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Chemical Ecology of Cerambycids

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5.1 Introduction

Given their popularity with naturalists and collectors, and in some cases their economic importance, it is remarkable how little is known about the basic biology of most cerambycid species. This is particularly true of cerambycid semiochemistry, which remains largely unexplored. In a 1999 review of cerambycid mate location and recognition, Hanks exhaustively reviewed the available data, which suggested that pheromones that act over long distances appeared to be uncommon in the Cerambycidae (Hanks 1999). Similarly, in a 2004 review of cerambycid chemical ecology, Allison et al. (2004) stated that most cerambycids did not use sex or aggregation pheromones. However, studies over the past decade have shown that, if anything, cerambycid species that do not use some form of attractant pheromones actually may be in the minority. Even more surprising is the fact that careful studies of a number of economically important species (e.g., the *Monochamus* and *Megacyllene* species, reviewed in Hanks 1999) had concluded that these species did not use long-range attractant pheromones, whereas we now have abundant evidence—from multiple species in the five major subfamilies—that the use of volatile pheromones is widespread within the family and that these compounds are often powerful attractants of one or both sexes.

There are several possible causes of the initial erroneous dogma that attractant pheromones were rare among the cerambycids. First, in species with relatively long-lived, feeding adults, such as the *Monochamus* species, a sexual maturation period and/or host feeding may be required before the adults produce or respond to pheromones (see Chapter 3). Second, in many cases, the pheromone is strongly synergized by host plant volatiles—in extreme cases to the extent that the pheromone alone is completely unattractive (see next section). Furthermore, a number of species are attracted to host volatiles independently of pheromones, which may have helped to obscure the fact that pheromones also were being used. Third, pheromone-mediated behavior may be much less obvious than in other types of insects. For example, male moths presented with the sex pheromones of females (during their normal activity period) immediately become active, wing-fanning and then initiating upwind flight (e.g., Hagaman and Cardé 1984). In contrast, cerambycids presented with male-produced aggregation pheromones have not been observed to display such overt behaviors. However, among those species that have female-produced sex pheromones, males may indeed activate rapidly when presented with odors from females (e.g., Cervantes et al. 2006). Fourth, cerambycids may only produce and respond to pheromones during specific daily time windows, and in fact, this appears to be one mechanism by which sympatric and seasonally synchronic species, which share one or more pheromone components, are able to maintain reproductive isolation (Mitchell et al. 2015). Fifth, there is growing evidence that adults of at least some cerambycids are highly stratified within forests, with some species rarely leaving the canopy. Thus, such species are unlikely to be captured during field bioassays using traps in the understory (e.g., Graham et al. 2012). Sixth, early investigators may not have appreciated that relatively high doses and high release rates of synthetic pheromones typically are required to attract those species that use male-produced aggregation pheromones. That is, studies have shown that individual males may release many micrograms of pheromones per hour (e.g., Iwabuchi 1986; Iwabuchi et al. 1987; Hall et al. 2006a; Lacey et al. 2007a), which translates into release rates of ~1 mg/day or more from a passive pheromone dispenser that releases pheromones constantly in order to match the release rate from a single male. Release rates lower than this may result in weak or no attraction to the male-produced aggregation pheromones (e.g., Lacey et al. 2004). Finally, it has become clear that use of appropriate trap designs is critically important in trapping cerambycids, with more than 10-fold differences in trap catch among different trap types (e.g., Graham et al. 2010; Allison et al. 2011, 2014). Any one, or any subset of these reasons may have obscured evidence of pheromone-mediated attraction among conspecifics and contributed to the erroneous impression that cerambycids generally did not use long-range sex or aggregation pheromones. As should become clear in the sections that follow, several cumulative factors contributed to the reversal of this dogma and resulted in our current working hypothesis that the use of attractant pheromones is widespread among the Cerambycidae.

5.2 Use of Pheromones in Cerambycid Reproduction

As with most insects, cerambycids use two distinct types of chemical signals to mediate reproductive interactions: volatile attractants that act over a distance to bring conspecifics together and less volatile to nonvolatile cuticular lipids for close-range recognition of sex and species. There is also increasing evidence that male beetles may use nonvolatile compounds deposited by females on substrates on which they have walked as a form of trail pheromone, allowing males to track and locate females.

The earlier literature reviewed for this chapter suggested three general scenarios for bringing the sexes together for mating:

1. One sex produces a pheromone that attracts the other sex, or both sexes, over long distances, with no additive or synergistic effects from host plant odors. As discussed here, earlier reports of this behavior may have been lacking due to inappropriate bioassay conditions, such as insufficient pheromone release rates or inefficient traps. Since then, a large number of species that fit this scenario have been discovered.

2. One sex produces an attractant pheromone, which acts additively or synergistically with host plant volatiles, to attract one or both sexes. It has become clear that this is a common scenario and that different species display a range of responses—from essentially no attraction to pheromones or host volatiles alone but strongly synergistic attraction to blends of the two, to weaker, additive attraction to blends as compared to pheromones alone.
3. Neither sex produces long-range attractant pheromones; instead, males and females are brought together by their mutual attraction to larval host plants (Linsley 1959), with attraction mediated by plant volatiles (e.g., Hanks et al. 1996; Lu et al. 2007; Flaherty et al. 2013). *Phoracantha semipunctata* (F.) may represent an example of this type of strategy because repeated attempts by the authors and others have failed to find any evidence of behaviors mediated by volatile pheromones. Alternatively, both sexes may be drawn by visual or olfactory cues to flowers or other food sources upon which adults feed and so are brought into contact (e.g., Wang et al. 1996; Reagel et al. 2002; Wang and Chen 2005).

These probably cover the main scenarios and strategies for mate location. Nevertheless, it is entirely possible that there are other scenarios still waiting to be discovered, given the great number and diversity of cerambycid species.

To date, attractant pheromones have been identified from five of the eight currently recognized subfamilies within the Cerambycidae (see Švácha and Lawrence 2014). The pheromones are of two types:

1. Male-produced pheromones that attract both sexes. By the standard definition, these would be classified as aggregation pheromones (produced by one or both sexes and attracting both sexes). But, in actuality, it is likely that they primarily serve to bring the sexes together for mating or to enhance mating in other ways, and so it may be more appropriate to refer to them as aggregation-sex pheromones (see discussion in Cardé 2014).
2. Female-produced sex pheromones that attract males exclusively.

Although these two types of pheromones likely serve the same overall purpose of bringing the sexes together for mating, some further discussion of the differences between them is warranted because these differences are almost certainly correlated with the ecology and life history of the producing species. Thus, the male-produced aggregation pheromones are produced in large amounts, sometimes more than 30 μg/h (Iwabuchi 1986; Iwabuchi et al. 1987; Hall et al. 2006a; Lacey et al. 2007a). These amounts far exceed the amount required to be detected by females because, in electroantennogram assays, antennae of females are sensitive to nanogram quantities of the pheromones (e.g., Zhang et al. 2002; Hall et al. 2006a; Pajares et al. 2010). It also is likely that these compounds, as their name implies, are involved in the formation of the conspecific aggregations that have been commonly observed among some species (see Chapter 4). Furthermore, there is some evidence that calling males stimulate other males to call in a type of "chorusing" behavior (Lemay et al. 2010). In combination, these three points suggest that aggregation pheromones also are involved in sexual selection, with males competing to advertise their fitness to females by their production of voluminous (and costly) amounts of pheromone.

In contrast, the female-produced sex pheromones appear to be emitted in much smaller amounts, perhaps on the order of a few nanograms per female per hour (Rodstein et al. 2009; Ray et al. 2012b). Furthermore, in at least some instances, it has been shown that they elicit immediate activation and upwind orientation by males (Cervantes et al. 2006; Rodstein et al. 2011) and that males can detect and respond to pheromone sources over distances of hundreds of meters (Maki et al. 2011a). Among the species that use these sex pheromones, it is likely that scramble competition prevails, with the first male to find a calling female immediately attempting to mate with her, and later arriving males challenging the paired male (see Chapter 4). These species also may be more likely to have nonfeeding adults, so that there is some urgency to find a mate before they run out of energy and die (see Chapter 4).

From among the ~115 species for which pheromones or likely pheromones are known (Table 5.1), without exception to date, the use of these two types of pheromones breaks out along taxonomic lines. Thus, all known attractant pheromones or likely pheromones for species in the subfamilies Prioninae (identified for ~25 species) and Lepturinae (~10 species) are female-produced sex pheromones, whereas

TABLE 5.1

Summary of Published Research from Field Trials on Volatile Pheromones, Attractants, Synergists, and Antagonists of Cerambycid Beetles

Taxonomy	Volatiles emitted (Pher = confirmed attractant)	Sex	Attractant (Attr), enhancer (Enh), antagonist (Antag)	References
CERAMBYCINAE				
Anaglyptini				
Anaglyptus colobotheoides Bates	–	–	Attr: 3-C6-ketol	Sweeney et al. 2014
Anaglyptus subfasciatus Pic	Pher: 3*R*-C6-, 3*R*-C8-ketol	M	Attr and Enh: floral volatiles	Nakashima et al. 1994; Leal et al. 1995
Cyrtophorus verrucosus (Olivier)	Pher: 3*R*-C6-ketol, nonan-2-one	M	Antag: (2,3)-C6-diol, plant volatiles	Hanks and Millar 2013; Mitchell et al. 2013, 2015
Callidiini				
Callidiellum rufipenne (Motschulsky)	Pher: 3*R*-, 3*S*-, 2*R*-, 2*S*-C6-ketol	M	Enh: 1-(1*H*-pyrrol-2-yl)-1,2-propanedione	Zou et al. 2016
Hylotrupes bajulus (L.)	Pher. 3*R*-C6-ketol, (2*S*,3*R*)-, (2*R*,3*R*)-C6-diol, (2,3)-C6-dione	M	–	Fettköther et al. 1995
Phymatodes aereus (Newman)	Pher: 3*R*-, 3*S*-C6-ketol	M	Attr: 3-C6-ketol + 3-C8-ketol; Enh: (2,3)-C6-diol; Antag: 2-methylbutan-1-ol	Hanks and Millar 2013; Mitchell et al. 2015
Phymatodes amoenus (Say)	Pher: 3*R*-C6-ketol, (*R*)-2-methylbutan-1-ol	M	Antag: plant volatiles	Hanks and Millar 2013; Mitchell et al. 2015
Phymatodes grandis (= lecontei) Casey	Pher: (*R*)-2-methylbutan-1-ol	M	Attr: 3*R*-, 3*S*-C6-ketol	Hanks et al. 2007
Phymatodes lengi Joutel	Pher: 3*R*-C6-ketol, (*R*)-2-methylbutan-1-ol	M	–	Hanks et al. 2012; Mitchell et al. 2015
Phymatodes pusillus (F.)	1-hexanol, 1-butanol, 1-octanol	M	–	Schröder 1996
Phymatodes testaceus (L.)	Pher: (*R*)-2-methylbutan-1-ol	M	Attr: 3-C6-ketol + (2,3)-C6-diol; Antag: plant volatiles	Sweeney et al. 2004; Hanks and Millar 2013
Phymatodes varius (F.)	Pher: 3*R*-C6-ketol, (*R*)-2-methylbutan-1-ol	M	Attr: *syn*-C6-diol; Antag: plant volatiles	Hanks and Millar 2013; Mitchell et al. 2015
Pyrrhidium sanguineum (L.)	3*R*-C6-ketol, (2*R*,3*R*)-, (2*S*,3*R*)-C6-diol	M	–	Schröder et al. 1994
Clytini				
Clytus arietis (L.)	3*R*-, 2*S*-C8-ketol, (2,3)-C8-diol	M	–	Schröder 1996
Clytus ruricola (Olivier)	–	–	Attr: plant volatiles	Montgomery and Wargo 1983
Curius dentatus Newman	–	–	Attr: *anti*-C6-diol; Antag: *syn*-C6 diol	Lacey et al. 2004; Hanks and Millar 2013
Demonax balyi Pascoe	–	–	Attr: 2*S*-C10-ketol	Hall et al. 2006a
Demonax gracilestriatus Gressitt & Rondon	–	–	Attr: 3-C6-ketol	Wickham et al. 2014

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Demonax l. literalis Gahan	–	–	Attr: 3-C6-ketol	Wickham et al. 2014
Demonax ordinatus Pascoe	–	–	Attr: *syn*-C8-diol	Wickham et al. 2014
Demonax theresae Pic	–	–	Attr: *anti*-C8-diol	Wickham et al. 2014
Megacyllene caryae (Gahan)	Pher: (2*R*,3*S*)-, (2*S*,3*R*)-C6-diol, (*S*)-(–)-limonene, 2-phenylethanol, (–)-α-terpineol, nerol, neral, geranial	M	Attr: citral, *syn*-C6-diol; Antag: plant volatiles	Lacey et al. 2008b; Hanks and Millar 2013; Handley et al. 2015
Neoclytus a. acuminatus (F.)	Pher: (2*S*,3*S*)-C6-diol	M	Attr: plant volatiles; Antag: *anti*-C6-diol, 3-C6-ketol, plant volatiles	Lacey et al. 2004; Hanks et al. 2012; Hanks and Millar 2013
Neoclytus balteatus LeConte	3*R*-C6-ketol, (2*S*,3*S*)-C6-, C8-diol	M	–	Ray et al. 2015
Neoclytus caprea (Say)	Pher: 3*R*-C6-ketol	M	Antag: plant volatiles	Hanks and Millar 2013; Ray et al. 2015
Neoclytus conjunctus (LeConte)	Pher: 3*R*-C6-ketol	M	–	Ray et al. 2015
Neoclytus irroratus (LeConte)	Pher: 3*R*-C6-ketol	M	Antag: 3*S*-C6-ketol	Ray et al. 2015
Neoclytus m. modestus Fall	Pher: 3*R*-C6-ketol	M	Antag: 3*S*-C6-ketol	Ray et al. 2015
Neoclytus m. mucronatus (F.)	Pher: 3*R*-C6-ketol	–	Attr: plant volatiles; Antag: (2,3)-C6-diol	Lacey et al. 2007a; Hanks et al. 2012; Miller et al. 2015a, 2015b; Ray et al. 2015
Neoclytus mucronatus vogti Linsley	3*R*-C6-ketol	M	–	Ray et al. 2015
Neoclytus scutellaris (Olivier)	Pher: 3*R*-C6-ketol	M	–	Ray et al. 2015
Neoclytus tenuiscriptus Fall	Pher: (2*S*,3*S*)-C6-diol	M	Antag: *anti*-C6-diol	Ray et al. 2015
Plagionotus arcuatus L.	3*R*-, 2-C10-ketol	M	–	Schröder 1996
Plagionotus christophi (Kraatz)	2-C8-ketol, (2,3)-C8-diol	M	–	Iwabuchi 1999
Rhaphuma horsfieldi (White)	–	–	Attr: *syn*-C6-, *syn*-C8-diol	Wickham et al. 2014
Rhaphuma laosica Gressitt & Rondon	–	–	Attr: *anti*-C6-diol	Wickham et al. 2014
Sarosesthes fulminans (F.)	Pher: 3*R*-C6-ketol, (2*S*,3*R*)-C6-diol	M	Attr: *anti*-C6-diol	Lacey et al. 2009; Hanks and Millar 2013
Xylotrechus antilope Schönh.	2*S*-, 3*R*-, 3*S*-C8-ketol	M	–	Schröder 1996
Xylotrechus atronotatus draconiceps Gressitt	–	–	Attr: 3-C6-ketol	Wickham et al. 2014
Xylotrechus chinensis (Chevrolat)	2*S*-, 3-C8-ketol, (2*S*,3*S*)-C8-diol	M	–	Iwabuchi et al. 1987; Kuwahara et al. 1987
Xylotrechus colonus (F.)	Pher: 3*R*-, 3*S*-C6-ketol, (2*R*,3*R*)-, (2*S*,3*S*)-, (2*R*,3*S*)-, (2*S*,3*R*)-C6-diol	M	Attr: plant volatiles; Antag: (2,3)-C6-diol	Lacey et al. 2009; Hanks et al. 2012; Hanks and Millar 2013, LMH, unpublished data

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Xylotrechus incurvatus (Chevrolat)	–	–	Attr: 3-C6-ketol	Wickham et al. 2014
Xylotrechus longitarsus Casey	–	–	Attr: plant volatiles	Morewood et al. 2002
Xylotrechus nauticus (Mannerheim)	Pher: 3*R*-, 3*S*-C6-ketol	M	–	Hanks et al. 2007
Xylotrechus pyrrhoderus Bates	Pher: (2*S*,3*S*)-C8-diol, 2*S*-C8-ketol	M	Antag: 2*R*-C8-ketol	Sakai et al. 1984; Iwabuchi et al. 1986; Narai et al. 2015
Xylotrechus quadripes Chevrolat	Pher: 2*S*-, 3-C10-ketol, 2-C8-ketol, (2*S*,3*S*)-C10-diol, (2,3)-C10-dione, 2-phenylethanol	M	–	Jayarama et al. 1998; Hall et al. 2006a
Xylotrechus rufilius Bates	–	–	Attr: 2-C8-ketol; Antag: *syn*-C8-diol	Iwabuchi 1999; Narai et al. 2015
Xylotrechus s. sagittatus (Germar)	–	–	Attr: plant volatiles	Miller et al. 2011, 2015a, 2015b; Hanks and Millar 2013
Xylotrechus undulatus (Say)	–	–	Attr: plant volatiles	Chénier and Philogène 1989
Xylotrechus villioni (Villard)	2-C8-ketone, (2,3)-C8-diol	M	–	Iwabuchi 1999
Compsocerini				
Rosalia funebris Motschulsky	Pher: (*Z*)-3-decenyl (*E*)-2-hexenoate	M	–	Ray et al. 2009a
Elaphidiini				
Anelaphus inflaticollis Chemsak	Pher: 3*R*-, 2*S*-C6-ketol, (2*R*,3*R*)-, (2*R*,3*S*)-C6-diol	M	–	Ray et al. 2009b
Anelaphus parallelus (Newman)	–	–	Attr: *syn*-C6-diol; Antag: 3-C6-ketol + *anti*-C6-diol	Hanks and Millar 2013
Anelaphus pumilus (Newman)	Pher: 3*R*-C6-ketol	M	–	Mitchell et al. 2015
Anelaphus villosus (F.)	–	–	Attr: *syn*-C6-diol, plant volatiles; Antag: plant volatiles	Montgomery and Wargo 1983; Hanks and Millar 2013
Elaphidion mucronatum (Say)	–	–	Attr: plant volatiles	Dunn and Potter 1991
Enaphalodes rufulus (Haldeman)	(2*S*,3*S*)-, (2*S*,3*R*)-C6-diol	M	–	Dahl 2006
Orwellion gibbulum arizonense (Casey)	3*R*-C6-ketol, decan-2-one	M	–	Mitchell et al. 2013
Parelaphidion aspersum (Haldeman)	3*R*-C6-ketol, nonan-2-one	M	–	Mitchell et al. 2013

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Hesperophanini				
Tylonotus bimaculatus Haldeman	Pher: (2*S*,4*E*)-2-hydroxy-4-octen-3-one; (3*R*,4*E*)-3-hydroxyoct-4-en-2-one, (*E*)-4-octen-2,3-dione, 2,3-C8-dione	M	–	Zou et al. 2015
Molorchini				
Molorchus minor (L.)	–	–	Attr: 3-C8-ketol + plant volatiles	Sweeney et al. 2014
Molorchus umbellatarum Schreb.	–	–	Attr: *anti*-C8-diol	Imrei et al. 2013
Obriini				
Obrium maculatum (Olivier)	–	–	Attr: fuscumol acetate	Mitchell et al. 2011; Hanks and Millar 2013
Tillomorphini				
Euderces picipes (F.)	3*R*-C6-ketol	M	Antag: 2-methylbutan-1-ol, nonan-2-one	Mitchell et al. 2015
Trachyderini				
Tragidion armatum brevipenne Linsley	3*R*-C6-ketol	M	–	Hanks et al. 2007
LAMIINAE				
Acanthocerini				
Acanthocinus aedilis (L.)	–	–	Attr: plant volatiles	Schroeder and Weslien 1994
Acanthocinus nodosus (F.)	–	–	Attr: plant volatile + bark beetle pheromones	Miller et al. 2015a, 2015b
Acanthocinus obliquus (LeConte)	–	–	Attr: plant volatile + bark beetle pheromones	Costello et al. 2008
Acanthocinus obsoletus (Olivier)	–	–	Attr: Plant volatiles and/or bark beetle pheromones	Miller and Asaro 2005; Miller et al. 2015a, 2015b
Acanthocinus princeps (Walker)	–	–	Attr: plant volatile + bark beetle pheromones	Macias-Samano et al. 2012
Acanthocinus spectabilis (LeConte)	–	–	Attr: plant volatile + bark beetle pheromones	Costello et al. 2008
Astyleiopus variegatus (Haldeman)	Pher: *S*-fuscumol, *S*-fuscumol acetate	M	Enh: plant volatiles; Antag: plant volatiles	Mitchell et al. 2011; Hanks et al. 2012; Hanks and Millar 2013; Hughes et al. 2013

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Taxonomy	Volatiles emitted (Pher = confirmed attractant)	Sex	Attractant (Attr), enhancer (Enh), antagonist (Antag)	References
Astylidius parvus (LeConte)	–	–	Attr: fuscumol, fuscumol + fuscumol acetate; Enh: plant volatiles	Mitchell et al. 2011; Hanks et al. 2012
Astylopsis macula (Say)	–	–	Attr: fuscumol + fuscumol acetate, plant volatiles	Hanks and Millar 2013
Astylopsis sexguttata (Say)	–	–	Attr: plant volatiles and/or bark beetle pheromones; Enh: bark beetle pheromones	Miller et al. 2011, 2015a, 2015b; Hanks and Millar 2013
Graphisurus fasciatus (Degeer)	–	–	Attr: fuscumol + fuscumol acetate, fuscumol acetate, plant volatiles; Enh: plant volatiles; Antag: plant volatiles	Mitchell et al. 2011; Hanks et al. 2012; Hanks and Millar 2013
Leptostylus transversus (Gyllenhal)	–	–	Attr: fuscumol	Mitchell et al. 2011
Lepturges angulatus (LeConte)	–	–	Attr: fuscumol acetate, fuscumol + fuscumol acetate; Enh: plant volatiles	Mitchell et al. 2011; Hanks et al. 2012; Hanks and Millar 2013
Lepturges confluens (Haldeman)	–	–	Attr: fuscumol + fuscumol acetate; Enh: plant volatiles	Hanks and Millar 2013
Acanthoderini				
Acanthoderes quadrigibba (Say)	–	–	Attr: fuscumol + fuscumol acetate; Antag: plant volatiles	Hanks and Millar 2013
Aegomorphus modestus (Gyllenhal)	–	–	Attr: fuscumol acetate, fuscumol + fuscumol acetate; Antag: plant volatiles	Mitchell et al. 2011; Hanks et al. 2012; Hanks and Millar 2013
Hedypathes betulinus (Klug)	Fuscumol acetate, geranylacetone, fuscumol	M	–	Fonseca et al. 2010
Sternidius alpha (Say)	–	–	Attr: plant volatiles, fuscumol, fuscumol acetate; Antag: plant volatiles	Mitchell et al. 2011; Hanks and Millar 2013
Steirastoma breve (Sulzer)	Fuscumol	M	–	Liendo-Barandiaran et al. 2010b
Urgleptes querci (Fitch)	–	–	Attr: plant volatiles	Montgomery and Wargo 1983
Agniini				
Acalolepta formosana (Breuning)	–	–	Attr: monochamol	Wickham et al. 2014
Dorcaschematini				
Dorcaschema alternatum (Say)	–	–	Attr: *anti*-C6-diol; Antag: 3-C6-ketol + *syn*-C6-diol	Hanks and Millar 2013

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Lamiini				
Pharsalia subgemmata (Thomson)	–	–	Attr: monochamol	Wickham et al. 2014
Pseudomacrochenus antennatus (Gahan)	–	–	Attr: monochamol	Wickham et al. 2014
Xenohammus bimaculatus Schwarzer	–	–	Attr: monochamol	Wickham et al. 2014
Monochamini				
Anoplophora chinensis (Forster)	Pher: 4-(heptyloxy)butan-1-ol	M	–	Hansen et al. 2015
Anoplophora glabripennis (Motschulsky)	Pher: 4-(heptyloxy)butanal, 4-(heptyloxy) butan-1-ol, (*E*,*E*)-α-farnesene	M	Attr: plant volatiles	Zhang et al. 2002; Nehme et al. 2010, 2014; Crook et al. 2014
Monochamus alternatus Hope	Pher: monochamol	M	Attr and Enh: plant volatiles	Fan et al. 2007a, 2007b; Teale et al. 2011
Monochamus bimaculatus Gahan	–	–	Attr: monochamol	Wickham et al. 2014
Monochamus carolinensis (Olivier)	Pher: monochamol	M	Attr, Enh, and Antag: plant volatiles	Phillips et al. 1988; Allison et al. 2012; Hanks et al. 2012; Hanks and Millar 2013; Ryall et al. 2015
Monochamus clamator (LeConte)	–	–	Attr: monochamol + plant volatiles; Enh: bark beetle pheromones	Miller and Borden 1990; Allison et al. 2001, 2003; Morewood et al. 2003; Costello et al. 2008; Macias-Samano et al. 2012
Monochamus galloprovincialis (Olivier)	Pher: monochamol	M	Attr and Enh: plant volatiles	Ibeas et al. 2007; Pajares et al. 2010; Jurc et al. 2012, Rassati et al. 2012
Monochamus leuconotus LeConte	2-(4-heptyloxy-1-butyloxy)ethan-1-ol	M	–	Hall et al. 2006b; Pajares et al. 2010
Monochamus marmorator Kirby	–	–	Attr: monochamol + plant volatiles	Ryall et al. 2015
Monochamus mutator LeConte	–	–	Attr: monochamol + plant volatiles	Ryall et al. 2015
Monochamus notatus (Drury)	–	–	Attr: monochamol, *syn*-C6-diol + plant volatiles, plant volatiles, bark beetle pheromones; Enh: plant volatiles	Allison et al. 2001, 2012; Fierke et al. 2012; Hanks and Millar 2015; Ryall et al. 2015
Monochamus obtusus Casey	–	–	Attr: monochamol + plant volatiles, plant volatiles, bark beetle pheromones	Allison et al. 2001; Macias-Samano et al. 2012

(Continued)

TABLE 5.1 ***(Continued)***

Summary of Published Research from Field Trials on Volatile Pheromones, Attractants, Synergists, and Antagonists of Cerambycid Beetles

Taxonomy	Volatiles emitted (Pher = confirmed attractant)	Sex	Attractant (Attr), enhancer (Enh), antagonist (Antag)	References
Monochamus saltuarius (Gebler)	–	–	Attr: monochamol	Ryall et al. 2015
Monochamus s. scutellatus (Say)	Pher: monochamol	M	Attr and Enh: plant volatiles, bark beetle pheromones; Antag: bark beetle pheromones	Chénier and Philogène 1989; Allison et al. 2001, 2003; Morewood et al. 2003; Fierke et al. 2012; Macias-Samano et al. 2012; Hanks and Millar 2013; Ryall et al. 2015
Monochamus sutor (L.)	Pher: monochamol	M	Attr: Bark beetle pheromones	Pajares et al. 2013
Monochamus titillator (F.)	–	–	Attr: monochamol + plant volatiles, plant volatiles, bark beetle pheromones	Billings and Cameron 1984; Phillips et al. 1988; Miller and Asaro 2005; Allison et al. 2012
Monochamus urussovii (Fischer)	–	–	Attr: monochamol + plant volatiles, plant volatiles	Sweeney et al. 2004; Ryall et al. 2015
LEPTURINAE				
Desmocerini				
Desmocerus a. aureipennis Chevrolat	Pher: (*R*)-desmolactone	F	–	Ray et al. 2014
Desmocerus a. cribripennis Horn	–	–	Attr: (*R*)-desmolactone	Ray et al. 2014
Desmocerus a. lacustris Linsley and Chemsak	–	–	Attr: (*R*)-desmolactone	Ray et al. 2014
Desmocerus c. californicus Horn	Pher: (*R*)-desmolactone	F	–	Ray et al. 2012
Desmocerus californicus dimorphus Fisher	–	–	Attr: (*R*)-desmolactone; Antag: (*S*)-desmolactone	Ray et al. 2014
Desmocerus palliatus (Forster)	–	–	Attr: (*R*)-desmolactone; Antag: (*S*)-desmolactone	Ray et al. 2014
Lepturini				
Analeptura lineola (Say)	–	–	Attr: plant volatiles	Montgomery and Wargo 1983
Ortholeptura valida (LeConte)	Pher: *cis*-vaccenyl acetate	F	–	Ray et al. 2011
Rhagiini				
Acmaeops proteus (Kirby)	–	–	Attr: monoterpenes, plant volatiles; Enh: bark beetle pheromones	Chénier and Philogène 1989; Costello et al. 2008; Miller et al. 2015a, 2015b

(Continued)

TABLE 5.1 ***(Continued)***

Summary of Published Research from Field Trials on Volatile Pheromones, Attractants, Synergists, and Antagonists of Cerambycid Beetles

Taxonomy	Volatiles emitted (Pher = confirmed attractant)	Sex	Attractant (Attr), enhancer (Enh), antagonist (Antag)	References
Rhagium inquisitor (L.)	–	–	Attr: plant volatiles, bark beetle pheromones	Schroeder and Weslien 1994; Miller et al. 2011; Jurc et al. 2012; Hanks and Millar 2013; Miller et al. 2015a, 2015b
PRIONINAE				
Megopidini				
Megopis costipennis White	Pher: (2*R*,3*S*)-C8 diol	F	Attr: *anti*-C8-diol	Wickham et al. 2014, 2016
Meroscelisini				
Tragosoma depsarium “harrisi” LeConte	–	–	Attr: (2*S*,3*R*)-C6-diol; Antag: *syn*-C6-diol	Ray et al. 2012a
Tragosoma depsarium **“**sp. nov. Laplante**”**	Pher: (2*R*,3*R*)-C6 diol	F	Antag: *anti*-C6-diol	Ray et al. 2012a
Tragosoma pilosicorne Casey	–	–	Attr: (2*S*,3*R*)-C6-diol	Ray et al. 2012a
Prionini				
Dorythenes granulosus (Thomson)	–	–	Attr: prionic acid	Wickham et al. 2016a
Prionus aztecus Casey	–	–	Attr: prionic acid	Barbour et al. 2011
Prionus californicus Motschulsky	Pher: prionic acid	F	–	Rodstein et al. 2009, 2011
Prionus coriarius (L.)	–	–	Attr: prionic acid	Barbour et al. 2011
Prionus imbricornis (L.)	–	–	Attr: prionic acid	Barbour et al. 2011
Prionus integer LeConte	–	–	Attr: prionic acid	Barbour et al. 2011
Prionus laticollis (Drury)	–	–	Attr: prionic acid	Barbour et al. 2011
Prionus lecontei Lameere	–	–	Attr: prionic acid	Barbour et al. 2011
Prionus linsleyi Hovore	–	–	Attr: prionic acid	Barbour et al. 2011
Prionus pocularis Dalman	–	–	Attr: plant volatiles	Miller et al. 2015a, 2015b

(Continued)

TABLE 5.1 ***(Continued)***

Summary of Published Research from Field Trials on Volatile Pheromones, Attractants, Synergists, and Antagonists of Cerambycid Beetles

Taxonomy	Volatiles emitted (Pher = confirmed attractant)	Sex	Attractant (Attr), enhancer (Enh), antagonist (Antag)	References
SPONDYLIDINAE				
Asemini				
Arhopalus rusticus (L.)	–	–	Attr: plant volatiles	Jurc et al. 2012; Miller et al. 2015a, 2015b
Arhopalus ferus (Mulsant)	–	–	Attr: plant volatiles; Antag: plant volatiles	Suckling et al. 2001; Wang and Leschen 2003
Asemum striatum (L.)	–	–	Attr: plant volatiles	Chénier and Philogène 1989; Sweeney et al. 2004; Miller et al. 2011, 2015a, 2015b; Hanks and Millar 2013
Tetropium castaneum (L.)	–	–	Attr: plant volatiles; Enh: fuscumol + fuscumol acetate	Sweeney et al. 2004, 2010, 2014
Tetropium cinnamopterum (Kirby)	Pher: *S*-fuscumol	M	Attr and Enh: plant volatiles	Silk et al. 2007; Sweeney et al. 2010; Hanks and Millar 2013
Tetropium fuscum (F.)	Pher: *S*-fuscumol	M	Attr and Enh: plant volatiles	Sweeney et al. 2004, 2010; Silk et al. 2007
Tetropium schwarzianum Casey	–	–	Attr: fuscumol + fuscumol acetate; Enh: plant volatiles	Hanks and Millar 2013
Spondylidini				
Spondylis buprestoides (L.)	–	–	Attr: plant volatiles	Sweeney et al. 2004; Jurc et al. 2012

Note: The sex that emits volatiles is indicated by M (male) and F (female). Confirmed pheromones (indicated by “Pher”) that were produced by males attracted both sexes, whereas those produced by females attracted only males (see text). Compound abbreviations: carbon chainlength indicated by C6, C8, or C10; ketol, 2- or 3-hydroxyalkanone; diol, (2,3)-alkanediol; dione, (2,3)-alkanedione. Blends of chemicals tested in field trials are indicated by “+”.

all known attractant pheromones or likely pheromones from species in the subfamilies Cerambycinae, Lamiinae, and Spondylidinae are male-produced aggregation pheromones (Table 5.1). Thus, through evolutionary time, the subfamilies appear to have diverged in their use of different types of pheromones, but the underlying causes for this divergence are not yet clear.

No attractant pheromones are known for any species in the remaining three subfamilies, (Dorcasominae, Necydalinae, Parandrinae), but it should be pointed out that these subfamilies are relatively small. It also must be pointed out that pheromones have been identified for two species, *Migdolus fryanus* Westwood (Leal et al. 1994) and *Vesperus xatarti* Mulsant (Boyer et al. 1997), which formerly were considered in the Cerambycidae, but taxonomic revisions have now placed these species in their own family, the Vesperidae (Švácha and Lawrence 2014). Hence, the pheromones of these two species will not be discussed here.

5.3 Volatile Pheromones from the Various Subfamilies

5.3.1 Subfamily Cerambycinae

The first volatile pheromone found in the Cerambycidae was identified from the Japanese cerambycine *Xylotrechus pyrrhoderus* Bates (Sakai et al. 1984; Iwabuchi 1986). The pheromone is produced by males and consists of two components, (*S*)-2-hydroxyoctan-3-one and (2*S*,3*S*)-2,3-octanediol (Figure 5.1 and Table 5.1). Wind tunnel and field cage experiments showed that the ketol component was somewhat attractive on its own, whereas the diol was not, but it synergized attraction to the ketol (Iwabuchi et al. 1986; Iwabuchi 1988). Furthermore, the "nonnatural" enantiomer (*R*)-2-hydroxyoctan-3-one inhibited attraction. The same two gross structures were found in the congener *X. chinensis* (Chevrolat), but it was not possible to determine which stereoisomers were produced (Iwabuchi et al. 1987). Over the next 15 years, male-produced pheromones were reported from another four cerambycine species (Table 5.1), including *Pyrrhidium sanguineum* (L.), *Hylotrupes bajulus* (L.), *Anaglyptus subfasciatus* Pic, and *Xylotrechus quadripes* Chevrolat. Remarkably, the structures of the pheromones of all six of these cerambycine species, from different areas of the world, were all very similar, with all of them consisting of unbranched 6-, 8-, or 10-carbon chains with either a ketone and an alcohol function in the two and three positions or alcohols in both positions (Figure 5.1). On this basis, we synthesized and (with the help of numerous collaborators) tested a library of these types of structures in field screening trials in North America and other parts of the world, with remarkable results (see Table 5.1). To summarize a decade of trials, these types of compounds now are known to be male-produced pheromone components for numerous cerambycine species and likely pheromones for many more that have been attracted in significant numbers in field trials but that have not yet been shown to produce the compounds to which they were attracted. The cumulative data have elucidated a number of trends:

1. Chain lengths of the hydroxyketones and 2,3-alkanediols appear to be restricted to 6, 8, or 10 carbons.
2. Although 6-, 8-, and 10-carbon 2,3-alkanediones frequently are found in extracts of headspace volatiles from males, they do not appear to be active components of the pheromones. Rather, they may be biosynthetic intermediates or artifacts from degradation of the corresponding ketols during analysis (Sakai et al. 1984; Leal et al. 1995; Millar et al. 2009).
3. In the hydroxyketones, the ketone can be in the 2- or 3-position. When in the 2-position, for example, 3-hydroxyalkan-2-one, the (*R*)-configuration is strongly favored, whereas when the ketone is in the 3-position (2-hydroxyalkan-3-one), the (*S*)-configuration appears most common (Table 5.1). For reasons that are not known, 3-hydroxyalkan-2-ones appear to be much more common than the isomeric 2-hydroxyalkan-3-ones, but this may be due to the fact that more field screening trials have been carried out with the former. Furthermore, beetles generally appear to be insensitive to the enantiomeric purity of the hydroxyketones (but see Iwabuchi et al. 1986 for an example where they are not), whereas there are a number of examples of beetles being inhibited by other structural analogs (Table 5.1).

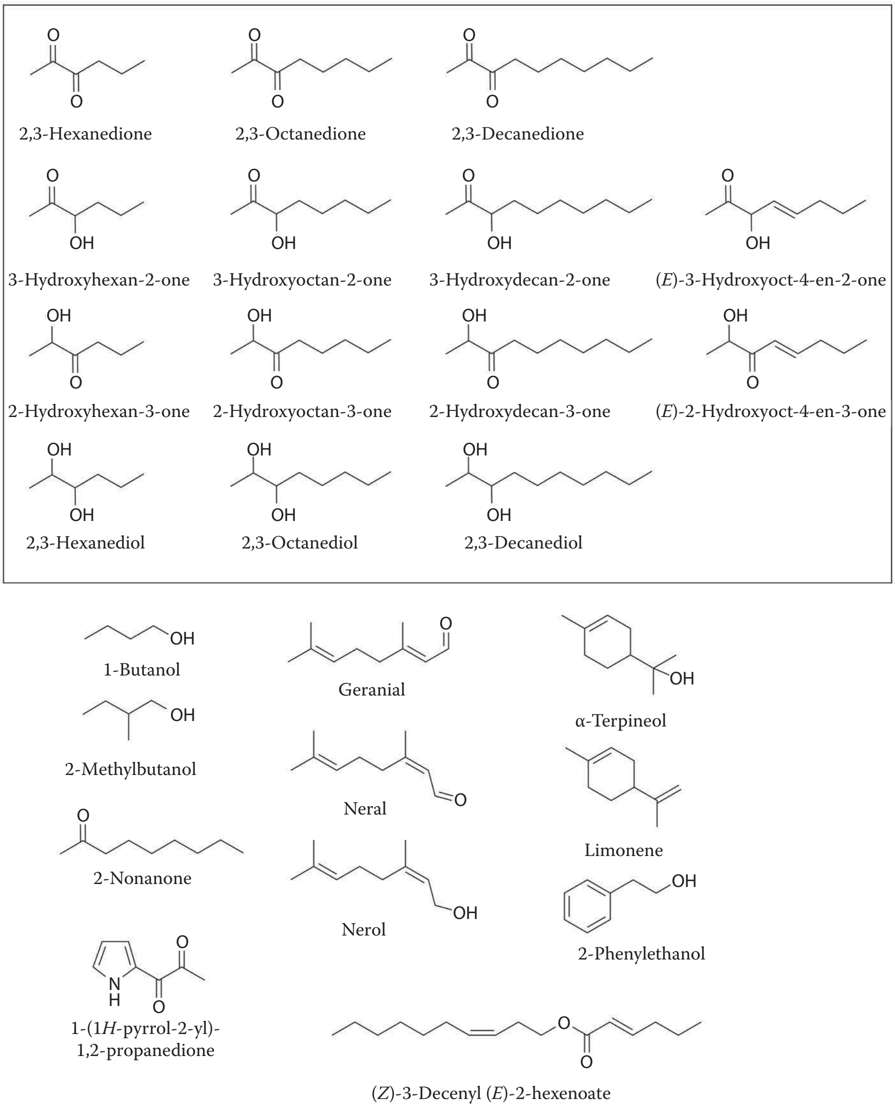

FIGURE 5.1 Pheromone structures and related compounds identified from species in the subfamily Cerambycinae. The structures in the box are the fairly well-defined group of 2,3-alkanediones, 2-hydroxyalkan-3-ones, 3-hydroxylalkan-2-ones, and 2,3-alkanediols. The remaining structures belong to various classes of compounds.

4. The 2,3-alkanediols each have four possible stereoisomers (two diastereomeric pairs of enantiomers). For those species using 2,3-alkanediol pheromone components, there are no examples known of inhibition by the "non-natural" enantiomer, but there are several examples known of species being inhibited by one or both of the diastereomers (Table 5.1).
5. All known examples of volatile pheromones from species in the subfamily Cerambycinae are male-produced, and many of the pheromones appear to be produced from glandular tissue in the prothorax (see following).

To date, the only variation that has appeared on these hydroxyketone and diol structures is the addition of a double bond between carbons 4 and 5, for the cerambycine *Tylonotus bimaculatus* Haldeman, males of which produce (2*S*,4*E*)-2-hydroxy-4-octen-3-one and lesser amounts of relatively unstable (3*R*,4*E*)-3-hydroxy-4-octen-2-one (Figure 5.1 and Table 5.1).

However, it is rapidly becoming clear that cerambycine species use a wide variety of other compounds as male-produced pheromone components, and these compounds currently defy ready classification into related structural groups (see Figure 5.1 and Table 5.1). For example, several species use 2-methylbutan-1-ol as a pheromone component, either as a single component or in combination with other components such as 3-hydroxyhexan-2-one. Several others produce a novel diketopyrrole structure (1-[1*H*-pyrrol-2-yl]-1,2-propanedione) (Zou et al. 2016). The North American species *Megacyllene caryae* (Gahan) produces a complicated blend consisting of two 2,3-hexanediols, along with several terpenoids and aromatic compounds. Whereas initial field trials suggested that most of the components were necessary to attract beetles, subsequent bioassays over several years have shown that an isomeric blend of geranial and neral (= citral), among the most abundant components in the blend, is highly attractive without the remaining minor components (e.g., Handley et al. 2015). Other compounds appear to be unique; for example, the North American species *Rosalia funebris* Motschulsky uses (*Z*)-3-decenyl (*E*)-2-hexenoate as its male-produced pheromone, which has not attracted any other cerambycid species in field trials in North America, Asia, or Europe. Overall though, based on the trends that have emerged so far, it seems safe to say that most of the compounds mentioned earlier in this chapter will turn out to be pheromone components of additional species. Conversely, it is certain that other entirely new cerambycine pheromone structures remain to be discovered.

Two general types of glandular tissues that produce volatile pheromones have been identified within the Cerambycidae. The first type, typified by males of many cerambycine species, consists of sex-specific multicellular glands in the endocuticle that connect via ducts to pores in the prothorax. These were first identified in males of the cerambycine *X. pyrrhoderus* by Iwabuchi (1986), who also noted that the pheromone-producing tissues were undeveloped in newly emerged males but developed and became functional as the males became sexually mature. More recently, Iwabuchi and coworkers published a follow-up study in which the glandular structures were illustrated in much greater detail in *X. pyrrhoderus* and a number of other species (Hoshino et al. 2015). Males of the cerambycines *Neoclytus a. acuminatus* (F.) (Lacey et al. 2007b), *A. subfasciatus* (Nakamuta et al. 1994), and *H. bajulus* (Noldt et al. 1995) have prothoracic pores similar to those of *X. pyrrhoderus*, and these pores also have been associated with production of pheromones. In a more comprehensive examination of males and females of 65 species in 24 tribes within the Cerambycinae, Ray et al. (2006) found male-specific prothoracic gland pores in 49 species across 15 tribes, whereas neither sex of the remaining 16 species appeared to have pores, even though at least one of these species (*R. funebris*) is known to have a male-produced volatile pheromone (Ray et al. 2009a). However, it must be noted that the structure of its pheromone ([*Z*]-3-decenyl [*E*]-2-hexenoate) is quite different than those of any other pheromones known from cerambycines (see Figure 5.1), and so the pheromone may be produced by glands elsewhere on the body. Furthermore, Ray et al. (2006) did not find consistent patterns within tribes or even within a genus. For example, males of one species in the genus *Lissonotus* had gland pores, whereas they were absent in a congener. Male-specific gland pores also were found in all nine species in another study of cerambycine species in the tribe Clytini (Li et al. 2013). In a more recent study comparing 12 Asian cerambycine species in the tribes Clytini and Anaglyptini, males of 11 species, including four *Xylotrechus* species, had gland pores, whereas a fifth species, *X. cuneipennis* (Kraatz), did not (Hoshino et al. 2015).

The large number of examples now known suggests that the presence of male-specific pores is a likely indication of aggregation pheromone production within the subfamily Cerambycinae. In fact, 11 species shown by Ray et al. (2006) to have pores were subsequently found to use male-produced pheromones (Lacey et al. 2008b, 2009; Mitchell et al. 2013, 2015; Ray et al. 2015; Zou et al. 2016). However, no conclusions can be drawn about pheromone use in cerambycine species in which the pores are absent because at least one species without pores (*R. funebris*) clearly does use male-produced pheromones. Thus, the prothoracic pores offer a one-sided test: If they are present, the species probably uses a male-produced pheromone, but if absent, it cannot be predicted whether or not pheromones are used.

In addition to having specialized morphological structures for pheromone production, cerambycine species have evolved specific behaviors that aid in the dissemination of volatile pheromones. Thus, calling male *N. a. acuminatus* adopt a “push-up stance” in which the head and thorax are raised, which increases air flow over the pheromone-releasing prothoracic structures (Lacey et al. 2007b). Since then, similar behaviors have been noted in males of a number of other cerambycine species that have prothoracic pores (Lacey et al. 2007a, 2009; Ray et al. 2009b).

5.3.2 Subfamily Lamiinae

To date, all known volatile pheromones of species within the Lamiinae are male-produced aggregation pheromones. Two general motifs have been found—one clearly terpenoid based and the other based on hydroxyethers (Figure 5.2). The first lamiine pheromone was identified from males of *Anoplophora glabripennis* (Motschulsky), the Asian longhorned beetle, and consisted of a blend of 4-(heptyloxy)butanol and the corresponding aldehyde, 4-(heptyloxy)butanal (Zhang et al. 2002). However because of the relatively weak activity of the pheromone in numerous field trials conducted in both the United States (Nehme et al. 2014) and this beetle's native region, China (Nehme et al. 2010; Meng et al. 2014), it remains uncertain whether the pheromone has been completely identified. In fact, a recent paper suggested that (*E*,*E*)-α-farnesene may comprise a third component of the pheromone but, to date, only laboratory bioassays have been reported (Crook et al. 2014). Combinations of host plant volatiles with the pheromone lure do seem to increase attraction, but the overall levels of attraction remain relatively weak (Nehme et al. 2010; Meng et al. 2014).

Not unexpectedly, males of the sympatric congener *A. chinensis* (Forster) also have been shown to produce 4-(heptyloxy)butanol but not the aldehyde, and in field trials, beetles were attracted to blends

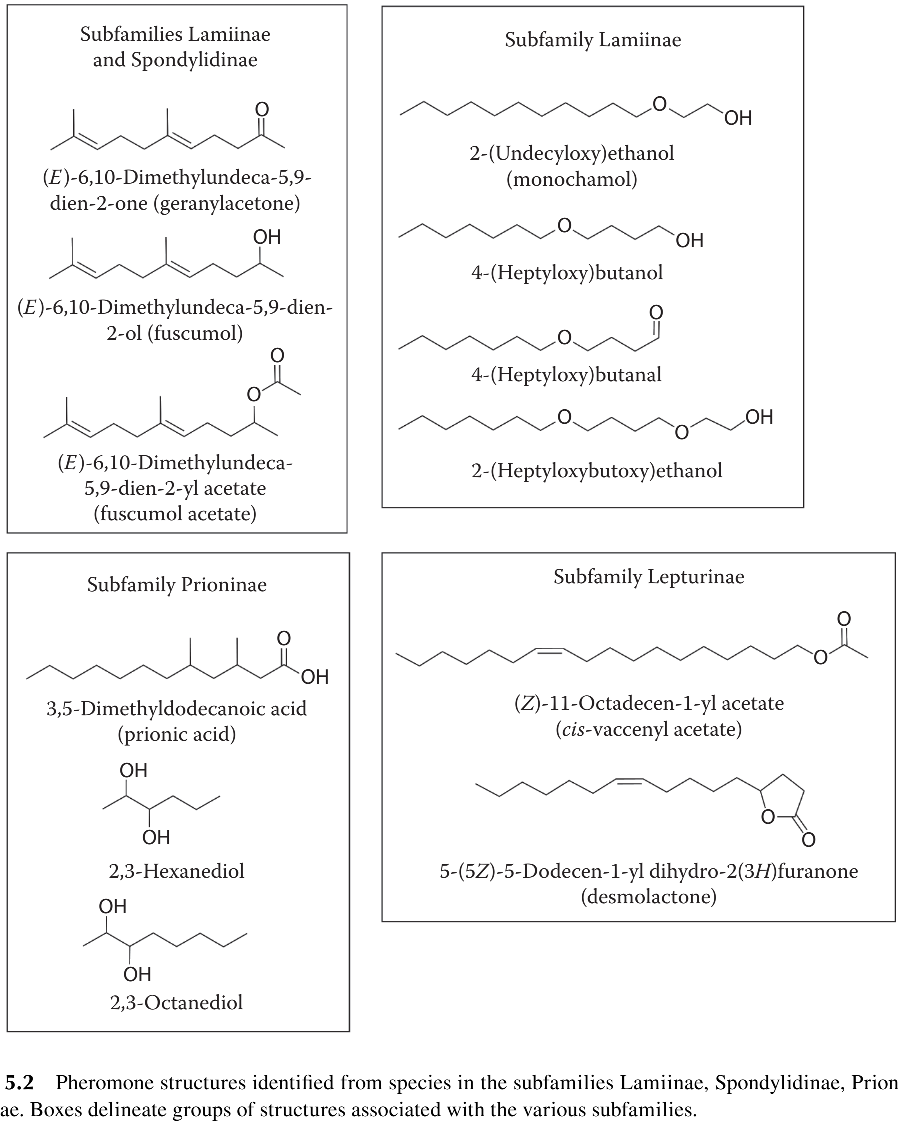

FIGURE 5.2 Pheromone structures identified from species in the subfamilies Lamiinae, Spondylidinae, Prioninae, and Lepturinae. Boxes delineate groups of structures associated with the various subfamilies.

of the pheromone when released with α-pinene and ethanol as crude mimics of host plant volatiles (Hansen et al. 2015).

Another example of the hydroxyether motif was identified in the European species *Monochamus galloprovincialis* (Olivier) (Pajares et al. 2010), males of which produce 2-(undecyloxy)ethanol (given the common name monochamol). This pheromone, in combination with host plant volatiles and bark beetle pheromone synergists, is an excellent attractant for both sexes, and lures have been commercialized for trapping this species, specifically because it is a major vector of pinewood nematode in Europe (Sousa et al. 2001). Monochamol now has been identified as a pheromone component for five additional *Monochamus* species and as a likely pheromone component for another eight (Table 5.1). For some species, the pheromone alone is attractive, whereas with others, the pheromone is synergized by plant volatiles and/or bark beetle pheromones (see Section 5.7). Extending the biosynthetic parsimony further, monochamol has now been identified as a likely pheromone for beetles in four other genera in the same tribe as *Monochamus* (Monochamini), specifically *Acalolepta formosana* (Breuning), *Pharsalia subgemmata* (Thomson), *Pseudomacrochenus antennatus* (Gahan), and *Xenohammus bimaculatus* Schwarzer (Table 5.1). However, it must be noted that even within the genus *Monochamus*, there is some variation in pheromone structures. Specifically, males of the African species *Monochamus leuconotus* (Pascoe) produce 2-(heptyloxybutoxy)ethanol, almost a hybrid structure of the other two (Figure 5.2 and Table 5.1). To date, no field trials have been reported for this species.

Given the similarities among these hydroxyether type pheromones, and the overall high degree of conservation of pheromone structures among related cerambycid taxa, we synthesized and field tested four analogs of these compounds (2-[nonyloxy]ethanol, 4-[nonyloxy]butanol, 2-[heptyloxy]ethanol, and 6-[heptyloxy]hexanol) in the United States, China, and Costa Rica (unpublished data). None of them attracted any cerambycids, suggesting that if there are other pheromones with these types of structures, they likely consist of only a few specific structures. From the three known pheromones of this type (four if you also count 4-[heptyloxy]butanal), one consistent structural feature that may be important is that the nonfunctionalized end of the molecule consists of a fragment with an odd number of carbons (7 or 11), whereas the second part of the chain contains an even number of carbons (2 or 4; Figure 5.2).

The second major pheromone structural type found from lamiine species to date is based on the sesquiterpene degradation product geranylacetone, the corresponding alcohol ([*E*]-6,10-dimethylundeca-5,9-dien-2-ol, originally called fuscol, but now generally referred to as fuscumol), and the acetate ester of the alcohol ([*E*]-6,10-dimethylundeca-5,9-dien-2-yl acetate, or fuscumol acetate; Figure 5.2). The alcohol and acetate can exist in two enantiomeric forms, each of which will likely have different biological activities. This structural motif was first identified in two species in the genus *Tetropium* (subfamily Spondylidinae; Silk et al. 2007; see following text), with fuscumol being named after *T. fuscum* (F.), but fuscumol and/or fuscumol acetate were later shown to attract adults of a number of lamiine species as well (Mitchell et al. 2011). In the Lamiinae, components with this structural motif were first identified from the South American species *Hedypathes betulinus* (Klug), males of which produce fuscumol acetate as a major component, with lesser amounts of fuscumol and geranylacetone (Table 5.1). In laboratory bioassays, fuscumol acetate was not attractive to females as a single component, but blends of fuscumol acetate with the two minor components, or with host plant volatiles, were attractive. Further studies showed that the males produced pure (*R*)-fuscumol acetate but, unexpectedly, a ~4:1 mixture of (*R*)- and (*S*)-fuscumol (Vidal et al. 2010). Similarly, fuscumol has been identified from male-produced volatiles of the South American lamiine *Steirastoma breve* (Sulzer), and females were attracted to extracts of males in laboratory bioassays (Table 5.1). There have been no published reports of field trials for either species to date.

Fuscumol and fuscumol acetate, as single components or blended, have now been shown to attract a number of North American lamiine species (Table 5.1), usually in screening trials that used racemic fuscumol and fuscumol acetate (e.g., Hanks et al. 2012) or even “technical grade” mixtures of the (*E*)- and (*Z*)-isomers of the two compounds (Mitchell et al. 2011; Wong et al. 2012; Hanks and Millar 2013; Hanks et al. 2014). However, for almost all of these species, it is not yet known which enantiomer (or blend of enantiomers) of fuscumol and/or fuscumol acetate is produced. The single exception is *Astyleiopus variegatus* (Haldeman), which has been shown to produce the (*S*)-enantiomer of both compounds (Hughes et al. 2013). The results of field trials to determine whether the “non-natural” (*R*)-enantiomers either inhibit or have no effect on attraction have not yet been reported.

Despite the rapidly increasing number of pheromones known from the Lamiinae, little is known about where these compounds are produced. Prothoracic pores were found in *Hedypathes betulinus* (Klug), males of which produce fuscumol, fuscumol acetate, and geranylacetone, but the pores were present in both sexes (Fonseca et al. 2010). By analyzing extracts of body sections of males, Zarbin et al. (2013) found that pheromones were concentrated in the prothorax; furthermore, isotopically labeled precursors applied to the prothoraces of males were converted to labeled pheromone (Zarbin et al. 2013). Thus, the evidence suggests that pheromone production likely occurs somewhere in the prothorax, even though the role of the identified pores is equivocal. Similarly, males of *M. s. scutellatus* (Say), which produce the pheromone monochamol (Fierke et al. 2012), were found to have prothoracic pores, but no females were examined so it is not known whether the pores are sex-specific (Brodie 2008). Thus, all that can really be said is that the pheromone-producing structures of lamiine species are not yet known.

5.3.3 Subfamily Spondylidinae

Male-produced volatile pheromones, including fuscumol and fuscumol acetate (Figure 5.2), have been identified from two species in this subfamily (Table 5.1). As already mentioned, fuscumol was first identified from the congeners *Tetropium fuscum*, native to Europe but established in North America since about 1999, and the North American *T. c. cinnamopterum* Kirby (Silk et al. 2007; Sweeney et al. 2010). Both species produce and respond to (*S*)-fuscumol, but they respond equally well to racemic fuscumol, indicating that the (*R*)-enantiomer is not inhibitory (Sweeney et al. 2010). Also, the pheromone alone is minimally active for both species, as well as for the European congener *T. castaneum* (L.), but there is strong synergism between the pheromone and host volatiles (Sweeney et al. 2010). Fuscumol and fuscumol acetate also attracted the congener *T. schwarzianum* Casey in field screening trials (Hanks and Millar 2013), providing more evidence that this is likely a conserved and widely shared pheromone motif.

Within the subfamily Spondylidinae, Mayo et al. (2013) reported that neither sex of *T. fuscum* and *T. c. cinnamopterum* has the prothoracic gland pores that have been correlated with pheromone production in cerambycine species. However, isotopically labeled precursors applied to the abdominal sternites were incorporated into the pheromone, leading the authors to hypothesize that pheromone production might be occurring in the midgut, but this remains to be verified. It has also been observed that calling males of *Tetropium* species adopt a "push-up" stance, analogous to that noted with cerambycine species (Section 5.3.1), as a mechanism to more effectively disperse their pheromones (Lemay et al. 2010; Mayo et al. 2013). The presence of calling males also stimulates other males to call, increasing the strength of the signal (Lemay et al. 2010).

5.3.4 Subfamily Prioninae

Švácha and Lawrence (2014) suggested that pheromones of prionine species were likely to be produced by females based on the fact that females of many species are flightless, or at least incapable of flight until they have laid some of their eggs and reduced their mass, whereas males fly readily. In contrast, few cerambycine species have flightless females (Švácha and Lawrence 2014). To date, two disparate types of female-produced sex pheromones have been identified from prionine species (Figure 5.2 and Table 5.1). The first was identified from *Prionus californicus* Motschulsky as 3,5-dimethyldodecanoic acid (prionic acid) (Rodstein et al. 2009), and this compound as a mixture of all four possible stereoisomers subsequently was shown to attract males of at least six *Prionus* species in North America as well as the European *P. coriarius* L. (Barbour et al. 2011). The pheromone appears to be produced from an eversible gland on the dorsum of the ovipositor: a calling female elevates her abdomen, extrudes her long ovipositor, and the gland everts on the dorsal surface (Barbour et al. 2006). Other researchers have reported similar behaviors by females of other prionine species (Rotrou 1936; Linsley 1962; Benham and Farrar 1976; Gwynne and Hostetler 1978; Paschen et al. 2012), suggesting that the eversible gland on the ovipositor may be widespread in some but not all tribes of the Prioninae (see following for examples of other pheromone gland structures).

Extracts of the pheromone glands of female *P. californicus* were found to contain a number of analogs and homologs of prionic acid, some of which also were attractive to males; but prionic acid as a single component was as attractive as any blend, showing that the single compound was both necessary and sufficient for attraction (Maki et al. 2011b). Very recently, males of an Asian prionine species in another genus, *Dorysthenes granulosus* (Thomson), have been shown to be attracted by prionic acid (Table 5.1; Wickham et al. 2016a), indicating that this compound is a likely pheromone for this species as well and that the structure has been conserved across genera of the tribe Prionini on different continents. It has not been reported whether females of *D. granulosus* display the same type of calling behavior, with an eversible gland on the ovipositor. Furthermore, given the high degree of conservation of pheromone structures within closely related taxa of cerambycids, it seems likely that prionic acid, or a closely related compound, will be found to attract males of other *Dorysthenes* species that are important pests in Asia (Hill 2008).

The second type of female-produced sex pheromones are comprised of 2,3-alkanediols, which have been identified within the Prioninae (Figure 5.2 and Table 5.1). Females of the North American *Tragosoma depsarium* "sp. nov. Laplante" (tribe Meroscelisini) produce (2*R*,3*R*)-2,3-hexanediol, and only males were attracted by the synthesized compound in field bioassays (Ray et al. 2012a). During those field trials, males of the congeners *T. depsarium "harrisi"* LeConte and *T. pilosicorne* Casey were specifically attracted by the (2*S*,3*R*)-enantiomer, strong evidence that it is likely to be their female-produced sex pheromone. Similarly, females of the Asian prionine *Nepiodes* (formerly *Megopis*) *c. costipennis* White (tribe Megopidini) produce (2*R*,3*S*)-2,3-octanediol, and only males were attracted by the synthetic compound in field bioassays (Wickham et al. 2016b). These 2,3-alkanediols are unrelated to prionic acid biosynthetically and, furthermore, apparently are produced from entirely different glands than prionic acid. Remarkably, females of these diol-producing prionine species have prothoracic gland pores analogous to the pheromone-producing gland pores in male cerambycines (Ray et al. 2012a; Wickham et al. 2016b), some species of which produce exactly the same 2,3-alkanediols as aggregation pheromones. Thus, the compounds and the morphological structures from which they are produced have been conserved across subfamilies, even though the sexes producing the compounds are different, and the contexts in which the pheromones are used also are different.

5.3.5 Subfamily Lepturinae

The first attractant pheromone of a lepturine species was identified in 2011 for the North American species *Ortholeptura valida* (LeConte) (Ray et al. 2011). The compound, (*Z*)-11-octadecen-1-yl acetate (*cis*-vaccenyl acetate; Figure 5.2), is a female-produced sex pheromone but also is produced by male fruit flies in the genus *Drosophila* as an aggregation pheromone (Bartelt et al. 1985) and as an anti-aphrodisiac that males apply to females (Jallon et al. 1981).

The other sex pheromone structure that has been identified from lepturine species, (4*R*,9*Z*)-hexadec-9-en-4-olide (desmolactone; Figure 5.2), is likely to be biosynthetically related to *cis*-vaccenyl acetate, both probably being derived from fatty acid precursors. Desmolactone was initially described from *Desmocerus californicus californicus* Horn (Ray et al. 2012b) but has since been shown to be a pheromone, or likely pheromone, for several other North American species and subspecies of *Desmocerus*, including the threatened *D. californicus dimorphus* Fisher (Ray et al. 2014; Table 5.1).

Nothing is known of the site of pheromone production in lepturine species. Hoshino et al. (2015) noted that males of the lepturine *Leptura o. ochraceofasciata* (Motschulsky) lacked the prothoracic gland pores that have been found in males of many cerambycine species, but this may be largely irrelevant because the evidence suggests that lepturine species use female-produced sex pheromones rather than male-produced aggregation pheromones.

5.4 Contact Pheromones

As with most other insect species, cerambycids use relatively nonvolatile compounds as close range or contact pheromones for the recognition of species and sex, and specifically, so that males can recognize females for mating. This dependence on contact for mate recognition was reported quite early (e.g., Heintze 1925), and it has since been reported for cerambycid species in all of the major subfamilies (e.g., Bouhelier and Hudault 1936; Michelsen 1963; Farrar 1967; Pilat 1972; Godinez-Aguilar et al. 2009). Thus, upon contacting females with their antennae, males display a sequence of characteristic behavioral steps, including arrestment and orientation toward the female, alignment of the male's body with that of the female and mounting on her back, culminating in coupling of the genitalia and copulation (see Chapter 4). It has been demonstrated repeatedly that the contact pheromone is a subset of the cuticular lipids, by solvent extraction of freshly killed female carcasses. Males readily try to mate with carcasses of females before extraction but ignore the carcasses after the cuticular lipids have been removed (reviewed in Ginzel 2010). The fact that males readily attempt copulation with female carcasses also precludes the possibility of acoustic signals or behavioral responses on the part of the female being critical components in close-range sexual recognition. The cuticular extract can then be transferred onto a previously washed female or male carcass, or a model such as a glass rod, resulting in at least partial restoration of the activity, with males orientating toward and attempting to copulate with the treated models. In fact, successful interspecific copulations can be induced by treating a live female of one species with the cuticular extract of another (e.g., *Phoracantha semipunctata* and *Phoracantha recurva* Newman; JGM, LMH, unpublished data; *Megacyllene* spp.; Galford 1980a). However, components of the active pheromones have been identified in only a few cases, which is due in part to the complexity of the cuticular lipids and the difficulty in purifying or obtaining pure standards of individual compounds for tests of function in bioassays.

In the first study in which a cerambycid contact pheromone was identified, Fukaya and Honda (1992) conducted a sequence of methodical studies with the yellow-spotted longicorn, *Psacothea hilaris* (Pascoe) (Lamiinae), in which they first described the sequence of male mating behaviors, then showed that the pheromone was removed by extraction with organic solvents and could be reapplied to previously extracted carcasses or neutral substrates, and finally showed that antennae, palpi, and tarsi were all involved in various steps of the behavioral sequence. In this and subsequent papers (e.g., Fukaya and Honda 1995; Fukaya et al. 1996), the authors also presented data indicating that the different steps in the behavioral sequence were elicited by different components, with the compound(s) eliciting the initial orientation response being localized on the female's prothorax, whereas the component(s) eliciting abdominal bending/genital coupling by the male were likely distributed over the entire body surface. A major component of the pheromone was identified as the methyl-branched alkene (*Z*)-21-methylpentatriacont-8-ene, which elicited mating behaviors from males, although at lower levels than the crude extract from females, suggesting that other components might be involved (Fukaya et al. 1996). In particular, the authors noted that this compound did not induce the orientation behavioral step of males upon initial contact with females. Furthermore, because of the presence of the double bond and a chiral center in the molecule, the compound has four possible stereoisomers. Synthesis and bioassay of all four isomers showed that, somewhat surprisingly, all four isomers elicited some degree of response. The (*Z*)-isomers elicited stronger responses than the "non-natural" (*E*)-isomers, but there were no significant differences in responses of males to the (*R*)- or (*S*)-enantiomers of the (*Z*)-alkene, suggesting that the males could not discriminate the absolute configuration (Fukaya et al. 1997). Fukaya and Honda (1996) showed that the size and shape of models treated with extracts of females were also important, with the best responses being obtained with models that approximated the size and shape of a female beetle. Somewhat surprisingly, these authors also reported that extracts of males could elicit partial mating responses from other males (Fukaya and Honda 1992, 1996), suggesting that the relevant components were not sex-specific. However, no chromatographic comparisons of males and females were presented, so this finding remains speculative.

Fukaya and coworkers followed this work with a comprehensive study of the contact pheromone of a Japanese population of another lamiine species, *Anoplophora malasiaca* (Thomson). Although this species was synonymized with *A. chinensis* by Lingafelter and Hoebeke (2002), more recent evidence suggests that the two may indeed be separate species (e.g., Muraji et al. 2011). The pheromone was perceived only after the male contacted the female with his antennae. Liquid chromatographic fractionation of cuticular extracts of females showed that the pheromone consisted of both saturated hydrocarbon(s) and more polar compounds (Fukaya et al. 1999, 2000). Although the hydrocarbon fractions of extracts from males and females had some components in common, they were clearly different both qualitatively and quantitatively (Akino et al. 2001). A reconstruction of the eight major alkanes from females, when mixed with a more polar fraction, elicited the full suite of mating behaviors, and of the eight compounds tested, the 9-methylalkanes (9-methylheptacosane and 9-methylnonacosane) and the 15-methylalkanes (15-methylhentriacontane and 15-methyltritriacontane) appeared to be most important in eliciting responses from males. Initial analyses of the more polar fraction identified a blend of four straight-chain ketones (heptacosan-10-one, [*Z*]-18-heptacosen-10-one, [18*Z*,21*Z*]-heptacosa-18,21-dien-10-one, and [18*Z*,21*Z*,24*Z*]-heptacosa-18,21,24-trien-10-one) as additional active components, whereas a fifth component, heptacosan-12-one, appeared to be inhibitory (Yasui et al. 2003). However, an additional subfraction from the polar fraction was required for full activity. Further analyses identified three complex bicyclic lactones, termed gomadalactones A, B, and C, as the missing components (Yasui et al. 2007a). Their absolute configurations were inferred by comparison of their circular dichroism spectra with those of synthesized model compounds containing the bicyclic lactone core (Mori 2007). As with *P. hilaris*, visual cues also were important in directing males toward females at short range (Fukaya et al. 2004, 2005). To our knowledge, this contact pheromone blend consisting of eight hydrocarbons, four ketones, and three lactones is the most complex insect pheromone blend yet identified.

Contact sex pheromone components also have been identified from one other lamiine species, *A. glabripennis*, a congener of *A. malasiaca*. Zhang et al. (2003) identified five alkenes ([*Z*]-9-tricosene, *Z*9-C_{23}, subsequent abbreviations follow this pattern, *Z*9-C_{25}, *Z*7-C_{25}, *Z*9-C_{27}, *Z*7-C_{27}) that were consistently more abundant in extracts of female *A. glabripennis* than in corresponding extracts of males. Individually, the compounds were inactive, but the blend of all five elicited mating behaviors from males analogous to those elicited by crude extracts of females. Subsets of these five compounds were not tested, so it remains unclear as to whether all five components are required for activity.

Within the subfamily Spondylidinae, contact pheromones have been identified from two species in the genus *Tetropium*. Thus, bioassay evidence suggested that (*S*)-11-methylheptacosane, present in extracts of females in much larger amounts than in extracts of males, is a contact pheromone component of *T. fuscum*, with the synthetic enantiomer eliciting copulation attempts by males (Silk et al. 2011). In contrast, the racemic mixture and the (*R*)-enantiomer did not elicit mating attempts, indicating that the males could clearly discriminate between the enantiomers and that the (*R*)-enantiomer was inhibitory. Because of the relatively small amounts available for analysis, and the very small specific rotations of long-chain methyl-branched hydrocarbons, it was not possible to verify that the females produced the (*S*)-enantiomer by analytical means. Addition of several other methylalkanes that were present in higher proportions in extracts of females than in extracts of males did not increase the activity. However, only the (*S*)-enantiomers were tested. For the congeneric *T. c. cinnamopterum*, a blend of (*S*)-11-methylheptacosane with *Z*9-C_{25} was required to elicit significant levels of arrestment, mounting, and copulation attempts (Silk et al. 2011).

In the subfamily Cerambycinae, contact sex pheromones have been identified from five species. Thus, the contact pheromone of *N. a. acuminatus* consists of a major component, 7Me-C_{27}, and two synergistic minor components, 7Me- and 9Me-C_{25} (Lacey et al. 2008a). In a follow-up study, Hughes et al. (2015) proved that the insect-produced 7Me-C_{25} had the (*R*)-configuration by isolating the compound, measuring its optical rotation, and comparing the rotation to those of the pure synthesized enantiomers. It was not possible to isolate the other two components to measure their optical rotations, but bioassays with the enantiomers of the two compounds suggested that they also were likely to have the (*R*)-configuration.

For the cerambycine *Callidiellum rufipenne* (Motschulsky), the synthesized mixture of the four isomers of the female-specific 5,17-dimethylnonacosane proved sufficient to elicit complete mating sequences from males (Rutledge et al. 2009). Similarly, *Z*9-C_{25}, the most abundant hydrocarbon on the cuticle of female *Megacyllene robiniae* (Forster), elicited the full array of mating responses from males (Ginzel et al. 2003), whereas females of the congeneric *M. caryae* used the analogous *Z*9-C_{29} as a contact pheromone component (Ginzel et al. 2006). In both of these *Megacyllene* species, there were marked differences in the cuticular hydrocarbon profiles of males and females, suggesting that other components probably are involved in the pheromones as well. Finally, three contact pheromone components, C_{25}, 9Me-C_{25}, and 3Me-C_{25}, were identified from female *Xylotrechus colonus* (F.) (Ginzel et al. 2003), and the absolute configuration of the latter compound was subsequently shown to be (*R*) by isolation and measurement of its optical rotation (Bello et al. 2013). In fact, a recent study of the absolute configurations of 36 methyl-branched cuticular hydrocarbons from 20 species in 9 insect orders, including three cerambycid species [*Brothylus gemmulatus* LeConte, *Monochamus titillator* (F.), *Monochamus c. clamator* (LeConte)] determined that they all had the (*R*)-configuration (Bello et al. 2015). Thus, it seems that the majority of methyl-branched hydrocarbons from cerambycids are likely to have the (*R*)-configuration. However, in some species, gas chromatographic (GC) analyses have shown the cuticular hydrocarbon profiles of males and females to be very similar, even though males can clearly discriminate between females and other males upon antennal contact with the cuticle (e.g., *P. semipunctata*; Hanks et al. 1996; JGM and LMH, unpublished data). However, the enantiomers of cuticular hydrocarbons cannot be separated chromatographically, and so one possible explanation for this ability to discriminate among what superficially appear to be similar cuticular profiles could be that females produce the (*S*)-enantiomer of one or more of the hydrocarbons to create a sex-specific signal.

Overall, these studies illustrate several important points about cerambycid contact pheromones. First, considerable information about the possible pheromone components can be obtained by simple fractionation steps that break down crude extracts from females into distinct chemical classes, which can then be bioassayed to determine which classes of chemicals are involved (see Bello et al. 2015). Second, the pheromones may be simple, consisting of one or a few compounds, or remarkably complex, as in the case of *A. malasiaca*. In fact, it is likely that the incomplete recovery of the full activity of many insect contact pheromones is due to the reconstructions of the blends with synthetic compounds being incomplete. Stated another way, it is likely that the contact pheromones of at least some insects contain far more compounds than the few that have been identified and associated with activity, particularly given the relatively large number of compounds present in crude cuticular extracts. Third, contact pheromones of females may be entirely sufficient to elicit the complete suite of mating behaviors in males of at least some species (Fukaya and Honda 1996; Wang et al. 2002; Crook et al. 2004; Lu et al. 2007; Luo et al. 2011). In others, physical cues, such as size and shape, or acoustic cues such as substrate-borne vibrations from walking beetles also may be important (e.g., Wang et al. 1990, 1996; Fukaya and Honda 1996; Fukaya et al. 2004, 2005; Wang and Chen 2005; Lu et al. 2007; Tsubaki et al. 2014).

5.5 Trail Pheromones

As described here, contact sex pheromones have been shown to induce a very characteristic sequence of behavioral steps in males whose antennae come in contact with the pheromones, including mounting and copulation attempts. However, there are also a number of cases in which it has been noted that males can detect where females have walked, and they will follow this trail or at least slow down when the trail is perceived. It is not known whether females actively apply compounds to the substrate or whether the trail is deposited simply by compounds rubbing off the cuticle as the female walks. Galford (1977) appeared to have been the first to demonstrate this phenomenon by showing that males of *M. robiniae* remained longer on sticks or filter papers upon which females had walked than on controls. Wang et al. (2002) showed that male *Nadezhdiella cantori* Hope followed trails deposited by walking females and that the walking responses were even stronger to extracts of females that were painted onto a substrate. In the only example to date in which cerambycid trail pheromone components have been identified, Hoover et al. (2014) identified two major components (2Me-C_{22} and *Z*9-C_{23}) and two minor components (*Z*9-C_{25} and *Z*7-C_{25}) from residues deposited on filter papers by walking virgin or mated females but not males of *A. glabripennis*. In bioassays, males followed trails of a reconstructed blend of the four components, and virgin but not mated males followed trails comprised of the two major components alone. It should be noted that the three alkene components had been previously identified as contact sex pheromone components for this species (Zhang et al. 2003). Thus, not surprisingly, there appears to be considerable overlap in both the function and the components of female-produced contact sex pheromones and trail pheromones. The authors of the present chapter have heard anecdotal evidence and seen videos of similar instances of male cerambycids tracking the "footprints" of their females, and it seems likely that this will prove to be a common mate-location strategy within the family, given the propensity of males of many species to patrol host trees, sampling the substrate with their antennae, and ready to pounce on a female as soon as they contact her with their antennae (see Chapter 4).

5.6 Mechanisms for Maintaining Reproductive Isolation

From the earlier descriptions of the types of pheromones found within the different subfamilies, it is clear that pheromone structures are often highly conserved within the Cerambycidae, with the same compound(s) being shared by species within the same genus, tribe, subfamily or, in the cases of the 2,3-alkanediols and fuscumol, even among species in different subfamilies (see Table 5.1). Superficially, this might seem to create multiple opportunities for cross-attraction among species, and at first glance, catches in pheromone-baited traps would appear to bear this out, with traps baited with a single compound often catching beetles of multiple species simultaneously (e.g., Hanks and Millar 2012). However, it must be remembered that pheromone lures are passive devices that release pheromones continuously, whereas the available data suggest that different cerambycid species have distinct diel activity patterns, including specific time windows in which they produce and respond to pheromones (see Chapter 4). Thus, catches in traps baited with lures that release pheromones continuously may be deceiving.

Generally speaking, there are multiple, complimentary mechanisms that assure prezygotic reproductive isolation among sympatric cerambycid species, including spatial, temporal, and chemical factors. Thus, species that are geographically separated can obviously use the same pheromone components without interfering with each other. However, even species that are sympatric can remain spatially separated in one or both of two ways. First, because of the frequent strong synergism of pheromones with host plant volatiles, species that share one or more pheromone components may avoid cross-attraction if they infest hosts that have distinctly different odor profiles. For example, adults of species whose larvae develop in oaks may be repelled by blends of their pheromones with conifer host odors (Collignon et al. 2016). Furthermore, adult males may not call unless they are on suitable hosts (e.g., Fonseca et al. 2010). Second, there is growing evidence that different species segregate themselves at different heights within the forest—from ground level to the upper canopy of host trees. Remarkably, this segregation by height can be absolute, with some species only being caught at ground level, others only being caught in the upper canopy, and another subset of species demonstrating no clear preference for one height over the other (Graham et al. 2012; Dodds 2014; Webster et al. 2016).

With regard to temporal factors, most cerambycids have distinct seasonal activity patterns, with the adults of most species of temperate zones being present for only a few weeks per year (see Chapter 4). Thus, the same compound can be used as a pheromone by a succession of sympatric species as long as their seasonal activity periods have minimal overlap, and this has indeed been shown to be the case (Hanks and Millar 2013; Hanks et al. 2014; Handley et al. 2015; Mitchell et al. 2015). In fact, some species have taken this to extremes, such as two *Megacyllene* species native to the eastern United States. Thus, adults of *M. caryae* emerge very early in spring, whereas adults of *M. robiniae* emerge very late in the fall, in both cases avoiding overlap with other cerambycid species with which they share pheromone components (Hanks et al. 2014; JGM and LMH, unpublished data). In the mountains of California, adults of *Semanotus ligneus amplus* (Casey) and *Callidium pseudotsugae* Fisher emerge so early in spring that there is still snow on the ground (I. P. Swift, personal observation). Emerging very early may have additional advantages, such as obtaining first choice of the oviposition sites created by trees and branches that have fallen during the winter.

Even sympatric species that have similar seasonal activity patterns can minimize cross-attraction by producing and responding to pheromones at different times of day. It is well known that cerambycid species are limited in their daily flight periods, being strictly diurnal, crepuscular, or nocturnal (Linsley 1959), and this phenology likely extends to their pheromone-mediated behavior as well. For example, males of *H. betulinus* produced pheromones primarily between four and six hours after the onset of photophase (Fonseca et al. 2010). These types of observational data have now been reinforced with data from traps on timers, which have clearly shown that sympatric species that share pheromone components have largely nonoverlapping diel response windows (Mitchell et al. 2015).

There is a growing body of evidence that, similar to other insect taxa, cerambycid species may use blends of pheromone components that inhibit cross-attraction in both a positive and a negative sense. That is, the pheromone blends of some species consist of two or more components, with each individual component having no activity, or much reduced activity, in comparison to the blend. For example, Mitchell et al. (2015) reported that two cerambycine species that overlap in seasonal and daily activity periods have very similar pheromones: males of *Euderces pini* (Olivier) produce (*R*)-3-hydroxyhexan-2-one, while the pheromone of male *Phymatodes amoenus* (Say) is composed primarily of the same compound but with (*R*)-2-methylbutanol as a minor component. Nevertheless, the two species remain segregated by that minor component because it is a critical synergist for adult *P. amoenus*, while simultaneously antagonizing attraction of *E. pini*. Similarly, the cerambycines *X. colonus* and *Sarosesthes fulminans* (F.) both have (*R*)-3-hydroxyhexan-2-one as their dominant pheromone component but differ in the stereochemistry of their 2,3-hexanediol minor components (Lacey et al. 2009). Cross-attraction is averted because attraction of each species is synergized by its natural minor component(s) and antagonized by the minor component(s) produced by the other species. In another subfamily, the Prioninae, female *T. depsarium* "nov. sp. Laplante" produce (2*R*,3*R*)-2,3-hexanediol as their sex pheromone, and attraction of males is antagonized by one or both of the diastereomers, which are produced by its sympatric and synchronic congeners (Ray et al. 2012a).

There are also many examples known of species whose responses are inhibited by isomers or other analogs of their pheromone components, even though it is not yet clear which sympatric species might potentially interfere with their pheromone communication channels. This was first observed in the cerambycine *X. pyrrhoderus*, whose pheromone consists of a blend of (*S*)-2-hydroxyoctan-3-one + (2*S*,3*S*)-2,3-octanediol, and that is inhibited by (*R*)-2-hydroxyoctan-3-one (Iwabuchi et al. 1986). Similarly, *H. bajulus* (Reddy et al. 2005) and *Neoclytus m. mucronatus* (F.) (Lacey et al. 2007a) both use (*R*)-3-hydroxyhexan-2-one as a major pheromone component, and both are inhibited by (*S*)-3-hydroxyhexan-2-one. In another example, males of *N. a. acuminatus* produce (2*S*,3*S*)-2,3-hexanediol as their sole pheromone component. This species is not inhibited by the enantiomeric (2*R*,3*R*)-2,3-hexanediol, but it is inhibited by one or both of the diastereomeric (2*R*,3*S*)- or (2*S*,3*R*)-2,3-hexanediols (Lacey et al. 2004), and by (*R*)-3-hydroxyhexan-2-one (Hanks et al. 2012). An analogous situation was found more recently for the western congener *N. tenuiscriptus* Fall, males of which also produce (2*S*,3*S*)-2,3-hexanediol as their sole pheromone component (Ray et al. 2015). Further examples of inhibition by isomers and analogs of a particular species' pheromone can be found in Table 5.1.

The high degree of conservation of pheromone structures, with identical pheromone structures being shared by species on different continents, may have important consequences for invasion biology. That is, a new invader must overcome Allee effects, whereby low population densities reduce population growth due to the difficulty of males and females finding each other in order to reproduce. Below a certain minimum density, populations will become extinct (Courchamp et al. 1999). Thus, any environmental effect that interferes with mate location will reinforce Allee effects, further hindering the chances of an invasive species becoming established. This concept is the foundation of the authors' working hypothesis that an invasive (cerambycid) species whose sex or aggregation pheromone is also used by one or more endemic species in the country being invaded (i.e., where the native species can interfere with mate location by the invasive species in a form of natural mating disruption) will have a reduced chance of becoming established. Conversely, an invasive species that has a pheromone that is not shared by native species (i.e., that has a "pheromone-free space" to invade) will be more likely to establish. In consequence, we suggest that knowledge of the pheromone of an invasive species, and whether or not the pheromone is shared by native species, should be a factor to consider during risk analysis for potentially invasive pest species.

5.7 Exploitation of Plant Volatiles and Bark Beetle Pheromones as Kairomones

In 1930, Beeson observed that adults of the cerambycine *Hoplocerambyx spinicornis* Newman were attracted from at least a half mile away by volatile chemicals emanating from newly felled host trees. Since that time, there has been abundant observational evidence that cerambycids use plant volatiles to locate hosts for their larvae, based on the behavior of adults (e.g., Hughes and Hughes 1982; Kobayashi et al. 1984; Zeh et al. 1992). These observations have been further supported by formal experiments that tested attraction of beetles to host material in the laboratory (e.g., Hanks et al. 1996; Fujiwara-Tsujii et al. 2012) and in the field (e.g., Liendo-Barandiaran et al. 2010a, 2010b; Coyle et al. 2015). In many cases, both sexes are attracted by host plant volatiles (reviewed in Hanks 1999; Allison et al. 2004; also see Chapter 4) and with both sexes being equally capable of discriminating the odors of stressed trees from those of healthy trees that would be less suitable hosts. Plant volatiles therefore serve to bring the sexes of many cerambycid species together on larval hosts, suggesting that host plant location and mate location are intimately associated (Linsley 1959; Hanks 1999). Further evidence for this mode of mate location is provided by observations of the independent arrival of males and females on larval hosts (see Chapter 4).

The oviposition behavior of female cerambycids also may be strongly influenced by plant volatiles. For example, in laboratory bioassays, Li et al. (2007) showed that female *Monochamus alternatus* Hope were not attracted to volatiles from non-host plants and would not oviposit on natural hosts to which such chemicals had been applied. Laboratory studies (e.g., Hanks et al. 1995; Mazaheri et al. 2011) and field studies (e.g., Collignon et al. 2016) designed to evaluate the potential host range of cerambycid species further attest to the ability of females to use chemical cues to distinguish host from nonhost species.

Larvae of many wood-boring insects (bark and ambrosia beetles, buprestids, cerambycids, and wood wasps) require hosts that are in a particular physiological condition, often attacking trees that have been stressed by adverse environmental conditions such as water deficit, fire, or air pollution (Wood 1982; Hanks 1999). However, it can be difficult to gauge the physiological status of plants when they first become attractive to beetles. A tree that appears perfectly healthy to a human observer may in fact be suffering severe stress, and any one measure of vigor, such as leaf water potential or branch growth increment, may be an unreliable indicator of the potential to resist attacks by wood-boring insects (e.g., Flaherty et al. 2011). Researchers often have assumed that trees that already have been colonized by larvae are representative of a vulnerable physiological condition, and the volatiles that these trees produce therefore are likely attractants (e.g., Sweeney et al. 2004). However, the larvae inevitably alter the condition of their host by destroying tissues and disrupting the vascular system, with concomitant changes in the host odor profile. Thus, the opportunity to identify the particular blend of odor constituents that attracted the first adult colonizers to the host tree has already passed by the time developing larvae are present. Even designating a tree as alive or dead may not be straightforward. For example, felling a tree does not immediately kill it because at least some tissues remain alive for some time; a freshly felled tree or fallen branch is not dead but slowly dying. Many cerambycids colonize such hosts, whereas they will not colonize completely dead hosts in which the tissues are hard and dry (Linsley 1959). The ability to discriminate among suitable and unsuitable hosts may be mediated by both chemical cues (e.g., water content, odors, and possibly contact chemical cues) and physical cues (e.g., bark or wood hardness).

Because many cerambycids are attracted to stressed hosts, research on host plant attractants naturally has centered on volatiles that are associated with plant stress (e.g., Fan et al. 2007b). Females of most cerambycid species have quite broad oviposition preferences, attacking plant species in multiple genera and even families (see volumes indexed in Linsley and Chemsak 1997). It therefore seems plausible that the volatile cues used by adults of a given species for host location may be common to all its hosts. Consistent with this hypothesis, ethanol is produced by stressed or diseased plants, or by plants that are long dead and decaying, and ethanol attracts many species of wood-boring insects (reviewed by Allison et al. 2004; Byers 2004; Kelsey et al. 2014). Thus, ethanol can serve as one possible cue to attract insects that require stressed hosts, including freshly fallen trees or branches (reviewed by Joseph et al. 2001), but by itself, it may not be a completely reliable cue because of the wealth of other possible sources of ethanol—for example, from decay of organic matter. This situation may in part explain why ethanol alone is not a general attractant for cerambycids that attack stressed hosts; in field experiments, ethanol lures typically attract only a few cerambycid species in large numbers, with many more species represented by a few specimens that may be random captures (e.g., Montgomery and Wargo 1983; Miller et al. 2015a, 2015b). Species that are not attracted by ethanol alone likely use other types of plant volatiles, alone or in combination with ethanol, as more reliable cues to locate hosts in the particular condition that is most suitable for their larvae. Nevertheless, high-release rate ethanol lures have been used in a nationwide trapping program to monitor for invasive wood-borers in the United States (Rabaglia et al. 2008).

Consistent with attraction to ethanol, some cerambycid species whose larvae develop in deciduous woody plants are attracted to fermenting molasses or sugar solutions, often with other ingredients such as beer, wine, or decaying fruit added (Linsley 1959). Attraction of insects to such baits has been summarized by Champlain and Kirk (1926), Frost and Dietrich (1929), Champlain and Knull (1932), and Galford (1980b). It also has been suggested that fermenting baits might attract cerambycids because the baits simulate the volatiles of fermenting sap on which adult beetles feed rather than volatiles from larval hosts (Champlain and Knull 1932). This hypothesis is supported by the trapping surveys cited here because all of the species attracted were in the Cerambycinae and Lepturinae, the only two subfamilies in which sap feeding is common (Linsley 1959). Conversely, lamiines were poorly represented in these studies, whereas they would have been expected to be attracted if the fermenting baits did indeed emulate the odor of larval hosts.

Much of the research on host attractants of wood-boring insects has centered on bark and ambrosia beetles that attack conifers, largely due to their importance as forest pests. Stressed conifers may produce ethanol as well as increased amounts of a broad spectrum of terpenes (e.g., Fan et al. 2007b). The monoterpene α-pinene is among the dominant volatiles of many conifers as well as being a major component of the distilled essential oils known as turpentines (Kozlowski and Pallardy 1997; Byers and Zhang 2011). Many species of wood-boring insects have long been known to be attracted by α-pinene and turpentines, including cerambycids that feed on conifers (e.g., Gardiner 1957; Byers 2004). In addition to α-pinene, conifer essential oils contain a variety of other monoterpenes and sesquiterpenes, and blends of these compounds have been formulated as attractants for wood-boring insects, including cerambycids (reviewed in Allison et al. 2004; Sweeney et al. 2004; Fan et al. 2007b; Collignon et al. 2016). Reconstruction of these blends can be complicated by the difficulty in identifying the complex structures of some sesquiterpenes, particularly those that exist in two or more stereoisomeric forms and/or that are not commercially available (e.g., see Millar et al. 1986; Barata et al. 2000; Sweeney et al. 2004; Crook et al. 2008).

Terpenes also may play a role in host location and/or recognition for cerambycids that infest deciduous hosts. In detailed studies of the attraction of cerambycids to host volatiles, Yasui and coworkers showed that the cuticle of both sexes of *A. malasiaca* acquired host plant odors by contact, feeding, or passive adsorption, and that these odors were subsequently used as mate location cues (see Yasui et al. 2007b, 2008; Yasui 2009). Thus, analysis of volatiles from the elytra of adult beetles reared on satsuma mandarin trees (*Citrus unshiu* Marcovitch) showed them to contain the same sesquiterpenes as were released by the host after feeding or other types of damage. However, *A. malasiaca* is polyphagous, and further investigations revealed that the attraction of males was affected by the host upon which they had been reared. For example, males reared on satsuma mandarin, species of willow (*Salix*), or blueberry (*Vaccinium*) were most strongly attracted to the volatiles of the host from which they had been reared or collected, and to those odors released from the elytra of females exposed to plants of those same species (Yasui et al. 2011; Fujiwara-Tsujii et al. 2012, 2013). Thus, the host plant volatiles appeared to act in two sequential ways—first as longer-range attractants to bring the sexes together on the same host plants and then, over shorter ranges, by attraction to host plant volatiles being released from the cuticle of conspecifics. At close range, both visual signals and contact sex pheromones were important in the final steps of mate location and recognition (Yasui 2009).

Field studies have revealed that attraction to terpenes is synergized by ethanol for some conifer-feeding cerambycids (e.g., Kobayashi et al. 1984; Chénier and Philogène 1989). For example, Sweeney et al. (2004) found that adults of the spondylidines *T. fuscum*, *T. castaneum*, and *Spondylis buprestoides* (L.) were attracted to a blend of monoterpenes associated with host plant stress, and attraction was strongly synergized by ethanol. The synergistic combination of monoterpenes (especially α-pinene) and ethanol as an attractant for many cerambycids has resulted in the combination being considered a general "plant volatile" treatment by researchers (e.g., Costello et al. 2008; Campbell and Borden 2009; Miller et al. 2015a, 2015b). However, the two components do not always act synergistically and are by no means a general attractant for all cerambycid species (e.g., Collignon et al. 2016). For example, a fourth spondylidine species captured by Sweeney et al. (2004), *Asemum striatum* (L.), was attracted by α-pinene alone but not influenced by ethanol. Species of *Monochamus* also vary as to whether ethanol synergizes attraction to terpenes (e.g., Chénier and Philogène 1989; Allison et al. 2001; Ibeas et al. 2007). This variation among wood-boring insects in their responses to terpenes and ethanol again may be due to interspecific differences in the host condition required for their larvae (see Phillips et al. 1988; Schroeder and Lindelöw 1989) and/or the types of hosts that they attack (e.g., conifers versus deciduous trees).

Some cerambycid species are strongly attracted to smoke volatiles from forest fires, with the dead, dying, or severely stressed trees providing a large but ephemeral resource for the development of their larvae (reviewed by Suckling et al. 2001; Allison et al. 2004). For example, Boulanger et al. (2013) found three species of cerambycids colonizing fire-damaged spruce, including the lamiine *Monochamus s. scutellatus* and the lepturine congeners *Acmaeops pratensis* (Laicharting) and *Acmaeops proteus proteus* (Kirby). Kelsey and Joseph (2003) reported that pines damaged by fire produced ethanol, with emission rates increasing with the severity of tissue damage. In addition to several species of bark and ambrosia beetles, the cerambycid *Spondylis upiformis* (Mannerheim) was attracted to scorched pines, with the numbers attracted increasing with the concentration of ethanol in the sapwood, suggesting that ethanol was at least in part responsible for attracting adult beetles to potential larval hosts. Adults of other pyrophilous species also are attracted to fire-damaged hosts by smoke volatiles. For example, Gardiner (1957) found that smoke from smoldering pine slash attracted the lepturines *A. p. proteus* and *Stictoleptura c. canadensis* (Olivier) (formerly *Anoplodera canadensis*) as well as the spondylidines *T. c. cinnamopterum* and *Asemum striatum* (formerly *A. atrum*). Hovore and Giesbert (1976) reported that *Tragidion annulatum* LeConte were strongly attracted to brushfires and burning vegetation, and this was corroborated by Swift and Ray (2008). Suckling et al. (2001) found that females of the spondylidine *Arhopalus ferus* (Mulsant) preferred to oviposit on pines that had been burned and used smoke to locate burned hosts. To our knowledge, none of the volatile components of smoke that mediate the attraction of pyrophilous species have been identified, although a recent study showed that specific olfactory neurons on the antennae of adults of both sexes of *Monochamus galloprovincialis* were stimulated by typical smoke volatiles (Álvarez et al. 2015).

Because many cerambycid species are known to exploit volatiles from woody plants as host location cues, it should come as no surprise that volatiles from unsuitable hosts also may influence the behavior of adult beetles. For example, Yatagai et al. (2002) found that adults of the cryptomeria bark borer, *Semanotus japonicus* Lecordaire, were repelled by essential oils of *Cryptomeria* species that are resistant to their larvae. Yamasaki et al. (1997) found that attraction of *Monochamus alternatus* to monoterpenes of its pine hosts was antagonized by the sesquiterpene (–)-germacrene D, which characterizes healthy trees that would be unsuitable larval hosts. Moreover, Suckling et al. (2001) found that attraction of *Arhoplaus ferus* to smoke volatiles was effectively blocked by release of green leaf volatiles that presumably contradict the signal that fire has rendered the upwind host vulnerable to attack. A recent study also has found that species that attack deciduous hosts are inhibited by monoterpene blends characteristic of conifers (Collignon et al. 2016).

The odor blends from both coniferous and deciduous woody plants can be complex, consisting as they do of compounds as variable in properties and chemistry as ethylene (a gas at room temperature), through relatively small and volatile compounds such as green leaf volatiles and monoterpenes, to less volatile compounds such as sesquiterpene hydrocarbons and oxygenated sesquiterpenes (e.g., Kimmerer and Kozlowski 1982; Yatagai et al. 2002). The problem of identifying even individual chemicals is compounded for those components that have two or more stereoisomers because each of these is perceived by biological receptors as a distinct entity. Thus, in theory, the problem of reconstructing the specific subset of compounds that comprise the attractant cue for a particular insect species, including the correct relative ratios, can be daunting (e.g., Millar et al. 1986). Consequently, in practice, many researchers have resorted to using only crude approximations of host volatiles as test attractants, such as the α-pinene or turpentine baits mentioned earlier. In part, these crude baits may work reasonably well for polyphagous species, which presumably have flexible host plant attractant "templates" in order to be able to respond to the varying odor profiles of the variety of species that they infest.

Many researchers have used electroantennography (EAG) or, even better, gas chromatography coupled with electroantennographic detection (GC-EAD) to aid in identifying potential host plant attractants (Millar and Haynes 1998). For example, there is no evidence that the cerambycine *Phoracantha semipunctata* uses volatile pheromones for long-range attraction; instead, both sexes are strongly attracted to the odors of fallen trees, cut logs, or dying foliage (Hanks et al. 1996; Barata and Araújo 2001). The beetle's known host range is restricted to a single genus, *Eucalyptus*, but *Eucalyptus* is among the largest plant genera (~750 species; Elliot and Jones 1990), and the phytochemistry of the various species is both variable and complex (e.g., Boland et al. 1991). Barata et al. (2000) conducted GC-EAD studies with *P. semipunctata* and found that the beetle antennae detected 43 host volatiles—about a third of which the authors could not identify. It also must be remembered that the EAD response of an antenna to a particular compound provides no insight into behavioral response. Thus, some of the compounds eliciting antennal responses may mediate behavioral responses other than attraction and may even be repellent. Because of the complexity of the blend and the resulting uncertainty as to which components might form part of the attractant bouquet, to our knowledge it has not been possible to reconstruct a blend of *Eucalyptus* volatiles that is as attractive as crude host material for *P. semipunctata*. Similarly, Fan et al. (2007a, 2007b) conducted GC-EAD studies with *Monochamus alternatus* and found that antennae of males responded most strongly to α-pinene, β-pinene, 3-carene, and terpinolene. Further complicating matters, males were attracted only by α- and β-pinene in olfactometer bioassays, but they were significantly attracted to all four compounds when they were tested as individual components in field bioassays. Females of *M. alternatus* showed much weaker responses to these compounds, suggesting to the authors that the sexes were brought together by males first arriving on larval hosts and then producing a pheromone that attracts beetles of both sexes. The recent identification of a male-produced pheromone for *M. alternatus* (Teale et al. 2011) has added credence to this theory.

As mentioned here, much of the research on cerambycid host plant attractants has focused on species that attack stressed hosts, with few studies of those that attack healthy hosts or those whose larvae feed in totally dead or decaying hosts. Among the cerambycids that attack healthy hosts are those that render only part of a tree highly stressed, irrespective of its original condition, by disrupting the vascular system. Such species include (1) branch-girdling lamiines, females of which chew a trench through the bark encircling the branch and then oviposit distal to the trench so that the developing larvae are isolated from any host plant reaction; and (2) “pruning” cerambycine species whose larvae girdle branches from within and then feed distally to the girdle, so that they again are protected from host responses (Linsley 1959; Solomon 1995). For such beetle species, any tree of the appropriate species may be suitable as a larval host, and the volatiles that adults use to find hosts are likely to be those that are produced by hosts of any physiological condition.

Little is known of host attractants or other cues used by cerambycids whose larvae develop in hosts that are completely dead. The larvae of parandrines and lepturines commonly develop in decaying hosts, while a few species of cerambycines, spondylidines, and necydalines develop in dead and seasoned wood (Švácha and Lawrence 2014). Species that feed in dead hosts are among the most polyphagous of cerambycids, with some species developing in both coniferous and deciduous hosts (Linsley 1959). This polyphagy is likely due to the fact that the larvae of these species derive their nutrition primarily from the tissues of fungi growing in the dead wood rather than from the dead wood itself (see Švácha and Lawrence 2014). One such species in this category is the old house borer, *Hylotrupes bajulus*, whose larvae develop in dead and seasoned wood (Linsley 1959). This species is an important pest because the larvae can damage structural timber (White 1954; Noldt et al. 1995, and references therein). Higgs and Evans (1978) first showed that female *H. bajulus* preferred to oviposit in host material that was already infested, with oviposition being stimulated by (–)-verbenone present in the larval frass and thus probably derived from the host. Subsequent attempts to identify volatile attractants from hosts and frass in olfactometer studies were hindered by the incomplete responses of adults under experimental conditions (e.g., Fettköther et al. 2000). Nevertheless, these studies indicated that females responded from a distance to crude extracts of host material and larval frass as well as to (–)-verbenone and several other monoterpenes from pines. Males, on the other hand, also responded to the crude extracts but differed from females somewhat in their response to the various monoterpenes—for example, by not responding to (–)-verbenone. A later study by Reddy et al. (2005) revealed that host monoterpenes synergized attraction of females to synthetic blends of the primary components of the male-produced pheromone blend ([*R*]-3-hydroxyhexan-2-one + 1-butanol; Table 5.1).

It also has been determined that cerambycids that share hosts with bark and ambrosia beetles can exploit the pheromones of the latter as kairomones (reviewed by Ibeas et al. 2007). This chemical eavesdropping is adaptive because it directs adult cerambycids to trees that are the highest quality hosts for their larvae—for example, those whose defenses have been compromised by bark beetle attack and that can provide their larvae with added nutrition from facultatively preying upon bark beetle larvae (e.g., Billings and Cameron 1984; Allison et al. 2001, 2003; Dodds et al. 2001). There is a wealth of literature on pheromones of scolytine bark beetles, with many different structures identified (reviewed in Francke and Dettner 2005). Among the most common—and most studied—pheromone components are ipsenol and ipsdienol (e.g., Wood 1982; Seybold et al. 1995, and references that follow). As with host plant volatiles, cerambycid species vary in how they respond to the particular bark beetle pheromones that they exploit as kairomones. Thus, no particular bark beetle compound can be considered a truly general attractant. For example, pheromone components of various bark beetle species may act as attractants, antagonists, or be entirely neutral for sympatric species of *Monochamus* (reviewed by Ibeas et al. 2007). To further complicate matters, the sexes may differ in their responses to plant volatiles and other kairomones. For example, Costello et al. (2008) found that males of *M. c. clamator* were most strongly attracted to host plant volatiles alone, whereas ipsdienol acted synergistically with host volatiles to attract females. The response of a cerambycid species to pheromone components of a given bark beetle species likely depends on whether they share hosts (i.e., the cerambycid depends on bark beetles to weaken host defenses) and on their coevolutionary history (i.e., whether they evolved in sympatry).

Host plant volatiles may strongly influence the response of cerambycids to bark beetle pheromones—for example, by providing “context” to the pheromone signal, indicating that bark beetles are not only present but are colonizing a vulnerable plant. Cerambycid species vary in how they are influenced by the host plant volatiles—again probably due to their ecological relationships with the bark beetles and their host plants. For example, an extensive trapping survey conducted by Miller et al. (2015a, 2015b) revealed that the cerambycid *Astylopsis sexguttata* (Say) was significantly attracted by the blend of ipsenol and ipsdienol, and attraction was synergized by ethanol plus α-pinene. However, adults of *Acanthocinus obsoletus* (Olivier) were attracted only by the combination of bark beetle pheromones and the plant volatiles but not to either tested separately. Additional species that were attracted by plant volatiles alone were not influenced by bark beetle pheromones.

Little is known of the sensory cues used by adult cerambycids to locate the host plants upon which they feed as opposed to the larval hosts upon which they oviposit. In some groups, adults and larvae exploit the same host plants, whereas in others, adults and larvae feed on quite different hosts (see Linsley 1959; also see Chapter 4). For example, adult lamiines typically feed on foliage or tender bark tissues of their larval host species. In contrast, adult lepturines and some groups of cerambycines feed on pollen and nectar from flowers, whereas their larvae develop in dying and dead wood. Other cerambycine adults feed on plant sap or do not feed at all as adults. For flower feeders, mutual attraction of both sexes to plants may be sufficient to bring the sexes together, analogous to species that are attracted to larval hosts for mating. For example, males and females of the cerambycine *Zorion guttigerum* (Westwood) are independently attracted to flowers, and so it has been suggested that they may not require a long-range pheromone (Wang and Chen 2005). Adults of the cerambycine *A. subfasciatus* feed on nectar and pollen; in a field bioassay, Ikeda et al. (1993) found that the adults were attracted to floral volatiles produced by the host, including benzyl acetate, phenylethyl propionate, and linalool. In a screening trial of floral volatiles in Japan, Sakakibara et al. (1998) found that two lepturine species were significantly attracted to benzyl alcohol, another lepturine species to methyl benzoate, and a fourth lepturine and one cerambycine species to methyl phenylacetate. Many other species, including another 20 lepturines, showed no significant treatment effect, most likely because the selected test chemicals were dissimilar to the odor profiles of their floral hosts. Overall, this study highlights the fact that, whereas odors of hosts fed on by adults may be useful for sampling particular species, these odors will not attract a representative sample of the cerambycid community.

The recent advances described here showing that volatile pheromones are common, and perhaps almost ubiquitous, among cerambycids have revealed another role for plant volatiles as pheromone synergists. The accumulated literature shows that, for some groups of cerambycids, pheromones alone are sufficient to strongly attract adults and thus may be effective as trap lures for a variety of species that differ in their larval hosts (e.g., Hanks and Millar 2013). Conversely, plant volatiles are critical synergists of pheromones for other cerambycid species. For example, adults of *Tetropium* species (Spondylidinae) are not attracted to the male-produced pheromone fuscumol but are strongly attracted to traps baited with a combination of the pheromone, ethanol, and a synthetic blend of monoterpenes mimicking volatiles of the spruce host plants (Sweeney et al. 2004; Silk et al. 2007). The blend of ethanol and the monoterpenes was attractive in its own right, but attraction was strongly synergized by fuscumol.

In an experiment that tested attraction of cerambycids to a blend of synthetic pheromones from multiple species, Hanks et al. (2012) found that attraction to pheromones was synergized by ethanol but not affected by α-pinene for the cerambycine *Neoclytus m. mucronatus* and the lamiines *Astyleiopus variegatus* and *Astylidius parvus* (LeConte). In contrast, for the lamiine *Graphisurus fasciatus* (Degeer), ethanol synergized and α-pinene antagonized attraction to the pheromone. The fact that α-pinene was neutral or even repellent to these species is consistent with their larval hosts being deciduous trees (Lingafelter 2007) that do not release large amounts of α-pinene. For the conifer-feeding species *Monochamus carolinensis* Olivier, however, neither the host volatile α-pinene nor the male-produced pheromone monochamol was attractive alone, but they strongly synergized each other. Allison et al. (2012) confirmed this strongly synergistic interaction for *M. carolinensis*.

Monochamol is now known to be a pheromone or likely pheromone for more than a dozen *Monochamus* species (Table 5.1). Among these species, the activity of monochamol varies from being attractive as a single component, through facultative synergism by host plant volatiles and/or bark beetle pheromones, to obligate synergism between monochamol and host plant volatiles. For example, monochamol alone attracts the Eurasian *M. galloprovincialis*, *M. saltuarius* (Gebler), *M. sutor* (L.), and *M. urussovii* (Fischer), and the North American *M. notatus* (Drury) and *M. s. scutellatus*, and attraction may be synergized by host plant volatiles and/or bark beetle pheromones (Pajares et al. 2010, 2013; Fierke et al. 2012; Ryall et al. 2015). On the contrary, the Asian *M. alternatus* and North American *M. titillator* are attracted only by the combination of monochamol and plant volatiles (α-pinene, ethanol) and are not attracted to monochamol or plant volatiles alone (Teale et al. 2011; Allison et al. 2012). Macias-Samano et al. (2012) further showed that *M. c. clamator* and *M. o. obtusus* Casey also are attracted by monochamol released with synergistic plant volatiles and bark beetle kairomones.

Pheromones of cerambycids also may be synergized by volatiles from host plants of the adults. For example, Nakamuta et al. (1997) found that females of the cerambycid *A. subfasciatus* were not attracted by synthetic components of the male-produced pheromone ([*R*]-3-hydroxyhexan-2-one + [*R*]-3-hydroxyoctan-2-one) nor to a floral volatile of the host plant of adults (methyl phenylacetate), but they were attracted by the combination of the pheromone and the floral volatile. This synergism may also occur to a greater or lesser extent with species in which the adult and larval hosts are the same (see earlier examples).

5.8 Chemical Defenses of Cerambycids

Several authors have commented in general terms that many cerambycids produce defensive secretions from metasternal glands or mandibular glands (Linsley 1959; Moore and Brown 1971; Dettner 1987), but there are remarkably few actual cases of defensive compounds being identified from cerambycids. Unfortunately, the first identification of a defensive compound from a cerambycid, the European cerambycine species *Aromia moschata* (L.), as 2-hydroxybenzaldehyde (salicylaldehyde) (Hollande 1909), appears to have been incorrect because more than 60 years later, Vidari et al. (1973) identified two rose oxide and two iridodial isomers as the main components of the secretion. The scent of *A. moschata* is perceptible to humans from a distance of many meters and has earned the species the common name of musk beetle (Duffy 1949). Such strong scents are characteristic of the tribe to which *A. moschata* belongs, the Callichromatini, with the glands being associated with the metasternal coxae (Linsley 1959). The scents are believed to be defensive in nature (Švácha and Lawrence 2014). Iridodials have also been identified in the defensive secretions of a Japanese species in that tribe, *Chloridolum loochooanum* Gressitt (Ohmura et al. 2009).

There is anecdotal evidence from cerambycid collectors that the supposed defensive chemicals of callichromatine species are used as alarm pheromones, but to date, there appears to be only a single published report, for the Central American species *Schwarzerion holochlorum* (Bates). Greeney and DeVries (2004) noted that when individuals of that species were handled, resulting in the production of a strong sweet, ammonia-like odor, nearby conspecifics dispersed. The experiment was repeated a number of times, and all indications were that the dispersal signal was indeed a volatile chemical rather than a visual or acoustic signal. Similar behavior, triggered by a similar odor, was also observed in the congener, *S.* nr. *euthalia* Bates (Greeney and DeVries 2004).

Moore and Brown (1972) identified an analog of salicylaldehyde, 2-hydroxy-6-methylbenzaldehyde, from the Australian species *Phoracantha semipunctata*, along with (5-ethylcyclopent-1-enyl)methanol the corresponding aldehyde, and several isomeric aldehydes. The chemicals were exuded when beetles were agitated—such as when handled. Adults of the congener *P. synonyma* Newman also produced 2-hydroxy-6-methylbenzaldehyde as well as several cyclic esters (macrolides) with 10-14 membered rings (Moore and Brown 1976). The "pineapple-like" odor of the secretion was found to be due to a series of short-chain methyl and ethyl esters, such as methyl and ethyl 2-methylbutyrate. As with the callichromatines, the defensive glands of the *Phoracantha* species are in the metasternum.

Moore and Brown (1971) also identified toluene and 2-methylphenol (*o*-cresol), which exude from mandibular glands on the frons of the cerambycids *Stenocentrus ostricilla* (Newman) and *Syllitus grammicus* (Newman), commenting that beetles in these genera are commonly known as "stinking longhorns" because of the distinctive odor of 2-methylphenol. It was thought likely that other members of these genera had similar defensive compounds because congeneric adults have similar pungent odors.

It also had been suggested that cerambycids might sequester toxins from their hosts for use in their own defense. For example, aposematic beetles in the lamiine genus *Tetraopes* are specialists on milkweed plants (*Asclepias* species; Asclepiadaceae), which contain toxic cardenolides. However, analyses of several *Tetraopes* species determined that they contained only microgram amounts of cardenolides, probably not enough to deter predators (Isman et al. 1977). In a second example, cerambycids in the genus *Elytroleptus* mimic and prey upon lycid beetles in the genera *Calopteron* and *Lycus*, which produce the toxin lycidic acid ([5*E*,7*E*]-octadeca-5,7-dien-9-ynoic acid; Eisner et al. 2008). Remarkably, the *Elytroleptus* species do not sequester this toxin but rather may derive indirect protection by mingling within aggregations of their toxic hosts. Similar comingling of cerambycid mimics of lyctid beetles with the lyctids has been reported for a number of South American species (do Nascimento et al. 2010).

There has also been a single report of a cerambycid using a venom. Specifically, the South American species *Onychocerus albitarsis* Pascoe has a sting-like terminal antennal segment with associated glandular tissue (Berkov et al. 2008). When molested, it flicks the antennae at its target to drive the antennal tip home, causing a painful sting.

5.9 Practical Applications of Cerambycid Semiochemicals

Semiochemicals which mediate insect behaviors have four basic practical applications:

1. Detection of a target species to determine presence/absence
2. Sampling or monitoring to follow seasonal phenology and the size, growth, and decline of populations for both invasive and endemic species
3. Sampling insect communities to assess species richness and diversity
4. Management of populations that have become pests

The first three applications are clearly related and so will be discussed together.

5.9.1 Use of Semiochemicals for Detection and Monitoring of Cerambycids

Cerambycid beetles are dichotomous in that they perform essential ecosystem functions by initiating the colonization, decomposition, and recycling of woody biomass, but these characteristics can also render them important pests of living trees, cut timber, and wooden structures (e.g., Solomon 1995). Thus, at one end of the scale, the presence and population sizes of native species reflect the health of ecosystems, whereas at the other end of the scale, they can be some of the most important invasive species, with their introductions into new areas of the world having the potential to cause both enormous economic losses and major disruptions of natural ecosystems. A case in point is the introduction of *Anoplophora glabripennis* into North America and Europe, where it has the potential to devastate natural and urban forests as well as plantation-grown trees and orchards (Haack et al. 2010; Faccoli et al. 2015). In fact, this insect has been listed among the 100 most dangerous invasive insects (Simberloff and Rejmánek 2011). The potential for damage by invasive species is further enhanced if they vector plant pathogens, as is the case with *Monochamus* species that vector pinewood nematode [*Bursaphelenchus xylophilus* (Steiner and Buehrer); Nematoda; Aphelenchoididae], the causative agent of the often lethal pine wilt disease (Mamiya 1983). On the other end of the scale, some cerambycids have been listed as threatened or endangered, such as *Desmocerus c. dimorphus* in central California (Holyoak et al. 2010) or the European species *Rosalia alpina* (L.), which is on the red list of threatened species of the International Union for the Conservation of Nature (World Conservation Monitoring Centre 1996).

For both threatened and invasive species, the basic problem is the same, that is, to detect the presence (and/or monitor population size and phenology) of a target species with the maximum degree of sensitivity and selectivity. As with many other types of insects, semiochemical-baited traps may be the most successful and cost-effective method of accomplishing this for any cerambycid species for which pheromones or related attractants are known. Several specific case studies may serve to emphasize this point. For example, in a recent two-year survey of cerambycid fauna in U.S. forest fragments in the state of Delaware, pheromone-baited traps captured cerambycids of 69 species, including seven species that were new state records (Handley et al. 2015). In another example, 34 male *Desmocerus c. dimorphus* were captured in a small field survey for this threatened species, a number that exceeded the total number of known museum specimens when the species was originally listed as threatened (Ray et al. 2014). A further 63 males were captured in a subsequent pheromone dose-response study (Ray et al. 2014). Other examples of multiple individuals of supposedly rare species being collected in straightforward, short-term field trials include *Curius dentatus* Newman (Lacey et al. 2004), *Anelaphus inflaticollis* Chemsak (Ray et al. 2009b), and *Neoclytus tenuiscriptus* Fall (Ray et al. 2015). Furthermore, the general concept of using pheromone-baited traps as a method of surveying poorly known endemic cerambycid fauna has been tested with success in Russia (Sweeney et al. 2014), China (Wickham et al. 2014), and Australia (Hayes et al. 2016).

Traps baited with combinations of pheromones and host plant volatiles, or other synergists such as bark beetle pheromones, have now been in use for several years for detection and monitoring of range expansions of several invasive cerambycids, including *Anoplophora glabripennis* in North America and Europe (reviewed in Meng et al. 2015), *Tetropium fuscum* in North America (Rhainds et al. 2011), and several *Monochamus* species in Europe (Rassati et al. 2012; Álvarez et al. 2014). To date, these appear to be the only cerambycid pheromones that have been incorporated into operational detection programs, but the great progress in the identification of cerambycid pheromones and attractants in the past decade will undoubtedly provide many more candidate compounds for use in surveillance programs for invasive species. For example, a likely pheromone has been identified for the Asian species *Xylotrechus rufilius* Bates, which recently was intercepted in shipping entering Baltimore, Maryland (Narai et al. 2015), and a pheromone blend was very recently identified for the Asian species *Callidiellum rufipenne*, which invaded the northeastern United States almost two decades ago (Zou et al. 2016). In terms of North American species invading other continents, attractant pheromones are known for North American species such as *Neoclytus a. acuminatus*, which has invaded Europe (Cocquempot and Lindelöw 2010). Pheromone-based attractants have now been identified for at least 12 *Monochamus* species, many of which have the potential to invade or have invaded areas outside their native ranges (Table 5.1). All these *Monochamus* species are attracted to the same, single pheromone component, monochamol, either alone or in combination with host plant volatiles or other synergists.

Ecological studies are also increasingly benefiting from the availability of effective tools for sampling large numbers of cerambycids. Pheromone-baited traps have now been used in several studies of cerambycid species richness and diversity, and these efforts are greatly enhanced by the two complimentary factors that the pheromone structures are often shared by multiple species and that the pheromones can be deployed in blends to attract species from both the same and different subfamilies simultaneously (see the following for further discussion of these points). Thus, a relatively small numbers of traps baited with a few different lure blends can trap beetles of more than 100 species in a given area (e.g., Graham et al. 2012; Hanks and Millar 2013; Wickham et al. 2014; Dodds et al. 2015; Handley et al. 2015).

5.9.1.1 Trap Efficacy

In parallel with the identifications of substantial numbers of pheromones/attractants for cerambycids over the past decade, a number of studies have assessed operational parameters such as trap design, trap placement, and lure design, with the goal of increasing trapping efficiency. In short, attractants are only effective if they are released in appropriate amounts, and the responding insects are indeed trapped. Trap designs have been driven by three main concerns: the efficiency with which an insect that reaches a trap is captured, the retention of the insects once they have been captured, and trap cost. In what follows, we have not attempted an exhaustive recitation of all studies designed to test trap design because essentially all of the earlier papers are cited in the studies described here. Instead, we have focused primarily on the more recent innovations and conclusive studies from the past decade.

From several comparisons of various types and shapes of traps, cross-vane panel traps or multiple funnel Lindgren traps—both of which present a vertical silhouette—have emerged as the most effective general designs (e.g., Graham et al. 2012; Allison et al. 2014; Álvarez et al. 2014; Dodds et al. 2014; Rassati et al. 2014, and references therein), but there are nuances depending upon the specific application. For example, Dodds et al. (2014) found that Malaise traps deployed in the canopy tended to catch larger numbers of species overall, and more rare species, than funnel or panel traps. In addition, Allison et al. (2014) reported that trap efficiency was improved by increasing the diameter of the bottom funnel of traps, which directs insects into the collection bucket, and by using a killing solution in the collection cup to improve retention of captured beetles. However, the single most important factor in improving trap efficacy, demonstrated in a number of trials, was treating the trap surfaces and collection cup with a lubricant such as the Teflon dispersion Fluon® which prevents beetles from clinging to traps when they land and prevents escape from collection buckets (Graham et al. 2010, 2012; Allison et al. 2011, 2014; Álvarez et al. 2014). Various designs of cross-vane intercept traps are available commercially, including traps precoated with Fluon (e.g., Alpha Scents Inc., West Linn, Oregon, USA; Synergy Semiochemical Corp., Burnaby, BC, Canada; ChemTica Internacional SA, San Jose, Costa Rica).

The design of lures is also critically important in order to provide semiochemical release rates that are optimally attractive. Because cerambycid males producing aggregation pheromones can release amounts of many tens of micrograms per hour, or possibly more, pheromone lures should release analogous or greater amounts, which translates to several milligrams per day. Thus, pheromone-impregnated rubber septa that are commonly used as slow release devices for pheromones of Lepidoptera, scale insects, and mealybugs, among other insects, are not used with cerambycid pheromones because the release rates generally are not high enough. Instead, effective lures have been constructed from thin-walled plastic sachets. For example, the authors have used both low-density polyethylene (LDP) resealable plastic bags and heat-sealed plastic tubing as release devices (Hanks et al. 2014). The former have the advantages that they are cheap and readily available anywhere in the world, and they seem to work reasonably well for most cerambycid pheromones, but the disadvantages that they cannot be shipped or stored when loaded, and they tend to leak, so they are obviously not suitable for commercialization. Nevertheless, they have proven very useful and convenient for research-type field trials testing various individual compounds and blends of compounds. In contrast, lures made from heat-sealable plastic tubing avoid most of the disadvantages of the plastic bags, with the added advantages that the tubing comes in a variety of different sizes, wall thicknesses, and chemistries, allowing for easy adjustment of release rates. Most of the cerambycid pheromone lures that pheromone companies are developing are of this type (e.g., Alpha Scents Inc., Synergy Semiochemical Corp., ChemTica Internacional SA). Similar but larger plastic pouches are used to obtain even higher daily release rates (grams per day) of pheromone synergists such as α-pinene and ethanol.

Another factor that may well be neglected in trapping programs is the possible stratification of different cerambycid species from ground level up to the upper canopy. For example, Graham et al. (2012) compared catches in pheromone-baited traps placed at heights of ~1.5 m versus in the upper canopy; from a total of 72 species caught, 21 species were caught exclusively at one of the two heights. Webster et al. (2016) obtained similar results in cerambycid trapping studies carried out in eastern Canada. A number of other studies showed similar trends, but their results may not be as clear-cut because those studies either used passive traps with no attractant (Su and Woods 2001; Vance et al. 2003; Ulyshen and Hanula 2007; Wermelinger et al. 2007; Sugimoto and Togashi 2013) or traps baited with host plant volatiles or kairomones such as bark beetle pheromones (Dodds 2014). Thus, it is unclear to what extent a pheromone lure might alter these results by attracting beetles to canopy strata outside their normal ranges.

5.9.1.2 Generic Lures and Pheromonal Parsimony

One of the bottlenecks of many programs for detecting incursions of invasive insects—and particularly Lepidoptera—is that, as a general rule, lures are formulated to attract only a single species. That is, the pheromones of multiple species are not mixed to form generic lures that might attract multiple species because of the potential for antagonistic interactions among the components (but see Brockerhoff et al. 2013). With cerambycid pheromones, this may be less of a problem for two reasons. First, because of the biosynthetic parsimony that has become evident, it is already common to attract multiple sympatric species to a single compound (e.g., Hanks and Millar 2013; Wickham et al. 2014) in part because the various species use other segregation methods, such as having species-specific, nonoverlapping daily activity cycles of both pheromone production and response (e.g., Mitchell et al. 2015). Second, although the pheromones within a genus, tribe, or even subfamily may be highly conserved, they usually are not conserved across subfamilies. For example, cerambycine species use pheromones (e.g., short-chain alcohols, hydroxyketones, and 2,3-alkanediols) that are in entirely different chemical classes than the pheromones of lamiines (terpenoid derivatives and straight-chain hydroxyethers) or some prionines (prionic acid; Figures 5.1 and 5.2). Two exceptions have been identified to date. First, 2,3-alkanediols are used as female-produced sex pheromones of species in the prionine genera *Tragosoma* and *Megopis* and as male-produced aggregation pheromones by some cerambycine species (see earlier text and Table 5.1). Second, fuscumol and fuscumol acetate are male-produced pheromones for species in both the Spondylidinae and Lamiinae (Table 5.1 and Figure 5.2). In general terms, though, a number of studies on several continents have shown that cerambycid pheromones from different structural classes can be mixed to form generic lures that attract multiple species, thus enabling detection and sampling at far less cost than using multiple traps with a single pheromone per trap (Hanks et al. 2012; Mitchell et al. 2011; Graham et al. 2012; Wong et al. 2012; Hanks and Millar 2013, Sweeney et al. 2014, Wickham et al. 2014; Handley et al. 2015). This concept has now resulted in a commercial version of a multicomponent cerambycid pheromone lure (ChemTica Internacional SA).

However, when the goal is to have the most sensitive trap for a certain species, more caution may be required because there is increasing evidence that there can indeed be inhibition of attraction within cerambycid communities (see Table 5.1), such as inhibition of the (2*S*,3*S*)-2,3-hexanediol pheromone of *Neoclytus a. acuminatus* by (*R*)-3-hydroxyhexan-2-one (Hanks et al. 2012) or inhibition of responses of *Tragosoma* species to their 2,3-hexanediol pheromones by one or more of the "nonnatural" diastereomers for a particular species (Ray et al. 2012a) or inhibition by minor components of the pheromone blends of sympatric species (Mitchell et al. 2015). That being said, generic lures may still be very useful for detecting the presence of a broad spectrum of species because some species are somewhat attracted to blends even though they contain antagonistic components. For example, *N. a. acuminatus* was still attracted in significant numbers to a blend containing its 2,3-hexanediol pheromone despite antagonism from the 3-hydroxyhexan-2-one that was also in the blend (Hanks and Millar 2013). Also, some species apparently will come to relatively weak attractants if there is no stronger attractant in the vicinity. For example, *Prionus californicus* males are attracted to the methyl ester of the female-produced pheromone, prionic acid, if prionic acid itself it not present (Maki et al. 2011b).

5.9.2 Pheromone-Based Tactics for Control of Cerambycids

There are several ways in which pheromones or related semiochemicals could be exploited in programs to control cerambycids. First, it might be possible to disrupt mating using arrays of dispensers releasing pheromones that interfere with mate location, as has been successfully developed for a number of lepidopteran species (e.g., Witzgall et al. 2010). Second, mass trapping with pheromone-baited traps could be used to eliminate a large fraction of the population. This strategy has worked very successfully for groups of large tropical weevils (e.g., Faleiro 2006). Third, pheromone-based attract-and-kill might be possible, using bait stations containing an attractant along with either a toxicant or an entomopathogen such as fungi or nematodes (e.g., Hajek and Bauer 2009; Brabbs et al. 2015).

Pheromone-based mating disruption has been tested twice—both times using the sex pheromone of *Prionus* species. The first trial targeted *P. californicus* in hopyards, where the larvae feed on roots of hop plants. Arrays of lures containing the female sex pheromone resulted in an 84% reduction in males finding a sentinel trap (Maki et al. 2011a). However, because the life cycle of this pest is three to five years, longer-term experiments would be required to determine the efficacy of mating disruption in terms of decreased densities of larvae and damage rates and, ultimately, reduced levels of infestation. The second experiment was done with *P. californicus* in sweet cherries, where a 94% reduction in males locating sentinel traps in an array of pheromone dispensers was achieved (J. D. Barbour, personal communication). Over a two-year period, catches of males in pheromone-baited traps decreased from 234 to 32, suggesting that this strategy could indeed be effective in reducing population densities (Alston et al. 2015).

Pheromone-based mass trapping of cerambycids has been tested several times. For example, Maki et al. (2011a), again working with *P. californicus*, found that surrounding a sentinel trap with a grid of pheromone-baited traps resulted in a very promising 88% reduction in the number of males reaching the sentinel trap. In a longer-term trial with *P. californicus* in sweet cherries, after five years of trapping with pheromone-baited traps, trap catches were reduced from 265 to 2 males, indicating that mass trapping this species has an excellent chance of success if continued for several years (Alston et al. 2015). Similar mass trapping trials targeting *Prionus* species are ongoing in other crops (e.g., pecans; Dutcher 2013) and are likely to be attempted with other prionine species that have powerful female-produced sex pheromones. For example, the prionine species *Dorysthenes granulosus*, a major pest on more than one million hectares of sugarcane in southern China, also appears to use prionic acid as its female-produced sex pheromone (Wickham et al. 2016a) and so is another likely target for pheromone-based mass trapping.

Two other tests of pheromone-based mass trapping have been undertaken with species that use male-produced aggregation pheromones. First, Sweeney et al. (2011) tested attractant-baited traps set out in 10 by 10 m grids for the invasive species *Tetropium fuscum* and found lower infestation rates in spruce bait logs and fewer larvae per log in treated plots, indicating that this tactic might be useful for controlling or eliminating beetles from small areas, such as newly established populations of this invasive species. Over larger areas, the initial cost of traps and lures, and the cost of servicing traps, would probably be prohibitive. Finally, following up on their development of very effective lures containing a blend of monochamol, bark beetle pheromones, and α-pinene for *Monochamus galloprovincialis*, Pajares and coworkers tested the efficacy of mass trapping this species (Sanchez-Husillos et al. 2015). Using mark-recapture experiments to estimate beetle population sizes, these researchers estimated that less than one trap per hectare could reduce beetle populations by 95%, concluding that this method could be highly effective in both controlling the beetle and containing the spread of the beetle-vectored pinewood nematode.

5.10 Summary

It is no understatement to say that our knowledge and general understanding of cerambycid beetle semiochemistry have changed dramatically, if not diametrically, in the last decade. Specifically, a frequently cited 2004 review of the chemical ecology of cerambycids listed volatile pheromones from only six cerambycine and one lamiine species and concluded that most Cerambycidae do not use sex or aggregation pheromones as attractants (Allison et al. 2004). In contrast, volatile sex and aggregation pheromones now have been identified from more than 100 species in the five major cerambycid subfamilies, and likely pheromones have been identified from many more species based on their strong attraction to known pheromone components in field screening studies (Table 5.1). Thus, the large volume of recent studies indicates that lack of volatile pheromones may be the exception rather than the rule in the Cerambycidae. In parallel with the surge in identifications of pheromones, major improvements in lure and trap designs have greatly improved the efficiency with which beetles are attracted and captured. In combination, these advances in pheromone chemistry and trap technology have provided valuable new tools for detection and monitoring of cerambycids—whether it be for detecting invasive species, surveys for rare or endangered species, routine monitoring of endemic species, or surveys to assess species richness. For at least some species, it also may be possible to develop practical control methods using pheromone-based mass trapping or mating disruption. Clearly, we have only scratched the surface of what there is to be learned about the use of semiochemicals by this large insect family, and the next few years should see continuing advancements as the pace of research accelerates.

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