). Larvae of phloeophagous species that are associated with fungi feed (at least in most stages) in woody tissues, not on mats of fungal hyphae. The earliest research into mycetangia revealed their presence in phloeophagous as well as xylomycetophagous species (Francke-Grosmann, 1956a, b, 1963a, b, 1965, 1966; see Kirisits, 2004). Francke-Grosmann (cited above) reported mycetangia in typical phloeophagous species in *Hylastes*, *Hylurgops*, and *Ips*. The potential nutritional benefits of fungi in species that are not ambrosia beetles are now being explored in detail (Six and Paine, 1998; Ayres *et al.*, 2000; Bentz and Six, 2006; Adams and Six, 2007; recent reviews by Six, 2012, 2013; Chapters 6 and 8).

Several phloeophagous *Ips* species have mycangia, including the Eurasian *Ips acuminatus* (Gyllenhal) (Francke-Grosmann, 1963a). This *Ips* transports two mycetangial fungi (Francke-Grosmann, 1963a, 1967; Guérard *et al.*, 2000). Larval mines in phloem that is obviously discolored by fungi are notably shorter than those in phloem with no discoloration. When the fungus is clearly well established, one can see that larvae double-back in their own feeding tunnels and feed on the white fungus growing on the tunnel walls; the first action of eclosed young adults is to completely graze white fungal conidia and hyphae, which have grown on the walls of their pupal chambers (Kirkendall, unpubl.). Several unrelated North American *Ips* species seem to have a similar biology (summarized in Harrington, 2005). *Tomicus minor* is a common Eurasian scolytine breeding in pine trunks and thicker branches; first

TABLE 3.2 Number of Scolytinae Genera and Tribes with at Least one Species Exhibiting the Given Larval Feeding Mode (247 total genera, 26 total tribes)

Number of Taxa with at Least One Species	Phl	Xym	Spm	Myc	Mye	Xyl	Hbv	?
Genera	121	63	9	2	14	21	17	31
Tribes	20	10	5	1	6	11	9	14

Some genera and tribes are represented in more than one category. Phl = phloeophagous (feeding in inner bark); Xym = xylomycetophagous (ambrosia beetles); Spm = spermatophagous (feeding in seeds, fruits); Myc, mycophagous (feeding on non-symbiotic fungi); Mye = myelophagous, feeding on pith; Xyl = xylophagous, feeding in sapwood; Hbv = herbiphagous (herbivorous), feeding in non-woody plant tissues; "?," unknown larval feeding habits. Data from Appendix.

and second instar larvae feed in inner bark, but later instars move into the xylem where they become strict fungus feeders (Harrington, 2005). Both *I. acuminatus* and *T. minor* would seem to be intermediate between true phloeophages and obligate fungus feeders. They are both associated with *Ambrosiella* fungi (as well as bluestain fungi), which are ambrosia fungi in xylomycetophagous species.

The relationship of symbiotic fungi with certain species of *Dendroctonus* and *Ips* is not an obligate one, but successful establishment of their fungi definitely enhances larval fitness in some species. Southern pine beetle (*Dendroctonus frontalis* Zimmermann) larvae feeding in the absence of their two mycetangial fungi have significantly reduced offspring survivorship (Barras, 1973), and females breeding without these mutualistic fungi lay only half as many eggs as controls (Goldhammer *et al*., 1990). Similar fitness effects of mutualistic fungi are seen in the mountain pine beetle, *D. ponderosae* Hopkins (Six and Paine, 1998). Southern pine beetle mutualistic fungi raise the nitrogen content of the phloem and increase its digestibility (Ayres *et al*., 2000). Fox *et al.* (1992) found evidence for enhanced growth of *Ips paraconfusus* Lanier larvae when the associated fungus was present in the phloem, and Yearian *et al.* (1972) found that reproduction by females of *I. avulsus* (but not for two other *Ips* species) is increased by the establishment of their associated fungus. The terms "phloemycetophagous" and "mycophloeophagous" have been suggested for inner bark-breeding species that regularly feed on phloem plus fungus (Kirisits, 2004; Six, 2012).

We have focused on fungi here, but the nutritional quality of substrates consumed by bark beetles results from a complex interaction between the physical and biochemical attributes of the tissues consumed (Kirkendall, 1983; Haack and Slansky, 1987; Reid and Robb, 1999; Six, 2012) and a complex community of fungi, yeasts, bacteria, and other microbes (Cardoza *et al*., 2006b; Hofstetter *et al*., 2006; Six, 2012, 2013; Chapter 6).

3.2 Xylomycetophagy (Ambrosia Beetles)

The larvae and adults of xylomycetophagous species eat cultivated fungi growing on woody tissues (Schedl, 1958; Browne, 1961; S. L. Wood, 1982: see Box 3.1, Table 3.1, and Figure 3.5C, D), and are referred to as ambrosia beetles

BOX 3.1 Terminology

Most specialized terms are defined in the text. However, there are a few that are not, or that deserve special comment. We largely follow well-established conventions in bark and ambrosia beetle research (e.g., S. L. Wood, 1982), but have tried to align terms regarding mating systems and social behavior with the vocabulary being used more generally in behavioral ecology (Wilson, 1975; Shuster and Wade, 2003).

Alloparental—Refers to parenting by individuals other than the biological parents of the offspring, such as of ambrosia beetle larvae by siblings or aunts.

Ambrosia beetles—Ambrosia beetles are those Scolytinae (plus all Platypodinae) whose larvae feed primarily on coevolved symbiotic "ambrosia fungi," which adult females cultivate in tunnel systems in woody tissues. They may consume wood in the process (xylomycetophagy *sensu* Hulcr *et al.* in Chapter 2) or not (mycophagy *sensu* Hulcr *et al.* in Chapter 2), but we will not make this distinction (see also "xylomycetophagy," below).

Bark—Shorthand for inner bark, the secondary phloem tissue of woody dicots.

Bark beetles—In the literature, this term is used (confusingly) in two senses, with three different meanings. Taxonomically, "bark beetles" refers to the subfamily Scolytinae; for clarity, we will avoid this usage. The expression is used two ways in an ecological sense: it can mean species breeding in inner bark (live and dead phloem tissues), but many authors also use it in apposition to ambrosia beetles (that is, to include all species that are not xylomycetophagous). To avoid confusion, we will mainly use "phloeophagous" to indicate Scolytinae that breed in inner bark; occasionally, as in discussions primarily focused on ambrosia beetles, we use bark beetles (or "non-ambrosia beetles") as an umbrella term for all feeding modes other than xylomycetophagy. We will not use it taxonomically.

Bark and ambrosia beetles—This expression is often used as a collective term for Scolytinae. "Bark beetles," in this phrase, refers to all feeding modes other than obligate fungus feeding. We use this compound phrase broadly, to encompass both Scolytinae and Platypodinae, in order to avoid the excessively long "bark and ambrosia beetles and pinhole borers" when referring collectively to these two lineages.

Declivity—The downward-sloping posterior portion of the elytra: the back end of the beetle.

Frass—boring dust; the variegated mixture of feces and wood bits (digested or not) resulting from the tunneling activities of wood-boring insect larvae or adults.

Frons—Front of the head: the area between the eyes, from the vertex (top of the head) to epistoma (upper margin of the mandibles).

Hardwoods—Non-monocot angiosperm trees, as opposed to conifers. We use "broadleaf trees" synonymously, though technically this term also includes monocots.

Harem polygyny—Also known as simultaneous polygyny (as opposed to serial polygyny) in anthropology and behavioral ecology literature; in a harem polygynous scolytine, at least some gallery systems have multiple females. "Polygamy" (see below) is often used incorrectly as a synonym.

Continued

BOX 3.1 Terminology—cont'd

Herbiphagy—Biologists often call feeding on any plant tissue "herbivory." Bark and ambrosia beetle researchers use the related term "herbiphagy" for taxa feeding on fleshy (not woody) plant tissues, such as plant leaves, leaf stalks, or stems and branches of non-woody plants.

Monocots—Monocots are one of the two major groups of flowering plants, the other being dicots. Monocots comprise a monophyletic clade of plants that develop from a single cotyledon; monocot host plants of bark and ambrosia beetles include grasses (especially bamboos), palms, agaves, lilies (*Yucca* trees), and orchids.

Mycophagy—Used by us in a very narrow sense, for feeding on free-living fungi; other authors use this term broadly for any form of feeding on fungal hyphae and conidia (e.g., Harrington, 2005).

Monogyny—In monogynous species, only one female breeds in a gallery system.

Parasitoids—Parasitoids are insects that live on or in their hosts for some time before eventually killing them. Parasitoids of bark and ambrosia beetles are usually wasps, most commonly chalcidoids, pteromaloids, proctotrupoids, or ichneumonoids.

Pinhole borers—Currently, "pinhole borer" is often used to refer to Platypodinae as a group, though in older literature it may refer to any ambrosia beetle. "Shothole borer" has also been used as a generic term for ambrosia beetles, though at some point it seems to have been co-opted by North American entomologists for the phloeophagous bark beetle *Scolytus rugulosus* (Müller), a minor pest of fruit trees.

Polygamy—Also known as communal breeding, colonial breeding, or promiscuous breeding; in Scolytinae, a mating system where several males and several females are involved in constructing egg tunnel systems. In zoology, usually refers to a mating system in which both sexes mate with multiple partners, and have roughly equal variation in mating success.

Spermatophagy—Used (only) by Scolytinae researchers to classify species breeding in seeds and their encasing fruit tissues, and the viviparous propagules of mangrove trees. In the latter two cases, spermatophagy overlaps with herbiphagy, as the beetles are breeding in fleshy tissues. Other biologists call insects breeding in seeds "seed predators" or "seed parasites." Outside of bark beetle research, the term refers to phagocytosis of spermatozoa.

Xylomycetophagy—We use this term to refer collectively to the feeding category for ambrosia beetles: taxa whose larvae and adults feed primarily on cultivated co-evolved fungi. We do not distinguish between fungus farming species that do and do not ingest wood as well as fungus. Tunnel elongation, egg niche enlargement, and construction of pupal chambers (such as by all Platypodinae) may lead to ingesting wood, and in some taxa, species may be consuming wood incidentally while feeding on mycelia. For many ambrosia beetles, wood consumption is an aspect of their feeding ecology that is simply unknown; if "xylomycetophagy" is used narrowly to refer to ambrosia beetles known to feed on wood as well as fungi, and "mycophagy" used for taxa known to ingest fungi exclusively, then there remains no formal term (of the sort "phloeophagy," "xylophagy," etc.) to categorize feeding behavior of all ambrosia beetles, or to refer to ambrosia beetles for which relevant feeding behavior details are not known.

Xylophagy—Scolytinae that breed in tunnels in sapwood, and do not cultivate fungi.

(Schmidberger, 1836; Hubbard, 1897). Ambrosia beetles actively cultivate coevolved mutualistic fungi. The fungus forms layers of nutritious ambrosial growth within a few days (Francke-Grosmann, 1967). This growth is predominantly composed of fruiting structures of a single species of ascomycete fungus, which serves as major food source for adults and larvae. These fungi typically grow as mycelia, but form fruiting structures in the presence of the tending beetles (Batra, 1967; French and Roeper, 1972a; Biedermann, 2012).

Xylomycetophagy (cultivation of fungi growing in wood) is found in 63 genera in 10 tribes of Scolytinae (Table 3.2) and in all but the most basal Platypodinae. Based on the most recent phylogenetic analyses (Jordal and Cognato, 2012), it has evolved 10 or 11 times in Scolytinae, depending on details of the analysis (Figure 3.4), and it has originated once in Platypodinae (Jordal *et al.*, 2011). Two of these origins are recent, being single species in large scolytine genera (*Hypothenemus*, *Scolytodes*). Ambrosia beetles usually tunnel in sapwood or pith, but some can breed in seeds, leafstalks, or the tissues of woody monocots. Several corthyline ambrosia beetle species, for example, have only been collected from the woody petioles of large, fallen *Cecropia* leaves (Wood, 1983, 2007; Jordal and Kirkendall, 1998), which are also utilized by generalist ambrosia beetles such as *Xylosandrus morigerus* (Blandford) (Andersen *et al.*, 2012) and *X. crassiusculus* (Motschulsky) (Kirkendall and Ødegaard, 2007). All Platypodinae are tightly associated with fungi and usually colonize broadleaf trees; all but *Schedlarius* (xylophagous in rotted wood) and *Mecopelmus* (phloeophagous) are ambrosia beetles.

Most xylomycetophagous species transport their fungi in mycetangia or the gut (Schneider-Orelli, 1911; Francke-Grosmann, 1975). Vectoring of fungi within the gut is probably the ancestral mode of spore transmission, but still seems to be the dominant mechanism in some ambrosia beetles, including examples of both Scolytinae and Platypodinae that have no or reduced mycetangia. *Xyleborinus saxesenii*, for example, has very small elytral mycetangia (Francke-Grosmann, 1956a) and transmits its principal ambrosial fungus via the gut (Francke-Grosmann, 1975). In others like *Anisandrus dispar* (F.) with well-developed mycetangia, mycetangia and gut may harbor different fungi (see also *X. saxesenii*: Biedermann *et al.*, 2013); such redundancy may serve as an insurance mechanism in case one of the organs is infected by parasites. However, some others lack mycetangia completely because they rely on the fungal gardening of neighboring beetles of other species.

Fungus stealing was suspected by Kalshoven (1960a) and Beaver (1976), but was first thoroughly documented by Hulcr and Cognato (2010), who termed it "mycocleptism." The latter researchers found mycocleptism to be the main foraging strategy for at least 16 species mainly from the xyleborine genera *Ambrosiophilus* (eight species) and *Diuncus* (five species), but also including *Xylosandrus hulcri* Dole and Cognato, the scolytine *Camptocerus suturalis* (F.), and one Platypodinae, *Crossotarsus imitatrix* (Schedl). The "mycocleptae" tunnel close to the tunnel of an established "provider" species, in some instances breaking into the adjacent gallery system and destroying neighboring brood. The walls of the mycocleptae's tunnels then begin to produce ambrosia fungus, which had been introduced by the provider species. At least the genus *Diuncus* has lost mycetangia all together, and is completely dependent on this parasitic strategy.

3.3 Xylophagy (Breeding in Wood)

Species in which larvae feed wholly in sapwood occur in only 21 genera spread among 11 tribes. The most species-rich xylophagous lineage occurs in the Micracidini, in which three genera of wood feeders, *Hylocurus*, *Micracis*, and *Thysanoes*, include 119 species. Four Hylesinini genera seem to be entirely xylophagous, *Dactylipalpus*, *Hapalogenius*, *Phloeoborus* and *Rhopalopselion*, and *Hylesinopsis* partially so (see Appendix). The remainder of xylophagous examples is single species or small clades. Xylophagy has originated about nine times (Figure 3.4; see the more detailed phylogeny in Jordal and Cognato, 2012). Wood is nutritionally a very poor resource for insects (Cowling and Merrill, 1966; Kramer and Kozlowsky, 1979; Haack and Slansky, 1987). Many organisms feeding on wood are known to be dependent on the contributions of gut microbes. This has long been suspected to be the case for xylophagous bark beetles as well, but there has been relatively little research on this aspect of their biology. Xylophagous species often have low fecundity, relative to phloeophagous species (Kirkendall, 1984). The primary benefit to adopting xylophagy in these beetles would seem to be lower larval mortality from predators and parasites, but it may also be important that the physical environment (temperature, wood moisture, food quality, persistence of resource quality) is relatively stable, much more so than would be expected for inner bark.

Browne (1961) treats pith and twig breeders as xylophagous; we prefer to separate the two, since pith and sapwood are considerably different in structure, density and hardness, and possibly in nutritional quality, though levels of nitrogen are roughly similar (Cowling and Merrill, 1966; Kramer and Kozlowsky, 1979).

3.3.1 Breeding in Wood Nutritionally Improved by Fungi

Currently, this is a hypothetical group, as no wood-breeding scolytines have been studied in any detail. The xylophagous genera *Dactylipalpus* and *Phloeoborus* have distinctive mycetangia, but do not appear to be true ambrosia beetles. Beaver and Löyttyniemi (1985) report that *Dactylipalpus camerunus* Hagedorn is polyphagous, monogynous, and xylophagous, and attacks moderate to large logs and dying or dead stems. Females have pronotal mycetangia, suggesting that they may be closely associated with fungi. In addition, Browne (1963) reports *Dactylipalpus* as xylophagous. Similarly, as far as is known, *Phloeoborus* are xylophagous, but females have mycetangia (Wood, 1986).

3.4 Herbiphagy

Some genera or single species breed in herbaceous plant tissues, and are classified as herbiphagous (Box 3.1, Table 3.1). It is a rare feeding strategy in Scolytinae, being found in only 17 genera (6%) in nine tribes (Table 3.2), and has evolved only about eight times (Figure 3.4). Half of the genera in which herbiphagy is represented are specialized to this lifestyle (Appendix). One radiation in the Dryocoetini accounts for about two-thirds of all herbiphagous species.

Feeding habits in this category include breeding in herbaceous plants, ivy, *Clematis*, grass stems including bamboos, cacti and succulent euphorbs, leaf petioles, and the viviparous propagules of mangrove trees. We include here two species that breed in roots of herbaceous plants: (1) *Hylastinus obscurus* (Marsham) is a minor pest of clover in North America, where it is an introduced species, though there are no records of it breeding in clover from Europe where it is native (Webster, 1910; Koehler *et al.*, 1961); and (2) the recently discovered *Dryocoetes krivolutzkajae* Mandelshtam, which breeds in roots of *Rhodiola rosea* (Crassulaceae), the only bark beetle of treeless tundra landscapes (Mandelshtam, 2001; Smetanin, 2013). And we include the only galling bark beetle, *Scolytodes ageratinae* Wood, which attacks live plants of a herbaceous montane species of *Ageratina* (Asteraceae) in Costa Rica (Wood, 2007; Kirkendall, unpubl.; see Section 3.9)

Thamnurgus is a typical example of a herbiphagous genus. *Thamnurgus euphorbiae* Küster has been approved for biological control of *Euphorbia esula* L. (leafy spurge), an invasive weed in the USA (Campobasso *et al*., 2004). Females oviposit in the stem, starting at the top of the plants. Apparently, females have high lifetime fecundity (88 eggs) but lay relatively few eggs per plant. Colonized plants are weakened structurally and break easily, producing fewer seeds. *Thamnurgus pegani* Eggers breeds in stems of *Peganum harmala* L. (Nitrariaceae), a perennial plant toxic to grazing animals (Güclü and Özbek, 2007). One or a few eggs are laid between the stem and a lateral branch junction, and larvae tunnel down the inside of the stem in the pith. The tissue on which larvae are feeding becomes blackish-brown due to presence of *Fusarium oxysporum* Schltdl.; the fungus was also isolated from the bodies of the bark beetles. A couple of weeks after eggs are laid, larval tunnels are still very short (6 mm); this and the presence of white mycelia on the surface of the stained pith tissues suggest that the species may be gaining significant nutrition from the fungus.

An entire scolytine community (29 species, six genera, three tribes) can be found in the cactus-like, shrubby, and tree-like euphorbs of the Canary Islands, Madeira, Cape Verde, and North Africa (Jordal, 2006). Species are narrowly host specific, but up to half a dozen species could be found in one branch. Like the *Thamnurgus* mentioned above, these herbiphagous species are characterized by unusually low (within-plant) fecundity, though they likely oviposit in several plants. The scolytines breed only in dead branches and twigs, but differ ecologically in moisture preferences and host diameter.

The seeds of some mangrove trees (like those of *Rhizophora* or *Bruguiera*) grow while still on the mother plant; these viviparous propagules later drop from the tree and float until they strand on muddy sediments, after which they begin to root. *Coccotrypes* species breeding in the propagules of mangrove trees are sometimes categorized as spermatophagous, but we classify them here as herbiphagous since they are actually breeding in live, non-ligneous (not woody) plant tissues and not in seeds or fruit tissues. Hanging or (usually) newly beached seedlings are attacked by *Coccotrypes rhizophorae* (Hopkins), *C. fallax* (Eggers), and *C. littoralis* (Beeson) (Beeson, 1939, 1941; Kalshoven, 1958; Browne, 1961). These species specialize in mangroves, as opposed to most *Coccotrypes*, which are host generalists and breed in seeds, bark, or leafstalks with some, such as *C. cyperi* (Beeson), breeding on all three. The mangrove *Coccotrypes* are not found in other hosts, or in branches or trunks of mangroves. Interpreting this feeding behavior as herbaceous gets some support from the observation that *C. rhizophorae* also attacks the soft, growing tips of aerial roots of *Rhizophora mangle* L.; it does not, however, breed in the older, woody portions of the roots (Aktinson and Equihua-Martínez, 1985b). In Neotropical mangroves, only *C. rhizophorae* is found; it occurs in mangrove forests throughout the world, and may have dispersed to the New World on its own, as have the mangrove species in these forests (Atkinson and Peck, 1994). Little has been published on the biology of mangrove *Coccotrypes*, but there have been two ecological studies of the effects of *C. rhizophorae* in the Neotropics, where it seems that the high levels of propagule attacks can have significant effects on the mangrove ecosystem (Rabinowitz, 1977; Sousa *et al*., 2003).

Herbiphagy is a difficult category to define precisely, especially without detailed knowledge of plant anatomy. *Dendrocranulus*, for example, breeds in stems of cucurbit vines. We choose to classify *Dendrocranulus* as myelophagous (as do Atkinson and Peck, 1994) but it could also have been classified as herbiphagous. Which is more important physiologically, ecologically, and evolutionarily? That it breeds in non-woody plants (herbiphagous), or that it colonizes pithy tissues (myelophagous)? Petioles, too, are problematic. Those of large fallen *Cecropia* leaves are very woody, at one extreme, in contrast to those of *Gunnera*, which although stiff, are quite moist and rather fleshy (Figure 3.6). *Scolytodes*, a large neotropical genus comprised primarily of phloeophagous and myelophagous species, has radiated into both.

Lineages moving from bark to herbaceous tissues probably are moving to food with similar or even higher nutritional quality (with the exception of petioles: Jordal and Kirkendall, 1998), but herbaceous tissues differ from those of trees and woody shrubs tissues in their anatomy, biochemistry, and especially in moisture content. The distribution of herbiphagy in Scolytinae, and what we know of the biology of herbiphagous species, suggest that adopting herbiphagy is not readily accomplished and demands a suite of new adaptations (including major life history adjustments), though perhaps less so in those cases that most resemble woody branches (such as the highly lignified petioles of *Cecropia* leaves).

FIGURE 3.6 An example of herbiphagy: cave-type egg gallery of *Scolytodes gunnerae* Wood in live fleshy leafstalk of *Gunnera insignis* in Costa Rica. Eggs are laid loose in the gallery; the leafstalk is ca. 3 cm in diameter.

3.5 Myelophagy (Pith Breeders)

Pith breeding is very uncommon in Scolytinae. Only 14 genera in six tribes have species that regularly breed in pith (Table 3.2). Pith is composed of undifferentiated parenchyma cells, which function in storage of nutrients, and in eudicots is located in the center of the stem. It is mainly present in young growth; in older branches and stems it is often replaced by woodier xylem cells. Pith is poor in nutrients, being about equivalent to young sapwood in terms of nitrogen content (Cowling and Merrill, 1966) or somewhere in between sapwood and inner bark (Haack and Slansky, 1987). It is, however, easy to tunnel through. This combination of features is illustrated by the breeding biology of *Scolytodes atratus* Wood and Bright in *Cecropia* petioles, the centers of which are composed of a relatively large cylinder of soft white pith: tunnels can be several tens of cm in length yet produce only four or five offspring (Wood, 1983; Jordal and Kirkendall, 1998).

Typically, pith breeders construct irregular chambers or meandering egg tunnels, often going both up and down the twig from the entrance. Twig breeders are generally monogynous, even in otherwise harem polygynous genera such as *Pityophthorus*, *Araptus*, or *Scolytodes* (Kirkendall, 1983).

Twigs of many woody plants are largely pith, so twig breeders are classified as myelophagous; often, an entire twig is hollowed out by adult and larval feeding, but most of the tissue consumed is pith. There are a handful of *Pityophthorus* species that breed mainly or only in twigs and that are categorized here as myelophagous. In tropical hardwoods, the tribe Bothrosternini comprises mainly pith borers (some *Cnesinus* are phloeophagous), some of which have evolved fungus farming in pith (Beaver, 1973; S. L. Wood, 1982, 2007; Kolarik and Kirkendall, 2010; Section 3.2, Appendix).

3.6 Spermatophagy (Seed Breeders)

Spermatophagy (or spermophagy) as used by bark beetle researchers denotes species breeding in seeds and the surrounding fruit tissues. This term has been applied very broadly to encompass true seed predators (Janzen, 1971) but also species collected from fleshy fruits, woody seedpods, mangrove propagules (which we treat as herbiphagous), or cones (Schedl, 1958; Browne, 1961; S. L. Wood, 1982, 2007; Kirkendall, 1983; Atkinson and Equihua-Martínez, 1986b). As such, the category is rather heterogeneous with respect to actual feeding adaptations. Normally, exposed seeds from fallen fruits (or defecated seeds) are preferred both by seed specialists and by generalists when they breed in seeds.

Nine genera in five tribes have spermatophagous species, and true seed breeding has originated at least eight times (Table 3.2; Figure 3.4). Two genera of Scolytinae only breed in seeds (*Pagiocerus*, neotropical, five species; *Dactylotrypes*, one species endemic to the Canary Islands), as does possibly *Spermophthorus* (Wood, 2007).

3.6.1 Pagiocerus

Pagiocerus frontalis (F.), found in Central and South America, is often collected from seeds of Lauraceae, including commercial avocado (*Persea americana* Mill.). In Mexico, it bores into partially or completely exposed seeds lying on the ground and does not attack fruits on the tree (Atkinson and Equihua-Martínez, 1985b; Atkinson *et al*., 1986). In South America, it has been recorded as a pest of maize since at least 1930; the seeds are attacked on the plant and in storage, and it has been collected from coffee berries in Ecuador (Yust, 1957; Okello *et al*., 1996b; Gianoli *et al*., 2006). In the laboratory, it can be bred on cassava chips as well as maize (Okello *et al*., 1996a). The biology of other *Pagiocerus* species is not known, except that *P. punctatus* Eggers has been collected from male strobili of *Araucaria angustifolia* (Bertol.) Kuntze in Brazil (Mecke and Galileo, 2004).

3.6.2 Coccotrypes

Many species of *Coccotrypes* breed in small hard seeds, especially palms. Most *Coccotrypes* that breed in seeds also breed in bark, leafstalks, or other tissues, but some are known to be seed specialists (e.g., *C. carphophagus* (Hornung), *C. dactyliperda* F.), and there are many species that are not often collected but have only been found in seeds (Beeson, 1939, 1941; Browne, 1962). *Coccotrypes* only colonize seeds that have fallen, i.e., seeds that are at least partly exposed or completely bare of fruit tissues. Within seeds, beetles experience similar selective pressures as many ambrosia beetles (e.g., Xyleborini) by inhabiting a "bonanza type" resource that is protectable and may provide ample food for several offspring generations. Hence, this habitat favors the evolution of inbreeding, biased sex ratios, dispersal polymorphism, and advanced social behavior (Hamilton, 1978, 1979), which characterizes *Coccotrypes* (Herfs, 1950; 1959; Gottlieb *et al*., 2014) and many *Hypothenemus* species (see below) as well as Xyleborini.

3.6.3 Other Seed Breeders

Most *Araptus* species are phloeophagous or myelophagous, but at least 19 species breed in seeds (S. L. Wood, 1982, 2007); half of these are apparently legume seed specialists. Most *Hypothenemus* are highly polyphagous, but a few regularly or most commonly breed in seeds (Beeson, 1941; Browne, 1961; S. L. Wood, 1982, 2007; Atkinson and Equihua-Martínez, 1985c; Chapter 11) and a few species in other genera at least sometimes breed in seeds (see Appendix). In addition, species of *Conophthorus* that breed in developing cones of Pinaceae are also classified as spermatophagous.

3.6.4 Economically Significant Seed Breeders

Only one example of a spermatophagous species attacking fruits still on the plant is known to us: the coffee berry borer, *Hypothenemus hampei* (Ferrari) (Chapter 11). The coffee berry borer is the most serious pest of coffee in most coffee growing countries (LePelley, 1968; Benavides *et al*., 2005; Jaramillo *et al*., 2006; Chapter 11). It attacks healthy coffee berries, and breeds in the developing endosperm. This is the only example known to us of scolytines attacking live, attached fruits, and is by far the most economically important spermatophage and the most widely known tropical bark beetle. The congeneric tropical nut borer (*Hypothenemus obscurus* (F.)) is a pest of macadamia in Hawaii and Australia (Jones, 1992; Delate, 1994; Mitchell and Maddox, 2010; Chapter 11). It breeds in both seeds and bark, but primarily breeds in seeds and nuts of a wide variety of plants (S. L. Wood, 1982, 2007).

3.6.5 Cone Breeders

Conophthorus (Chapter 12) have the unique habit of breeding in the developing cones of gymnosperms (Miller, 1915; Lyons, 1956; Chamberlin, 1958; Keen, 1958; Ruckes, 1963; Hedlin *et al*., 1980; Flores and Bright, 1987; Furniss, 1997). Females bore in from the base of a developing cone, severing the conductive tissues and killing the cone whether or not brood is successfully produced (Ruckes, 1963; Godwin and Odell, 1965; Hedlin *et al*., 1980). Seed crop loss to *Conophthorus* species can be over 50% (Cognato *et al*., 2005). Conifer seeds are particularly high in nitrogen, higher than bark (Kramer and Kozlowsky, 1979). *Conophthorus* are relatively host specific; each species breeds in one *Pinus* host, or in a few closely related *Pinus* species (Hedlin *et al*., 1980; Cognato *et al*., 2005). *Conophthorus ponderosae*, the one species that is recorded from many pine host species, may be a species complex (Cognato *et al*., 2005; but see Menard and Cognato, 2007).

Curiously, regular breeding in gymnosperm cones has evolved only once, in North America (Cognato *et al*., 2005). *Conophthorus* has likely evolved from a *Pityophthorus* ancestor such as the closely related *P. schwerdtfergeri* (Schedl), which breeds in both twigs and cones (Cognato *et al*., 2005). It should be noted that some *Conophthorus* feed on shoots, e.g., *C. coniperda* Schwarz, especially when all cones are occupied (Morgan and Mailu, 1976), and *C. resinosae* Hopkins both feeds and breeds in shoots as well as cones (McPherson *et al*., 1970; de Groot and Borden, 1992). Additionally, several *Pityophthorus* species have been collected from cones in North America (Godwin and Odell, 1965). Given these facts, it seems odd that the habit has not also evolved in Eurasian conifer scolytines.

3.7 Mycophagy (Fungus Feeders)

Other than galling (one species), mycophagy is the rarest feeding mode in Scolytinae, known from only two genera in two tribes. At least some species in the rarely collected genus *Trischidias* breed in the fruiting bodies of ascomycete fungus growing in dead twigs or wood (Deyrup, 1987). Similarly, the rare *Lymantor decipiens* (LeConte) (but not other *Lymantor*) is found in dry sapwood with black fungi, upon which they are thought to feed (Swaine, 1918; Blackman, 1922; S. L. Wood, 1982; Kirkendall, unpubl.).

3.8 Breeding in Monocots

Interestingly, there are only a few host-specific phloeophages breeding regularly in the outer tissues of monocots, and there seem to be relatively few records of polyphagous ambrosia beetles breeding in woody monocots. Generally, for bark and ambrosia beetles, the preferred tissues of woody plants are the vascular tissues: cambium plus phloem for phloeophages, and xylem for xylophages and most ambrosia beetles. The vascular tissues taken together constitute a thick cylinder in gymnosperm trees and dicot angiosperms. In monocot angiosperms, xylem and phloem occur together in small bundles scattered in a matrix of nutrient-poor ground tissue. Thus, in monocots, there are no thick rings of relatively favorable tissue for phloeophages as there are in dicots and gymnosperms. It may also be that this radically different distribution of vascular tissues precludes normal phloeophagous gallery construction by bark beetles, and may also hinder normal fungus development in ambrosia beetles. Monocot specialists include few species of *Chramesus* (a genus with phloeophagous and xylophagous species) and of *Corthylus* (ambrosia beetles) that breed in native bamboos in the neotropics (S. L. Wood, 1982, 2007; Atkinson and Equihua-Martínez, 1986b). Otherwise, breeding by non-ambrosia beetle scolytines in monocots is restricted to leaves of yuccas and agaves (species of *Chramesus*, *Cactopinus*, *Pseudothysanoes*, *Hypothenemus*: Atkinson and Equihua-Martínez, 1985a, b, c; Atkinson, 2010) and stems, pseudobulbs, or flowering stalks of bromeliads and orchids (*Chramesus annectans* (Wood), Atkinson *et al*., 1986; *Tricolus coloreus* Wood, an ambrosia beetle, Wood, 2007; *Xylosandrus* ambrosia beetles, Reitter, 1916, Dekle and Kuitert, 1968, and Dole *et al*., 2010). In addition, several *Hypothenemus* species and *Chramesus exilis* Wood breed in woody *Smilax* vines (Atkinson and Equihua-Martínez, 1985a, b); *Hypothenemus pubescens* (Hopkins) breeds in the stems of grasses (S. L. Wood, 1982; Atkinson and Peck, 1994). With the exception of the *Hypothenemus* and *Xylosandrus* ambrosia beetles, all of these seem to be monocot specialists, though some are rarely collected, so their true host breadth is not known. Trunks and woody parts of palm leaves are colonized by generalist (polyphagous) ambrosia beetles, but the species richness of ambrosia beetles in palms seems to be much lower than that in dicots in the same forests. Sufficiently large, hard monocot seeds, on the other hand, which have similar structure to those of angiosperms, are readily colonized by both seed specialists and seed generalists.

3.9 Breeding in Live Hosts

Although bark and ambrosia beetles are primarily adapted to colonizing recently dead woody plants, many lineages have evolved to find and breed in living tissues. For species feeding directly on plant tissues (not cultivating fungi), living resources have the advantages of being generally more nutritious than dead tissues, and may have fewer intraspecific and interspecific competitors. Older dead resource units may also have experienced a buildup of predators, parasites, and potentially hostile microbes. The disadvantages of breeding in live resources are that they not only have an array of preformed anatomical and chemical defenses but can also mobilize further physical and chemical weapons. In this section, we present information on Scolytinae and Platypodinae that can tackle living tissues, e.g., wood, seeds, or seedlings. We discuss tree killing, but not the mass attacks on conifers by *Dendroctonus* or *Ips*, which are covered in Chapters 8 and 9, respectively, or in other recent works (Raffa *et al*., 2008; Kausrud *et al*., 2011, 2012; Lindgren and Raffa, 2013). We will focus instead on the less well-known instances of bark and ambrosia beetles killing hardwoods or breeding in living plant parts.

Insects breeding in live as opposed to dead plant tissues must adapt to active plant defenses. A clear consequence is that those regularly colonizing living tissues are more host specific than species breeding in the same tissue type but only in dead tissues. *Coccotrypes* and *Hypothenemus*, which breed in seeds, attack seeds of many plant families as long as they are big enough and hard enough (Browne, 1961; Schedl, 1960b, 1961). *Coccotrypes* breeding in mangrove propagules do not breed in any other hosts, or even in branches or trunks of mangrove trees. *Hypothenemus hampei* is the only *Hypothenemus* species that can breed in developing *Coffea* seeds, though many other species have been collected from *Coffea* trees; interestingly, it has been collected from hard seeds and woody pods produced by plants of several different families, but the only live fruits it is known to regularly colonize are those of *Coffea* (Schedl, 1960b, 1961; Vega *et al*., 2012). A very few ambrosia beetles are known only to attack standing, live trees, and in each case they are unusually host specific. The rare species *Xyleborus vochysiae* Kirkendall has only been collected from one host species (see below), in contrast to other tropical *Xyleborus*, which usually can be found in dead hosts of several to many different plant families. Three platypodine ambrosia beetles breed exclusively in live trees. The West African *Trachyostus ghanaensis* Schedl breeds only in *Triplochiton scleroxylon* K. Schum. (Sterculiaceae) (Roberts, 1960), while the Malayan *Dendroplatypus impar* (Schedl) breeds only in the certain *Shorea* species (Dipterocarpaceae) (Browne, 1965). The Australian *A. incompertus* is restricted to one genus, *Eucalyptus* (Kent, 2002). As with *Xyleborus*, platypodine ambrosia beetles are usually quite polyphagous. Another West African platypodine, *Doliopygus dubius* (Sampson), is polyphagous when colonizing felled trees and logs, but attacks live (apparently healthy) trees of only one species, *Terminalia superba* Engls. and Diels (Combretaceae) (Browne, 1961). There is one exception to this trend, however. *Corthylus columbianus* Hopkins breeds in live trees, but does not seem to be very host specific (Crozier and Giese, 1967a, b).

3.9.1 *Killing Entire Trees*

Relatively few bark and ambrosia beetles are able to colonize and kill entire trees, but those that do can have major ecological and economic impacts. Species of *Dendroctonus* (Chapter 8) and *Ips* (Chapter 9), in particular, kill millions of trees each year in North America, Europe, and Asia. Given the worldwide local and regional importance of tree killing by *Dendroctonus* and *Ips*, there is an erroneous but widespread notion that tree killing is by and large restricted to Pinaceae, as reflected in the title of a paper by the Australian forest entomologist Clifford P. Ohmart, who asks "Why are there so few tree-killing bark beetles associated with angiosperms?" (Ohmart, 1989). The article's claim, that the ability to kill trees has only evolved in taxa breeding in Pinaceae, seems to have been accepted uncritically in the few papers citing this work (e.g., Hulcr and Dunn, 2011). Ohmart (1989) argues for a key difference in how angiosperm vs. conifer host trees react physiologically to beetle attack. However, the article is flawed by a bias towards temperate (primarily North American) Scolytinae; this bias is frequently encountered in discussions of bark and ambrosia beetles by forest entomologists (e.g., Stark, 1982). Ohmart's (1989) hypothesis depends on assumptions about differences in temperate vs. tropical scolytine–host tree interactions, but not one article on tropical scolytine biology is cited.

The main tree-killing bark beetle in Europe is *Ips typographus* L., which breeds in spruce (*Picea*), but it is nevertheless not clearly a primary attacker. It mainly kills healthy trees during irregular outbreaks triggered by massive population buildups; otherwise, it kills trees that are highly stressed or attacks recently dead and dying trees

(Berryman, 1982; Kausrud *et al*., 2012; Chapter 9). *Sphaerotrypes hagedorni* Eggers (Diamerini) can kill its savannah host tree *Anogeissus leiocarpus* (DC.) Guill. and Perr. (Combretaceae), but does so only in the dry season, when trees are water stressed; attacks on living trees in the wet season fail due to active tree defenses, i.e., gum exudation (Roberts, 1969).

A century ago, the hickory bark beetle *Scolytus quadrispinosus* Say was a focus of attention by forest entomologists. It was causing huge losses of hickory timber, particularly trees under moisture stress, in the eastern USA (Schwarz, 1901; Hopkins, 1904, 1908; Blackman, 1924; Blackman and Stage, 1924; Beal and Massey, 1945). During periods of drought, this species kills large tracts of hickory trees in the eastern USA. Normally, it attacks only weakened trees; galleries started in vigorous trees soon fill with sap, and fail (Blackman, 1924; Blackman and Stage, 1924). Felt (1914) and Blackman (1924) used precipitation data to show that significant tree killing only occurred in years with deficiencies of rainfall.

Early in the 20th century, *S. rugulosus* was reported to be regularly killing "large numbers" of scrubby wild plum (*Prunus serotina* Ehrh.), with highest densities on trees injured by ground fires used to clear weeds (Blackman, 1922). Normally, these bark beetles colonize injured branches or trunks, but when numerous they attack healthy hosts (Blackman, 1922; Beal and Massey, 1945). Orchard practices have since changed considerably, and *S. rugulosus* is no longer considered an important pest of *Prunus* fruit trees.

Similarly, the peach bark beetle *Phloeotribus liminaris* (Harris) was studied in the early 1900s because it was damaging and even killing peach, black cherry, wild cherry trees, and mulberry in the northeast USA (Wilson, 1909; Beal and Massey, 1945). Though it was originally collected and described because of its association with "peach yellows" in the 1850s (Harris, 1852), it was not considered an economic problem until the turn of the century, when plantings of peach and cherry had grown (Wilson, 1909). Population buildups due to breeding in slash or windthrown trees can lead to massive attacks on healthy trees during breeding, but normally the main damage is due to gum spotting (gumosis), the result of the tree's reaction to beetles overwintering under the bark in healthy tissues (Beal and Massey, 1945); gum spot defects reduce the veneer value of black cherry by 50–90% (Hanavan *et al*., 2012). Beetles tunneling in healthy trees usually are either pitched out or killed by the gum reaction (Rexrode, 1982).

These are just a few of many examples of phloeophagous bark beetles locally killing native or ornamental trees, regularly or in occasional outbreaks. A few hardwood examples not yet mentioned include species of *Alniphagus aspericollis* (LeConte) killing alders (Chamberlin, 1958; Borden, 1969); *Dryocoetes betulae* Hopkins killing birches (Hopkins, 1904); four *Phloeotribus* species that can occasionally kill *Prunus* trees (Blackman, 1922; Atkinson and Equihua-Martínez, 1985a; Atkinson *et al*., 1986); *Scolytodes guyanensis* Schedl killing thousands of mahogany trees "of all sizes" (*Swietenia*) in plantations (Gruner, 1974); *Scolytus ratzeburgi* Jansen killing birches (Tredl, 1915); and *Taphrorhychus villifrons* Dufour killing dwarfed oaks ("*nains*"; Balachowsky, 1949).

Ambrosia beetles, too, occasionally or regularly attack and kill live hardwood trees. The newly described xyleborine ambrosia beetle *Coptoborus ochromactonus* Smith and Cognato was discovered and named because it was killing large proportions of young trees in commercial balsa plantations in Ecuador (Stilwell *et al*., 2014). Most mortality occurred in the dry season and to the smallest trees; deaths were attributed to the establishment of the beetles' primary ambrosia fungus, a *Fusarium* (Stilwell *et al*., 2014). A few ambrosia beetle species such as this one can colonize live trees, though usually hosts are stressed or diseased. If their ambrosia fungus thrives in live trees, when density of attacks is high enough, the fungus's rapid spread in xylem tissues can disable water conduction and effectively throttle the host. In a similar fashion, laurel wilt disease is caused by the symbiotic *Raffaelea* fungus of the Asian ambrosia beetle *Xyleborus glabratus* Eichhoff, which is called the redbay ambrosia beetle in the USA. Laurel wilt disease is killing thousands of mature forest, ornamental, and plantation trees in the family Lauraceae (particularly redbay *Persea borbonia* (L.) Spreng. and sassafras, *Sassafras albidum* (Nutt.) Nees) and is a potential threat to two endangered species and to the southeastern US avocado industry (Fraedrich *et al*., 2008; Hanula *et al*., 2008).

Other examples of ambrosia beetles killing hardwoods include *Xylosandrus germanus* (Blandford) (oaks: Heidenreich, 1960); *Xyloterinus politus* Say (birches: Schwartz, 1891); *Euplatypus parallelus* (F.) (Beaver, 2013); *Platypus quercivorus* (Murayama) (oaks: Kamata *et al*., 2002); *Platypus subgranosus* Schedl (*Nothofagus*: Howard, 1973); and *Euplatypus hintzi* (Schaufuss) (*Eucalyptus* in plantations: Roberts, 1969).

A few examples of gymnosperms being killed by otherwise innocuous species include *Pseudohylesinus grandis* Swaine, which normally breeds in weakened or dying Douglas-fir but occasionally attacks and kills "a considerable quantity of young timber" (Chamberlin, 1918); and *Phloeosinus rubundicollis* Swaine, which has been observed killing thousands of ornamental *Chamaecyparis* (Chamberlin, 1958).

Some species that are considered harmless in their native ecosystems ("secondary") become deadly when introduced to naive forests (Kühnholz *et al*., 2001; Ploetz *et al*., 2013). *Dendroctonus valens* LeConte females breed singly or in small numbers at the bases and in the roots of pines, and attacks by this species have no impact on trees in their native forests in North America. Meanwhile, in China, where the species has recently become established, it kills thousands of pines each year (Yan *et al.*, 2005; Sun *et al.*, 2013; Chapter 8). Similarly, the secondary North American bark beetle *Ips grandicollis* (Eichhoff) is a lethal pest of exotic *Pinus resinosa* in plantations in Australia (Morgan, 1967).

Considering these examples, it is important to be cautious in concluding that only certain bark beetle species have evolved to kill trees, or that bark and ambrosia beetles only kill Pinaceae (Ohmart, 1989). While a handful of notorious *Dendroctonus* species are specialists at tree killing, there is a continuum of aggressiveness in Scolytinae and Platypodinae, from species that only breed in live tissues to species that come to a tree months after its death. Many species can and do kill their hosts under the right conditions, even perfectly healthy individuals. In many of the examples cited above, the individual trees that were killed were known or suspected to be stressed. The point is, however, that these trees would likely have survived had the above-mentioned bark or ambrosia beetles not colonized them.

While the greatest ecological and economic impacts of tree killing are by *Dendroctonus* species in low diversity, widespread conifer forests, there is a large and growing number of instances of serious tree pathogens vectored by Scolytinae and Platypodinae in forests around the world, primarily involving angiosperm hosts (Hulcr and Dunn, 2011; Ploetz *et al.*, 2013). There has been considerable research into a few examples, such as Dutch elm disease, vectored in North America by both the native elm bark beetle *Hylurgopinus rufipes* (Eichhoff) and the invasive *Scolytus multistriatus* (Marsham), and in Europe by several native species of *Scolytus*. Other cases, many of which are only recently documented, are just beginning to be investigated (Hulcr and Dunn, 2011; Ploetz *et al.*, 2013). The impacts of attacks by these beetle–fungus partnerships vary from mild economic losses due to wood discoloration to major ecological and economic consequences due to massive tree mortality, mainly mortality of angiosperms, *contra* Ohmart (1989).

3.9.2 Killing Plant Parts, Seedlings, and Seeds

Much less appreciated are the impacts of perhaps hundreds of species, which affect live host plants in more subtle ways, by killing branches or twigs, patches of bark, seedlings, or seeds (Blackman 1922; Beeson, 1941; Chamberlin 1958; Browne, 1961; S. L. Wood, 1982; Postner, 1974). These bark beetles can nonetheless significantly reduce the growth and reproduction of their hosts and repeated branch killing can lead to death of entire trees.

A number of phloeophagous Scolytinae have been described as progressive branch killers. Several ash bark beetle species (*Hylesinus*) kill branches year after year, eventually moving onto the trunk, perhaps because branch losses have crippled the tree's defenses (Doane, 1923; McKnight and Aarhus, 1973; Postner, 1974; Gast *et al.*, 1989). Progressive branch killing has also been reported for *Hylesinus oleiperda* F. in olive trees and ashes (Postner, 1974; Graf, 1977), *S. ratzeburgi* in birches (Tredl, 1915), and *Pityophthorus costatulus* Wood in *Thevetia* (Apocynaceae) (Atkinson *et al.*, 1986a), to give just a few examples.

A few bark beetles that attack branches have been researched because the damage they cause is of sufficient economic import to warrant attention. The ambrosia beetle known now as the black twig borer, *Xylosandrus compactus* (Eichhoff), is well known as a pest of coffee and cocoa in West Africa, and tea in Asia (Kalshoven, 1925; Brader, 1964; Kaneko *et al.*, 1965; Entwistle, 1972), and where introduced is a pest of a wide variety of ornamental and native trees (Kalshoven, 1958; Browne, 1961, 1968; Beaver, 1988; Chong *et al.*, 2009). The adults bore into healthy young stems, branches or twigs; concentrated attacks can lead to death of the plant (Brader, 1964). Sadly for coffee aficionados, the black twig borer is a major impediment to coffee production in the Kona region of Hawaii (Greco and Wright, 2013.)

A palearctic phloeophagous species reproducing harmlessly in trunks of dead or dying pines is *Tomicus piniperda* (L.) (Chapter 10). Like most other *Tomicus* (Kirkendall *et al.*, 2008), its impact is due not to its breeding habits, but rather to the behavior of recently emerged young adults, which feed in the pith of healthy tree tops and branch tips (maturation feeding), killing them (Chararas, 1962; Långström, 1983; Långström and Hellqvist, 1993; Amezaga, 1997). Shoot pruning by *T. piniperda* in Nordic pine forests has been estimated to reduce forest productivity by up to 45% of the annual volume growth (Eidmann, 1992). Maturation feeding is especially intense in the Chinese *Tomicus yunnanensis* Kirkendall and Faccoli, and trees are so weakened by it that they can later be attacked and killed by this species (Ye, 1997; Ye and Ding, 1999; Lieutier *et al.*, 2003).

A number of phloeophagous and myelophagous species have evolved to breed in small plant parts incapable of defending themselves (such as the *Tomicus* described above). These species either tolerate local host defenses, or can mechanically disable or overwhelm them. Whether or not microbes are an important weapon (as they clearly are in almost all tree killers) is not generally known but is to be expected.

Pityophthorus puberulus (LeConte) offers an example of apparent tolerance. Females breeding in terminal twigs can be seen to be practically swimming in resin, and use a mixture of frass and resin to plug the entrance (males being absent in this parthenogenetic species) (Deyrup and Kirkendall, 1983; Kirkendall, unpubl.). At least several

Pityophthorus species originally described in *Myeloborus* seem to have the same biology, breeding in and killing pitchy twigs of pine trees (Blackman, 1928).

The monogynous ambrosia beetle *Corthylus punctatissimus* (Zimmermann) girdles stems and roots of saplings of a wide variety of angiosperm trees in eastern North America (Merriam, 1883; Schwarz, 1891; Roeper *et al*., 1987a, b). At high population densities, such girdling could have significant ecological effects: as recounted by Merriam (1883): "...in Lewis county [New York, USA] alone hundreds of thousands of young sugar maples perished from the ravages of this Scolytid during the summer of 1882." However, Schwarz (1891) commented that *C. punctatissimus* pairs destroy the underground stems but not the roots, and that plants later re-sprout. Regardless, the loss of a significant amount of biomass at such a young stage must severely affect plant fitness.

Anisandrus dispar (F.) girdles and kills branches and young trees in fruit tree orchards in the USA, where it is introduced (Hubbard, 1897). It is likely that there are other ambrosia beetles with similar behavior.

Conophthorus females bore in from the base of a developing pinecone and girdle it, cutting the conductive tissues and killing the cone whether or not a brood is successfully produced (Hedlin *et al*., 1980; Mattson, 1980). After girdling the cone, they tunnel in a more or less straight line along the cone axis.

Curiously, unlike with other wood borers, there seem to be few species, which have been recorded as girdling branches, twigs, or the stems of seedlings or saplings. Girdling not only disables plant defenses, but it also alters physical and nutritional qualities of the resource (Forcella, 1982; Dussourd and Eisner, 1987; Hanks, 1999). Girdling is a widely used strategy in Cerambycidae (Forcella, 1982; Ferro *et al*., 2009) and in addition to mitigating plant defenses such as sap flow (e.g., *Sthenias grisator*: Duffy, 1968), girdling may alter favorably the nutritional quality of the girdled twig by trapping and concentrating nutrients normally transported from the leaves (Forcella, 1982). Interestingly, Forcella (1982) reports that the cerambycid *Oncideres cingulata* (Say) cuts phloem tissues when girdling, but not xylem, so parts distal to the girdle remain alive. To our knowledge, nobody has investigated this behavior in bark and ambrosia beetles to determine if girdling concentrates nutrients, or simply disarms plant defenses (Dussourd and Eisner, 1987; Hanks, 1999).

On the surface, it would seem that girdling by cerambycids and scolytines are not analogous, in that cerambycids girdle a branch or twig first and oviposit distal to the girdle afterwards, while the girdling of scolytines is primarily during egg gallery construction and goes on over days. Indeed, that scolytines girdle small diameter breeding material in the course of constructing egg tunnels may simply be the optimal behavior for spacing of offspring in the resource medium. Nevertheless, the girdling benefits mentioned above are substantial, and could select for such behavior in scolytines: there are species of *Carphobius* and *Thysanoes* that seem to be specialized to breeding in twigs and branches girdled by cerambycids (S. L. Wood, 1982), suggesting that scolytines reap the same girdling benefits as do longhorn beetles. Depending on the temperature and the size of the beetle with respect to the diameter of the host material, a tunnel that completely severs phloem tissues (the first 360-degree turn) might take only a day or two to complete. It seems clear that girdling is an adaptive strategy in at least *Conophthorus*. If girdling is more than incidental in, for example, twig-breeding species or species breeding in herbaceous stems or vines, we would expect to see that spiraling tunnel construction is always outwards from the initial spot of entry (as described for *Xylocleptes bispinus* (F.) in *Clematis* vines: Lövendal, 1898), while it would be random if girdling was not important.

Herbiphagy is relatively rare in Scolytinae, but many herbiphagous species do attack live plants (see Section 3.4). Attacks on stems can kill the plants.

Spermatophagous species (Section 3.6) usually kill the live seeds in which they breed, and may well have significant impacts on regeneration of certain host trees (Janzen, 1971, 1972; Wood, 2007). Palm seed mortality due to *Coccotrypes* can be up to 100%, though it varies much from place to place and year to year (Janzen, 1972; Kirkendall, unpubl.). Other *Coccotrypes* species breed in and often kill live seedlings (the viviparous propagules) of mangrove trees, affecting mangrove forest communities (Sousa *et al*., 2003; see Section 3.4).

3.9.3 Breeding in Live Plant Parts without Causing much Damage

In exceptional cases, bark and ambrosia beetles breed in live plants seemingly with little or no damage to the host. Two unique examples can be found in the large neotropical genus *Scolytodes*, both in Costa Rica; both were discovered by the extraordinary young naturalist Kenji Nishida, who was then doing his Master's research at the University of Costa Rica. *Scolytodes ageratinae* Wood galls a small, high elevation herbaceous plant, *Ageratina* cf. *ixiocladon* (Asteraceae) (Nishida, pers. commun.); galled plants seem otherwise healthy, but may have lower fitness than ungalled. No other galling Scolytinae are known anywhere in the world. The congener *Scolytodes gunnerae* Wood breeds in the leaf petioles of two montane *Gunnera* species. The plants, known locally as poor man's umbrella (*la sombrilla de pobre*), have extremely large, rounded leaves 1–2 m in diameter and sprout in a whorl from a very short central stem. The beetles breed in irregular cave-type galleries in the several-cm-thick, fleshy petioles of healthy leaves (Figure 3.6). Old tunnels heal over, and though plant fitness has not been measured, the large leaves seem unaffected by the presence of a few small bark beetle galleries, and plants with colonized leaves seem to flower and fruit normally (Kirkendall, unpubl.). Again, this feeding mode, i.e., breeding in the fleshy petioles of large leaves, was totally unexpected and is unique to *S. gunnerae*.

In addition, a handful of ambrosia beetles tunnel in the wood of healthy live trees. *Xyleborus vochysiae* Kirkendall is a large inbreeding ambrosia beetle that has only been observed to colonize standing live *Vochysia ferruginea* Mart. (Vochysiaceae) in Costa Rica (Kirkendall, 2006). About three-quarters of the standing trees in a 7-year-old plantation were attacked (but multiple felled trees were not), and almost every tree surveyed in a 20-year-old secondary forest had the characteristic entry holes of this species, although it appeared that most attempted colonizations had failed. The interaction between the beetles and their host plants was not studied, but there were no signs of wilting or loss of leaves in the affected trees as might be the case if they were vectoring an aggressive fungus. This rare species has only been collected from this one host species, in contrast to other tropical *Xyleborus*, which usually can be found in hosts of several to many different plant families.

Corthylus columbianus is a common ambrosia beetle species in hardwood forests of eastern North America (S. L. Wood, 1982; Majka *et al.*, 2007), where it breeds in trunks of healthy, vigorous trees. Hosts appear to be unaffected, and old beetle entrance tunnels are gradually covered over by secondary tree growth. Fungal staining from old tunnel systems remains in the wood, making possible the study of historical distributions and population density fluctuations (Crozier and Giese, 1967b; McManus and Giese, 1968; Milne and Giese, 1969). Interestingly, a different *Corthylus* with similar biology does kill its host trees. *Corthylus zulmae* Wood breeds in the trunks of live native alders (*Alnus acuminata* Kunth; Betulaceae) in plantations in Colombia (Gil *et al.*, 2004; Jaramillo *et al.*, 2011). Fungi associated with this species seem to be responsible for tree death. Their biologies being so similar, the lack of harm caused by *C. columbianus* must be due to the low virulence of its ambrosial fungus.

In most of the examples of Scolytinae or Platypodinae breeding in live trees there is little damage to the tree itself, though the value as a timber resource may be reduced. However, the tunneling of *Megaplatypus mutatus* (Chapuis) in the trunks of various hardwoods can weaken the structural integrity of its hosts to result in stem breakage and mortality, and it is considered a pest of plantations (Santoro, 1963; Giménez and Etiennot, 2003; Girardi *et al.*, 2006; Alfaro *et al.*, 2007; Zanuncio *et al.*, 2010).

4. EVOLUTIONARY ECOLOGY OF REPRODUCTIVE BEHAVIOR

Bark and ambrosia beetles do not dazzle the eye as do longhorn and jewel beetles, or please the ear as do crickets and katydids, but few if any insect groups exhibit such an intriguing variety of reproductive behavior as do bark and ambrosia beetles (Kirkendall, 1983, 1993; Kirkendall *et al.*, 1997; Costa, 2010). In most insects, males leave females immediately or soon after copulation; in most bark beetle species, males remain with females in their tunnel systems until most or all eggs have been laid. Only a few examples are known where males do not join females in galleries and remain for at least a week or more. Most insects, and most bark and ambrosia beetles, outbreed, and the dangers of inbreeding are well documented; nonetheless, species reproducing by brother/sister mating are widespread and abundant, and have been mating incestuously for tens of millions of years. Outbreeding taxa vary in how the two sexes meet (mate location), how long males stay with females (male residency), and with how many females individual males are mated simultaneously (mating systems). Among outbreeders we find male/female pairs (which in some species mate for life), males with harems, and numerous instances of bigyny, i.e., species in which males nearly always mate with exactly two females, a mating system virtually unheard of outside of Scolytinae. There are also four forms of parthenogenesis (clonal reproduction) in this group: thelytoky, in which females produce only daughters; pseudogamy (also known as gynogenesis), in which females mate with males but produce only daughters, and only the mother's genes are passed on to offspring; arrhenotoky, in which daughters are formed sexually and are diploid, but sons are produced by the hatching of unfertilized eggs and are haploid; and pseudoarrhenotoky, or paternal genome elimination, in which daughters are formed sexually and are diploid, and males arise from fertilized eggs but express and pass on only genes from their mothers.

4.1 Mating Behavior

4.1.1 *Fighting*

Newly arriving conspecifics are easily repelled by bark and ambrosia beetles ensconced in tunnel entrances. Physical combat between members of the same sex takes place primarily early in the colonization phase, usually while a member of the pioneering sex is beginning to tunnel or shortly after pairs have formed (Blackman, 1931; Goeden and Norris, 1965; Fockler and Borden, 1972; Salonen, 1973; Beaver, 1976; Petty, 1977; Vernoff and Rudinsky, 1980; Kirkendall, 1983; Swedenborg *et al.*, 1988, 1989; Jordal, 2006; Smith and Cognato, 2011). Wandering males will also try to enter active gallery systems, but are blocked from entering by resident males (McGehey, 1968; Oester and Rudinsky, 1975; Rudinsky and Ryker, 1976; Oester *et al*., 1978, 1981). Only rarely do intruding males succeed in replacing males already in tunnels (Vernoff and Rudinsky, 1980). Male/male competition is common in female-initiated mating systems (such as in *Tomicus*, *Dendroctonus*, *Pseudohylesinus*, or *Scolytus*) but females have been observed fighting in male-initiated mating systems (Nord, 1972).

4.1.2 Courtship

Courtship in both Scolytinae and Platypodinae takes place with both individuals facing forward, so physical interactions during courtship are between the front of the courting individual and the back end of the courted one. Ancestrally, males court females, as is the general rule in insects and other arthropods (and indeed in animals as a whole). However, females court males in all known cases of harem polygyny and in some monogynous species as well, such as in all Platypodinae, monogynous species of *Scolytodes*, and the monogynous genera of Corthylini; it has been hypothesized that, for most cases, monogynous species with such sex role reversal are likely derived from harem polygynous lineages (Kirkendall, 1983).

Acoustic communication is a key component of intersexual selection during courtship, but may not always be sufficient by itself for species discrimination (Lewis and Cane, 1992). It appears that almost all Scolytinae and Platypodinae stridulate (Barr, 1969; Sasakawa and Yoshiyasu, 1983; Lyal and King, 1996), though stridulation has been secondarily lost in some species (Barr, 1969; Sasakawa and Yoshiyasu, 1983). Stridulation at the entrance to or inside the gallery system is a key component of courtship in Scolytinae (Barr, 1969; Swaby and Rudinsky, 1976; Rudinsky *et al*., 1978; Rudinsky, 1979; Rudinsky and Vallo, 1979; Oester *et al*., 1981; Ryker, 1984; Garraway, 1986; Ytsma, 1988; Swedenborg *et al*., 1989; Lewis and Cane, 1992; Ohya and Kinuura, 2001), and in Platypodinae (Chapman, 1870; Ytsma, 1988; Ohya and Kinuura, 2001; Kobayashi and Ueda, 2002). Stridulation is also used in male/male and female/female competition (Rudinsky and Michael, 1974; Rudinsky, 1976; Swaby and Rudinsky, 1976; Oester and Rudinsky, 1979; Rudinsky and Vallo, 1979; Oester *et al*., 1981; Swedenborg *et al*., 1988, 1989) and when predators attempt to enter a gallery system (Roberts, 1960); Wood (2007) reports that *Dendrosinus bourreriae* Schwarz adults working under bark in a branch "buzzed" for several minutes when the branch was disturbed, sounding like a nest of bees had been disturbed.

Courtship involves an interaction between acoustic and chemical communication (Rudinsky *et al*., 1976; Rudinsky, 1979), and where it has been studied in detail, courtship behavior also may include bumping (frons to declivity), antennal tapping or drumming on the declivity, brushing of antennae or the antennal scape setae against the elytra, and mandibular gnawing (Blackman and Stage, 1924; Petty, 1977; Oester *et al*., 1981; Swedenborg *et al*., 1988; Jordal, 2006; Smith and Cognato, 2011). In the platypodine *Doliopygus conradti* Strohmeyer, females and males engage in a "tug-of-war," where females attempt to pull males out of newly started tunnels with their mandibles and males resist; if they ultimately succeed, the female can then enter the gallery, and mating takes place with the male on the surface and the tip of the female's abdomen protruding from the entrance (Browne, 1962). In a similar fashion, courting females tug on male *Platypus quercivorus* Murayama (Ohya and Kinuura, 2001), so this behavior may be common in Platypodinae.

Besides the tactile components of bumping, brushing, stroking, and other rhythmic forms of physical contact between males and females during courtship, there is likely an olfactory or "taste" component as well: though little investigated in bark and ambrosia beetles, interspecific differences in cuticular hydrocarbons are important in species recognition in other insects (Singer, 1998; Howard and Blomquist, 2005) and such differences have been found when looked for in bark and ambrosia beetles (Page *et al*., 1990a, b, 1997; Sullivan *et al*., 2012).

Although courtship mostly occurs at or in the entrance or nuptial chamber, for at least some Scolytinae, mating can also occur during pre-dispersal feeding in the previous year's breeding material, hibernating sites, or feeding tunnels in branches or twigs (Kirkendall, 1993; McNee *et al*., 2000). Although it is likely that courtship patterns, including which sex courts, are similar to those that occur around or in gallery systems of the same species, nothing is known about mating behavior before dispersal and colonization of fresh breeding material.

4.1.3 Copulation

Females of at least outbreeding Scolytinae and Platypodinae copulate more than once, even if with the same individual male. Evidence comes from both watching individuals in nature and observing beetles in semi-natural conditions such as thick sheets of bark between plates of glass. Many authors have reported that bark and ambrosia beetles mate repeatedly during gallery construction (Gossard, 1913; Blackman and Stage, 1924; Doane and Gilliland, 1929; Hadorn, 1933; Hansen, 1956; Reid, 1958; Gouger *et al*., 1975; Petty, 1977; Garraway, 1986). In some cases, copulation seems to be restricted to the period when females are still on or near the surface or only in the early stages of oviposition (Hadorn, 1933; Gouger *et al*., 1975; Campobasso *et al*., 2004).

Copulations themselves are brief, lasting from 10 seconds to a few minutes at most (Blackman and Stage, 1924; Hadorn, 1933; Reid, 1958; Gouger *et al.*, 1975; Garraway, 1986). In the mountain pine beetle (*Dendroctonus ponderosae* Hopkins), coupling lasts 10–60 seconds and is repeated about once per day, and less frequently after egg laying commences (Reid, 1958). For two species of harem polygynous *Ips*, Garraway (1986) reports that copulation takes ca. 10 seconds, and that females beginning oviposition are mated "frequently." In *I. avulsus*, copulation averages 35 seconds and females mated three times at 10-minute intervals, after which the female walled herself off from the nuptial chamber with tightly packed frass in the egg arm (Gouger *et al.*, 1975).

Platypodinae presumably mate only in the earliest stages of tunneling; copulation is probably not possible inside the gallery system, and takes place with the male on the bark surface and the female in the tunnel entrance. Courtship and copulation in Platypodinae is described and illustrated in Jover (1952). There is no nuptial chamber in the tunnel systems of these ambrosia beetles, and copulation is accomplished by the male exiting the tunnel entrance and allowing the courting female to enter, then copulating with the male on the surface and the female in the tunnel entrance. No deviations from this general pattern have been reported for Platypodinae.

4.1.4 Repeated Mating: the Key to Evolution of Prolonged Male Residency?

The fact that females are receptive during part or most of the egg laying period provides an explanation for the evolution of mate guarding, and ultimately of male residence. Lissemore (1997) attributed male residency in *Ips pini* (Say) to the need for males to copulate repeatedly with females in order to fully displace sperm from previous matings. Many *Ips* females joining males already have sperm stored in their spermathecae; in such cases, Lissemore (1997) found that males require about 5–7 days of repeated copulations to attain near-complete paternity. Repeated copulations may function generally as paternity assurance: half of all *T. piniperda* females colonizing breeding material have been inseminated during the previous year's maturation feeding in shoots or while overwintering at the bases of trees (Janin and Lieutier, 1988), and in an Israeli population Mendel (1983) found nearly all females of *Orthotomicus erosus* (Wollaston) had been inseminated after overwintering in dense aggregations. Much lower levels of pre-colonization insemination are probably more usual (reviewed by Kirkendall, 1993; Bleiker *et al.*, 2013), but there is a clear potential for sperm competition in many Scolytinae, and the evolutionary response has been repeated copulation. Mating prior to gallery system construction may, however, be largely confined to species that are not ambrosia beetles, species in which aggregations of young adults occur during fall maturation feeding or in overwintering clusters before young adults emerge and disperse. The importance of this distinction will become apparent in our discussion of the evolution of alloparental care (Section 5.3).

We have discussed repeated copulation from the point of view of males. From a female point of view, repeated copulations (continuous sexual receptivity) may be an adaptation for extending male residency, thus gaining the benefits of male burrow blocking and frass removal. But it also may increase the fitness of her offspring by diluting and eventually replacing sperm from pre-dispersal matings; this becomes an advantage when some proportion of early matings are with relatives, and using early sperm then produces offspring with inbreeding depression.

Thus, males that stay in order to mate repeatedly with the same female gain offspring through increased paternity as well as increased female oviposition rates, while females gain in fecundity (as long as males remove frass) and produce outbred offspring. It is a short step from males staying long enough to ensure maximum paternity to the evolution of paternal care (Section 5.3).

4.2 Mating Systems

Most bark beetles outbreed, as do most insects, but both regular inbreeding and parthenogenesis (clonal reproduction) have evolved in Scolytinae. Outbreeding taxa vary in how the two sexes meet (mate location), how long males stay with females (male residency), and with how many females individual males are mated simultaneously (mating systems).

Mating system diversity and evolution has been reviewed by Kirkendall (1983; see also Kirkendall, 1993). Outbreeding bark and ambrosia mating systems are classified by how many females breed simultaneously with the same male: one, monogyny; regularly two, bigyny; several to many, harem polygyny. For consistency, inbreeding is referred to as inbreeding polygyny, when classifying mating systems based on numbers of females (Kirkendall, 1983). In a handful of species, it appears that both multiple males and multiple females are in contact and mating is indiscriminate: these systems are referred to as colonial mating or polygamy.

Another mating system factor is male residency, how long males remain with females after copulation. Males do stay with females in most species. The species in which males do not stay for an appreciable amount of time are scattered among four unrelated tribes (Hylesinini, Diamerini, Scolytini, and Corthylini (subtribe Pityophthorina) (Kirkendall, 1983). We will treat male residency in Section 5, where we discuss it in the contexts of the evolution of subsocial behavior and paternal care. A detailed overview of variation in how long males remain in gallery systems can be found in Kirkendall (1983), and arguments for the evolution of prolonged male residency are developed in that review and in Kirkendall (1993), and in Section 5.

Generally, the pioneering sex initiates tunneling in fresh breeding material, and is located by the following sex; the second-arriving sex is attracted either to host odors, odors from boring dust, pheromones, or a combination. Members of the pioneer sex are also attracted, which often results in densely colonized host material. In the vast majority of species, males stay for a week or more, guarding the entrance and removing frass; commonly, males depart near or after females have finished ovipositing, and they may even die in the tunnel system (Kirkendall, 1983).

4.2.1 Monogyny

The ancestral mating system for Scolytinae is almost certainly female-initiated monogyny, and it is still the predominant mating system in bark and ambrosia beetles (Kirkendall, 1983; Figure 3.4). Nearly half of all genera have monogynous species, and nearly all tribes (Table 3.3), and most of these (especially in more basal lineages) are female initiated.

Male-initiated monogyny is the rule in Platypodinae, but rare in Scolytinae. In Bothrosternini, it is found at least in pith-breeding species, in *Sternobothrus* and certain *Cnesinus* (Beaver, 1973). The sex initiating mating is not known for most species in the tribe, but it does seem that all species are monogynous (Kirkendall, 1983). Monogynous species of *Scolytodes* (a genus with both monogyny and harem polygyny) are male initiated (Kirkendall, 1983; Kirkendall, pers. observ., *Scolytodes* species in *Cecropia* petioles). The remaining examples are from the Corthylini, a tribe with both monogynous and harem polygynous genera. As far as is known, almost all Corthylini are male initiated, including the monogynous genera, both those that are phloeophagous and those that are xylomycetophagous (Kirkendall, 1983). Exceptions occur in the large phloeophagous genus *Pityophthorus*, where female initiation may have re-evolved in a few twig breeders; cone beetles in the close related genus *Conophthorus* are also monogynous and female initiated (see next subsection).

As far as is known, without exception, Platypodinae are monogynous, and males seek out new host material and initiate tunnel construction (Jover, 1952; Kalshoven, 1960b; Browne, 1961; Kirkendall, 1983). That almost all Platypodinae are male-initiated monogynous species suggests that, once evolved, male initiation is evolutionarily stable (Kirkendall, 1983). Details of mating systems are not known for *Mecopelmus*, which is phloeophagous, and *Schedlarius*, which breeds in fungus-rotted wood of *Bursera* (Wood, 1993). Jover (1952) describes the outcome (apparently with several platypodine species) of introducing a second female to tunnel systems occupied by mated pairs. These females were accepted by the male, but the second female soon abandoned the gallery and left. His observations suggest that monogyny in Platypodinae may be maintained by the decisions of secondary females, rather than by any active resistance by males or primary females, but it would be informative to see if similar experiments confirmed these briefly reported results.

Male-initiated monogyny in Scolytinae tends to occur in species or genera that otherwise are dominated by harem polygyny (Kirkendall, 1983). These species breed in resources where more than one female cannot breed simultaneously without dramatic larval mortality due to intrabrood competition; hence, it is not advantageous for females to join already-mated males.

4.2.2 Reversions to Female-initiated Mating Systems

Kirkendall (1983) argued that colonization by males should be a stable strategy, especially when sex attractant pheromones are involved. Females coming to already established males avoid considerable risks and time investment associated with finding usable host material; when they can enter tunnels immediately, they also reduce their risk of being consumed by surface-active predators such as checkered beetles (Cleridae), ants, and foraging birds. Nonetheless, reversion to female colonization has occurred in cone beetles (*Conophthorus*) and in a few twig-breeding *Pityophthorus* species, both corthylines. In almost all Corthylini, males initiate gallery construction. Cone beetles

TABLE 3.3 Number of Scolyinae Genera and Tribes with at Least One Species having the Given Mating System (247 total genera, 26 total tribes)

Number of Taxa with at Least One Species	MG	BG	HP	Col	Inbr	?
Genera	118	19	27	3	54	45
Tribes	24	8	8	2	9	17

Some genera and tribes are represented in more than one category. MG = monogyny; BG = bigyny; HP = harem polygyny; Col = colonial polygyny (polygamy); Inbr = inbreeding; "?" = mating system unknown. Data from Appendix.

are a monophyletic corthyline group similar to *Pityophthorus* genetically, morphologically, and in pheromone components (pityol, conophthorin) (S. L. Wood, 1982; Dallara *et al*., 2000; Rappaport *et al*., 2000; Cognato *et al*., 2005; *Conophthorus* biology is also discussed in Section 3.6). An example from *Pityophthorus* is *P. pubescens* (Marsham). Most *Pityophthorus* are harem polygynous phloeophages in branches or trunks of hardwoods and conifers, and are distributed around the world; males initiate gallery systems, and where known, produce attractant pheromones. *Pityophthorus pubescens* is one of several twig breeders that have reverted to monogyny, and in this species females initiate gallery construction and also produce a sex pheromone (López *et al*., 2013).

What these species seem to have in common is that females spread their oviposition among many host resource units, rather than putting a large number of eggs in one resource over a long period of time as is the case in most bark and ambrosia beetles. Perhaps the short female residency time reduces advantages to males of staying with females, which in turn leads to females needing to initiate at least subsequent galleries alone. Once that behavior is in place, it is possible for female initiation of the first egg tunnel to evolve, though it is not clear what balance of selective forces would lead to its evolution.

Females also colonize in parthenogenetic (thelytykous) species (*Pityophthorus puberulus* (LeConte): Deyrup and Kirkendall, 1983) and of course in inbreeders (since males do not disperse), including lineages likely derived from outbreeders with male initiation such as the *Araptus laevigatus* Wood complex. In *Pityophthorus* and *Araptus*, this may have evolved either after female initiation re-evolved, or directly from male initiation (which predominates in these genera and their allies).

4.2.3 Bigyny

Regular bigyny has evolved repeatedly in Scolytinae, from both harem polygynous and monogynous ancestors. Systems in which males regularly have two females are found in 19 different genera, in eight tribes; seven genera are from the Micracidini, in which most genera are bigynous. Several otherwise monogynous genera have one or a few species that are bigynous. In the Phloeosinini, bigynous species are found in two otherwise monogynous and (mainly) phloeophagous genera, *Phloeosinus* and *Chramesus*. *Chramesus* has the bigynous species *C. incomptus* Wood, which makes biramous diagonal galleries in *Clematis* shrub stems (S. L. Wood, 1982).

We can find no references to regular, simultaneous bigyny in other animals. In fish and birds, at least, occasional bigyny in monogynous species seems to occur when male territories are of sufficient size and quality to overlap territories of two females. In such cases, most males are monogynous, and a few (in fish, usually larger males) are bigynous. That regular bigyny is only known from Scolytinae must, then, be related to geometric constraints on egg tunnel construction (situations that force tunnels to diverge at 180°). But this does not explain why the vast majority of bark beetles with transverse or longitudinal biramous tunnel systems (i.e., systems in which the two tunnels do diverge at or nearly at 180°) remain monogynous or are only occasionally, not regularly, bigynous.

That bigynous species rarely have more than two females is easier to understand. When egg tunnels are constrained to run either parallel to the wood grain or perpendicular to it, adding the work of a new female means adding a tunnel parallel to, and close by, the tunnel of another ovipositing female, which should result in extremely high larval mortality in species where larvae must tunnel long distances to acquire enough resources (Kirkendall, 1984; Løyning and Kirkendall, 1999). In most such situations, females should be selected to avoid joining bygynous systems.

By the same reasoning, for species where egg tunnels are all longitudinal or all transverse, polygyny is only possible where resource quality is high and larval tunnels correspondingly short; in such cases, most males have four (maximum of two parallel arms running in one direction) or less females. In cases where females join males with four females, the joining female(s) will suffer large losses of offspring due to competition (Schlyter and Zhang, 1996; Latty *et al*., 2009; Kirkendall, 1989). This constraint on harem size is weak or nonexistent in harem polygynous species producing star-shaped gallery systems with long egg tunnels, however; egg tunnels diverge more and more, as they progress, steadily reducing intraharem competition for resources. Star-shaped systems are especially common in genera such as *Pityophthorus*, *Scolytodes*, *Pityogenes*, *Pityokteines*, and *Polygraphus*.

4.2.4 Harem Polygyny

Simultaneous polygyny (harem polygyny and bigyny) has evolved only sporadically in more basal taxa (Figure 3.7; reviewed in detail in Kirkendall, 1983). Altogether, 39 genera in 11 tribes have species that are harem polygynous or bigynous (Appendix). Based on Figure 3.7, it appears that polygyny has evolved at least 12 times in Scolytinae; the number of independent origins is certainly higher, given that there are multiple occurrences of polygyny in each of the predominantly monogynous genera *Scolytus* and *Phloeosinus*, and at least some of the polygynous species are not related to other polygynous species in the same genus. Harem polygyny is found in 26 genera in eight tribes. It is the predominant mating system in Ipini, and common in Corthylini and Polygraphini.

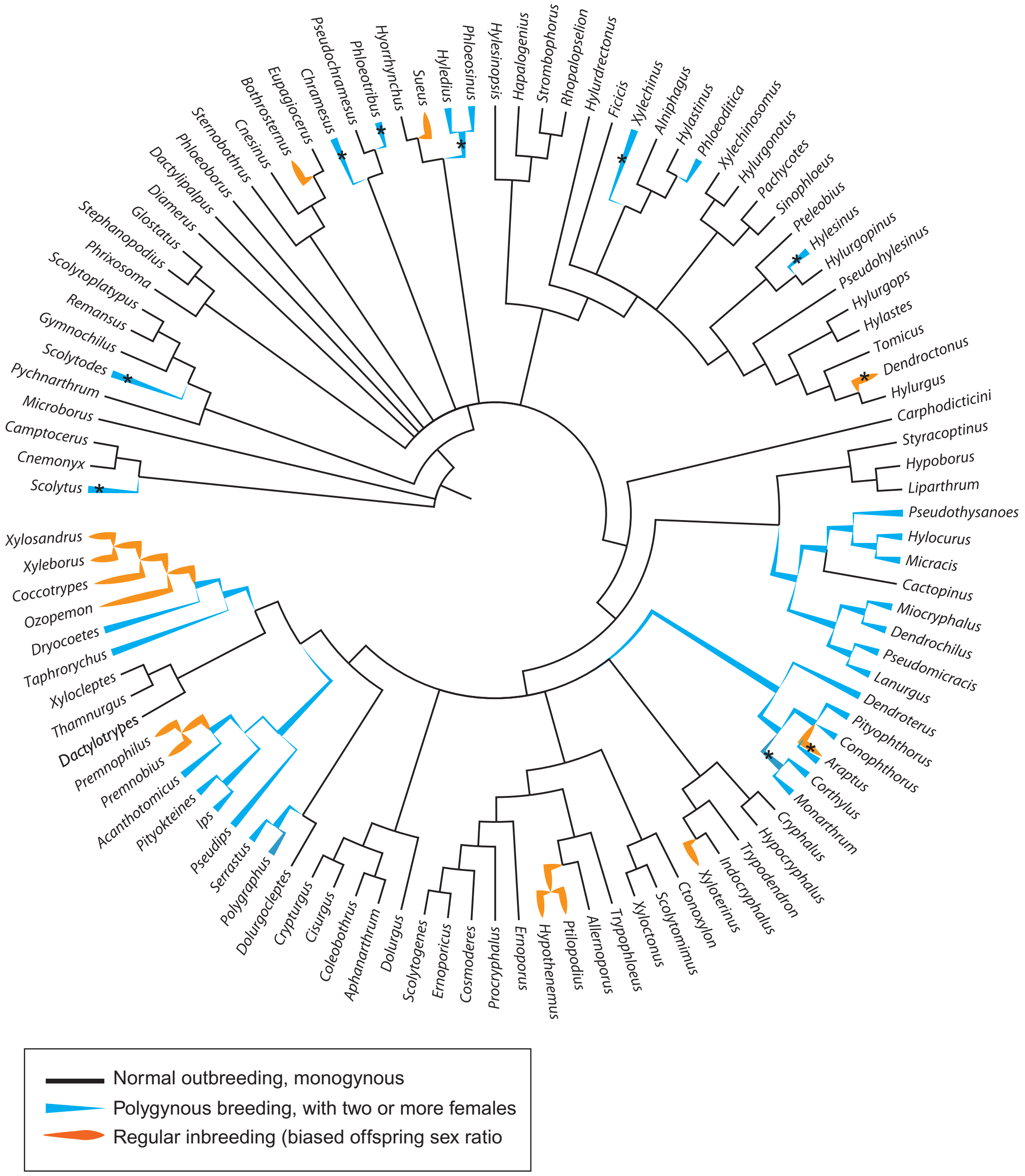

FIGURE 3.7 **Phylogenetic tree of Scolytinae with mating systems indicated (see inset legend).** Harem polygyny includes bygyny. Stars indicate genera or lineages in which the mating system is rare (one or just a few species).

Harem polygyny is relatively rare in animals. In bark and ambrosia beetles, polygyny takes the form of resource defense polygyny, where males accrue multiple mates because they control critical breeding resources capable of supporting the reproduction of more than one female (Emlen and Oring, 1977; see also Searcy and Yasukawa, 1989). The key question in polygynous mating systems is why females join already mated males, if unmated males are available. Females joining a mated male rather than an unmated (or less mated) one may suffer decreased fecundity in more crowded systems and decreased offspring survivorship due to within-harem competition (Kirkendall, 1989). This must be outweighed by the costs in time, energy, and predation risk of searching for an unmated (or less mated) male. If mated males control sufficiently high quality breeding resources, the positive effects of resource quality on fitness can outweigh the costs of joining a mated male. This resource-based argument for the evolution of simultaneous polygyny is encapsulated in the polygyny threshold model, which though developed and tested in the context of bird mating systems, would seem to apply well to bark and ambrosia beetles (Kirkendall, 1983). Kirkendall (1983) postulates that the harem polygyny threshold model is most likely to lead to the evolution of polygyny in these beetles when resource quality is highly variable (not uniformly high or low). Variable resource quality leads to some males being in high quality resource patches capable of supporting high fecundity of several females, while other males sit in low quality patches and will be largely ignored by searching females. See Kirkendall (1983) for a more detailed development of the argument and for data supporting it.

For species where egg tunnels are all longitudinal or all transverse and hence run parallel to each other if on the same side of the gallery system, polygyny is only possible where resource quality is sufficiently high and larval tunnels correspondingly short. Support for this hypothesis comes from observations that males in fact refuse entry to additional females after having acquired their normal complement (Borden, 1967; Swaby and Rudinsky, 1976), and that once having achieved large harems, males of several species have been shown to be less attractive or to reduce pheromone emission (Kirkendall *et al*., 1997).

Kirkendall (1983) suggests that females in large harems do not suffer a fitness cost to joining harems. Available data also suggest that in harems with only three of four females, it is possible for females to avoid within-harem competition if they space their egg galleries optimally, even in systems where egg tunnels run parallel to each other as they do in *Ips* (Kirkendall, 1989; Schlyter and Zhang, 1996; Latty *et al*., 2009).

In the extreme case of no available solo-male territories, the only option for females is to join mated males (i.e., harems). Mortality of the initiating sex is thought to be quite high in bark and ambrosia beetles, due to the difficulties of locating breeding material before exhausting energy resources, mortality from above-bark predation, and deaths due to residual or active host tree defenses. If males are the pioneer sex, and if mortality is high enough, then one would expect considerable pressure from late-arriving females on blocking males to allow them entry, even when one female is already in the gallery system. Polygyny can then evolve as long as the net change to male fitness is positive and the fitness of joining females greater than zero, and assuming that the first-arriving females cannot prevent entry of further females. Put more simply, polygyny can evolve if it pays males to allow more than one female to enter, and if females joining mated males can successfully produce offspring. Note, however, that in current harem polygynous species, unmated males are relatively frequent (review and original data in Kirkendall, 1983; Schlyter and Zhang, 1996; Latty *et al*., 2009).

4.2.5 Colonial Polygyny

We have categorized three genera in two tribes as having species with colonial polygyny (Table 3.3): *Aphanarthrum* and *Crypturgus* (Crypturgini), and *Cyrtogenius* (Dryocoetini). None of the species we call colonial have been studied in detail, but they appear to have multiple males and multiple females in the tunnel systems. It is possible that some of these instances are of multiple male/female pairs sharing a system of tunnels, but it seems more likely that no pair bonds are formed and both sexes mate with several individuals of the opposite sex. It must be difficult for males to maintain exclusive access to females in a many-branched tunnel system. In the phloeophagous *Cyrtogenius brevior* (Eggers) in Fiji, gallery systems are described as having many branches, with several adults in each branch; Roberts (1976) collected 20 males and 32 females from 11 or 12 galleries. Other species in the genus are monogynous, and phloeophagous or xylophagous (Browne, 1961, 1963; Roberts, 1976). Similarly, all *Crypturgus* species are found in networks of interconnected tunnels with many females and males in the same colony (Blackman and Stage, 1918; Chararas, 1962). Jordal (2006) reported on systems of interconnected tunnels with multiple individuals in *Aphanarthrum* species breeding in succulent *Euphorbia* species and suggested that promiscuous systems such as these evolve in lineages of inquilines, i.e., species that regularly use tunnels of other species as a starting point for their own egg galleries. This behavior is the norm, for *Crypturgus* species, and has also been observed in *Aphanarthrum* (Jordal, 2006).

4.2.6 Inbreeding Polygyny

Inbreeding polygyny is not unique to Scolytinae; regular brother/sister mating is found in a wide range of organisms, ranging from eyelash mites to naked mole rats, but it has evolved especially often in bark beetles. Extreme inbreeding has evolved eight times in Scolytinae, and is represented in nine different tribes (Table 3.3). About 27% of all described Scolytinae are thought to breed regularly by brother/sister mating. Of all inbreeding species, 97% come from two major species radiations. The largest inbreeding clade is that of 1336 species from 37 genera of Xyleborini plus three genera of inbreeding Dryocoetini, 22% of all Scolytinae (Tables 3.3 and 3.4, Appendix). This clade has been inbreeding regularly for about 20 million years (Jordal and Cognato, 2012). The second largest clade, the inbreeding Cryphalini, comprises 238 species divided among six genera. Its age is estimated to be ca. 50 million years (Jordal and Cognato, 2012). Despite the evolutionary success of the two major clades and ecological success of many inbreeding species, there is no evidence that inbreeding leads to diversification (Jordal and Cognato, 2012).

While many inbreeding clades are ambrosia beetles, there is no evidence that ambrosia feeding in itself predisposes a lineage to evolving inbreeding. Inbreeding has not

TABLE 3.4 Occurrences of Inbreeding in Scolytinae (after Kirkendall, 1993; see also Phylogeny in Jordal and Cognato, 2012)

Lineage	Tribe	Inbr. spp.	Biology
Bothrosternus	Bothrosternini	11	Ambrosia beetles
Araptus laevigatus complex	Corthylini	9	Seeds, pods, leafstalks, fruits
Cryptocarenus, Hypothenemus, Margadillius, Periocryphalus, Ptilopodius, Trischidias	Cryphalini	238	Highly variable, but few strictly phloeophagous (see text); one ambrosia beetle
Coccotrypes, Ozopemon, Dryocoetiops	Dryocoetini	168	Seeds, fruits; many highly polyphagous; *Ozopemon* is phloeophagous.
+ Xyleborini	Xyleborini	1168	Ambrosia beetles
Dendroctonus micans, D. punctatus	Hylurgini	2	Phloeophagous
Sueus	Hyorrhynchini	5	Ambrosia beetles
Premnobius, Premnophilus	Ipini	25	Ambrosia beetles
Xyloterinus	Xyloterini	1	Ambrosia beetles

evolved in Platypodinae, Corthylina (the ambrosia beetle subtribe of Corthylini), or *Camptocerus*. In six lineages in which ambrosia feeding and inbreeding co-occur, fungus farming preceded inbreeding in only three (Jordal and Cognato, 2012). Actually, the highest transition rates to xylomycetophagy are from lineages with regular inbreeding (Jordal and Cognato, 2012).

What is striking from Table 3.4 is that inbreeders mainly have feeding modes other than the predominant one of phloeophagy. Kirkendall (1993) analyzed the association between inbreeding and larva feeding modes for the bark and ambrosia beetles of North and Central America and for those of Thailand, Malaysia, and Indonesia. For both regions, inbreeders are most commonly ambrosia beetles. For North and Central America, 93% breed either as ambrosia beetles or in pith, seeds, and fruits, or "diverse" tissues. In the Southeast Asia fauna, too, those that are not ambrosia beetles are mainly myelophagous and spermatophagous. Conversely, inbreeding has never evolved in purely herbiphagous lineages (Kirkendall, 1993), though a few inbreeders have evolved herbiphagy and some generalists (both ambrosia beetles and phloeophages) are able to breed in herbaceous tissues. Both *Xylosandrus*, which breed in orchids (Dole *et al.*, 2010), and *Hypothenemus*, which breed in fleshy tissues, are tissue generalists, with the exception of *H*. pubescens, which may breed exclusively in grass stems (Atkinson and Peck, 1994). *Coccotrypes*, which attack mangrove propagules, are also herbiphagous (Sections 3.4 and 3.9). These examples all come from inbreeding clades.

The few phloeophagous inbreeders are atypical for species breeding in inner bark: both *Ozopemon* and *Dendroctonus* breed in large chambers with larvae feeding communally, as do phloeophagous *Hypothenemus* and *Coccotrypes* (Kirkendall, 1993). Communal larval feeding is a common theme in inbreeders, and one of the most important factors in the evolution of regular inbreeding. Communal feeding is associated with all inbreeding lineages whether they are ambrosia beetles, pith breeders, seed breeders, or phloem feeders (Kirkendall, 1993; Jordal and Cognato, 2012). In seeds, if colonized only once, a single family develops in close contact within the confines of a single seed. In pith, the larvae feed in close proximity in one long cylinder.

As argued by Kirkendall (1983, 1993), the first step in the evolution of inbreeding must be pre-dispersal mating. However, for pre-dispersal mating to be incestuous, young adults must have developed in close proximity. In most bark beetle systems, larvae tunnel away from the maternal egg gallery, and most bark beetles breed in relatively dense aggregations: any mating before dispersing will usually be between offspring of different broods. Inbreeding can only evolve in an outbreeding species if young adults are in close contact with each other when they mature, as will happen if they develop together in a common nest as larvae of one family.

Inbreeding is characterized by two major ecological patterns (Kirkendall, 1993; Jordal *et al.*, 2001). There is a latitudinal gradient in close inbreeding: the proportion of inbreeders in the Scolytinae fauna increases from just a few species in the far north or far south to being roughly half of the fauna of lowland tropics. It is likely that there is also a corresponding elevational gradient (inbreeding decreases with increasing altitude), though this has not been thoroughly investigated (but see Kirkendall, 1993). Inbreeding is also disproportionately common on small islands, not because outbreeders evolve incestuous mating, but because inbreeders are more successful colonizers (Kirkendall, 1993; Jordal *et al*., 2001). The species–area relationship differs for the two mating behaviors: numbers of outbreeding species decrease more rapidly with area than do numbers of inbreeding species. Jordal *et al.* (2001) showed that this pattern was not due to differences between outbreeders and inbreeders in resource utilization (feeding modes) or by sampling biases (undercollecting). Rather, outbreeders are poor colonizers because they are constrained by Allee effects, density-dependent behavioral and ecological factors disproportionately impacting small populations (Gascoigne *et al*., 2009; Kramer *et al*., 2009). Jordal *et al.* (2006) postulate that outbreeders have difficulties successfully establishing new populations because they are more vulnerable to random extinctions of small populations, suffer inbreeding depression, and have difficulties finding mates. Inbreeders, by virtue of investing minimally in males, and by not expending time and energy on mate location, have higher intrinsic rates of increase, and thus are exposed to the dangers of stochastic extinctions for a shorter period than are outbreeders.

Repeated inbreeding rapidly produces homozygotic genomes, which are then passed on intact from one generation to the next. Regular inbreeding, then, can be considered to be quasiclonal reproduction, "quasi-" because outbreeding is always a possibility in inbeeding lineages, while in most cases truly clonal, parthenogenetic organisms cannot suddenly shuffle their genes in a bout of sexual reproduction. Reproduction by extreme inbreeders (species for which interfamilial inbreeding is the norm), then, is "clonal" as long as inbreeding continues, but is "reset" for females mating with unrelated males who manage to get into a foreign gallery system. Outbreeding individuals then produce a genetically variable brood with a burst of heterozygosity.

How often does outbreeding occur in inbreeding lineages, and how does it happen? This is a key question for understanding why inbreeding has been so successful in these beetles. Population structure has been investigated recently for the seed borers *Coccotrypes dactyliperda* (F.) (Gottlieb *et al*., 2009; Holzman *et al*., 2009) and *H. hampei* (Benavides *et al*., 2005); all found low rates of genetic variation, and large genetic differences between populations, patterns consistent with high rates of inbreeding. Experiments with *X. germanus* (Peer and Taborsky, 2005) found outbreeding depression but no inbreeding depression, as expected for regular inbreeders. Gottlieb *et al.* (2009) estimated inbreeding rates and found that they vary highly between populations but generally reflect high amounts of inbreeding.

Extreme inbreeders, then, potentially reap the benefits of clonal reproduction, i.e., replication of successful genomes from one generation to the next, preserving combinations of genes that work well together and conserving local adaptation. All inbreeders that have been studied in any detail have evolved adaptive, strongly female-biased sex ratios, further increasing advantages to inbreeding; outbreeders invest half their resources in males, while inbreeders invest minimally. However, this nearly two-fold advantage in reproductive rate would be largely mitigated if males significantly increase the reproductive output of their partners. For this reason, the fitness effects of male residency are particularly relevant, in understanding the factors favoring or disfavoring the evolution of regular inbreeding. It should also be more difficult for inbreeding to evolve in species where male presence significantly increases female fecundity or the survivorship of the male's offspring (see Section 5.3). There should then be strong selection on females to bind males to them, which they do by being continuously receptive, even if females have mated previously and have sufficient sperm to fertilize all their eggs. Females breeding alone (and hence using only sperm from a predispersal mating) would have low reproductive success relative to outbreeding females.

4.2.7 *Partial Inbreeding*

As far as can be determined from the literature on inbreeding Solytinae, almost all instances are examples of extreme inbreeding, and reproduce regularly by brother/sister mating (Kirkendall, 1993). The likely exception is the Palearctic *D. micans* and its Nearctic sister species *D. punctatus* LeConte. These two species may be the best examples of scolytine species with populations that regularly experience intermediate levels of inbreeding (but see Holzman *et al*., 2009). All other inbreeding lineages in Scolytinae exhibit most characteristics of what Hamilton (1967) termed a biofacies of extreme inbreeding, but this *Dendroctonus* clade does not; their males are only statistically shorter and lighter in weight than females, and can fly (Kirkendall, 1993; Meurisse *et al*., 2008). Further, *D. micans* seem to produce more than minimum numbers of males per brood; typical families have 10–30 males (Kirkendall, 1993). *Dendroctonus punctuatus* have similarly large broods with multiple males, and have an average of about five females per male ($N = 37$ broods: M. Furniss, pers. commun.). Other inbreeding scolytines normally produce broods with just one or very few males, sufficient to fertilize all their sisters (Kirkendall, 1993). However, as with all other inbreeding scolytines, mating in *D. micans* and *D. punctatus* occurs before females disperse, and males do not participate in gallery construction. Inbreeding as a breeding strategy has not been studied in *D. micans* or *D. punctatus*, but the only genetic study (using protein electrophoresis) supports a hypothesis of intermediate levels of inbreeding, with modest but reduced levels of heterozygosity found in both species (Kegley *et al*., 1997).

That *D. micans* and *D. punctatus* do not seem to be fully committed to inbreeding could have arisen in two ways. First, it is possible that they are under strong selection to inbreed and do so most of the time, but that inbreeding has evolved too recently for males to fully adapt. In this case, the relatively high numbers of males might be maladaptive, but females might have poor control over the sex of their eggs. Alternatively, these two species may indeed be balancing inbreeding and outbreeding, and the numbers of males produced may be optimal for the levels of outbreeding occurring in natural populations as well as for regular partial brood mortality due to *Rhizophagus grandis* Gyllenhal predation (discussed in Kirkendall, 1993). We lean towards the latter hypothesis. Inbreeding must have evolved before *D. micans* and *D. punctatus* split. This split may have been as recent as the Wisconsin glaciation 85,000–11,000 years ago, as argued by Furniss (1996), but as he pointed out, they differ in 10 discrete morphological characters, and they also differ in karyotype (Zúñiga *et al*., 2002a, b). Whether or not this level of differentiation can occur in such a relatively short time is an interesting question.

Broods regularly merge in epidemic outbreaks of *D. micans*, and under endemic conditions, males are fully capable of wandering from one brood gallery to another, or even flying to another colonized tree (Meurisse *et al*., 2008). Whether or not interfamily matings represent genetic outbreeding is not known. When there are multiple broods on a single tree, these may often stem from related females (Grégoire, 1988).

4.2.8 Parthenogenetic Reproduction

Four forms of parthenogenetic reproduction have evolved in Scolytinae. In thelytoky and pseudogamy, females are produced clonally and are genetic copies of their mothers. In the former, no males are involved and populations consist solely of females, while in the latter, fertilization is required (by males of the same or a related species) but male genomes are not used to build the phenotype and are not passed along to offspring. In arrhenotoky and pseudoarrhenotoky, daughters are sexually produced, but males express and pass on only genes from their mother. Males are thus functionally haploid in both, though in pseudoarrhenotoky, fertilization takes place but then the paternal genome is eliminated. Since male genomes are produced by meiosis, males are not clonal.

Obligate or facultative thelytoky is relatively frequent in weevils, and occurs at least sporadically in over 80 families of Hexapoda (Normark and Kirkendall, 2009); it has arisen at least once in Scolytinae, in Corthylini, though there are several lineages in which it may also occur. Deyrup and Kirkendall (1983) examined over 500 *Pityophthorus puberulus* (LeConte) individuals collected from Indiana, Michigan, and Maine; *P. puberulus* is the most common scolytine in dead twigs of native and exotic pines. All were female, and none contained sperm, not even those taken from galleries with eggs and larvae. In no case were two parent adults found in a gallery system. In taxonomic treatments of the genus, Bright (1981) and S. L. Wood (1982) describe *P. puberulus* males simply as being identical to females; but as found by Deyrup and Kirkendall (1983), Bright (1981) reports that galleries contain only one individual. Thus, while it is possible that one or more sexual populations exist in this widespread species, no confirmed males are known, and *P. puberulus* should be considered parthenogenetic. There have been no subsequent investigations into this interesting case of thelytoky.

A possible second instance of all-female lineages comes from *S. rugulosus*. Gurevitz (1975) reported breeding repeated all-female generations in the laboratory, from beetles collected in Israel. *Scolytus rugulosus* has been occasionally studied as a pest of fruit trees in its native Eurasia and as an invasive species in North America, but no deviations from 1:1 sex ratios have been reported by other authors, and it seems to be a normally reproducing monogynous bark beetle everywhere else other than the Middle East (Gossard, 1913; Kemner, 1916; Chodjaï, 1963; Kirkendall, unpubl.). Parthenogenesis in *S. rugulosus* needs to be confirmed.

Finally, there are several groups (*Bothrosternus foveatus* Wood and Bright; *Dryocoetiops*) that have been treated as inbreeding (Kirkendall, 1993) but where males have still not been found; in both, close relatives are inbreeders. Given that males of inbreeders are often tiny and are rarely collected, it is possible that these groups inbreed.

In pseudogamy, a form of sperm-dependent parthenogenesis, eggs must be fertilized to develop, but sperm do not contribute genetically to the offspring and inheritance is strictly mother to daughter (Beukeboom and Vrijenhoek, 1998; Schlupp, 2005). It is a rare reproductive system, occurring among hexapods in just a few other orders; in beetles, it is found in a spider beetle (Ptinidae). Pseudogamy as a reproductive system has evolved at least twice in Scolytinae, in North American spruce-breeding *Ips*, and in a Eurasian pine-breeding *Ips* (Lanier and Kirkendall, 1986).

In North America, pseudogamy occurs in the *tridens* complex of spruce-breeding *Ips* (Hopping, 1964; Lanier and Oliver, 1966; Lanier and Kirkendall, 1986). Three types of individuals, pseudogamous females, sexual females, and males, are found in *Ips borealis* Swaine, *I. tridens* (Mannerheim), *I. pilifrons* Swaine, and *I. perturbatus* (Eichhoff). In all four "species," pseudogamous females are triploid

(Lanier and Kirkendall, 1986). As is usually the case (Schlupp, 2005), pseudogamy has probably originated via interspecific hybridization. These pseudogamous lineages form a monophyletic clade (Cognato and Sperling, 2000), so the phenomenon may have evolved only once in this species group. For the most part, only the taxonomy and systematics of these pseudogamous populations have been studied; virtually nothing is known of the nature of pseudogamy in these lineages. It seems likely that predominantly or entirely sexual populations were studied in the ecological investigations of *I. perturbatus*, which in these papers seems to have typical *Ips* biology and equal sex ratios (Gobeil, 1936; Robertson, 2000).

Interspecific hybridization is much less likely the origin in *I. acuminatus*, the Eurasian example of pseudogamy, though here, too, the parthenogenetic females are triploid (Lanier and Kirkendall, 1986). Though this pine breeder occurs from Western Europe to eastern Siberia, China, and Japan, its reproductive behavior and population dynamics have only been studied in Europe (Bakke, 1968b; Kirkendall, 1989, 1990; Kirkendall and Stenseth, 1990; Løyning and Kirkendall, 1996; Løyning, 2000; Meirmans *et al*., 2006).

Arrhenotoky has arisen once in Scolytinae, producing the remarkably successful haplodiploid clade comprising Xyleborini (nearly 1200 species in 37 genera) and three inbreeding genera previously placed in Dryocoetini, *Coccotrypes* (129 spp.), *Ozopemon* (21 spp.), and *Dryocoetiops* (18 spp.) (Jordal *et al*., 2002; Cognato *et al*., 2011; Jordal and Cognato, 2012). It is well known that bees, wasps, and ants are haplodiploid, but this system is also found in the one species of Micromalthidae, many thrips, a few whiteflies and scale insects, most rotifers, most mites, and some nematodes. The entire scolytine clade is considered haplodiploid, but this is based on the observations of just a few species of *Coccotrypes* and *Xylosandrus* (Kirkendall, 1993). However, there are no data that falsify the hypothesis that the entire clade is haplodiploid, and finding all-male broods in many species supports the hypothesis (these represent reproduction by unfertilized females).

Pseudo-arrhenotoky is known from one inbreeding lineage, *Hypothenemus*, having been demonstrated in *H. hampei* (Brun *et al*., 1995a, b; Borsa and Kjellberg, 1996a, b; Chapter 11). The phenomenon was discovered serendipitously while studying the evolution of resistance to insecticides, when it was observed that males always had the resistance phenotype of their mother, regardless of the father's phenotype. Worldwide, there are 181 described species in the genus (Chapter 11), but only *H. hampei* has been studied in this context. It is believed that the entire genus inbreeds, since in all cases where broods have been examined, males are rare, and all males known are reduced in size and flightless, which are characteristics of regular inbreeders. Further, the most closely related genera also inbreed. Pseudo-arrhenotoky is a rare breeding system, but is known in some mites and in mealy bugs (Coccidae). Variation in reproductive systems among closely related coccids, though, raises a red flag, and the hypothesis that pseudo-arrhenotoky is characteristic of all inbreeding *Hypothenemus* its relatives should be verified.

4.3 Gallery System Form

The general hiking and camping public, including most entomologists, rarely encounter the insects themselves, but may well be aware of the consequences of their activities: dead and dying trees during bark beetle outbreaks, and the striking engravings seen in older dead wood. Forest entomologists have long classified these etchings based on their general form (Barbey, 1901; Swaine, 1918; Blackman, 1922; Chamberlin, 1939), and they are still used today.

Generally, one can deduce the mating system of a species (especially those breeding in inner bark) from the form of the tunnel system: single egg tunnels result from monogyny, a variable number of egg tunnels per system from polygyny (Figure 3.6). However, when there are two tunnels, this may result either from a single female working in two directions or, in a few lineages, from bigyny. Variously shaped large chambers lacking defined egg tunnels—cave-type systems—are formed by monogynous species.

Females of phloeophagous Scolytinae disperse eggs in a wide variety of ways. Most commonly, all eggs laid by a single female during a given bout of reproduction are deposited in a single long gallery or in two long galleries bored in opposite directions. In a few genera, a single female makes several short tunnels leading away from a central nuptial chamber; an especially interesting example is *Ips latidens* (LeConte), a monogynous species in an otherwise uniformly harem polygynous genus (Reid, 1999). Most Cryphalini, and a few genera or species from other lineages, make elongate to roundish chambers, where the eggs are either spaced around the periphery in egg niches (as in *Procryphalus mucronatus* (LeConte), *Dacryostactus kolbei* Schauffuss, or *Styracoptinus murex* (Blandford)), deposited in egg pockets (*Cryphalus kurilensis* Krivolutskava, *C. exiguus* Blandford), or simply laid in clusters loose in the gallery (*Cryptocarenus*, some *Cryphalus*, many *Hypothenemus*, *Trypophloeus populi* Hopkins). Some specialists, such as Blackman (1922), Browne (1961), and S. L. Wood, (1982), have thought that cave-type galleries were "primitive" in bark beetles, but this seems unlikely given that basal taxa in current phylogenies all make long egg tunnels.

Ambrosia beetle tunnel systems also show variation in egg deposition strategies (Browne, 1961). Again, in most groups, each female constructs a single tunnel or a few long branches. Tunnels constructed in smaller branches may completely encircle the branch, and in very small-diameter breeding material tunnel systems usually spiral. Eggs are placed in niches constructed by the mother beetle in *Camptocerus*, Corthylini, and Xyloterini, reflecting their derivation from phloeophagous ancestors with egg niches; they are laid in batches loose in tunnels or lenticular chambers in Xyleborini, as they are in other members of this clade (spermatophagous or phloeophagous *Coccotrypes*, *Ozopemon*, and relatives), suggesting that the ancestors of this large inbreeding clade lost the practice of placing eggs singly in niches. Interestingly, Platypodinae lays eggs in clusters and larvae feed in the tunnel system, but the last instar larvae form cradles in which they pupate singly.

Long tunnels give females options for optimally dispersing offspring in space, both with respect to resource quality, resource quantity, host plant defenses, and intrabrood competition. At the same time, females themselves must feed continuously in order to produce large, protein-rich eggs. In Scolytinae, eggs are generally one-quarter to one-third or more their mother's body length (Kirkendall, unpublished data), while plant tissues they consume are critically low in nitrogen (White, 1993; Kirkendall, 1983; Haack and Slansky, 1987; Ayres *et al.*, 2000). Tunneling, then, fulfills both needs: spacing of eggs and acquiring nutrients for oviposition. Spatial orientation of tunnels, placement of eggs in the tunnels, and spacing of eggs all are highly variable in Scolytinae and almost certainly are adaptations, but there has been little research in this area.

4.3.1 Spatial Orientation

Broadly considered, phloeophagous tunnel systems are classified by the number of egg tunnels (arms) in a system and by the orientation of the tunnels. Most monogynous systems can have one (uniramous), two (biramous), or (exceptionally) more egg tunnels (polyramous). These tunnels can run with the wood grain (longitudinal or vertical), or perpendicular to the grain of the wood (transverse or horizontal); biramous systems can also be V-shaped. Tunnels of some *Dendroctonus* are long and very irregular in shape. *Chaetophloeus* species make single nearly circular egg tunnels; *Pseudips* construct C- or S-shaped systems (uni- or biramous). Polygynous systems are also classified by egg tunnel orientation, although less often so than are monogynous systems. In many polygynous taxa, egg tunnels are clearly oriented either longitudinally (e.g., most *Ips*) or transversely (*Pityokteines*), but others are simply fairly evenly spaced from each other and form star-shaped patterns (*Polygraphus*, most *Pityophthorus*). Gallery systems of regularly bigynous species usually are biramous, with each arm being the work of one female, and these run directly opposite one another, either longitudinally or transversely, though some species make V-shaped systems (one female in each arm). Females of *Pseudothyanoes* each make both arms of a "V," the system as a whole resembling an "X" or "H."

The adaptive significance of variation in egg tunnel orientation has not been rigorously analyzed, though hypotheses have been proposed (see Kirkendall, 1983). It is clear that there are associations with host plants: bark beetles in oaks (*Quercus*) and firs (*Abies*) tunnel horizontally, for example, even though congeners tunnel vertically in other hosts (Kirkendall, unpubl.). Since newly hatched larvae tunnel at least initially perpendicularly to the egg tunnel, the best orientation of the egg tunnel may be determined by factors selecting for larval tunneling direction: if it is optimal for larvae to tunnel with the grain of the wood, for example, then the egg tunnel should be transverse. Selection on adult or larval tunneling direction can result from host–plant defenses and physical characteristics of the host. If the inner bark is too thin to completely contain larvae as they feed, or if there are other reasons for larvae to tunnel deeper such that they begin to feed partly in sapwood, then the more fibrous nature of sapwood becomes a significant factor, as pointed out by Trägårdh (1930). Trägårdh (1930) also found that larval mines when engraved into the sapwood run strictly longitudinally and parallel to each other, but if the larval mines are purely in the inner bark, the mines can wander and can be transverse to one another. Both oaks and the woody leafstalks of *Cecropia* are quite fibrous, and especially small larvae probably cannot tunnel transversely; tunnels of bark beetles in oaks, and the smaller species in the cortex of *Cecropia* petioles, are transverse, and larvae feed perpendicularly to the gallery arms (with the wood fibers rather than across them).

It is also conceivable that, in some hosts, it is adaptive for females to oviposit where larvae are forced to partly chew through sapwood. This forces larvae to tunnel in straight lines (and thus they do not accidentally cross paths with neighbors), and allows for females to lay eggs right next to each other, if tighter egg packing is advantageous. A test of this hypothesis would be to compare related species with different egg arm orientations, transverse vs. longitudinal. Egg spacing (eggs per mm gallery) should be "tighter" (i.e., a higher number of eggs/mm) in species with transverse galleries.

4.3.2 Placement of Eggs

Most commonly, including among most basal taxa, eggs are placed in niches (egg-sized pockets) along both sides of an egg tunnel. Though usually these are evenly spaced on either side, some species (such as *Dendroctonus simplex* LeConte: Hopkins, 1909) alternate laying several eggs on one side. In species in which tunnels characteristically curve strongly, eggs are placed exclusively on the outer side of the curve. But also when generally straight or mildly curved tunnels curve more strongly, eggs will be placed only on the outer side. In at least some species, but possibly all or most, phloeophagous females seem to be able to adjust their egg placement adaptively. For example, *Pseudoips mexicanus* (Hopkins) tunnels are usually curved but can be straight; eggs are laid on both sides if straight, but just the outer side if curved (Smith *et al.*, 2009). An advantage of a curved gallery is that larvae emanating from the outer side can fan out, reducing the chance of accidentally coming in contact with each other (though two cases of incidental cannibalism were seen by Smith *et al.* (2009)).

The vast majority of phloeophagous species construct egg-sized niches, and lay just one egg in a niche. Interestingly, a few scattered instances of multiple eggs per niche have evolved: examples include *Chaetophloeus heterodoxus* (Casey) (Swaine, 1918); *Pseudoips* (Trimble, 1924; Chamberlin, 1958; S. L. Wood, 1982; Smith *et al.*, 2009; Zhang *et al.*, 2010); *Orthotomicus caelatus* (Eichhoff) (Swaine, 1918); and *Liparthrum mexicanum* Wood (Atkinson and Equihua-Martínez, 1985b). Such egg pockets are wider and deeper than normal egg niches, and may contain a few eggs (e.g., 1–4 in *Pseudoips*) or many (e.g., 6–12 in *C. heterodoxus*).

Furthermore, some species deposit eggs in widened portions of the egg tunnel rather than in single egg niches or egg pockets. Examples include *Dendroctonus pseudotsugae* Hopkins, *D. piceaperda* Hopkins, *D. rufipennis* (=*D. engelmanni* Hopkins), *D. micans*, *D. punctatus*, *D. valens*, *D. terebrans* (Olivier), *Hylurgops pinifex* (Fitch), *Dryocoetes americanus* Hopkins (=*D. autographus* (Ratzeburg)), and *Orthotomicus laricis* (F.) (Lövendal, 1898; Hopkins, 1909; Swaine, 1918; Balachowsky, 1949). In some cases, these are protected by a layer of frass, just as are normal egg niches. Intermediate between these grooves and the egg pockets is the pattern of *D. simplex*, which places three or four eggs side by side at the bottom of an elongate shallow pocket or groove (Swaine, 1918), and *Xylechinosomus valdivianus* (Eggers), where clusters of up to 30 eggs are placed in shallow troughs along the tunnel wall (Rühm, 1981). *Pseudothysanoes dislocatus* (Blackman) seems to have similar behavior (Blackman, 1922). *Hylurdrectonus piniarius* Schedl lays eggs loose in frass in indefinite tunnels in the cortex of *Araucaria* branches (Brimblecombe, 1953).

The selective advantages of clustering single niches or laying more than one egg in an egg pocket are not obvious. At least with regards to egg pockets, there would seem to be a cost of greater intra-family resource competition when larvae hatch so close to each other, and a risk of accidental siblicide. Perhaps clues can be found in the biology of the inbreeding *D. micans*, where clustered larval feeding significantly increases growth (Figure 3.6A). *Dendroctonus micans* breed solitarily in trunks of live spruces or other conifers. Storer *et al.* (1997) suggest that larval aggregation might be important in dealing with host defenses. This hypothesis suggests that egg clustering in phloeophagous species will be associated with breeding in live (vs. dead) plant tissues, particularly in hosts with strong chemical defenses.

5. SOCIAL EVOLUTION

It is not generally known that bark and ambrosia beetles exhibit an extraordinary diversity of social systems. Higher forms of sociality have evolved repeatedly in these insects, and the only eusocial beetle is the platypodine ambrosia beetle, *A. incompertus* (Kent and Simpson, 1992). Bark and ambrosia beetles are also the only social insects with closely related haplodiploid and diploid social lineages (Normark *et al.*, 1999; Jordal *et al.*, 2000), which would allow comparative studies to contribute to the long-debated role of haplodiploidy for social evolution (Hamilton, 1964; Bourke, 2011). Unfortunately, our knowledge of the detailed behaviors of social species is still superficial, as sociality has rarely been the primary focus of researchers working with these insects. This is primarily because studying insect behavior in tunnel systems under the bark or in the wood of trees is almost impossible. Exciting progress is now being made, however, because evolutionary biologists interested in social behavior have discovered these beetles as an illustrative alternative to classical hymenopteran model systems (Hamilton, 1967, 1978; Kirkendall, 1983, 1993; Kirkendall *et al.*, 1997; Peer and Taborsky, 2007; Biedermann *et al.*, 2009, 2011, 2012; Biedermann and Taborsky, 2011, submitted; Jordal *et al.*, 2011; Boomsma, 2013), and because several ambrosia beetles have been successfully reared in artificial media (Saunders and Knoke, 1967; French and Roeper, 1972b; Roeper *et al.*, 1980b; Mizuno and Kajimura, 2002; Biedermann *et al.*, 2009; Lake Maner *et al.*, 2013), which allows behavioral observations, experimental manipulations, and, due to their often short generation times, even artificial selection experiments (Biedermann and Taborsky, submitted).

5.1 Social Behaviors and Ecology of Bark and Ambrosia Beetles: an Overview

Animal social systems range from simple gregariousness, to family groups with parental care, to complex cooperative breeding or eusocial societies with reproductive altruism (Wilson, 1971; Alexander *et al.*, 1991; Costa, 2006; Boomsma, 2013). In bark and ambrosia beetles, all these forms are present: (1) gregarious feeding is typical for the phloeophagous larval offspring in certain *Dendroctonus* species, many cryphalines, *Ozopemon*, and some phloeophagous and some spermatophagous *Coccotrypes* species;

it is the norm for Xyleborini and Platypodinae. Gregariousness of adults is particularly apparent in cooperative mass attack in some primary *Dendroctonus* and *Ips* species, but also is found during overwintering or maturation feeding of many species. (2) Parental investment in the form of brood care by the mother, the father, or both—also termed "subsociality"—is ancestral for bark and ambrosia beetles and thus typical for the whole group. (3) Adult offspring refrain from dispersal and engage in "alloparental" brood care of young siblings at the natal nest, which is likely confined to some ambrosia beetles (see below) and potentially also *Coccotrypes* species breeding in seeds. Some of these species may form true beetle "societies" with division of labor between adult and immature offspring present in communal tunnel systems. These can be further split into "facultatively eusocial" or "obligately eusocial" societies, depending on whether adult offspring refrain temporarily or permanently from reproduction (Boomsma, 2009). Currently, we know of three facultatively eusocial (*Xyleborinus saxesenii* (Ratzeburg), *X. affinis* Eichhoff, *Trachyostus ghanaensis* Schedl) and one possibly obligately eusocial ambrosia beetle (*A. incompertus*), but there are likely more eusocial species awaiting discovery.

Larvae of phloem-feeding bark beetles construct their own tunnels in the phloem during feeding and gradually move away from their maternal tunnel. As larvae also pack these mines with frass, there is often no physical contact between the parents and their offspring. This is not true for all bark beetles, however, as some *Dendroctonus* species and also many non-phloem feeders like *Hypothenemus* and *Coccotrypes* species live in communal galleries. Communal galleries are also present in many ambrosia beetles, but tunnels may or may not be altered by ambrosial grazing by larvae and adults. Larvae and adults can move and interact freely in such galleries. However, this is not true for all ambrosia beetles; in *Camptocerus*, Xyloterini and Corthylini, larvae are separated from each other because they develop in individual larval niches and do not move freely in the galleries. Nevertheless, they still closely interact with their parents that freely move within the galleries. Consequently, as there are many more interactions between individuals in galleries of many ambrosia beetles and non-phloem feeders than in galleries of true bark beetles, the potential for advanced sociality to evolve is much higher in the first groups (Kirkendall *et al.*, 1997).

5.2 Basic Concepts of Social Evolution Theory

The evolution of behavior is fundamentally based on maximizing the direct fitness of individuals (i.e., individual-level selection; Alexander, 1974; Clutton-Brock, 2009). As Darwin (1859) realized, this cannot explain the evolution of alloparental care and eusociality, however, because the beneficiaries of care are not offspring of the caregivers but rather kin to them with varying degrees of relatedness. This problem was resolved by William Hamilton's theory of inclusive fitness (kin selection theory), which incorporates both the direct and indirect fitness effects of costly behaviors: an altruistic behavior can evolve if it benefits the spread of a cooperative gene, not necessarily by self reproduction (direct fitness), but also through the reproduction of relatives bearing that gene (indirect fitness) (Hamilton, 1964). More precisely, altruism is selected, for if the genetic relatedness (r) between social partners is greater than the ratio of fitness costs (c) to the performer over the fitness benefits (b) to the recipient: $r > c/b$. Accordingly, social behaviors typically arise in kin groups and under ecological conditions that yield higher inclusive fitness gains when remaining in the natal nest.

Ever since the publication of Hamilton's paper (Hamilton, 1964), several ecological conditions have been identified to generally facilitate social evolution across various animal groups, which can be roughly grouped in two categories: environmental constraints on solitary breeding and benefits of philopatry (Korb and Heinze, 2008; Bourke, 2011). Aiding kin becomes a viable alternative to breeding oneself when independent breeding is very costly. Environmental factors that increase the costs of solitary breeding include high mortality during dispersal, breeding sites being limiting, and high population densities (Emlen, 1982). Philopatry (not dispersing before breeding) can be beneficial if there is an opportunity to inherit the nest or a possibility of co-breeding (direct fitness benefits), or by helping related individuals to increase their reproductive output (indirect fitness benefits) (Stacey and Ligon, 1991).

5.3 Subsociality and Parental Care in Bark and Ambrosia Beetles

Subsociality is characterized by reproductive investment of parents beyond egg laying: post-ovipositional care increasing survival, growth, and development of offspring (Wilson, 1971). In insects, it has evolved repeatedly, typically in connection with abundant but ephemeral resources and high competition or predation pressure (Tallamy and Wood, 1986). The bark of dead trees is a prime example of an environment facilitating subsocial life. Wood suitable for insect attack is unpredictably distributed and difficult to locate, but offers an abundant, defendable resource, which may persist for several generations. The physical properties of woody tissues and plant defenses like resin flow and toxic chemical metabolites are likely major obstacles for small larvae, problems more easily overcome with the help of adult individuals (Hamilton, 1978; Chapters 1 and 5). Parents can also assist with food provisioning, in particular by increasing the quality or digestibility of food. By inoculating the wood with microorganisms, they can increase its nitrogen content and can make plant tissues easier to assess and assimilate. Wood-feeding insects can only utilize lignocellulosic resources by engaging in symbioses with bacteria, fungi, or protozoa (Tallamy and Wood, 1986). As parent beetles can significantly reduce physical and nutritional limitations for their offspring (see below), it is not surprising that wood is one of the most favorable habitats for the origin of subsociality in insects as well as of insect–microbe associations (Hamilton, 1978, 1996; Tallamy, 1994; Jordal *et al*., 2011).

Excavation of tunnels by adults for reproduction is universal in bark and ambrosia beetles. One or both parents typically remain in the tunnel system, providing nest protection and removing frass. This behavior is not common among other weevils that typically lay their eggs singly on the outside of plants or in small pre-bored cavities, where the larvae feed solitarily (Lengerken, 1939). The parental care of bark and ambrosia beetles is no exception in this habitat, as subsociality has evolved repeatedly in other weevil clades that bore in wood, such as Cossoninae and Conoderinae (Kuschel, 1966; Jordal *et al*., 2011) and Bostrychidae and Ciidae (Hamilton, 1979; Kirkendall, unpubl.). Parental care takes similar forms in these groups, being characterized by one or both sexes boring oviposition tunnels, keeping them free of frass, and protecting them against predators and competitors (Kuschel, 1966; Jordal *et al*., 2011). This suggests that selective factors specific to wood, like the difficulties faced by immature offspring mentioned above and pressures from competitors and natural enemies, have repeatedly selected for adult beetles which bore oviposition tunnels through the outer bark instead of laying their eggs freely on the plant surface or in simple slits. Following the successful excavation of a tunnel in the phloem, there is no reason for a female to leave this proto-nest after laying the first egg; tunnel excavation is energetically costly and the habitat offers a nutritious, defendable, and abundant food resource, which can support both her own nutritional needs and those of many more offspring. Studies on predation pressure within and outside the gallery are rare, but it is likely that, once under the bark surface, females are also much safer from predation by vertebrates and invertebrates alike. Beetles in tunnels are invisible to foraging vertebrates such as birds or lizards, and invertebrate wood borer predators like ants or checkered beetles (Cleridae) preferentially attack adult beetles on the bark as they have considerable difficulty with extracting them from tunnels (Wichmann, 1967).

Bark and ambrosia beetle females invest relatively heavily in individual offspring, via egg provisioning and maternal care. Eggs are unusually large, ranging from one-sixth the length of the female's body in *Tomicus pilifer* (Spessivtsev) (Wang, 1981) to one-third the size in *X. affinis* (Roeper *et al*., 1980b), *T. populi* (Petty, 1977), and *Pagiocerus frontalis* (F.) (Yust, 1957). Clutch sizes are modest (commonly, 70–90 eggs, but often smaller: Browne, 1961), and some bark beetles (such as those colonizing woody petioles of large leaves) lay fewer than a dozen eggs (Beaver, 1979b; Jordal and Kirkendall, 1998); these are among the insects with the lowest recorded fecundity (Hinton, 1981; Nyland, 1995).

Many males and females commit to one or two breeding sites (Kirkendall, 1983). For holarctic, outbreeding non-xylomycetophagous species, it is often reported that females re-emerge after finishing their first egg tunnel (Kirkendall, 1983); Browne (1961), however, believed that in the humid tropics, females of most species breed in only one bout. Pairs often die in their gallery system in species from a variety of genera: *Conophthorus lambertianae* Hopkins (Chamberlin, 1958), *Scolytus unispinosus* LeConte (Chamberlin, 1918), *Pseudohylesinus nebulosus* (LeConte) (Chamberlin, 1918), *Dactylipalpus camerunus* Hagedorn (Browne, 1963), *T. populi*, *Procryphalus mucronatus* (LeConte) (Petty, 1977), and *C. columbianus* (Milne and Giese, 1969). Committing strongly to a bout of breeding selects for increased parental investment (Wilson, 1975; Tallamy and Wood, 1986). Where it has been investigated, scolytine beetles as diverse as *Dendroctonus*, *Phloeosinus*, *Ips*, *Hypothenemus*, and *Conophthorus* digest (histolyze) their wing muscles once they have begun breeding (Chapman, 1956; Reid, 1958; Lekander, 1963; Borden and Slater, 1969; Morgan and Mailu, 1976; Garraway, 1986; Robertson and Roitberg, 1998; López-Guillén *et al*., 2011); whether or not Platypodinae do this as well is not known, and how common the phenomenon is within the Scolytinae is similarly unknown. For females, autolysis of wing muscles must free up quantities of protein for egg production; the advantages to males are less clear (Robertson, 1998b). While some females can regenerate their muscles after a post-ovipositional period of feeding, in many species most or all re-emerging females cannot fly, e.g., *Dendroctonus* (Lawko and Dyer, 1974; Langor, 1987; Grégoire, 1988); *Hypothenemus* (Ticheler, 1961; López-Guillén *et al*., 2011); and *Phloeosinus* (Garraway and Freeman, 1981). Regeneration in *Ips* males depends on body size and time spent in the tunnel system (Robertson, 1998a). Scolytines that do not regenerate wing muscles can and often do walk to new sites on the same host to start a second egg tunnel, though they cannot disperse to new breeding material (Fuchs, 1907; Reid, 1958; Sauvard, 2004).

In at least some Platypodinae, both sexes lose their tarsal segments after some weeks in the gallery and are thought to be incapable of dispersing anew (reviewed in Kirkendall *et al*., 1997). Here, commitment to one bout of reproduction seems assured.

This variation in reproductive strategies reflects varying optimal solutions to the problem of balancing the number of eggs laid with investment in offspring being produced, and (especially for males) balancing investment in current vs. future offspring. Over time, breeding material degrades, intraspecific and interspecific competition increase, and pressure from parasites and predators increases. Offspring produced late are smaller and consequently have lower fitness than those produced earlier in the same host (Kajimura and Hiiji, 1994). At some point, these factors shift the balance in favor away from laying more eggs towards either investing more in maternal care, or departing the brood and attempting further reproduction elsewhere.

5.3.1 Removing or Packing Frass

The simplest and most widespread form of parental care common to all bark and ambrosia beetles is clearing frass from the egg tunnel. Females and their offspring produce large amounts of frass during tunneling and feeding, which is pushed back towards the entrance by the mother; it is expelled from the gallery system by the male, if present, or by the female, or in some cases packed tightly into the base of the tunnel. Though modifications exist, frass is typically shuffled out of the nest by sliding it backwards beneath their body with the legs and then using their elytral declivity as a shovel to eject it (Wichmann, 1967). Although the fitness benefits of frass removal have not been studied, it is likely highly advantageous, as it is invariably present in all wood-boring weevils. Apart from enabling free movements within the gallery (females face forward while tunneling but must turn around and back up to lay eggs in newly constructed niches), keeping egg galleries free of frass likely serves two major purposes: ventilation of the nest, and nest hygiene by removing potential substrate for parasites and pathogens (e.g., mites, nematodes, fungi, bacteria). Ventilation of phloeophagous tunnels is important enough that it has been proposed as one possible function for entrance blocking, nuptial chambers, and especially holes bored upwards through the bark from the oviposition tunnels (Swaine, 1918; Blackman, 1922; Morgan, 1998; see below). Both ventilation and hygiene are especially important in ambrosia beetles, as fungus cultures grow only under specific moisture content and are very sensitive to pathogens (Francke-Grosmann, 1967). Likewise *X. saxesenii* females have been shown not only to shuffle frass and sawdust outside of the gallery but may also remove intruding mites, spores of fungal pathogens, and diseased individuals (Biedermann, 2012).

Although females of almost all species begin by removing frass, in at least a few species it has a been observed that, some time after commencing oviposition, females instead begin packing the frass behind them, forming an impenetrable plug between the active part of the egg tunnel and the nuptial chamber or even the tunnel entrance. Oviposition tunnels become plugged with tightly packed frass in *D. ponderosae* (Reid, 1958); some *Ips* species (Morgan, 1967; Gouger *et al*., 1975; Garraway, 1986); and some *Pityophthorus* species (Blackman, 1922). When frass blocks off the nuptial chamber, females chew small lateral (sometimes vertical) tunnel extensions in which they can turn around.

Reid and Roitberg (1994) and Robertson (1998b) used male removal experiments to study the effects of male residence on female reproduction in the harem polygynous *I. pini*. Males usually remain with females for several weeks, during most of the time that females are ovipositing. Reid and Roitberg (1994) found that after only 3 or 4 days, females breeding without males present had laid 11% fewer eggs. Robertson (1998b) found that there was considerably more frass in the tunnels of females in systems with no male, and that females with no male present laid fewer eggs and produced fewer emerging offspring. Kirkendall *et al*. (1997) reported similar effects of frass-removing males on female reproduction in a different harem polygynous species, *Pityogenes chalcographus* (L.). They also summarized published field studies on monogynous *Hylesinus*, *Scolytus* (two species), *Trypodendron*, and *Camptocerus*, in which data could be found for both females breeding with a male present and females breeding alone. In all cases, females produced many more eggs when a male was present (Kirkendall *et al*., 1997). Existing data, then, though covering relatively few genera and species, all support the hypothesis that the most important feature of prolonged male residency is the benefits to offspring production of aiding females with frass removal.

5.3.2 Burrow Blocking or Plugging

Males staying with females is likely ancestral in bark and ambrosia beetles; there are few species (and no entire genera) of outbreeding Scolytinae or Platypodinae in which males do not remain at least some days, and they block the burrow entrance while there (Kirkendall, 1983). Furthermore, male residence and in some cases egg tunnel guarding, seems to have evolved in unrelated insect groups in which females tunnel to oviposit, such as passalids, bostrychids, ciids, subsocial cockroaches, and lower termites (Hamilton, 1979; Tallamy, 1994).

However, males are not always present during periods when it is beneficial to block. In a very few species, males may or may not guard females after surface copulations, but stay with females for at most a few days (reviewed in Kirkendall, 1983); these include species of *Dendroctonus* (Reid, 1958), *Strombophorus* (Schedl, 1960a; Browne, 1963), *Scolytus* (Gossard, 1913; Blackman, 1922; Fisher, 1931; McMullen and Atkins, 1962), an *Alniphagus* (Borden, 1969), a *Pityophthorus* (Hedlin and Ruth, 1970), and a *Conophthorus* (Mattson, 1980). As far as is known, *P. puberulus* is parthenogenetic, and males do not exist (Deyrup and Kirkendall, 1983). Even in species in which males do normally stay, some males may leave early or die, leaving the female alone. When no males are available during some or all oviposition, females may either block the entrance themselves (especially if oviposition is complete), or plug the entrance solidly with frass mixed with resin or possibly oral secretions (Kirkendall, 1984; Kirkendall *et al*., 1997). Further evidence for the importance of blocking entrances (even late in the breeding cycle) comes from the only ambrosia beetle species in the large inbreeding genus *Hypothenemus*, i.e., *H. curtipennis* (Schedl). If an *H. curtipennis* mother dies or departs, the entrance is blocked by adult offspring (Beaver, 1986). In several platypodines, males block the entrance with long cylinders of wood fibers; if these are removed experimentally, they are rapidly replaced (Jover, 1952; Husson, 1955). Females or males die blocking the entrance in a number of species (Kirkendall, 1984), suggesting a role for blocking even late in the reproductive cycle.

Blocking of the entrance has long been hypothesized to have a protective function. Burrow blocking was discussed at length by Blackman (1922). He hypothesized that it serves to exclude parasites and predators that might otherwise harm eggs and young larvae (see discussion in Kirkendall *et al*., 1997) and observed that any disturbance of the entrance or even the passing of a shadow over the opening would cause a male deeper in the gallery system to promptly return to his post. The clearest example of parental protection was given by Darling and Roberts (1999), who observed guarding males of the platypodine *Crossotarsus barbatus* Chapuis killing planidia larvae of *Monacon robertsi* Boucek (Hymenoptera: Perilampidae), parasitoids that try to enter the galleries. In *I. pini* male removal experiments, both Robertson (1998b) and Reid and Roitberg (1994) found much higher mortality of females in harems from which males had been removed, suggesting that male presence indeed has an important protective effect. To the extent that males staying with females protect offspring, male residency can be interpreted as paternal care.

In the case of inbreeding species, blocking by mothers or daughters may also hinder the intrusion of unrelated males (Peer and Taborsky, 2005), and in ambrosia beetles with communally feeding offspring they have been shown to protect larvae from accidentally leaving the nest (*X. saxesenii*: Biedermann and Taborsky, 2011).

Blocking could also be important for microclimate. By plugging and unplugging the entrance with their bodies, individuals can possibly regulate the microclimate within the nest, which (as argued above) is especially important in ambrosia beetles. This too, would be a form of paternal care when carried out by males, as is normally the case in outbreeding species. Kalshoven (1959) observed male *Scolytoplatypus eutomoides* Blandford (an outbreeding ambrosia beetle) to perform "…pumping movements, rapidly jerking to and fro…" in the gallery entrance, which he interpreted to serve the ventilation of the nest.

Prolonged male residency (during which they accrue fitness benefits from both blocking and frass removal) could also be favored by intrasexual selection, if males who leave too soon risk being supplanted by new males, or if males of harem polygynous species who leave early forgo opportunities to acquire further mates. However, there is little support for this hypothesis (Kirkendall *et al*., 1997; Robertson, 1998b), and it likely only applies to the first week or so of gallery construction. Colonization of new breeding material in most species seems to be highly synchronized. When aggregation pheromones are not involved, the attractiveness of colonized breeding material seems to decline rapidly, and for taxa with pheromone systems it is often found that "masking" or "anti-aggregation" pheromones are produced after pairing (Rudinsky, 1969; D. L. Wood, 1982; Birch, 1984; Borden, 1985). Thus, the likelihood of new males entering an open tunnel is low after just a few days, and for harem polygynous species there are few or no new females arriving after a short period. Thus, in a study of harem polygynous *I. pini*, Reid and Roitberg (1994) found just a 4% replacement rate over 6 days, for gallery systems from which males had been removed experimentally.

5.3.3 Ventilation Holes

As mentioned above, females of many species chew special openings to the outside from the egg tunnels, usually referred to as ventilation holes or ventilation tunnels. In species that pack frass rather than expelling it, these must also serve as turning niches. If they do function as ventilation holes then they likely increase the survivorship of young larvae, and hence represent maternal care; however, they also present possible new entry points for natural enemies. Melnikova (1964) demonstrated experimentally that for *Scolytus ratzeburgi* Janson breeding in beech, these holes regulate humidity, after rejecting the hypothesis that they could be used for copulation. Broods with sealed ventilation holes were flooded with sap. The holes were only made by females, and were still being constructed or enlarged after the female was finished ovipositing (=maternal care). The observations of McKnight and Aarhus (1973) support this view: in two *Hylesinus* species breeding in ash, the species breeding in live tissues (*H. californicus* (Swaine)) makes ventilation holes, while the species breeding in dead tissues (*H. criddlei* (Swaine)) does not.

5.3.4 Fungus Tending as Maternal Care

The most elaborate forms of maternal care are found in ambrosia beetles. In these, offspring survival and growth is largely dependent upon female fungus farming. Ambrosia beetle females plant and maintain a fungal food supply and hold pathogens in check. During construction of the egg tunnels, they disseminate fungal spores from their mycetangia to the tunnel walls. Subsequent beetle tending behavior strongly stimulates the growth in unknown ways (Francke-Grosmann, 1966; Happ *et al*., 1975, 1976). *Crossotarsus japonicus* Blandford ambrosia beetles with oral mycetangia have been observed to spread oral secretions containing fungal spores on other individuals and on tunnel walls, via grooming and tending (Nakashima, 1971). The mother's cleaning and tending activity is essential for keeping fungal garden pathogens in check and to keep the ambrosia fungus from overgrowing immobile eggs and pupae (Hadorn, 1933; L. R. Batra, 1966; Francke-Grosmann, 1967; Biedermann and Taborsky, 2011). Oral applications of secretions to pathogen-infested areas by *D. rufipennis* females (not an ambrosia beetle) have clear antimicrobial effects (Cardoza *et al*., 2006b). In ambrosia beetles of the tribe Xyleborini, mothers frequently groom their eggs, larvae, and pupae with their mouth parts and relocate brood with behaviors similar to shuffling frass (French and Roeper, 1975; Kingsolver and Norris, 1977a; Roeper *et al*., 1980a; Biedermann and Taborsky, 2011). A remarkable development of relocation behavior is seen in females of some *Crossotarsus* species (Platypodinae) that have deep hollows in the frons, in which they can carry their eggs (and maybe small larvae) through the tunnel systems (Browne, 1961; Darling and Roberts, 1999). Finally, there are hints of active food provisioning in *Monarthrum fasciatum* (Say) and *Gnathotrichus* species (Scolytinae), in which larvae live in separate niches, where females have been observed to feed them with pieces of fungal mycelium (Hubbard, 1897; Doane and Gilliland, 1929).

5.3.5 Paternal Care

The benefits of prolonged male residency can be attributed to a mixture of sexual and natural selection, as indicated above. Some of the consequences of burrow blocking and frass removal increase the number of offspring, and some increase the survival of those offspring and hence can be considered paternal care. Paternal care is rare in insects and hence is of special interest; in the vast majority of species, males leave females after copulating with them and are not present when eggs are laid, precluding the evolution of males contributing directly to offspring survivorship. Given that mate abandonment is the norm, it is striking that male postcopulatory residency is so common in bark and ambrosia beetles and that male residency seems to significantly increase offspring survivorship as well as male fecundity (Kirkendall 1983; Reid and Roitberg, 1994, 1995; Kirkendall *et al*., 1997; Lissemore, 1997; Robertson, 1998a, b; Robertson and Roitberg, 1998).

In *I. pini*, Robertson (1998b) found that the longer that males stay with females, the more eggs are laid, the longer the female egg tunnels are, and the less competition there is between larval progeny thus increasing offspring survivorship. Such paternal care has long-lasting effects, as competition during larval development affects adult size; larger males attract more females (Robertson and Roitberg, 1998) and larger males and females produce larger broods (Foelker and Hofstetter, 2014). Experimental male removal in this species also had dramatic effects on increased predation by tenebrionid and colydiid beetles (Reid and Roitberg, 1994).

Thus, evidence from *I. pini*, *Crossotarsus*, and *Scolytoplatypus* supports interpreting male residence as being a form of paternal care. It is not at all clear yet if this conclusion applies more generally. As emphasized by Kirkendall *et al.* (1997), male residence is a key feature of almost all bark and ambrosia beetle mating systems, and the vast majority of outbreeding species are monogynous. Is male residency selected more strongly by sexual or natural selection? Comparative studies in genera with large variation in male behavior (such as in *Scolytus*, which includes a few species with no male residency at all) could provide key insights into the features selecting for and against postcopulatory residency, and the extent to which paternal care is a significant factor in species in which males stay for all or most of a female's reproduction.

The variability and evolution of male residency is discussed in detail in Kirkendall (1983) and in Kirkendall *et al.* (1997). There is little support in general for the hypothesis that males remain to increase their own mating success via mate guarding or attracting further females. Mate guarding, however, may be important in species in which males leave before oviposition commences; more importantly, mate guarding may have been the initial selective advantage to remaining some time with females after copulating with them. Mate guarding is posited to have preceded evolution of offspring care in other insects (Tallamy, 1994; Costa, 2010), and this is likely the case for bark and ambrosia beetles. Once males are regularly highly related to the offspring they are guarding (as would be assured by strict monogamy or repeated copulations with the same male), male and female reproductive interests are fully aligned, and division of labor between the sexes can evolve.

5.3.6 Males in Inbreeders

Despite the importance of males in outbreeding bark and ambrosia beetles, in inbreeding taxa, the significance of males for productivity appears to be negligible. Although all cooperative behaviors that are shown by adult females other than blocking are also present in male offspring of *X. saxesenii* and *X. affinis*, and all-male colonies (arising from unfertilized females that lay haploid eggs) are almost as productive as normal colonies, there are typically only one to three males per nest. With so few males present, male behaviors can have little impact on nest productivity (Biedermann, 2010, 2012; Biedermann and Taborsky, 2011).

What selects for diminished roles of males in these taxa? Sibling mating within subdivided family groups provides an arena for mate competition between relatives (Charnov, 1982), which favors producing lower numbers of males (i.e., local mate competition *sensu* Hamilton, 1967). In the most extreme cases this may lead to neoteny, as all resources that would have been utilized by males can be invested in dispersing females instead (Jordal *et al.*, 2002). Fighting may be expected among brothers, as in some sib-mating parasitoid wasps (Hamilton, 1978, 1979), but currently there is no evidence that sibling fighting takes place in inbreeding bark or ambrosia beetles; in many species it is extremely unlikely because they regularly produce only one male per brood, unless broods become so large that one male may not be able to fertilize all of his sisters (Kirkendall, 1983, 1993). The pronotal horns in males of several Xyleborini species (see Hubbard, 1897), which have been proposed to have a fighting role (Hamilton, 1979; Costa, 2006), have been observed to function as hooks to attach to the tunnel wall during copulation in *X. affinis* males (Biedermann, 2012). The only exception might be species with less biased sex ratios, in which male dispersal and outbreeding occurs regularly (*D. micans*, *D. punctatus*: Section 4.2). The possibility remains that the unusually large males of some inbreeders, or hooks or horns on inbreeding males, might be important in competition with unrelated, intruding males, but little is known as yet of how often unrelated males successfully enter nests and inseminate non-sisters.

5.4 Delayed Dispersal and Alloparental Care

The evolution of parental care given by siblings (a form of alloparental care) requires that generations overlap, i.e., that immatures are still present when the first offspring reach adulthood, and that caring for related juveniles for some time results in higher inclusive fitness than dispersing immediately and producing own offspring. The first stage in the evolution of alloparental care, given overlap of generations, is delayed dispersal. Once adults are present in the nest because they have delayed leaving, there is a potential for evolving to aid the reproductive efforts of their mother. No new behavior need evolve, beyond not dispersing or delaying dispersal: simply by carrying out the same behaviors they would normally employ while breeding themselves (burrow blocking, frass removal, fungus tending), they can increase the survivorship of their mother's family and perhaps increase their mother's total reproductive output as well by relieving her of some of her duties. Because bark and ambrosia beetles produce large eggs over a period of weeks or even months, overlap of generations is universal, so the potential for the evolution of alloparental care is high. What factors might create delayed dispersal, and can delayed dispersal lead to significant alloparental care giving? What do we know about the costs and benefits of delayed dispersal for young adults? Can non-dispersing individuals breed further in the same host material?

5.4.1 Delayed Dispersal

Any plant tissues break down once dead, but wood degrades slowly, and woody tissues can potentially support several generations of wood-boring insects. The wood of live trees, however, is well protected, and can potentially support insect colonies as long as the tree lives. Dead wood, even in small branches, is a very large resource unit for tiny beetles, but one that is scattered and unpredictable in the environment. For scolytines and platypodines, locating new breeding material is energetically costly and associated with high levels of mortality. Dead wood degrades slowly but surely, with the rate of deterioration of individual resource units depending on the temperature and what other organisms have colonized the wood. Inner bark degrades much more rapidly than sapwood so more advanced forms of social behavior are more likely to evolve in xylomycetophagous species than phloeophagous species. Unconsumed, usable woody food resources are often still available for further breeding, even while offspring of the current brood are still maturing. Young adult beetles, then, have the options of (1) remaining in the current tunnel system for at least some time; (2) extending the current tunnel system and breeding in it; or (3) leaving and attempting to breed elsewhere. If they do remain, do they do anything that increases the survivorship of current juveniles?

Delayed dispersal of adult offspring is not common in nature, though characteristic of social taxa (Wilson, 1971; Costa, 2006). Adult offspring of bark and ambrosia beetle species are commonly observed to remain in the natal gallery system for days, weeks, or months after maturation (Fuchs, 1907; Kalshoven, 1962; Kirkendall *et al.*, 1997; McNee *et al.*, 2000; Peer and Taborsky, 2007; López-Guillén *et al.*, 2011; Biedermann *et al.*, 2012).

Direct and indirect fitness benefits at the natal nest can select for prolonged delayed dispersal. Delayed dispersal of females in *X. saxesenii* is affected by the quality and amount of ambrosia fungi (Biedermann and Taborsky, submitted). These gains might be either (1) direct through feeding up body reserves for later reproduction, through co-breeding within the natal nest, or through becoming the lone breeder, or (2) indirect through engaging in brood care and fungus tending, thus helping relatives to produce more brood and increasing offspring survivorship. Benefit (2) is especially relevant in species with extended egg laying periods of the mother, where adult and immature offspring stages overlap considerably and brood that is dependent on adult care are still present when the mother dies (e.g., *X. saxesenii*; Biedermann *et al.*, 2012).

The delayed dispersal of adult offspring in bark and ambrosia beetles was recognized by the pioneers of bark beetle research (Ratzeburg, 1839; Eichhoff, 1881; Hopkins, 1909). Typically, it has been attributed to having to build up energy reserves before dispersal, and this period of the life cycle is termed pre-emergence feeding or maturation feeding in these beetles (Eichhoff, 1881; Botterweg, 1982; McNee *et al.*, 2000). Other reasons for at least short delays are adverse environmental conditions (especially cold temperatures or strong winds) that do not allow dispersal or host finding. Typical for poikilothermic animals, bark and ambrosia beetles are only active above certain temperatures and the favorable season for host finding of temperate species is typically in spring or early summer; the beetles are active year round in subtropical and tropical forests, barring prolonged dry seasons. Hence, adults often hibernate within their natal galleries instead of dispersing immediately after reaching adulthood.

Evidence that maturation feeding promotes delayed dispersal comes from phloem-feeding mountain pine beetles, where females were experimentally prevented from feeding after molting to adult. They matured normally, but were less likely to breed successfully, and laid smaller eggs (Elkin and Reid, 2005). Weather has been repeatedly shown to limit dispersal: dispersal is facilitated by sunny weather with little wind, minimum temperatures being in the range of 10–20 °C depending on the species (Bakke, 1968a, 1992; Salom and McLean, 1989, 1991; Faccoli and Rukalski, 2004) and high air pressure (Biedermann, 2012). Adults of some species live through unfavorable seasons or weather periods within their natal nests (other species survive in leaf litter, under bark of live trees, or in twigs of live branches).

Although maturation feeding and waiting for favorable environmental conditions are of primary importance in many taxa, especially in bark beetles in which individuals feed separately in their own cradles, it certainly cannot explain the extraordinarily long philopatric periods of adults in some ambrosia beetle species. Female ambrosia beetles were found to lay eggs only after growing their own fungus garden on which they fed (French and Roeper, 1975; Kingsolver and Norris, 1977b; Roeper *et al.*, 1980a; Beaver, 1989). Hence, it is unlikely that reserves accumulated before emergence will raise the productivity of those beetles sufficiently to outweigh the fitness costs of delayed dispersal (the time lost from potential breeding). In some xyleborine ambrosia beetles, daughters even remain all their lives within their natal nests, e.g., *X. affinis* (Schneider, 1987) and *X. saxesenii* (Peer and Taborsky, 2007; Biedermann *et al.*, 2012). Laboratory studies with *X. affinis* galleries in artificial medium showed that remaining adult females are fully capable of breeding independently when they are experimentally removed from their natal nest (Biedermann *et al.*, 2011), which suggests that maturation feeding is not essential for egg laying. Surprisingly, and in contrast to the maturation feeding hypothesis, delayed dispersal comes at a cost for females. *Xyleborus affinis* females that disperse after their philopatric period produced fewer eggs than females removed from the gallery before their philopatric period (Biedermann *et al.*, 2011). This cost may result from cobreeding or from engaging in alloparental brood care during the philopatric period at the natal nest.

It is likely that a combination of both direct and indirect benefits select for delayed dispersal in many ambrosia beetle species, as (1) ovary dissections revealed that one-quarter of staying females in *X. saxesenii* field galleries (Biedermann *et al.*, 2012) and one-half in *X. affinis* laboratory galleries (Biedermann *et al.*, 2011) lay eggs in the natal nest during their philopatric period, and (2) correlative studies indicate that staying and helping in the nest is triggered by demands of brood dependent on care. The latter was shown by increased social behavior of staying females and later dispersal in relation to both increasing numbers of sibling larvae and pupae (which depend on brood care) and decreasing numbers of adult "helpers" in both species (Biedermann *et al.*, 2011; Biedermann and Taborsky, 2011). Numbers of egg layers correlated with neither the number of staying adult females nor with the number of eggs, which suggests that egg numbers are regulated and adjusted to fungus productivity (Biedermann *et al.*, 2012).

A selection experiment on timing of dispersal in *X. saxesenii* showed that delayed dispersal and helping in this species and are probably genetically linked (Biedermann and Taborsky, submitted).

Finally, helping in adults can probably evolve relatively easily, as it seems not to strongly curtail a helper's future reproduction because helping is risk free and does not reduce a helper's energy stores. The tradeoff between helping and future reproduction (Queller and Strassmann, 1998; Korb and Heinze, 2008) may thus be weak in such ambrosia beetles. This may also explain why helping is even present in male offspring of the haplodiploid *X. saxesenii* and *X. affinis*. Unexpectedly, recent observations indicate that they take part in all cooperative behaviors that are shown by adult females except for blocking (Biedermann, 2010, 2012; Biedermann and Taborsky, 2011), which suggests that relatedness asymmetries caused by haplodiploidy, which would favor female-biased help, are probably offset by inbreeding in these species (Hamilton, 1972). Nevertheless, because of strong local male competition, there are only one or two males and up to 80 females per gallery, and thus their help is of minor importance.

Several factors disfavor the evolution of delayed dispersal of adult offspring, even when food conditions would allow adult offspring to establish a second generation at the natal nest site (Gandon, 1999): (1) a buildup during the breeding period of predators, parasites (e.g., mites, nematodes, parasitoids) and pathogens (e.g., fungal saprobes) (Dahlsten, 1982; Hofstetter *et al*., 2006; Cardoza *et al*., 2008; Hofstetter and Moser, 2014); (2) problems in relation to inbreeding, if unrelated mates are not available (Thornhill, 1993; Gandon, 1999); (3) competition among closely related individuals (Kirkendall *et al*., 1997; West *et al*., 2002); and (4) the relatively small potential for indirect fitness benefits at the natal nest for beetles that live within their food compared to other social insects that need to forage for their food (Mueller *et al*., 2005; Biedermann, 2012).

These four factors may all present serious obstacles that might often hinder the evolution of forms of sociality beyond parental care, although the importance of these factors has not been studied in bark and ambrosia beetles. Consequently, bark and ambrosia beetle social systems exceeding subsociality must have evolved mechanisms to overcome or handle these obstacles. Mechanisms increasing social immunity (blocking out of predators and parasites, and gallery hygienic tasks to keep pathogens and diseases in check), and fungiculture techniques that assure a long-term food supply, have likely improved in the course of bark and ambrosia beetle social evolution, as seen in other fungus-farming social insects (Cremer *et al*., 2007; Hölldobler and Wilson, 2009; Wilson-Rich *et al*., 2009). Pseudo-arrhenotoky in *H. hampei* (Brun *et al*., 1995a, b; Borsa and Kjellberg, 1996a, b) and haplodiploidy in the Xyleborini clade (Normark *et al*., 1999) may mitigate the potential hindrance of inbreeding, by allowing the purging of deleterious mutations through haplodiploid males (Hamilton, 1967; Smith, 2000).

5.5 Larval Cooperation

Some bark and ambrosia beetles not only have adult helpers at the natal nest, but can also have larvae that cooperate and may engage in division of labor with the adults (Biedermann and Taborsky, 2011). Although data on larval behavior in these beetles are mostly anecdotic, it could be a common phenomenon in species with gregariously feeding offspring and in which adults and larvae can move freely within their nests. Larval cooperation has been experimentally proven only in the ambrosia beetle *X. saxesenii* (Biedermann and Taborsky, 2011), but observations suggesting larval cooperation come also from the phloem feeding *D. micans*, *D. valens*, and *D. punctatus* (Grégoire *et al*., 1981; Deneubourg *et al*., 1990; Furniss, 1995) and from other ambrosia feeding Xyleborini (*X. affinis*: Biedermann, 2012) and Platypodinae, *Platypus cylindrus* (F.) (Strohmeyer, 1906), *Trachyostus ghanaensis* Schedl, *T. aterrimus* (Schaufuss), *T. schaufussi* Schedl (Roberts, 1968), *Doliopygus conradti* (Strohmeyer), and *D. dubius* (Sampson) (Browne, 1963).

Remarkably, this division of labor between adult and immature stages is almost unique among social insects. Helper or worker castes in insects without metamorphosis (Hemimetabola), like aphids or termites, are always formed by immature individuals, whereas in insects with metamorphosis (Holometabola), such as beetles and Hymenoptera, workers are typically adults, as immature individuals in ant, wasp, and bee societies are largely immobile, helpless, and often dependent on adults to be moved and fed (Wilson, 1971; Choe and Crespi, 1997). There are very few exceptions of cooperatively behaving immatures in Hymenoptera, including nest-building-silk producing weaver ant larvae (Wilson and Hölldobler, 1980) and nutrient and enzyme producing larvae of some wasp and ant species (Ishay and Ikan, 1968; Hunt *et al*., 1982).

What does larval cooperation in bark and ambrosia beetles look like? In phloem feeders larvae cooperate primarily by feeding side by side, which helps them to overcome plant defenses, and aggregation is effected by pheromones (Grégoire *et al*., 1981; Deneubourg *et al*., 1990; Storer *et al*., 1997). Gregarious feeding is also known from the ambrosia beetle genus *Xyleborinus*, in which larvae feed not only on fungal mycelia (as typical), but also on fungus-infested wood. Aggregation pheromones have not been studied in ambrosia beetle larvae, but it is likely that gregarious feeding may more effectively control fungal saprobes threatening their primary ambrosia food fungus (Biedermann, unpubl.; Biedermann and Taborsky, 2011). Like gregarious feeding on plants, gregarious feeding on fungi has been repeatedly found to be an adaptation of arthropods to overcome the induction of secondary fungal defenses (Rohlfs, 2005; Rohlfs and Churchill, 2011).

Larvae take part in gallery hygiene, by relocating frass and by grooming eggs, pupae, each other, and adults; these behaviors have been widely reported from different bark and ambrosia beetle species. In *X. saxesenii*, larvae ball up frass, which can then be more easily removed by their adult siblings (Biedermann and Taborsky, 2011). In *D. micans*, larvae pack frass at specific locations, allowing free movement within the brood chamber (Grégoire *et al*., 1981); they also block tunnels to hinder access by *R. grandis* predators (Koch, 1909). Fifth instar larvae in some Platypodinae also relocate frass to unused gallery parts or for plugging artificial nest openings (Hadorn, 1933; Beeson, 1941; Kalshoven, 1959) and expel frass and parasitoid planidia through the nest entrance (Darling and Roberts, 1999). These larvae have a plug-like last abdominal segment, which can be used both as a shovel and as a device to fully plug the gallery entrance against intruders (Strohmeyer, 1906). These larvae have been observed to overtake the role of entrance blocker during times when their parents are deep inside the nest (Strohmeyer, 1906; Roberts, 1968). In both

Platypodinae and many Xyleborini, larvae also engage in excavation of new tunnels or chambers to create more surface for the developing ambrosia fungus (Strohmeyer, 1906; Kent, 2002; Biedermann and Taborsky, 2011). The flat brood chambers that are typically found in the genus *Xyleborinus* are almost exclusively accomplished by the larval habit of feeding on fungus-infested wood (Biedermann and Taborsky, 2011; De Fine Licht and Biedermann, 2012). The same is true for the long transverse tunnels in nests of several Platypodinae that are bored by fifth instar larvae (Roberts, 1962, 1968; Browne, 1972).

The ultimate cause for the larval specialization for tunneling shown by many ambrosia beetles may relate to their repeated molting: mandibles of adults gradually wear down during excavation, and adult females that bore extensively would suffer from substantial long-term costs. In contrast, larval mandibles regenerate at each molt (Biedermann and Taborsky, 2011).

Xyleborinus saxesenii larvae that feed on fungus-infested wood likely fertilize the growing ambrosia fungus with the finely fragmented woody sawdust in their feces, which gets smeared on the gallery walls after defecation (Hubbard 1897; Biedermann and Taborsky, 2011). This larval frass probably also contains enzymes for further wood degradation, as a recent study showed that *X. saxesenii* larvae possess hemicellulases, which are not found in their adult siblings (De Fine Licht and Biedermann, 2012). Furthermore, bark and ambrosia beetle larvae may spread associated bacterial and fungal symbionts within the galleries, which have been shown to have defensive functions against pathogens, detoxify poisonous plant metabolites, degrade lignocellulose plant cell walls, or fix nitrogen from the air (Cardoza *et al.*, 2006b; Adams *et al.*, 2008; Scott *et al.*, 2008; Morales-Jiménez *et al.*, 2013; Chapter 6). This suggests that cooperation, and division of labor among larvae and adults, goes far beyond behavioral interactions, but may also include microbial, biochemical, and enzymatic processes.

Larval contributions to gallery extension and to hygiene reduce the workload for adults. Indeed, and against the common preconception that larvae only compete for resources among each other, positive effects of larval numbers on group productivity have been observed in *X. saxesenii* (Biedermann and Taborsky, 2011), *D. micans* (Storer *et al.*, 1997), and several Platypodinae species, in which females only lay second egg clutches in the presence of fifth instar larval helpers (Roberts, 1968).

In summary, larvae in some bark and many ambrosia beetle species are free to move within the natal nest, and are not confined to small areas or brood cells like those of most hymenopteran social societies (Wilson, 1971; Hölldobler and Wilson, 1990). This, in combination with different capabilities of larvae and adults, predisposes especially ambrosia beetles for division of labor between larval and adult stages. Importance and specific roles of larvae in the galleries appear to vary between species (Biedermann, 2012).

One aspect that has not been studied at all in bark and ambrosia beetles is the possibility of delayed development of larvae. If larvae play such an important role in the nests of many gregarious bark and ambrosia beetle species and there are possibilities for larvae to gain indirect fitness benefits by cooperating in the natal nest, selection may favor prolonged development (e.g., by additional larval instars). Prolonged development or even permanently immature helper/worker castes are the rule in hemimetabolous social insects like termites, aphids, or thrips, in which individuals only mature to become reproductive queens or kings (Choe and Crespi, 1997; Korb and Heinze, 2008). There are two hints for prolonged development also in larvae of bark and ambrosia beetles. First, the number of larval instars varies between two and five among species in bark and ambrosia beetles; it is unknown what factors select for more or fewer instars. The numbers of instars are sometimes, but not always, related to size of the adult (Lekander, 1962; Lekander, 1968a, b). Second, among species with helping larvae (*Dendroctonus*, Xyleborini, Platypodinae) and for reasons that remain unclear, there appears to be high variability in the developmental periods of larvae (Wichmann, 1927). Koch (1909) observed that from *D. micans* eggs laid the same day, the progeny pupated over a period of 44 days without any obvious reasons. While the first larval instars are typically short and quite fixed in time, the length of the last instar is highly plastic and in some cases two to four times longer than all previous instars together (Koch, 1909; Baker, 1963; Browne, 1963; Biedermann *et al.*, 2009). Generally, the last instar is typically the one that overtakes most helping and has evolved even some morphological adaptations for helping (see above). The maximum of five instars and the longest development of larvae (which can be several years) relative to the oviposition period of adults are both found in Platypodinae (Kirkendall *et al.*, 1997). Unfortunately, researchers have rarely reported larval numbers when dissecting galleries, and experimental studies are lacking, so prolonged development of larvae as an investment in siblings must remain speculative.

5.6 The Evolution of Reproductive Altruism

The frequent occurrence of overlapping generations and cooperative brood care in this group of beetles suggests that reproductive altruism may be more widespread than currently known. In Xyleborini, Corthylini, and Platypodinae, there are several species in which adult females have been observed to delay reproduction. In a single species, *X. affinis*, delayed dispersal and helping at the natal nest have been experimentally shown to involve fitness costs on future independent breeding. Adult daughters remaining longer in their mother's nest produced a significantly smaller brood when given their own choice to breed, than adult females experimentally removed from the nest before their delayed dispersal period (Biedermann *et al.*, 2011). As only some of the females that delayed breeding bred together with the mother, this implies that helping at the natal nest is costly for adult females in ambrosia beetles. Similarly, in *X. saxesenii*, there are hints that some daughters remain, never breed, and die within their mother's nests (Peer and Taborsky, 2007). Sterile adult female worker castes seem to be present in *A. incompertus* (Harris *et al.*, 1976; Kent and Simpson, 1992), although it has not yet been fully proven that sterility is non-reversible in the case when the mother dies (Kirkendall *et al.*, 1997). Furthermore, while many cooperative behaviors of larvae and adults are probably relatively inexpensive in terms of fitness, blocking of the gallery entrance is dangerous and costly (Kirkendall *et al.*, 1997). Feeding and blocking are incompatible and blocking individuals have been observed to be attacked by parasitoids (Beaver, 1986) or killed by predators (Wichmann, 1967). Hence, blocking can be interpreted as self-sacrificing altruism in those Cryphalini, Xyleborini, and Platypodinae in which larvae (*P. cylindrus*: Strohmeyer, 1906) or non-reproducing adult offspring (*H. curtipennis*: Beaver, 1986; *X. saxesenii*: Biedermann and Taborsky, 2011; *X. germanus*: Peer and Taborsky, 2004; *A. incompertus*: Kent, 2002) have been observed to take turns in blocking of the nest. This suggests that facultative (or even obligate) eusociality, defined by overlap of parental and offspring generations, alloparental brood care, and facultative (or permanent) reproductive altruism of some individuals (S. W. T. Batra, 1966; Wilson, 1971) have evolved multiple times in ambrosia beetles.

How is reproductive altruism favored by natural selection? Similar factors that facilitate the evolution of alloparental care also predispose for reproductive altruism. Kin selection is certainly essential, and all current evidence indicates that altruism can only evolve in groups of relatives, in which individuals invest in the reproduction of own genes via related individuals (Hamilton, 1964; Boomsma, 2013). More specifically, studies have shown that permanently sterile castes can only evolve if colony foundation is by a single, monogamously mated female, which assures high relatedness within her offspring group. This way, relatedness between colony females equals relatedness of a female to her own potential offspring; then, any constraint on individual reproduction can favor the evolution of staying, helping, and ultimately (under the right conditions) of sterility of helpers (Boomsma, 2009, 2013). Single gallery foundation and monogamy can be found in some bark beetles and is the rule in ambrosia beetles (Kirkendall, 1993), which suggests that the precondition for altruism to evolve is present in many species.

There are severe constraints on dispersal and individual reproduction in bark and ambrosia beetles. Costs of dispersal depend on the species, but in general it seems difficult for beetles to find suitable host trees and establish galleries (Berryman, 1982). Mortality during dispersal flight is about 50% for bark beetles (Klein *et al.*, 1978; Garraway and Freeman, 1981) and 70–80% for an ambrosia beetle (Milne and Giese, 1970), and survival decreases rapidly after the first day of host search (Pope *et al.*, 1980), typically because individuals are exposed to predation pressure and adverse weather conditions, but also because they exhaust fat reserves necessary for flying. Successful gallery establishment is also difficult as bark and ambrosia beetles have specific requirements for their breeding material, like plant taxon, size of material, moisture content, and the presence or absence of certain fungi or other microorganisms. Although ambrosia beetles are typically less specialized to host taxa (Browne, 1958; Beaver, 1977, 1979a; Atkinson and Equihua-Martínez, 1986b), boring in solid wood, overcoming host tree defenses (e.g., resins), and planting of fungal cultivars are risky tasks. Often, less than half of females successfully manage the last step (Fischer, 1954; Hosking, 1972; Nord, 1972; Weber and McPherson, 1983; Biedermann *et al.*, 2009), typically because either the ambrosia fungus does not grow or fungal pathogens overgrow the initial cultures (Biedermann, 2012; Biedermann *et al.*, 2013). All these factors render pre-dispersal cooperation and altruism more profitable, if longevity of the natal gallery allows adults to gain inclusive fitness benefits.

The longevity of the breeding material is likely the crucial factor that will affect evolution of cooperation and reproductive altruism. This depends on competition with other ambrosia beetles and microorganisms, timing of beetle attack in the dying process of a tree (in cases where breeding is in dead hosts), and size and type of host material that is attacked. Reproductive altruism without sterility can evolve in species attacking dying or dead trees of large diameter as long as they provide resources for several generations of offspring, as seen in *X. affinis*, *X. saxesenii*, and probably other Platypodinae and Xyleborini (see above; Biedermann, 2012). Facultative suppression of oviposition assures that females can disperse and breed independently should the breeding substrate degenerate, and permits further inclusive fitness gains from helping at the natal nest. In *X. saxesenii*, many galleries need to be abandoned after a single generation, despite the fact that other galleries are productive for several offspring cycles. Obligate sterility of adults, however, is expected only to evolve under conditions that consistently provide non-breeding females with indirect fitness gains. This is the case when beetles colonize living trees, which can provide food for many consecutive offspring generations. The only currently known case of obligate eusociality in beetles is found in *A. incompertus*, which attacks living trees and constructs galleries that may last for more than 30 years (Kent and Simpson, 1992). Several more ambrosia beetles breed in living trees, so more cases of obligate eusociality may be discovered in the future (Kirkendall *et al.*, 1997). These systems should have evolved elaborate techniques for maintaining long-term fungiculture and social immunity, such as mechanisms to suppress the spread of fungus-garden pathogens and insect diseases, as have evolved in societies of fungus-farming ants (Currie, 2001). Unexpected discoveries are likely when more researchers have started to work with platypodine ambrosia beetles, especially those in living trees.

6. INTRACELLULAR BACTERIA AND BARK BEETLE EVOLUTION

Because of their potential influences on the evolution of bark and ambrosia beetles, we conclude with a brief discussion of what little we know about intracellular bacteria in Scolytinae (nothing is known for Platypodinae). Intracellular symbionts in the alpha-proteobacterial genera *Wolbachia* and *Rickettsia* are widespread in arthropods and nematodes, with *Wolbachia* present in 70% of all insects (Werren *et al.*, 2008). Bark beetles are no exception and despite the lack of a detailed survey, single screenings have identified *Wolbachia* bacteria in Ipini (*I. typographus*: Stauffer *et al.*, 1997; *P. chalcographus*: Arthofer *et al.*, 2009), Xyleborini (*X. germanus*: Kawasaki *et al.*, 2010), Dryocoetini (*H. hampei*: Vega *et al.*, 2002), and Cryphalini (*Coccotrypes dactiliperda*: Zchori-Fein *et al.*, 2006). In the evolution of insect mating systems, these symbionts are important, as they have repeatedly been shown to be able to manipulate host reproductive biology and evolution (see review by Werren *et al.*, 2008).

Wolbachia, the best studied of these intracellular parasites, is vertically transmitted with the egg from an infected female to her progeny and not via males. *Wolbachia* has a variety of phenotypic effects on its host, including (1) feminization (genetic males develop into females); (2) parthenogenesis; (3) selective male killing; and (4) cytoplasmic incompatibility (prevents infected males from successfully fertilizing eggs of females that lack the same *Wolbachia* types) (Werren *et al.*, 2008). In bark beetles, the role of *Wolbachia* and other intracellular symbionts for host reproduction remains largely unstudied.

It would be interesting to determine if extreme sex ratios in inbreeding Scolytinae are in any way caused by *Wolbachia* infections. This is unlikely, however, given that the extremely female biased sex ratios in regular inbreeders are predicted by local mate competition theory, and in most cases are extremely precise (Hamilton, 1967; Kirkendall, 1983, 1993; Borsa and Kjellberg, 1996a, b; Biedermann, 2010). In the only study on this topic, Zchori-Fein et al. (2006) found no evidence for an influence of *Wolbachia* on sex ratios in *C. dactyliperda*. Instead, these authors showed that the elimination of both *Wolbachia* and *Rickettsia* by antibiotic treatment led to unfertile females with no sign of oogenesis. Accordingly, also *Xyleborus ferrugineus* (F.) ambrosia beetles cannot reproduce after elimination of their unknown intracellular symbionts (Peleg and Norris, 1973; Norris and Chu, 1980). This may indicate that *Wolbachia* have changed their phenotype from reproductive parasitism to obligate mutualism in these inbreeding scolytids and the hosts are now dependent on the symbionts for oogenesis and/or nutrition, as clearly shown for other arthropods (Dedeine *et al.*, 2001; Hosokawa *et al.*, 2010). However, does *Wolbachia* also affect the evolution of their hosts? Generally, there is strong evidence that infections lead to inbreeding and thus drive speciation (Bordenstein *et al.*, 2001; Brucker and Bordenstein, 2012). Superinfection with up to five different *Wolbachia* strains per female (Kawasaki *et al.*, 2010) is likely responsible for smaller broods produced by females mated with males other than their brothers in the xyleborine ambrosia beetle *X. germanus* (Peer and Taborsky, 2005). This outbreeding depression could be caused by cytoplasmic incompatibility, as egg numbers between outbreeding and inbreeding broods were equal, but hatching rates differed (Peer and Taborsky, 2005). Whether such outbreeding depression is common in other inbreeding bark beetles has not been investigated. Finally, *Wolbachia* have also been hypothesized to play a role in the evolution of haplodiploidy in inbreeding taxa (Normark, 2004). Engelstädter and Hurst (2006) showed that paternal genome exclusion, which can be a predecessor of haplodiploidy, could be caused by cytoplasmic incompatibility-inducing bacteria in eggs of incompatible crosses, rendering the embryo functionally haploid. Paternal genome exclusion as well as *Wolbachia* are present in *H. hampei* (Brun *et al.*, 1995a, b; Vega *et al.*, 2002), which strongly suggests that the genetic system of bark beetles may be influenced by intracellular bacterial symbionts.

The abundance and effect of *Wolbachia* across outbreeding bark and ambrosia beetle is largely unknown. *Wolbachia* are present in *I. typographus* (Stauffer *et al.*, 1997) and *P. chalcographus* (Arthofer *et al.*, 2009) at low titer (35.5% of all sampled individuals infected) and at low density within infected individuals, and no correlation between infection titer and host population or geographic location was found. At least for *P. chalcographus* this suggests either that populations currently evolve towards the loss of *Wolbachia* or unidentified fitness advantages conserve the infection by the symbiont under certain environmental conditions (Arthofer *et al.*, 2009). Hypothetically, bark beetle associated fungi may help beetle hosts to cure themselves from parasitic symbionts (Arthofer *et al.*, 2009), as these fungi are known to produce a rich array of antibiotics (Zrimec *et al.*, 2004). It is possible that *Wolbachia* is repeatedly reacquired by the beetles within their feeding habitat (e.g., Stahlhut *et al.*, 2010).

7. CONCLUSION

Over 100 million years ago, several early lineages of weevils began laying eggs in tunnels under bark rather than in slits cut with their snouts. Two of these, Scolytinae (6000 species) and Platypodinae (1400 species), achieved notable evolutionary and ecological success. Their shift from an herbivorous to a saproxylic lifestyle led rapidly to a series of morphological and behavioral adjustments, adaptations we also see in a variety of other wood-boring beetles. Subsequent key innovations included male residence and monogyny, the development of active fungus cultivation, the evolution of alternative mating systems such as inbreeding and simultaneous polygyny, and haploidiploidy. Central was the adoption of living in tunnels within their food source: tunnels in wood are easily defended, and encourage long residency, which in turn fosters various elements of social behavior.

The variation we have documented in this chapter illustrates the potential for testing a multitude of general hypotheses in behavioral ecology and evolutionary biology. We will soon have the tools to test such hypotheses using the comparative method. Until very recently, most phylogenetic work has been limited in resolution and extent and is therefore of limited value for this purpose. These problems will be resolved in the next few years by several current projects dealing with large-scale weevil and scolytine phylogenetics. The 1000-Curculionidae project is based in part on phylogenomics work using conserved anchored genome regions; it is expected that most weevil relationships will be well resolved, including the position of Scolytinae, Platypodinae, and Cossoninae. The same technology is currently used to develop data matrices for Cryphalini and Xyleborini, and ultimately to develop further a soon-to-be published 20-gene phylogeny of Scolytinae (Pistone and Jordal, in progress).

Hopefully, advances being made by applying the comparative method to a broad selection of taxa will be accompanied by (or will inspire) complementary experimental research. From the perspective of evolutionary biology, four areas discussed in detail in this chapter seem especially promising for such a combined approach: mating system evolution, sexual selection, inbreeding, and social behavior. But in addition, for a topic not covered by us, we would point out that the application of sound phylogenies to existing data on pheromone components will generate important insights into how pheromone systems evolve over time, and into the broad question of how such signaling behavior does or does not constrain the adoption of new hosts (since some components of pheromones are modified plant compounds). Analyses such as these would also point out the major gaps in our knowledge of bark and ambrosia beetle pheromones: almost nothing is known, for example, of the pheromone systems of tropical genera.

7.1 Mating System Evolution

As we have documented, bark and ambrosia beetles provide behavioral ecologists with multiple origins of mating systems otherwise rare in invertebrates (and often rare or nonexistent in vertebrates). Surely, both comparative and experimental studies of selected Scolytinae (but also of conoderine and cossonine weevils with convergent biology) would contribute considerably to our general understanding of mating system evolution and allow testing of hypotheses largely investigated only in birds or fishes. As noted above, there are genera and even species (or species complexes) that vary in their mating systems, and that make tempting targets for such research. There are many abundant and widespread temperate species that are amenable to research into the details of monogyny, harem polygyny, and inbreeding. Phloeophagous and spermatophagous species in particular are easily reared in the laboratory, and both fecundity and egg to adult survivorship easily measured. The fact that most species commonly occur in dense breeding aggregations makes it easy to gather large amounts of data and facilitates thorough replication of experimental treatments (such as removal or addition of males or females).

7.2 Sexual Selection

Although complete sexual role reversal is rare in insects, there are surprisingly many cases of males being selective about which females they mate with. Male mate choice is believed to occur in at least 58 insect species from 37 families and 11 orders, including *I. pini* and *I. acuminatus*, which we discussed earlier (Bonduriansky, 2001). Bonduriansky (2001) finds that male choosiness in Coleoptera is favored, for example, when both sexes occur in dense aggregations and there are low search costs, a common scenario for bark and ambrosia beetles. Also favoring male choosiness is costly male investment in mating, which could be the case with male-initiated tunnels and subsequent helping activities. Male choosiness can evolve if there is large variation in female quality; in bark beetles, this can be reflected in body size variation (strongly correlated with fecundity). Investigating the extent and nature of sex role reversal in Scolytinae and Platypodinae should be a priority for bark beetle behavioral ecologists. This should be done both as a broad comparative study and by the close study of key genera with such variation (such as *Scolytus*, *Phloeosinus*, *Hylesinus*, and *Pityophthorus* + *Conophthorus*) and species in which role reversal seems to be actively evolving (e.g., *H. varius*). Whether males select females or vice versa is controversial for *I. pini*, a common and widespread North American species deserving further attention in this regard.

We rely heavily on features of the declivity for identifying species of bark and ambrosia beetles, yet we know little of the adaptive significance of the enormous variation we encounter in this key feature. Extreme developments of sharp points and edges combined with deep declivities seems to be associated with taking over the nests of other species, but exactly how such structures are employed is unknown. It is tempting to attribute more modest variation in declivity form and ornamentation to sexual selection in the context of courtship, but there is considerable variation in the declivities of female Xyleborini as well, all of which are inbreeders, which as far as is known have only rudimentary courtship and presumably no intersexual selection. So, the questions arise, how do sexual selection and natural selection interact in sculpting this part of beetle bodies, in outbreeding species, and how does the adoption of inbreeding impact selection on declivities?

7.3 Inbreeding

We have only begun to understand the evolution and ecology of inbreeding in insects, and in these beetles in particular. There are several outstanding questions with regards to Scolytinae that inbreed.

Generally, the distribution of genetic variation (at single loci, but also variation in combinations of alleles over several loci) within individuals, families, populations, and regions has important consequences for the evolutionary fate and ecological impact of species. Extreme inbreeding is expected to generate homozygotic genotypes, and small populations should lose variation among genotypes to genetic drift. Small amounts of outbreeding, however, could have enormous consequences. How often do inbreeders outbreed? How often do males disperse, and how often do they succeed in entering other nests and mating with non-sisters? Are matings between non-siblings "effective" outbreeding: in a local population, what is the degree of relatedness between females and foreign males? How are populations of regular inbreeders structured? Besides these key questions, it is important to investigate the extent of outbreeding depression in regular inbreeders.

A few genetic studies of inbreeders are mentioned in Section 4.2, but these only begin to scratch the surface. We need ecological genetics studies of both indigenous and invasive species, and of lineages with a wide variety of ecological specializations.

We repeat that the highly unusual paternal genome loss system reported for *H. hampei* has only been demonstrated for that one species. Taken together with the related inbreeding genera, this is a lineage of over 200 species. It would be interesting to know if other inbreeders from this clade share this rare breeding system.

7.4 Social Evolution

As with inbreeding, we are only beginning to explore the rich variation in adult and larval social behaviors in these beetles. Only a few of the many potentially social species have been studied behaviorally. The most interesting forms of cooperative behavior seem to be in ambrosia beetles, but these are particularly difficult to observe since they tunnel deep in wood. Observing ambrosia beetle behavior requires establishing them on semi-artificial media in the laboratory, which is quite labor intensive. The last decade has seen major advances in the ability to rear and observe ambrosia beetles, making this group more accessible to researchers interested in social behavior, and should lead to the development of several more potential model systems. Thus far, though, only xyleborine ambrosia beetles have been reared, and a broader understanding of the ecology of social behavior in bark and ambrosia beetles will depend on establishing species from other lineages in the laboratory.

The relative importance of genetic and ecological factors in social evolution is still unclear. Scolytinae and Platypodinae vary in the way they colonize new breeding material (in large aggregations, or single individuals), uni- or biparental care, alloparental care by larvae or adults, and occurrence of division of labor. Further, subsocial species breed in a wide variety of substrates and ecosystems.

Fungus farming seems to provide a variety of opportunities for division of labor, hence the repeated evolution of alloparental care and forms of larval cooperation in ambrosia beetles. Future research, using well-established model systems, should investigate the mechanisms by which these beetles can actively promote the growth of their fungal cultivars and protect them from pathogens, and can induce the specialized "ambrosial" growth forms seen in their tunnels. Careful observations of larvae and adults can elucidate the roles they each play, and look for previously unknown expressions of altruistic behavior.

APPENDIX

Larval feeding modes and adult mating systems in Scolytinae, with the total number of species given for each genus. Rare occurences in a genus (one or a few species) are coded "(x)" and unknown mating behavior or feeding modes are indicated by "?". Abbreviations, larval (and usually adult) feeding: Phl, phloeophagy (feeding in inner bark); Xlm, xylomycetophagy (farming fungus); Spm, spermatophagy (feeding in seeds); Myc, feeding on free-living fungi; Mye, myelophagy (feeding in pith); Xyl, xylophagy (feeding in wood); Hbv, herbiphagy (feeding in non-woody plants); feed?, unknown larval feeding habits. Abbreviations, mating systems: MG, monogyny; HP, harem polygyny; BG, bigyny; Col, colonial polygyny (several males and several females in a gallery system); Inbr, inbreeding; MS?, unknown mating system. The list of tribes and genera and the numbers of species were compiled by T. H. Atkinson (see Chapter 2).

Tribe	Genus	Phl	Xlm	Spm	Myc	Mye	Xly	Hbv	feed?	MG	HP	BG	Col	Inbr	MS?	Spp
Amphiscolytini	*Amphiscolytus*								?						?	1
Bothrosternini	*Akrobothrus*								?						?	1
	Bothrosternus					x								(x)		11
	Cnesinus	x	(x)			x				x						95
	Eupagiocerus		(x)			x									?	3
	Pagiocerus			x						x						5
	Sternobothrus					x				x						16
Cactopinini	*Cactopinus*							x		x						21
Carphodicticini	*Carphodicticus*	x								x						1
	Craniodicticus						x								?	3
	Dendrodicticus								?						?	1
Corthylini	*Amphicranus*		x							x	(x)					66
	Araptus	x		(x)							x	(x)		(x)		172
	Brachyspartus								?						?	1
	Conophthorus			x						x						13
	Corthylocurus		x							x						15
	Corthyloxiphus		x							x						21
	Corthylus		x							x	(x)					159
	Dacnophthorus	x								x						5
	Dendroterus	x									x					15
	Glochinocerus									x						2
	Gnatharus								?						?	1
	Gnatholeptus	x									x					4
	Gnathotrichus		x							x						16
	Gnathotrupes		x							x						30
	Metacorthylus		x							x						13
	Microcorthylus		x							x						38
	Mimiocurus	x					x			x						15
	Monarthrum		x								x					140

continued

Tribe	Genus	Phl	Xlm	Spm	Myc	Mye	Xly	Hbv	feed?	MG	HP	BG	Col	Inbr	MS?	Spp
	Phelloterus	x									x					3
	Phloeoterus	x									x					1
	Pityoborus		x							x						7
	Pityodendron								?						?	1
	Pityophthorus	x				x				x	x	(x)				385
	Pityotrichus	x								x						3
	Pseudopityophthorus	x								x						27
	Sauroptilius								?						?	1
	Spermophthorus			x											?	2
	Styphlosoma	x									x					4
	Tricolus		x							x						50
	Urocorthylus								?						?	1
Cryphalini	*Acorthylus*	x								x						6
	Allernoporus	x								x						1
	Allothenemus								?						?	1
	Coriacephilus	x													?	5
	Cosmoderes					?									?	20
	Cryphalogenes							x		x						2
	Cryphalus	x								x						190
	Cryptocarenus		no?	(x)		x								x		16
	Eidophelus	x										?				5
	Ernocladius	LK								x						2
	Ernoporicus	x								x						15
	Ernoporus	x								x						16
	Hemicryphalus														?	7
	Hypocryphalus	x								x						52
	Hypothenemus	x	(x)	x		x		(x)						x		183
	Margadillius			x					?					x		13
	Neocryphus								?						?	2

	Periocryphalus					x								x		2
	Procryphalus	x								x						3
	Ptilopodius	x												1?		17
	Scolytogenes	x				x				x						107
	Stegomerus	x								x						7
	Stephanopodius	x					x			x						6
	Trischidias				x									x		7
	Trypophloeus	x								x						17
Crypturgini	*Aphanarthrum*							x		x			(x)			29
	Cisurgus							x		x						9
	Crypturgus	x											x			15
	Deropria	x					(x)								?	1
	Dolurgus	x								x						1
Diamerini	*Acacicis*	x								x						11
	Bothrosternoides								?						?	1
	Diamerus	x								x						34
	Peronophorus	x								x						5
	Pseudodiamerus	x								x						3
	Sphaerotrypes	x								x						47
	Strombophorus	x					x			x						31
Dryocoetini	*Chiloxylon*								?						?	1
	Coccotrypes	x		x				x						x		129
	Cynanchophagus								?							1
	Cyrtogenius	x					x			x			x			106
	Dactylotrypes			x						x						1
	Dendrocranulus					x				x						43
	Dryocoetes							(x)			x	(x)				37
	Dryocoetiops					x								x?		18
	Lymantor				x					x						4
	Ozopemon	x												x		21

continued

Tribe	Genus	Phl	Xlm	Spm	Myc	Mye	Xly	Hbv	feed?	MG	HP	BG	Col	Inbr	MS?	Spp
	Peridryocoetes	?													?	6
	Pseudothamnurgus								?							5
	Taphronurgus							x								1
	Taphrorychus	x									x					19
	Thamnurgus							x								33
	Tiarophorus	?													?	8
	Triotemnus	x													?	15
	Xylocleptes							x		x						26
Hexacolini	*Gymnochilus*	x								x						9
	Microborus	x								x						8
	Pycnarthrum	x								x						18
	Scolytodes	x	(x)					(x)		x	x					207
Hylastini	*Hylastes*	x								x						32
	Hylurgops	x								x						21
	Scierus	x								x						2
Hylesinini	*Alniphagus*	x								x						3
	Cryptocurus								?						?	1
	Dactylipalpus						x			x						11
	Ficicis	x								x						14
	Hapalogenius						x								?	32
	Hylastinus	x						x		x						4
	Hylesinopsis	x					(x)			x						16
	Hylesinus	x								x		(x)				37
	Kissophagus	x								x						3
	Longulus	x										x				1
	Neopteleobius	x													?	1
	Phloeoborus				?		x			x						27
	Pteleobius	x								x						2
	Rhopalopselion						x			x						11

Hylurgini	*Chaetoptelius*	x								x						7
	Dendroctonus	x								x				(x)		20
	Dendrotrupes	x													?	2
	Hylurdrectonus	x								x						4
	Hylurgonotus						x			x						4
	Hylurgopinus	x								x						1
	Hylurgus	x								x						3
	Pachycotes						x			x						9
	Pseudohylesinus	x								x						13
	Pseudoxylechinus	x								x						9
	Sinophloeus	x													?	1
	Tomicus	x								x						7
	Xylechinosomus	x														11
	Xylechinus	x								x	x					40
Hyorrhynchini	*Hyorrhynchus*		x							x						11
	Pseudohyorrhynchus		x							x						3
	Sueus		x											x		5
Hypoborini	*Chaetophloeus*	x								x						24
	Cryphyophthorus								?						?	2
	Dacryostactus	x								x						1
	Glochiphorus								?						?	2
	Hypoborus	x								x						2
	Liparthrum	x						x		x						37
	Styracoptinus	x								x						4
	Trypanophellos								?							1
	Zygophloeus								?						?	1
Ipini	*Acanthotomicus*	x					(x)			(x)	x					94
	Dendrochilus						x								?	9
	Ips	x									x					45
	Orthotomicus	x									x					20

continued

Tribe	Genus	Phl	Xlm	Spm	Myc	Mye	Xly	Hbv	feed?	MG	HP	BG	Col	Inbr	MS?	Spp
	Pityogenes	x									x					24
	Pityokteines	x									x					10
	Premnobius		x											x		23
	Premnophilus		x											x		2
	Pseudips	x										x				3
Micracidini	*Afromicracis*								?						?	17
	Hylocurus	(x)					x				(x)	x				78
	Lanurgus	x						x		x						22
	Micracis						x					x				26
	Micracisella					x				x						20
	Miocryphalus	x				(x)						?				
	Phloeocleptus	x										x				11
	Phloeocurus	x													?	1
	Pseudomicracis	x								x	x					8
	Pseudothysanoes	x					(x)	(x)				x				92
	Saurotocis	x									x					2
	Stenoclyptus	x										x				2
	Stevewoodia								?						?	1
	Thysanoes						x					x				15
Phloeosinini	*Asiophilus*								?						?	2
	Carphotoreus	x								x						1
	Catenophorus								?						?	1
	Chramesus	x				(x)	(x*)	(x)		x		(x)				92
	Cladoctonus	x								x						14
	Cortisinus								?						?	1
	Dendrosinus						x			x						7
	Hyledius	x								x	(x)					24
	Hyleops	x								x						1
	Microdictica								?						?	1

	Phloeocranus	x								x						1
	Phloeoditica	x										x				2
	Phloeosinopsioides								?						?	3
	Phloeosinus	x					(x*)			x		(x)				66
	Pseudochramesus	x								x						11
Phloeotribini	*Aricerus*	x								x						3
	Dryotomicus								?						?	4
	Phloeotribus	x								x		(x)				103
Phrixosomatini	*Phrixosoma*	x								x						25
Polygraphini	*Bothinodroctonus*	x													?	3
	Cardroctonus								?						?	3
	Carphobius	x								x						3
	Carphoborus	x									x					34
	Chortastus	x								x	x					5
	Dolurgocleptes								?						?	2
	Halystus	x													?	2
	Polygraphus	x								(x)	x					100
	Serrastus	x								x						2
Scolytini	*Camptocerus*		x							x						31
	Ceratolepsis	x								x						7
	Cnemonyx	x								x						23
	Loganius	x								x						16
	Scolytopsis	x								x						6
	Scolytus	x								x	(x)	(x)				126
Scolytoplatypodini	*Remansus*		x							?						4
	Scolytoplatypus		x							x						49
Xyleborini	*Amasa*		x											x		41
	Ambrosiodmus		x											x		80
	Ambrosiophilus		x											x		8
	Ancipitis		x											x		1

continued

Tribe	Genus	Phl	Xlm	Spm	Myc	Mye	Xly	Hbv	feed?	MG	HP	BG	Col	Inbr	MS?	Spp
	Anisandrus		x											x		14
	Arixyleborus		x											x		32
	Beaverium		x											x		7
	Cnestus		x											x		32
	Coptoborus		x											x		23
	Coptodryas		x											x		36
	Cryptoxyleborus		x											x		18
	Cyclorhipidion		x											x		86
	Debus		x											x		16
	Diuncus		x											x		17
	Dryocoetoides		x											x		25
	Dryoxylon		x											x		1
	Eccoptopterus		x											x		6
	Euwallacea		x											x		45
	Fortiborus		x											x		6
	Hadrodemius		x											x		3
	Immanus		x													2
	Leptoxyleborus		x											x		6
	Microperus		x											x		16
	Planiculus		x											x		7
	Pseudowebbia		x											x		6
	Sampsonius		x											x		22
	Schedlia		x											x		6
	Stictodex		x											x		2
	Streptocranus		x											x		11
	Taurodemus		x											x		15
	Theoborus		x											x		11
	Truncaudum		x											x		7
	Wallacellus		x											x		3

	Webbia		x											x		38
	Xyleborinus		x											x		76
	Xyleborus		x											x		404
	Xylosandrus		x											x		39
Xyloctonini	*Cryphalomimus*								?						?	3
	Ctonoxylon	x								x						28
	Glostatus	x								x						18
	Scolytomimus	x								x						14
	Xyloctonus	x								x						15
Xyloterini	*Indocryphalus*		x							x						8
	Trypodendron		x							x						13
	Xyloterinus		x											x		1

[*] *Feeding and reproductive behavior for Scolytinae genera of the world. For most genera, larval feeding mode and mating system information are in the review of world genera by (Wood, 1986; see also 1982, 2007), or regional works of Beeson (1941), Schedl (1958, 1959, 1977), Browne (1961, 1963), and Chararas (1962); overlooked or recent information for poorly known genera or exceptional species is in Kalshoven (1958), Roberts (1969, 1976), Beaver and Löyttyniemi (1985), Noguera-Martínez and Atkinson (1990), and Jordal (2006).*

ACKNOWLEDGMENTS

The taxonomic distributions of feeding behaviors and reproductive systems would not have been possible without the taxonomic data compilation kindly supplied by T. H. Atkinson. Roger Beaver, Sarah Smith, and Anthony Cognato replied promptly to repeated requests for natural history information, which greatly improved the manuscript. We thank them and all the others who supplied facts or research reprints. P.H.W.B. is funded by an SNSF Postdoctoral Research Grant (P300P3_151134).

REFERENCES

Adams, A.S., Six, D.L., 2007. Temporal variation in mycophagy and prevalence of fungi associated with developmental stages of *Dendroctonus ponderosae* (Coleoptera: Curculionidae). Environ. Entomol. 36, 64–72.

Adams, A.S., Six, D.L., Adams, S.M., Holben, W.E., 2008. *In vitro* interactions between yeasts and bacteria and the fungal symbionts of the mountain pine beetle (*Dendroctonus ponderosae*). Microb. Ecol. 56, 460–466.

Ahnlund, H., 1996. Saproxylic insects on a Swedish dead aspen. Entomologisk Tidskrift 117, 137–144.

Alexander, R.D., 1974. The evolution of social behavior. Annu. Rev. Ecol. Syst. 5, 325–383.

Alexander, R.D., Noonan, K.M., Crespi, B.J., 1991. The evolution of eusociality. In: Sherman, P.W., Jarvis, J.U.M., Alexander, R.D. (Eds.), The Biology of the Naked Mole Rat. Princeton University Press, Princeton, pp. 1–44.

Alfaro, R.I., Humble, L.M., Gonzalez, P., Villaverde, R., Allegro, G., 2007. The threat of the ambrosia beetle *Megaplatypus mutatus* (Chapuis) (=*Platypus mutatus* Chapuis) to world poplar resources. Forestry 80, 471–479.

Amezaga, I., 1997. Forest characteristics affecting the rate of shoot pruning by the pine shoot beetle (*Tomicus piniperda* L.) in *Pinus radiata* D. Don and *P. sylvestris* L. plantations. Forestry 70, 129–137.

Anderbrandt, O., Schlyter, F., Birgersson, G., 1985. Intraspecific competition affecting parents and offspring in the bark beetle *Ips typographus*. Oikos 45, 89–98.

Andersen, J., Nilssen, A.C., 1983. Intrapopulation size variation of free-living and tree-boring Coleoptera. Can. Entomol. 15, 1453–1464.

Andersen, H., Jordal, B., Kambestad, M., Kirkendall, L.R., 2012. Improbable but true: the invasive inbreeding ambrosia beetle *Xylosandrus morigerus* has generalist genotypes. Ecol. Evol. 2, 247–257.

Arthofer, W., Riegler, M., Avtzis, D.N., Stauffer, C., 2009. Evidence for low-titre infections in insect symbiosis: *Wolbachia* in the bark beetle *Pityogenes chalcographus* (Coleoptera, Scolytinae). Environ. Microbiol. 11, 1923–1933.

Atkinson, T.H., 2010. New species and records of *Cactopinus* Schwarz with a key to species (Coleoptera, Curculionidae, Scolytinae). ZooKeys. 17–33.

Atkinson, T.H., Equihua-Martínez, A., 1985a. Lista comentada de los coleópteros Scolytidae y Platypodidae del Valle de México. Folia Entomol. Mexic. 65, 63–108.

Atkinson, T.H., Equihua-Martínez, A., 1985b. Notes on biology and distribution of Mexican and Central American Scolytidae (Coleoptera). I. Hylesininae, Scolytinae except Cryphalini and Corthylini. Coleopterists Bulletin 39, 227–238.

Atkinson, T.H., Equihua-Martínez, A., 1985c. Notes on biology and distribution of Mexican and Central American Scolytidae (Coleoptera). II. Scolytinae: Cryphalini and Corthylini. Coleopterists Bulletin 39, 355–363.

Atkinson, T.H., Equihua-Martínez, A., 1986a. Biology of the Scolytidae and Platypodidae (Coleoptera) in a tropical deciduous forest at Chamela, Jalisco. Mexico. Fla. Entomol. 69, 303–310.

Atkinson, T.H., Equihua-Martínez, A., 1986b. Biology of bark and ambrosia beetles (Coleoptera, Scolytidae and Platypodidae) of a tropical rain forest in southeastern Mexico with an annotated checklist of species. Ann. Entomol. Soc. Am. 79, 414–423.

Atkinson, T.H., Peck, S.B., 1994. Annotated checklist of the bark and ambrosia beetles (Coleoptera: Platypodidae and Scolytidae) of tropical southern Florida. Fla. Entomol. 77, 313–329.

Atkinson, T.H., Saucedo Céspedes, E., Martínez Fernández, E., Burgos Solorio, A., 1986. Coleópteros Scolytidae y Platypodidae asociados con las comunidades vegetales de clima templado y frío en el estado de Morelos, México. Acta Zool. Mex. 17, 1–58 (ns).

Ausmus, B.S., 1977. Regulation of wood decomposition rates by arthropod and annelid populations. Ecol. Bull. 25, 180–192.

Ayres, M.P., Wilkens, R.T., Ruel, J.J., Lombardero, M.J., Vallery, E., 2000. Nitrogen budgets of phloem-feeding bark beetles with and without symbiotic fungi. Ecology 81, 2198–2210.

Baker, J.M., 1963. Ambrosia beetles and their fungi, with particular reference to *Platypus cylindrus* Fab. In: Mosse, B., Nutman, P.S. (Eds.), Symbiotic Associations; Thirteenth Symposium of the Society for General Microbiology. The Syndics of the Cambridge University Press, London, pp. 232–265.

Bakke, A., 1968a. Ecological studies on bark beetles (Coleoptera: Scolytidae) associated with Scots pine (*Pinus sylvestris* L.) in Norway with particular reference to the influence of temperature. Meddelelser Norske Skogforsøksvesen 21, 441–602.

Bakke, A., 1968b. Field and laboratory studies on sex ratio in *Ips acuminatus* (Coleoptera: Scolytidae) in Norway. Can. Entomol. 100, 640–648.

Bakke, A., 1992. Monitoring bark beetle populations: effects of temperature. J. Appl. Entomol. 114, 208–211.

Balachowsky, A., 1949. Coléoptères Scolytidae. Libraire de la Faculte des Sciences, Paris.

Barbey, A., 1901. Les Scolytides de L'Europe Centrale. H. Kündig, Geneva.

Barr, B.A., 1969. Sound production in Scolytidae (Coleoptera) with emphasis on the genus *Ips*. Can. Entomol. 101, 636–672.

Barras, S.J., 1973. Reduction of progeny and development in southern pine beetle following removal of symbiotic fungi. Can. Entomol. 105, 1295–1299.

Batra, L.R., 1963. Ecology of ambrosia fungi and their dissemination by beetles. Trans. Kansas Acad. Sci. 66, 213–236.

Batra, L.R., 1966. Ambrosia fungi: extent of specificity to ambrosia beetles. Science 153, 193–195.

Batra, L.R., 1967. Ambrosia fungi—a taxonomic revision and nutritional studies of some species. Mycologia 59, 976–1017.

Batra, S.W.T., 1966. Nests and social behaviour of halictine bees of India. Indian J. Entomol. 28, 375–393.

Beal, J.A., Massey, C.L., 1945. Bark beetles and ambrosia beetles (Coleoptera: Scolytoidea) with special reference to the species occurring in North Carolina. Duke University School of Forestry Bulletin 10, 1–178.

Beaver, R.A., 1973. Biological studies of Brazilian Scolytidae and Platypodidae (Coleoptera) II. The tribe Bothrosternini. Pap. Avulsos Dep. Zool. 26, 227–236.

Beaver, R.A., 1976. Biological studies of Brazilian Scolytidae and Platypodidae (Coleoptera). 5. The tribe Xyleborini. Z. angew. Entomol. 80, 15–30.

Beaver, R.A., 1977. Bark and ambrosia beetles in tropical forests. Biotrop Special Publication 2, 133–149.

Beaver, R.A., 1979a. Host specificity in temperate and tropical animals. Nature 281, 139–141.

Beaver, R.A., 1979b. Leafstalks as a habitat for bark beetles (Col.: Scolytidae). Z. angew. Entomol. 88, 296–306.

Beaver, R.A., 1986. The taxonomy, mycangia and biology of *Hypothenemus curtipennis* (Schedl), the first known cryphaline ambrosia beetle (Coleoptera: Scolytidae). Entomol. Scand. 17, 131–135.

Beaver, R.A., 1988. Biological studies on ambrosia beetles of the Seychelles (Col., Scolytidae and Platypodidae). J. Appl. Entomol. 105, 62–73.

Beaver, R.A., 1989. Insect-fungus relationships in the bark and ambrosia beetles. In: Wilding, N., Collins, N.M., Hammond, P.M., Webber, J.F. (Eds.), Insect-Fungus Interactions. Academic Press, London, pp. 121–143.

Beaver, R.A., 2000. Studies on the genus *Diapus* Chapuis (Coleoptera: Platypodidae) new species and new synonymy. Serangga 5, 247–260.

Beaver, R.A., 2013. The invasive neotropical ambrosia beetle *Euplatypus parallelus* (Fabricius, 1801) in the oriental region and its pest status. The Entomologist's Monthly Magazine 149, 143–154.

Beaver, R.A., Browne, F.G., 1975. The Scolytidae and Platypodidae (Coleoptera) of Thailand. A checklist with biological and zoogeographical notes. Oriental Insects 9, 283–311.

Beaver, R.A., Gebhardt, H., 2006. A review of the Oriental species of *Scolytoplatypus* Schaufuss (Coleoptera, Curculionidae, Scolytinae). Dtsch. Entomol. Z. 53, 155–178.

Beaver, R.A., Löyttyniemi, K., 1985. Bark and ambrosia beetles (Coleoptera: Scolytidae) of Zambia. Revue zoologiques africaine 99, 63–85.

Beeson, C.F.C., 1939. New species and biology of *Coccotrypes* and *Thamnurgides* (Scolytidae, Col.). *Indian Forest Records (N. S.)*. Entomology 5, 279–308.

Beeson, C.F.C., 1941. The Ecology and Control of the Forest Insects of India and the Neighbouring Countries. The Vasant Press, India.

Benavides, P., Vega, F.E., Romero-Severson, J., Bustillo, A.E., Stuart, J.J., 2005. Biodiversity and biogeography of an important inbred pest of coffee, coffee berry borer (Coleoptera: Curculionidae: Scolytinae). Ann. Entomol. Soc. Am. 98, 359–366.

Bentz, B.J., Six, D.L., 2006. Ergosterol content of fungi associated with *Dendroctonus ponderosae* and *Dendroctonus rufipennis* (Coleoptera: Curculionidae, Scolytinae). Ann. Entomol. Soc. Am. 99, 189–194.

Berryman, A.A., 1982. Population dynamics of bark beetles. In: Mitton, J.B., Sturgeon, K.B. (Eds.), Bark Beetles in North American Conifers. A System for the Study of Evolutionary Biology. University of Texas Press, Austin.

Beukeboom, L.W., Vrijenhoek, R.C., 1998. Evolutionary genetics and ecology of sperm-dependent parthenogenesis. J. Evol. Biol. 11, 755–782.

Biedermann, P.H.W., 2010. Observations on sex ratio and behavior of males in *Xyleborinus saxesenii* Ratzeburg (Scolytinae, Coleoptera). ZooKeys 56, 253–267.

Biedermann, P.H.W., 2012. The evolution of cooperation in ambrosia beetles. Ph.D. thesis, University of Bern.

Biedermann, P.H.W., Taborsky, M., 2011. Larval helpers and age polyethism in ambrosia beetles. Proc. Natl. Acad. Sci. U. S. A. 108, 17064–17069.

Biedermann, P. H. W., and Taborsky, M. (submitted). Experimental social evolution: philopatry and cooperation co-evolve in an ambrosia beetle.

Biedermann, P.H.W., Klepzig, K.D., Taborsky, M., 2009. Fungus cultivation by ambrosia beetles: behavior and laboratory breeding success in three xyleborine species. Environ. Entomol. 38, 1096–1105.

Biedermann, P.H.W., Klepzig, K.D., Taborsky, M., 2011. Costs of delayed dispersal and alloparental care in the fungus-cultivating ambrosia beetle *Xyleborus affinis* Eichhoff (Scolytinae: Curculionidae). Behav. Ecol. Sociobiol. 65, 1753–1761.

Biedermann, P.H.W., Peer, K., Taborsky, M., 2012. Female dispersal and reproduction in the ambrosia beetle *Xyleborinus saxesenii* Ratzeburg (Coleoptera; Scolytinae). Mitteilungen der Deutschen Gesellschaft für allgemeine und angewandte Entomologie 18, 231–235.

Biedermann, P.H.W., Klepzig, K.D., Taborsky, M., Six, D.L., 2013. Abundance and dynamics of filamentous fungi in the complex ambrosia gardens of the primitively eusocial beetle *Xyleborinus saxesenii* Ratzeburg (Coleoptera: Curculionidae, Scolytinae). FEMS Microbiol. Ecol. 83, 711–723.

Birch, M.C., 1984. Aggregation in bark beetles. In: Bell, W.J., Cardé, R.T. (Eds.), Chemical Ecology of Insects. Chapman and Hall, New York, pp. 331–353.

Blackman, M.W., 1922. Mississippi bark beetles. Miss., Agric. Exp. Stn., Tech. Bull, 11,130 pp., 18 pls.

Blackman, M.W., 1924. The effect of deficiency and excess in rainfall upon the hickory bark beetle (*Eccoptogaster quadrispinosus* Say). J. Econ. Entomol. 17, 460–470.

Blackman, M.W., 1928. The genus *Pityophthorus* Eichh. in North America: a revisional study of the Pityophthori, with descriptions of two new genera and seventy-one new species, 25, New York State College of Forestry at Syracuse, Technical Publication, 1–184.

Blackman, M.W., 1931. The Black Hills beetle (*Dendroctonus ponderosae* Hopk.). Bulletin of the New York State College of Forestry at Syracuse University 4, 1–97.

Blackman, M.W., Stage, H.H., 1918. Notes on insects bred from the bark and wood of the American larch, 10,Technical Publication, New York State College of Forestry at Syracuse University, 1–115.

Blackman, M.W., Stage, H.H., 1924. On the succession of insects living in the bark and wood of dying, dead and decaying hickory. New York State College of Forestry at Syracuse University, Technical Publication 17, 1–268.

Bleiker, K.P., Heron, R.J., Braithwaite, E.C., Smith, G.D., 2013. Preemergence mating in the mass-attacking bark beetle, *Dendroctonus ponderosae* (Coleoptera: Curculionidae). Can. Entomol. 145, 12–19.

Bonduriansky, R., 2001. The evolution of male mate choice in insects: a synthesis of ideas and evidence. Biol. Rev. 76, 305–339.

Boomsma, J.J., 2009. Lifetime monogamy and the evolution of eusociality. Philos. Trans. R. Soc., B 364, 3191–3207.

Boomsma, J.J., 2013. Beyond promiscuity: mate-choice commitments in social breeding. Philos. Trans. R. Soc. B 368,20120050.

Borden, J.H., 1967. Factors influencing the response of *Ips confusus* (Coleoptera: Scolytidae) to male attractant. Can. Entomol. 99, 1164–1193.

Borden, J.H., 1969. Observations on the life history and habits of *Alniphagus aspericollis* (Coleoptera: Scolytidae) in southwestern British Columbia. Can. Entomol. 101, 870–878.

Borden, J.H., 1985. Aggregation pheromones. In: Kerkut, G.A. (Ed.), Behaviour. Pergamon Press, Oxford, pp. 257–285.

Borden, J.H., Slater, C.E., 1969. Flight muscle volume change in *Ips confusus* (Coleoptera: Scolytidae). Can. J. Zool. 47, 29–31.

Bordenstein, S.R., O'Hara, F.P., Werren, J.H., 2001. *Wolbachia*-induced incompatibility precedes other hybrid incompatibilities in *Nasonia*. Nature 409, 707–710.

Borsa, P., Kjellberg, F., 1996a. Experimental evidence for pseudo-arrhenotoky in *Hypothenemus hampei* (Coleoptera: Scolytidae). Heredity 76, 130–135.

Borsa, P., Kjellberg, F., 1996b. Secondary sex ratio adjustment in a pseudo-arrhenotokous insect, *Hypothenemus hampei* (Coleoptera: Scolytidae). Comptes Rendus de l'Academie des Sciences Serie Iii-Sciences de la Vie-Life Sciences 319, 1159–1166.

Botterweg, P.F., 1982. Dispersal and flight behavior of the spruce bark beetle *Ips typographus* in relation to sex, size and fat-content. Z. angew. Entomol. 94, 466–489.

Bourke, A.F.G., 2011. Principles of Social Evolution. Oxford University Press, Oxford.

Brader, L., 1964. Étude de la relation entre le scolyte des rameaux du caféir, *Xyleborus compactus* Eichh. (*X. morstatti* Hag.), et sa plantehôte. Mededelingen van de Landbouwhogeschool te Wageningen 64, 1–109.

Bright, D.E., 1981. Taxonomic monograph of the genus *Pityophthorus* Eichhoff in North and Central America (Coleoptera: Scolytidae). Mem. Entomol. Soc. Can. 118, 1–378.

Bright, D.E., Poinar Jr., G.O., 1994. Scolytidae and Platypodidae (Coleoptera) from Dominican Republic Amber. Ann. Entomol. Soc. Am. 87, 170–194.

Bright, D.E., Stark, R.W., 1973. The bark and ambrosia beetles of California. Coleoptera: Scolytidae and Platypodidae. Bulletin of the California Insect Survey 16, 1–169.

Brimblecombe, A.R., 1953. An annotated list of the Scolytidae occurring in Australia. Queensl. J. Agric. Sci. 10, 167–205.

Browne, F.G., 1958. Some aspects of host selection among ambrosia beetles in the humid tropics of south-east Asia. Malayan Forest Records 21, 164–182.

Browne, F.G., 1961. The Biology of Malayan Scolytidae and Platypodidae. Malayan Forest Records 22, 1–255.

Browne, F.G., 1962. The emergence, flight and mating behaviour of *Doliopygus conradti*. West African Timber Borer Research Unit 5, 21–27.

Browne, F.G., 1963. Notes on the habits and distribution of some Ghanaian bark beetles and ambrosia beetles (Coleoptera: Scolytidae and Platypodidae). Bull. Entomol. Res. 54, 229–266.

Browne, F.G., 1965. Types of ambrosia beetle attack on living trees. Proc. Int. Cong. Entomol. 12, 680.

Browne, F.G., 1968. Pests and Diseases of Forest Plantation Trees. Clarendon, Oxford.

Browne, F.G., 1972. Larvae of principal old world genera of Platypodinae. Trans. R. Entomol. Soc. Lond. 124, 167–190.

Brucker, R.M., Bordenstein, S.R., 2012. Speciation by symbiosis. Trends Ecol. Evol. 27, 443–451.

Brun, L.O., Borsa, P., Gaudichon, V., Stuart, J.J., Aronstein, K., Coustau, C., Ffrench-Constant, R.H., 1995a. 'Functional' haplodiploidy. Nature 374, 506.

Brun, L.O., Stuart, J.J., Gaudichon, V., Aronstein, K., Ffrench-Constant, R.H., 1995b. Functional haplodiploidy—a mechanism for the spread of insecticide resistance in an important international insect pest. Proc. Natl. Acad. Sci. U. S. A. 92, 9861–9865.

Cai, Y., Cheng, X., Xu, R., Duan, D., Kirkendall, L.R., 2008. Genetic diversity and biogeography of red turpentine beetle *Dendroctonus valens* in its native and invasive regions. Insect Sci. 15, 291–301.

Campobasso, G., Terragitti, G., Mann, K., Quimby, P.C., 2004. Field and laboratory biology of the stem-feeding beetle *Thamnurgus euphorbiae* (Kuster) (Col., Scolytidae) in Italy, a potential biological control candidate of leafy spurge in the USA and Canada. J. Appl. Entomol. 128, 1–5.

Cardoza, Y.J., Paskewitz, S., Raffa, K.F., 2006a. Travelling through time and space on wings of beetles: a tripartite insect-fungi-nematode association. Symbiosis 41, 71–79.

Cardoza, Y.J., Klepzig, K.D., Raffa, K.F., 2006b. Bacteria in oral secretions of an endophytic insect inhibit antagonistic fungi. Ecol. Entomol. 31, 636–645.

Cardoza, Y.J., Moser, J.C., Klepzig, K.D., Raffa, K.F., 2008. Multipartite symbioses among fungi, mites, nematodes, and the spruce beetle, *Dendroctonus rufipennis*. Environ. Entomol. 37, 956–963.

Chamberlin, W.J., 1918. Bark beetles infesting the Douglas fir. Bull. Oregon Agric. College Exp. Sta. 147, 1–40.

Chamberlin, W.J., 1939. The Bark and Timber Beetles of North America. North of Mexico, Oregon State College Cooperative Association, Corvallis, Oregon.

Chamberlin, W.J., 1958. The Scolytoidea of the Northwest: Oregon, Washington, Idaho, and British Columbia. Oregon State College, Corvallis.

Chapman, T.A., 1870. On the habits of *Platypus cylindrus*. Entomologists Monthly Magazine 7, 103–107, 132–135.

Chapman, J.A., 1956. Flight muscle changes during adult life in a scolytid beetle, *Trypodendron*. Nature 177, 1183.

Chararas, C., 1962. Étude biologique des scolytidae des conifères. P. Lechevalier, Paris.

Charnov, E.L., 1982. The Theory of Sex Allocation. Princeton University Press, Princeton.

Chodjaï, M., 1963. Étude écologique de *Rugoscolytus mediterraneus* Eggers (Col. Scolytidae) en Iran. Rev. Path. Vég. Entomol. Agr. Fr. 42, 139–160.

Choe, J.C., Crespi, B.J., 1997. The Evolution of Social Behaviour in Insects and Arachnids. Cambridge University Press, Cambridge.

Chong, J.-H., Reid, L., Williamson, M., 2009. Distribution, host plants, and damage of the black twig borer, *Xylosandrus compactus* (Eichhoff), in South Carolina. J. Agric. Urban Entomol. 26, 199–208.

Civetta, A., Singh, R.S., 1999. Broad-sense sexual selection, sex gene pool evolution, and speciation. Genome 42, 1033–1041.

Clutton-Brock, T., 2009. Cooperation between non-kin in animal societies. Nature 462, 51–57.

Cognato, A.I., 2013. Molecular phylogeny and taxonomic review of Premnobiini Browne 1962 (Coleoptera: Curculionidae: Scolytinae). Front. Ecol. Evol. 1http://dx.doi.org/10.3389/fevo.2013.00001.

Cognato, A.I., Grimaldi, D., 2009. 100 million years of morphological conservation in bark beetles (Coleoptera: Curculionidae: Scolytinae). Syst. Entomol. 34, 93–100.

Cognato, A.I., Sperling, F.A.H., 2000. Phylogeny of *Ips* DeGeer species (Coleoptera: Scolytidae) inferred from mitochondrial cytochrome oxidase I DNA sequence. Mol. Phylogenet. Evol. 14, 445–460.

Cognato, A.I., Seybold, S.J., Sperling, F.A.H., 1999. Incomplete barriers to mitochondrial gene flow between pheromone races of the North American pine engraver, *Ips pini* (Say) (Coleoptera: Scolytidae). Proc. R. Soc. London B 266, 1843–1850.

Cognato, A.I., Gillette, N.E., Bolaños, R.C., Sperling, F.A.H., 2005. Mitochondrial phylogeny of pine cone beetles (Scolytinae, *Conophthorus*) and their affiliation with geographic area and host. Mol. Phylogenet. Evol. 36, 494–508.

Cognato, A.I., Hulcr, J., Dole, S.A., Jordal, B.H., 2011. Phylogeny of haplo-diploid, fungus-growing ambrosia beetles (Curculionidae: Scolytinae: Xyleborini) inferred from molecular and morphological data. Zool. Scr. 40, 174–186.

Costa, J.T., 2006. The Other Insect Societies. Belknapp Press of Harvard University. Press, Cambridge.

Costa, J.T., 2010. Social evolution in "other" insects and arachnids. In: Breed, M.D., Moore, J. (Eds.), Encyclopedia of Animal Behavior. Academic Press, Oxford, pp. 231–241.

Cowling, E.B., Merrill, W., 1966. Nitrogen in wood and its role in wood deterioration. Can. J. Bot. 44, 1533–1544.

Cremer, S., Armitage, S.A.O., Schmid-Hempel, P., 2007. Social immunity. Curr. Biol. 17, R693–R702.

Crowson, R.A., 1974. Observations on Histeroidea, with descriptions of an apterous male, and of the internal anatomy of male *Sphaerites*. J. Entomol. Series B, Taxonomy 42, 133–140.

Crozier, R.G., Giese, R.L., 1967a. The Columbian timber beetle, *Corthylus columbianus* (Coleoptera: Scolytidae). III. Definition of epiphytotics. J. Econ. Entomol 60, 55–58.

Crozier, R.G., Giese, R.L., 1967b. The Columbian timber beetle, *Corthylus columbianus* (Coleoptera: Scolytidae). IV. Intrastand population distribution. Can. Entomol. 99, 1203–1214.

Currie, C.R., 2001. A community of ants, fungi, and bacteria: a multilateral approach to studying symbiosis. Annu. Rev. Microbiol. 55, 357–380.

Dahlsten, D.L., 1982. Relationship between bark beetles and their natural enemies. In: Mitton, J.B., Sturgeon, K.B. (Eds.), Bark Beetles in North American Conifers. A System for the Study of Evolutionary Biology. University of Texas Press, Austin, pp. 140–182.

Dallara, P.L., Seybold, S.J., Meyer, H., Tolasch, T., Francke, W., Wood, D.L., 2000. Semiochemicals from three species of *Pityophthorus* (Coleoptera: Scolytidae): identification and field response. Can. Entomol. 132, 889–906.

Darling, D.C., Roberts, H., 1999. Life history and larval morphology of *Monacon* (Hymenoptera: Perilampidae), parasitoids of ambrosia beetles (Coleoptera: Platypodidae). Can. J. Zool. 77, 1768–1782.

Darwin, C., 1859. The Origin of Species. John Murray, London.

De Fine Licht, H.H., Biedermann, P.H.W., 2012. Patterns of functional enzyme activity in fungus farming ambrosia beetles. Front. Zool. 9, 13.

de Groot, P., Borden, J.H., 1992. Host acceptance behaviour of the jack pine tip beetle, *Conophthorus banksianae* and the red pine cone beetle. C. resinosae. Entomol. Exp. Appl. 65, 149–155.

De Leon, D., 1952. Insects associated with *Sequoia sempervirens* and *Sequoia gigantea* in California. Pan-Pac. Entomol. 28, 75–91.

Dedeine, F., Vavre, F., Fleury, F., Loppin, B., Hochberg, M.E., Boulétreau, M., 2001. Removing symbiotic *Wolbachia* bacteria specifically inhibits oogenesis in a parasitic wasp. Proc. Natl. Acad. Sci. U. S. A. 98, 6247–6252.

Dekle, G.W., Kuitert, L.C., 1968. Orchid insects, related pests and control. Florida Department of Agriculture, Bulletin of the Division of Plant Industry 8, 1–28.

Delate, K.M., 1994. Postharvest control treatments for *Hypothenemus obscurus* (F.) in macadamia nuts. J. Econ. Entomol. 87, 120–126.

Deneubourg, J.L., Grégoire, J.-C., LeFort, E., 1990. Kinetics of larval gregarious behaviour in the bark beetle *Dendroctonus micans* (Coleoptera: Scolytidae). J. Insect Behav. 3, 169–182.

Deyrup, M., 1987. *Trischidias exigua* Wood, new to the United States, with notes on the biology of the genus. Coleopterists Bulletin 41, 339–343.

Deyrup, M., Kirkendall, L.R., 1983. Apparent parthenogenesis in *Pityophthorus puberulus* (Coleoptera: Scolytidae). Ann. Entomol. Soc. Am. 76, 400–402.

Doane, R.W., 1923. *Leperisinus californicus* Sw. killing ash trees. Can. Entomol. 55, 217.

Doane, R.W., Gilliland, O.J., 1929. Three California ambrosia beetles. J. Econ. Entomol. 22, 915–921.

Dole, S.A., Jordal, B.H., Cognato, A.I., 2010. Polyphyly of *Xylosandrus* Reitter inferred from nuclear and mitochondrial genes (Coleoptera: Curculionidae: Scolytinae). Mol. Phylogenet. Evol. 54, 773–782.

Duffy, E.A.J., 1968. A monograph of the immature stages of oriental timber beetles (Cerambycidae). British Museum (Natural History), London.

Dussourd, D.E., Eisner, T., 1987. Vein-cutting behavior: insect counterploy to the latex defense of plants. Science 237, 898–901.

Eichhoff, W., 1881. Die Europäischen Borkenkäfer. Julius Springer, Berlin.

Eidmann, H.H., 1992. Impact of bark beetles on forests and forestry in Sweden. J. Appl. Entomol. 114, 193–200.

Elkin, C.M., Reid, M.L., 2005. Low energy reserves and energy allocation decisions affect reproduction by mountain pine beetles, *Dendroctonus ponderosae*. Funct. Ecol. 19, 102–109.

Emlen, S.T., 1982. The evolution of helping. I. An ecological constraints model. Am. Nat. 119, 29–39.

Emlen, S.T., Oring, L.W., 1977. Ecology, sexual selection, and the evolution of mating systems. Science 197, 215–223.

Engelstädter, J., Hurst, G.D.D., 2006. Can maternally transmitted endosymbionts facilitate the evolution of haplodiploidy? J. Evol. Biol. 19, 194–202.

Entwistle, P.F., 1972. Pests of Cocoa. Longman, London.

Faccoli, M., Rukalski, J.P., 2004. Attractiveness of artificially killed red oaks (*Quercus rubra*) to ambrosia beetles (Coleoptera, Scolytidae). In: Ceretti, P., Hardersen, S., Mason, F., Nardi, G., Tisato, M., Zapparoli, M. (Eds.), Invertibrati di una Foresta della Pianura Padana, Bosco della Fontana. Cierre Grafica Editore, Verona, pp. 171–179.

Farrell, B.D., Sequeira, A.S., O'Meara, B.C., Normark, B.B., Chung, J.H., Jordal, B.H., 2001. The evolution of agriculture in beetles (Curculionidae: Scolytinae and Platypodinae). Evolution 55, 2011–2027.

Felt, E.P., 1914. Notes on forest insects. J. Econ. Entomol. 7, 373–375.

Ferro, M.L., Gimmel, M.L., Harms, K.E., Carlton, C.E., 2009. The beetle community of small oak twigs in Louisiana, with a literature review of Coleoptera from fine woody debris. Coleopterists Bulletin 63, 239–263.

Fischer, M., 1954. Untersuchungen über den kleinen Holzbohrer (*Xyleborus saxeseni*). Pflanzenschutzberichte 12, 137–180.

Fisher, R.C., 1931. Notes on the biology of the large elm bark-beetle, *Scolytus destructor* Ol. Forestry 5, 120–131.

Flores, L.J., Bright, D.E., 1987. A new species of *Conophthorus* from Mexico: descriptions and biological notes. Coleopterists Bulletin 41, 181–184.

Fockler, C.E., Borden, J.H., 1972. Sexual behavior and seasonal mating activity of *Trypodendron lineatum* (Coleoptera: Scolytidae). Can. Entomol. 104, 1841–1853.

Foelker, C.J., Hofstetter, R.W., 2014. Heritability, fecundity, and sexual size dimorphism in four species of bark beetles (Coleoptera: Curculionidae: Scolytinae). Ann. Entomol. Soc. Am. 107, 143–151.

Forcella, F., 1982. Twig nitrogen content and larval survival of twig-girdling beetles, *Oncideres cingulata* (Say) (Coleoptera: Cerambycidae). Coleopterists Bulletin 35, 211–212.

Fox, J.W., Wood, D.L., Akers, R.P., Parmeter, J.R., 1992. Survival and development of *Ips paraconfusus* Lanier (Coleoptera, Scolytidae) reared axenically and with tree–pathogenic fungi vectored by cohabiting *Dendroctonus* species. Can. Entomol. 124, 1157–1167.

Fraedrich, S.W., Harrington, T.C., Rabaglia, R.J., Ulyshen, M.D., Mayfield, A.E., Hanula, J.L., et al., 2008. A fungal symbiont of the redbay ambrosia beetle causes a lethal wilt in redbay and other Lauraceae in the southeastern United States. Plant Dis. 92, 215–224.

Francke-Grosmann, H., 1956a. Hautdrüsen als Träger der Pilzsymbiose bei Ambrosiakäfern. Zeitschrift für Ökologie und Morphologie der Tiere 45, 275–308.

Francke-Grosmann, H., 1956b. Zur Übertragung der Nährpilze bei Ambrosiakäfern. Naturwissenschaften 43, 286–287.

Francke-Grosmann, H., 1963a. Die Übertragung der Pilzflora bei dem Borkenkäfer *Ips acuminatus*. Z. angew. Entomol. 52, 355–361.

Francke-Grosmann, H., 1963b. Some new aspects in forest entomology. Annu. Rev. Entomol. 8, 415–438.

Francke-Grosmann, H., 1965. Ein Symbioseorgan bei dem Borkenkäfer *Dendroctonus frontalis* Zimm. (Coleoptera Scolytidae). Naturwissenschaften 52, 143.

Francke-Grosmann, H., 1966. Über Symbiosen von xylo-mycetophagen und phloeophagen Scolitoidea mit holzbewohnenden Pilzen. Material und Organismen 1, 503–522, Beiheft.

Francke-Grosmann, H., 1967. Ectosymbiosis in wood-inhabiting beetles. In: Henry, S.M. (Ed.), Symbiosis. Academic Press, New York, pp. 141–205.

Francke-Grosmann, H., 1975. Zur epizoischen und endozoischen Übertragung der symbiotischen Pilze des Ambrosiakäfers *Xyleborus saxeseni* (Coleoptera: Scolitidae). Entomologica Germanica 1, 279–292.

French, J.R.J., Roeper, R.A., 1972a. Interactions of ambrosia beetle, *Xyleborus dispar* (Coleoptera, Scolytidae), with its symbiotic fungus *Ambrosiella hartigii* (Fungi imperfecti). Can. Entomol. 104, 1635–1641.

French, J.R.J., Roeper, R.A., 1972b. In vitro culture of the ambrosia beetle *Xyleborus dispar* (Coleoptera: Scolytidae) with its symbiotic fungus, *Ambrosiella hartigii*. Ann. Entomol. Soc. Am. 65, 719–721.

French, J.R.J., Roeper, R.A., 1975. Studies on the biology of the ambrosia beetle *Xyleborus dispar* (F.) (Coleoptera: Scolytidae). J. Appl. Entomol. 78, 241–247.

Fuchs, G., 1907. Über die Fortpflanzungsverhältnisse der rindenbrütenden Borkenkäfer verbunden mit einer geschichtlichen und kritischen Darstellung der bisherigen Literatur. Ludwig-Maximilians-University, Munich, Doctoral Dissertation.

Furniss, M.M., 1995. Biology of *Dendroctonus punctatus* (Coleoptera: Scolytidae). Ann. Entomol. Soc. Am. 88, 173–182.

Furniss, M.M., 1996. Taxonomic status of *Dendroctonus punctatus* and *D. micans* (Coleoptera: Scolytidae). Ann. Entomol. Soc. Am. 89, 328–333.

Furniss, M.M., 1997. *Conophthorus ponderosae* (Coleoptera: Scolytidae) infesting lodgepole pine cones in Idaho. Environ. Entomol. 26, 855–858.

Gandon, S., 1999. Kin competition, the cost of inbreeding and the evolution of dispersal. J. Theor. Biol. 200, 345–364.

Garraway, E., 1986. The biology of *Ips calligraphus* and *Ips grandicollis* (Coleoptera: Scolytidae) in Jamaica. Can. Entomol. 118, 113–121.

Garraway, E., Freeman, B.E., 1981. Population-dynamics of the juniper bark beetle *Phloeosinus neotropicus* in Jamaica. Oikos 37, 363–368.

Garrick, R.C., Nason, J.D., Fernandez-Manjarres, J.F., Dyer, R.J., 2013. Ecological co-associations influence species' responses to past climatic change: an example from a Sonoran Desert bark beetle. Mol. Ecol. 22, 3345–3361.

Gascoigne, J., Berec, L., Gregory, S., Courchamp, F., 2009. Dangerously few liaisons: a review of mate-finding Allee effects. Popul. Ecol. 51, 355–372.

Gast, S.J., Furniss, M.M., Johnson, J.B., Ivie, M.A., 1989. List of Montana Scolytidae (Coleoptera) and notes on new records. Great Basin Nat. 49, 381–386.

Gianoli, E., Ramos, I., Alfaro-Tapia, A., Valdéz, Y., Echegaray, E.R., Yábar, E., 2006. Benefits of a maize-bean-weeds mixed cropping system in Urubamba Valley, Peruvian Andes. Int. J. Pest Manage. 4, 283–289.

Gil, Z.N., Bustillo, A.E., Gómez, D.E., Marín, P., 2004. *Corthylus* n. sp. (Coleoptera: Scolytidae), plaga del aiso en la cuenca del Río Blanco en Colombia. Revista Colombiana de Entomología 30, 171–178.

Gillett, C.P.D.T., Crampton-Platt, A., Timmermans, M.J.T.N., Jordal, B., Emerson, B.C., Vogler, A.P., 2014. Bulk *de novo* mitogenome assembly from pooled total DNA elucidates the phylogeny of weevils (Coleoptera: Curculionoidea). Mol. Biol. Evol. http://dx.doi.org/10.1093/molbev/msu154.

Giménez, R.A., Etiennot, A.E., 2003. Host range of *Platypus mutatus* (Chapuis, 1865) (Coleoptera: Platypodidae). Entomotropica 18, 89–94.

Girardi, G.S., Giménez, R.A., Braga, M.R., 2006. Occurrence of *Platypus mutatus* Chapuis (Coleoptera: Platypodidae) in a Brazilwood experimental plantation in southeastern Brazil. Neotrop. Entomol. 35, 864–867.

Gobeil, A.R., 1936. The biology of *Ips perturbatus* Eichhoff. Can. J. Res. 14, 181–204.

Godwin, G., Odell, T.M., 1965. The life history of the white-pine cone beetle, *Conophthorus coniperda*. Ann. Entomol. Soc. Am. 58, 213–219.

Goeden, R.D., Norris, D.M., 1965. Some biological and ecological aspects of ovipositional attack in *Carya* spp. by *Scolytus quadrispinosus* (Coleoptera: Scolytidae). Ann. Entomol. Soc. Am. 58, 771–777.

Goldhammer, D.S., Stephen, F.M., Paine, T.D., 1990. The effect of the fungi *Ceratocystis minor* (Hedgecock) Hunt, *Ceratocystis minor* (Hedgecock) Hunt var. Barrasii Taylor, and SJB 122 on reproduction of the southern pine beetle, *Dendroctonus frontalis* Zimmermann (Coleoptera: Scolytidae). Can. Entomol. 122, 407–418.

Gossard, H.A., 1913. Orchard bark beetles and pin hole borers. Bulletin of the Ohio Agricultural Experiment Station 264, 1–68.

Gottlieb, D., Holzman, J.P., Lubin, Y., Bouskila, A., Kelley, S.T., Harari, A.R., 2009. Mate availability contributes to maintain the mixed-mating system in a scolytid beetle. J. Evol. Biol. 22, 1526–1534.

Gottlieb, D., Lubin, Y., Harari, A.R., 2014. The effect of female mating status on male offspring traits. Behav. Ecol. Sociobiol. 68, 701–710.

Gouger, R.J., Yearian, W.C., Wilkinson, R.C., 1975. Feeding and reproductive behaviour of *Ips avulsus*. Fla. Entomol. 58, 221–229.

Graf, P., 1977. A contribution on the biology and control of *Hylesinus oleiperda* F. (Coleopt., Scolytidae) on olive in the Tadla (Morocco). Z. angew. Entomol. 83, 52–62.

Greco, E.B., Wright, M.G., 2013. Dispersion and sequential sampling plan for *Xylosandrus compactus* (Coleoptera: Curculionidae) infesting Hawaii coffee plantations. Environ. Entomol. 42, 277–282.

Grégoire, J.-C., 1988. The greater European spruce bark beetle. In: Berryman, A.A. (Ed.), Dynamics of Forest Insect Populations. Patterns, Causes, Implications. Plenum, New York, pp. 455–478.

Grégoire, J.-C., Braekman, J.-C., Tondeur, A., 1981. Chemical communication between the larvae of *Dendroctonus micans* Kug (Coleoptera: Scolytidae). Les colloques de l'INRA, 7. Les Médiateurs chimiques, 253–257.

Gruner, L., 1974. Biologie et dégats d'*Hexacolus guyanensis* Schedl, dans les plantations d'acajou rouge (*Swietenia macrophylla* King., Méliacée) en Guadeloupe (Coleoptera: Scolytidae). Ann. Sci. Forest. 31, 111–128.

Güclü, C., Özbek, H., 2007. Biology and damage of *Thamnurgus pegani* Eggers (Coleoptera: Scolytidae) feeding on *Peganum harmala* L. in Eastern Turkey. Proc. Entomol. Soc. Wash. 109, 350–358.

Guérard, N., Dreyer, E., Lieutier, F., 2000. Interactions between Scots pine, *Ips acuminatus* (Gyll.) and *Ophiostoma brunneo-ciliatum* (Math.): estimation of the critical thresholds of attack and inoculation densities and effects on hydraulic properties in the stem. Ann. For. Sci. 57, 681–690.

Gurevitz, E., 1975. Contribution a l'étude des Scolytidae I. Comportement de différents stades du scolyte méditerranéen, *Scolytus* (*Rugoscolytus*) *mediterraneus* Eggers en Israël. Annales de zoologie—écologie animale 7, 477–489.

Haack, R.A., Slansky, F., 1987. Nutritional ecology of wood-feeding Coleoptera, Lepidoptera, and Hymenoptera. In: Slansky, F., Rodriguez, J.G. (Eds.), The Nutritional Ecology of Insects, Mites, Spiders, and Related Invertebrates. Wiley, New York, pp. 449–486.

Hadorn, C., 1933. Recherches sur la morphologie, les stades evolutifs et l'hivernage du bostryche lisere (*Xyloterus lineatus* Oliv.). Beiheft zu den Zeitschriften des Schweizerischen Forstvereins 11, 1–120.

Hamilton, W.D., 1964. The genetical evolution of social behavior, I and II. J. Theor. Biol. 7 (1–16), 17–52.

Hamilton, W.D., 1967. Extraordinary sex ratios. Science 156, 477–488.

Hamilton, W.D., 1972. Altruism and related phenomena, mainly in social insects. Annu. Rev. Ecol. Syst. 3, 193–232.

Hamilton, W.D., 1978. Evolution and diversity under bark. In: Mound, L.A., Waloff, N. (Eds.), Diversity of Insect Faunas. Blackwell, Oxford, pp. 154–175.

Hamilton, W.D., 1979. Wingless and fighting males in fig wasps and other insects. In: Blum, M.S., Blum, N.A. (Eds.), Reproductive Competition, Mate Choice, and Sexual Selection in Insects. Plenum, New York, pp. 167–220.

Hamilton, W.D., 1996. Funeral feasts: evolution and diversity under bark. In: Narrow Roads of Gene Land: The Collected Papers of W. D. Hamilton: Volume 1: Evolution of Social Behaviour. Spektrum Academic Publishers, Oxford, pp. 387–420.

Hammond, H.E., Langor, D.W., Spence, J.R., 2001. Early colonization of *Populus* wood by saproxylic beetles (Coleoptera). Can. J. For. Res. 31, 1175–1183.

Hanavan, R.P., Adams, K.B., Allen, D.C., 2012. Abundance and distribution of peach bark beetle in northern hardwood stands of New York. N. J. Appl. Forest 29, 128–132.

Hanks, L.M., 1999. Influence of the larval host plant on reproductive strategies of cerambycid beetles. Annu. Rev. Entomol. 44, 483–505.

Hansen, V., 1956. Biller. XVIII Barkbiller. Danmarks Fauna bind 62, G. E. C. Gads Forlag, Copenhagen.

Hanula, J.L., Mayfield, A.E., Fraedrich, S.W., Rabaglia, R.J., 2008. Biology and host associations of redbay ambrosia beetle (Coleoptera: Curculionidae: Scolytinae), exotic vector of laurel wilt killing redbay trees in the southeastern United States. J. Econ. Entomol. 101, 1276–1286.

Happ, G.M., Happ, C.M., Barras, S.J., 1975. Bark beetle fungal symbioses III. Ultrastructure of conidiogenesis in a Sporothrix ectosymbiont of the southern pine beetle. Can. J. Bot, 53, 2702–2711.

Happ, G.M., Happ, C.M., Barras, S.J., 1976. Bark beetle fungal symbioses. II. Fine structure of a basidiomycetous ectosymbiont of the southern pine beetle. Can. J. Bot. 1049–1062.

Haran, J., Timmermans, M.J.T.N., Vogler, A.P., 2013. Mitogenome sequences stabilize the phylogenetics of weevils (Curculionoidea) and establish the monophyly of larval ectophagy. Mol. Phylogenet. Evol. 67, 156–166.

Harrington, T.C., 2005. Ecology and evolution of mycophagous bark beetles and their fungal partners. In: Vega, F.E., Blackwell, M. (Eds.), Insect-Fungal Associations: Ecology and Evolution. Oxford University Press, New York, pp. 257–295.

Harris, T.W., 1852. A Treatise on some of the Insects of New England which are Injurious to Vegetation, Second ed. White & Potter, Boston.

Harris, J.A., Campbell, K.G., Wright, G.M., 1976. Ecological studies on the horizontal borer *Austroplatypus incompertus* (Schedl) (Coleoptera: Platypodidae). J. Entomol. Soc. Aust. (N. S. W.) 9, 11–21.

Hedlin, A.F., Ruth, D.S., 1970. A Douglas-fir twig mining beetle, *Pityophthorus orarius* (Coleoptera: Scolytidae). Can. Entomol. 102, 105–108.

Hedlin, A.F., Yates, H.O., Tovar, D.C., Ebel, B.H., Koerber, T.W., Merkel, E.P., 1980. Cone and seed insects of North American conifers. Environment Canada, Canadian Forest Service, Ottawa.

Heidenreich, E., 1960. Primärbefall durch *Xylosandrus germanus* an Jungeichen. Anz. Schädlingskd. 23, 5–10.

Herfs, A., 1950. Studien an dem Steinnußborkenkäfer, *Coccotrypes tanganus* Eggers. Höfchen-Briefe für Wissenschaft und Praxis 3, 3–31.

Herfs, A., 1959. Über den Steinnußborkenkäfer *Coccotrypes dactyliperda* F. Anz. Schädlingskd. 32, 1–4.

Hinton, H.E., 1981. Biology of Insect Eggs, Vol. 1, Pergamon Press, New York.

Hofstetter, R.W., Moser, J.C., 2014. The role of mites in insect-fungus associations. Annu. Rev. Entomol. 59, 537–557.

Hofstetter, R.W., Cronin, J.T., Klepzig, K.D., Moser, J.C., Ayres, M.P., 2006. Antagonisms, mutualisms and commensalisms affect outbreak dynamics of the southern pine beetle. Oecologia 147, 679–691.

Hölldobler, B., Wilson, E.O., 1990. The Ants. The Belknap Press of Harvard University Press, Cambridge.

Hölldobler, B., Wilson, E.O., 2009. The Superorganism: The Beauty, Elegance, and Strangeness of Insect Societies. W. W. Norton & Company, Inc., New York.

Holzman, J., Bohonak, A., Kirkendall, L., Gottlieb, D., Harari, A., Kelley, S., 2009. Inbreeding variability and population structure in the invasive haplodiploid palm-seed borer (*Coccotrypes dactyliperda*). J. Evol. Biol. 22, 1076–1087.

Hopkins, A.D., 1904. Insects injurious to hardwood forests. U.S. Department of Agriculture, Yearbook for 1903, 313–328.

Hopkins, A.D., 1908. Notable depredations by forest insects. U.S. Department of Agriculture, Yearbook for 1907, 149–164.

Hopkins, A.D., 1909. Contributions toward a monograph of the scolytid beetles. I. The genus *Dendroctonus, 17 U.S. Department of Agriculture, Bureau of Entomology, Technical Bulletin* 1–164.

Hopping, G.R., 1964. The breeding evidence indicating two genetic types of females of *Ips tridens*. Can. Entomol. 96, 117–118.

Hosking, G.B., 1972. *Xyleborus saxeseni*, its life-history and flight behaviour in New Zealand. N. Z. J. For. Sci. 3, 37–53.

Hosokawa, T., Koga, R., Kikuchi, Y., Meng, X.-Y., Fukatsu, T., 2010. *Wolbachia* as a bacteriocyte-associated nutritional mutualist. Proc. Natl. Acad. Sci. U. S. A. 107, 769–774.

Howard, T.M., 1973. Accelerated tree death in mature *Nothofagus cunninghamii* Oerst forests in Tasmania. Victorian Natur. 90, 343–345.

Howard, R.W., Blomquist, G.J., 2005. Ecological, behavioral, and biochemical aspects of insect hydrocarbons. Annu. Rev. Entomol. 50, 371–393.

Hubbard, H.G., 1897. The ambrosia beetles of the United States. In: Howard, L.O. (Ed.), Some Miscellaneous Results of the Work of the Division of Entomology, pp. 9–13, U.S. Dept. of Agriculture Bureau of Entomology Bull. No. 7.

Hulcr, J., Cognato, A., 2010. Repeated evolution of theft in fungus farming ambrosia beetles. Evolution 64, 3205–3211.

Hulcr, J., Dunn, R.R., 2011. The sudden emergence of pathogenicity in insect-fungus symbioses threatens naive forest ecosystems. Proc. R. Soc. B 278, 2866–2873.

Hulcr, J., Mogia, M., Isua, B., Novotny, V., 2007. Host specificity of ambrosia and bark beetles (Col., Curculionidae: Scolytinae and Platypodinae) in a New Guinea rainforest. Ecol. Entomol. 32, 762–772.

Hulcr, J., Beaver, R.A., Puranasakul, W., Dole, S.A., Sonthichai, S., 2008a. A comparison of bark and ambrosia beetle communities in two forest types in northern Thailand (Coleoptera: Curculionidae: Scolytinae and Platypodinae). Environ. Entomol. 37, 1461–1470.

Hulcr, J., Novotny, V., Maurer, B.A., Cognato, A.I., 2008b. Low beta diversity of ambrosia beetles (Coleoptera: Curculionidae: Scolytinae and Platypodinae) in lowland rainforests of Papua New Guinea. Oikos 117, 214–222.

Hunt, J.H., Baker, I., Baker, H.G., 1982. Similarity of amino-acids in nectar and larval saliva—the nutritional basis for trophallaxis in social wasps. Evolution 36, 1318–1322.

Husson, R., 1955. Sur la biologie du Coléoptère xylophage *Platypus cylindrus* Fabr. Annales Univeristatis Saraviensis—Scientia 4, 348–356.

Ishay, J., Ikan, R., 1968. Food exchange between adults and larvae in *Vespa orientalis* F. Anim. Behav. 16, 298–303.

Janin, J.L., Lieutier, F., 1988. Early mating in the life-cycle of *Tomicus piniperda* L. (Coleoptera, Scolytidae) in the forest of Orleans (France). Agronomie 8, 169–172.

Janzen, D.H., 1971. Seed predation by animals. Annu. Rev. Ecol. Syst. 2, 465–492.

Janzen, D.H., 1972. Association of a rainforest palm and seed-eating beetles in Puerto Rico. Ecology 53, 258–261.

Jaramillo, J., Borgemeister, C., Baker, P., 2006. Coffee berry borer *Hypothenemus hampei* (Coleoptera: Curculionidae): searching for sustainable control strategies. Bull. Entomol. Res. 96, 223–233.

Jaramillo, J.L., Ospina, C.M., Gil, Z.N., Montoya, E.C., Benavides, P., 2011. Advances on the biology of *Corthylus zulmae* (Coleoptera: Curculionidae) in *Alnus acuminata* (Betulaceae). Revista Colombiana de Entomología 37, 48–55.

Jones, V.P., 1992. Effect of harvest interval and cultivar on damage to macadamia nuts caused by *Hypothenemus obscurus*. J. Econ. Entomol. 85, 1878–1883.

Jordal, B.H., 1998. New species of *Scolytodes* (Coleoptera: Scolytidae) from Costa Rica and Panama. Rev. Biol. Trop. 46, 407–419.

Jordal, B.H., 2001. The origin and radiation of sib-mating haplodiploid beetles (Coleoptera, Curculionidae, Scolytinae), PhD thesis, University of Bergen.

Jordal, B.H., 2006. Community structure and reproductive biology of bark beetles (Coleoptera: Scolytinae) associated with Macaronesian *Euphorbia* shrubs. Eur. J. Entomol. 103, 71–80.

Jordal, B.H., 2013. Deep phylogenetic divergence between *Scolytoplatypus* and *Remansus*, a new genus of Scolytoplatypodini from Madagascar (Coleoptera, Curculionidae, Scolytinae). ZooKeys 9–33.

Jordal, B.H., 2014a. Cossoninae. In: Leschen, R.A.B., Beutel, R. (Eds.), Handbook of Zoology, Band IV Arthropoda: Insecta. Part 38: Coleoptera, Beetles, Vol. 3. de Gruyter, Berlin, pp. 345–349.

Jordal, B.H., 2014b. Platypodinae. In: Leschen, R.A.B., Beutel, R. (Eds.), Handbook of Zoology, Band IV Arthropoda: Insecta. Part 38: Coleoptera, Beetles, Vol. 3. de Gruyter, Berlin, pp. 358–364.

Jordal, B.H., 2014c. Scolytinae. In: Leschen, R.A.B., Beutel, R. (Eds.), Handbook of Zoology, Band IV Arthropoda: Insecta. Part 38: Coleoptera, Beetles, Vol. 3. de Gruyter, Berlin, pp. 349–358.

Jordal, B., Cognato, A., 2012. Molecular phylogeny of bark and ambrosia beetles reveals multiple origins of fungus farming during periods of global warming. BMC Evol. Biol. 12, 133.

Jordal, B.H., Kambestad, M., 2014. DNA barcoding of bark and ambrosia beetles reveals excessive NUMTs and consistent east-west divergence across Palearctic forests. Mol. Ecol. Resour. 14, 7–17.

Jordal, B.H., Kirkendall, L.R., 1998. Ecological relationships of a guild of tropical beetles breeding in *Cecropia* petioles in Costa Rica. J. Trop. Ecol. 14, 153–176.

Jordal, B.H., Normark, B.B., Farrell, B.D., 2000. Evolutionary radiation of an inbreeding haplodiploid beetle lineage (Curculionidae, Scolytinae). Biol. J. Linn. Soc. 71, 483–499.

Jordal, B.H., Beaver, R.A., Kirkendall, L.R., 2001. Breaking taboos in the tropics: incest promotes colonization by wood-boring beetles. Glob. Ecol. Biogeogr. 10, 345–357.

Jordal, B.H., Beaver, R.A., Normark, B.B., Farrell, B.D., 2002. Extraordinary sex ratios and the evolution of male neoteny in sib-mating *Ozopemon* beetles. Biol. J. Linn. Soc. 75, 353–360.

Jordal, B.H., Emerson, B.C., Hewitt, G.M., 2006. Apparent "sympatric" speciation in ecologically similar herbivorous beetles facilitated by multiple colonizations of an island. Mol. Ecol. 15, 2935–2947.

Jordal, B., Gillespie, J.J., Cognato, A.I., 2008. Secondary structure alignment and direct optimization of 28S rDNA sequences provide limited phylogenetic resolution in bark and ambrosia beetles (Curculionidae: Scolytinae). Zool. Scr. 37, 43–56.

Jordal, B.H., Sequeira, A.S., Cognato, A.I., 2011. The age and phylogeny of wood boring weevils and the origin of subsociality. Mol. Phylogenet. Evol. 59, 708–724.

Jover, H., 1952. Note préliminaire su la biologie des Platypodidae de basse Côte d'Ivoire. Revue de pathologie végétale et d'entomologie agricole de France 31, 73–81.

Kajimura, H., Hijii, N., 1994. Reproduction and resource utilization of the ambrosia beetle, *Xylosandrus mutilatus,* in field and experimental populations. Entomol. Exp. Appl. 71, 121–132.

Kalshoven, L.G.E., 1925. Primaire aantasting van houtige gewassen door *Xyleborus*-soorten. *Overdruk uilhet Verslag van de resde Vergadering van de Vereeniging van Proefstation-personeel Gehouden te Djocja*, 7 Oct 1925, 1–14.

Kalshoven, L.G.E., 1958. Studies on the biology of Indonesian Scolytoidea I. Tijdschr. Entomol. 101, 157–184.

Kalshoven, L.G.E., 1959. Studies on the biology of Indonesian Scolytoidea II. Tijdschr. Entomol. 102, 135–173.

Kalshoven, L.G.E., 1960a. A form of commensalism occurring in *Xyleborus* species? Entomologische Berichten 20, 118–120.

Kalshoven, L.G.E., 1960b. Studies on the biology of Indonesian Platypodidae. Tijdschr. Entomol. 103, 31–53.

Kalshoven, L.G.E., 1962. Note on the habits of *Xyleborus destruens* Bldf., the near-primary borer of teak trees on Java. Entomologische Berichten 22, 7–18.

Kamata, N., Esaki, K., Kato, K., Igeta, Y., Wada, K., 2002. Potential impact of global warming on deciduous oak dieback caused by ambrosia fungus *Raffaelea* sp. carried by ambrosia beetle *Platypus quercivorus* (Coleoptera: Platypodidae) in Japan. Bull. Entomol. Res. 92, 119–126.

Kaneko, T., Tamaki, Y., Takagi, K., 1965. Preliminary report on the biology of some Scolytid beetles, the tea root borer, *Xyleborus germanus* Blanford, attacking tea roots, and the tea stem borer, *Xyleborus compactus* Eichhoff, attacking tea twigs. Japanese Journal of Applied Entomology and Zoology 9, 23–28.

Kausrud, K.L., Grégoire, J.-C., Skarpaas, O., Erbilgin, N., Gilbert, M., Økland, B., Stenseth, N.C., 2011. Trees wanted dead or alive! Host selection and population dynamics in tree-killing bark beetles. PLoS One 6, e18274.

Kausrud, K., Okland, B., Skarpaas, O., Grégoire, J.C., Erbilgin, N., Stenseth, N.C., 2012. Population dynamics in changing environments: the case of an eruptive forest pest species. Biol. Rev. 87, 34–51.

Kawasaki, Y., Ito, M., Miura, K., Kajimura, H., 2010. Superinfection of five *Wolbachia* in the alnus ambrosia beetle, *Xylosandrus germanus* (Coleoptera: Curculionidae). Bull. Entomol. Res. 100, 231–239.

Keen, F.P., 1958. Cone and Seed Insects of Western Forest Trees. U.S. Department of Agriculture, Technical Bulletin no. 1169, Washington, DC.

Kegley, S.J., Furniss, M.M., Grégoire, J.-C., 1997. Electrophoretic comparison of *Dendroctonus punctatus* LeConte and *D. micans* (Kugelann) (Coleoptera: Scolytidae). Pan-Pac. Entomol. 73, 40–45.

Kemner, N.A., 1916. Några nya eller mindre kända skadedjur på fruktträd. *Medd. nr. 133 från Centralanstalten för Försöksväsendet på Jordbruksområdet, Entomol. avd. nr. 25*, 21 pp.

Kent, D., 2002. Biology of the ambrosia beetle *Austroplatypus incompertus Aust.* J. Entomol. 41, 378.

Kent, D.S., Simpson, J.A., 1992. Eusociality in the beetle *Austroplatypus incompertus* (Coleoptera: Platypodidae). Naturwissenschaften 79, 86–87.

Kingsolver, J.G., Norris, D.M., 1977a. The interaction of the female ambrosia beetle, *Xyleborus ferrugineus* (Coleoptera: Scolytidae), with her eggs in relation to the morphology of the gallery system. Entomol. Exp. Appl. 21, 9–13.

Kingsolver, J.G., Norris, D.M., 1977b. The interaction of *Xyleborus ferrugineus* (Fabr.) (Coleoptera: Scolytidae) behavior and initial reproduction in relation to its symbiotic fungi. Ann. Entomol. Soc. Am. 70, 1–4.

Kirejtshuk, A.G., Azar, D., Beaver, R.A., Mandelshtam, M.Y., Nel, A., 2009. The most ancient bark beetle known: a new tribe, genus and species from Lebanese amber (Coleoptera, Curculionidae, Scolytinae). Syst. Entomol. 34, 101–112.

Kirisits, T., 2004. Fungal associates of European bark beetles with special emphasis on the ophiostomatoid fungi. In: Lieutier, F., Keith, R.D., Battisti, A., Grégoire, J.-C., Evans, H.F. (Eds.), Bark and Wood Boring Insects in Living Trees in Europe, a Synthesis. Springer, Dordrecht, pp. 181–237.

Kirkendall, L.R., 1983. The evolution of mating systems in bark and ambrosia beetles (Coleoptera: Scolytidae and Platypodidae). Zool. J. Linn. Soc. 77, 293–352.

Kirkendall, L.R., 1984. Notes on the breeding biology of some bigynous and monogynous Mexican bark beetles (Scolytidae: *Scolytus*, *Thysanoes*, *Phloeotribus*) and records for associated Scolytidae (*Hylocurus*, *Hypothenemus*, *Araptus*) and Platypodidae (*Platypus*). Z. angew. Entomol. 97, 234–244.

Kirkendall, L.R., 1989. Within-harem competition among *Ips* females, an overlooked component of density-dependent larval mortality. Holarctic Ecol. 12, 477–487.

Kirkendall, L.R., 1990. Sperm is a limiting resource in the pseudogamous bark beetle *Ips acuminatus* (Scolytidae). Oikos 57, 80–87.

Kirkendall, L.R., 1993. Ecology and evolution of biased sex ratios in bark and ambrosia beetles. In: Wrensch, D.L., Ebbert, M.A. (Eds.), Evolution and Diversity of Sex Ratio in Insects and Mites. Chapman & Hall, New York, pp. 235–345.

Kirkendall, L., 2006. A new host-specific, *Xyleborus vochysiae* (Curculionidae: Scolytinae), from Central America breeding in live trees. Ann. Entomol. Soc. Am. 99, 211–217.

Kirkendall, L., Ødegaard, F., 2007. Ongoing invasions of old-growth tropical forests: establishment of three incestuous beetle species in southern Central America (Curculionidae: Scolytinae). Zootaxa. 53–62.

Kirkendall, L.R., Stenseth, N.C., 1990. Ecological and evolutionary stability of sperm-dependent parthenogenesis: effects of partial niche overlap between sexual and asexual females. Evolution 44, 698–714.

Kirkendall, L.R., Kent, D.S., Raffa, K.F., 1997. Interactions among males, females and offspring in bark and ambrosia beetles: the significance of living in tunnels for the evolution of social behavior. In: Choe, J.C., Crespi, B.J. (Eds.), The Evolution of Social Behavior in Insects and Arachnids. Cambridge University Press, Cambridge, pp. 181–215.

Kirkendall, L.R., Faccoli, M., Ye, H., 2008. Description of the Yunnan shoot borer, *Tomicus yunnanensis* Kirkendall & Faccoli sp n. (Curculionidae, Scolytinae), an unusually aggressive pine shoot beetle from southern China, with a key to the species of *Tomicus*. Zootaxa 1819, 25–39.

Klein, W.H., Parker, D.L., Jensen, C.E., 1978. Attack, emergence, and stand depletion trends of mountain pine beetle in a lodgepole pine stand during an outbreak. Environ. Entomol. 7, 732–737.

Kleine, R., 1931. Die Biologie der Brenthidae. Entomologische Rundschau 48, 149–167, 189–193.

Knee, W., Forbes, M.R., Beaulieu, F., 2013. Diversity and host use of mites (Acari: Mesostigmata, Oribatida) phoretic on bark beetles (Coleoptera: Scolytinae): global generalists, local specialists? Ann. Entomol. Soc. Am. 106, 339–350.

Knížek, M., 2010. Five new species of *Triotemnus* (Coleoptera, Curculionidae, Scolytinae) from Morocco and Yemen. ZooKeys 191–206.

Kobayashi, M., Ueda, A., 2002. Preliminary study of mate choice in *Platypus quercivorus* (Murayama) (Coleoptera: Platypodidae). Appl. Entomol. Zool. 37, 451–457.

Koch, R., 1909. Das Larvenleben des Riesenbastkäfers *Hylesinus (Dendroctonus) micans*. Naturwissenschaftliche Zeitschrift für Land- und Forstwirtschaft 7, 319–340.

Koehler, C.S., Gyrisco, G.G., Newsom, L.D., Schwardt, H.H., 1961. Biology and control of the clover root borer, *Hylastinus obscurus* (Marsham). Memoirs of the Cornell University Agricultural Experiment Station 376, 1–36.

Kolarik, M., Kirkendall, L.R., 2010. Evidence for a new lineage of primary ambrosia fungi in *Geosmithia* Pitt (Ascomycota: Hypocreales). Fungal Biol. 114, 676–689.

Korb, J., Heinze, J., 2008. Ecology of Social Evolution. Springer, Berlin.

Kramer, P., Kozlowsky, T.T., 1979. Physiology of Woody Plants. Academic Press, New York.

Kramer, A.M., Dennis, B., Liebhold, A.M., Drake, J.M., 2009. The evidence for Allee effects. Popul. Ecol. 51, 341–354.

Kühnholz, S., Borden, J.H., Uzunovic, A., 2001. Secondary ambrosia beetles in apparently healthy trees: adaptations, potential causes and suggested research. Integrated Pest. Manag. Rev. 6, 209–219.

Kuschel, G., 1966. A cossonine genus with bark-beetle habits with remarks on relationships and biogeography. N. Z. J. Sci. 9, 3–29.

Lachat, T., Nagel, P., Cakpo, Y., Attignon, S., Goergen, G., Sinsin, B., Peveling, R., 2006. Dead wood and saproxylic beetle assemblages in a semi-deciduous forest in southern Benin. Forest Ecol. Manage. 225, 27–38.

Lachat, T., Wermelinger, B., Gossner, M.M., Bussler, H., Isacsson, G., Müller, J., 2012. Saproxylic beetles as indicator species for dead-wood amount and temperature in European beech forests. Ecol. Indic. 23, 323–331.

Lake Maner, M., Hanula, J.L., Kristine Braman, S., 2013. Rearing redbay ambrosia beetle, *Xyleborus glabratus* (Coleoptera: Curculionidae: Scolytinae), on semi-artificial media. Fla. Entomol. 96, 1042–1051.

Langor, D.W., 1987. Flight muscle changes in the eastern larch beetle, *Dendroctonus simplex* LeConte. Coleopterists Bulletin 41, 351–357.

Långström, B., 1983. Life cycle and shoot feeding of the pine shoot beetles. Stud. For. Suec. 163, 1–29.

Långström, B., Hellqvist, C., 1993. Induced and spontaneous attacks by pine shoot beetles on young Scots pine trees—tree mortality and beetle performance. J. Appl. Entomol. 115, 25–36.

Lanier, G.N., Kirkendall, L.R., 1986. Karyology of pseudogamous *Ips* bark beetles. Hereditas 105, 87–96.

Lanier, G.N., Oliver Jr., J.H., 1966. “Sex-ratio” condition: unusual mechanisms in bark beetles. Science 150, 208–209.

Latty, T.M., Magrath, M.J.L., Symonds, M.R.E., 2009. Harem size and oviposition behaviour in a polygynous bark beetle. Ecol. Entomol. 34, 562–568.

Lawko, C.M., Dyer, E.D.A., 1974. Flight ability of spruce beetles emerging after attacking frontalin-baited trees. Canada Department of the Environment, Canadian Forestry Service, Bi-monthly Research Note 30, 17.

Lekander, B., 1962. Die Borkenkäerlarven, ein vernachlässigter Teil der Forstentomologie. Dtsch. Entomol. Z. 9, 428–432.

Lekander, B., 1963. *Xyleborus cryptographus* Ratzb. (Col. Ipidae), Ein Beitrag zur Kenntnis seiner Verbreitung und Biologie. Entomologisk Tidskrift 84, 96–109.

Lekander, B., 1968a. Scandinavian bark beetle larvae. Department of Forest Zoology, Stockholm.

Lekander, B., 1968b. The number of larval instars in some bark beetle species. Entomologisk Tidskrift 89, 25–34.

Lengerken, H., 1939. Die Brutfürsorge- und Brutpflegeinstinkte der Käfer. Akademische Verlagsgesellschaft m.b.H, Leipzig.

LePelley, R.H., 1968. Pests of Coffee. Longmans, Green and Co., London.

Lewis, E.E., Cane, J.H., 1992. Inefficacy of courtship stridulation as a premating ethological barrier for *Ips* bark beetles (Coleoptera: Scolytidae). Ann. Entomol. Soc. Am. 85, 517–524.

Lieutier, F., Ye, H., Yart, A., 2003. Shoot damage by *Tomicus* sp (Coleoptera: Scolytidae) and effect on *Pinus yunnanensis* resistance to subsequent reproductive attacks in the stem. Agr. Forest Entomol. 5, 227–233.

Lieutier, F., Day, K.R., Battisti, A., Grégoire, J.-C., Evans, H.F. (Eds.), 2004. Bark and Wood Boring Insects in Living Trees in Europe, a Synthesis. Kluwer Academic Publishers, Dordrecht.

Lindgren, B.S., Raffa, K.F., 2013. Evolution of tree killing in bark beetles (Coleoptera: Curculionidae): trade-offs between the maddening crowds and a sticky situation. Can. Entomol. 145, 471–495.

Linnaeus, C., 1758. *Systema Naturae per Regna Tria Naturae: Secundum Classes, Ordines, Genera, Species, Cum Characteribus, Differentiis, Synonymis, Locis* (10th ed.) (in Latin). Laurentius Salvius, Stockholm.

Lissemore, F.M., 1997. Frass clearing by male pine engraver beetles (*Ips pini*; Scolytidae): paternal care or paternity assurance? Behav. Ecol. 8, 318–325.

López, S., Quero, C., Iturrondobeitia, J.C., Guerrero, A., Goldarazena, A., 2013. Electrophysiological and behavioural responses of Pityophthorus pubescens (Coleoptera: Scolytinae) to (E, E)-α-farnesene, (R)-(+)-limonene and (S)-(−)-verbenone in Pinus radiata (Pinaceae) stands in northern Spain. Pest Manage. Sci. 69, 40–47.

López-Guillén, G., Carrasco, J.V., Cruz-López, L., Barrera, J.F., Malo, E.A., Rojas, J.C., 2011. Morphology and structural changes in flight muscles of *Hypothenemus hampei* (Coleoptera: Curculionidae) females. Environ. Entomol. 40, 441–448.

Lövendal, E.A., 1898. De danske barkbiller (Scolytidæ et Platypodidæ danicæ) og deres betydning for skov- og havebruget. Det Schubotheske Forlag, J.L, Lybecker og E.A. Hirschsprung, Copenhagen.

Løyning, M.K., 2000. Reproductive performance of clonal and sexual bark beetles (Coleoptera: Scolytidae) in the field. J. Evol. Biol. 13, 743–748.

Løyning, M., Kirkendall, L., 1996. Mate discrimination in a pseudogamous bark beetle (Coleoptera: Scolytidae): male *Ips acuminatus* prefer sexual to clonal females. Oikos 77, 336–344.

Løyning, M.K., Kirkendall, L.R., 1999. Notes on the mating system of *Hylesinus varius* (F.) (Col., Scolytidae), a putatively bigynous bark beetle. J. Appl. Entomol. 123, 77–82.

Lyal, C.H.C., King, T., 1996. Elytro-tergal stridulation in weevils (Insecta: Coleoptera: Curculionoidea). J. Nat. Hist. 30, 703–773.

Lyons, L.A., 1956. Insects affecting seed production in red pine: Part I *Conophthorus resinosae* Hopk. (Coleoptera: Scolytidae). Can. Entomol. 88, 599–608.

Majka, C.G., Anderson, R.S., McCorquodale, D.B., 2007. The weevils (Coleoptera: Curculionoidea) of the Maritime Provinces of Canada, II: New records from Nova Scotia and Prince Edward Island and regional zoogeography. Can. Entomol. 139, 397–442.

Mandelshtam, M.Y., 2001. New synonymy and new records in Palaearctic Scolytidae (Coleoptera). Zoosystematica Rossica 9, 203–204.

Maroja, L.S., Bogdanowicz, S.M., Wallin, K.F., Raffa, K.F., Harrison, R. G., 2007. Phylogeography of spruce beetles (*Dendroctonus rufipennis* Kirby) (Curculionidae: Scolytinae) in North America. Mol. Ecol. 16, 2560–2573.

Mattson, W.J., 1980. Cone resources and the ecology of the red pine cone beetle, *Conophthorus resinosae* (Coleoptera, Scolytidae). Ann. Entomol. Soc. Am. 73, 390–396.

McGehey, J.H., 1968. Territorial behaviour of bark-beetle males. Can. Entomol. 100, 1153.

McKenna, D.D., 2011. Towards a temporal framework for “inordinate fondness”: Reconstructing the macroevolutionary history of beetles (Coleoptera). Entomologica Americana 117, 28–36.

McKenna, D.D., Sequeira, A.S., Marvaldi, A.E., Farrell, B.D., 2009. Temporal lags and overlap in the diversification of weevils and flowering plants. Proc. Natl. Acad. Sci. U. S. A. 106, 7083–7088.

McKnight, M.E., Aarhus, D.G., 1973. Bark beetles, *Leperisinus californicus* and *L. criddlei* (Coleoptera: Scolytidae), attacking green ash in North Dakota. Ann. Entomol. Soc. Am. 66, 955–957.

McManus, M.L., Giese, R.L., 1968. Columbian timber beetle *Corthylus columbianus. VII. Effect of climatic integrants on historic density fluctuations*. For. Sci. 14, 242–253.

McMullen, L.H., Atkins, M.D., 1962. The life history and habits of *Scolytus unispinosus* Leconte (Coleoptera: Scolytidae) in the interior of British Columbia. Can. Entomol. 94, 17–25.

McNee, W.R., Wood, D.L., Storer, A.J., 2000. Pre-emergence feeding in bark beetles (Coleoptera: Scolytidae). Environ. Entomol. 29, 495–501.

McPherson, J.E., Stehr, F.W., Wilson, L.F., 1970. A comparison between *Conophthorus* shoot-infesting beetles and *Conophthorus resinosae* (Coleoptera: Scolytidae). 1. Comparative life history studies in Michigan. Can. Entomol. 102, 1008–1015.

Mecke, R., Galileo, M.H.M., 2004. A review of the weevil fauna (Coleoptera, Curculionoidea) of *Araucaria angustifolia* (Bert.) O. Kuntze (Araucariaceae) in South Brazil. Revista Brasileira de Zoologia 21, 505–513.

Meirmans, S., Skorping, A., Løyning, M.K., Kirkendall, L.R., 2006. On the track of the Red Queen: bark beetles, their nematodes, local climate and geographic parthenogenesis. J. Evol. Biol. 19, 1939–1947.

Melnikova, N.I., 1964. Biological significance of the air holes in egg tunnels of *Scolytus ratzeburgi* Jans. (Coleoptera, Ipidae). Entomol. Rev. 43, 16–23.

Menard, K.L., Cognato, A.I., 2007. Mitochondrial haplotypic diversity of pine cone beetles (Scolytinae: *Conophthorus*) collected on food sources. Environ. Entomol. 36, 962–966.

Mendel, Z., 1983. Seasonal history of *Orthotomicus erosus* (Coleoptera: Scolytidae) in Israel. Phytoparasitica 11, 13–24.

Merriam, C.H., 1883. Ravages of a rare scolytid beetle in the sugar maples of northeastern New York. Am. Nat. 17, 84–86.

Meurisse, N., Couillien, D., Grégoire, J.-C., 2008. Kairomone traps: a tool for monitoring the invasive spruce bark beetle *Dendroctonus micans* (Coleoptera: Scolytinae) and its specific predator, *Rhizophagus grandis* (Coleoptera: Monotomidae). J. Appl. Entomol. 45, 537–548.

Miller, J.M., 1915. Cone beetles: Injury to sugar pine and western yellow pine. U.S. Department of Agriculture Bulletin 243, 1–12.

Milne, D.H., Giese, R.L., 1969. Biology of the Columbian timber beetle, *Corthylus columbianus* (Coleoptera: Scolytidae). IX. Population biology and gallery characteristics. Entomol. News 80, 225–237.

Milne, D.H., Giese, R.L., 1970. Biology of the Columbian timber beetle, *Corthylus columbianus* (Coleoptera: Scolytidae). X. Comparison of yearly mortality and dispersal losses with population densities. Entomol. News 81, 12–24.

Mitchell, A., Maddox, C., 2010. Bark beetles (Coleoptera: Curculionidae: Scolytinae) of importance to the Australian macadamia industry: an integrative taxonomic approach to species diagnostics. Aust. J. Entomol. 49, 104–113.

Mitton, J.B., Sturgeon, K.B., 1982. Biotic interactions and evolutionary change. In: Mitton, J.B., Sturgeon, K.B. (Eds.), Bark Beetles in North American Conifers. A System for the Study of Evolutionary Biology. University of Texas Press, Austin, pp. 3–20.

Mizuno, T., Kajimura, H., 2002. Reproduction of the ambrosia beetle, *Xyleborus pfeili* (Ratzeburg) (Col., Scolytidae), on semi-artificial diet. J. Appl. Entomol. 126, 455–462.

Morales-Jiménez, J., Vera-Ponce de León, A., García-Domínguez, A., Martínez-Romero, E., Zúñiga, G., Hernández-Rodríguez, C., 2013. Nitrogen-fixing and uricolytic bacteria associated with the gut of *Dendroctonus rhizophagus* and *Dendroctonus valens* (Curculionidae: Scolytinae). Microb. Ecol. 66, 200–210.

Morgan, F.D., 1967. *Ips grandicollis* in South Australia. Aust. For. 31, 137–155.

Morgan, C., 1998. The assessment of potential attractants to beetle pests: improvements to laboratory pitfall bioassay methods. J. Stored Prod. Res. 34, 59–74.

Morgan, F.D., Mailu, M., 1976. Behavior and generation dynamics of the white pine cone beetle *Conophthorus coniperda* (Schwarz) in central Wisconsin. Ann. Entomol. Soc. Am. 69, 863–871.

Mueller, U.G., Gerardo, N.M., Aanen, D.K., Six, D.L., Schultz, T.R., 2005. The evolution of agriculture in insects. Annu. Rev. Ecol. Evol. Syst. 36, 563–595.

Nakashima, T., 1971. Notes on the associated fungi and the mycetangia of the ambrosia beetle, *Crossotarsus niponicus*. Appl. Entomol. Zool. 6, 131–137.

Nobuchi, A., 1969. A comparative morphological study of the proventriculus in the adult of the superfamily Scolytoidea (Coleoptera). Bull. Gov. For. Exp. Stn. (Jpn.) 224, 39–110.

Nobuchi, A., 1972. The biology of Japanese Scolytidae and Platypodidae (Coleoptera). Rev. Plant Prot. Res. 5, 61–75.

Noguera-Martínez, F.A., Atkinson, T.H., 1990. Biogeography and biology of bark and ambrosia beetles (Coleoptera: Scolytidae and Platypodidae) of a mesic montane forest in Mexico, with an annotated checklist of species. Ann. Entomol. Soc. Am. 83, 453–466.

Nord, J.C., 1972. Biology of the Columbian timber beetle, *Corthylus columbianus* (Coleoptera: Scolytidae). Ann. Entomol. Soc. Am. 65, 350–358.

Normark, B.B., 2004. Haplodiploidy as an outcome of coevolution between male-killing cytoplasmatic elements and their hosts. Evolution 58, 790–798.

Normark, B.B., Kirkendall, L.R., 2009. Parthenogenesis in insects and mites. In: Resh, V.H., Cardé, R.T. (Eds.), Encyclopedia of Insects, Second Edition. Academic Press, Amsterdam, pp. 753–757.

Normark, B.B., Jordal, B.H., Farrell, B.D., 1999. Origin of a haplodiploid beetle lineage. Proc. R. Soc. B 266, 2253–2259.

Norris, D.M., Chu, H.M., 1980. Symbiote-dependent arrhenotokous parthenogenesis in the eukaryote *Xyleborus*. In: Schwemmler, W., Schenk, H.E.A. (Eds.), Endocytobiology: Endosymbiosis and Cell Biology. Walter de Gruyter & Co., Berlin, pp. 453–460.

Novotny, V., Miller, S.E., Hulcr, J., Drew, R.A.I., Basset, Y., Janda, M., et al., 2007. Low beta diversity of herbivorous insects in tropical forests. Nature 448, 692–698.

Novotny, V., Miller, S.E., Baje, L., Balagawi, S., Basset, Y., Cizek, L., et al., 2010. Guild-specific patterns of species richness and host specialization in plant-herbivore food webs from a tropical forest. J. Anim. Ecol. 79, 1193–1203.

Nunberg, M., 1963. Zur Systematik und Synonomie der Scolytoidea (Coleoptera). *Ann. Zool.* Warszawa 20, 357–361.

Nyland, B.C., 1995. Lowest lifetime fecundity. In: Walker, T.J. (Ed.), Insect Book of Records. Available online:http://entnemdept.ifas.ufl.edu/walker/ufbir/chapters/chapter_17.shtml, Last accessed: June 27, 2015.

Ødegaard, F., 2000. The relative importance of trees versus lianas as hosts for phytophagous beetles (Coleoptera) in tropical forests. J. Biogeogr. 27, 283–296.

Ødegaard, F., 2004. Species richness of phytophagous beetles in the tropical tree *Brosimum utile* (Moraceae): the effects of sampling strategy and the problem of tourists. Ecol. Entomol. 29, 76–88.

Ødegaard, F., 2006. Host specificity, alpha- and beta-diversity of phytophagous beetles in two tropical forests in Panama. Biodiv. Conserv. 15, 83–105.

Ødegaard, F., Diserud, O.H., Engen, S., Aagaard, K., 2000. The magnitude of local host specificity for phytophagous insects and its implications for estimates of global species richness. Conserv. Biol. 14, 1182–1186.

Ødegaard, F., Diserud, O.H., Østbye, K., 2005. The importance of plant relatedness for host utilization among phytophagous insects. Ecol. Lett. 8, 612–617.

Oester, P.T., Rudinsky, J.A., 1975. Sound production in Scolytidae: stridulation by “silent” *Ips* bark beetles. Z. angew. Entomol. 79, 421–427.

Oester, P.T., Rudinsky, J.A., 1979. Acoustic behavior of three sympatric species of *Ips* (Coleoptera-Scolytidae) co-inhabiting Sitka spruce. Z. angew. Entomol. 87, 398–412.

Oester, P.T., Rykar, L.C., Rudinsky, J.A., 1978. Complex male premating stridulation of the bark beetle *Hylurgops rugipennis* (Mann). Coleopterists Bulletin 32, 93–98.

Oester, P.T., Rudinsky, J.A., Ryker, L.C., 1981. Olfactory and acoustic behavior of *Pseudohylesinus nebulosus* (Coleoptera, Scolytidae) on Douglas-fir bark. Can. Entomol. 113, 645–650.

Ohmart, C.P., 1989. Why are there so few tree-killing bark beetles associated with angiosperms? Oikos 54, 242–245.

Ohya, E., Kinuura, H., 2001. Close range sound communications of the oak platypodid beetle *Platypus quercivorus* (Murayama) (Coleoptera: Platypodidae). Appl. Entomol. Zool. 36, 317–321.

Okello, S., Reichmuth, C., Schulz, F.A., 1996a. Observations on the biology and host specificity of *Pagiocerus frontalis* (Fabricius) (Coleoptera: Scolytidae) at 20 °C and 25 °C and 75% rh. Zeitschrift für Pflanzenkrankheiten und Pflanzenschutz 103, 377–382.

Okello, S., Reichmuth, C., Schulz, F.A., 1996b. Laboratory investigations on the developmental rate at low relative humidity and the developmental temperature limit of *Pagiocerus frontalis* (Fab) (Col, Scolytidae) at high and low temperatures. Anz. Schädlingskd. 69, 180–182.

Page, R.E., Willis, M.A., 1983. Sexual dimorphism in ventral abdominal setae in *Scolytus multistriatus* (Coleoptera: Scolytidae): possible role in courtship behavior. Ann. Entomol. Soc. Am. 76, 78–82.

Page, M., Nelson, L.J., Haverty, M.I., Blomquist, G.J., 1990a. Cuticular hydrocarbons as chemotaxonomic characters for bark beetles: *Dendroctonus ponderosae*, *D. jeffreyi*, *D. brevicomis*, and *D. frontalis* (Coleoptera: Scolytidae). Ann. Entomol. Soc. Am. 83, 892–902.

Page, M., Nelson, L.J., Haverty, M.I., Blomquist, G.J., 1990b. Cuticular hydrocarbons of eight species of North American cone beetles, *Conophthorus* Hopkins. J. Chem. Ecol. 16, 1173–1198.

Page, M., Nelson, L.J., Blomquist, G.J., Seybold, S.J., 1997. Cuticular hydrocarbons as chemotaxonomic characters of pine engraver beetles (*Ips* spp.) in the grandicollis subgeneric group. J. Chem. Ecol. 23, 1053–1099.

Paine, T.D. (Ed.), 2006. Invasive Forest Insects, Introduced Forest Trees, and Altered Ecosystems. Springer, Dordrecht.

Paine, T.D., Raffa, K.F., Harrington, T.C., 1997. Interactions among scolytid bark beetles, their associated fungi, and live conifers. Annu. Rev. Entomol. 42, 179–206.

Peer, K., Taborsky, M., 2005. Outbreeding depression, but no inbreeding depression in haplodiploid ambrosia beetles with regular sibling mating. Evolution 59, 317–323.

Peer, K., Taborsky, M., 2007. Delayed dispersal as a potential route to cooperative breeding in ambrosia beetles. Behav. Ecol. Sociobiol. 61, 729–739.

Peleg, B., Norris, D.M., 1973. Oocyte activation in *Xyleborus ferrugineus* by bacterial symbionts. J. Insect Physiol. 19, 137–145.

Petty, J.L., 1977. Bionomics of two aspen bark beetles, *Trypophloeus populi* and *Procryphalus mucronatus* (Coleoptera: Scolytidae). Western Great Basin Nat. 37, 105–127.

Pfeffer, A., 1955. Fauna CSR, Kurovci—Scolytoidea. Nakaldatelství CSAV, Praha.

Pfeffer, A., 1995. Zentral- und westpaläarktische Borken- und Kernkäfer (Coleoptera: Scolytidae, Platypodidae). Entomologica Brasiliensia 17, 5–310.

Ploetz, R.C., Hulcr, J., Wingfield, M.J., de Beer, Z.W., 2013. Destructive tree diseases that are associated with ambrosia and bark beetles: black swan events in tree pathology? Plant Dis. 97, 856–872.

Pope, D.N., Coulson, R.N., Fargo, W.S., Gagne, J.A., Kelly, C.W., 1980. The allocation process and between-tree survival probabilities in *Dendroctonus frontalis* infestations. Res. Popul. Ecol. 22, 197–210.

Postner, M., 1974. Scolytidae (=Ipidae), Borkenkäfer. In: Schwenke, W. (Ed.), Die Forstschädlinge Europas. Bind 2, Käfer. Paul Parey, Hamburg, pp. 334–482.

Pureswaran, D.S., Borden, J.H., 2003. Is bigger better? Size and pheromone production in the mountain pine beetle, *Dendroctonus ponderosae* Hopkins (Coleoptera: Scolytidae). J. Insect Behav. 16, 765–782.

Queller, D.C., Strassmann, J.E., 1998. Kin selection and social insects. BioScience 48, 165–175.

Rabinowitz, D., 1977. Effects of a mangrove borer, *Poecilips rhizophorae,* on propagules of *Rhizophora harrisonii* in Panamá. Fla. Entomol. 60, 129–134.

Raffa, K.F., Aukema, B.H., Bentz, B.J., Carroll, A.L., Hicke, J.A., Turner, M.G., Romme, W.H., 2008. Cross-scale drivers of natural disturbances prone to anthropogenic amplification: the dynamics of bark beetle eruptions. BioScience 58, 501–517.

Rappaport, N.G., Stein, J.D., del Rio Mora, A.A., Debarr, G.L., De Groot, P., Mori, S., 2000. Cone beetle (*Conophthorus* spp.) (Coleoptera: Scolytidae) responses to behavioral chemicals in field trials: a transcontinental perspective. Can. Entomol. 132, 925–937.

Ratzeburg, J.T.C., 1839. Die Forst-Insecten. Nicolaische Buchhandlung, Berlin.

Reid, R.W., 1958. Internal changes in the female mountain pine beetle, *Dendroctonus monticolae* Hopk., associated with egg laying and flight. Can. Entomol. 90, 464–468.

Reid, M.L., 1999. Monogamy in the bark beetle *Ips latidens:* ecological correlates of an unusual mating system. Ecol. Entomol. 24, 89–94.

Reid, M.L., Robb, T., 1999. Death of vigorous trees benefits bark beetles. Oecologia 120, 555–562.

Reid, M.L., Roitberg, B.D., 1994. Benefits of prolonged male residence with mates and brood in pine engravers (Coleoptera, Scolytidae). Oikos 70, 140–148.

Reid, M.L., Roitberg, B.D., 1995. Effects of body-size on investment in individual broods by male pine engravers *Can.* J. Zool. 73, 1396–1401.

Reitter, E., 1916. Fauna Germanica. V Band. Die Käfer des Deutschen Reiches, K. G. Lutz, Stuttgard.

Rexrode, C.O., 1982. Bionomics of the peach bark beetle *Phloeotribus liminaris* (Coleoptera: Scolytidae) in black cherry. J. Georgia Entomol. Soc. 17, 388–398.

Roberts, H., 1960. *Trachyostus ghanaensis* Schedl (Col., Platypodidae) an ambrosia beetle attacking Wawa, *Triplochiton scleroxylon* K. Schum. *West Afr. Timber Borer Res. Unit Tech.* Bull. No. 3, 1–17.

Roberts, H., 1962. A description of the developmental stages of T*rachyostus aterrimus* a West African Platypodina, and some remarks on its biology. Fifth Report West African Timber Borer Research Unit 1961–62, 29–46.

Roberts, H., 1968. Notes on biology of ambrosia beetles of genus *Trachyostus* Schedl (Coleoptera—Platypodidae) in West Africa. Bull. Entomol. Res. 58, 325–352.

Roberts, H., 1969. Forest insects of Nigeria with notes on their biology and distribution. Commonwealth Forestry Institute Paper 44, 1–206.

Roberts, H., 1976. Observations on the biology of some tropical rain forest Scolytidae (Coleoptera) from Fiji I. Subfamilies—Hylesininae, Ipinae (excluding Xyleborini). Bull. Entomol. Res. 66, 373–388.

Robertson, I.C., 1998a. Flight muscle changes in male pine engraver beetles during reproduction: the effects of body size, mating status and breeding failure. Physiol. Entomol. 23, 75–80.

Robertson, I.C., 1998b. Paternal care enhances male reproductive success in pine engraver beetles. Anim. Behav. 56, 595–602.

Robertson, I.C., 2000. Reproduction and developmental phenology of *Ips perturbatus* (Coleoptera: Scolytidae) inhabiting white spruce (Pinaceae). Can. Entomol. 132, 529–537.

Robertson, I.C., Roitberg, B.D., 1998. Duration of paternal care in pine engraver beetles: why do larger males care less? Behav. Ecol. Sociobiol. 43, 379–386.

Roeper, R.A., 1995. Patterns of mycetophagy in Michigan ambrosia beetles. Michigan Academian 27, 153–161.

Roeper, R.A., Treeful, L.M., Foote, R.A., Bunce, M.A., 1980a. *In vitro* culture of the ambrosia beetle *Xyleborus affinis* (Coleoptera: Scolytidae). Great Lakes Entomologist 13, 33–35.

Roeper, R., Treeful, L.M., O'Brien, K.M., Foote, R.A., Bunce, M.A., 1980b. Life history of the ambrosia beetle *Xyleborus affinis* (Coleoptera: Scolytidae) from *in vitro* culture. Great Lakes Entomologist 13, 141–144.

Roeper, R.A., Zestos, D.V., Palik, B.J., Kirkendall, L.R., 1987a. Distribution and host plants of *Corthylus punctatissimus* (Coleoptera: Scolytidae) in the lower peninsula of Michigan. Great Lakes Entomologist 20, 69–70.

Roeper, R.A., Palik, B.J., Zestos, D.V., Hesch, P.G., Larsen, C.D., 1987b. Observations of the habits of *Corthylus punctatissimus* (Coleoptera, Scolytidae) infesting maple saplings in Central Michigan. Great Lakes Entomologist 20, 173–176.

Rohlfs, M., 2005. Density-dependent insect–mold interactions: effects on fungal growth and spore production. Mycologia 97, 996–1001.

Rohlfs, M., Churchill, A.C.L., 2011. Fungal secondary metabolites as modulators of interactions with insects and other arthropods. Fungal Genet. Biol. 48, 23–34.

Ruckes Jr., H., 1963. Cone beetles of the genus *Conophthorus* in California (Coleoptera: Scolytidae). Pan-Pac. Entomol. 39, 43–50.

Rudinsky, J.A., 1969. Masking of the aggregating pheromone in *Dendroctonus pseudotsugae* Hopk. Science 166, 884–885.

Rudinsky, J.A., 1976. Various host–insect interrelations in host-finding and colonization behavior of bark beetles on coniferous trees. Symp. Biol. Hung. 16, 229–235.

Rudinsky, J.A., 1979. Chemoacoustically induced behavior of *Ips typographus* (Col, Scolytidae). Z. angew. Entomol. 88, 537–541.

Rudinsky, J.A., Michael, R.R., 1974. Sound production in Scolytidae: "rivalry" behaviour of male *Dendroctonus* beetles. J. Insect Physiol. 20, 1219–1230.

Rudinsky, J.A., Ryker, L.C., 1976. Sound production in Scolytidae—rivalry and premating stridulation of male Douglas-fir beetle. J. Insect Physiol. 22, 997–999.

Rudinsky, J.A., Vallo, V., 1979. The ash bark beetles *Leperisinus fraxini* and *Hylesinus oleiperda*: stridulatory organs, acoustic signals, and pheromone production. Z. angew. Entomol. 87, 417–429.

Rudinsky, J.A., Ryker, L.C., Michael, R.R., Libbey, L.M., Morgan, M.E., 1976. Sound production in Scolytidae: female sonic stimulus of male pheromone release in two *Dendroctonus* beetles. J. Insect Physiol. 22, 1675–1681.

Rudinsky, J.A., Vallo, V., Ryker, L.C., 1978. Sound production in Scolytidae: attraction and stridulation of *Scolytus mali* (Col., Scolytidae). Z. angew. Entomol. 86, 381–391.

Rühm, W., 1981. Zur Biologie und Ökologie von *Pteleobius* (*Xylechinus*) *valdivianus* (Eggers, 1942) (Col., Scolytidae), einer vorwiegend an unterständigen Araukarien, *Araucaria araucana* (Mol.) Koch, brütenden Borkenkäferart. Entomologische Mitteilungen aus dem Zoologischen Museum Hamburg 7, 13–20.

Ryker, L.C., 1984. Acoustic and chemical signals in the life cycle of a beetle. Sci. Am. 250, 112–123.

Safranyik, L., 1976. Size- and sex-related emergence, and survival in cold storage, of mountain pine beetle adults. Can. Entomol. 108, 209–212.

Salom, S.M., McLean, J.A., 1989. Influence of wind on the spring flight of *Trypodendron lineatum* (Olivier) (Coleoptera, Scolytidae) in a second-growth coniferous forest. Can. Entomol. 121, 109–119.

Salom, S.M., McLean, J.A., 1991. Environmental influences on dispersal of *Trypodendron lineatum* (Coleoptera, Scolytidae). Environ. Entomol. 20, 565–576.

Salonen, K., 1973. On the life cycle, especially on the reproduction biology of *Blastophagus piniperda* L. (Col., Scolytidae). Acta For. Fenn. 127, 1–72.

Santoro, F.H., 1963. Bioecología de *Platypus sulcatus* Chapuis (Coeloptera, Platypodidae). Revista de Investigaciones Forestales 4, 47–79.

Santos, M.F., de, A., Mermudes, J.R.M., da Fonseca, V.M.M., 2011. A specimen of Curculioninae (Curculionidae, Coleoptera) from the Lower Cretaceous, Araripe Basin, north-eastern Brazil. Palaeontology 54, 807–814.

Sasakawa, M., Yoshiyasu, Y., 1983. Stridulatory organs of the Japanese pine bark beetles (Coleoptera, Scolytidae). Kontyu 51, 493–501.

Saunders, J.L., Knoke, J.K., 1967. Diets for rearing the ambrosia beetle *Xyleborus ferrugineus* (Fabricius) in vitro. Science 157, 460–463.

Sauvard, D., 2004. General biology of bark beetles. In: Lieutier, F., Day, K.R., Battisti, A., Grégoire, J.-C., Evans, H.F. (Eds.), Bark and Wood Boring Insects in Living Trees in Europe, A Synthesis. Kluwer Academic Publishers, Dordrecht, pp. 63–88.

Schedl, K.E., 1931. Morphology of the bark beetles of the genus *Gnathotrichus* Eichhoff. Smithson. Misc. Collect. 82, 1–88.

Schedl, K.E., 1958. Breeding habits of arboricole insects in Central Africa. Tenth International Congress of Entomology, Proceedings,183–197.

Schedl, K.E., 1959. Scolytidae und Platypodidae Afrikas. Band 1. Familie Scolytidae. Revista de Entomologia de Moçambique 2, 357–422.

Schedl, K.E., 1960a. Scolytidae und Platypodidae Afrikas. Band 1 (forts.). Familie Scolytidae. Revista de Entomologia de Moçambique 3, 75–154.

Schedl, K.E., 1960b. Insectes nuisibles aux fruits et aux graines. Publications de l'Institut National pour l'étude agronomique du Congo Belge, Série Scientifique 82, 1–133.

Schedl, K.E., 1961. Scolytidae und Platypodidae Afrikas. Band 1 (forts.). Familie Scolytidae. Revista de Entomologia de Moçambique 4, 335–742.

Schedl, K.E., 1962a. Scolytidae und Platypodidae Afrikas. Band 2. Familie Scolytidae. Revista de Entomologia de Moçambique 5, 1–594.

Schedl, K.E., 1962b. Scolytidae und Platypodidae Afrikas. Band 3. Familie Platypodidae. Revue Entomologique de Moçambique 5, 595–1352.

Schedl, K.E., 1972. Monographie der Familie Platypodidae Coleoptera. W. Junk, Den Haag.

Schedl, K.E., 1974. Scolytoidea from the Galapagos and Cocos Islands. Studies of the Neotropical Fauna 9, 47–53.

Schedl, K.E., 1977. Die Scolytidae und Platypodidae Madagaskars und einiger naheliengender Inselgruppen. 303 Bietrag. Mitt. Forstl. Bundes-Versuchanstalt, Wien 119, 5–326.

Schlupp, I., 2005. The evolutionary ecology of gynogenesis. Annu. Rev. Ecol. Evol. Syst. 36, 399–417.

Schlyter, F., Zhang, Q.-H., 1996. Testing avian polygyny hypotheses in insects: harem size distribution and female egg gallery spacing in three *Ips* bark beetles. Oikos 76, 57–69.

Schmidberger, J., 1836. Naturgeschichte des Apfelborkenkäfers *Apate dispar*. Beiträge zur Obstbaumzucht und zur Naturgeschichte der den Obstbäumen schädlichen Insekten 4, 213–230.

Schneider, I., 1987. Distribution, fungus-transfer and gallery construction of the ambrosia beetle *Xyleborus affinis* in comparison with *X. mascarensis* (Coleoptera, Scolytidae). Entomologia Generalis 12, 267–275.

Schneider-Orelli, O., 1911. Die Uebertragung und Keimung des Ambrosiapilzes von *Xyleborus (Anisandrus) dispar* F. Naturwissenschaftliche Zeitschrift für Land- und Forstwirtschaft 8, 186–192.

Schrey, N.M., Schrey, A.W., Heist, E.J., Reeve, J.D., 2011. Genetic heterogeneity in a cyclical forest pest, the southern pine beetle, *Dendroctonus frontalis*, is differentiated into east and west groups in the southeastern United States. J. Insect Sci. 11, 110.

Schwarz, E.A., 1891. Notes on the breeding habits of some scolytids. Proc. Entomol. Soc. Wash. 2, 77–80.

Schwarz, E.A., 1901. Note on *Scolytus quadrispinosus*. Proc. Entomol. Soc. Wash. 4, 344.

Scott, J.J., Oh, D.C., Yuceer, M.C., Klepzig, K.D., Clardy, J., Currie, C.R., 2008. Bacterial protection of beetle-fungus mutualism. Science 322, 63.

Searcy, W.A., Yasukawa, K., 1989. Alternative models of territorial polygyny in birds. Am. Nat. 134, 323–343.

Sforzi, A., Bartolozzi, L., 2004. Brenthidae of the World. Museo Regionale di Scienze Naturali. Torino, Italy.

Shimizu, A., Tanaka, R., Akiba, M., Masuya, H., Iwata, R., Fukuda, K., Kanzaki, N., 2013. Nematodes associated with *Dryocoetes uniseriatus* (Coleoptera: Scolytidae). Environ. Entomol. 42, 79–88.

Shuster, S.M., Wade, M.J., 2003. Mating Systems and Strategies. Princeton University Press, Princeton and Oxford.

Singer, T., 1998. Roles of hydrocarbons in the recognition systems of insects. Am. Zool. 38, 394–405.

Six, D.L., 2003. Bark beetle-fungus symbioses. In: Bourtzis, K., Miller, T.A. (Eds.), Insect Symbiosis. CRC Press, Boca Raton, pp. 97–114.

Six, D.L., 2012. Ecological and evolutionary determinants of bark beetle–fungus symbioses. Insects 3, 339–366.

Six, D., 2013. The bark beetle holobiont: Why microbes matter. J. Chem. Ecol. 1–14.

Six, D.L., Paine, T.D., 1998. Effects of mycangial fungi and host tree species on progeny survival and emergence of *Dendroctonus ponderosae* (Coleoptera: Scolytidae). Environ. Entomol. 27, 1393–1401.

Smetanin, A.N., 2013. A new bark beetle species, *Dryocoetes krivolutzkajae* Mandelshtam, 2001 (Scolytidae), discovered in Kamchatka. Contemp. Probl. Ecol. 6, 43–44.

Smith, N.G.C., 2000. The evolution of haplodiploidy under inbreeding. Heredity 84, 186–192.

Smith, S.M., Cognato, A.I., 2010. A taxonomic revision of *Camptocerus* Dejean (Coleoptera: Curculionidae: Scolytinae). Insecta Mundi 148, 1–88.

Smith, S.M., Cognato, A.I., 2011. Observations of the biology of *Camptocerus* Dejean (Coleoptera: Curculionidae: Scolytinae) in Peru. Coleopterists Bulletin 65, 27–32.

Smith, G.D., Carroll, A.L., Lindgren, B.S., 2009. Life history of a secondary bark beetle, *Pseudips mexicanus* (Coleoptera: Curculionidae: Scolytinae), in lodgepole pine in British Columbia. Can. Entomol. 141, 56–69.

Sousa, W.P., Quek, S.P., Mitchell, B.J., 2003. Regeneration of *Rhizophora mangle* in a Caribbean mangrove forest: interacting effects of canopy disturbance and a stem-boring beetle. Oecologia 137, 436–445.

Speight, M.R., Wainhouse, D., 1989. Ecology and Management of Forest Insects. Clarendon Press, Oxford.

Stacey, P.B., Ligon, J.D., 1991. The benefits-of-philopatry hypothesis for the evolution of cooperative breeding variation in territory quality and group-size effects. Am. Nat. 137, 831–846.

Stahlhut, J.K., Desjardins, C.A., Clark, M.E., Baldo, L., Russell, J.A., Werren, J.H., Jaenike, J., 2010. The mushroom habitat as an ecological arena for global exchange of *Wolbachia*. Mol. Ecol. 19, 1940–1952.

Stark, R.W., 1982. Generalized ecology and life cycle of bark beetles. In: Mitton, J.B., Sturgeon, K.B. (Eds.), Bark Beetles in North American Conifers. A System for the Study of Evolutionary Biology. University of Texas Press, Austin, pp. 21–45.

Stauffer, C., van Meer, M.M.M., Riegler, M., 1997. The presence of the protobacteria *Wolbachia* in European *Ips typographus* (Col, Scolytidae) populations and the consequences for genetic data. Mitteilungen der Deutschen Gesellschaft für allgemeine und angewandte Entomologie 11, 709–711.

Stilwell, A.R., Smith, S.M., Cognato, A.I., Martinez, M., Flowers, R.W., 2014. *Coptoborus ochromactonus,* n. sp. (Coleoptera: Curculionidae: Scolytinae), an emerging pest of cultivated balsa (Malvales: Malvaceae) in Ecuador. J. Econ. Entomol. 107, 675–683.

Stone, C., 1990. Parasitic and phoretic nematodes associated with *Ips grandicollis* (Coleoptera, Scolytidae) in New-South-Wales. Nematologica 36, 478–480.

Storer, A.J., Wainhouse, D., Speight, M.R., 1997. The effect of larval aggregation behaviour on larval growth of the spruce bark beetle *Dendroctonus micans*. Ecol. Entomol. 22, 109–115.

Strohmeyer, H., 1906. Neue Untersuchungen über Biologie, Schädlichkeit und Vorkommen des Eichenkernkäfers, *Platypus cylindrus* var. *cylindriformis*. Naturwissenschaftliche Zeitschrift fur Land- und Forstwirtschaft 4, 329–341, 408–421, 506–511.

Strohmeyer, H., 1918. Die Morphologic des Chitinskeletts der Platypodiden. Archiv fuer Naturgeschichte Berlin Abt A 84, 1–42.

Sullivan, B.T., Niño, A., Moreno, B., Brownie, C., Macías-Sámano, J., Clarke, S.R., et al., 2012. Biochemical evidence that *Dendroctonus frontalis* consists of two sibling species in Belize and Chiapas. Mexico. Ann. Entomol. Soc. Am. 105, 817–831.

Sun, J.H., Lu, M., Gillette, N.E., Wingfield, M.J., 2013. Red turpentine beetle: innocuous native becomes invasive tree killer in China. Annu. Rev. Entomol. 58, 293–311.

Susoy, V., Herrmann, M., 2014. Preferential host switching and codivergence shaped radiation of bark beetle symbionts, nematodes of *Micoletzkya* (Nematoda: Diplogastridae). J. Evol. Biol. 27, 889–898.

Swaby, J.A., Rudinsky, J.A., 1976. Acoustic and olfactory behaviour of *Ips pini* (Say) (Coleoptera: Scolytidae) during host invasion and colonisation. Z. angew. Entomol. 81, 421–432.

Swaine, J.M., 1918. Canadian bark-beetles, part II. A preliminary classification, with an account of the habits and means of control. Canadian Department of Agriculture, Division of Entomology, Bulletin 14, 1–143.

Swedenborg, P.D., Jones, R.L., Ascerno, M.E., Landwehr, V.R., 1988. *Hylurgopinus rufipes* (Eichhoff) (Coleoptera: Scolytidae): attraction to broodwood, host colonization behavior, and seasonal activity in central Minnesota. Can. Entomol. 120, 1041–1050.

Swedenborg, P.D., Jones, R.L., Ryker, L.C., 1989. Stridulation and associated behavior of the native elm bark beetle *Hylurgopinus rufipes* (Eichhoff) (Coleoptera: Scolytidae). Can. Entomol. 121, 245–252.

Swift, M.J., 1977. The roles of fungi and animals in the immobilization and release of nutrient elements from decomposing branchwood. Ecol. Bull. 25, 193–202.

Tallamy, D.W., 1994. Nourishment and the evolution of paternal investment in subsocial arthropods. In: Hunt, J.H., Nalepa, C.A. (Eds.), Nourishment and Evolution in Insect Societies. Westview Press, Boulder, pp. 21–55.

Tallamy, D.W., Wood, R.F., 1986. Convergence patterns in subsocial insects. Annu. Rev. Entomol. 31, 369–390.

Thompson, R.T., 1996. The species of *Phaenomerus* Schönherr (Coleoptera: Curculionidae: Zygopinae) of the Australian region. Invertebrate Taxonomy 10, 937–993.

Thornhill, N.W., 1993. The Natural History of Inbreeding and Outbreeding: Theoretical and Empirical Perspectives. University of Chicago Press, Chicago.

Ticheler, J.H.G., 1961. An analytical study of the epidemiology of the coffee berry borer in the Ivory Coast. Mededelingen van de Landbouwhogeschool te Wageningen 61 (11), 1–49, 1–13.

Trägårdh, I., 1930. Studies on the galleries of bark beetles. Bull. Entomol. Res. 21, 469–480.

Tredl, R., 1915. Aus dem Leben des Birkensplintkäfers, *Scolytus ratzeburgi*. Entomologische Blätter 11, 146–154.

Trimble, F.M., 1924. Life history and habits of two Pacific coast bark beetles. Ann. Entomol. Soc. Am. 17, 382–391.

Tykarski, P., 2006. Beetles associated with scolytids (Coleoptera, Scolytidae) and the elevational gradient: diversity and dynamics of the community in the Tatra National Park. Poland. Forest Ecol. Manage. 225, 146–159.

Ulyshen, M.D., Hanula, J.L., Horn, S., Kilgo, J.C., Moorman, C.E., 2004. Spatial and temporal patterns of beetles associated with coarse woody debris in managed bottomland hardwood forests. Forest Ecol. Manage. 199, 259–272.

Vega, F.E., Benavides, P., Stuart, J.A., O'Neill, S.L., 2002. *Wolbachia* infection in the coffee berry borer (Coleoptera: Scolytidae). Ann. Entomol. Soc. Am. 95, 374–378.

Vega, F.E., Davis, A.P., Jaramillo, J., 2012. From forest to plantation? Obscure articles reveal alternative host plants for the coffee berry borer, *Hypothenemus hampei* (Coleoptera: Curculionidae). Biol. J. Linn. Soc. 107, 86–94.

Vega, F.E., Simpkins, A., Bauchan, G., Infante, F., Kramer, M., Land, M.F., 2014. On the eyes of male coffee berry borers as rudimentary organs. PLoS One 9 (1), e85860.

Vernoff, S., Rudinsky, J.A., 1980. Sound production and pairing behavior of *Leperisinus californicus* Swaine and *L. oreganus* Blackman (Coleoptera: Scolytidae) attacking Oregon ash. Z. angew. Entomol. 90, 58–74.

Wallace, A.R., 1860. Notes on the habits of Scolytidae and Bostrichidae. Transactions of the Entomological Society of London (n. s.) 5 (Part IV), 218–220.

Wang, C.S., 1981. A study of the Korean pine bark beetle (*Blastophagus pilifer* Spess). Kunchong Zhishi [Insect Knowledge] 18, 165–167 [in Chinese, with English abstract].

Weber, B.C., McPherson, J.E., 1983. Life history of the ambrosia beetle *Xylosandrus germanus* (Coleoptera: Scolytidae). Ann. Entomol. Soc. Am. 76, 455–462.

Webster, F.M., 1910. The clover root-borer (*Hylastinus obscurus* Marsham.). U.S. Department of Agriculture, Bureau of Entomology Circular no 119, 1–5.

Werren, J.H., Baldo, L., Clark, M.E., 2008. *Wolbachia*: master manipulators of invertebrate biology. Nat. Rev. Microbiol. 6, 741–751.

West, S.A., Pen, I., Griffin, A.S., 2002. Cooperation and competition between relatives. Science 296, 72–75.

White, T.C.R., 1993. The Inadequate Environment. Nitrogen and the Abundance of Animals. Springer-Verlag, Berlin.

Wichmann, H.E., 1927. Ipidae. In: Schulze, P. (Ed.), Biologie der Tiere Deutschlands. Gebrüder Bornträger, Berlin, pp. 347–381.

Wichmann, H.E., 1967. Die Wirkungsbreite des Ausstoßreflexes bei Borkenkäfern. J. Pest Sci. 40, 184–187.

Wilson, H.F., 1909. The peach-tree barkbeetle. *U.S.* Department of Agriculture, Bureau of Entomology, Bulletin 68, 91–108.

Wilson, E.O., 1971. The Insect Societies. Belknap Press of Harvard University, Cambridge.

Wilson, E.O., 1975. Sociobiology: The New Synthesis. Harvard University Press, Cambridge.

Wilson, E.O., Hölldobler, B., 1980. Sex-differences in cooperative silk-spinning by weaver ant larvae. Proc. Natl. Acad. Sci. U. S. A. 77, 2343–2347.

Wilson-Rich, N., Spivak, M., Fefferman, N.H., Starks, P.T., 2009. Genetic, individual, and group facilitation of disease resistance in insect societies. Annu. Rev. Entomol. 54, 405–423.

Wood, S.L., 1978. A reclassification of the subfamilies and tribes of Scolytidae (Coleoptera). Annales de la Société entomologique de France (Neauveau Series) 14, 95–122.

Wood, D.L., 1982. The role of pheromones, kairomones, and allomones in the host selection and colonization behavior of bark beetles. Annu. Rev. Entomol. 27, 411–446.

Wood, S.L., 1982. The bark and ambrosia beetles of North and Central America (Coleoptera: Scolytidae), a taxonomic monograph. Great Basin Nat. Mem. 6, 1–1359.

Wood, S.L., 1983. *Scolytodes atratus panamensis* (Escarbajito de guarumo, *Cecropia* petiole borer). In: Janzen, D.H. (Ed.), Costa Rican Natural History. University of Chicago Press, Chicago, pp. 768–769.

Wood, S.L., 1986. A reclassification of the genera of Scolytidae (Coleoptera). Great Basin Nat. Mem. 10, 1–126.

Wood, S.L., 1993. Revision of the genera of Platypodidae (Coleoptera). Great Basin Nat. 53, 259–281.

Wood, S.L., 2007. Bark and Ambrosia Beetles of South America (Coleoptera, Scolytidae). Brigham Young University, Provo.

Wood, S.L., Bright, D.E., 1987. A catalog of Scolytidae and Platypodidae (Coleoptera), Part 1: Bibliography. Great Basin Nat. Mem. 11, 1–685.

Wood, S.L., Bright Jr., D.E., 1992. A catalog of Scolytidae and Platypodidae (Coleoptera), Part 2: Taxonomic Index. Volumes A and B. Great Basin Nat. Mem. 13, 1–1553.

Yan, Z.L., Sun, J.H., Don, O., Zhang, Z.N., 2005. The red turpentine beetle, *Dendroctonus valens* LeConte (Scolytidae): an exotic invasive pest of pine in China. Biodivers. Conserv. 14, 1735–1760.

Ye, H., 1997. Mass attack by *Tomicus piniperda* L. (Col., Scolytidae) on *Pinus yunnanensis* tree in the Kunming region, southwest China. In: Grégoire, J.-C., Liebhold, A.M., Stephen, F.M., Day, K.R., Salom, S.M. (Eds.), Proceedings: Integrating Cultural Tactics into the Management of Bark Beetle and Reforestation Pests, pp. 225–227, USDA Forest Service General Technical Report NE-236.

Ye, H., Ding, X.S., 1999. Impacts of *Tomicus minor* on distribution and reproduction of *Tomicus piniperda* (Col., Scolytidae) on the trunk of the living *Pinus yunnanensis* trees. J. Appl. Entomol. 123, 329–333.

Yearian, W.C., Gouger, R.J., Wilkinson, R.C., 1972. Effects of the bluestain fungus, *Ceratocystis ips*, on development of Ips bark beetles in pine bolts. Ann. Entomol. Soc. Am. 65, 481–487.

Ytsma, G., 1988. Stridulation in *Platypus apicalis*, *P. caviceps*, and *P. gracilis* (Col., Platypodidae). J. Appl. Entomol. 11, 256–261.

Yust, H.R., 1957. Biology and habits of *Pagiocerus fiorii* in Ecuador. J. Econ. Entomol. 50, 92–96.

Zanuncio, A.J.V., Pastori, P.L., Kirkendall, L.R., Lino-Neto, J., Serrão, J.E., Zanuncio, J.C., 2010. *Megaplatypus mutatus* (Chapuis) (Coleoptera: Curculionidae: Platypodinae) attacking hybrid *Eucalyptus* clones in southern Espirito Santo, Brazil. Coleopterists Bulletin 61, 81–83.

Zanzot, J.W., Matusick, G., Eckhardt, L.G., 2010. Ecology of root-feeding beetles and their associated fungi on longleaf pine in Georgia. Environ. Entomol. 39, 415–423.

Zchori-Fein, E., Borad, C., Harari, A.R., 2006. Oogenesis in the date stone beetle, *Coccotrypes dactyliperda,* depends on symbiotic bacteria. Physiol. Entomol. 31, 164–169.

Zhang, L.L., Chen, H., Ma, C., Tian, Z.G., 2010. Electrophysiological responses of *Dendroctonus armandi* (Coleoptera: Curculionidae: Scolytinae) to volatiles of Chinese white pine as well as to pure enantiomers and racemates of some monoterpenes. Chemoecology 20, 265–275.

Zrimec, M.B., Zrimec, A., Slanc, P., Kac, J., Kreft, S., 2004. Screening for antibacterial activity in 72 species of wood-colonizing fungi by the *Vibrio fisheri* bioluminescence method. J. Basic Microbiol. 44, 407–412.

Zúñiga, G., Cisneros, R., Hayes, J.L., Macias-Samano, J., 2002a. Karyology, geographic distribution, and origin of the genus *Dendroctonus* Erichson (Coleoptera: Scolytidae). Ann. Entomol. Soc. Am. 95, 267–275.

Zúñiga, G., Salinas-Moreno, Y., Hayes, J.L., Grégoire, J.C., Cisneros, R., 2002b. Chromosome number in *Dendroctonus micans* and karyological divergence within the genus *Dendroctonus* (Coleoptera: Scolytidae). Can. Entomol. 134, 503–510.