Insectes soc. 44 (1997) 289–296
0020-1812/97/030289-09 $ 1.50+0.20/0

Insectes Sociaux

Research article

Suicidal defensive behaviour by frontal gland dehiscence in *Globitermes sulphureus* Haviland soldiers (Isoptera)

C. Bordereau[1,*], A. Robert[1], V. Van Tuyen[2] and A. Peppuy[1]

[1] *Université de Bourgogne, UMR CNRS 5548, 6, Bd Gabriel, F-21000 Dijon, France*
[2] *Trung Tam Nghien Cuu Phong Tru Moi, 2 Chua Boc Street, Hanoï, Vietnam*

Key words: Defensive behaviour, autothysis, termites.

Summary

Globitermes sulphureus is a well-known termite for the suicidal behaviour of the soldiers which liberate a sticky defensive secretion by rupturing their body. We have shown that this secretion is elaborated in a highly transformed frontal gland occupying a large part of the abdomen and the thorax, and not in the salivary glands as had been assumed until now. This special frontal gland without an outside opening is ruptured by violent contractions of the abdominal wall at the level of a weakness area of the sternal thoracic integument, just before the forecoxae. This soldier autothysis is efficient but represents only one of the components of the defensive strategy of the species which also uses a mechanical defense with mandibles and the intervention of an alarm pheromone recruiting congeners.

Introduction

Termite colonies are protected by soldiers which have developed various defensive strategies using mechanical and/or chemical weapons (Deligne et al., 1981; Prestwich, 1984). A remarkable case, first described by Bathellier (1927), is the suicidal behaviour by autothysis observed in *Globitermes sulphureus* soldiers. When attacking, these soldiers expel a large amount of yellow liquid which entangles both the termites and their enemies. According to this author, this defensive secretion originating from hypertrophied salivary glands is ejected through the mouth or, in very excited soldiers showing violent contractions of their whole body, by rupturing of the salivary gland wall and of the integument near the basis of the legs. *G. sulphureus* soldiers have been so called walking chemical bombs (Oster and Wilson, 1978), exploding termites (Mill, 1984) or kamikaze termites (Prestwich, 1988) and have drawn the attention of sociobiologists for their altruistic behaviour.

* Author for correspondence. E-mail: Christian.Bordereau@u-bourgogne.fr.

We here report observations carried out on *G. sulphureus* soldiers from Vietnam, showing that the defensive behaviour is not always suicidal and that the secretion is released not from salivary glands, but from a very modified frontal gland.

Material and methods

Globitermes sulphureus Haviland (Termitidae, Termitinae) is a very common species in Central and South Vietnam where it is considered as a major pest, because it causes extensive damages to wood structures. This species builds an epigeous dome-like nest which may reach one to one and half meters in height. It is made of earth, excremental matter and non-assimilitated vegetative material. A thin bark covering the nest and a wall made of a dense network of fine and large galleries protect the colony (Noirot, 1959).

The colonies comprize tens of thousands of individuals. Soldiers represent 5 to 10 percent of the active population. Soldiers are characterized by the yellow colour of their abdomen due to the accumulation of the defensive secretion in a gland occupying the thorax and a large part of the abdominal cavity. They also possess two well developed slender and curved mandibles of the slashing-piercing type (Fig. 1).

Field observations have been carried out in the province of Ban May Thuot, Central Vietnam, in May 1993 and May 1994.

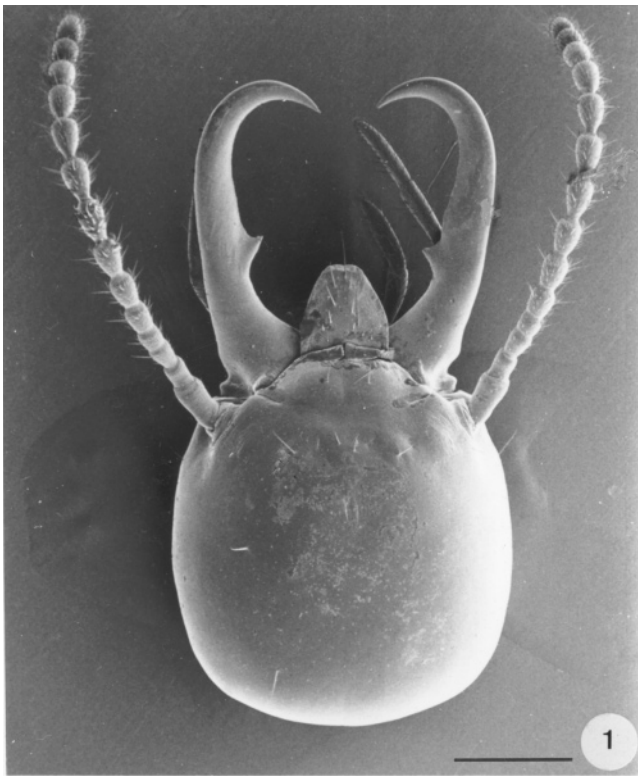
Soldier head capsules were dehydrated by alcohol and acetone and were observed with a scanning electron microscope JEOL JSM 35 CS.

For histological studies, specimens were fixed in Duboscq-Brasil's mixture and embedded in paraffin wax. Sagittal sections (7 µm) were stained with Heidenhain's azan. Three to five individuals were observed for each stage of the soldier morphogenesis.

Results

Behavioural observations

The defensive behaviour of *Globitermes sulphureus* soldiers was observed many times in the field after the artificial removing of a small part of the superficial bark of the nest. This induced the arrival of soldiers and workers at the breach of the nest. The soldiers showed an alert behaviour by keeping still, standing up on their legs and scanning all around with their antennae. The workers rapidly started to repair the nest breach by depositing new material. When the colonies were attacked by ants, such as *Oecophylla smaragdina*, the workers immediately escaped and many soldiers rapidly arrived at the surface of the nest where very violent fights occurred. In a first step, termite soldiers tried to catch and pierce their adversaries with their mandibles. Ants could be so repelled. Sometimes, termite soldiers pursued their enemies, but most often they escaped inside the nest. However, some very excited soldiers rapidly showed under their neck a droplet of yellowish liquid which gently flowed out and was never projected against the adversary. This secretion could be emitted even before a physical contact with enemies. Soldiers with excreted defensive secretion generally remained still, but were able to fight for several



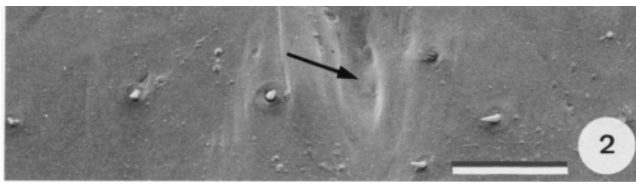


Figure 1. Scanning electron micrograph of the soldier head capsule of *Globitermes sulphureus* showing the shape of hooks of the two long slender mandibles and the absence of a frontal pore. (scale bar: 300 µm)

Figure 2. Detail of the fontanelle area showing the slight depression of the cuticular surface (arrow) and the absence of a glandular aperture. (scale bar: 30 µm)

minutes against ants. In this case, ants and termites most often became stuck in the viscous termite secretion which rapidly congealed in the air.

Origin of the defensive secretion

The observation of rupturing soldiers under stereomicroscope shows that the yellowish defensive secretion flows out on the thoracic sternal face, just behind the forecoxae. In intact soldiers, no opening is visible in this area.

The dissection of soldiers shows that the defensive gland is an unpaired gland occupying the thorax and a great part of the abdomen, with a dorsal position in relation to the digestive tube and the salivary glands. This gland does not enter into the head capsule and does not open to the outside. In the thorax, it shows a horse-saddle shape with lateral expansions reaching the sternal wall. No relation is observed between this gland and the normally developed salivary gland reservoirs filled with hyaline liquid and opening into the buccal cavity. Therefore, the defensive secretion of the soldiers of *G. sulphureus* does not come from the salivary glands.

The position of the defensive gland of *G. sulphureus* corresponds to that of hypertrophied frontal glands observed in some species of Rhinotermitidae, which open to the outside in the fontanelle area of the cephalic capsule by a frontal pore. However, in *G. sulphureus*, no frontal pore is visible on the head capsule. Under scanning electron microscope, only a slight depression can be recognized at the level of the fontanelle (Figs. 1, 2).

Histological sections of soldiers show that the wall of the defensive gland is made of a thin monolayered epithelium (5–10 µm). The anterior extremity of the gland is located between the pro and the mesothorax. Sometimes, a small duct is reaching or even penetrating slightly into the head, but this duct is blind. On the other hand, a very tight contact is observed between the wall of the gland and the wall of the sternal arthrodial integument at the level of the forecoxae. In ruptured soldiers, this is precisely the point of the released secretion.

Figures 3–10. Differentiation of the frontal gland during the morphogenesis of the soldier of *Globitermes sulphureus*

Figure 3. Worker molting into presoldier (stage just before ecdysis). Inside the cephalic capsule, the frontal gland (fg) appears as a small spherical vesicle containing flocculent secretion and is located above the brain, just behind the fontanelle area. (scale bar: 500 µm)

Figure 4. Detail of Figure 3 showing the absence of communication between the frontal gland and the outside. The thinning of the glandular epithelium in front of the vesicle and the cells present between the vesicle and the cephalic epidermis probably correspond to a vestigial canal (arrow). (scale bar: 100 µm)

Figure 5. Presoldier. At this stage, the frontal gland (fg) increases in volume and takes an ovoid shape indicating a beginning of migration. (scale bar: 500 µm)

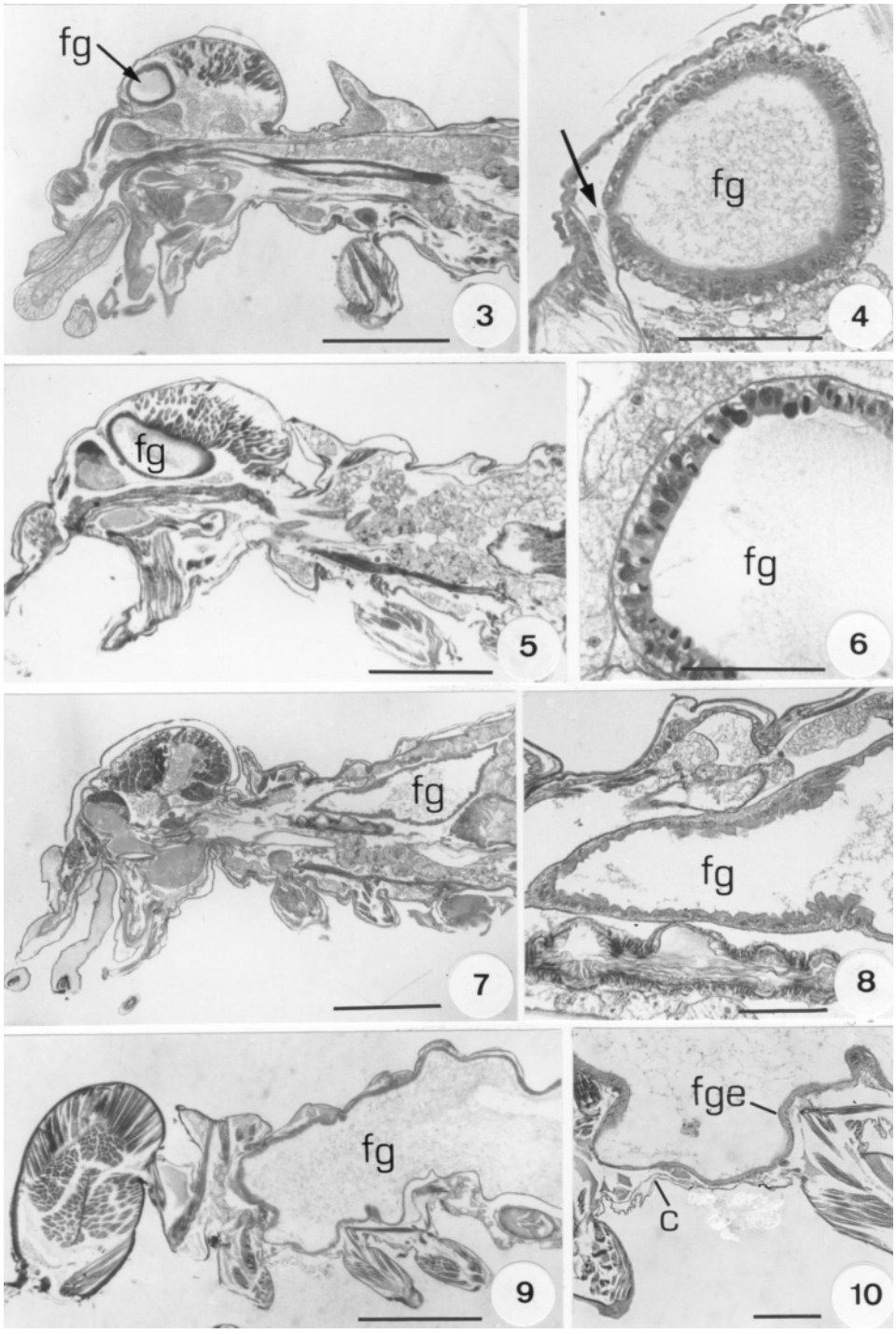
Figure 6. Detail of Figure 5 showing epithelial mitoses in the epithelium of the frontal gland (fg). (scale bar: 100 µm)

Figure 7. Presoldier molting into soldier. Before the ecdysis of the presoldier into soldier, the frontal gland (fg) migrates into the thorax. (scale bar: 500 µm)

Figure 8. Detail of Figure 7 showing the epithelium of the frontal gland (fg) and the flocculent secretion. (scale bar: 100 µm)

Figure 9. Soldier. At this stage, the frontal gland (fg) filled up with defensive secretion occupies a large part of the thorax and the abdomen. The glandular epithelium is in an intimate relation with the integument (scale bar: 500 µm)

Figure 10. Detail of Figure 9 showing the intimate contact between the epithelium of the defensive gland (fge) and the arthrodial cuticle of the sternal integument (c). (scale bar: 100 µm)


fg
3
fg
4
fg
5
fg
6
fg
7
fg
8
fg
9
fge
c
10

Only the study of the differentiation of the defensive gland during the soldier morphogenesis allowed the understanding of its origin (Figs. 3–10, Fig. 11). In *G. sulphureus*, soldiers develop from workers, and as in all termites, they differentiate through 2 successive molts. The first molt gives rise to the presoldier, the second to the final soldier.

In non molting workers, no frontal gland is visible inside the cephalic capsule. In workers molting into presoldiers (Figs. 3, 4), just before the ecdysis, a vesicle containing flocculent material is differentiated just above the brain, posteriorly to the attachment of the tentorial-fontanellar muscles. This spherical vesicle of 100–200 µm in diameter has a monolayered epithelium of 20–30 µm in thickness. It is not clearly related to the epidermis. However, there is a thinning of the glandular wall near the fontanelle area and some cells are present between the glandular epithelium and the epidermis.

In presoldiers (Figs. 5, 6), this glandular vesicle is enlarged by epithelial mitoses and becomes ovoid. Just before the molting of the presoldier into soldier, the vesicle migrates into the thorax and the abdomen where it has a dorsal position in relation to the digestive tract (Figs. 7, 8).

In the young soldier (Figs. 9, 10), it occupies its final place in the thorax and the abdomen. There, it progressively enlarges due to the secretion and the accumulation of the defensive liquid. The epithelium grows by stretching and flattening of the cells. The glandular wall is in intimate contact with the integument, especially in the area of the sternal thoracic area where the rupture of the soldier body occurs because of the contraction of the abdominal muscles.

Discussion

The defensive gland of *Globitermes sulphureus* soldiers is an unpaired dorsal hypertrophied gland which is mainly located in the abdominal cavity. This gland does not open to the outside. It is very similar to that of *Serritermes serrifer* soldiers which has also been interpreted as a frontal gland by Costa-Leonardo and Kitayama (1991). The frontal gland of termite soldiers is a defensive exocrine gland which has no equivalent in other insects, it is an invagination of the cephalic epidermis of the median frontal region at the level of the fontanelle (Noirot, 1969). Its development greatly varies according to the species. It often appears as a small spherical vesicle entirely located in the cephalic capsule and opening to the outside by a frontal pore. However, it may take up almost the entire body of the soldier as in many species of Rhinotermitidae (Quennedey, 1984; Prestwitch, 1984). This last situation is observed in *Serritermes serrifer* and *G. sulphureus*, the main difference being the absence of any frontal pore. However, in *G. sulphureus*, the cells observed in the presoldier between the frontal vesicle and the cephalic epidermis probably represent vestigial cells of the frontal invagination. Moreover, our study clearly shows that the defensive gland of *G. sulphureus* is a frontal gland which undergoes an actual metamorphosis during the presoldier stage. From a small spherical frontal vesicle linked to the cephalic epidermis at the beginning of the stage, it becomes a blind hypertrophied reservoir migrating in the abdominal cavity at the end of the presoldier stage. This perfectly illustrates the possibilities of anatomical differentiations allowed by the

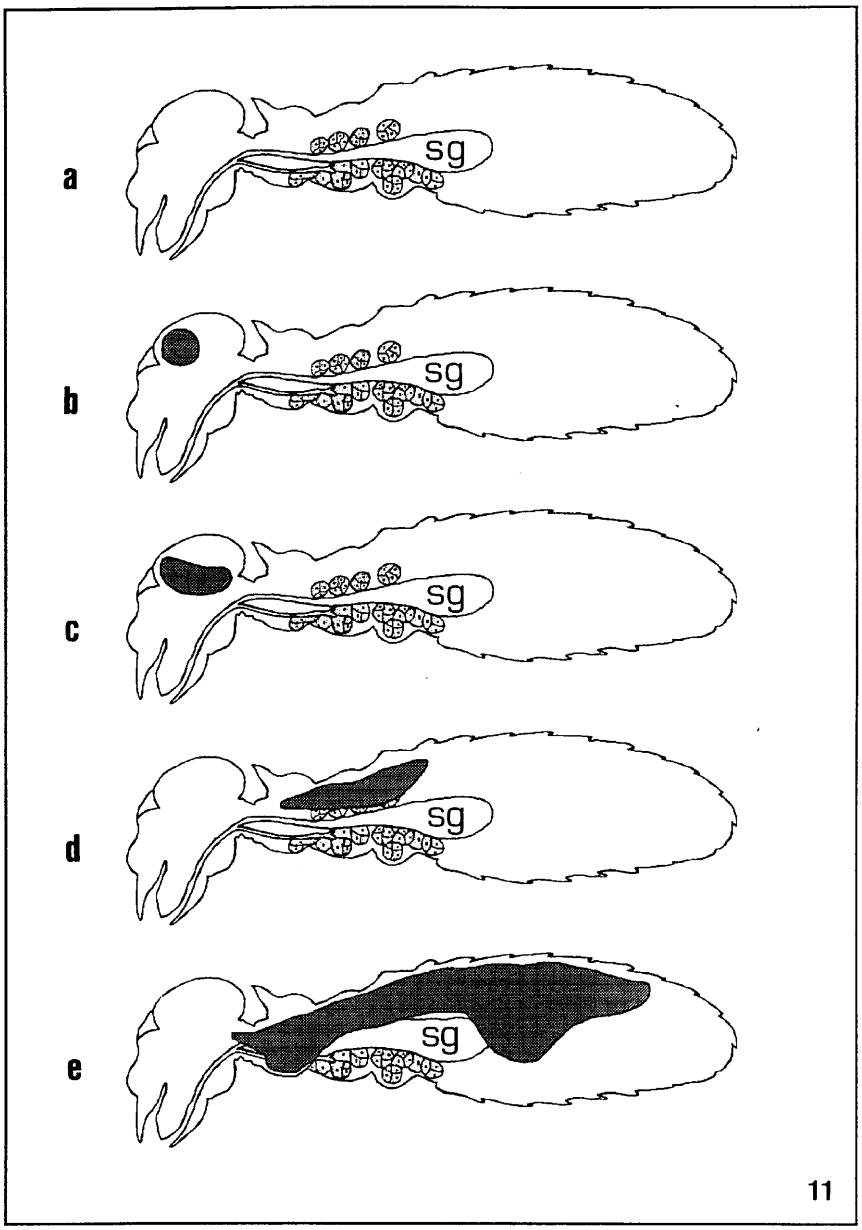


Figure 11. Sketches summarizing the differentiation of the defensive gland (in grey) of soldiers in *Globitermes sulphureus* (sg: salivary glands). a: Worker stage from which is developing the presoldier, b: Worker molting into presoldier, c: Presoldier, d: Presoldier molting into soldier, e: Soldier.

development of termite soldiers. It is clear that the presoldier stage which could be compared to the nymph of holometabolous insects (Deligne, 1970) is at the origin of the high evolutive diversity of the termite soldiers from a morphological point of view, as well as from a biochemical or a behavioural one (Noirot, 1990).

From a functional point of view, the frontal gland of termites is known to be a defensive gland whose secretion acts against the enemies either toxically or physically (Deligne et al., 1981; Prestwich, 1984). This secretion is often released through the frontal pore thanks to the action of the mandibular muscles which compress the glandular walls (Noirot, 1969; Deligne, 1970). In the species of Rhinotermitidae with a hypertrophied frontal gland extending into the abdomen, the defensive secretion is ejected by the contraction of the abdominal muscles. The same mechanism is observed in *G. sulphureus*. However, because of the absence of a frontal pore, the defensive secretion only exudes after the rupture of the glandular wall and the integument. This behaviour was observed in the ant *Camponotus saundersi* by Maschwitz and Maschwitz (1974) who coined the term autothysis for such a mechanism. In *G. sulphureus*, the exudation consists of a slow flow of the defensive secretion which accumulates as a droplet at the inner face of the head capsule. The expressions of "walking bomb" used by Oster and Wilson (1978) or "exploding termites" by Mill (1984) appear therefore exaggerated. The comparison with the Bre'r Rabbit's "Tar-baby" effect (Sands, 1982) is more judicious, as the predatory ants trying to catch the exuding soldiers are immediately entangled with the sticky termite. The chemical analysis of this special defensive secretion is now in progress.

G. sulphureus and *S. serrifer* are the only known examples until now of altruistic defense by autothysis due to the dehiscence of the frontal gland of soldiers. But other examples of soldier autothysis have been reported in many species of neotropical termites, such as in *Dentispicotermes*, *Genuotermes* and *Orthognathotermes* (Mathews, 1977; Mill, 1984). They are believed to be involved with the dehiscence of salivary glands. However, the descriptions given by the authors are close to what is observed in *G. sulphureus* and *Serritermes serrifer*. Their soldiers possess long thin mandibles of the reaping type (Deligne, 1971; Deligne and Quennedey, 1977) and have a defensive gland extending into the thorax and the forepart of the abdomen. The defensive secretion is a yellow liquid that coagulates rapidly into a gummy, rubbery consistency in the air. The line of rupture is located either laterally in front of the abdomen or even, in *Orthognathotermes*, between the forecoxae as in *G. sulphureus* (Mathews, 1977; Mill, 1984). So, it would be very useful to reinvestigate the precise origin of the defensive gland in these species. The examples of *G. sulphureus* (Termitidae) and that of *S. serrifer* (Rhinotermitidae) at least, and possibly those of neotropical Termitinae show that suicidal defensive strategy by soldiers is polyphyletic in termites.

A similar mechanism of autothysis involving the sacrifice of the individual for the benefit of the society is known in the workers of several species of the soldierless Apicotermitinae *Grigiotermes* and *Ruptitermes* (Mathews, 1977; Sands, 1982; Mill, 1984). According to Sands (1982), this worker caste autothysis would be the most effective of all forms of termite defense. It could even surpass the chemical defense of soldiers of Rhinotermitidae and Nasutitermitinae, since isolated individuals are able to block the narrow galleries penetrating inside the nest, and since the one-for-one exchange in the fights implied a high energy cost to predators. The

defensive strategy developed by *G. sulphureus* appears still more efficient as the soldier autothysis is only one of the components of this defense, the soldiers being able to use their mandibles to fight their opponents without suicidal behaviour and also to emit an alarm pheromone recruiting congeners on the site of the fights (Robert et al., 1995). This multi-defensive strategy probably is a key element of the ecological success of *G. sulphureus* in Southeast Asia.

Acknowledgements

The study was supported with funds of the French Ministry of Foreign Affairs, the Vietnamese Ministry of Water Resources and the United Nations Development Programme, Hanoï (Project VIE 94/016 – Bio-ecology and Control of Termites in Vietnam). We would especially like to thank Prof. C. Noirot for his helpful comments on the manuscript and Mrs E. Mc Lellan for linguistic revision.

References

Bathellier, J., 1927. Contribution à l'étude systématique et biologique des Termites de l'Indo-Chine. *Faune colonies françaises 1*:125–365.

Costa-Leonardo, A.M. and K. Kitayama, 1991. Frontal gland dehiscence in the brazilian termite *Serritermes serrifer* (Isoptera: Serritermitidae). *Sociobiology 19*:333–338.

Deligne, J., 1970. Thèse Sciences, Université de Bruxelles, Belgique, 424 pp.

Deligne, J., 1971. Mécanique du comportement de combat chez les soldats de termites (Insectes Isoptères). *Forma et Functio 4*:176–187.

Deligne, J. and A. Quennedey, 1977. Morphological approach to defensive mechanisms in Termites. Proc. VIII Int. Congr. IUSSI, Wageningen.

Deligne, J., A. Quennedey and M.S. Blum, 1981. The enemies and defense mechanisms of Termites. In: *Social Insects*, Vol. 2, (H.R. Hermann, Ed.), New-York, Academic Press, pp. 1–76.

Maschwitz, U. and E. Maschwitz, 1974. Platzende Arbeiterinnen: Eine neue Art der Feindabwehr bei sozialen Hautflüglern. *Oecologia Berlin 14*:289–294.

Mathews, A.G.A., 1977. Studies on Termites from the Mato Grosso State, Brazil. Acad. Bras. Cienc. ed., Rio de Janeiro, 267 pp.

Mill, A.E., 1984. Exploding termites – An unusual defensive behaviour. *Ent. Mont. Mag. 120*: 179–184.

Noirot, C., 1959. Les nids de *Globitermes sulphureus* Haviland au Cambodge. *Insectes soc. 6*:259–268.

Noirot, C., 1969. Glands and secretions. In: *Biology of Termites* (K. Krishna, F.M. Weesner, Eds.), New-York, Academic Press,Vol. I, pp. 89–123.

Noirot, C., 1990. La caste des soldats chez les termites: originalité, évolution. *Actes Coll. Insectes Sociaux 6*:21–26.

Oster, G.F. and E.O. Wilson, 1978. *Caste and ecology in the social insects.* Princeton University Press, New Jersey, USA, 352 pp.

Prestwich, G.D., 1984. Defense mechanisms of termites. *Ann. Rev. Entomol. 29*:201–232.

Prestwich, G.D., 1988. Chemicals of termites societies. *Sociobiology 14*:175–186.

Quennedey, A., 1984. Morphology and ultrastructure of termite defense glands. In: *Defensive Mechanisms in Social Insects*, (H.R. Hermann, Ed.) New-York, Praeger Press, pp. 151–200.

Robert, A., V. Van Tuyen and C. Bordereau, 1995. Stratégies défensives chez *Globitermes sulphureus*. *Actes Coll. Insectes Sociaux 10*:165–168.

Sands, W.A., 1982. Agonistic behavior of African soldierless Apicotermitinae (Isoptera, Termitidae). *Sociobiology 7*:12–17.

Received 27 February 1997;
revised 20 May 1997;
accepted 30 May 1997.