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Gary J. Blomquist and Anne-Genevieve Bagnères

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Part I

Chemistry, Biochemistry, and Physiology

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Introduction: history and overview of
insect hydrocarbons*Gary J. Blomquist and Anne-Geneviève Bagnères*

The long-chain hydrocarbons of insects play central roles in the waterproofing of the insect cuticle and function extensively in chemical communication where relatively non-volatile chemicals are required. The recognition of the critical roles that hydrocarbons serve as sex pheromones, kairomones, species and gender recognition cues, nestmate recognition, dominance and fertility cues, chemical mimicry, primer pheromones and task-specific cues has resulted in an explosion of new information in the past several decades, and, indeed, served as the impetus for this book.

A number of reviews and chapters on specific topics related to insect hydrocarbons have been published over the past few decades (Jackson and Blomquist, 1976a; Blomquist and Jackson, 1979; Howard and Blomquist, 1982, 2005; Blomquist and Dillwith, 1985; Blomquist *et al.*, 1987; Lockey, 1988, 1991; Howard, 1993; Nelson and Blomquist, 1995; Gibbs, 2002), and in this book we attempt to bring this information up-to-date and in one place. At the time the first insect hydrocarbons were chemically identified in the 1960s and early 1970s, no one could have predicted the amount of interest that they would generate. Indeed, a pioneer in this field advised one of the authors (GJB) to go into a field other than insect hydrocarbons as he began his independent research career in the early 1970s, as he saw no future in this area. This prophecy proved very wrong and illustrates how difficult it is to predict the future of any scientific field.

The ability of insects to withstand desiccation was recognized in the 1930s to be due to the epicuticular layer of the cuticle. Wigglesworth (1933) described a complex fatty or waxy substance in the upper layers of the cuticle which he called “cuticulin”. The presence of hydrocarbons in this wax of insects was suggested by Chibnall *et al.* (1934) and Blount *et al.* (1937), and over the next few decades the importance of hydrocarbons in the cuticular wax of insects was established (Baker *et al.*, 1963 and references therein). The first relatively complete chemical analyses of the hydrocarbons from any insect, the American cockroach, *Periplaneta americana* (Baker *et al.*, 1963), occurred after the development of gas-liquid chromatography (GLC). The three major components of the hydrocarbons of this insect, *n*-pentacosane, 3-methylpentacosane and (*Z,Z*)-6,9-heptacosadiene, represent the three major classes of hydrocarbons on insects, *n*-alkanes, methyl-branched alkanes and alkenes. Baker and co-workers (1963) were able to identify *n*-pentacosane by its elution time on GLC to a standard and its inclusion in a 5-angstrom molecular sieve. 3-Methylpentacosane

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was identified by its failure to be absorbed in a 5-angstrom molecular sieve and mass spectral data. Silver nitrate column chromatography separated the C27 diene from other hydrocarbon components, and the double-bond positions and isomeric composition were determined by a variety of techniques including infrared analysis and oxidative cleavage of the double bonds. The composition of the hydrocarbons of *P. americana* is unique in their simplicity, with over 90% of the hydrocarbons comprised of only three components (Jackson, 1972), and it was a fortunate choice of insect species for Baker *et al.* (1963). In general, the hydrocarbon composition of insects is much more complex, and sometimes consists of well over a hundred components. In an earlier analysis of the cuticular wax of the Mormon cricket, *Anabrus simplex* (Baker *et al.*, 1960), the complexity of the hydrocarbon mixture (Jackson and Blomquist, 1976b) made it impossible for individual components to be characterized in the early 1960s (Baker *et al.*, 1960). The development and application of combined gas–liquid chromatography and mass spectrometry was key to the rapid and efficient analysis of insect hydrocarbons. In the late 1960s and during the next few decades, GC–MS analysis of insect hydrocarbons was established (Nelson and Sukkestad, 1970; Martin and MaConnell, 1970), and over the next several decades the hydrocarbons of hundreds of insect species were analyzed, first on packed columns and then much more efficiently on capillary columns. It was recognized that for many insect species, very complex mixtures of normal (straight-chain), methyl-branched and unsaturated components exist, with chain lengths ranging from 21 to 50 or so carbons. In retrospect, the occurrence of extremely complex mixtures of components might have suggested that hydrocarbons could play important roles in chemical communication, but only after the recognition of the number and variety of roles they do play have we come to more fully appreciate the importance of insect hydrocarbons in chemical communication. The variety of chain lengths and the number and positions of the methyl branches and double bonds provide the insect with the chemical equivalent of the visually variable colored plumage of birds. Cvačka *et al.* (2006) reported hydrocarbons of up to 70 carbons in chain length using MALDI–TOF mass spectrometry, indicating that the earlier chain-length limits of 50 or so carbons might be a limitation of GC–MS techniques and not the ability of the insect to make longer chain components. The structure and chemical analysis of insect hydrocarbons are covered in Chapter 2 (Blomquist, this book).

A series of studies in the 1960s demonstrated that labeled acetate was incorporated into insect cuticular hydrocarbons (Vroman *et al.*, 1965; Lamb and Monroe, 1968; Nelson, 1969) establishing the *de novo* biosynthesis of the majority of components. Because of the simple hydrocarbon composition and the ease of isolating 3-methylpentacosane and (Z,Z)-6,9-heptacosadiene from the *P. americana*, early *in vivo* biosynthetic studies concentrated on this insect (Conrad and Jackson, 1971; Blomquist *et al.*, 1975; Major and Blomquist, 1978; Dwyer *et al.*, 1981). Work with radiolabeled precursors established the elongation–decarboxylation pathway for hydrocarbon biosynthesis (Major and Blomquist, 1978) and the incorporation of propionate, as a methylmalonate unit, to form the methyl-branching unit (Blomquist *et al.*, 1975). Over the next several decades, studies evolved from *in vivo* studies to the use of microsomal preparations to gain an understanding of how the major

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components were made and regulated. In the final step of hydrocarbon formation, the elongated acyl-CoA is reduced to aldehyde and oxidatively decarbonylated to hydrocarbon (Reed *et al.*, 1994, 1995). The biosynthesis of insect hydrocarbons is presented in Chapter 3 (Blomquist, this book). Only recently have the powerful tools of molecular biology been applied to studies of insect hydrocarbon biosynthesis, and this is covered in Chapter 4 (Wicker-Thomas and Chertemps, this book).

In the mid-1960s, Locke (1965) presented an illustration of insect cuticular lipids in which the newly synthesized hydrocarbons exited the epidermal oenocyte cells where they were synthesized, were transported through pore canals and then formed an outer layer on the cuticle. He pictured the polar head groups of fatty acids interacting with the cuticle, and then the hydrocarbons layered on top of the acyl chains of fatty acids. This served as an excellent model in which to test a number of hypotheses, many of which are still unanswered. It is now clear that newly synthesized hydrocarbons are taken up first by lipophorin and transported via the hemolymph (Bagnères and Blomquist, Chapter 5, this book). How they get transferred to the surface of the insect is unknown, although a number of species are able to selectively transport shorter chain hydrocarbon pheromones and pheromone precursors to the pheromone gland on the abdomen, whereas longer chain cuticular hydrocarbons are transported to cover the entire cuticle (Schal *et al.*, 1998; Jurenka *et al.*, 2003). In many cases, hydrocarbons comprise the majority of the cuticular lipids, making the proposed role of fatty acids of lesser importance, and the arrangement of hydrocarbons on the surface of the insect is unknown, although suggestions have been made that the components of most importance in chemical communication may be on the outer surface (Ginzel *et al.*, 2003; Ginzel, Chapter 17, this book). A clear understanding of hydrocarbon transport to the cuticle and arrangement of hydrocarbons on the surface of insects is, at this time, unavailable.

The large surface-to-volume ratio of insects makes it important that excessive evaporation be prevented. The first recognized and perhaps still primary function of insect cuticular lipids, especially hydrocarbons, is to restrict water loss, a fact first recognized by Ramsay (1935). Early investigations centered on the measurement of transpiration of water and the role of cuticular lipids in preventing water loss, and these early studies were reviewed in Barton-Brown (1964), Beament (1961, 1964), Edney (1957), Richards (1951), and Locke (1965). It is now clear that the cuticle is permeable to water vapor, and that the cuticular lipid layer plays a major role in reducing transpiration. Cuticles from which the surface lipids are removed with organic solvents are relatively permeable to water. Vegetable oils, lecithin and a series of wetting agents and detergents show widely different effects on permeability of the cuticle to water (Beament, 1945). The waterproofing observed with intact insects is closely duplicated when extracted cuticular lipids are deposited on collodion membranes or intact wing membranes (Beament, 1945). The transpiration rate from an insect is found to increase rather abruptly at a temperature that closely corresponds to the transition point or change of phase point of the lipids on the cuticle of a particular species. This transition point is near the melting range of the extractable lipid (Wigglesworth, 1945; Beament, 1945). Rapid desiccation occurs as a result of scratching the outer surface

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of the epicuticle with abrasive dusts. The abrasion needs to be only deep enough to penetrate the epicuticle. Adsorption of the lipids onto the dust may also play a role to a certain extent, especially on insects where the lipids are soft (Wigglesworth, 1945). If the abraded insect is kept in a moist atmosphere to prevent desiccation, the lipid layer is apparently restored, along with the ability to resist desiccation. The lipid melting model achieved textbook status (Randall *et al.*, 1997; Chapman, 1998), although a number of researchers have pointed out its limitation. In the last several decades, Gibbs and Rajpurohit (Chapter 6, this book) have re-examined this phenomenon, and presents our current understanding of the role of cuticular hydrocarbons and other lipids in restricting water loss from insects.

The cuticular hydrocarbons of many insect species are extremely complex and involve mixtures of normal, mono-, di- and tri-unsaturated and mono-, di-, tri-, tetra- and pentamethyl-branched components of chain lengths between 21 and 50 carbons. The number of known components is very large and the number of possible isomers much larger. Insects biosynthesize the vast majority of their hydrocarbon components, and thus hydrocarbon composition may be considered a part of an insect's genotype and therefore available for taxonomic use. The early studies by Jackson (1970), Jackson and Baker (1970), Jackson and Blomquist (1976a), Lockey (1980) and Carlson and collaborators (Carlson and Service, 1979, 1980; Carlson and Brenner, 1988; Carlson, 1988) recognized the special role of cuticular hydrocarbons in chemical taxonomy. The importance of using hydrocarbons in chemical taxonomy has continued to grow, with more recent efforts centered on Drosophilidae and termites. This work is covered in Chapter 7 (Bagnères and Wicker-Thomas, this book).

In order to more fully understand and interpret mass spectra and retention indices of methyl-branched and unsaturated hydrocarbons, standard known hydrocarbon compounds were synthesized and analyzed (Pomonis *et al.*, 1978, 1980). The availability of standards with one or more methyl branches and specific double bonds allowed for better understanding of the roles individual components and hydrocarbon classes played in determining critical transition temperatures and waterproofing characteristics of hydrocarbons (Gibbs and Pomonis, 1995). With the increasing recognition that many hydrocarbon components play important roles in chemical communication, the importance of synthesizing hydrocarbon standards to determine the exact role of individual compounds became more important. The first review of the chemical synthesis of long-chain hydrocarbons is presented in Chapter 8 (Millar, this book).

While the hydrocarbon fraction of insect cuticular lipids is certainly the most studied and has been shown to play a key role in a wide range of chemical communication, other lipids are often present on the surface of insects. The most common cuticular lipids in addition to hydrocarbons include a variety of types of esters, free fatty acids, primary and secondary alcohols, ketones and sterols. Triacylglycerols and the more polar phospholipids are not common components of insect cuticular lipids. In some cases, hydrocarbons are hydroxylated and metabolized to oxygenated components, and these products include some of the short range and contact pheromones of the housefly (Blomquist, 2003) and the German cockroach (Schal *et al.*, 2003). The oxygenated cuticular lipids are discussed in Chapter 9 (Buckner, this book).

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The recognition of the role of cuticular hydrocarbons in chemical communication has evolved over the last 38 years from a point where it was noteworthy when cuticular hydrocarbons functioned in chemical communication to where it is now noteworthy if the hydrocarbons don't serve a function in chemical communication. Carlson *et al.* (1971) first demonstrated the role of hydrocarbons in chemical communication when they showed that a component (Z-9-tricosene) of the hydrocarbons of the female housefly, *Musca domestica*, served as a short-range attractant for males. At about the same time, the *n*-alkanes docosane, tricosane, tetracosane and pentacosane (Jones *et al.*, 1973), and the branched chain hydrocarbon 13-methylhentriacontane (Jones *et al.*, 1971) were shown to be host-seeking stimulants (kairomones) for the egg parasite *Trichogramma evanescens* and the parasite *Microplitis croceipes*, respectively. The activity of the straight chain hydrocarbons, C₂₂, C₂₃, C₂₄ and C₂₅ might appear surprising at first glance, considering that these compounds are so widespread. On the other hand, a highly specific kairomone would hardly serve a parasite that has a broad latitude in the selection of insect hosts such as *T. evanescens*. Since the young of this parasite will develop in eggs of most Lepidoptera, a kairomone common to many species might be anticipated (Jones *et al.*, 1973).

It is becoming increasingly clear that a major function of cuticular hydrocarbons in arthropods is to serve as recognition signals between two or more individuals. One or more components of the complex mixture of hydrocarbons found on the cuticle of almost all arthropods is often the primary chemical cue that answers questions such as: "Are you a member of my species? Are you the same gender as me? For subsocial insects, are you a member of my family, cohort or group? For eusocial insects, are you a member of my colony? Are you a member of my nest? To which caste do you belong? Are you a queen or perhaps a brood? Are you a worker trying to convey to me the need to accomplish a certain task? Are you closely related kin? And, for many arthropods that exist asinquilines in the nest of social insects, can you recognize that I am alien?" (Howard and Blomquist, 2005).

Although a few early authors predicted that contact between cuticle and antenna was crucial for chemical recognition in insects, technical difficulties prevented proof of this concept until relatively recently. As a result of this delay, the study of volatile signals long dominated that of pheromone (and allomone) chemoreception. One of the first to implicate antennae in inter- and intra-specific recognition in ants was Adèle Fielde in 1904 and 1905. Shortly after, in 1907, W. Barrows (reference in Stocker and Rodrigues, 1999, and deBruyne, 2003) demonstrated that adult *Drosophila* detect odors using their antennae. Prokopy *et al.* (1982) appears to have been the first to use a combination of electrophysiological and behavioral techniques to identify the production source of contact pheromones in female *Rhagoletis pomonella* (from Stadler's 1984 review on contact chemoreception). Hodgson and Roeder (1956), Clément (1981, 1982), Rence and Loher (1977) and Le Moli *et al.* (1983) were among the first to implicate the antenna in the reception of chemical cues from insect cuticle. Further confirmation was obtained in experimental works by Venard and Jallon (1980), Antony and Jallon (1982), Howard *et al.* (1982a), Bonavita-Cougourdan *et al.* (1987), Getz and Smith (1983, 1987), Morel *et al.* (1988), and Bagnères *et al.* (1991) (see also later references in Chapter 10). The aforementioned authors almost consistently showed direct or

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indirect evidence that behavioral responses to total cuticular mixture extracts or individual compounds depended on antennal reception. Recent insect studies (Heifetz *et al.*, 1997; Brockmann *et al.*, 2003; Batista-Pereira *et al.*, 2004; Châline *et al.*, 2005; Ozaki *et al.*, 2005; Saïd *et al.*, 2005; Guerrieri and d'Ettorre, 2008) using one or two compounds or mixtures demonstrated direct olfactory sensitivity to long-chain hydrocarbons. Ozaki and Wada-Katsumata review the perception of cuticular hydrocarbons in Chapter 10.

Early studies on perception and olfaction of cuticular hydrocarbons were performed in social insects because of their sociobiological implications in kin and nestmate recognition processes. Adèle Fielde made her visionary predictions about the “power of recognition” (1904) and the “specific, progressive and incurred odor” (1905) based on observations in ants. Emerson (1929) and Dropkin (1946) suggested that species odor in social insects might be environmentally induced (in Howse, 1975). Wilson (1971) stated that conspecific recognition was acquired over time in insect colonies, whereas Wallis (1962, 1964, refs in Howse, 1975) found that environmental factors had little effect on colony odor that appeared soon after emergence. Crozier and Dix (1979), Hölldobler and Michener (1980), Shellman and Gamboa (1982), Carlin and Hölldobler (1983), Pfennig *et al.* (1983), Lacy and Sherman (1983), and Howse (1984), who were among the first to implicate contact pheromones as nestmate recognition cues, studied this aspect on various species of social insects.

Nestmate recognition is part of kin recognition in social insects. Genetic relatedness, as well as phenotype matching, play a key role in social insects (Hamilton, 1964; Lacy and Sherman, 1983). As stated by Howard (1993) and Passera and Aron (2005), the first proof that cuticular hydrocarbons play a role in colonial recognition was provided by Bonavita-Cougourdan *et al.* in 1987. Bonavita-Cougourdan and colleagues were also the first to suggest that methyl-branched hydrocarbons exhibited the greatest variation between colonies and to discuss preliminary data implicating the postpharyngeal gland in the colony odor. Nevertheless, proof of kin recognition using cuticular hydrocarbons, i.e., based on cues correlated with genetic relatedness, has been presented in only a few eusocial species, e.g., honeybees (Arnold *et al.*, 1996), wasps (Gamboa, 2004) and termites (Dronnet *et al.*, 2006). Most examples have involved nestmate recognition. There have been even fewer reports on kin recognition with contact cues in gregarious species such as cockroaches (Lihoreau *et al.*, 2007; Lihoreau and Rivault, 2009) and also solitary species (Lizé *et al.*, 2006), and most have involved incest avoidance and/or mate choice (Simmons, 1989; Lihoreau *et al.*, 2007). In this book, the role of cuticular hydrocarbons in nestmate recognition is presented in Chapter 11, along with a review of the nestmate recognition models proposed by van Zweden and d'Ettorre.

The use of cuticular hydrocarbon as task-specific cues was suggested by Howard *et al.* (1982a) and Bagnères *et al.* (1998) and illustrated by caste-specific mixtures in termites. Bonavita-Cougourdan *et al.* (1993) also reported evidence of a hydrocarbon cueing between functional castes of *Camponotus* ants. Several studies by Gordon, Greene and collaborators recently proved the involvement of cuticular compounds in task decisions in ants (Greene and Gordon, 2003, 2007). Green reviews this aspect of chemical communication of social insects in Chapter 12.

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Introduction

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A particularly well-documented example of the cueing function of cuticular hydrocarbons involves fertility and dominance signals. Because age is often an important factor for task, fertility and dominance cues (Wilson, 1963; Robinson, 1992; Keller and Nonacs, 1993), some of the first studies were carried out using foundresses and young wasps as models (Bonavita-Cougourdan *et al.*, 1991; Brown *et al.*, 1991). There have also been studies on queen and brood odor in ants (Monnin and Peeters, 1997; Dahbi and Lenoir, 1998; Monnin *et al.*, 1998; Monnin, 2006; Liebig *et al.*, 1999, 2005), bees (Francis *et al.*, 1985) and bumble bees (Ayasse *et al.*, 1995). Recently cuticular hydrocarbons were even described as putative primer pheromones (Le Conte and Hefetz, 2008). Liebig reviews the literature describing social insects' use of cuticular hydrocarbons as dominance and fertility cues in Chapter 13.

Some insect (and non-insect) species use cuticular hydrocarbons for chemical deception/mimicry to gain some advantage from another species. In Chapter 14 Bagnères and Lorenzi review the wide range of multitrophic level mimicry relationships that have been described between plants and insects, social insects and nonsocial insects and non-insects, and various social insect interactions including other aspects of mimicry, for example artificial mixed social insect colonies and intraspecific mimicry. Howard *et al.* (1982b, 1990), Vander Meer and Wojcik (1982) and Vander Meer *et al.* (1989) were the first to report chemical mimicry with cuticular hydrocarbons. Subsequent reports included those of Espelie and collaborators on parabiotic associations in social insects (Espelie and Hermann, 1988), Franks *et al.* (1990) on chemical disguise phenomenon in a leptothoracine cuckoo ant, and Yamaoka (1990) on various chemical interactions. Scott (1986) described sexual mimicry in *Drosophila*. Since those different reports, two main theories have been proposed to account for the appearance of specific hydrocarbons used for chemical mimicry phenomena: de novo biosynthesis by the intruder or acquisition from the host by contact. These two processes are not mutually exclusive. Other possible integration processes could be involved for newborn insects with low amounts of hydrocarbon, parasite cuticular chemical insignificance that has often been observed, and odor change with age that was observed long ago by Fielde (1905).

The cuticular hydrocarbons of solitary insects have also been thoroughly studied. A wide range of functions has been documented in diptera behavior (aggregation dominance, courtship, mate discrimination) and reproduction (fecundity, sex-ratio). Ferveur and Cobb emphasize the evolutionary aspect of those various cuticular hydrocarbon functions in Chapter 15. A number of authors earlier studied dipteran cuticular hydrocarbons, including Rogoff *et al.* (1964), Butterworth (1969), Leonard *et al.* (1974) and Leonard and Ehrman (1976). Most authors focused on sexual selection using pheromones in *Drosophila* and, since the 1980s, the group of Jallon and associated people (Antony and Jallon, 1981, 1982; Jallon, 1984, reference found in Ferveur, 2005). The involvement of hydrocarbons in housefly sexual behavior was studied by Blomquist *et al.* (1987) and Carlson *et al.* (1971).

In Chapter 16 Trabalon and Bagnères present an overview of non-insect contact pheromones with emphasis on long-chain hydrocarbons and derivative compounds in Arachnids. Apart from studies on spider and scorpion venoms, the first semiochemical studies in these

close insect relatives focused on permeability properties of cuticular lipids (Hadley, 1970, 1981; Hadley and Filshie, 1979; Hadley and Hall, 1980). Several early studies described contact pheromones on female spider webs and cuticle (Hegdekar and Dondale, 1969; Blanke, 1975; Dijkstra, 1976; Tietjen, 1979). Krafft (1982) showed that tactochemical stimuli obtained by body contact played an important role in spider recognition of conspecifics. One of the chapter authors (M. Trabalon) presented the first complete description of spider cuticular hydrocarbons. Since data on scorpion recognition mechanisms using cuticular contact pheromones has been rare, the other chapter author (A-C Bagnères) has provided personal results (obtained in collaboration with Phil Brownell) that have never been published elsewhere.

Chapter 18 by Millar describes the role of longer polyene hydrocarbons and their derivatives as sex pheromones in lepidopterans. Non-oxygenated polyenes were identified as moth pheromones before the oxygenated derivatives. Indeed, Roelofs *et al.* (1982) identified (Z,Z,Z)-1,3,6,9-nonadecatetraene as the sex pheromone of the winter moth *Operophtera brumata*. This finding was supported by trap tests showing that the synthetic compound was highly attractive. At that time, the finding that *O. brumata* males responded optimally to a conspecific female sex pheromone at temperatures between 7°C and 15°C was unique among pheromone studies. Conner *et al.* (1980) identified the sex pheromone produced by female *Utetheisa ornatrix* moths as (Z,Z,Z)-3,6,9-heneicosatriene. Shortly thereafter, further studies carried out by the same authors for the chemical determination of female sex attractants in other moth populations showed that a Z-C21 tetraene ((Z,Z,Z)-1,3,6,9-heneicosatetraene), along with a new C21 diene (Z,Z)-6,9-heneicosadiene, was a major component, and that both compounds were EAG-active (Jain *et al.*, 1983). In 2004, Ando *et al.* classified polyene hydrocarbons as type II pheromones (15% of the lepidopteran sex pheromones) generally found in the geometridae and arctiidae families.

Chapter 19 by Bartelt is devoted to the pheromonal role of short-chain hydrocarbons, especially short methyl/ethyl-branched and unsaturated components in beetles. The most abundant components in *Carpophilus hemipterus* (Coleoptera, Nitidulidae) have been identified as (2E,4E,6E,8E)-3,5,7-trimethyl-2,4,6,8-decatetraene and (2E,4E,6E,8E)-3,5,7-trimethyl-2,4,6,8-undecatetraene (Bartelt *et al.*, 1990). Later studies showed that male *C. hemipterus* emit nine all-*E* tetraene hydrocarbons and one all-*E* triene hydrocarbon in addition to the two previously reported pheromonally active tetraenes (Bartelt *et al.*, 1992). In their review of biologically active compounds in beetles, Francke and Dettner (2005) listed only a few dozen of those pheromonal compounds, most of which were identified by Bartelt.

While it is always difficult to predict where a given scientific field is headed, Chapter 20 summarizes some of the gaps in our understanding of insect cuticular hydrocarbons and points out areas where work is needed.

In addition to providing a thorough up-to-date compilation of current data, this book gives new perspective in several areas. Chapters 2–9 of this book significantly expand discussion of the chemistry, biochemistry and physiology of cuticular hydrocarbons. Chapter 8 provides the first review of the chemical synthesis of long-chain hydrocarbons. Chapters 11–13 provide new insight into the role of chemical communication in various social insect

functions. Chapter 14 is specifically devoted to chemical mimicry. Chapters 15–19 focus on hydrocarbons as sex pheromones, including those of solitary insects such as Diptera, Coleoptera, and Lepidoptera as well as spiders and scorpions. In an effort to cover all aspects of cuticular hydrocarbons (and derivatives) functions and analyses, the authors of this book have included a wide range of data, not only from the large recent reviews but also from ongoing and unpublished studies.

References

- Ando, T., Inomata, S. I. and Yamamoto, M. (2004). Lepidopteran sex pheromones. In *The Chemistry of Pheromones and other Semiochemicals I*. Topics in Current Chemistry, Vol. 229. Berlin: Springer, pp. 51–96.
- Antony, C. and Jallon, J.-M. (1981). Evolution des hydrocarbures comportementalement actifs des *Drosophila melanogaster* au cours de la maturation sexuelle. *C. R. Acad. Sci. Paris Serie D*, **292**, 239–242.
- Antony, C. and Jallon, J.-M. (1982). The chemical basis for sex recognition in *Drosophila melanogaster*. *J. Insect Physiol.*, **28**, 873–880.
- Arnold, G., Quenet, B., Cornuet, J.-M., Masson, C., De Schepper, B., Estoup, A. and Gasqui, P. (1996). Kin recognition in honeybees. *Nature*, **379**, 498.
- Ayasse M., Maelovits T., Tengö J., Taghizadeh T. and Francke W. (1995). Are there pheromonal dominance signals in the bumblebee *Bombus hypnorum* L. (Hymenoptera, Apidae)? *Apidologie*, **26**, 163–180.
- Bagnères, A.-G., Killian, A., Clément, J.-L and Lange, C. (1991). Interspecific recognition among termites of the genus *Reticulitermes*: Evidence for a role for the hydrocarbons. *J. Chem. Ecol.*, **17**, 2397–2420.
- Bagnères A.-G., Rivière G. and Clément J.-L. (1998). Artificial neural network modeling of caste odor discrimination based on cuticular hydrocarbons in termites. *Chemoecology*, **8**, 201–209.
- Baker, G., Pepper, J. H., Johnson, L. H. and Hastings, E. (1960). Estimation of the composition of the cuticular wax of the Mormon cricket, *Anabrus simplex* Hald. *J. Insect Physiol.*, **5**, 47–60.
- Baker, G. L., Vroman, H. E. and Padmore, J. (1963). Hydrocarbons of the American cockroach. *Biochem. Biophys. Res. Commun.*, **13**, 360–365.
- Bartelt, R. J., Dowd, P. F., Plattner, R. D. and Weisleder, D. (1990). Aggregation pheromone of dried-fruit beetle, *Carpophilus hemipterus*. Wind-tunnel bioassay and identification of two novel tetraene hydrocarbons. *J. Chem. Ecol.*, **16**, 1015–1039.
- Bartelt, R. J., Weisleder, D., Dowd, P. F. and Plattner, R. D. (1992). Male-specific tetraene and triene hydrocarbons of *Carpophilus hemipterus*: Structure and pheromonal activity. *J. Chem. Ecol.*, **18**, 379–402.
- Barton-Browne, L. B. (1964). Water regulation in insects. *Annu. Rev. Entomol.*, **9**, 63–78.
- Batista-Pereira, L. G., dos Santos, M. G., Corrêa, A. G., Fernandes, J. B., Arab, A., Costa-Leonardo, A.-M., Dietrich, C. R. R. C., Pereira, D. A. and Bueno O. C. (2004). Cuticular hydrocarbons of *Heterotermes tenuis* (Isoptera: Rhinotermitidae): Analyses and electrophysiological studies. *Z. Naturforsch.*, **59c**, 135–139.
- Beament, J. W. L. (1945). The cuticular lipoids of insects. *J. Exp. Biol.*, **21**, 115–131.
- Beament, J. W. L. (1961). The water relations of insect cuticle. *Biol. Rev.*, **36**, 281–320.