3

Feeding Biology of Cerambycids

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3.1 Introduction

There are more than 36,000 species of Cerambycidae recognized throughout the world (see Chapter 1), occurring on all continents except Antarctica (Linsley 1959). Given such numbers, it is not surprising that cerambycids display great diversity in their feeding habits. Both adults and larvae are almost exclusively phytophagous. Some adults appear not to feed at all, while others feed daily. Larvae primarily utilize woody host plants, but some species develop within herbaceous plants. Cerambycid larvae infest nearly all plant parts, especially stems, branches, and roots, as well as feed on nearly all plant tissues, especially bark, cambium, and wood. As expected in such a large insect family, some cerambycids are strictly monophagous while others are highly polyphagous. Similarly, some cerambycids infest live, healthy plants while others develop in dead plants; likewise, some species prefer moist wood, while others prefer dry wood. Cerambycid larvae are able to digest woody tissues with the aid of enzymes that they sometimes secrete themselves or that they obtain from symbionts. Many details on the feeding biology of cerambycids will be provided in this chapter, including the types of food consumed by adults and larvae, the common parts of plants that larvae infest and the tissues they consume, and aspects of wood digestion.

3.2 Adult Feeding Habits

Although few detailed studies have been conducted on the feeding habits of cerambycid adults, some general trends are apparent at the subfamily level (Duffy 1953). For example, parandrine, prionine, and spondylidine adults appear not to feed at all (Benham and Farrar 1976; Bense 1995; Švácha and Lawrence 2014). By contrast, it appears that all Lamiinae as well as most Lepturinae feed as adults. Although in the Cerambycinae, some adults are known to feed, while others do not—such as *Hylotrupes* and *Stromatium* (Duffy 1953).

3.2.1 Types of Adult Food

Butovitsch (1939) categorized the general types of food consumed by adult cerambycids as flowers, bark, foliage, cones, sap, fruit, roots, and fungi. Most lepturine adults, as well as many cerambycine (e.g., *Batyle, Euderces, Megacyllene*, and *Molorchus*) and a few lamiine (e.g., *Phytoecia* and *Tetrops*) adults, visit flowers and feed on pollen and nectar (Duffy 1953; Linsley 1959; see Figure 3.1). The bark and stem feeders are almost entirely lamiines (e.g., *Acanthocinus, Lamia*, and *Monochamus*; Duffy 1953). Leaves are consumed primarily by lamiines (e.g., *Batocera, Oberea*, and *Saperda*) as well as needles and developing cones (e.g., *Monochamus*; Butovitsch 1939; Duffy 1953). Adults of some lamiine species feed on both bark and foliage (e.g., *Goes, Monochamus, Plectrodera*, and *Saperda*; Webb 1909; Brooks 1919; Nord et al. 1972; Solomon 1974, 1980; see Figure 3.2). Various cerambycine (e.g., *Cerambyx* and *Hoplocerambyx*) and lamiine (e.g., *Moneilema*) adults feed on fruit and sap exudates (Duffy 1953). Roots of grasses are fed on by both the larvae and, at times, the adults of the soil-dwelling lamiine genus *Dorcadion* (Duffy 1953; Linsley 1959). Only a few adult cerambycids are known to feed on fungi, such as members of the lamiine genus *Leiopus* (Craighead 1923; Duffy 1953; Michalcewicz 2002).

FIGURE 3.1 *Megacyllene robiniae* (Forster) adult feeding on pollen of goldenrod (*Solidago*) flowers. The larval hosts of this North American cerambycine are locust trees in the genus *Robinia*. (Courtesy of David Cappaert [Bugwood image 2106090].)

FIGURE 3.2 An example of maturation feeding by the Asian lamiine *Anoplophora glabripennis* (Motschulsky) on maple (*Acer*) branches. (Courtesy of Dean Morewood [Bugwood image 1193003].)

3.2.2 Food and Adult Reproduction

As mentioned earlier, many cerambycids do not feed as adults and are typically capable of reproducing soon after emergence. For example, the cerambycine *Xylotrechus pyrrhoderus* Bates was capable of flight, responding to pheromones, mating, and egg laying at the time of emergence from its host plant without any additional feeding (Iwabuchi 1982). However, for species that feed after emergence, such as the Lamiinae, adults typically feed for one to three weeks before becoming sexually mature (Alya and Hain 1985; Hanks 1999), a period of time referred to as maturation feeding (Edwards 1961; Slipinski and Escalona 2013). For example, in the lamiine *Anoplophora glabripennis* (Motschulsky), adult females become sexually mature about 10 days after emergence, and maturation feeding is required for ovary development (Li and Liu 1997). Similarly, Keena (2002) and Smith et al. (2002) reported that the mean time from adult emergence to first oviposition in *A. glabripennis* varied from 9 to 17 days. Members of the lamiine genus *Monochamus* often feed for 7–12 days after emergence before becoming sexually mature (Akbulut and Stamps 2012). Similarly, in the lamiine *Glenea cantor* (F.), Lu et al. (2013) noted that adults required an average of five to seven days of feeding before mating and about another week of feeding before initiating oviposition.

The type of food consumed by cerambycid adults can influence their longevity and fecundity. In *A. glabripennis*, for example, the species of tree selected as the source of twigs to feed the adults influences their fecundity (Smith et al. 2002; Hajek and Kalb 2007). Similarly, for the cerambycine borers *Phoracantha recurva* Newman and *Phoracantha semipunctata* F., which as larvae develop in *Eucalyptus* trees and as adults feed on *Eucalyptus* pollen, adult longevity and fecundity increased when adults were maintained on a diet rich in *Eucalyptus* pollen compared with other pollen sources (Millar et al. 2003).

3.2.3 Food and Adult Flight, Pollination, and Disease Transmission

Many of the feeding habits of adult cerambycids have a direct influence on their dispersal behavior as well as on their role in pollination and disease transmission. For example, in the flower-feeding cerambycids, such as the Lepturinae, the flowers visited by adults typically are on different plant species than the larval hosts. Therefore, these adults need to disperse at least twice after emerging—first to flowers where they feed and often mate and then to the larval host plants to oviposit (Duffy 1953; Linsley 1959; Bílý and Mehl 1989; Bense 1995; Hanks 1999). By contrast, cerambycid adults that feed on bark and foliage usually feed on the same species of plants that serve as the larval hosts (Duffy 1953; Solomon 1995; Hanks 1999); therefore, adult dispersal may be minimal if the original host plant is still suitable for oviposition (see Chapter 2). For example, in *A. glabripennis*, which typically is univoltine, the same tree is often reinfested for several years until it dies, although a small portion of the progeny may disperse more widely (Haack et al. 2006, 2010). Many of the flower-feeding cerambycids pollinate their food plants as they feed on pollen and nectar (Willemstein 1987; Gutowski 1990; Hawkeswood and Turner 2007). With respect to disease transmission, the fact that adults of the pine-infesting lamiine genus *Monochamus* conduct maturation feeding on the bark, twigs, and foliage of pines (*Pinus*) enables them to be efficient vectors of the pinewood nematode, *Bursaphelenchus xylophilus* (Steiner & Buhrer) Nickle, given that the nematodes depart the adult's body during feeding and enter the trees through the feeding wounds created in the bark (Linit 1990; Akbulut and Stamps 2012; see Chapter 6).

3.2.4 Predatory Cerambycids

Although nearly all cerambycid adults that are known to feed are phytophagous, there is at least one cerambycine genus (*Elytroleptus*) where the species are carnivorous, preying on adult lycid beetles (net-winged beetles). Most *Elytroleptus* species are native to Mexico and the southwestern United States (Linsley 1962). In general, lycid adults are protected chemically from predation, and they often have aposematic coloration and form dense aggregations on plants (Eisner et al. 2008; Grzymala and Miller 2013). *Elytroleptus* adults mimic the appearance of these lycid beetles, allowing them to join their aggregations and prey on them (Linsley et al. 1961; Eisner et al. 1962; Selander et al. 1963).

3.3 Larval Feeding Habits

Cerambycid larvae are phytophagous (Linsley 1959; Hanks 1999; Slipinski and Escalona 2013), although facultative inter- and intraspecific predation has been observed when larvae encounter other individuals within the host plant as they construct their galleries (Togashi 1990; Victorsson and Wikars 1996; Dodds et al. 2001; Ware and Stephen 2006; Schoeller et al. 2012). Cerambycid larvae feed on a wide diversity of plant species, plant parts, plant tissues, as well as on plants in various conditions from living and healthy to dead and decaying. Before looking at these trends in host usage, readers need to be aware that information on larval hosts is best known for the economically important species but usually is incomplete for most cerambycids or entirely lacking for others. Moreover, larval host information is at times incorrect, often as a result of inaccurate plant or insect identification, changes in taxonomic status of a species or species complex, in situations when the plant on which an adult beetle is collected is assumed to be the larval host, or when such information is not presented clearly in the literature or on museum specimen labels. Nevertheless, for those world regions where the larval hosts are relatively well known for the local cerambycids, the clear trend is for most species to develop in woody plants, especially conifers and hardwood (broadleaf) trees (see Section 3.3.1).

3.3.1 Larval Host Plants

Information in Table 3.1 shows the number of cerambycid species that develop in various groupings of host plants for Montana (89% of species with known hosts; Hart et al. 2013) and Florida (77%; Thomas et al. 2005) in the United States; as well as the geographic regions of Fennoscandia (comprising Norway, Sweden, Finland, and a small part of neighboring Russia) and Denmark (100%; Bílý and Mehl 1989); Israel (91%; Sama et al. 2010); and Korea (57%; Lim et al. 2014). The checklist provided in Hart et al. (2013) for the cerambycids of Montana was supplemented with host data from the "Montana Wood Boring Insect Project" database (http://www.mtent.org/Cerambycidae.html) and, occasionally, from

TABLE 3.1

Percent of Cerambycids with Known Larval Hosts that Feed as Larvae in Various Types of Host Plants in Five World Regions

	Percent of Cerambycids that Develop in Different Hose Groupings[b]				
Larval Hosts[a]	**Montana**	**Florida**	**Fennoscandia and Denmark**	**Israel**	**Korea**
C	45.2	16.2	30.1	5.3	15.5
H	19.3	69.3	44.7	41.1	49.7
S	5.2	3.0	0	3.2	2.2
V	0.7	1.7	0	1.0	3.9
HC	5.9	5.6	14.6	5.3	8.8
HS	7.4	0.6	5.7	6.3	9.9
HCS	0.7	0	0.8	1.0	1.1
HCSV	0.7	0	0	0	1.1
HV	0	1.1	0	2.1	2.8
HSV	3.7	0	0.8	0	0.6
P	10.4	1.7	3.2	32.6	1.1
Cactus	0.7	0	0	0	0
Palm	0	1.1	0	2.1	0
HP	0	0	0	0	1.1
VP	0	0	0	0	0.6
HVB	0	0	0	0	0.6
HB	0	0	0	0	1.1
No. spp. With host data	135	179	123	95	181
Total No. spp.	152	233	123	104	318

Source: Data were based on Hart et al. (2013), http://www.mtent.org/Cerambycidae.html, and occasionally on other sources (see Section 3.3.1) for Montana, United States; Thomas et al. (2005) for Florida, United States; Bílý and Mehl (1989) for Fennoscandia and Denmark; Sama et al. (2010) for Israel; and Lim et al. (2014) for Korea.

[a] Larval host categories: B = bamboo; C = conifers; H = hardwood trees; S = woody shrubs; P = herbaceous plants; V = woody vines. Categories with more than one letter or plant group represent cerambycids that utilize plant genera in each of the listed plant groups.

[b] Percentage values based on only those cerambycid species with known larval hosts.

Linsley (1962a, 1962b, 1963, 1964) and Linsley and Chemsak (1972, 1976, 1984, 1995). These five world regions were selected because they represent different parts of the Northern Hemisphere where there is a good knowledge of the local larval host plants. In each of these world regions, assuming the information is accurate and complete, the majority of the cerambycid species develop strictly in trees, shrubs, and woody vines, with these woody plants constituting the larval hosts of about 89% of the cerambycids in Montana, 98% in Florida, 97% in Fennoscandia/Denmark, 65% in Israel, and 96% in Korea (Table 3.1). Coniferous trees are the most commonly utilized group of host plants for the cerambycids of Montana, although hardwood trees are the most common larval hosts in the other four world regions (Table 3.1). The dominance of woody plants serving as larval hosts likely is the general pattern for cerambycids worldwide. For example, recent larval host records for 180 South American cerambycids indicated that about 92% of the species listed developed strictly in trees, shrubs, and woody vines (Machado et al. 2012). Likewise, in Hawaii, Gressitt and Davis (1972) reported that nearly all of the 120 endemic cerambycids developed in trees and shrubs.

Herbaceous plants that traditionally are considered nonwoody, as well as cacti (Cactaceae) and various monocots that have some "woody" parts, occasionally are used by cerambycids as larval hosts—for example, some agave (Asparagaceae, formerly in Liliaceae), orchids (Orchidaceae), palms (Arecaceae), and yucca (Asparagaceae). About 11% of the cerambycids in Montana develop in herbaceous plants and cacti, 3% of Florida species develop in herbaceous plants and palms, 3% of Fennoscandian species develop in herbaceous plants, 35% of Israeli species develop in herbaceous plants and palms, and 5% of Korean species develop in herbaceous plants and bamboo (Table 3.1). Both annual and perennial herbaceous plants are used as hosts by certain cerambycids (Linsley 1959).

Several examples of cerambycids that feed on herbaceous plants, cacti, and woody monocots are listed in Table 3.2. In general, larvae of these cerambycids feed inside the roots and stems of their hosts, but some larvae live in the soil and feed externally on host tissues. For example, larvae of the prionine *Prionus emarginatus* Say and the lamiine *Dorcadion pseudopreissi* Breuning feed externally on the roots of grasses (Poaceae) (Craighead 1923; Gwynne and Hostetler 1978; Kumral et al. 2012), and larvae of the lepturine *Pseudovadonia livida* (F.) feed on decaying roots and stalks of grasses as well as fungal mycelium (Burakowski 1979; Bense 1995).

Larvae of many cerambycids are economic pests on herbaceous plants in various parts of the world. For example, the lamiine *Apomecyna binubila* Pascoe is a pest of melons (*Cucurbita* sp.) in Africa (Pollard 1954); the lamiine *Dectes texanus* LeConte is a pest of soybeans [*Glycine max* (L.) Merr.] in the United States (Tindall et al. 2010); the prionine *Dorysthenes buqueti* (Guérin-Méneville) is a pest of sugarcane (*Saccharum officinarum* L.) in Asia (Sugar Research Australia 2013); the lamiine *Acalolepta mixta* (Hope) and the cerambycine *Xylotrechus arvicola* (Olivier) are pests of grapes (*Vitis*) in Australia and Spain, respectively (Goodwin and Pettit 1994; García-Ruiz et al. 2012); the lamiine *Agapanthia cardui* L. is a pest of artichokes (*Cynara scolymus* L.) in the Mediterranean region (Baragaño Galán et al. 1981); and the cerambycine *Plagionotus floralis* (Pallas) is a pest of alfalfa (*Medicago sativa* L.) in Europe (Toshova et al. 2010). Likewise, a few of the cerambycids that develop in woody monocots are economic pests, such as the cerambycines *Jebusaea hammerschmidti* Reiche, a pest of date palms (*Phoenix dactilifera* L.) in the Middle East (Giblin-Davis 2001), and *Chlorophorus annularis* F., a pest of bamboo (*Bambusa* sp.) in Asia (Barak et al. 2009). With respect to the cactus-feeding cerambycids, a few species are of concern in the United States because they infest rare species of cacti that are protected under the U.S. Federal Endangered Species Act. For example, the lamiines *Moneilema armatum* LeConte and *Moneilema semipunctatum* LeConte infest at least five species of endangered and threatened cacti in the western United States (Kass 2001; Ferguson and Williamson 2009; USDA 2013; Figure 3.3).

3.3.2 Plant Parts Utilized by Larvae

Cerambycids develop in nearly all parts of their host plants but mainly in the stems, branches, and roots. Some species develop primarily in twigs (Figure 3.4), such as the lamiine *Oberea tripunctata* (Swederus) and the cerambycine *Tessaropa tenuipes* (Haldeman) in North America (Linsley 1962b, Solomon 1995) and the lamiine *Pogonocherus hispidus* (L.) in Europe (Bílý and Mehl 1989; Bense 1995). Some species oviposit primarily along the lower trunk of their hosts, such as the cerambycines *Enaphalodes rufulus* (Haldeman) (Donley and Rast 1984) and *Megacyllene robiniae* (Forster) (Harman and Harman 1990) in the United States. Still others oviposit predominantly at the base of trees such as the prionines *Mallodon* (= *Stenodontes*) *dasystomus* (Say) in the United States (Linsley 1962a, Solomon 1995) and the prionine *Prionus coriarius* (L.) in Europe (Bílý and Mehl 1989; Bense 1995).

To further illustrate the utilization of various tree parts among different cerambycids, several species are listed in Table 3.3 that develop primarily in the twigs, branches, trunks, and roots of oak (*Quercus*) and pine trees in the United States and northern Europe. The typical range in adult body length is given for each of the species listed in Table 3.3 and, assuming these sizes are typical of cerambycids that infest these different parts of a tree, there is an apparent trend where twig- and branch-infesting cerambycids generally are smaller than root- and trunk-infesting cerambycids. Such a pattern in beetle size is logical given the differences in physical size of these plant parts and the faster decay rates of twigs and branches compared with trunks and stumps (Cornelissen et al. 2012) and thus reflect the constraints that would be placed on potential beetle size and voltinism in twig- versus trunk-infesting cerambycids, for example. Similar lists of cerambycids that infest different parts of trees could be developed for many other tree genera throughout the world.

Although most cerambycid larvae develop in the roots, stems, and branches of their host plants, a few develop in other plant parts such as seeds, pods, fruits, and cones (Table 3.4 and Figure 3.5).

TABLE 3.2

Examples of Cerambycids that Develop in Nonwoody Plants

Species	Sub-Family[a]	Common Host Genera in Nature	Host Plant Family	Plant Part Infested	Source
Agapanthia villosoviridescens (DeGeer)	Lam	*Cirsium, Angelica, Carduus, Senecio*	Apiaceae, Asteraceae	Stem	Bílý and Mehl 1989
Ataxia hubbardi Fisher	Lam	*Ambrosia, Erigeron Helianthus, Vernonia, Heracleum*	Asteraceae	Root, stem	Rogers 1977; Schwitzgebel and Wilbur 1942; Twinn and Harding 1999
Brachysomida californica (LeConte)	Lep	*Lomatium*	Apiaceae	Root	Swift 2008
Chlorophorus annularis (Fabricius)	Cer	*Phyllostachys, Sasa*	Poaceae	Stem	Friedman et al. 2008; Lim et al. 2014
Coenopoeus palmeri (LeConte)	Lam	*Opuntia*	Cactaceae	Stem, branch	Raske 1972
Cortodera flavimana (Waldl)	Lep	*Ranunculus*	Ranunculaceae	Root	Özdikmen 2003
Dectes texanus LeConte	Lam	*Ambrosia, Anoda, Glycine, Xanthium*	Asteraceae, Fabaceae, Malvaceae	Stem	Tindall et al. 2010
Diaxenes dendrobii Gahan	Lam	*Coelogyne, Dendrobium, Laelia, Odontoglossum*	Orchidaceae	Stem	MacDougall 1900
Hemierana marginata (Fabricius)	Lam	*Ambrosia, Erigeron, Vernonia*	Asteraceae	Stem	Schwitzgebel and Wilbur 1942
Hippopsis lemniscata (Fabricius)	Lam	*Ambrosia, Vernonia, Xanthium*	Asteraceae	Stem	Piper 1977; Rogers 1977
Jebusaea hammerschmidti Reiche	Cer	*Phoenix*	Arecaceae	Stem	Giblin-Davis 2001
Mecas cana saturnina (LeConte)[b]	Lam	*Ambrosia, Helianthus, Iva*	Asteraceae	Root, stem	Rogers 1977
Moneilema appressum LeConte	Lam	*Echinocereus, Opuntia*	Cactaceae	Root, stem	Lingafelter 2003
Moneilema armatum LeConte	Lam	*Astrophytum, Opuntia*	Cactaceae	Root, stem	Ferguson and Williamson 2009
Nealcidion cereicola (Fisher)	Lam	*Cereus, Cleistocactus, Echinopsis, Monvillea, Stetsonia*	Cactaceae	Stem, branch	Machado et al. 2012; McFadyen and Fidalgo 1976
Phytoecia cylindrica (L)	Lam	*Anthriscus, Daucus*	Apiaceae	Stem	Bílýand Mehl 1989; Twinn and Harding 1999
Prionus emarginatus Say	Prio	*Grasses*	Poaceae	root	Craighead 1923; Gwynne and Hostetler 1978
Tetraopes tetraophthalmus (Forster)	Lam	*Asclepias*	Asclepidacae	Root	Matter 2001
Tragidion agave Swift & Ray	Cer	*Agave*	Asparagaceae	Flower stalk	Chemsak and Powell 1966; Swift and Ray 2008
Tragidion armatum LeConte	Cer	*Agave, Yucca*	Asparagaceae	Stem	Craighead 1923; Linsley 1962a; Waring and Smith 1987
Zagymnus clerinus (LeConte)	Cer	*Chamaerops*	Arecaceae	Leaf stem	Beutenmuller 1896; Blatchley 1928

[a] Cer = Cerambycinae; Lam = Lamiinae; Lep = Lepturinae; Prio = Prioninae.

[b] In the original publication, *Mecas cana saturnina* (LeConte) was reported as *Mecas inornata* Say; see Linsley and Chemsak (1995).

FIGURE 3.3 Adult lamiine *Moneilema armatum* LeConte, a flightless cerambycid that feeds on and develops in cacti in the western United States. (Courtesy of Whitney Cranshaw [Bugwood image 5393466].)

FIGURE 3.4 Larvae, galls, and larval galleries of the lamiine *Oberea delongi* Knull on its larval host, eastern cottonwood (*Populus deltoides* Bartram ex Marsh.), in the eastern United States. (Courtesy of James Solomon [Bugwood image 3056084].)

TABLE 3.3

Examples of Cerambycids that Develop in Various Parts of Oak (*Quercus*) and Pine (*Pinus*) Trees Growing in the United States and in Fennoscandia and Denmark[a]

	Species, Subfamily,[b] and Adult Length (mm)[c]					
Tree Part	**United States**			**Fennoscandia and Denmark**		
Oak-Infesting Cerambycids						
Twig	*Anelaphus parallelus* (Newman)	Cer	10–15	*Anaesthetis testacea* (Fabricius)	Lam	5–10
Twig	*Psyrassa unicolor* (Randall)	Cer	9–15	*Phymatodes pusillus* (Fabricius)	Cer	5–10
Branch	*Goes debilis* LeConte	Lam	10–16	*Pyrrhidium sanguineum* (L.)	Cer	6–15
Branch	*Purpuricenus axillaris* Haldeman	Cer	12–29	Xylotrechus antilope (Schönherr)	Cer	7–14
Trunk	*Enaphalodes rufulus* (Haldeman)	Cer	23–33	*Cerambyx cerdo* L.	Lam	24–53
Trunk	*Goes tigrinus* (De Geer)	Lam	22–38	*Rhagium sycophanta* (Schrank)	Lep	17–26
Root	*Archodontes melanopus melanopus* (L.)	Prio	33–57	*Prionus coriarius* (L.)	Prio	19–45
Root	*Prionus imbricornis* (L.)	Prio	31–42	*Stenocorus meridianus* (L.)	Lep	15–25
Pine-Infesting Cerambycids						
Twig and branch	*Phymatodes hirtellus* (LeConte)	Cer	5–7	*Pogonocherus decoratus* Fairmaire	Lam	4–7
Branch	*Haplidus testaceus* LeConte	Cer	8–16	*Molorchus minor* (L.)	Cer	6–16
Branch	*Neoclytus muricatulus* Kirby	Cer	5–9	*Pogonocherus fasciculatus* (DeGeer)	Lam	5–8
Trunk	*Callidium antennatum* Newman	Cer	9–15	*Ergates faber* (L.)	Prio	23–60
Trunk	*Monochamus titillator* (Fabricius)	Lam	17–31	*Monochamus sutor* (L.)	Lam	15–25
Root	*Typocerus zebra* (Olivier)	Lep	10–16	*Judolia sexmaculata* (L.)	Lep	8–14
Root	*Ulochaetes leoninus* LeConte	Nec	20–30	*Pachyta quadrimaculata* (L.)	Lep	11–20

[a] Craighead (1923) and Solomon (1995) for the United States; Bílý and Mehl (1989) for Fennoscandia and Denmark.

[b] Cer = Cerambycinae; Lam = Lamiinae; Lep = Lepturinae; Nec = Necydalinae (formerly a tribe in Lepturinae); Prio = Prioninae.

[c] Adult length data from Bílý and Mehl 1989; Furniss and Carolin 1977; Linsley 1962b, 1964; Solomon 1995; Yanega 1996.

Seed-infesting cerambycids have been recorded from trees in the families Rhizophoraceae and Sapindaceae, pod-infesting species from both herbaceous and woody Leguminosae, and cone-infesting species from conifers in the Cupressaceae and Pinaceae (Table 3.4). All the dicot-infesting cerambycids listed in Table 3.4 are members of the subfamily Lamiinae, while the conifer-infesting species represent the subfamilies Cerambycinae, Lepturinae, and Spondylidinae. It is surprising that so few cerambycids have evolved to develop in seeds, pods, fruits, and cones—or perhaps many more await discovery. The cerambycids that develop inside seeds and fruit generally are small in size. For example, adults of the seed-infesting lamiine *Ataxia falli* Breuning are 12–16 mm in length (Linsley and Chemsak 1984), and adults of the fruit-infesting lamiine *Leptostylus gibbulosus* Bates are 8–11 mm in length (Linsley and Chemsak 1995; Table 3.4).

Leaves are seldom mined by cerambycid larvae, but there are a few exceptions. The lamiine *Microlamia pygmaea* Bates, for example, is a small (adults are about 2–4 mm long) cerambycid in New Zealand that develops in fallen twigs and dead leaves of kauri trees, *Agathis australis* (D. Don) Lindley (Martin 2000). Another example is the cerambycine *Jebusaea hammerschmidti* Reiche (syn. *Pseudophilus testaceus* Gah.), a large cerambycid (21–40 mm) native to the Middle East that, as larvae, first mines the

TABLE 3.4

Records of Cerambycid Species that Feed on Seeds, Pods, and Cones

		Plant Host and Plant Part Infested				
Species	**Sub-Family**[a]	**Genus or Species**	**Plant Family**	**Part**	**Country or Location of Study**	**Source**
Ataxia sulcata Fall (= *Ataxia falli* Breuning)	Lam	*Rhizophora mangle*	Rhizophoraceae	Seed	United States (Florida)	Craighead 1923
Chlorophorus strobilicola Champion	Cer	*Pinus roxburghii*	Pinaceae	Cone	India	Champion 1919; Pande and Bhandari 2006
Cortodera femorata (Fabricius)	Lep	*Picea* *Pinus*	Pinaceae Pinaceae	Cone	Serbia, Latvia	Pil and Stojanovic 2005; Barševskis and Savenkov 2013
Enaretta castelnaudii Thomson	Lam.	*Acacia*	Leguminosae	Pod	Africa	Schabel 2006
Leptostylus gibbulosus Bates	Lam	Sapindus saponaria	Sapindaceae	Fruit	United States (Texas), Mexico, Colombia	Vogt 1949; Romero Nápoles et al. 2007; Hernandez-Jaramillo et al. 2012
Leptostylus gundlachi Fisher [= *Leptostylopsis gundlachi* (Fisher), and *Styloleptus gundlachi* (Fisher)]	Lam	*Erythrina fusca*	Leguminosae	Pod	Puerto Rico	Wolcott 1948
Leptostyulus spermovoratis Chemsak	Lam	*Diospyros*	Ebenaceae	Fruit	Costa Rica	Chemsak 1972
Leptostylus terracolor Horn, [= *Leptostylopsis terraecolor* (Horn)]	Lam	*Rhizophora mangle*	Rhizophoraceae	Seed	United States (Florida)	Craighead 1923
Lepturges guadeloupensis Fleutiaux & Salle [= *Urgleptes guadeloupensis* (Fleutiaux & Salle)]	Lam	*Acacia farnesiana*	Leguminosae	Pod	Puerto Rico	Wolcott 1948
Lepturges spermophagus Fisher [= *Atrypanius spermophagus* (Fisher)]	Lam	*Vigna*	Leguminosae	Pod	Mexico	Fisher 1917
Lophopoeum timbouvae Lameere (= *Baryssinus leguminicola* Linell)	Lam	*Enterolobium, Gleditsia, Inga, Prosopis, Tamarindus*	Leguminosae	Pod	Argentina, Brazil, Paraguay	Duffy 1960
Paratimia conicola Fisher	Spo	*Pinus attenuate, Pinus contorta ssp. bolanderi*	Pinaceae	Cone	United States (California, Oregon)	Craighead 1923; Linsley 1962a
Phymatodes nitidus LeConte	Cer	*Sequoia sempervirens, Sequoiadendron giganteum*	Cupressaceae	Cone	United States (California)	Keen 1958; Stecker 1980
Xylotrechus schaefferi Schott	Cer	*Pinus banksiana, Pinus rigida*	Pinaceae	Cone	United States (New York)	Hoebeke and Huether 1990

[a] Cer = Cerambycinae; Lam = Lamiinae; Lep = Lepturinae; Spo = Spondylidinae.

FIGURE 3.5 Larvae of the cerambycine *Chlorophorus strobilicola* Champion construct galleries in pine (*Pinus*) cones. (Courtesy of the Pennsylvania Department of Conservation and Natural Resources [Bugwood image 5017026].)

leaf petioles of date palms *(Phoenix dactylifera* L.) before entering the main stem of the plant where they complete larval development and pupate (Carpenter and Elmer 1978; Giblin-Davis 2001).

3.3.3 Host Tissues Utilized

The host tissues in the major roots, trunks, and branches of woody plants form distinctive bands, starting first (from the outside) with the outer bark and then the inner bark, cambium, sapwood, and heartwood. Cerambycid larvae have evolved to feed on all of these tissues, with some developing almost entirely in a single tissue and others feeding on several tissues. For example, the lepturine *Encyclops caeruleus* (Say) and the cerambycine *Microclytus gazellula* (Haldeman) develop mainly in the outer bark of various North American hardwoods; the lamiine *Acanthocinus* species develop almost entirely in the inner and outer bark of conifers (Figure 3.6); and the cerambycine *Eburia quadrigeminata* (Say) and the lepturine *Pyrotrichus vitticollis* LeConte develop primarily in the heartwood of hardwoods (Craighead 1923; Hardy 1944; Linsley 1962b; Baker 1972; Dodds et al. 2002; Yuan et al. 2008). In most cases when larvae utilize multiple tissues, they complete early larval development in the cambial region and then tunnel deeper into the sapwood—and possibly the heartwood—during late larval development. There are exceptions to this rule, such as the hardwood trunk-infesting species of the lamiine genus *Goes* and the cerambycine *Neoclytus caprea* Say where the newly hatched larvae enter the sapwood with little feeding in the cambial region (Craighead 1923; Solomon 1995). In this chapter, the term cambial region includes the inner bark, cambium, and outer sapwood.

Several hardwood-infesting cerambycids that are native to eastern North America are listed in Table 3.5. The species are grouped by the host tissues typically consumed during larval development, starting with species that feed primarily on the bark and ending with species that feed primarily on wood. Host condition can influence which host tissues are utilized by cerambycid larvae. For example, in the *Ulmus*-infesting cerambycine *Physocnemum brevilineum* (Say), larvae typically feed and later construct pupal cells in the outer bark when developing in living trees, but in cut logs, the larvae develop in the cambial region and construct pupal chambers in the outer sapwood (Haliburton 1951).

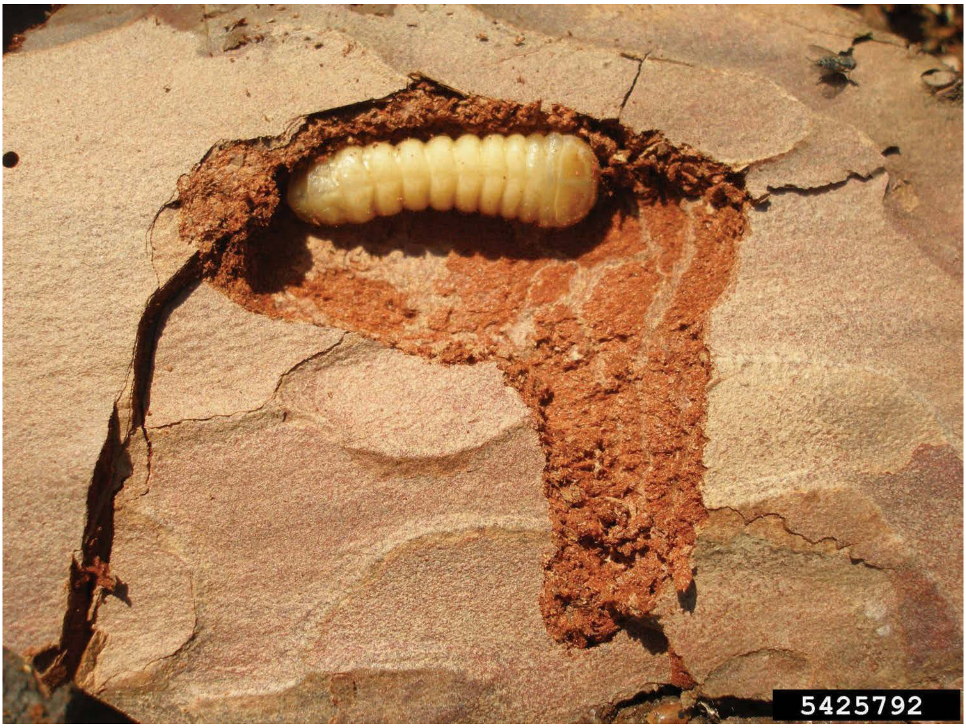

FIGURE 3.6 Larvae of the lamiine *Acanthocinus aedilis* (L.) construct galleries primarily in the outer bark of their coniferous hosts. (Courtesy of Valentyna Meshkova [Bugwood image 5425792].)

3.3.4 Host Range

The larval host range of cerambycids varies from some that feed on a single species or genus of plants (monophagous) to cerambycids that develop on multiple plant species, either all within a single plant family (oligophagous) or multiple families (polyphagous). For the cerambycids of Montana (Hart et al. 2013, supplemented with data from http://www.mtent.org/Cerambycidae.html; Linsley 1962a, 1962b, 1963, 1964; Linsley and Chemsak 1972, 1976, 1984, 1995), Fennoscandia and Denmark (Bílý and Mehl 1989), Israel (Sama et al. 2010), and Korea (Lim et al. 2014), for which host genera were provided, the average number of plant genera used as larval hosts was 3.9 genera per cerambycid species (range 1–26 genera) in Montana, 4.4 genera (range 1–16) in Fennoscandia and Denmark, 3.3 genera (1–19) in Israel, and 3.5 genera (1–27) in Korea. These numbers would likely be higher if complete larval host data were known for all cerambycids.

Examples of monophagous North American species would include the cerambycine *Megacyllene robiniae* that develops in *Robinia* trees (Solomon 1995; Figure 3.7) and all species of the lepturine genus *Desmocerus* that develop in species of *Sambucus* (Burke 1921; Figure 3.8). Similarly, in Europe, the lamiine *Saperda punctata* (L.) mostly infests *Ulmus*, and the cerambycine *Xylotrechus antilope* (Schönherr) mostly infests *Quercus* (Bense 1995). One North American example of a polyphagous species is the cerambycine *Neoclytus acuminatus* (Fabricius), which has developed in at least 26 genera of hardwood trees (Linsley 1964; Solomon 1995; Hart et al. 2013) and has also become established in Europe (Cocquempot and Lindelöw 2010). European examples of polyphagous species include the lepturine *Rhagium bifasciatum* Fabricius, which develops in at least 16 genera of conifers and hardwoods (Bílý and Mehl 1989), and the cerambycine *Penichroa fasciata* (Stephens), which develops in at least 19 genera of conifers and hardwoods (Sama et al. 2010).

Several cerambycids have been introduced to new countries as biological control agents for both herbaceous and woody plants because of their high host specificity. For example, the lamiine *Apagomerella versicolor* (Boheman) from Argentina is a potential biological control agent of *Xanthium* species in

TABLE 3.5

Typical Generation Time for Selected Cerambycids Native to the Northeastern United States that Infest Hardwood Trees, Organized by the Host Tissues Consumed by the Larvae, Starting from the Outer Bark and Moving Inward to the Heartwood

Species	Sub-Family[a]	Common Larval Hosts[b]	Adult Length (mm)	Larval Host Tissues[c]	Generation Time (yr)	Tree Parts Infested
Enaphalodes cortiphagus (Craighead)	Cer	*Quercus*	16–30	OB, CAM	3	Trunk
Parelaphidion incertum (Newman)	Cer	*Morus, Quercus*	9–17	OB, CAM	2–3	Trunk
Physocnemum brevilineum (Say)	Cer	*Ulmus*	9–20	OB, CAM, SW	1–2	Trunk, branch
Strophiona nitens (Forster)	Lep	*Castanea, Quercus*	10–15	OB, SW	2	Trunk, branch
Saperda discoidea (Fabricius)	Lam	*Carya, Juglans*	10–11	CAM	1	Trunk
Saperda tridentata Olivier	Lam	*Ulmus*	9–17	CAM	1	Trunk, branch
Enaphalodes rufulus (Haldeman)	Cer	*Quercus*	23–33	CAM, SW	2	Trunk, branch
Glycobius speciosus (Say)	Cer	*Acer*	22–27	CAM, SW	2	Trunk, branch
Neoclytus acuminatus (Fabricius)	Cer	*Fraxinus, Quercus*	4–18	CAM, SW	1	Trunk, branch
Tylonotus bimaculatus Haldeman	Cer	*Fraxinus, Ligustrum*	10–18	CAM, SW	2	Trunk
Xylotrechus quadrimaculatus (Haldeman)	Cer	*Betula, Fagus*	8–16	CAM, SW	1	Branch
Dorcaschema alternatum (Say)	Lam	*Morus, Maclura*	7–16	CAM, SW	1–2	Trunk, branch
Dorcaschema wildii Uhler	Lam	*Morus, Maclura*	16–22	CAM, SW	1–2	Trunk, branch
Plectrodera scalator (Fabricius)	Lam	*Populus, Salix*	25–40	CAM, SW	1–2	Root
Saperda calcarata Say	Lam	*Populus*	20–30	CAM, SW	2–3	Trunk
Saperda cretata Newman	Lam	*Malus, Crateagus*	10–20	CAM, SW	2–3	Trunk, branch
Saperda fayi Bland	Lam	*Crateagus*	12–13	CAM, SW	2	Branch
Saperda inornata Say	Lam	*Populus, Salix*	8–13	CAM, SW	2	Trunk
Megacyllene robiniae (Forster)	Cer	*Robinia*	12–19	CAM, SW, HW	1	Trunk, branch
Aegomorphus morrisi (Uhler)	Lam	*Nyssa*	20–26	CAM, SW, HW	2	Trunk
Saperda candida Fabricius	Lam	*Cydonia, Malus*	13–25	CAM, SW, HW	2–4	Trunk
Saperda vestita Say	Lam	*Tilia*	12–21	CAM, SW, HW	3	Trunk
Purpuricenus axillaris Haldeman	Cer	*Quercus, Castanea*	12–29	SW	2	Branch
Goes debelis LeConte	Lam	*Quercus*	10–16	SW	3–4	Branch
Goes pulcher (Haldeman)	Lam	*Carya, Juglans*	17–25	SW	3–5	Trunk
Goes pulverulentus (Haldeman)	Lam	*Fagus, Quercus*	18–25	SW	3–5	Trunk, branch

(Continued)

TABLE 3.5 *(Continued)*

Typical Generation Time for Selected Cerambycids Native to the Northeastern United States that Infest Hardwood Trees, Organized by the Host Tissues Consumed by the Larvae, Starting from the Outer Bark and Moving Inward to the Heartwood

Species	Sub-Family[a]	Common Larval Hosts[b]	Adult Length (mm)	Larval Host Tissues[c]	Generation Time (yr)	Tree Parts Infested
Goes tesselatus (Haldeman)	Lam	*Quercus*	20–27	SW	3–5	Trunk
Goes tigrinus (De Geer)	Lam	*Quercus*	22–38	SW	3–4	Trunk
Oberea ruficollis (Fabricius)	Lam	*Sassafras*	17	SW	2–3	Trunk
Oberea schaumii LeConte	Lam	*Populus*	12–16	SW	2–3	Branch
Desmocerus palliatus (Forster)	Prio	*Sambucus*	18–27	SW	2–3	Trunk
Dryobius sexnotatus (Linsley)	Cer	*Acer*, *Tilia*	20–26	SW, HW	2–3	Trunk
Xylotrechus aceris Fisher	Cer	*Acer*	10–14	SW, HW	2	Trunk, branch
Neandra brunnea (Fabricius)	Par	*Juglans*, *Carya*	8–12	SW, HW	3–4	Trunk
Prionus imbricornis (L.)	Prio	*Quercus*, *Castanea*	31–42	SW, HW	3–5	Root

Source: Data based almost entirely on Solomon, J. D., *Guide to insect borers in North American broadleaf trees and shrubs.* USDA Forest Service, Washington, DC, 1995.

[a] Cer = Cerambycinae; Lam = Lamiinae; Lep = Lepturinae; Par = Parandrinae; Prio = Prioninae.

[b] Primary larval hosts listed in Solomon (1995).

[c] Host tissues include OB = outer bark; CAM = cambial region, including inner bark and outer sapwood; SW = sapwood, and HW = heartwood.

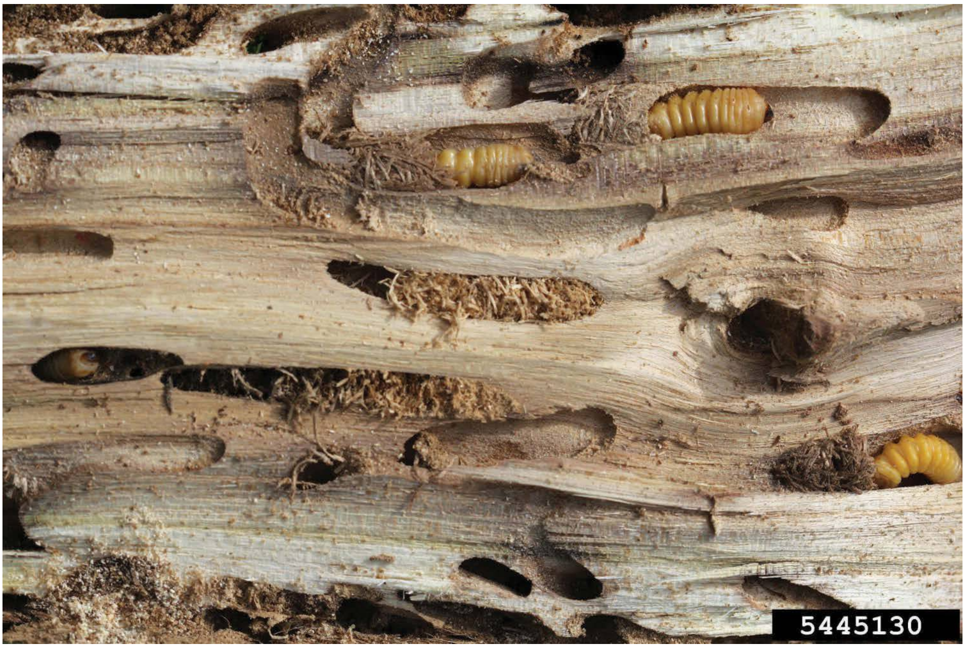

FIGURE 3.7 Larvae of the cerambycine *Megacyllene robiniae* (Forster) construct galleries throughout the sapwood and heartwood of their typical larval host, black locust (*Robinia pseudoacacia* L.). (Courtesy of Whitney Cranshaw [Bugwood image 5445130].)

FIGURE 3.8 Pupae of the lepturine *Desmocerus palliatus* (Forster) in the larval galleries that extend downward in the stems to the base of the plant—primarily in the pith of its host elder (*Sambucus*). (Courtesy of James Solomon [Bugwood image 3066074].)

the United States (Logarzo et al. 2002); the cerambycine *Megacyllene mellyi* (Chevrolat) from South America was introduced into Australia to control *Baccharis halimifolia* L. (McFadyen 1983); the lamiine *Nealcidion cereicola* (Fisher) from South America was introduced into Australia for biological control of *Harrisia* (= *Eriocereus*) *martinii* (Labouret) Britton (McFadyen and Fidalgo 1976); the lamiine *Oberea erythrocephala* (Schrank) from Europe was introduced into North America to control *Euphorbia esula* L. (Hansen et al. 1997); and the lamiines *Aerenicopsis championi* Bates and *Plagiohammus spinipennis* (Thoms.) from Mexico were introduced into Hawaii to control *Lantana camara* L. (Davis et al. 1993).

Typically, species that develop in healthy live plants tend to be monophagous or oligophagous, while those that develop in dead or decaying hosts tend to be polyphagous (Hanks 1999). However, given that there are thousands of cerambycid species worldwide, there are always exceptions. For example, the two Asian lamiines, *Anoplophora chinensis* (Forster) and *A. glabripennis* (Motschulsky), can develop in dozens of genera of apparently healthy hardwood trees and eventually kill them, which is the key reason why active eradication programs have been initiated in Europe and North America—where these two beetles have been introduced (MacLeod et al. 2002; Haack et al. 2010; Turgeon et al. 2015; Rassati et al. 2016; see Chapter 13).

3.3.5 Host Condition

Cerambycid larvae develop in host plants that vary in condition from healthy to dead and from moist to dry. Hanks (1999) noted the following general trends in the condition of the host plants selected for oviposition by adult females in several of the cerambycid subfamilies: Lepturinae, Prioninae, and Spondylidinae often develop in dead and decaying wood; Lamiinae usually develop in living and weakened hosts but seldom in dead hosts, whereas Cerambycinae develop in living, dying, and dead hosts. Many cerambycids that develop in living trees—but not all (see as follows) can complete development even in dead wood, especially when moisture levels are maintained at suitable levels. Although most cerambycids show an ovipositional preference for hosts in a particular condition, this relationship can be altered when the insect encounters new hosts. For example, in its native range of Europe, the spondylidine *Tetropium fuscum* F. tends to infest stressed or recently cut *Picea* trees, whereas in Canada, where it was introduced, it infests apparently healthy *Picea* trees (Flaherty et al. 2011). Another widespread European species, the cerambycine *Xylotrechus arvicola*, whose larvae generally feed on dead and decaying wood of hardwood trees, has recently been found to infest and damage living grape stems, branches, and roots (García-Ruiz et al. 2012).

Examples of cerambycid genera whose species are commonly associated with living hosts include *Anoplophora, Enaphalodes, Goes, Lamia, Megacyllene, Oberea, Oncideres, Plectrodera*, and *Saperda* (Figure 3.9). Similarly, examples of cerambycids that typically infest dead hosts are members of the genera *Arhopalus, Ergates, Parandra*, and *Rhagium* (Craighead 1923; Linsley 1959; Bílý and Mehl 1989; Solomon 1995). The requirement for living hosts appears to be particularly strong in species of the lamiine genera *Goes* and *Saperda*, given that their larvae seldom complete development when an infested tree is cut (Craighead 1923; Linsley 1959). Similarly, cerambycids that develop in the roots and stems of herbaceous plants usually select living hosts for oviposition (Piper 1978; Bense 1995; Rejzek et al. 2001), but some, such as the lamiines *Lepromoris gibba* (Brulle) (Duffy 1953) and *Parmena pubescens* (Dalman) (Duffy 1957), infest dead stalks of herbaceous Euphorbiaceae, perhaps because less milky sap is present in the dead tissue (Duffy 1953). When considering wood moisture content, several species of *Mallodon, Rhagium*, and *Rutpela* (=*Stragalic*) generally favor moist, decaying wood, while many species of *Chlorophorus, Gracilia, Hylotrupes*, and *Stromatium* develop in dry wood (Craighead 1923; Duffy 1953; Linsley 1959; Bense 1995). As logs decompose from the time of initial death or cutting to wood in advanced stages of decay, there are successional changes in the wood borer community structure, including cerambycids, providing further evidence that cerambycids vary in their preferences for hosts of a particular condition (Blackman and Stage 1924; Graham 1925; Savely 1939; Parmelee 1941; Howden and Vogt 1951; Haack et al. 1983; Khan 1985; Harmon et al. 1986; Hanula 1996; Saint-Germain et al. 2007; Costello et al. 2013; Lee et al. 2014; Ulyshen 2016).

FIGURE 3.9 Larva, larval galleries, pupa, and adult of the lamiine *Saperda calcarata* on its larval host, eastern cottonwood (*Populus deltoides* Bartram ex Marsh.), in the eastern United States. (Courtesy of James Solomon [Bugwood image 0284067].)

3.4 Larval Development, Nutrition, and Voltinism

As mentioned in Sections 3.3.2 and 3.3.3, cerambycid larvae feed and develop in almost every major plant part (roots, stems, branches, fruit, and seeds) and plant tissue (outer bark, inner bark, cambium, sapwood, and heartwood). These plant tissues differ greatly in thickness, nutrient levels, amount of living cells, degree of lignification (toughness), and their functional role within plants (Kramer and Kozlowski 1979; Haack and Slansky 1987; Pallardy 2008) and therefore can have a strong influence on cerambycid development rates and voltinism.

A brief discussion follows on the major physical and nutritional differences among these tree tissues based largely on the work by Kramer and Kozlowski (1979), Haack and Slansky (1987), and Pallardy (2008). The outer bark is largely dead, dense, corky tissue that functions in protecting the underlying tissues and reducing water loss. Outer bark generally is low in water and nutrients. By contrast, the inner bark (often called phloem) largely is soft living tissue, consisting of thin-walled cells. The inner bark is rich in water and nutrients and is the major tissue for the transport of photosynthates. The vascular cambium (or simply the cambium) is the ring of living cells that produces phloem cells to the outside and xylem (wood) cells to the inside. Because the cambium consists of living cells and is meristematically active, it likely has the highest water and nutrient levels of any major tissue within a woody plant. The sapwood consists mostly of dead, highly lignified cells that function in water and mineral transport. About 5–35% of the sapwood is living parenchyma cells, depending on the tree species (Panshin and de Zeeuw 1980). The water content of sapwood generally is high, being similar to inner bark, but the nutrient levels are usually much lower than the cambium or inner bark. The most nutritious portion of the sapwood is the outer portion closest to the cambium. Parenchyma cells die during the transition from sapwood to heartwood, and thus heartwood consists of dead tissue (Spicer 2005). Heartwood, in comparison with sapwood, generally is similar in density and lower in nutrients but is higher in secondary compounds. The water content of heartwood usually is similar to that of sapwood in hardwoods but is lower in conifers (Peck 1959; Skarr 1972).

Considering the overall nutritional quality of these tissues, cambium would rank highest, followed by inner bark, then sapwood, with heartwood and outer bark being lowest. Of course, the volume of each of these tissues available for larval consumption also varies considerably. For example, in the trunk of a large tree, the cambium would provide the smallest volume of these major tissues, followed by the inner bark, and likely then the outer bark, sapwood, and heartwood. However, great variation can occur in the thickness of these tissues, depending on plant age and diameter, as well as among and within plant families, genera, and species (Wilkins 1991; Sellin 1994; Pallardy 2008). Another tissue that varies dramatically in width is the pith, which commonly is found at the center of young stems and branches and initially consists of soft, spongy parenchyma cells. The pith usually is very distinct in young branches and stems of woody plants, but it becomes crushed and difficult to discern in older stem sections. In species of elderberry (*Sambucus*), which usually grow as shrubs or small trees, the pith is relatively wide and solid and is the primary tissue consumed by larvae of the North American lepturine *Desmocerus* species, especially the early instars (Burke 1921; Solomon 1995; Figure 3.8).

Many factors can influence cerambycid development time, including nutritional quality of the host tissues, host condition, and ambient temperatures. As detailed by Haack and Slansky (1987) for tree-infesting, temperate-zone cerambycids, development usually occurs in one to two years for larvae that feed primarily in the nutrient-rich cambial region, in two to three years when development occurs in both the cambial region and sapwood, and in three years or longer when most development occurs in the sapwood and heartwood. To demonstrate this pattern with cerambycids, several species native to the eastern United States are listed in Table 3.5 based on life-history data presented in Solomon (1995). These cerambycids are grouped by the host tissues commonly consumed by larvae of each species, starting with species that feed primarily on bark and ending with species that feed primarily on wood. An attempt was made to select species that were broadly similar in adult size so that voltinism patterns could be compared more on the basis of variation in nutritional quality of the host tissues consumed rather than on variation in final body size. Overall, for the species listed in Table 3.5, cerambycids that developed primarily in the outer and inner bark of tree trunks often required two to three years to complete one generation.

Those that developed primarily in the cambial region typically were univoltine. For species that developed in the cambial region as well as the sapwood, one to two years usually were required to complete development, although some species needed two to three years. For species that developed almost entirely in the sapwood or sapwood and heartwood, two to three years to as many as three to five years usually were required to complete one generation (Table 3.5).

There are exceptions to the aforementioned voltinism patterns. For example, the North American cerambycine *Megacyllene robiniae* is univoltine on its host (*Robinia*), although the larvae spend much of their life tunneling and feeding in the sapwood and heartwood (Galford 1984; Harman and Harman 1990). Similarly, the Asian lamiine *A. glabripennis*, which develops in dozens of species of living hardwood trees, generally is univoltine, although it too feeds extensively in sapwood and heartwood (Haack et al. 2010). The high microbial diversity in the guts of *A. glabripennis* larvae likely improves the digestion and assimilation of woody tissues and thereby may allow for their relatively short generation time (Geib et al. 2008, 2009a, 2009b; Scully et al. 2014).

Although most wood-infesting cerambycids complete development within a few years, there are numerous records of adults emerging from various wood products many years, or even decades, after the product was constructed. In these cases, oviposition is presumed to have occurred in the forest or lumberyard prior to milling the logs rather than sometime after construction of the wood products. This scenario can be assumed to have happened for most of the cerambycids reared from wood products given that these species require bark for oviposition, none of which usually is present on the final constructed product. Several examples of prolonged cerambycid development are shown in Table 3.6, with the longest being for the cerambycine *Eburia quadrigeminata* that emerged from a bookcase that was constructed more than 40 years earlier. More examples of protracted cerambycid development are given in Packard (1881) and Duffy (1953), and similar examples exist for several species of wood-boring Buprestidae (Coleoptera) (Spencer 1930; Linsley 1943; Smith 1962a, 1962b), with the longest records exceeding 50 years for *Buprestis aurulenta* L. (Smith 1962a). Although such records are exceptions, these data provide evidence that certain buprestids and cerambycids have the longest generation times of all insects.

Over the years, some authors have questioned the validity of these records of prolonged development, suggesting that oviposition could have occurred on the actual wood products sometime after final construction

TABLE 3.6

Summary Data for Cerambycids that Exhibited Prolonged Larval Development in Various Wood Items

Species	Sub-Family[a]	Country (State or Province)[b]	Wood Item	Min. Age (yr)[d]	References
Anaglyptus mysticus (L.)	Cer	The United Kingdom	*Fagus* drawer[c]	13	Hickin 1947
Phymatodes dimidiatus (Kirby)	Cer	Canada (BC)	*Abies* rafters	6	Spencer 1930
Eburia quadrigeminata (Say)	Cer	United States (IN)	*Acer* flooring	14	Webster 1889
Eburia quadrigeminata	Cer	United States (IA)	*Betula* bookcase	40	Jaques 1918
Eburia quadrigeminata	Cer	United States (IN)	*Fraxinus* door sill	19	McNeil 1886
Eburia quadrigeminata	Cer	United States (IN)	Bedstead *(Quercus)*[c]	20	Troop 1915
Eburia quadrigeminata	Cer	The United Kingdom	*Quercus* wardrobe	19	Hickin 1951
Ergates faber (L.)	Prio	The United Kingdom	*Pinus* pier	20	Fraser 1948
Hylotrupes bajulus (L.)	Cer	Canada	Dry wood in attic	12–15	Campbell et al. 1989
Hylotrupes bajulus	Cer	The United Kingdom	*Pinus* cupboard	17	Bayford 1938

[a] Cer = Cerambycinae; Prio = Prioninae.

[b] BC = British Columbia; IA = Iowa; IN = Indiana.

[c] Likely host, but not confirmed.

[d] Values represent the likely number of years since construction of the wood items prior to adult emergence and thus the estimated minimum number of years required to complete development.

(Spencer 1930; Beer 1949). However, some of the records are of buprestids and cerambycids that were native to the country where the furniture or wood product was constructed but that were not native to the country where the beetles emerged (Linsley 1943; Smith 1962a). Given that moisture content and nutrient levels decline as wood dries (Haack and Slansky 1987), it is not surprising that larval development would be prolonged when larvae are present in finished wood products that are relatively dry and kept indoors.

3.5 Wood Digestion

The woody environment is fibrous, tough, and nutritionally poor and therefore presents many challenges to wood-boring insects as they tunnel and feed in wood (Haack and Slansky 1987). For example, the nitrogen content of wood typically ranges from only 0.03% to 0.1% on a dry weight basis (Cowling and Merrill 1966). Considering the tree trunk in cross-section, the nitrogen content of sapwood generally decreases from the annual rings nearest the cambium inward to the sapwood–heartwood interface and then stays relatively constant throughout the heartwood until rising somewhat again near the pith at the center of the trunk or branch (Merrill and Cowling 1966). The toughness of wood results from the highly polymerized cell walls, which provide rigidity to woody plants and consist primarily of cellulose microfibrils, hemicellulose, and lignin (Gilbert 2010). Cellulose consists of thousands of glucose molecules, linked end-to-end in long straight chains that bind with other cellulose molecules to form microfibrils. By contrast, hemicellulose is a branched chain of mostly five carbon sugars that help link cellulose and lignin in each major layer of the cell wall. Lignin is an aromatic three-dimensional polymer that acts to cement the microfibrils together and gives woody plants their rigidity (Rowell et al. 2005). In North American conifers, for example, 40–45% of wood on a dry weight basis is cellulose, 7–14% is hemicellulose, and 26–34% is lignin. By contrast, in North American hardwoods, 38–49% of wood is cellulose, 19–26% is hemicellulose, and 23–30% is lignin (Rowell et al. 2005).

For more than two centuries, biologists have been interested in understanding how wood-boring insects are able to develop and survive in such a harsh environment as sapwood and heartwood. Mansour and Mansour-Bek (1934) and Parkin (1940) reviewed the early research in this field, including a discussion of the researchers involved, the test insects used, and their general findings and interpretations. A variety of techniques were utilized in these early studies but most involved comparing the chemical constituents of larval frass with the wood being consumed to detect differences as well as testing extracts from the borer's gut for their ability to enzymatically degrade specific wood constituents (Parkin 1940). As a result of these early studies, researchers developed a basic understanding that symbiotic microorganisms were involved in wood digestion in insects through enzymatic activity, including bacteria, fungi, and protozoans (Mansour and Mansour-Bek 1934; Parkin 1940; Graham 1967; Breznak 1982; Breznak and Brune 1994). More recently, using modern molecular and biochemical techniques, many more details have been elucidated about the symbionts, enzymes, and genes involved in wood degradation (Sugimura et al. 2003; Lee et al. 2004; Geib et al. 2008; Zhou et al. 2009; Watanabe and Tokuda 2010; Calderón-Cortés et al. 2012; Scully et al. 2013; Brune and Dietrich 2015). Moreover, it is recognized that wood-degrading enzymes in cerambycids are produced both exogenously (symbiont dependent) (Delalibera et al. 2005; Park et al. 2007; Zhou et al. 2009; Gieb et al. 2009b) and endogenously (symbiont independent) (Scrivener et al. 1997; Lee et al. 2005; Wei et al. 2006; Calderón-Cortés et al. 2012).

In the early 1900s, several cerambycids were known to harbor yeast-like fungi as endosymbionts in their midgut intestinal walls (Graham 1967). For example, Schomann (1937) reported that fungal endosymbionts were common in conifer-infesting cerambycid larvae but were rare in hardwood-infesting cerambycids. More recently, Grünwald et al. (2010) described several strains of ascomycetous yeasts in the guts of conifer-infesting cerambycids. In addition, Geib et al. (2008) demonstrated that certain gut fungi in *A. glabripennis* aided in lignin degradation. Transfer of symbiotic fungi between generations is accomplished during oviposition when fungi are deposited externally on the egg surface, with the new larvae becoming inoculated as they chew through the egg chorion (Schomann 1937; Graham 1967). In addition to fungal endosymbionts, several cerambycids utilize cellulolytic enzymes from fungi that they ingest while tunneling in wood (i.e., so-called acquired digestive enzymes). Cerambycids became the focus of this line of research in the 1980s, using species such as the conifer-infesting lamiine

Monochamus marmorator Kirby and the hardwood-infesting lamiine *Saperda calcarata* Say (Martin 1983; Kukor and Martin 1986a, 1986b; Martin 1992).

The role of bacteria in the digestion of cellulose, hemicellulose, and other polysaccharides in cerambycid larvae has been recognized for decades (Mansour and Mansour-Bek 1934; Parkin 1940). The bacterial diversity in the guts of cerambycid larvae has been elucidated in several species recently, with several classes of bacteria identified such as Actinobacteria and Gammaproteobacteria (Delalibera et al. 2005; Heo et al. 2006; Schloss et al. 2006; Park et al. 2007; Mazza et al. 2014). It is important to note that the bacterial community in the insect's gut is highly variable and can be influenced by the host plant. For example, Gieb et al. (2009a) demonstrated that the community of gut bacteria in *A. glabripennis* was most diverse when larvae fed in their preferred host trees (*Acer*) but much less diverse when they fed in nonpreferred hosts (*Pyrus*). Moreover, Schloss et al. (2006) reported that bacterial diversity was relatively high in the guts of *A. glabripennis* larvae, which have a broad host range, whereas bacterial diversity was relatively low in *Saperda vestita* Say, a lamiine with a narrow host range (primarily *Tilia*). It would be interesting to determine if bacterial diversity typically is greater in the gut tract of polyphagous cerambycid larvae compared to monophagous species. As for the transfer of bacteria between generations of cerambycids, it likely occurs during oviposition with bacteria being placed on the outside or inside of eggs or deposited near the oviposition site (Gieb et al. 2009b).

3.6 Summary and Future Directions

The thousands of cerambycid species found worldwide display great diversity in their feeding habits, including a wide variety of host plants, plant parts, and tissues consumed. The great success that cerambycids have had in exploiting the woody environment is related to their ability to enzymatically degrade many wood constituents through symbionts and endogenously produced enzymes. Knowledge of the feeding habits of adult and larval cerambycids can be used in developing integrated pest management programs for pest species. For example, knowing when and where adults feed is useful when scheduling detection surveys and pesticide applications. Similarly, knowing in which plant tissues the larvae feed and tunnel allows managers to judge the value, for example, of using systemic insecticides for their control, knowing that larvae that feed in or close to the cambial region would be much more susceptible to systemic insecticides than those that feed deep within the sapwood or heartwood (Poland et al. 2006). Although much has been learned about the feeding biology of the world's cerambycids, there are still many gaps in our basic understanding of their life history, larval and adult host plants, digestive symbionts, and wood-degrading enzymes; therefore, much more research remains to be conducted on these topics.

ACKNOWLEDGMENTS

The author thanks Toby Petrice for comments on an earlier draft of this chapter and the many photographers who supplied images to the Bugwood website at the University of Georgia.

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