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Chapter 1

HYDROCARBONS AND INSECTS' SOCIAL PHYSIOLOGY

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ABSTRACT

Since the middle of the 20th century, improvements in analytical technologies have permitted the identification of cuticular hydrocarbons present on the cuticle of almost all insects.

Concomitantly, a great deal of attention has been paid to the determination of their role at the individual, colonial, and populational level. Many studies pointed to the importance of the surface lipids which cover the insects' cuticle. They are important for the survival of individuals and at a higher level, to maintain colony integrity and species survival. The lipid layer is responsible for the water-repellent character of the cuticle which is its primary function. It reduces surface transpiration and protects terrestrial insects from desiccation. Furthermore, it creates a barrier against micro-organisms and inorganic chemical components. More recently, bioassays have shown that surface hydrocarbons are important tools for recognition systems for solitary insects but above all, for social insects where the chemical communications between individuals are complex. Cuticular hydrocarbons serve as contact pheromones when insects encounter each other. They permit insects to identify « friends » from « foes », nestmates from non-nestmates. They constitute a true chemical signature. They also maintain the social structure of insect colonies by separating individuals according to their functions within the colony, according to their physiological states and their hierarchical rank. They constitute a fertility signal for the queen which indicates its presence for the workers which retain their reproduction. Furthermore, cuticular hydrocarbons can play a major role in sexual behavior as an attractant or repellent. They can also be involved in courtship behavior. These are kairomones or allomones in host-parasite and prey-predator relationships, and contribute to mutualistic relations between insects.

Nowadays, the identification of all these functions allows biologists to use cuticular hydrocarbons as tools to conduct eco-ethological studies. For example, it is possible to use hydrocarbon composition as taxonomic character to identify cryptic species which are morphologically close. This could be useful in conservation planning. These components should equally allow a better understanding of ant colonies structure, for instance, the boundaries of polydomous colonies or especially in the context of an invasion when ants form super-colonies.

INTRODUCTION

The exoskeleton of insects (the cuticle) is covered by a lipidic layer. Hydrocarbons are by far the most abundant class of chemicals coating the cuticle of insects (Jackson and Blomquist, 1976; Nelson and Blomquist, 1995). They constitute a barrier against water loss, preventing lethal desiccation, and they provide protection against infection (e.g. Wigglesworth, 1945, 1986; Hadley, 1982; Lockey, 1988; Gibbs, 2002). Cuticular hydrocarbons (CHs) generally range in size from 20 to 40 (and even 48, Akino, 2006) carbon atoms in chain-length, with three structural classes: *n*-alkanes, *n*-alkenes and mono-, di-, and tri-methyl-branched alkanes (Howard, 1993). There are additional constituents: alkyl esters, fatty acids, long-chain alcohols, glycerides, sterols, ketones and aldehydes (Lockey, 1988; Buckner, 1993). Rates of water loss are correlated with the CH structure such as chain-length, degree and position of unsaturation and of methyl-branching (Gibbs and Pomonis, 1995; Gibbs, 1998). Alkanes are likely to form impermeable layers on the insect cuticle whereas alkenes are likely to form more permeable layers. Due to this solid-liquid phase separation, the primary function of alkanes would be resistance to desiccation, whereas that of alkenes would be chemical communication (Gibbs, 2002). It is generally admitted that CHs are synthesized by the oenocytes, cells located near the epidermis or dispersed inside the body. Oenocytes are often associated with fat bodies, a major source of fatty acids that could serve as precursors for hydrocarbon biosynthesis (for the biosynthetic pathways, see for example Diehl, 1975; Howard and Blomquist, 2005; Juarez and Fernandez, 2007). The CHs may also be produced by class III tegumentary glands (Guerino, 1999). Hydrocarbons were released to the hemolymph and transported by specific blood protein (lipophorins, see Chino, 1985) they were then delivered to both external and internal tissues, including the epicuticle, fat body and ovaries (Pho et al., 1996; Schal et al., 1998). In *Drosophila melanogaster* (Pho et al., 1996), it was demonstrated that lipophorin was associated with hydrocarbons, the same being found on the fly cuticle. In *Musca domestica*, the main female sex pheromone (Z)-9-tricosene was mostly found in the carcass and hemolymph. 90% of hemolymph hydrocarbons were associated with a high-density lipophorin, composed of two apoproteins, apolipophorin I (~240 kD) and apolipophorin II (~85 kD). This hydrocarbon carrier seems to be involved in the selective transport of sex pheromones on the cuticular surface (Schal et al., 2001).

Similarities between the CH composition and the hydrocarbons of the Dufour’s gland secretions have been reported in wasps and bees (Oldham et al., 1994, Dani et al., 2001). This was explained by the fact that the Dufour’s gland is an invagination of the epidermis. In ants, the study of hydrocarbons’ circulation in the organism is more advanced. The same hydrocarbons were found in the postpharyngeal gland (PPG) and on the cuticle (Bagnères and Morgan, 1991). This is the principle storage area for hydrocarbons. The PPG opens itself in the anterior part of the alimentary canal. Its contents may either go into the bucal cavity or towards the stomach which is the secondary storage area. Transfers between the PPG and the cuticle and between PPGs of different individuals have been characterized using radio-labeled markers (Soroker et al., 1995; Soroker and Hefetz, 2000). Radio-labeled acetate was injected into an individual whose mouth was blocked by bee wax, preventing her to perform selfgrooming. Hydrocarbons extracted 24 hours later, both in PPG and on the cuticle, presented approximately the same dose of radioactivity. Thus, a part of the hydrocarbons directly migrated to the cuticle while the other part was stocked in the PPG. When the individual was intact, the labeled hydrocarbons were found in the PPG in a greater amount, suggesting a role played by self-grooming in the circulation of hydrocarbons. When a treated individual was put together with another ant, after a few hours, labeled hydrocarbons were found in the PPG of the non-treated individual, demonstrating a transfer by trophallaxy (liquid exchange mouth to mouth), and allogrooming. Thus, hydrocarbons can be transferred between individuals within a colony by the means of trophallaxies, self- and allogroomings (see also Meskali et al., 1995b).

In this chapter, we reviewed the role of CHs as semiochemicals in solitary insects as well as in eusocial insects in several contexts of insect biology for regulating reproduction, nestmate recognition, task allocation, social parasitism, host-parasite and more generally interspecies relationships. The numerous studies performed on these areas indicate that CHs are the principal constituent of surface pheromone in insects. Given the extensive literature on this subject, we will not make an exhaustive review of the complexity of pheromonal communication, especially in social insects. References to numerous reviews are proposed to the reader so that he can acquire a more detailed understanding of the subject if he wishes. The study of these compounds has led to the development of additional tools for the biologist. Several examples will be given at the end of the chapter.

CHS AS NESTMATE RECOGNITION CUES

By definition, solitary insects do not share the same nest. What is most important for them is the ability to recognize both conspecifics from enemies and mates for reproduction. We will see later in this chapter that the CHs are species- and sex-specific.

Social insects have a highly developed recognition system that enables them to behave altruistically towards nestmates but generally act aggressively towards non-nestmates. Nestmate recognition is crucial for colony survival by protecting it against parasites and social parasites (Wilson, 1971; Dahbi and Lenoir, 1998). It protects the colony against conspecific intruders, preventing them from exploiting the colony's resources. Nestmate recognition decreases the likelihood of loss of fitness due to alien reproductive individuals, such as intra- and interspecific social parasites as noted by Zanetti and collaborators (2001) (fitness is the capability of certain genotype to reproduce-which usually is equal to the proportions of the individual's genes in all the genes of the next generation).

Such discrimination is largely based on chemical cues. Already at the end of 19th century and at the beginning of 20th century, some scientists (e.g. Fielde, 1904) proposed the hypothesis that the recognition between members of the same colony depended on the existence of a colony odor (reviewed by Provost, 1989). Howse (1975) suggested that this discrimination ability was based on a chemical signature carried by each individual on its cuticle. The work performed over the last 30 years had led to the belief that although other products may be active, CHs play a preponderant role in these mechanisms acting as a contact pheromone.

Many models have been developed to attempt to explain the mechanisms of nestmate recognition. Crozier and Dix (1979) proposed 2 models. Firstly, the individualistic model according to which each member of a colony keeps its own chemical characteristics genetically determined. In this model the individual estimate if the other individuals it meets are related or not according to whether they share at least an allele per locus which codes for an enzyme involving in the synthesis or the regulation of a particular recognition pheromone. Individuals use their own odor as a reference and compare it with that of the other individuals. Evidence supporting the individualistic model has been found in the sweat bee *Lasioglossum zephyrum* (Greenberg, 1979) and in ants (e.g. Crosland, 1989; Mintzer and Vinson, 1985; but see Provost, 1989). Secondly, the Gestalt model, according to which there is a transfer of recognition pheromones between all members of the group through licking, food exchange, allogrooming or simple contact. Chemical studies of nestmate recognition suggest that nestmate recogniton-cue phenotypes are specific to colonies, rather to individuals (Lacy and Sherman, 1983). In fact, almost all the studies of nestmate recognition have validated this model. The individuals are classified as « familiar » or not according to the level of resemblance of their odor with the learned colony odor. Thus, the individual receives a signal (« label », the term « recognition cue » is now employed) which he compares with the « memorized » model and which constitutes an internal standard for comparison (« template », Shelman and Gamboa, 1982). Templates are a neural or cognitive representation of the chemical phenotype of the colony to which the individual belongs. It develops through processes of learning or imprinting. This comparison between the label and the template is known as « phenotype matching » (Holmes and Sherman, 1982).

In fact the process may be more complex due to the temporal quantitative changes in CHs that have been found for adults in the fire ant *Solenopsis invicta* (Obin, 1986; Vander Meer et al., 1989b), in *Leptothorax lichtensteini* (Provost et al., 1993), in *Camponotus fellah* (Boulay et al., 2000), in the invasive Argentine ant (Suarez et al., 2002). The modification of the signal over the course of time suggests that the ants continually update the template with which they compare the chemical signal of non-nestmates. *L. lichtensteini* ants seem to have the ability of learning in the adult stage, since workers adopted by an alien colony of the same species acquire the odor of their new colony to the point where, after a few weeks they can fight against members of their old colony whose odor they seem to have forgotten (Provost, 1989). Template formation and plasticity were recently investigated using experimental mixed-species group of ants (Errard et al., 2006a; see also Breed et al., 2004a and Harano and Sasaki, 2006, for bees).

The acceptance threshold model has been developed by Reeve (1989) to describe nestmate recognition plasticity. In this model, colony members will accept conspecifics when levels of label-template dissimilarities are below the acceptance threshold. It varies according to the balance between costs and benefits of accepting non-nestmates. According to this model, aggression behavior will be an “all-or-none” response. In an alternative model, the graded response model, the individuals may vary their level of aggression according to the dissimilarities between the template and the label (Lenoir et al., 1999). Recognition process in *Aphaenogaster senilis* supports this graded response model (Ichinose et al., 2005).

The acceptance threshold model predicts that nestmate recognition is less developed in polygynous (multiple queens) colonies than in monogynous colonies. Indeed it is largely accepted that polygynous colonies possess weak recognition abilities relative to monogynous colonies, probably due to a broader exposure to heritable and environmentally derived nestmate recognition cues (Hölldobler and Wilson, 1977; review in Breed and Bennett, 1987; Morel et al., 1990; Provost et al., 1994). However several studies have shown that polygynous species workers were able to discriminate nestmates from non-nestmates (e.g. Rosset et al., 2007). Polydomy also influenced template breadth in *Iridomyrmex purpureus* where an incomplete transfer of colony odor between the nests was reported (van Wilgenburg et al., 2006). A negative relationship was found between nest number and aggression.

Another mechanism leading to weak nestmate recognition is reported from studies on the highly polygynous invasive ant *Linepithema humile*. It was suggested that a loss of genetic variability through a bottleneck may also result in a loss of the nestmate recognition system (Tsutsui et al., 2000) leading to unicoloniality and the formation of supercolonies (but see below Chapuisat et al., 2005)**.** An alternative theory is that there has been progressive and selective loss of less common alleles as recognition loci because groups of ants that do not fight among conspecific colonies have higher fitness (Giraud et al., 2002). Similarly, it was suggested that a loss of genetic variation decreases colony recognition efficiency leading to colony fusions for two ant siblings species *Temnothorax nylanderi* and *T. crassispinus* (Foitzik et al., 2007) and in laboratory experiments (Pusch et al., 2006). The cause of the reduction of genetic variation is yet unknown. These results evoke our data for *T. lichtensteini*, monogynous species whose colonies may be "open". The colonies merged in 60% of the experiments where we put together two colonies in the same arena (100 replicates), without aggression but with elimination of one of the two queens (Provost, 1985). A social insect society is defined "open" or "closed" when its members accept or refuse alien conspecific individuals (Wallis, 1964; Le Masne, 1985).

An absence of aggression between non-nestmates was reported for the primitive ant species *Myrmecia nigriceps* (van Wilgenburg et al., 2007) and in the monogynous ant *Lasius austriacus* (Steiner et al., 2007) and was possibly due to the cost of fighting intruders compared to the benefits of accepting or rejecting them. More studies, especially chemical studies are required on this subject.

As the aggressive behavior between individuals is easier to identify, it has frequently been used as a criteria for the existence of a recognition mechanism. However the absence of aggression between 2 individuals does not mean that they do not recognize each other. For example, workers of the unicolonial ant *Formica paralugubris*, for which little aggression was monitored, were able to discriminate nestmates from non-nestmates by performing significantly more trophallaxis with non-nestmates than nestmates (Chapuisat et al., 2005; see also Bjökman-Chiswell et al., 2008). Abandoning aggression while maintaining discrimination might be a first stage in supercolony formation (Steiner et al., 2007).

Aggression can be provoked by a number of factors such as the relatedness between the individuals (Provost, 1991), the history of the individuals (Provost, 1985), the eventual consequences for their own fitness and the social context within which the encounter takes place. An example where social context is primordial for nestmate recognition in ants was given by studies taking into account the proximity of colonies. Decreased aggressiveness towards non-nestmates sometimes occurs between neighboring colonies that nevertheless remain very aggressive towards non-neighboring con- or heterospecific ant colonies. This "dear enemy" effect reduces the cost of territorial defense. It has been reported in *Acromyrmex octospinosus* (Jutsum et al., 1979), in *Temnothorax nylanderi* that the agonistic interactions among non-nestmates increase with the distance between colonies (Heinze et al., 1996). Similarly, *Iridomyrmex purpureus* workers were more aggressive towards intruders from nests further away than neighboring nests (Thomas et al., 1999) as were two desert *Pheidole* ants (Langen et al., 2000). Some other cases are reported by Boulay and co-workers (2007a).

In contrast, workers of the ants *Pogonomyrmex barbatus* respond more strongly to neighboring conspecifics than to those from colonies separated from them by more than 150m (Gordon, 1989). This is also true for termites (Dunn and Messier, 1999) and for ant supercolonies (Thomas et al., 2006, 2007). The degree of aggression is not correlated to the geographic distance for *Cataglyphis iberica* (Dahbi et al., 1996) nor for *Camponotus cruentatus* (Boulay et al., 2007a). Two mechanisms could explain the "dear enemy" phenomenon. It may be a consequence of habituation to the chemical cues following frequent encounters between members of neighboring colonies or to reduced genetic differences between neighboring colonies leading to closer recognition cues for colonies living in a same area than for allopatric colonies.

Many reviews deal with nestmate recognition in social insects (ants: Vander Meer and Morel, 1998; termites: Clément and Bagnères, 1998; wasps: Singer et al., 1998; Gamboa, 2004; Dani, 2006; bees: Breed, 1998; see also Howard and Blomquist, 2005). An enormous quantity of studies (but not all: see for example Hernandez et al., 2006; Errard et al., 2008) have shown that CHs played a significant role in the recognition ability of social insects. Most of them established a correlation between differences in CHs profiles and nestmate recognition level and few studies reported direct experimental evidence that CHs are implicated in nestmate recognition **(**bioassays using removal and replacement of CHs by solvent extraction).

In the ant *Camponotus floridanus* the colony of origin, social caste, and social experience can be directly correlated to specific concentration patterns of cuticular compounds (Lavine et al., 1990). They demonstrated that foragers and callows (normal and naive) can be differentiated from one another on the basis of their CH profile. If the callows do not interact with the nurses (naive callow), they will not acquire the full colony label. This suggests an exchange of cuticular compounds between the nurses and callows. Aggressiveness between aliens is also correlated with differences in hydrocarbon compositions in *Cataglyphis cursor* (Nowbahari et al., 1990), in *Cataglyphis iberica* (Dahbi et al., 1996; Dahbi and Lenoir, 1998), in *Camponotus fellah* (Boulay et al., 2000). Using an immobilizing "joust" device with living ants of three closely related species of *Pachycondyla* and with different CH classes extracted from the ants, behavioral responses (mandibule opening and antennal retraction) were correlated with the CHs profiles and suggested that only internally branched methyl- and dimethylalkanes are involved (Lucas et al., 2005). *Camponotus cruentatus* workers possess an atypical profile of CHs with high proportions of trimethylalkanes. High aggression between *C. cruentatus* workers from different colonies was accompanied by dissimilarities in cuticular hydrocarbons among colonies (Boulay et al. 2007a). Nestmate recognition abilities of three species of the ant genus *Temnothorax* in relation to cuticular chemicals and intraspecific genetic diversity have been compared (Foitzik et al., 2007). Fusions in *T. nylanderi* and in *T. crassispinus* are common but rare in *T. unifasciatus*. While chemical profiles (*n*-alkanes, mono- di- and trimethylalkanes) of different colonies strongly overlapped in *T. crassispinus* and *T. nylanderi*, 97% of all *T. unifasciatus* samples were, in a discriminating analysis, correctly assigned to their respective colony. Chemical distances between colonies correlated with aggression levels in *T. unifasciatus*, but not in the other two species**.** In the Argentine ant *Linepithema humile*, genetic and cuticular hydrocarbon similarity between colony pairs was correlated with both levels of intraspecific aggression and colony fusion (Vasquez and Silverman, 2008).

Chemical supplementation studies (Breed, 1998) on the alteration of aggressiveness after coating an insect's surface with isolated hydrocarbon or cuticular extracts from another colony have provided strong evidence that CHs were the recognition cues. In *Camponotus vagus* ant, it has been demonstrated for the first time that the proportion of certain dimethylalkanes among the total mixture of CHs played the role of nestmate recognition cues (Bonavita-Cougourdan et al., 1987). A dead worker "A" coated with the chemical signature of a stranger "B" was attacked by its sisters whereas an alien dead worker "B" was not attacked by workers "A" if it was coated with the chemical signal of "A" workers. Similar experiments were carried out by Morel and co-workers (1988) in *Camponotus floridanus*. They showed that nestmate recognition cues change with age and highlighted the role of social experience in the acquisition of a colony-specific label.

Lahav and co-workers (1999) showed in *Cataglyphis niger* that the application of alien hydrocarbons (ant extracts and postpharyngeal gland extracts) on live workers elicited aggression in dyadic encounters of nestmates equivalent to that monitored between two alien ants. In contrast, application of nestmate hydrocarbons on an alien ant reduced aggression but not to the level displayed when two nestmates met. All the other more polar fractions are nonactive, suggesting that hydrocarbons are more important than oxygenated lipids as recognition pheromones. They noticed that the ants are more sensitive to label/template difference than to similarities. It should be noted that the postpharyngeal gland (present only in ants) contained the same hydrocarbons as those from the cuticle (Bagnères and Morgan, 1991; Soroker et al., 1995; Akino et al., 2004). It should be recalled that this gland is known to be a reservoir of CHs, a "Gestalt organ", according to Soroker and co-workers (1994, 1995), which plays an important role in homogenisation of the colony odor and nestmate recognition in *C. Niger*. Workers may regurgitate the content of their postpharyngeal gland to nestmates during trophallaxy, allogrooming, allowing the circulation of hydrocarbons throughout the colony (e.g. Vienne et al., 1995; Soroker et al., 1998). Meskali et al. (1995a) tested the response of *Camponotus vagus* workers towards nestmates treated with (Z)-9-tricosene. We found that nestmates clearly perceived the addition of the compound because the treatment influenced the number of antennations and mandible openings. They still accepted the treated individual and became habituated to it. In *Iridomyrmex purpureus*, filter paper covered with alien worker CHs provoked a stronger aggressive behavior than filter paper covered with the CHs of nestmates (Thomas et al., 1999). The role of CHs in nestmate recognition of the invasive ant *Linepithema humile* was investigated by behavioral assays testing the response of the ants to workers treated with colonymate or non-colonymate CHs. Chemical analyses revealed marked differences in the hydrocarbon profiles across supercolonies. Individuals treated without solvent but by contact with foreign CHs were aggressively rejected by their nestmates (Torres et al., 2007). Greene and Gordon (2007) demonstrated in two species, *Linepithema humile* and *Aphaenogaster cockerelli*, that information on species and colony membership is not in isolated components of the profile, but in the mixture of structural classes (*n*-alkanes, methyl-branched alkanes, and *n*-alkenes) found in cuticular hydrocarbon profiles. No single class of hydrocarbons was more important than the others. A combination of at least two hydrocarbon structural classes was necessary to provoke an aggressive species recognition response. Recognition appears to be based upon subtle differences in many components of the hydrocarbon profiles, and not on large differences in only a few hydrocarbon constituents.

Application of solvent-dissolved hydrocarbons has been also made on glass dummies. By this method, it has been shown that the harvester ant *Pogonomyrmex barbatus* displayed high levels of aggression towards small glass blocks coated with extracts from non-nestmate workers. The cuticular hydrocarbon fraction of extracts was sufficient to elicit agonistic behavior (Wagner et al., 2000). Using a similar method, Akino and collaborators (2004) demonstrated that in *Formica japonica* CHs serve as the nestmate discriminator for the workers and both *n*-alkanes and (Z)-9-alkenes with odd number of carbons from 25 to 33 are necessary to discriminate nestmates from foreign conspecifics. Only one of these 2 classes of hydrocarbons is not sufficient.

In many cases, environmental factors (ambient temperature, humidity, soil characteristics, food and nest material) may act synergistically with the genetic component of odor profiles. For example, colony odor was affected by plant material retrieved by the leaf-cutter ant *Acromyrmex octospinosus* foragers (Jutsum et al., 1979). When different colonies were provided with the same type of forage, they displayed lower levels of aggression toward each other than colonies that were provided with different forage. However, when colonies were divided and provided with different types of forage, they did not display harmful aggression when re-combined. In the Argentine ant *Linepithema humile*, diet altered the recognition cues. Aggression was recorded between nestmates reared on different insect prey (Liang and Silverman, 2000, Silverman and Liang, 2001). Richard (2007a, b, 2004) observed the same evidence of diet-derived CHs for the fungus-growing ant of genus *Acromyrmex.* Even contamination by simple contact with prey provoked nestmate aggression (Liang et al., 2001). Aggression diminished between colony pairs sharing a common diet when they were initially moderately aggressive. However, initially aggressive colony pairs still maintained high levels of aggression (Buczkowski et al., 2005).

The fine sensory mechanisms for nestmate recognition (e.g. HC blend perception mechanism) are not well known for insects. Ozaki and co-workers (2005) described a type of multiporous sensory sensillum on the antennae of the carpenter ant *Camponotus japonicus* that is involved in nestmate discrimination. Usually, multiporous chemosensilla are assumed to be olfactory rather than contact chemosensory. This sensillum responds only to non-nestmate CH blends, even in isolated antenna preparations. Moreover, these authors reported that lipophilic CHs might be transported owing to a member of the chemosensory protein family (CjapCSP) through hemolymph to putative receptor neurons housed by these sensilla.

The hydrocarbons are known to be implicated in nestmate recognition not only for ants but also for wasps, bees, and termites.

Exposure to nest material is required for a newly emerged *Polistes* to be able to recognize her nestmates (Shellman and Gamboa, 1982; Pfennig et al., 1983). Polistes nests are covered in colony-specific hydrocarbons (Espelie et al., 1990). The cues are learned from the nest material rather than from nestmates in the first hours of adulthood (Gamboa et al., 1986). CHs and hydrocarbons of the paper nest were the same, but in different proportion. Singer and Espelie (1992) found that newly emerged wasps *P. metricus* learned and acquired the colony-specific hydrocarbon profile from the nest surface, which allowed them to discriminate between nestmates and non-nestmates. In this species, the hydrocarbons found on the cuticle and on the surface of the nest were *n*-alkanes (mainly *n*-heptacosane and *n*-nonacosane), methylalkanes (methylhentriacontane and methyltritriacontane) and dimethylalkanes (Espelie et al., 1990). Different groups of compounds might be used by the wasps in different recognition contexts (Layton et al., 1994). Three hydrocarbons were identified as good candidates for colony recognition pheromone in *P. fuscatus* (Espelie et al., 1994). In the neotropical wasp *Polistes satan*, colony membership was correlated with CH profiles (Tannure-Nascimento et al., 2007). They established that three *n*-alkanes (*n*-C27, *n*-C29, *n*-C33) separated more significantly four colonies (but see below Dani et al., 2001).

Dani and co-workers (2003) showed that the secretion of the van der Vecht organ (sternal gland), located beneath the terminal gastral sternite segment, of *P. dominulus* was composed of a hydrocarbon mixture, which was similar in composition to that found on the cuticle. Dapporto and co-workers (2007c) showed that *Polistes gallicus* distinguish nestmates from alien individuals and queens from workers by the hydrocarbon mixtures of the van der Vecht organ. Another gland is also a candidate for this function: in *Polistes dominulus*, the Dufour's gland has been also shown to contain a complex mixture of hydrocarbons, which are the same as those found on the cuticle but differ in the proportions of the components. It was suggested that this gland plays an important role in the production of chemical cues used in nestmate recognition (Dani et al., 1996).

Chemical supplementation studies were carried out in *Polistes biglumis bimaculatus* (Lorenzi et al., 1997). Behavioral responses by the residents (acceptance or rejection of introduced wasps) have demonstrated that wasps are able to discriminate dead nestmates from dead non-nestmates and that they use CHs for this discrimination. Dani and collaborators (2001) tested the importance for nestmate recognition of a series of alkenes, methyl-branched alkanes and linear alkanes present in the cuticular profile of the social wasp *Polistes dominulus*. Compounds were deposited on the cuticle of live wasps. They analyzed the response of nestmates when the treated individual attempted to enter the nest. They showed that linear alkanes had no effect (in contrast with Ruther et al., 2002 for *Vespa crabro*), whereas wasps treated with methyl-branched alkanes or alkenes were attacked. Their results have also shown that an increase in a single alkene or methyl-branched alkane found on the cuticle may change the recognition signature. This suggests that it is the relative amount of some of the compounds within the profile that is perceived by the insect (see Breed et al., 2004a).

Application of solvent-dissolved hydrocarbons has also been performed on dummies for the European hornet *Vespa crabro* (Ruther et al., 1998). These same authors provided behavioral proof that the manipulation of cuticular hydrocarbon profiles can be detected. The perception of synthetic hydrocarbons deposited on dummies was sufficient to cause a significant increase in aggression (Ruther et al., 2002). Similarly, Zanetti and co-workers (2001) investigated the ability of females to recognize nestmates in the stenogastrine wasp *Parischnogaster striatula*. This species although phylogenetically close to *Polistinae* and *Vespinae* exhibits a primitive eusocial organization. By performing observations in the field of the reactions by resident females towards conspecifics (alive, dead and hexane-washed) present in their nests, they provided evidence that CHs mediate nestmate recognition. The wasp *Polybia paulista* is also able to distinguish nestmates from non-nestmates (Kudô et al., 2007) despite the fact this species is highly polygyne.

In honeybees, the evidence for the role of hydrocarbons in nestmate recognition is more controversial. Fröhlich and co-workers (2001) and Breed and co-workers (2004a) postulated that fatty acids are more important recognition cues in honeybees. However, CHs are colony-specific (Page et al., 1991) and have been reported to separate full-sisters from half-sisters (Arnold et al., 2000). Indeed, a bee colony contains between 7 and 20 different subfamilies due to the polyandry of the queen. The authors showed that in hive bees, subfamilies CH signatures tend to resemble each other without completely matching, thus restricting nepotistic behavior. Nevertheless a few subfamilies retain distinct profiles.

As with *Polistes* wasps, newly emerged bees carry no recognition cues ("blank slate", Breed et al., 2004b). A very short exposure (5min or less) to wax comb was sufficient for adult bees to acquire from it nestmate recognition cues which have genetically correlated components (Breed et al., 1995, 1998). Chemical analyses demonstrated that bees with exposure to wax comb have different chemical profiles than bees without such exposure. In an olfactometer, bees discriminated between wax combs and preferred the odors of previously learned wax combs. Chemical supplementation experiments revealed that bees treated with hexadecane, octadecane, tetracosanic acid or methyl docosanoate were less readily accepted by their sisters (Breed and Stiller, 1992). Hydrocarbons, together with esters, represent an important fraction of comb wax (Fröhlich et al., 2000). Nest material was reported as the most important source of recognition cues and more important than odors acquired from flowers (Downs et al., 2000). Chemicals acquired from the comb were transferred among bees in physical contact, resulting in a "Gestalt" colony odor (Breed et al., 1995). By swapping half the wax combs between two colonies, the effect of the wax comb on the acceptance of conspecific nestmates and non-nestmates by guards was investigated (D'Ettore et al., 2006). They demonstrated that this swapping experiment had a clear effect on nestmate recognition. Each of the two colonies became more tolerant towards non-nestmates due either to the modification of labels of the workers or to the change in the template of guards, or both. Moreover, swapping combs increased the similarity of CH profiles of workers from the different hives. Hydrocarbons were represented by a series of n-alkanes with chain lengths ranging from 23 to 33 carbon atoms and the corresponding alkenes (Martin et al., 2001).

In *Apis mellifera*, guard bees defend the nest against conspecific intruders or parasites. A guard would be able to accept all nestmates and reject all non-nestmates but recognition errors appeared when they have overlapping recognition cues (Reeve, 1989). Breed and co-workers (2004a) demonstrated that bee's recognition cues must completely match a colony's template to identify that bee as a colony member. Guard bees can develop a new recognition template when exposed to cue compounds so highlighting adaptability in the honeybees nestmate recognition system. They can assess the concentration of each among five compounds independently.

It was shown that, under natural conditions, where workers of many different patrilines are present in a colony, guards use only cues that are acquired as adults from the colony environment (Downs and Ratnieks, 1999). Thus, environmental cues were sufficient for the discrimination between nestmates and non-nestmates. Heritable cues might be used when the environmental cue heterogeneity was low between individuals (Grenberg, 1979; Mintzer, 1982). Using infrared thermography, Stabentheiner and co-workers (2002) have monitored that bees examined by guards heat up their surface, perhaps to enhance signaling by increasing the evaporation of compounds that help guards to identify them as a nestmate or to eliminate volatiles that disturb identification.

It was tested whether artificial changes in the cuticular profile through supplementing naturally occurring alkanes and alkenes in honeybees affect the behavior of nestmate guards. In all the experiments, bees treated with alkenes were attacked more intensively than bees treated with alkanes suggesting that this may correspond to differential importance in the recognition signature (Dani et al., 2005). This result is in agreement with what has already been reported by Breed (1998). The lack of an effect by *n*-alkanes is probably not due to a lack of perception because bees are able to learn and to discriminate between individual alkanes and alkenes found in the cuticular hydrocarbon profile (Châline et al., 2005). Using the proboscis extension reflex, these authors determined how well honeybees can learn long-chain linear alkanes and (Z)-alkenes present on the cuticle of bees and also how well they can discriminate between them. They showed that bees can discriminate between most of the 10 hydrocarbons tested but alkenes were much better learnt than alkanes. The ability of workers to learn shorter-chained alkenes of less than 29 carbons makes these compounds likely candidates for recognition cues.

Treatment with octopamine agonists improves the discrimination between related nestmates and unrelated non-nestmates in honeybees (Robinson, 1999).

Nestmate recognition also was investigated for stingless bees (e.g. *Scaptotrigona bipunctata*, Jungnickel et al., 2004; *Trigona fulviventris* and review, Buchwald and Breed, 2005; *Frieseomelitta varia*, Nunes et al., 2008). CHs are colony-specific in *S. bipunctata*. Seven out of 13 CHs identified in this species were sufficient to separate the two studied colonies. They were 3 alkenes, 3 alkanes and one methylalkane. Further analyses will be needed to confirm their role in nestmate recognition. Buchwald and Breed (2005) included fatty acids, alkanes, an alkene, wax esters and floral oils in their analysis of nestmate recognition for *T. fulviventris*. As for honeybees, fatty acids appear to be important in recognition processes but in contrast with honeybees, workers also used alkanes and floral oils. *F. varia* guards use chemical similarities to accept or reject incoming individuals. The cuticular compounds consist of linear and mono-methylalkanes from 24 to 31 carbon atoms, corresponding alkenes, some fatty acids and fatty acid esters.

For termites, the role of CHs in nestmate recognition has rarely been investigated. In 1998, Singer wrote: "To date there is little evidence that CHs play a role in the ability to distinguish between colonies of conspecific termites". Nevertheless, it has been demonstrated that CHs of different families of termites are species-specific (Haverty et al., 1988; Bagnères et al., 1991a). In dampwood termites, *Zootermopsis spp*., when individuals from different colonies containing different CH phenotypes were paired, high levels of aggression were found (Haverty and Thorne., 1989). Carrying out experiments with washed and re-treated dummies, some evidence have been reported that CHs were correlated with the recognition between members of different species or colonies, (Bagnères et al., loc. cit.; Takahashi and Gassa, 1995; Kaib et al., 2002, 2004). It was shown that CH composition can vary between colonies in close proximity (e.g. Kaib et al., 2002). In *Reticulitermes spp*., pairing groups or individuals from different colonies with the same CH phenotype resulted in little immediate aggression but high mortality was recorded after 24h whereas pairing groups or individuals from different CH phenotypes resulted in immediate aggression and in mortality in 99% of the tests (Haverty et al., 1999; Delphia et al., 2003). These authors concluded that these termites could differentiate CH penotypes and discriminate colonymates from alien workers. Taking into account CHs composition, agonistic behavior, genetic similarity, morphometric distances, and geographic distances between colonies of *Macrotermes subhyalinus*, it was reported that there is sufficient variation in the CH composition among colonies to allow nestmate recognition and that the level of aggression among colonies increases with an increase in the difference of CHs (Kaib et al., 2004). They recorded a positive correlation of the differences in hydrocarbon composition and of the aggression index with morphometric differences and a negative correlation with genetic similarity. These correlations were not due to local adaptations of the colonies. Termites were found to use a mixture of compounds rather than a single substance to recognize nestmates. Dronnet and co-workers (2006) investigated the possibility that CHs similarity and high genetic relatedness could explain the lack of intraspecific aggression among and within colonies of the introduced subterranean termite *Reticulitermes santonensis*. Short- *vs* long-chains and saturated- *vs* unsaturated-hydrocarbons were found to be associated with most genetic variations. Their results suggested that the absence of intraspecific aggression might result from a loss of diversity in genetically-derived recognition cues. The existence of caste and population specificity for cuticular hydrocarbons was confirmed for *R. lucifugus* (Klochkov et al., 2005). Using termites treated with hydrocarbons from various termite populations, they demonstrated the role of CHs in olfactory recognition of termite between castes and between populations.

In contrast, no correlation was found between CH composition and colony recognition in *Coptotermes formosanus* (Su and Haverty, 1991). In the same species, differences in CH profiles (but the authors only used visual observations of the chromatograms), as well as genetic distances between colonies determined by using microsatellite DNA markers showed no correlation with aggression (Florane et al., 2004). Their results demonstrated that termite diet played a significant role in determining the level of aggression suggesting that diet-derived cues may be involved in nestmate recognition. However, feeding on different diets could not induce aggression within the same colony. Italian populations of *Reticulitermes lucifugus* presented low levels of aggression between colonies regardless of geographical distance between them. CH patterns did not appear to be correlated with agonistic response in these populations (Uva et al., 2004).

Another hypothesis was presented by Matsuura (2001) for the termite *Reticulitermes speratus*. Differential intestinal bacteria composition leads to the production of chemical cues that enable nestmate recognition. This hypothesis was supported by the fact that the composition of the intestinal bacteria was colony-specific (Matsuura, 2001; Minkley et al., 2006 in *Hodotermes mossambicus*) and by experimental manipulations of the composition of bacteria by antibiotics which affected nestmate recognition in these species (Matsuura, 2001; Kirchner and Minkley, 2003).

In conclusion, correlative evidence for some ant and wasp species suggested that branched hydrocarbons account for most of the “between-colony” variability (ants: Bonavita-Cougourdan et al., 1987; Provost et al., 1993; Dahbi et al., 1996; wasps: Bonavita-Cougourdan et al., 1991; Espelie et al., 1994; Lahav et al., 1999). In the honeybee, *n*-alkenes and fatty acids have been found to be more significant than *n*-alkanes (Breed, 1998).

All the research performed on the recognition systems of social insects highlight the complexity of the chemical communication between group members. Nestmate recognition depends primarily on the perception of CHs, low volatility compounds of very different origins both between species and even within the same species. We will see that in addition to this self/nonself discrimination, social insects are able to discriminate nestmates by their function in the colony.

TASK-RELATED HYDROCARBONS IN SOCIAL INSECTS

Eusociality is characterized by an overlap of generations, a cooperative brood care and an intra-colony division of labor (Michener and Smith, 1987). Here we will focus our attention on the intra-colony division of labor. The division of labor within colony's workers (named polyethism) is based on the notion of caste. The division of labor linked with the reproductive function has been already developed in this chapter. In the following paragraphs, we will review functional subcastes. Polyethism is based on a workers polymorphism in 15% of ant genus (Passera and Aron, 2005), but when it does not exist, it is generally admitted that polyethism is related to the individuals' age (Wilson, 1963). Some studies analyzed the chemical signatures of workers performing different tasks to better understand the regulation of task allocation within a colony.

Examples of CHs as potential caste-recognition cues in termites were highlighted by Howard et al. (1982b), Haverty et al. (1996). The former showed that all castes of *Reticulitermes virginicus* (worker, soldier, nymph, neotenic) contained the same cuticular compounds and that the proportions of branched to normal alkanes, monomethyl to dimethylalkanes, saturated to unsaturated compounds were caste-specific. They also showed that the hydrocarbon mixtures of all four castes (worker, soldier, nymph, alates) were similar but quantitative differences existed. Nineteen peaks were statistically different between soldiers and workers but not between nymphs and alates. However, although evident, no caste-specific behavioral patterns were taken into account in these studies.

In *Camponotus floridanus* ants, foragers and callows can be differentiated following their CH profile (Lavine et al., 1990). Bonavita-Cougourdan and co-workers (1993) demonstrated by a retrieving behavior test that the two subcastes, foragers and nurses, of the ant *Camponotus vagus* are able to recognize each other. During the tests, some nurses and foragers were deposited outside the nest and the number of workers of each functional subcaste carried into the nest by foragers that had stayed in the nest was recorded. The authors established a correlation between the recognition process and the proportions of various cuticular hydrocarbons which differed between the two functional subcastes. These quantitative differences involved both alkanes and mono- and dimethylalkanes. As nest maintenance workers are younger than foragers, these variations in the proportions of CHs from one subcaste to another may be age-dependent.

Task-related hydrocarbon differences may be associated not only with age but also with such abiotic characteristics of the interior and exterior environment, as temperature, relative humidity (Wagner et al., 2001) and ultraviolet light. Gibbs (2002) thinks that the primary function of alkanes is resistance to desiccation, whereas that of alkenes is chemical communication. This is consistent with the work of Wagner and collaborators (1998). They compared the cuticular hydrocarbon composition of three categories of workers of the ant *Pogonomyrmex barbatus*: the patrollers who scout the foraging area each morning to locate and inform the colony of seed sources, the foragers who collect food as soon as patrollers have returned safely into the nest and the nest maintenance workers. Foragers and patrollers did not differ in hydrocarbon composition but both categories have a higher proportion of straight-chain alkanes relative to monomethylalkanes, dimethylalkanes and alkenes than nest maintenance workers. Moreover, when workers are forced to stay outside in a drier environment, the proportion of alkanes on their cuticle increases (Wagner et al., 2001).

Further to these experiments which confirmed the correlation between the chemical signature of individuals and the functional group to which they belong, field bioassays using artificial ants have been used (Greene and Gordon, 2003). The authors inhibited foraging by removing patrollers returning to the nest. Then, they simulated the returning patrollers by dropping 3-mm- diameter glass beads into the nest opening. The glass beads were coated with extracted patroller hydrocarbons, nest maintenance worker hydrocarbons or pentane for control, in amounts equivalent to that of one insect. They showed that only beads coated with patroller hydrocarbons extract elicited a foraging response from the colony. Thus an ant can assess the task status of another nestmate from its CH profile. This discrimination ability may play an adaptive role by regulating task assignment between workers.

A study of task-related variation of postpharyngeal and cuticular hydrocarbon compositions was carried out for the ant *Myrmicaria eumenoides* (Kaib et al., 2000). It suggests that chemical variations are not caused by environmental conditions. Task-specific differences in cuticular compositions were mainly in the amount of alkenes (high in foragers) and alkadienes (high in brood-tenders). In field colonies as well as in laboratory colonies fed on different diets, the intra-colonial differences between nestmates from different task groups were greater than inter-colonial variation among ants of the same task group. This result suggests that changes in hydrocarbon composition are controlled by internal factors within the colony. They also showed that the chemical variation is only partly correlated with age because, irrespective of their age, ants staying in the nest keep their CH ratios unchanged. On the contrary the CH variations are strongly correlated with the task allocation of individual ants. The influence of juvenile hormones (JH) on the composition of CHs and the division of labor were investigated in the same species (Lengyel et al., 2007). The application of exogenous JH III and a JH analogue (methoprene) did not result in an acceleration of task change but the authors mentioned a reduction of treated individuals' life expectancy. However quantitative changes from a brood-tender-type to a forager-type CH profile were accelerated by the application of JH III and methoprene. Thus, they obtained brood-tender workers that displayed forager-type CH profile. This indicates that changes in CHs recognition cues do not trigger task allocation. These results suggest a JH III-mediated, task-based recognition cue system in this species.

Our experiments (unpublished data) for the ant *Temnothorax lichtensteini* revealed that when foragers move into a new nest, they preferentially transport nurses. Thus, foragers are able to recognize nurses. We have found evidence of a correlation between functional subcastes and their CH profiles. Multivariate analysis (Figure 1) distinguished the two groups on the first axis which represents 37% of the variation. They only differ by relative amounts of some of individual hydrocarbons. Correlation circle of variables (Figure 2) reveals that foragers are characterized by higher proportions of a series of five monomethylalkanes, whereas nurses are characterized by a higher proportion of n-triacontane, of a mixture of two dimethylalkanes and of 8-methyl octacosane.

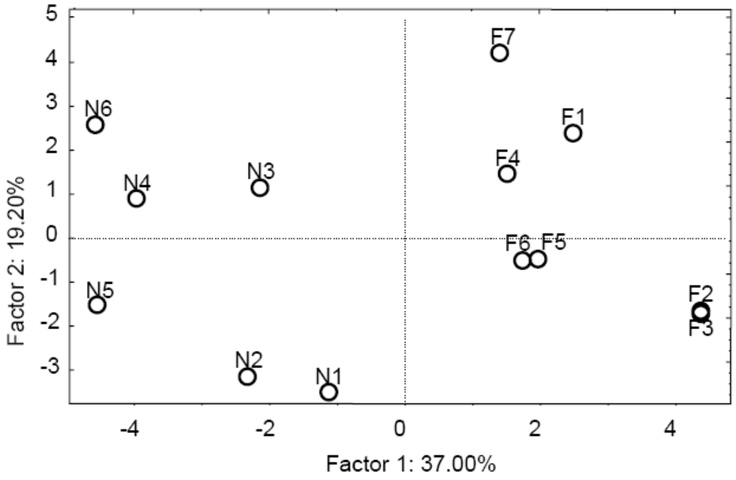

Figure 1. Principal Component Analysis of 48 variables (proportions of hydrocarbons) from six nurses (N1-N6) and seven foragers (F1-F7). The projection was performed on factorial plane 1-2. Axis 1 accounts for 37% of total variance and axis 2 for 19.2%.

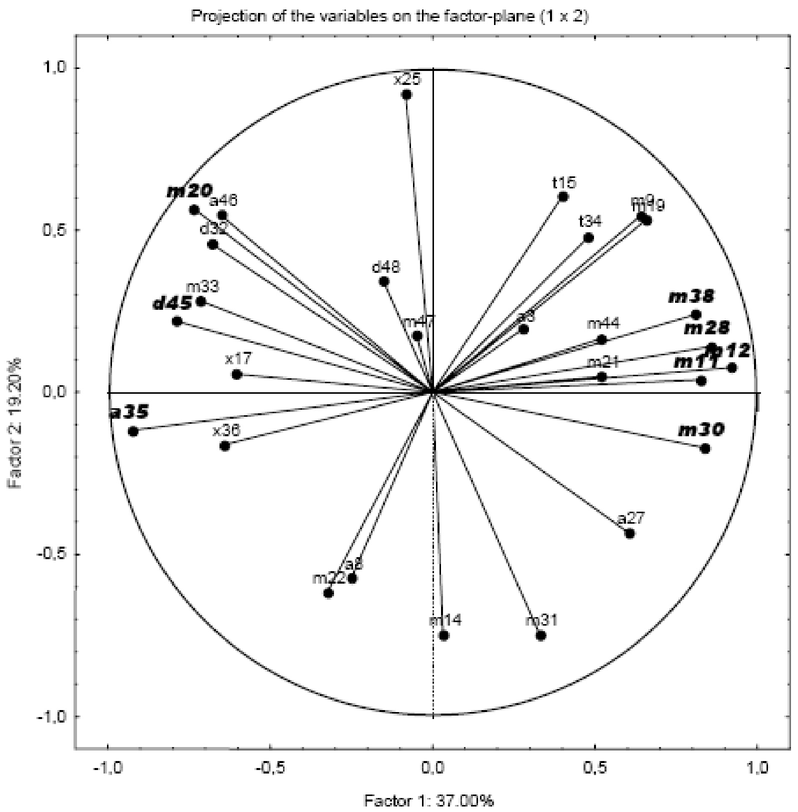

Figure 2. Correlation circle of variables. Symbols in bold character are the compounds that discriminate nurses from foragers. Abbreviations: a: *n*-alkanes; m: monomethylalkanes; d: dimethylalkanes; t: trimethylalkanes; e: alkene; x: unknown compounds.

Up until recently such chemical differentiation between nurses and foragers concerned ants living in colonies of several thousand individuals (*C. vagus, P. barbatus*, *M. eumenoides*). For these species, we could expect an uncompleted homogenisation of the colony odor according to the gestalt model (Cf nestmate recognition paragraph, this chapter). In *T. lichtensteini* for which colonies number about one hundred workers, nurses and foragers are distinguished by their CH profiles. This distinction exists despite the workers performing trophallaxis and intense allogroomings, behaviors known to be the cause of a unique colony odor (e.g. Soroker et al., 1994, 1995; Vienne et al., 1995). Our experiments are being conducted in laboratory under standard environmental conditions. Ants move on plaster of Paris, in and out of the nest, between the nest and the source of food. Ants are fed once a week, during one day. Then the food is taken away. Thus most of time, nurses and foragers are bordered inside the nest. In these conditions, it is unlikely that foragers' signatures are modified by the forage activity itself. Our study strongly suggests that the chemical differences between foragers and nurses are not environment-dependent but are correlated with the task allocation of individuals, as claimed by Kaib et al. (2000).

In this way, the possibility for a worker to recognize by touching antenna the membership of another worker, as nurse or forager category can play a fundamental role in task allocation. It could also allow social insects to have a rapid reaction to environmental changes and contribute to their ecological success.

RANK STATUS, REPRODUCTIVE STATUS AND CUTICULAR HYDROCARBONS

Rank status is often associated with the reproductive division of labor which is in turn correlated with ovarian development and variations in CH profiles.

Many studies show a correlation between reproductive activity and cuticular hydrocarbon profiles among different species of ants, wasps, bees (reviewed by Monnin, 2006).

Almost linear dominance hierarchies frequently appear in workers of queenless ant species. Only the alpha-worker mates and produces offspring, while other workers remain virgin. This is the case in the queenless ant *Dinoponera quadriceps*. In this species, the CH profile of the gamergates (mated egg-laying workers) differs from that of the other workers with a higher proportion of only two alkenes 9-C31:1 and 9-C33:1 (Monnin et al., 1998). Virgin alphas do not differ chemically from gamergates. Thus the authors assumed that CH signal is a fertility indicator rather than a mating status indicator. Peeters et al. (1999) confirmed that mated alpha workers have a higher proportion of an alkene, the 9-hentriacontene, than do virgin alphas. The proportion of 9-hentriacontene is lower in betas and even lower in low-ranking workers. They used solid-phase microextraction with gas chromatography to measure changes in the proportion of this alkene in beta workers after the removal of the alphas. They showed that the proportion of 9-C31:1 increased in beta workers at the same time as their fecundity increased. The authors concluded that this alkene provides information about egg-laying ability, enabling ants to recognize the different classes of nestmates. Application of the putative fertility signal, 9-hentriacontene, to beta females does not lead to differential treatment from subordinate or dominant individuals. The fertility signal is insufficient to denote rank (Monnin in Jackson, 2007).

Moreover, many studies in ants have shown that the surface of the eggs is covered with hydrocarbons. Selective destruction of worker-laid eggs by the gamergate takes place in this species. Gamergate-laid eggs are rich in 9-C31:1 and are not destroyed, whereas worker-laid eggs have a lower quantity of this alkene and are eaten by the gamergate (Monnin and Peeters, 1997). The control of reproduction by the gamergates does not stop there. Monnin et al. (2002) made an amazing discovery. They reported an unusual mechanism by which the dominant individual chemically marks any pretender who is then immobilized during several days by low-ranking females. The consequence is that the pretender loses its high rank. The gamergate marks the rival by rubbing its sting against him and by depositing chemicals from its Dufour's gland. These are mostly hydrocarbons (alkanes, alkenes and methyl-branched alkanes from 15 to 30 carbon atoms). The glands of gamergate have significantly more hydrocarbons than low-ranking workers (X3). By smearing beta workers with the Dufour's gland content of either a gamergate, or another beta or a low-ranking worker, they demonstrated that only Dufour's gland chemicals of gamergate are a pheromonal signal that induces immobilization, allowing gamergate to control reproduction.

In the queenless ant, *Diacamma ceylonense*, CHs ranging from C25 to C35 of nestmate workers vary in their proportions according to age and fertility. Several substances (*n*-C29 and two monomethylalkanes with 25 and 27 carbon atoms) discriminate callows egg-layers and foragers (Cuvillier-Hot et al., 2001). They found an inter-colony variation of the CHs much lower than intra-colony variation and qualitative differences between sexes (the males have a cuticular hydrocarbon profile with much more alkanes). Variations in cuticular profile reflected ovarian activity and could be used by ants as a fertility signal. The CH profile correlates with fertility in other queenless ants: *Streblognathus peetersi* (Cuvillier-Hot et al., 2004) and *Gnamptogenys striatula* (Lommelen et al., 2006).

Correlation between ovarian activity and a specific blend of CHs is also found in queenright ant colonies. Variations in cuticular hydrocarbons have been correlated with oogenesis both for queen and workers of the monogynous colony of Ponerine ant *Harpegnathos saltator* (Liebig et al., 2000). Gamergates and queen have similar CH profiles which differ from that of sterile workers by having a characteristic dimethylalkane, the 13,23-dimethylheptatriacontane and by long-chained hydrocarbons. Differences between reproductive and non-reproductive individuals' cuticular hydrocarbon profiles were independent of age or caste. The workers can accurately assess the ovarian activity of nestmates and adapt their behavior accordingly. The authors assumed that the ants use either the relative composition or the absolute amounts of cuticular hydrocarbons to be informed about each other's ovarian activity as qualitative and quantitative differences between the reproductive and non-reproductive individuals exist.

For the same species, following the tests made, scientists have shown that certain CHs can indicate dominance status whilst others are associated with ovarian activity. This is the case for the neotropical ponerine ant *Pachycondyla* cf. "*inversa*". Queens of this species may cooperate during colony founding. Division of labor is achieved by aggressive interactions between queens, which result in the formation of dominance hierarchies with the dominant queen specializing for brood guarding and the subordinate queens for foraging. Cuticular hydrocarbons analysis revealed consistent differences between queens with high versus low rank (Tentschert et al., 2001). Only high-ranking queens possess considerable amounts of two substances: pentadecane (*n*-C25) and heptadecene (*n*-C27:1). In contrast to the studies mentioned above, social status is apparently not associated with reproductive status because all foundresses lay eggs at similar rates. In this species, task and social status are tightly correlated but the authors assumed that the presence of the two substances is associated with social dominance alone. In their opinion it is unlikely that the two different tasks are likely to be the cause of the recorded differences in their cuticular profile. Heinze et al. (2002) showed in de-queened colonies of the same species that the composition of cuticular hydrocarbons of egg-laying workers is quantitatively and qualitatively different from that of non-egg-laying workers and is similar but not identical to the hydrocarbon blend of the queen. Using discriminant analyses and on the basis of their cuticular hydrocarbon profiles, the authors distinguished workers with four different classes of ovarian development (fertile queens; high-ranking egg-laying workers with fully developed ovaries; workers with slightly developed ovaries; and subordinate workers with undeveloped ovaries). 3,11-dimethylheptacosane represents 5% of the total hydrocarbons in subordinate workers, versus 35% in egg-laying orphaned workers, and 50% in the queen. The CHs profile does not simply indicate that an individual reproduces or not, it also advertises its level of reproductive activity. Social and reproductive statuses are closely correlated but the authors thought that the CH profile was more closely associated with ovarian activity than hierarchy rank. Using electroantennography and gas chromatography with electroantennographic detection, D'Ettore et al. (2004) showed that the branched hydrocarbon, 3,11 dimethylheptacosane was detected by the antennae of *P. inversa* workers. Thus, in *Pachycondyla* cf. *inversa*, 3,11 dimethylheptacosane constitutes, or at least contributes to, a signal of fertility that allows the queen to be distinguished from workers. In orphaned colonies 3,11 dimethylheptacosane allows workers with various levels of reproductive activity to be distinguished.

In the ant *Myrmecia gulosa*, workers can discriminate queens and fertile workers (after removal of the queen) from infertile individuals based on distinctive blends of long-chain hydrocarbons present both on the cuticle and in the postpharyngeal gland (Dietemann et al., 2003). Two compounds, 9-pentacosene and 3-methylpentacosane, were present in high proportions in reproductive individuals but were only present in trace quantities in non-reproductive individuals. The molecules characterizing reproductive are the same in all colonies. They suggest that these CHs function as pheromones allowing the recognition of the queen as well as egg-laying workers in orphaned colonies. The authors demonstrated that workers are capable of discriminating between queen and worker cuticular hydrocarbon profiles.

In *Camponotus vagus*, the queen and workers differ chemically during spring and summer, when the queen lays many eggs, but do not differ at the end of winter when the queen has not yet started to lay eggs (Bonavita-Cougourdan and Clément, 1994). Boulay et al. (2007b) investigated the reproductive strategy of the ant *Aphaenogaster senilis*. In this species, the inhibition of sexual production is apparently mediated by contact cues released by the queen. They have shown that the secretion of two exocrine gland, the Dufour's gland and the postpharyngeal gland possess caste-specific compositions which makes them potential candidates for the production of the queen pheromone. In the ectatommine ant *Ectatomma tuberculatum*, the visual appearance changes after mating and ovarian development (their cuticle turns from shiny to matt). This change seems to be caused by an accumulation of heptacosane and nonacosane which may give a physical protection to queens and may constitute a mating cue (Hora et al. 2008).

In the ant *Platythyrea punctata*, only one worker reproduces by thelytokous parthenogenesis. This worker differs chemically from sterile workers. After 27 days of isolation some sterile workers become egg-laying workers and after 47 days they acquire the CH profile typical of reproductive individuals (Hartmann et al., 2005).

Fertility signals have been reported in many other ant species belonging to various genus, for monogynous as well as polygynous colonies: *Temnothorax acervorum* and *T. gredleri*, (Tentschert et al., 2002); *Cataglyphis iberica*, (Dahbi and Lenoir, 1998). Surprisingly, a conflicting result was found in *C. niger* by Lahav and co-workers (2001) where the queen profile could not be discriminated from that of the workers.

In experimental digyne colonies of *Formica fusca*, queens contribute unequally to the brood because of the differences in their egg-laying capacity, but they do not form dominance hierarchies through physical aggression. This suggests that communication between queens is mediated by chemical signal (Hannonen et al., 2002). Using microsatellite markers to study reproductive partitioning in these *Formica fusca* experimental colonies, the authors found that the queens of different reproductive status differed in their CH profiles. A queen fecundity signal is encoded in her CH profile and acts as a pheromone for workers which pay more attention for queens having a higher fecundity.

Ant workers can perceive the queen fertility signal either directly by contact with the queen or indirectly by contact with queen-laid eggs whose surface is covered with the queen pheromone. Orphaned workers of the ant *Camponotus floridanus* refrain from reproducing when queen-laid eggs are added to the nest. A chemical signal located on their surface has been found (Endler et al., 2004). Queen- and worker-laid eggs differ in their surface hydrocarbons in a way similar to the way fertile queens differ from workers in the composition of their cuticular hydrocarbons (quantitative and qualitative differences). They concluded that queen-derived hydrocarbon labels inform workers about the presence of a fertile queen and thus regulate worker reproduction. Moreover orphaned workers destroy worker-laid eggs which do not have these protective CHs. Similarly, D'Ettorre et al., 2004 showed in *Pachycondyla inversa* that worker- and queen-laid eggs differ chemically by a higher quantity of 3,11-dimeC27 (the queen fertility signal, see above) in the queen-laid eggs.

Finally note the case of the highly polygynous invasive Argentine ant *Linepithema humile* where old reproductive queens, young mated queens, virgin non-laying queens and workers differ in their HC profiles. Queens are characterized by shorter chain length hydrocarbons than workers (de Biseau et al., 2004). The results of this study, in a species where workers lack ovaries, show that the variation in cuticular hydrocarbons with ovarian activity is not restricted to species with worker reproduction.

Correlation between ovarian activity and CH profile has been reported for social wasps *P. dominulus* (now *P. gallicus*) (Bonavita-Cougourdan et al., 1991). In this species whose colonies are composed of only one foundress and workers, we showed that the cuticular hydrocarbon profile of the foundress differs from that of its sterile daughters. In one orphaned colony without a foundress, we showed that one worker was reproducing and it had a foundress-like CH profile. Sledge et al. (2001) studied colonies of *P. sulcifer* with several foundresses. At the beginning of the foundation, all foundresses have the same ovarian development and have the same chemical profile. When the alpha foundress monopolizes reproduction, its CH profile differs of that of subordinate foundresses, which again differs from that of workers. They could chemically distinguish alpha females on the basis of one particular peak in their CH profiles. The removal of alpha allows beta to develop its ovaries and then present a profile typical of an alpha. These results suggest the existence of a fertility signal. However, Dapporto et al. (2007b) showed in *Polistes dominulus* that the relative positions of individuals in the dominance hierarchy were correlated with variable proportions of 17 cuticular hydrocarbons. This dominance signal might be different from the fertility signal (see Jackson, 2007). It might enable alpha individuals to control egg production, destroying eggs laid by other fertile subordinates.

Dapporto et al. (2007c) demonstrated that *Polistes gallicus* distinguish queens from workers by the hydrocarbon mixtures of the Van der Vecht organ (mainly linear and monomethyl-branched alkanes with odd-numbered carbon chains). This differentiation is based on a generalized queen signal.

CHs differences between breeders and non-breeders were also reported in *P. fuscatus* (Espelie et al., 1994), in the hornet *Vespa crabro* (Butts et al., 1995), in the bumblebees *Bombus hypnorum* (Ayasse et al., 1995) and *Bombus terrestris*. For this last species, it has been shown that workers of orphaned colonies refrain from reproducing when queen's cuticular extract is deposited onto a callow queen (Bloch and Hefetz, 1999).

Chemical profiles change in males as a result of social interactions were revealed in the cockroach *Nauphoeta cinerea*. Interactions between two males *Nauphoeta cinerea* cockroaches are characterized by an elaborate ritual that leads to a stable dominant-subordinate hierarchy between these two individuals (reviewed in Everaerts et al., 1997 and in Roux et al., 2002). Males reared in pairs for 30 days present significant differences in both CH profiles and sex pheromone of dominant and subordinate individuals (Everaerts et al., 1997). But in this study, CHs were not identified. We carried out dyadic agonistic encounters in three tests to determine the three-times dominant and three-times subordinate males (Roux et al., 2002). We showed that the dominant individuals were characterized by a higher proportion of three monomethylalkanes, whereas the subordinates were characterized by four other monomethylalkanes. Moreover, the four groups (three-times subordinate, two-times subordinate, two-times dominant and three-times dominant) lined up in their logical order on the first factorial axis in the principal component analysis taking into account the proportions of CHs. These findings suggested that cuticular hydrocarbon profiles are essential in establishing and maintaining dominance status. In this species, it is the males that attract females by means of three-components sex pheromone. The quantities of these volatile components vary with male status (Moore et al., 1995). By manipulating the quantities of these three components individually or in combinations, it has been demonstrated that the sex pheromone of males determines rather than reflects status (Moore et al., 1997). Female mate choice is based on pheromonal differences among males (Moore, 1988). However, the exact role of CHs of males in female mate choice is yet to be determined.

CHS AND SEXUAL BEHAVIOR

CHs intervene at different stages of sexual behavior and reproduction. They can allow long range sexual communication. Cuticular hydrocarbons are also involved in short-range sexual communication, enabling recognition and choice of sexual mates, causing aggregation, or acting as a courtship stimulant (aphrodisiac) or as a courtship inhibitor (antiaphrodisiac) to reduce the attractiveness of mated females (for reviews, see Howard and Blomquist, 1982; Blomquist et al., 1993; Ferveur, 2005)

CHs as Sex Pheromone

Long Range Attraction

There is extensive literature on the pheromonal role of cuticular hydrocarbons. The best known example concerns the sexual pheromone of flies. The female sex pheromone of the house fly *Musca domestica* is (Z)-9-tricosene (Carlson et al., 1971). In maturing female houseflies *M. domestica*, ovarian-produced ecdysteroids cause a modification in hydrocarbon production such that (Z)-9-tricosene becomes a major component, from day-2 until day-6 (Dillwith et al., 1983; Adams et al., 1984). The divergence in male and female wax production occurs at an early stage, less than one day (Mpuru et al., 2001). (Z)-9-tricosene first accumulates in the hemolymph, and then after more than 24 hours, is observed on the surface of the cuticle.

Similarly, in geometrid moths *Operophtera fagata*, unsaturated hydrocarbons secreted by apterous females strongly attract conspecific flying males (Szocs et al., 2004). The male mate-seeking and copulatory activity is stimulated by young female monoenes in the leaf-cutter bee *Megachile rotundata* (Paulmier et al., 1999).

In the ant *Formica lugubris*, the source of the sex pheromone is the Dufour's gland of the queen. It contains three hydrocarbons whose undecane represents 90% of the total of the Dufour's gland content. This product triggers the response of the male in inciting it to throw itself onto its partner and attempt to start copulating (Walter et al., 1993).

Short-Range Sexual Communication

The role of CHs in sexual communication was examined in a solitary burrowing bee, *Amegilla dawsoni* (Simmons et al., 2003). Washing CHs from the cuticle of emerging virgin females made them unattractive (as are nesting females) to mate-searching males. Chemical analyses revealed significant differences between male and female CHs and between virgin female and nesting female types. Higher concentrations of *n*-alkanes such as tricosane, pentacosane, and heptacosane indicate virgin females sexual receptivity.

The female of the rove beetle, *Aleochara curtula* (Staphylinidae) produces C21 and C23 monoenes which serve as a close-range sex pheromone (Peschke and Metzler, 1987).

Studies of two species of bee, *Osmia rufa* and *Andrena nigroaenea* suggest that CHs may also function as short-range sex attractants and repellents (Schiestl and Ayasse, 2000; Ayasse et al., 2001).

In the solitary bee *Colletes cunicularius*, the volatile linalool functions as a long range attractant for males but some less volatile CHs are necessary to induce complementary behavior when males approach the females (Mant et al., 2005).

Mate Choice

CHs can serve for choosing a mate within a species and play an important role in sexual isolation between related species (Coyne et al., 1994; Coyne and Oyama, 1995; Howard et al., 2003). Sexual isolation between two species of the genus *Chrysochus* (Coleoptera: Chrysomelidae) was due, at least in part, to males' preferences for conspecific females. This male choice is influenced by CH profiles. These profiles are both sex- and species-specific (Peterson et al., 2007).

In field crickets, there are differences in the CHs blends of males and females that facilitate sex recognition (Tregenza and Wedell, 1997). Female crickets *Gryllodes sigillatus* mark males with their chemical signature during mating, enabling females to recognize prior mates in subsequent encounters and to avoid re-mating with them (Ivy et al., 2005). Works on acridid grasshoppers and *Drosophila* have revealed sexual selection via female mating preferences based on the CHs of males (Blows and Allan, 1998; Blows, 1999; Higgie et al., 2000; Hine et al., 2002). CHs seem to play an important role in sexual isolation in *Drosophila elegans* (Ishii et al., 2001).

Contact pheromones are critical in mate recognition in longhorned beetles (Cerambycidae) (Ginzel and Hanks, 2003). All males attempted to mate with freeze-killed females,-mate recognition not depending on behavior of the female. None of the males responded to non-polar solvent-washed female, the recognition cues, mainly hydrocarbons having been removed by the solvent. The ball-roller scarab *Canthon cyanellus cyanellus* males recognize females by their cuticular compounds (Ortiz-Dominguez et al., 2006). Other studies showed that (Z)-9-pentacosene was a contact sex pheromone for the Cerambycid *Megacyllene robiniae* (Ginzel et al., 2003), and that (Z)-9-nonacosene is the major component of the contact sex pheromone of *M. caryae* (Ginzel et al., 2006). In longhorned beetle *Anoplophora malasiaca*, males attempted to mate with a glass dummy treated with the solvent extract of female elytra (Fukaya, 2003). The female sex pheromone perceived by direct contact is composed of saturated hydrocarbons and polar compounds that operated synergistically.

The changes in the hydrocarbon profile of the slave-making ant *Chalepoxenus muellerianus* induced by the host species *Temnothorax unifasciatus* influenced their mating preference (Beibl et al., 2007).

CHs as a Courtship Stimulant or as an Antiaphrodisiac

In *Cardiochiles nigriceps* (Braconidae), elements of male courtship behavior are provoked by a series of female-specific alkadienes (Syvertsen et al., 1995). Nonpolar hydrocarbon fractions from females arrest males and elicit courtship behavior in many Pteromalids (Sullivan, 2002; Steiner et al., 2005, 2006). In the parasitic wasp *Lariophagus distinguendus* (Hymenoptera: Pteromalidae), male courtship behavior is mediated by a female-produced sex pheromone (Steiner et al., 2007). They presented evidence that the sex pheromone is composed of a series of CHs but no bioassays were performed. Many monomethylalkanes and some alkenes were good candidates for mediating activity in this species.

Several species of fruit flies of the genus *Drosophilia* have sexually dimorphic hydrocarbon profiles. Certain hydrocarbons serve as contact sex pheromones which stimulate species-specific courtship behavior in males (reviewed by Singer et al., 1998). The attractiveness of *Drosophilia* females to the males changes according to the reproductive state of the female. 7-tricosene found in mated females of *D. melanogaster* acts as a courtship inhibitor which reduce the number of mating attempts by males upon females. This compound is the major hydrocarbon produced by mature male flies. In *D. virilis*, the application of both synthetic and natural (Z)-11-pentacosene on a dummy increased male courtship response (Oguma et al., 1992).

Similarly a polymethylalkene acts as antiaphrodisiac in tsetse flies *Glossina morsitans* (Carlson et al., 1991) and good evidence exists for the presence in females of a contact sex pheromone that provokes copulatory behavior by the males (Langley et al., 1975). This sex pheromone was identified and comprises of three high molecular weight hydrocarbons. The most active was 15,19,23-trimethylheptatriacontane, with 15,19-dimethylheptatriacontane and 17,21-dimethylheptatriacontane being less active (Carlson et al., 1978). Similarly, the CHs of the female tsetse fly *Glossina tachinoides* were found to be a contact sex stimulant for the sexual behavior of the males (Carlson et al., 1998). The greatest activity was provoked by a dimethylalkane, the 11,23-dimethylheptatriacontane. Chemoreceptors responsive to female sex pheromone are situated on the tarsi of sexually responding males and are the first structure to touch a female fly (Langley et al., 1987).

CHs as Trail Pheromone

Trail pheromones play an important part in the communication of social insects, allowing the optimal exploitation of food sources or the occupation of new nest sites (Wilson, 1971). The foragers of the yellow jacket *Vespula vulgaris* (Vespidae) usually walk through dark tunnels between the nest and cavity entrance, using the chemical trail for home orientation. An artificial trail made from an extract of cuticular lipids from the foragers was biologically as active as the trail laid by the foragers. Extracts of the naturally laid trail and cuticular extracts possess the same hydrocarbons in similar ratios (Steinmetz et al., 2003).

Three aphids parasitoids have been shown as presenting avoidance responses on leaves previously visited by two ladybird predators, *Coccinella septempunctata* and *Adalia bipunctata*. These responses were elicited by at least three n-alkanes present in the ladybirds' trails: *n*-tricosane, *n*-pentacosane, and *n*-heptacosane (Nakashima et al., 2006). The role of these compounds for the ladybirds must be investigated as they might play a role in oviposition deterrent behavior.

Lasius japonicus nestmate workers share footprint hydrocarbons that serve as the trail discrimination pheromone. As they are colony specific, they have the potential to serve as the territorial pheromone (Akino and Yamaoka, 2005). For this species, as for *L. nipponensis*, the footprint compounds consist mainly of hydrocarbons with a composition almost identical to that of CHs except for the absence of *n*-alkanes (Akino et al., 2005).

And finally note that CHs sometimes associated with more volatile compounds function as a pheromone in many other aspects of social life as an alarm pheromone (e.g. Walter et al., 1993), as a spacing pheromone (cf Howard and Blomquist, 1982; Kaib et al., 2002), and as an aggregation pheromone (Heifetz et al., 1997; Rivault et al., 1998; Saïd et al., 2005).

Host-Parasite Chemical Relationships

Many insect species are capable of exploiting the recognition system of eusocial insects to live as parasites or guests by mimicking the host colony's chemical signature (for a review see Dettner and Liepert, 1994). Indeed many studies showed that to usurp a host colony, social parasites use three different strategies. Some use force but most use chemical confusion by expressing a "blank slate", as newly emerged adult (Breed et al., 2004b), that is a substantially reduction of recognition cues to avoid being recognized and attacked. Others modify their own CH profile to match that of their host, either synthesizing them *de novo* or acquiring them from the host. Howard and co-workers (1990a), Sledge et al. (2001) distinguished true chemical mimicry from chemical camouflage according to the origin of the chemical signal. An individual uses chemical mimicry when it biosynthesizes *de novo* the host compounds whereas the term chemical camouflage is employed when the intruder acquires passively or actively the substances from the host. In this chapter we will comply with the opinion of Dettner and Liepert (1994) and we shall use the term chemical mimicry whatever the modality of the signal.

Colonies of social insects provide numerous forms of parasitic modes of life: dulotic ants which practice slave-making, inquiline species, ectoparasite, myrmecophily and termitophily (for a detailed classification of various forms of parasitism in ants, see Passera and Aron, 2005).

Slave-Making Ants

Slavery with ants is a form of social parasitism which can be either optional or obligatory. These species may have lost the ability not only to establish nests but also to raise their offspring. Such species are completely dependent on their hosts. The slave-making ants make raids on the nests of ants of different species with the objective to steal brood. Pupae are carried into the nest of the slave making ants. The adults descended from the stolen brood and born in the slave making ants nests ensure the correct functioning of the nest in looking after the brood of both types of ant and in collecting food. But at the time of the foundation, everything begins by the penetration of the newly mated queen of the slave-making ant (e.g. *Polyergus rufescens*) into the host nest. This queen presents no cuticular hydrocarbons (« blank slate »: Breed et al., 2004b; « chemically insignificant hypothesis »: Lenoir et al., 2001; Lambardi et al., 2007) which allows her to avoid being attacked by the host workers and to reach the resident queen to eliminate her (D'Ettore and Errard, 1998; Lenoir et al., 2001). This intrusion is also facilitated by physical adaptations and the emission of appeasement chemical compounds or propaganda substances. For example, n-heptadecene and n-heptadecadiene of the Dufour's gland are used by the slave-maker *Harpagoxenus sublaevis* as propaganda substances during nest usurpation of the host species *Leptothorax acervorum* (Ollet et al., 1987). In order to be well integrated, the parasite queen must acquire the host colony odor. This acquisition occurs by contact when the two queens are fighting (e.g. Mori et al., 1995). Similarly, just after the attack on the host *Formica* queen, the chemical profile of newly mated *Polyergus breviceps* queen was dramatically transformed. Before the attack it contained only simple normal alkanes. After the attack it contained complex mono- and dimethylalkanes, identical to those of the host queen (Johnson al., 2001). However it is not clear what happened to the n-alkanes initially present in the chemical profile of the new mated parasite queens but which are not found after the death of the host *Formica* queen.

Artificial mixed (heterospecific) colonies constitute a good model for the investigation of colony odor in eusocial insects (Errard, 1986) and permit a better understanding of the chemical signatures regulation of species living together. Using artificially mixed colonies of ants e.g. *Manica rubida*/*Formica selysi* (Bagnères et al., 1991b; Vienne et al., 1995), in termites *Reticulitermes santonensis*/*R. lucifugus grassei* (Vauchot et al., 1996, 1997, 1998) or in cockroaches *Nauphoeta cinerea/Leucophaea maderae* (Everearts et al., 1997), it has been shown that a homogenisation of CH profiles occurs between the two species' chemical signature. Workers from one species adsorb on their cuticle allospecific compounds as a result of transfer between individuals. A similar chemical mimicry by transfers of chemical compounds between individuals has been reported for a natural mixed colony made up by the slave-making ant *Harpagoxenus sublaevis* and either of its two host species: *Leptothorax acervorum* and *L. muscorum* (Kaib et al., 1993). When the three species live in a same colony, *H. sublaevis* chemical signature is a mix of the two slave species' cuticular hydrocarbons (Heinze et al., 1994). Identical data was provided by Beibl et al (2007) for the natural mixed colony *Chalepoxenus muelleniarus* and its two potential slaves, *Temnothorax unifasciatus* and *T. recedens* and by Yamaoka (1990) for the natural mixed colony *Polyergus samourai*/*Formica sp*. We reported a more complex pattern in the slave-making *Polyergus rufescens* and its two potential slaves, *Formica rufibarbis* and *F. cunicularia*. The three species have common hydrocarbons. Each of the two *Formica* species had its own specific compounds. The cohabitation with one or the other of slave species does not modified the qualitative profile of the slave-maker, (the slave-maker continues to produce alkenes, absent from *F. rufibarbis*). The *Polyergus* chemically resembled their *Formica* slaves, due to a tendency to adjust the proportions of some of the common hydrocarbons. There is no qualitative homogenisation of species profiles living in cohabitation (Bonavita-Cougourdan et al., 1996, 1997, 2004). In contrast, the slave-making ant *Rossomyrmex minuchae* and its host *Proformica longiseta* possess the same hydrocarbons but, despite their cohabitation, quantitative differences maintain their own chemical identity (Errard et al., 2006b).

Inquiline Species

These species have a worker caste highly reduced or even absent. After penetrated into a host colony, sexual individuals make raised their brood by host workers. They can eliminate the host queen but generally they conserve her. The cuckoo ant, *Doronomyrmex kutteri* (formely *Leptothorax kutteri*) is an inquiline workerless species closely related to the species *Leptothorax acervorum*. When initially entering the nest, the parasitic queen is violently attacked by host workers but once inside she is no longer attacked. She licks intensively the host queen and the resident workers. Chemical analyses (Franks et al., 1990) showed that the CH profiles including n-alkanes, monoenes, dienes and monomethylalkanes of *D. kutteri* queens and *L. acervorum* workers were similar as the result of their intensive grooming. Lambardi et al. (2007) studied the efficiency by which *Acromyrmex echinatior* leaf-cutting ants recognize intruding workers of the inquiline social parasite *A. insinuator*. The results were consistent with the "chemically insignificant" and not with the "chemical mimicry" hypothesis. In general social parasite workers produce fewer hydrocarbons. Moreover, their profiles have very low amounts of hydrocarbons in the C29-C35 range and large quantities of unusually heavy C43-C45 dienes which may blur the non-nestmate recognition cues. Low overall quantities of CH have also been reported in other ant inquilines (Lenoir et al., 2001) and in social parasites of *Polistes* wasps (Lorenzi and Bagnères, 2002).

Another process was reported for the ant *Formicoxenus nitidulus*. This social parasite is able to survive in at least 11 different ant host species. It was observed that when live or dead *F. nitidulus* are seized by their *Formica* host they are immediately dropped undamaged, indicating a chemical deterrent effect. Alkadienes were supposed to be the source (Martin et al., 2007).

In wasps, the obligatory workerless social parasite, *Polistes atrimandibularis*, can sequentially change the composition of its chemical signature to control the host nest of *P. biglumis bimaculatus* during the host's colonial cycle (Bagnères et al., 1996). Just before invasion of the host nest by the parasite queens, the cuticular signatures of the two species are distinct, *P. atrimandibularis* queens having many alkenes which were absent on the host queens' cuticle. After the invasion, the production of alkenes is disrupted but the CHs profiles of the two queens do not match. They become qualitatively and quantitatively similar at the time of emergence of *P. biglumis bimaculatus* workers. At the end of the colonial cycle, after the host queen left its nest, the parasite queen presents the pre-invasion signature whereas her female offspring presents an intermediate alkene-rich signature.

Polistes dominulus wasps are also parasitized by the permanent workerless social parasite *Polistes sulcifer*. Females of *P. sulcifer* usurp the host colony. After aggressively eliminating the dominant host foundress, the cuticular signatures of the *P. sulcifer* females change to match the host cuticular signature within 3 days of usurpation (Turillazzi et al., 2000). Sledge et al. (2001) showed that the parasite females are recognized as foreign individuals when they are introduced into other parasitized nests. Thus, they provide the first evidence that social parasites adopt not only species-specific but also colony-specific host odors by changing the proportions of their CHs, within 3 days of usurpation. This chemical mimicry, which facilitates their acceptance by host females, may result from intensive grooming and licking of host foundresses and workers by the parasites or may be acquired from the nest material (it is known that the surface of the nest is covered by hydrocarbons that are important for nestmate recognition).

The bumblebee *Bombus sylvestris* is an obligatory inquiline of *B. pratorum*. Females integrate themselves into host colonies, usually without aggressions. How *B. sylvestris* females integrated into colonies of natural versus non-natural hosts, *B. pratorum* and *B. terrestris* respectively was investigated. The *B. terrestris* and *B. sylvestris* species possess a species- and colony-specific chemical profile. The total quantity of cuticular chemicals in *B. sylvestris* females increases (x2.2) 24 hours after their introduction into the *B. terrestris* host colony to reach the same level of cuticular chemicals as their hosts. In order to facilitate their integration, these inquilines are initially chemically "invisible" (Dronnet et al., 2005).

In Melipone bees, Pianaro et al. (2007) show that abdominal waxes of *Melipona* bees, *M. scutellaris* and *M. rufiventris* are chemically similar, especially regarding *n*-alkanes, and *n*-alkenes. This is possibly how *M. rufiventris* workers invade *M. scutellaris* nests.

Ectoparasite

The ectoparasite is attached to the host's surface and there draw his resources. We evaluated the degree of chemical mimicry between the ectoparasite mite *Varroa jacobsoni* (now *Varroa destructor*) according to the developmental stage of its host honeybee *Apis mellifera* (Martin et al., 2001). We showed that *Varroa* profiles vary depending on the developmental stage of the host bee. The cuticular profile of adult mites follows their host cuticular profile at each of the host development stage. However, the degree of mimicry by *Varroa* is greater during larvae and pupal stages than the emerging adult bee stages. Chemical mimicry enables parasites to infest host colonies. Similar changes in chemical signature have been observed in the parasite *Polistes atrimandibularis* during development of its host *P. biglumis bimaculatus* (see above, Bagnères et al., 1996). Moreover, we showed that the CHs of larvae, pupae and emergent adults of parasitized bees were quantitatively different from the corresponding unparasitized individuals. Such a chemical modification could act as a signal for further invasion or could serve as parasite detection by bees (Salvy et al., 2001).

Myrmecophily, Termitophily

A large variety of insects live together with ants or termites, either at larval stage or as adults. Relationships between these myrmecophilous or termitophilous insects and the eusocial insects range from mutualism to obligatory parasitism, at least during a particular life-stage.

There is abundant literature on myrmecophily and termitophily (for reviews, see Hölldobler and Wilson, 1990; Dettner and Liepert, 1994; Howard and Blomquist, 2005; Passera and Aron, 2005). Myrmecophily was first described by Wasmann (1886). Myrmecophilous insects obtain many advantages such as access to food, access to ants as prey, protection from enemies and favorable climatic conditions (Hölldobler and Wilson, 1990). There again, myrmecophilous and termitophilous insects have to manipulate the nestmate recognition process of their hosts to cross the social boundaries, penetrate and live in the host colony without aggression. Diverse integration processes exist such as morphological mimic, behavioral mimic and appeasement secretion. In the following paragraphs we limit ourselves to chemical mimicry strategies.

One way for the integration into a social insect colony is to mimic the cuticular recognition cues of the host larvae. This strategy is used by some lycaenid butterfly larvae which live among ant brood. Akino and co-workers (1999) have studied the relationships between the social parasite butterfly *Maculinea rebeli* and its host, the ant *Myrmica schencki*. They showed that fourth-instar *Maculinea rebeli* caterpillars which have no previous contact with ants possess surface hydrocarbons (*n*-alkanes, mono- and dimethylalkanes) resembling the recognition chemicals of *Myrmica* larvae. Although not completely perfect, this chemical mimicry allows them to be recognized as ant larvae and carried by foraging *Myrmica schencki* ants into the nest brood chambers. They later acquired additional hydrocarbons within the ant nest to mimic their own host colony's odor. The deceived nurses feed the caterpillar as their own larvae. After finishing its nymphose with the ants, the adult butterfly leaves the ants nest.

The simulation of specific brood substances is also used by syrphid fly larvae of the genus *Microdon*. *M. albicomatus* and *M. piperi* are obligatory predators on the brood of their host ants, respectively *Myrmica incompleta* and *Camponotus modoc*. Chemical analyses of cuticular hydrocarbon profiles reveal that the CH profile of *M. albicomatus* larva contains n-alkanes, mono- and dimethylalkanes, and monoenes matching that of the pupae of its host-ant (Howard et al., 1990b). Comparable results were obtained for *M. piperi* larvae and *Camponotus modoc* larvae (Howard et al., 1990a). The authors suggest that the syrphid flies biosynthesize their CHs rather than acquire them from the host.

Eucharitid wasps of the genus *Orasema* use the same strategy to successfully prey on the brood of *Solenopsis invicta* (Vander Meer et al., 1989b). Five hydrocarbons (n-heptacosane, mono- and dimethylheptacosanes) were detected in the same proportions in ant and wasp pupae. Here the wasp larvae obtain its hydrocarbons by passive contact with its host. The authors reported that recently eclosed *Orasema* adults possess CH profiles that are 75% identical to those of the ants. Once these wasps leave the ant nest, the proportion of ant-like hydrocarbons rapidly diminishes to only 14%. This is consistent with Vauchot et al. (1997)

results that revealed the quick disappearance of allospecific compounds after the separation of two termites' species living in artificial mixed colonies.

Many species of Coleoptera are either myrmecophile or termitophile. Howard and co-workers (1980) provided evidence that the staphylinid beetle *Trichopsenius frosti* achieves its complete integration in a *Reticulitermes flavipes* termite colony by mimicking the cuticular hydrocarbons of its host. It is the first report of the role of these compounds in these host-parasites associations. By using radioactive markers, they showed that several species of termitophile staphylinid beetles synthesize the hydrocarbons of their host (Howard et al., 1980, 1982a). The termitophile may also acquire the termite's cuticular hydrocarbons by transfer as a result of frequent groomings and contacts with the host.

The scarabaeid beetle *Myrmecaphodius excavaticollis* (now *Martinezia duterteri*) also uses chemical mimicry to penetrate ant nest of the genus *Solenopsis* or *Iridomyrmex*. Within the nest, the beetle moves freely without being attacked by resident ants and feeds on ant larvae and on regurgitations obtained from ant workers. When he is experimentally transferred into another hosts' nest, *M. excavaticollis* mimics the CH profile of this new host. The beetle acquires the host odor by passive mechanisms as lickings or regurgitations (Vander Meer and Wojcik, 1982).

Two myrmecophilous beetles *Zyras comes* (Staphylinidae) and *Diaritiger fossulatus* (Pselaphidae) use chemical mimicry to enter the nest of their host ant *Lasius fuliginosus*. GC-MS analyses revealed that the two beetle species have identical hydrocarbon cocktails with the ant. The Nei's distance (which measures the degree of similarity between two profiles) between each beetle and its host workers is smaller than the distance between nestmates workers of the host colony but larger than between non-nestmates workers of the same ant species (Akino, 2002).

Myrmecophily in ant nest beetles Coleoptera Carabidae Paussinae was recently reviewed (Geiselhardt et al., 2007). Adult Paussini are accepted in Myrmicinae and Formicinae colonies although they are preying on the ant brood. However, a possible congruency between ants and Paussus species CH profiles, as well as the origin of the chemicals, remains to be investigated (Geiselhardt et al., loc. cit.).

Ant species that exploit several other species of ant even have the flexibility to match a variety of host species' chemical profiles (D'Etorre et al., 2002). In the same way a myrmecophile cricket often changes host ant species. When this happens, its cuticular hydrocarbon compounds change within several days to match those of the new host. The new host workers accept the cricket after several days when the two profiles match (Akino, 1996).

Stoeffler et al. (2007) reported another kind of chemical mimicry. Their results support the hypothesis that *Pella* beetles (Coleoptera: Staphylinidae) mimic alarm pheromones of their host, the ant *Lasius fuliginosus*. Undecane is secreted by the beetle and also serves as an aggressive-alarm- inducing pheromone for the ant.

A chemical mimicry mechanism in another social context, the competition for reproduction, was nicely reported by Cremer et al. (2002). In the ant *Cardicondyla obscurior*, there exist two kinds of males, winged males which participate in the nuptial flight and aggressive wingless males (ergatoids) that resemble workers. Wingless males attack each other competing for virgin queens but do not attack the winged males because the latter mimic the CHs profile of virgin queens. The disguise continues several days until the nuptial flight when they lose their odor's resemblance with queens.

As it can be seen, numerous solitary or social insects belonging to different taxa are capable of neutralizing the recognition systems between individuals. Although chemical mimicry is also reported for intruders that penetrate into nests of solitary insects, the majority of the works concern the exploitation of species living in societies which provide protection, food and an environment with stable physical characteristics.

CHs as Taxonomic Tools

The firsts studies were based on the comparison of CHs of two or more species and sometimes their geographical distribution in ants (e.g. Nelson et al., 1980 for *Solenopsis invicta*/ *S. richteri* and Vander Meer, 1986; Vander Meer and Lofgren, 1988, 1990 for the same species and their hybrids; Nowbahari et al., 1990 for 2 subspecies of *Cataglyphis cursor*), or in termites (Haverty et al., 1988; Bagnères et al., 1990; Kaib et al., 1991; for reviews see Lockey, 1991; Howard, 1993). Howard et al. (1988) used CHs as chemotaxonomic characters for two termite species, *Nasutitermes corniger* and *N. ephratae*. These two species were distinguished by 11 of their major hydrocarbon components. In 1988 they noted that 10 species of the genus *Reticulitermes* could be distinguished using hydrocarbon characters from the worker caste. More recently, Page et al. (2002) reviewed the use of CHs in termites' taxonomy. They used CH mixtures in a phylogenetic analysis. They discriminated three lineages in *Reticulitermes*, each characterized by a different set of dominant methyl-branched or unsaturated hydrocarbon components. By using CHs, Haverty and Nelson (1997) examined the taxonomy of *Reticulitermes* in northern California where two species had been described morphologically up to that time. They found five distinct hydrocarbon phenotypes which could correspond to unknown species. Takematsu and Yamaoka (1999) redefined the phylogeny of the different species of *Reticulitermes* from Japan and neighboring countries, giving greater importance to the chemical characteristics than to the morphological characteristics. Nine species belonging to two families (Kalotermitidae and Termopsidae) were examined in order to compare the hydrocarbon composition of termites' cuticle and those of their fecal pellets. They showed that hydrocarbons extracted from fecal pellets were qualitatively and quantitatively similar to cuticular extracts. Thus hydrocarbons from feces can be used to identify termites even though they are no longer present (Haverty et al., 2005).

In wasps *Polistes dominulus*, CH composition was used as a biogeographic tool for different populations of the Tuscan Archipelago (Dapporto et al., 2004).

In ants, we have investigated the CHs of six species belonging to the genus *Temnothorax* (*T. racovitzai*, *T. unifasciatus*, *T. lichtensteini*, *T. nylanderi*, *T. parvulus* and *T. recedens*) (unpublished data). Both qualitative and quantitative differences in their CHs were recorded (Figure 3 and Table 1) allowing these species to be differentiated. Chemotaxonomy is useful in this genus whose species are often difficult to distinguish by morphological characteristics, except for a few specialists.

Akino and co-workers (2002) analyzed CHs and morphological traits from 80 *Formica japonica* colonies from Japan. They found few morphological differences in workers but four different types of CH composition. They suggested that the colonies from these four chemical classes belong to separate species.

Table 1. Chemical identification of the cuticular hydrocarbons of six species of the *Temnothorax* genus

Hydrocarbons	Diagnostic ions EI ECL		T.rac	T.unif	T.lich	T.nyl	T.par	T.rec
n-C19	268	19.00	1					1
n-C21	296	21.00	2					2
C23:2	320	22.43	3					3
C23:1	322	22.79	4					
n-C23	324	23.00	5					5
12Me-C24	182/3,196/7,337 (M-l5)$^{+}$	24.37	6			6		6
n-C25	352	25.00	7	7		7		7
9+7-MeC25	112/3,140/1,252/3,280/1,351 (M-l5)$^{+}$	25.37	8		8	8		
5-MeC25	84/5,308/9,351 (M-l5)$^{+}$	25.52	9					
3-MeC25	56/7,336/7,351(M-l5)$^{+}$	25.74	10	10		10		
5,9-+5,11-+5,l3-DimeC25	84/5,154/5,182/3,196/7,210/1,224/5,252/3,365(M-l5)$^{+}$	25.91	11	11				
n-C26	366	26.00	12	12	12	12		12
8-MeC26	126/7,280/1,365(M-15)$^{+}$	26.27	13		13	13		
6-MeC26	98/9,308/9,365(M-l5)$^{+}$	26.44			14			
5-MeC26	84/5,322/3,365(M-l5)$^{+}$	26.50	15		15			
4-MeC26	70/1,336/7,365(M-l5)$^{+}$	26.56		16	16	16		
C27:1	378	26.80			17	17		17
n-C27	380	27.00	18	18	18	18	18	18
13-+11-+9-MeC27	140/1,168/9,196/7,210/1,224/5,252/3,280/1,379(M-l5)$^{+}$	27.34	19	19	19	19	19	19
7-MeC27	112/3,308/9,379(M-l5)$^{+}$	27.43	20	20	20	20	20	20
5-MeC27	84/5,336/7,379(M-l5)$^{+}$	27.50	21	21	21	21	21	21
11,15-+9,13-DimeC27	140/1,168/9,196/7,224/5,238/9,266/7,294/5,393(M-l5)$^{+}$	27.65		22	22	22		
3-MeC27	56/7,364/5,379(M-l5)$^{+}$	27.71	23	23	23	23	23	23
5,9-+5,l3-+5,15-+5,17-DimeC27	84/5,154/5,168/9,196/7,210/1,224/5,238/9,266/7,280/1,350/1,393(M-l5)$^{+}$	27.81	24	24		24	24	
5,9,15-TrimeC27	84/5,154/5,196/7,252/3,294/5,364/5,407 (M-l5)$^{+}$	27.82			25			
n-C28	394	28.00	26	26	26	26	26	26
3,7-+3,11-+3,15-+3,15-DimeC27	56/7,126/7,168/9,182/3,196/7,238/9,252/3,266/7,308/9,378/9,393(M-l5)$^{+}$	28.06	27	27	27	27	27	27
14-+12-MeC28	182/3,210/1,224/5,252/3,393(M-l5)$^{+}$	28.32	28	28	28	28	28	28
8-MeC28	126/7,322/3,393(M-l5)$^{+}$	28.37		29	29	29		
6-MeC28	98/9,336/7,393(M-l5)$^{+}$	28.45	30	30	30	30	30	
4-MeC28	70/1,364/5,393(M-l5)$^{+}$	28.60		31	31	31	31	31
8,12-+8,14-DimeC28	126/7,196/7,224/5,252/3,322/3,407 (M-l5)$^{+}$	28.72		32	32	32	32	32
4,8-DimeC28	70/1,140/1,308/9,378/9,407 (M-l5)$^{+}$	28.85		33	33	33		33
n-C29	408	29.00	34	34	34	34	34	34
15-+13-+11-+9-MeC29	140/1,168/9,196/7,224/5,252/3,280/1,308/9,407 (M-l5)$^{+}$	29.34	35	35	35	35	35	35
7-MeC29	112/3,336/7,407 (M-l5)$^{+}$	29.43		36	36	36	36	36
5-MeC29	84/5,364/5,407 (M-l5)$^{+}$	29.51	37	37	37	37	37	37
11,15-+11,17-+11,19-+9,13-DimeC29	140/1,168/9,196/7,210/1,224/5,238/9,252/3,266/7,296/7,322/3,421(M-l5)$^{+}$	29.63	38	38	38	38	38	38
7,17-DimeC29+3-MeC29	56/7,112/3,196/7,266/7,350/1,392/3,407+421(M-l5)$^{+}$	29.72	39	39	39	39	39	39

5,9-+5,17-DimeC29 84	/5,154/5,196/7,266/7,308/9,378/9,421 (M-15) +	29.83	40	40		40		40
5,9,15-TrimeC29	84/5,154/5,224/5,252/3,322/3,392/3, 421 (M-15) +	29.90			41		41	
N-C30+Chol+3,7-DimeC29	56/7,126/7,336/7,406/7,386(Chol),421 (M-15) +,422	30.00	42	42	42	42	42	42
14-+12-MeC30	182/3,210/1,238/9,280/1,421 (M-15)+	30.32	43	43	43	43	43	43
8-MeC30	126/7,350/1,421 (M-15)+	30.38	44	44	44	44	44	
6-MeC30	98/9,364/5,421 (M-15) +	30.42					45	45
5-MeC30	84/5,378/9,421 (M-15) +	30.50						46
4-MeC30	70/1,392/3,421 (M-15) +	30.59		47	47	47		
12,16-+12,2O-DimeC30	168/9,182/3,224/5,252/3,294/5,308/9,435(M-15) +	30.65	48	48	48	48	48	48
3-MeC30(+dimeC30)	56/7,406/7,421 (M-15) +	30.78	49					49
4,8-DimeC30	70/1,140/1,336/7,406/7,435(M-15) +	30.91		50	50			
n-C31	436	31.00	51	51	51	51	51	51
15-+13-+ 1l-+9-MeC31	140/1,168/9,196/7,224/5,252/3,280/1,308/9,336/7,435(M-15) +	31.32	52	52	52	52	52	52
7-MeC31	112/3,364/5,435(M-15) +	31.40				53	53	
5-MeC31	84/5,392/3,435(M-15) +	31.50	54					54
11,15-+ 11,17-+9,13-DimeC31	140/1,168/9,210/1,224/5,238/9,252/3,266/7,280/1,322/3,350/1,449(M-15) +	31.63	55	55	55	55	55	55
7,17-DimeC31+3-MeC31	56/7,112/3,380/1,420/1,435+449(M-15) +	31.76		56		56	56	56
5,9-+5,17-DimeC31	84/5,154/5,224/5,266/7,336/7,406/7 ,449(M-15) +	31.82	57			57	57	
n-C32+5,9,13- TrimeC31+5,9,15- TrimeC31	84/5,154/5,224/5,252/3,280/1,350/1,420/1,463(M-15) +,450	32.00	58	58	58	58	58	58
14-+12-+10-MeC32	140/1,182/3,210/1,266/7,308/9,336/7,449(M-15) +	32.32	59	59		59	59	59
12,18-+ 12,20-DimeC32+4-MeC32	70/1,182/3,196/7,224/5,280/1,308/9,322/3,420/1,449+463(M-15) +	32.62	60	60		60	60	60
dimeC32	463(M-15) +	32.74	61	61		61		61
n-C33	464	33.00	62	62		62	62	62
17-+15-+13-+11-MeC33	168/9,196/7,224/5,252/3,280/1,308/9,336/7,463(M-15) +	33.31	63	63	63	63	63	63
11,19-+ 11,21-+9,19-+9,21-DimeC33	140/1,168/9,196/7,224/5,294/5,322/3,350/1,378/9,477 (M-15) +	33.63	64	64	64	64	64	64
5,17-DimeC33+ 3-MeC33	56/7,84/5,224/5,294/5,434/5,448/9,463+477 (M-15) +	33.75	65	65		65	65	
nC34+X	478	34.00		66				
14-MeC34	210/1,294/5,477(M-15) +	34.28		67		67		
dimeC34	491(M-15) +	34.45		68				
3-MeC34	56/7,462/3,477 (M-15) +	34.72		69			69	
n-C35+dimeC34	492	35.00		70				70
17-+15-+13-+ 11-MeC35	168/9,196/7,224/5,252/3,280/1,308/9,336/7,364/5,491(M-15) +	35.27		71		71	71	
1l,19-DimeC35	168/9,224/5,322/3,378/9,505(M-15) +	35.57	72	72		72	72	
n-C36+X	506	36.00		73				
16-+14-MeC36	210/1,238/9,308/9,322/3,519(M-15) +	36.27		74				
3-MeC36	56/7,490/1,519(M-15) +	36.70		75				
n-C37	520	37.00		76				
dimeC37	533(M-15) +	37.50				77	77	

EI: Electronic Impact; ECL: Equivalent Chain Lenght; T.rac: *Temnothorax racovitzai;* T.unif: *T. unifasciatus;* T.lich: *T. lichtensteini;* T.nyl: *T. nylanderi;* T.par: *T. parvulus;* T.rec: *T. recedens.* Peak number: 1-77.

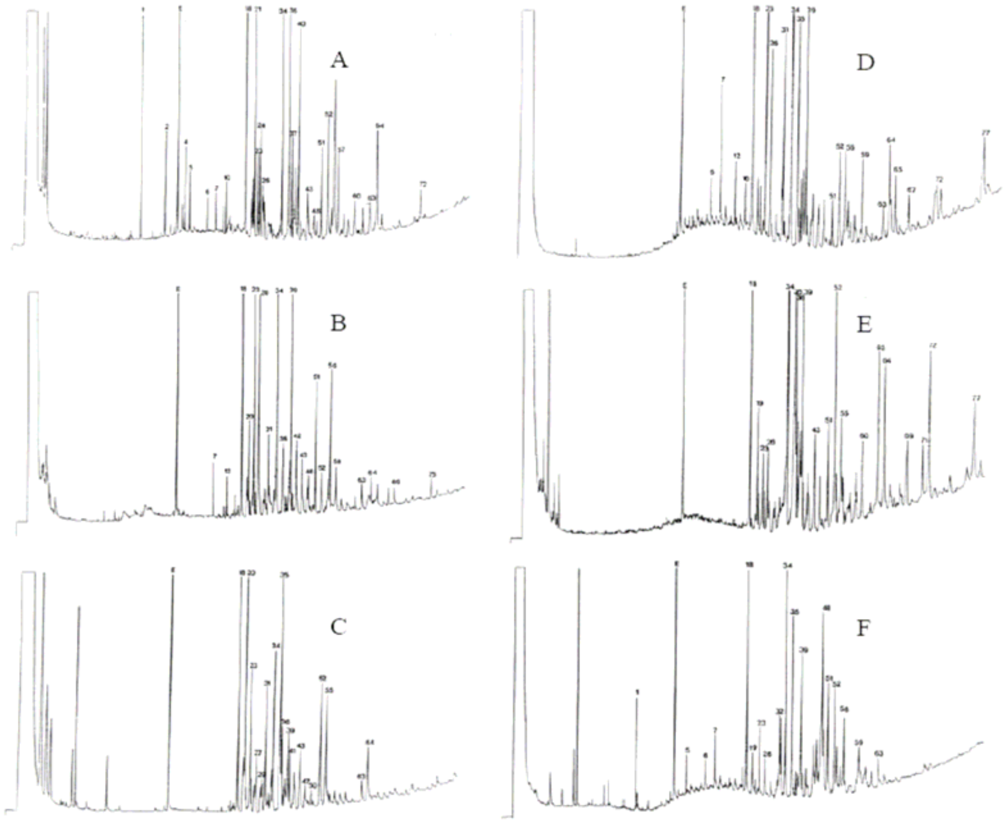

Figure 3. Cuticular hydrocarbon profiles (pentane extracts) of different species of the genus *Temnothorax*. A: *T. racovitzai*, B: *T. unifasciatus*, C: *T. lichtensteini*, D: *T. nylanderi*, E: *T. parvulus*, F: *T. recedens*. Standard peak E: *n*-C22. Peak number: 1-77.

For *Tetramorium* species from different countries, Steiner and collaborators (2002) reported congruence between chemical phenotypes and morphological determination in *T. ferox* and *T. moravicum* while six chemical phenotypes were found for two other species (*T. caespitum* and *T. impurum)*. This disparity could be explained by the possibility of hybridization and/or the existence of cryptic species (see below). With few exceptions (for an example, see Bagine et al., 1994), in all these studies CHs were described as being species-specific. This enabled the use of CH constituents as chemo-taxonomical tools for characterizing cryptic species complex i.e. a set of species that are reproductively isolated from each other but not readily or reliably distinguishable on a morphological basis (Howard, 1993). In the *Pachycondyla villosa* species complex (*Hymenoptera*), three closely related species were distinguished by their CH profiles (Lucas et al., 2002). The possibility of discriminating different species on the basis of their CHs can be used for systematical and biogeographical studies in *Lepidoptera*, in *Lasiommata megera/paramegaera* complex (Dapporto et al., 2007a). Triatomine insects (*Hemiptera*) are the vectors of Chagas disease. The presence, or absence, and relative quantities of their CHs are representative characteristics and are useful for differentiating genera, species, and populations (Juarez et al., 2002; Juarez and Fernandez, 2007).

In *Diptera*, CHs have been employed in differentiating species such as mosquitoes of *Anopheles* complex which is the most important malaria vector (e.g. Carlson and Service, 1979; Carlson et al. 1997), and flies such as *Glossina* species. A systematic comparison of methylalkanes from 26 species and subspecies of tsetse flies were carried out by Carlson and co-workers (1993). CHs were used as chemotaxonomic and philogenetic characters in beetles (*Ips spp*.) from the *grandicollis* subgeneric group (Page et al., 1997).

If the analysis of CHs proves to be useful as phenotypic markers in taxonomical studies, from an evolutionary point of view the use of cuticular compounds as phenotypic markers is controversial. It was clearly shown that depending on the type of genes used (mitochondrial or nuclear), the cuticular compounds may or may not constitute phylogenetic markers (Kutnik et al., 2004). Moreover the phylogenetic signals may be masked by the variations of CHs due to environmental conditions.

OTHER EXAMPLES OF APPLICATION FOR THE BIOLOGIST

Ginzel and Hanks (2002) claimed that CHs may be used for "mark-release-recapture" studies. They examined the potential for using blends of synthetic long-chain hydrocarbons, (*n*-C24 to *n*-C26, *n*-C28 and *n*-C30) which are structurally stable and non-volatile, to mark insects for field research. The total amount of synthetic hydrocarbons deposited on the elytra of the red milkweed beetle *Tetraopes tetrophthalmus* declined by only 25% over two months after the application. The invariability of hydrocarbon ratios was noted. The number of matings and the longevity of the beetle were not influenced by the hydrocarbon treatment. They concluded that application of blends of synthetic hydrocarbons offers an effective, convenient, and inexpensive means of uniquely marking insects for long-term field studies of population size and dispersal. However care must be taken in selecting hydrocarbons that will not influence intraspecific chemical communication.

The use of CHs analyses, agonistic behavioral and "mark-release-recapture" studies allowed monitoring in specific areas of chemical treatment against *Reticulitermes* termites. The origin of re-infestation was documented in insecticide-treated sites (Getty et al., 2000).

Social organization of colonies of a plant-ant *Cataulacus mckeyi* in Cameroon was determined by genetic, chemical and behavioral analyses. We showed that this species is monogynous and facultatively polydomous (i.e. a colony occupy one to several *Leonardoxa africana* trees). Using CHs analyses, it is possible to specify the colony boundaries by determining whether two neighboring trees contain workers belonging to the same colony or to different colonies (Figure 4) (Debout et al., 2003).

During forensic investigations it is necessary to be able to identify with certainty insects and their different stages of development. In Calliphoridae, it was assumed that the best philogenetic congruence between CHs and both morphological and molecular phylogenies were found for young adult female (Roux et al., 2006). CHs extracted from the pupal exuviae of six necrophagous flies were analyzed. They can be considered as valuable chemotaxonomic characteristics and feasibility for insects of forensic importance (Ye et al., 2007).

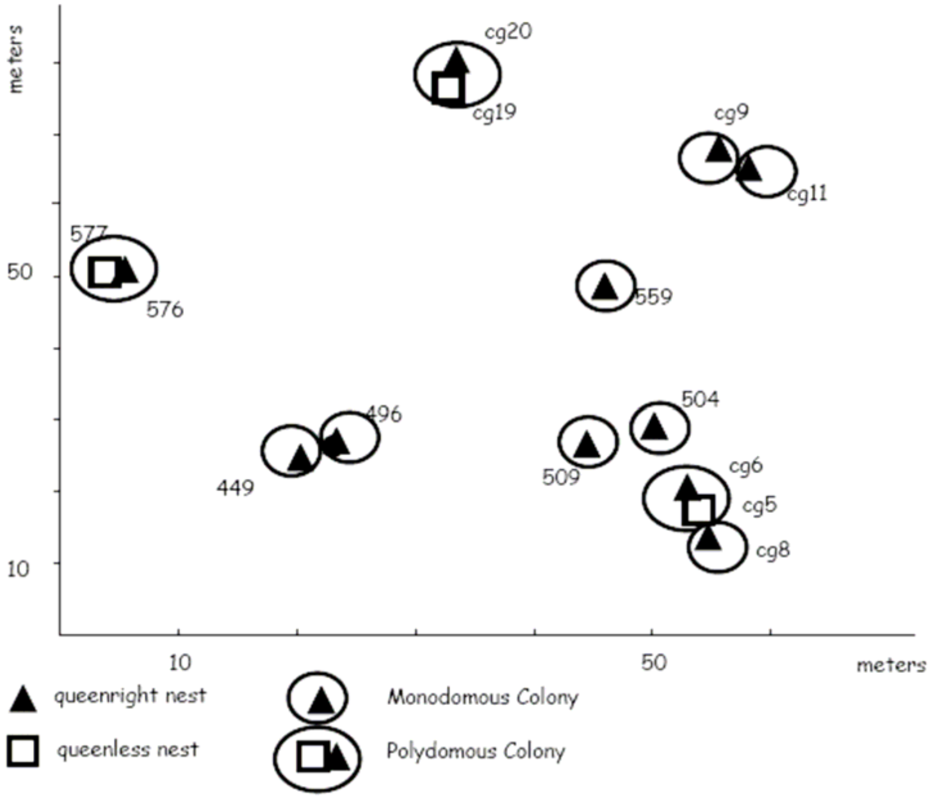

Figure 4. Example of nest distribution in the field: cg9 and cg11 (as 449 and 496) are two independent monodomous colonies, cg5 and cg6 (as cg19 and cg20) are two nests of the same polydomous colony, cg8 is a monodomous colony.

Finally, insects' cuticular lipids were proposed as a new target for insect control based on the disruption of their biosynthetic pathways (Juarez and Fernandez, 2007) or by altering the recognition signature (Tsutsui and Suarez, 2003; Torres et al., 2007).

CONCLUSION

According to its definition, pheromones are chemical compounds that are secreted by an individual (the sender) to the outside world and provoke a specific reaction in another individual of the same species (the receiver). Substances releasing reversible change in the behavior of the target organism are named releaser pheromones, while those provoking a physiological process in the receiver are called primer pheromones (Wilson and Bossert, 1963). Although CHs are involved in interspecific as well as intraspecific chemical communication, they are considered as semiochemicals that act as contact pheromone (they are perceived by other insects through direct contact or may be detected over a short distance). Usually, CHs are included in the class of releasers. In solitary insects, CH releaser pheromones play an important role, especially in the reproductive context. Within insect societies, the role of CH releaser pheromones is primordial, regulating queen-worker and worker-worker interactions. Up to recently, only a limited number of primer pheromones have been identified for ants. However a large number of primer pheromones have recently been discovered in bees (see Le Conte and Hefetz, 2008). Concerning the CHs, the border between releaser and primer pheromones often appears confusing. For example, queen fertility signals encoded in CHs are involved in the regulation of reproduction. They can be considered both as releaser and primer pheromones. They can both modify the behavior of the receiving workers, by eliciting aggression by policing workers and modify the physiology of the workers, by inhibiting their ovarian development. A queen-produced primer pheromone that has a profound effect on worker recognition or aggression toward conspecific workers and newly mated queens was found in *Solenopsis invicta* (Vander Meer and Alonso, 2002). This primer pheromone increases the sensitivity of workers to subtle within-species recognition cue differences. It might combine with releaser pheromones (CHs) that are involved in nestmate recognition. It has no effect in heterospecific recognition. Our review highlights the complexity of chemical communication in social insects.

With the CHs, we are far from the classic system of a pheromone, i.e. production and emission of a substance or a substances blend, species-specific, by an individual at a precise moment within a specific context to one or several receiver individuals of its own species. Social insects possess, on their cuticle, several dozen or often more than a hundred hydrocarbons whose origin is both genetic and environmental (physical or social). CHs seem to be produced, eventually modified by the environment and continuously emitted to any organism that the bearer meets. We conclude that certain CHs of the cuticular blend are involved in many different social contexts within a colony and can be different for the same social context among colonies, due to their environmental factors. This should open avenues for future research.

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