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Review

Chemical warfare in termites

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A R T I C L E I N F O

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Dedicated to the memory of Ivan Hrdý, our dear teacher and colleague, who introduced us to the fascinating world of termites.

A B S T R A C T

The rapid development of analytical methods in the last four decades has led to the discovery of a fascinating diversity of defensive chemicals used by termites. The last exhaustive review on termite defensive chemicals was published by G.D. Prestwich in 1984. In this text, we aim to fill the gap of the past 25 years and overview all of the relevant primary sources about the chemistry of termite defense (126 original papers, see Fig. 1 and online supplementary material) along with related biological aspects, such as the anatomy of defensive glands and their functional mechanisms, alarm communication, and the evolutionary significance of these defensive elements.

Contents

1. Termites: abundant, vulnerable, defended

The ability to defend is one of the most prominent life history traits common to eusocial animals; the strong pressure of predation and ecological constraints on independent reproduction are the factors promoting the evolution of social behavior (Crespi, 1994). The selection for defense has brought several taxa to the heights of eusociality through the evolution of specialized sterile defenders, the soldiers. Termites represent an excellent example in this respect. The vast majority of the species live in defendable cryptic habitats, alate imagoes are particularly vulnerable to predation, and the soldier caste has evolved as the first altruistic caste (Hare, 1937).

Due to their impressive abundance in the tropics, termites represent an important food source for numerous facultative and specialized predators; their richness includes many taxa of arthropods and vertebrates (reviewed in Deligne et al., 1981; Grassé, 1986). Nevertheless, termites undoubtedly suffer their main predation from ants. After termites, ants are the second clade to reach the most complex social organization, and at the same

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time a comparable ecological dominance but at different trophic levels, with ants being the dominant predators of arthropods. The arms race between these two superpowers determined the termites' defensive strategies (Hölldobler and Wilson, 1994). Another factor promoting the defensive adaptations in termites is the intra- and interspecific competition for nesting and foraging sites (see e.g. Thorne, 1982; Binder, 1988; Thorne and Haverty, 1991; Korb and Linsenmair, 2001; Thorne et al., 2003).

The defense *sensu lato* includes both passive and active elements that in concert allow termites to handle various threats. Among the passive elements, the life enclosed within tunnels, galleries and nests is of prime importance, as it separates the termites from possible predators. The nests of termites are often cited to be the most elaborate animal constructions in terms of structural and functional complexity, as well as size (Noirot, 1970; Grassé, 1984; Noirot and Darlington, 2000). The active elements consist in the behavioral and structural defensive adaptation of soldiers and workers, and alarm communication.

The role of the workers in termite defense should not be underestimated. First, they are always the most abundant caste and are fully responsible for the construction and repair of the passive defensive structures. Second, they indeed actively participate in defense (see e.g. Thorne, 1982; Binder, 1988). Nevertheless, it is in the soldier caste, fully devoted to defensive activities and liberated from the multitude of tasks performed by the workers, that we can find an impressive variety of defensive adaptations. These include mechanical weaponry, above all the enlarged and heavily sclerotized head, and the mandibles, allowing a classification into several categories of biting (e.g. crashing, slashing, piercing, reaping, etc.) or snapping (symmetric or asymmetric) (see Deligne et al., 1981; Prestwich, 1984a). As a complement to the mechanical weapons, the chemical defense occurs in soldiers, ensured by the exocrine glands: the labial glands, the labral gland, and above all, the frontal gland, the first of which evolved as a modification of glandular structures existing in the basic anatomic plan of insects, whereas the other two represent novel secretory organs, exclusive to termites.

2. Alarm communication

Collective handling of a threat requires effective communication allowing the escape of vulnerable individuals and the recruitment of defenders. The modes of alarm and recruitment in termites can be classified as follows: (i) general alarm elicited by substrate-borne vibrations or pheromones from the soldiers' frontal gland; (ii) specific alarm by physical contact between the alerted and the recruited termite. These modes can be combined and are not exclusive to soldiers, although soldiers play the prime role.

Body vibration is a widespread behavior observed in virtually all castes. It can be accompanied by drumming by the head or the abdomen against the floor or the roof of the nest or gallery (Stuart, 1963, 1988; Howse, 1964a,b, 1965; Leis et al., 1994). Even though these activities can be audible to man, the alarm signal is mediated by substrate-borne vibrations, perceived by the subgenual organ (Howse, 1964a,b). These vibrations act as an alarm in numerous species (Stuart, 1963, 1988; Howse, 1965; Kirchner et al., 1994; Connétable et al., 1998, 1999; Röhrig et al., 1999). A single or eventually a few termites close to the place of a disturbance are involved in producing the alarm in primitive termites, such as *Zootermopsis* and *Kalotermes* (Howse, 1965; Stuart, 1988; Kirchner et al., 1994), whereas in advanced species, the vibratory alarm reaches a higher level of complexity. First, it is restricted to soldiers, and second, the vibrations elicit an immediate positive feedback reaction of other soldiers, which start to vibrate as well (Stuart, 1988; Connétable et al., 1998, 1999; Röhrig et al., 1999). Synchronized vibrations of Macrotermitinae soldiers in the foraging territory are even audible as rhythmical hissing, supposedly acting as a warning signalization towards predators and/or competitors (Röhrig et al., 1999).

All known alarm substances are included in the soldier frontal gland secretion and released by fighting or excited soldiers (for a review, see Pasteels and Bordereau, 1998; Costa-Leonardo et al., 2009; or Ernst, 1959; Moore, 1968; Eisner et al., 1976; Kriston et al., 1977; Kaib, 1990; Reinhard and Clément, 2002; Reinhard et al., 2003). Despite numerous behavioral observations and the extensive list of identified frontal gland chemicals, the confirmations of particular alarm pheromones are rare, e.g. the monoterpenes α-pinene and limonene in *Nasutitermes rippertii* and *Velocitermes velox* (Vrkoč et al., 1978; Valterová et al., 1988a), carene and limonene in *N. costalis* (Vrkoč et al., 1978), α-pinene in *Nasutitermes princeps* (Roisin et al., 1990), and sesquiterpene (*E*,*E*)-α-farnesene in *Prorhinotermes canalifrons* (Šobotník et al., 2008). Reinhard et al. (2003) assigned the alarm function to several mono- and sesquiterpenes from the complex mixture of terpenoids of European *Reticulitermes* species. The participation of these compounds in communication is evidenced also by their high enantiomeric purity, characteristic for pheromones (Lindström et al., 1990; Everaerts et al., 1990; Valterová et al., 1992, 1993), and has been experimentally verified (Roisin et al., 1990).

The reactions of nestmates to the chemical alarm signaling are caste-specific. Soldiers tend to reach its source while other castes hide away or stay unalarmed; the alerted soldiers then propagate the alarm by active running and physical contacts with nestmates (Eisner et al., 1976; Šobotník et al., 2008) or through the release of further frontal gland secretion (Vrkoč et al., 1978; Roisin et al., 1990). The alarm signaling may also differ among particular subcastes; for example, the large soldiers of *Nasutitermes exitiosus* and the small soldiers of *Schedorhinotermes lamanianus* are devoted exclusively to alarm propagation, otherwise behaving non-combatively (Kriston et al., 1977; Kaib, 1990), whereas large workers of *Nasutitermes* participate in defense in response to an alarm pheromone and small workers show no reactions (Eisner et al., 1976; Roisin et al., 1990). In laboratory bioassays, the reactions depend on group composition; workers might be more curious and soldiers less precise in odor-source localization in single-caste groups (Roisin et al., 1990). The silencing of the alarm stimulus can be accelerated by deposition of feces and soil particles on an immobilized enemy (Eisner et al., 1976).

The second mode of alarm, the specific alarm, consists in the recruitment of defenders by direct physical contact accompanied by vibratory movements. The alerted nestmates follow the odor trail laid previously by the alarm initiator to the disturbance site (Stuart, 1963; Kettler and Leuthold, 1995).

3. Labial glands and their secretion

The labial glands are universally present in termites, irrespectively of species, caste, or developmental stage (Noirot, 1969; Billen et al., 1989; Šobotník and Weyda, 2003). Their function in workers is to produce the secretion involved in: (i) food digestion (especially cellulolysis), (ii) the feeding of dependent castes, (iii) building activities, and (iv) food-marking (Noirot, 1969; Grassé, 1982; Reinhard et al., 2002; Tokuda et al., 2002; Fujita et al., 2008).

As a derived function, the labial glands are used in defense, especially by soldiers. The soldiers of several taxa (*Mastotermes*, Macrotermitinae) possess hypertrophied glands with reservoirs extending deeply into the abdominal cavity (Quennedey, 1984). The secretion is released during a fight from the mouth, subsequently congeals in the air, and often fatally entangles the enemy. The soldiers of Macrotermitinae may stay locked with their mandibles to the body of the enemy while pumping with their abdominal musculature the content of the gland reservoirs into the