

FORUM

Chemical Communication in Isoptera

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Comunicação Química em Isoptera

RESUMO - Os semioquímicos dos cupins têm sido pouco estudados quando comparados aos de formigas e abelhas. Um dos fatores limitantes é o hábito críptico dos térmitas, aliado à dificuldade de manutenção de muitas espécies em laboratório. Entre os semioquímicos de Isoptera destacam-se os feromônios sexuais, de trilha, de alarme e uma mistura complexa de substâncias responsável pelo reconhecimento dos companheiros de ninho. Apesar de os semioquímicos dos cupins serem pouco conhecidos, os dados disponíveis indicam uma estratégia de parcimônia feromonal na comunicação química desses insetos, ou seja, algumas vezes o mesmo composto é secretado por diferentes glândulas, diferentes espécies e para diferentes funções.

PALAVRAS-CHAVE: Semioquímico, feromônio de trilha, feromônio de alarme, feromônio sexual, cupim

ABSTRACT - The semiochemicals produced by termites have been little studied compared to those of ants and bees. Among the limiting factors are the cryptic habits of termites, together with the difficulty in maintaining many species in the laboratory. The semiochemicals of Isoptera include trail, sex and alarm pheromones and a complex mixture of substances responsible for the recognition of nestmates. Although little is known about the semiochemicals of termites, available data indicate a strategy of pheromonal parsimony in the chemistry communication of these insects, i.e., the same compound is sometimes secreted by different glands, different species and for different functions.

KEY WORDS: Semiochemical, trail pheromone, alarm pheromone, sex pheromone, termite

Chemical communication in Isoptera depends on compounds secreted mostly by a wide variety of exocrine glands found throughout their bodies (Costa-Leonardo 2002). These substances are extremely important in termite societies as termites are blind, and these substances maintain the integration of the colony and social homeostasis. Castes in Isoptera include workers, soldiers and reproductives, which are specialized for different tasks in the nest. Reproductives are engaged in reproduction, whereas workers, which correspond to the most abundant caste, are responsible for food searching, nest building and brood care. In contrast, soldiers, due to their morphophysiological specialization, are primarily responsible for colony defense (Noirot & Darlington 2000).

The social organization of termite colonies depends on the proportion of the different castes and on efficient systems for communication and recognition. Semiochemicals in termite colonies are employed in many activities such as foraging, defense, attraction to and induction of feeding on food sources, colony segregation, mate location, and even

caste regulation. Several studies on termite pheromones have been published (Stuart 1969, 1970, Moore 1974, Prestwich 1984, Howse 1984, Pasteels & Bordereau 1998, Kaib 1999), but little is known on the identity of these semiochemicals. However, the data available to date indicate a strategy of pheromonal parsimony in the chemical communication of these insects when compared with other social insects. The chemical parsimony of termites is also functional, i.e., the same compound is secreted by different glands, different species and for different functions (Robert *et al* 2004).

Trail Pheromones

Trail pheromones are secreted by the sternal glands and are related to foraging behavior. The sternal gland is present in all castes of Isoptera. In Termitidae and Rhinotermitidae, sternal glands are modified epidermal cells located under the 5th abdominal sternite (Noirot 1969, Quennedey *et al* 2008).

In termites, foraging is a collective process in which the activities of hundreds or thousands of individuals are coordinated by trail pheromone. The pheromone is deposited when the insect presses its abdomen against the substrate, releasing the pheromonal secretion from the sternal gland. Termites lay exploratory trails during the search for a food source for latter nestmate recruitment to the food source. During the exploratory phase, scout workers leave the nest and lay a dotted trail of pheromone, i.e., constant intervals are maintained between deposition points, walking slowly in curves as the heads and antennae are constantly shaken. After traveling for a few centimeters, scout workers stop and rapidly return along the same path using the same trail. Other scout workers follow the same exploratory trail and extend it in the same direction or advance on a new territory. Once a food source is located, the scouts move very quickly and do not stop laying the trail, examining the food with the palpi and antennae. Then, scout workers return to the nest, laying a recruitment trail, which will attract other foragers to the newly discovered food source. The recruitment trail is thus laid from the food source to the nest but in a continuous manner (Reinhard & Kaib 2001).

Behavioral observations suggest that the trail pheromone of termites is a multi-component blend, with an active compound acting as a common orientation signal for different termite species and specific secondary compounds that determine the specificity of trails among species (Traniello 1982, Kaib 1999, Kaib *et al* 1982, Arab *et al* 2004). However, until now no species-specific compounds have been identified in Isoptera. The sternal gland of *Coptotermes gestroi* (Wasmann) (Rhinotermitidae) workers is characterized

by a complex structure consisting of various cells, a fact supporting the idea of multi-component pheromones (Costa-Leonardo 2006).

The common active compounds of termite trail pheromones identified until now include: dodecatrien-1-ol, neocembrene, dodecenol and dodecadienol (Sillam-Dussès *et al* 2005, 2006, Saran *et al* 2007). Dodecatrien-1-ol has been detected in many species of Rhinotermitidae, neocembrene in various termitid species of the subfamily Nasutitermitinae, and dodecadienol in *Ancistrotermes pakistanicus* (Ahmad), one termitid species of the subfamily Macrotermitinae. Table 1 illustrates the occurrence of these pheromones in some families and genera of Isoptera. According to Sillam-Dussès *et al* (2006), the active components of the trail pheromones are highly conservative and do not show a high species-specific diversity. However, from a phylogenetic point of view, there is a clear distinction between trail pheromones of Mastotermitidae, Termopsidae and Hodotermitidae when compared to those of more evolved families such as Kalotermitidae, Rhinotermitidae and Termitidae. In addition, there is a clear distinction between trail pheromones of fully and mandibulate nasutes, although the two groups belong to the same subfamily Nasutitermitinae (Table 1).

Most termite species also follow artificial trails produced by a wide variety of chemical compounds such as alcohols, fatty acids and saturated compounds. The ink of some ball-point pens elicits the trail-following behavior in subterranean termites of the genus *Reticulitermes* and in *Coptotermes formosanus* Shiraki due to the fact that the reported ink contains 2-phenoxyethanol whose structure is similar to that of dodecatrien-1-ol, the main component of the trail

Table 1 Occurrence of trail pheromone in Isoptera (Sillam-Dussès *et al* 2006).

Family	Subfamily	Genus	Trail pheromone
Termitidae	Nasutitermitinae (fully nasutes)	<i>Nasutitermes</i> , <i>Constrictotermes</i> , <i>Trinervitermes</i>	Mixture of Dodecatrienol and Neocembrene
	Nasutitermitinae (mandibulate nasutes)	<i>Syntermes</i> , <i>Cornitermes</i>	Dodecatrienol
	Termitidae	<i>Drepanotermes</i> , <i>Cubitermes</i>	Dodecatrienol
		<i>Pseudocanthotermes</i>	Dodecatrienol
	Macrotermitinae	<i>Ancistrotermes</i>	Dodecadienol
		<i>Macrotermes</i> , <i>Odontotermes</i>	Dodecenol
	Prorhinotermitinae	<i>Prorhinotermes</i>	Neocembrene
Rhinotermitidae	Heterotermitinae	<i>Heterotermes</i> , <i>Reticulitermes</i>	Dodecatrienol
	Coptotermitinae	<i>Coptotermes</i>	Dodecatrienol
	Rhinotermitinae	<i>Rhinotermes</i> , <i>Schedorhinotermes</i>	Dodecatrienol
Kalotermitidae		<i>Cryptotermes</i> , <i>Procryptotermes</i> , <i>Kalotermes</i> , <i>Neotermes</i> , <i>Postelectrotormes</i>	Dodecenol
Hodotermitidae	Hodotermitinae	<i>Hodotermes</i>	C18 molecule
	Termopsinae	<i>Zootermopsis</i>	Dodecanal
Termopsidae	Stolotermitinae	<i>Stolotermes</i>	Decadienol
	Porotermitinae	<i>Porotermes</i>	Decadienol
Mastotermitidae	Mastotermitinae	<i>Mastotermes</i>	Decadienol

pheromone of these species (Chen *et al* 1988). In addition, extracts of wood infested with the fungus *Gloeophyllum trabeum* (Persoon) also induce trail following and orientation in foraging termites because they contain dodecatrien-1-ol (Matsumura *et al* 1968, Rust *et al* 1996).

Aggregation and Phagostimulating Pheromones

Some subterranean termites such as *C. gestroi* secrete an aggregation pheromone that is also a feeding stimulant. Gnawing workers release saliva on the food which induces aggregation behavior on other workers (Casarin *et al* 2003). The aggregation pheromone is produced by the salivary glands and released on the food through the oral cavity. The advantage of this aggregation strategy is that it favors the defense work of soldiers, since it is easier to monitor aggregated workers than those spread over the food source. Additionally, this pheromone contributes to the survival of the worker caste (Kaib & Ziesmann 1992).

Alarm and Defense Pheromones

The defense of the colony is a collective process coordinated by a variety of signals. In addition to mechanical vibratory cues produced by termites by "banging" their heads on the substrate, chemical cues play an important role in the alarm and defense behavior of termites. This chemical defense is an individual behavior and may occur in soldiers or in workers, and it involves altruism and may be suicidal or not. Defensive compounds are produced by exocrine glands, being the frontal gland the most common (Costa-Leonardo 1998a, 1999, 2001).

The alarm behavior was demonstrated for the first time in *Nasutitermes*, as soldiers eject a viscous secretion produced by the frontal gland on their enemies from a considerable distance. Volatile compounds, mainly monoterpenes, sesquiterpenes and diterpenes (Prestwich 1984), then evaporate from the frontal secretion and attract more soldiers to the combat area. Detailed studies on various species of *Nasutitermes* demonstrated that workers and soldiers respond differently to alarm pheromones consisting of monoterpenes, and that these castes play a complementary role during defense (Roisin *et al* 1990). The alarm pheromones have been identified as α -pinene and limonene in *Nasutitermes rippertii* (Rambur), carene and limonene in *Nasutitermes costalis* (Holmgren), and α -pinene in *Nasutitermes princeps* (Desneux) (Vrkoc *et al* 1978, Roisin *et al* 1990).

The frontal gland produces and stores chemical substances and is present in soldiers and alates of some termite species (Costa-Leonardo 1989). Many of these substances are not pheromones; however, the content of the frontal gland represents a vast and peculiar arsenal of defensive products. In addition, various strategies of synthesis, storage and ejection of frontal secretion exist in Isoptera. Generally, the frontal gland content is eliminated through a fontanelle located on the head or in the terminal portion of a nose-like projection present in nasute soldiers. In soldiers of *Armitermes*

euamignathus Silvestri, the frontal secretion contains large amounts of tri-, tetra- and pentadecene, which has a slightly toxic effect on ants (Howse 1984). These compounds are common in the alarm pheromones of some ants (Blum 1981) and may act as "advertisement pheromones" (allomones), alerting ants and reducing their attack efficiency. Recent data showed (E,E)- α -farnesene as an alarm pheromone secreted by the soldier frontal gland of the termite *Protrichotermes canalifrons* (Sjöstedt) (Šobotník *et al* 2008).

The defense of termites may also involve suicidal altruism through rupture of an exocrine gland. In this case, the individual dies in defense of the society. Soldiers of *Serritermes serrifer* (Hagen & Bates) possess a hypertrophied frontal gland which does not contain an outer opening. In situations of danger, the gland explodes releasing a yellow secretion which becomes viscous in contact with air (Costa-Leonardo & Kitayama 1991, Costa-Leonardo 1998b). Workers of the soldierless *Ruptitermes* (Termitidae, Apicotermittinae) also show suicidal altruism characterized by the rupture of defense glands located between the metathorax and first abdominal segment (Costa-Leonardo 2004). In both cases, some alarm pheromones may exist in the composition of the viscous defense secretion of these individuals. However, these substances are not identified yet.

Sex Pheromones

In most termites, sex pheromones are produced by alate females, but in some cases the males or both sexes may be the source of this pheromone. Dodecatrien-1-ol is the main sex pheromone identified in termites (Table 2). The study of sex pheromones in termites is difficult since the mating flight occurs only once a year, lasts only a few minutes and the amount of pheromone is minimal. In addition, the purification of solvent-extracted glandular secretions is difficult. However, there are evidences suggesting that termite sex pheromones are multi-components and the constituents are synergists one to another (Clément 1982, Laduguie *et al* 1994).

The sex pheromone-producing exocrine glands include the tergal and the posterior sternal glands and the sternal gland of the 5th sternite (Table 2). Tergal glands produce sex pheromones involved during post-flight behavior of the reproductives. The location of these glands vary among the termite species (tergites 3-10 or 6-10, 8-10, 9 and 10 or only in the tergite 10). They may be found in both sexes, but may be restricted to females or even be absent, and their role is not well understood (Ampion & Quennedey 1981). Some sex pheromones produced by the reproductive sternal gland are identical to the worker trail pheromones, but are secreted in much higher quantities, especially in females whose sternal gland is larger (Pasteels & Bordereau 1998). This dual pheromonal function is particularly observed in species where females do not possess tergal glands, but have a hypertrophied sternal gland instead (Robert *et al* 2004).

The reproductive sexual behavior of termites involves the use of both long and short distance cues by females. Calling females generally expose the sternal gland of the 5th sternite for the release of long distance cues, while short distance cues

Table 2 Occurrence of sex pheromones in Isoptera.

Family	Subfamily	Genus / species	Sex of reproductives	Source of sex pheromone	Sex pheromone
Termitidae	Macrotermitinae	<i>Pseudacanthotermes spiniger</i>	Female	SG	Dodecatrienol
		<i>Pseudacanthotermes militares</i>			
		<i>Macrotermes annandalei</i>	Female	PSG	NI
		<i>Macrotermes barneyi</i>			
	Nasutitermitinae	<i>Ancistrotermes pakistanicus</i>	Female	SG / TG	Dodecadienol
		<i>Trinervitermes bettonianus</i>	Female	SG / TG	Neocembrene
Rhinoitermitidae	Coptotermitinae	<i>Syntermes dirus</i>	Female	TG	NI
		<i>Cornitermes bequaerti</i>	Female	TG	Dodecatrienol
	Heterotermitinae	<i>Coptotermes formosanus</i>	Female	TG	Trilinolein (?)
		<i>Reticulitermes</i>	Female	SG	Dodecatrienol
	Prorhinotermitinae	<i>Prorehinotermes</i>	Male	PSG	NI
Kalotermitidae	Hodotermitinae	<i>Kalotermes flavicollis</i>	Female, male	SG / TG	NI
Hodotermitidae		<i>Hodotermes mossambicus</i>	Male	SG	NI
Termopsidae	Termopsinae	<i>Zootermopsis nevadensis</i>	Female	SG	Decadienal
			Male	SG	Dodecanal
		<i>Stolotermes</i> , <i>Porotermes</i>	Male	PSG	NI
Mastotermitidae	Mastotermitinae	<i>Mastotermes darwiniensis</i>	Female, male	PSG	NI

SG = sternal gland; PSG = posterior sternal glands; TG = tergal glands; NI = not identified

are released by tergal glands. Short distance cues are involved in the final stages of male attraction and in the initiation of a tandem running behavior until the location of the nest site. In general, tergal glands correspond to thickenings of the last abdominal tergites and influence the pairing of reproductives, maintaining the cohesion of the tandem before mating. Nevertheless, in *Cornitermes bequaerti* Emerson, the three female tergal glands are involved in the calling posture (Bordereau *et al* 2002). Once attracted by the sex pheromone, the male touches the female, placing its prothoracic legs on the abdominal pleural membranes of the female. A nuptial promenade in tandem is rapidly started with the female as a leader (Fig 1), while the male licks the tergal secretions, and walks only with meso- and metathoracic legs. Trilinolein has been identified in the tergal glands of female alates of *C. formosanus* Shiraki, and has been interpreted as a nuptial gift for the male (Bland *et al* 2004, Raina *et al* 2005). However, this substance may also be a sex pheromone precursor in this species (Table 2).

Cuticular Hydrocarbons-Recognition Pheromones

Termite cuticle functions as an enormous exocrine gland, producing a mixture of chemical substances, mainly hydrocarbons (Kaib 1999), which are believed to be involved in nestmate recognition (Clément & Bagnères 1998, Batista-Pereira *et al* 2004, Kaib *et al* 2004). This belief is based on the fact that hydrocarbon cuticular composition differs among colonies of the same termite species (Howard 1993, Kaib *et al* 2002), and that these differences might be correlated

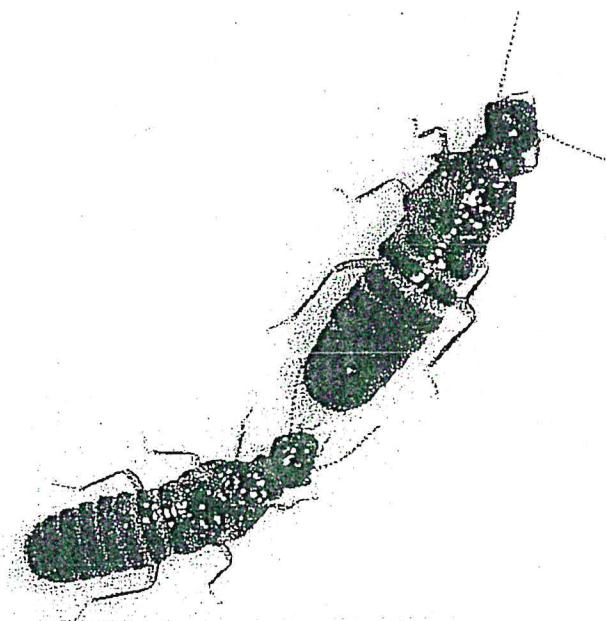


Fig 1 Tandem running of *Procornitermes araujoi* Emerson. The male follows the large female, which acts as a leader in this process.

with intercolonial aggressions (Jmhasly *et al* 1998). Recent studies in this area suggest a genetic mechanism for cuticular hydrocarbons, but current research has not ruled out environmental effects on the composition of these

substances in termites (Matsuura 2001, Florane *et al* 2004, Dronnet *et al* 2006).

Final Considerations

The available data indicate a great economy in chemical communication strategies of Isoptera. In some species such as *C. bequaerti*, the same compound, dodecatrien-1-ol, is used both as a sex and a trail pheromone. However, despite the ecological and economic role of termites, little is known on their semiochemicals as compared to what is already known for other social insects. Further information on these chemical mediators is essential both for a better understanding of the Isoptera society and for the development of alternative methods for termite control.

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