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Suicidal defence through a dehiscent frontal weapon in *Apilitermes longiceps* soldiers (Isoptera: Termitidae) *

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Abstract

Within the '*Cubitermes*-group' of Termitinae, the genus *Apilitermes* presents an atypical frontal weapon. Despite a well-developed frontal gland, the frontal pore is very small and probably non-functional. On the basis of occasional field observations as well as morphological studies and dissections of many museum specimens, we show that these soldiers use autothysis of the frontal gland as a suicidal defence mechanism. When attacked, they suddenly cross their mandibles while their frontal integument cracks along a median cleft. At the same time, the thin dorsal wall of the frontal gland is torn open, allowing the frontal defensive secretion to be poured out towards the enemy. During this action, the soldier is mortally wounded. The defensive breaking of the head in 'kamikaze' termite soldiers is recorded here for the first time. It provides a spectacular new example of extreme altruistic behaviour in this caste of social insects.

Keywords: autothysis, frontal gland, African termite.

Introduction

The monospecific genus *Apilitermes* Holmgren belongs to the Afrotropical '*Cubitermes*-group' of Termitinae, which contains a total of 26 genera and 163 species (KAMBHAMPATI & EGGLETON, 2000). This natural line of humivorous termites is defined notably by anatomical features of the workers' alimentary canal (NOIROT, 2001; BITSCH & NOIROT, 2002).

In this group, soldiers' weapons always consist in long mandibles either of the biting or the reaping type (DELIGNE *et al.*, 1981) and a well-developed

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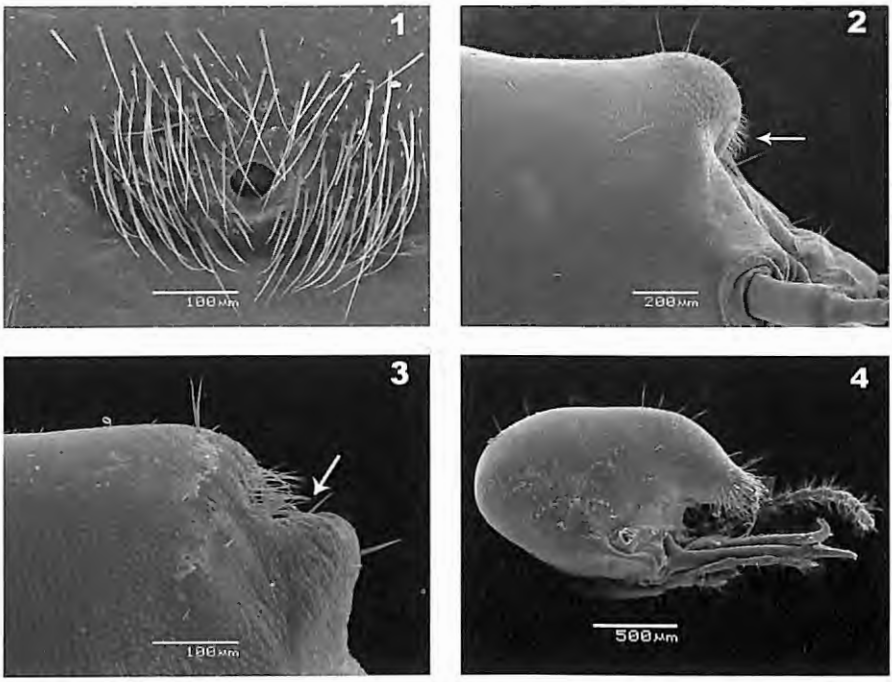


Figs 1-4. Typical soldiers of the '*Cubitermes*-group' (SEM micrographs). – Fig. 1. *Thoracotermes macrothorax*: detail of the frons showing the tuft of hairs surrounding the frontal pore. – Fig. 2. *Furculitermes* sp.: anterior part of the head showing the tuft of hairs and the marked frontal hump overhanging the frontal pore (arrow). – Fig. 3. *Orthotermes mansuetus*: anterior part of the head showing the frontal tuft of hairs, the 'cupule' (arrow) and the steep slope of the frons. – Fig. 4. *Proboscitermes tubuliferus*: profile of the head showing the hairy 'proboscis'.

frontal gland, whose secretions have been studied in three genera (*Cubitermes*, *Crenetermes* and *Noditermes*). The main chemicals identified consist in relatively non-volatile non-polar oily hydrocarbons, which appear to act as antihealants and/or irritants against ants (PRESTWICH, 1984, 1988). As a general rule, the pore of the gland is associated with characteristic features of the head, which may vary from one genus to another.

In 23 genera (amounting to 160 described species), a tuft of long curved hairs overhangs the frontal pore and flanks it on both sides (Fig. 1). In these genera, the frontal pore is generally situated under a marked frontal hump and above a steep anterior part of the frons, with a slope of 40° or more (Fig. 2). Furthermore, in some instances (e.g. *Orthotermes*), the frontal pore opens in a frontal 'cupule', i.e. a cup-shaped depression of the frons where the frontal secretion flows before being poured forth (Fig. 3). In *Proboscitermes* and *Unicornitermes*, the frontal pore opens at the extremity of a prominent frontal tube know as the 'proboscis' (Fig. 4).

In two other monospecific genera (*Mucrotermes* and *Forficulitermes*), the tuft of hairs is reduced but the frontal cupule is well developed.

So, in all these 25 genera, the frontal pore is accompanied by a tuft of hairs and/or specialised contours of the head, which most probably help to control the flow of its defensive secretion and to direct it against an enemy. Such devices strongly suggest that the frontal pore is in fact functional.

Within the '*Cubitermes*-group' of genera, *Apilitermes longiceps* (SJÖSTEDT) clearly appears to be an exception. Despite a well-developed frontal gland, their soldiers are deprived of any long hairs around the frontal pore (hence the name *A-pili-termes*) or of any of the features mentioned above for the other genera. Furthermore, the published descriptions are contradictory, as the frontal pore itself is either considered to be lacking (SJÖSTEDT, 1899, 1900) or minute and situated on the horizontal part of the head (HOLMGREN, 1912).

We therefore tried to understand the functioning of this atypical frontal weapon on the basis of field observations as well as morphological studies and dissections of museum specimens.

Materiel and methods

Occasional field observations took place in March 1962 in a secondary forest near Makokou (Gabon) on a few living soldiers of *Apilitermes longiceps* (SJÖSTEDT, 1899) found in superficial soil galleries.

The morphological studies are mainly based on 16 samples of *A. longiceps*, each containing at least a dozen of soldiers. The samples were mainly collected in Congo and are kept in the 'Albert BOUILLON collection' of the Royal Museum for Central Africa.

General examination and dissection of the specimens took place under a stereomicroscope. As regards dissection, the dorsal cuticle of the head was incised with micro-scissors and peeled off with fine forceps without touching or disturbing the internal organs.

Specimens observed with a scanning electron microscope (SEM) went through standard steps of serial ethanol dehydration and were subsequently treated with hexamethyl-disilazane. Specimens were then air-dried and covered with a 9 nm gold film in a Jeol JFC-1300 auto fine coater.

Photo-micrographs and SEM-micrographs were taken with a Leica stereomicroscope and a Jeol 6480 LV SEM respectively.

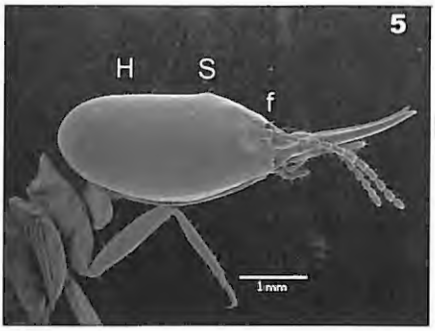
Field observations

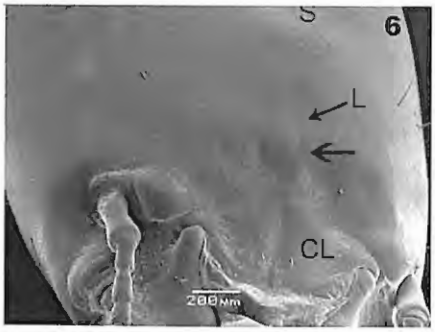
During field termite collecting, one of us (JD) observed an unusual defensive behaviour of *Apilitermes* soldiers. When gently seized with forceps, they suddenly crossed their mandibles while their frontal integument cracked along a median cleft, releasing a translucent liquid.

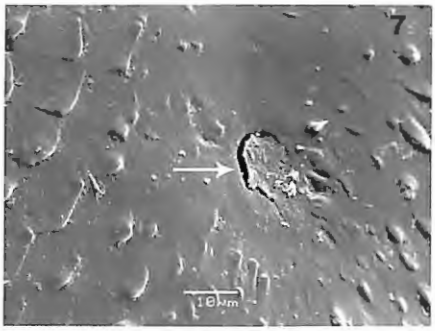
Due to a lack of living material, these field observations were not continued, but they incited us to conduct a close study of preserved specimens.

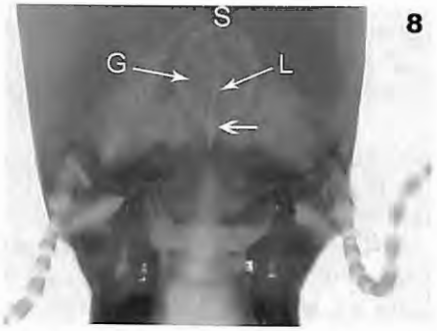
Morphological results

In all the examined samples of *Apilitermes longiceps*, we found two categories of soldiers: those with intact heads and those with a more or less pronounced crack along the frons.









Figs 5-7. Intact soldiers of *Apilitermes longiceps* (SEM micrographs). – Fig. 5. Profile of the head showing its 'horizontal' part (H), its summit (S) and the gentle slope of the frons (f). – Fig. 6. Front view of the frons showing the summit of the head (S), the frontal pore (arrow) and, between them, the smooth and slightly hollowed longitudinal band (L). Postclypeus = CL. – Fig. 7. Detail of the frons showing the very minute frontal pore blocked up by a dense material (arrow).

Fig. 8. Intact soldier of *Apilitermes longiceps*: photo-micrograph of the frons showing the summit of the head (S), the longitudinal band or 'yellow line' (L), the position of the frontal pore (arrow) and the frontal gland (G) observed through the cuticle.

A. All intact soldiers were found in collections with their mandibles open or directed forwards, or only slightly crossed. On the basis of these soldiers, we can be more precise about or correct previous descriptions, particularly regarding the five following points.

(1) In its rear 'horizontal' part, the head shows a slightly sinuous dorsal profile (Fig. 5). It culminates forward in a small rounded summit with a rough granular surface. A close examination with the scanning electron microscope shows that there is nothing resembling a frontal pore in that part of the head. Instead, a few very small orifices (measuring about 0.5 μm in diameter) are scattered on the whole surface of the integument. They clearly correspond to the openings of dermal glands.

(2) From the summit of the head, the frons slopes down gently (Fig. 5). It joins the 'horizontal' part of the head at an angle of about 30°. Like the rest of the head, it is very sparsely setose.

(3) A frontal pore is definitely present on the anterior part of the frons (Figs 6-7). It is twice as far from the summit of the head as from the postclypeus. This frontal pore is indeed very minute, measuring about 9 μm in diameter. It always appears blocked up by a dense material. There are no hairs in its immediate vicinity.

(4) From the summit of the head up to the frontal pore, the cuticle shows a smooth and slightly hollowed longitudinal band, contrasting with the more convex and scaly adjacent zones (Fig. 6). With the usual magnification of a stereomicroscope (x 100), this longitudinal band appears as a diffuse yellow line, while the frontal pore is difficult to discern, appearing as a little brownish spot in the distal part of this yellow line (Fig. 8).

(5) The frontal gland itself can easily be observed through the cuticle (Fig. 8) or in dissections (Fig. 12). In intact soldiers it is egg-shaped and quite well developed, measuring about 470 μm in width (i.e. about one-fourth of head width) and 540 μm in length (i.e. about one-fifth of head length).

B. Soldiers with a cracked frons were all fixed with their mandibles strongly crossed. These wounded soldiers show the following features:

(1) The frons is cracked along a line running at least from the summit of the head to the frontal pore, i.e. along the 'longitudinal band' or 'yellow line' already observed in intact soldiers (Fig. 9). Furthermore, it is generally creased along a transverse line halfway between the summit of the head and the frontal pore. The clypeus itself is often cleft open. In some cases, a long continuous cleft runs from the summit of the head up to the labrum (Fig. 10).

(2) Internal tissues are exposed and often spread out. In many specimens, the cuticle of the whole frons shows remains of spread-out tissues and liquids (Fig. 10).

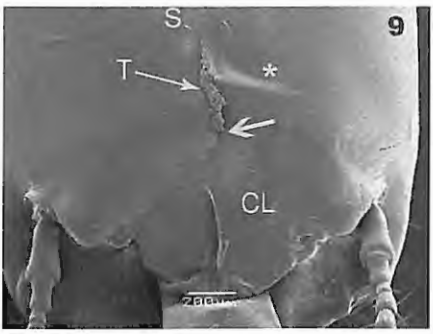
(3) In soldiers with a cracked frons, dissections confirm that the frontal gland was compressed and its dorsal wall torn open, thus allowing its secretion to be poured out (Fig. 11). By contrast, in the dissections of intact soldiers, the frontal gland is still well rounded and unhurt (Fig. 12).

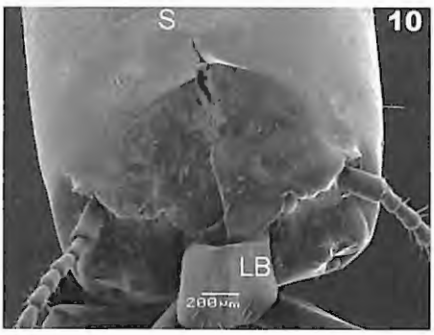
Discussion and conclusion

Contrary to SJÖSTEDT's statement, there is indeed a frontal pore on the head of *Apilitermes* soldiers, but contrary to HOLMGREN's description, this pore is situated on the front sloping part of the head at two-thirds of the distance between the summit of the head and the postclypeus.

The frontal pore is very small and devoid of any features such as hairs, a hump, a cupule, etc. It is probably non-functional or, at best, poorly efficient.

This defect is compensated by the dehiscence of the frontal weapon. In a close combat with an enemy, when the soldier strongly crosses its mandibles, its frons cleaves open along a definite line and the thin dorsal wall of the frontal gland is torn open, allowing the frontal defensive secretion to be poured out towards the enemy. During this action, the soldier is of course mortally wounded.





Figs 9-10. Wounded soldiers of *Apilitermes longiceps* (SEM micrographs). – Fig. 9. Front view of the head showing the frontal crack running from the summit of the head (S) to the frontal pore (arrow), a transverse frontal crease (asterisk) and a longitudinal crack through the postclypeus (CL). Internal tissues (T) are spread out. – Fig. 10. Front view of the head showing a long continuous cleft running from the summit of the head (S) up to the labrum (LB). The cuticle shows remains of spread-out tissues and liquids.

Figs 11-12. Dissected soldiers of *Apilitermes longiceps* (photo-micrographs). – Fig. 11. Wounded soldier: dissected head showing the compressed and torn-open frontal gland (arrow). – Fig. 12. Intact soldier: dissected head showing the egg-shaped and unhurt frontal gland (arrow).

A plausible evolution scenario is that a dehiscence line first appeared on the frons of soldiers and proved to be more efficient than the frontal pore which, as a consequence, progressively regressed and lost its typical tuft of hairs and

nearby specialised contours of the head. As is the case for other types of 'altruistic' behaviour, this suicidal defence mechanism of soldiers was probably selected in the course of evolution because it contributed to protecting the other individuals of the society and in particular the reproductives, which transmit the soldiers' genes to the next generation.

Defensive dehiscence of integument has already been documented in social insects. MASCHWITZ & MASCHWITZ (1974) coined the word 'autothysis' to describe this type of self-sacrificing mechanism, which they found in some *Camponotus* species (Formicinae). They applied the same term to designate the defensive manoeuvre of honeybee workers (Apinae), which possess a barbed sting that remains embedded when the insects pull away from their victim, causing part of their viscera – including the poison gland – to be torn out, and the bees to be fatally injured (SAGAKAMI & AKAHIRA, 1960). A similar defensive behaviour occurs in many polybiine wasps (WILSON, 1971).

As for termites, autothysis has appeared in a convergent way in different systematic groups and in both worker and soldier castes.

In termite workers, abdominal dehiscence was first reported by SANDS (1972, 1982) in one or more species within 10 soldierless African genera of Apicotermitinae. This dehiscence causes the gut and its offensive contents to burst out of the abdominal integument of the worker and to be scattered. A similar abdominal dehiscence has been observed by MATHEWS (1977) in *Ruptitermes*, a Neotropical soldierless genus of Apicotermitinae. In this genus however, the offensive liquid emitted comes from ruptured paired 'dehiscent glands' localised laterally between the metathorax and the first abdominal segment (COSTA-LEONARDO, 2004).

In termite soldiers, defence through dehiscence of thoracic or abdominal integument involving salivary reservoirs is mentioned by MILL (1974) in some Termitinae of the '*Amitermes*-group'. Two cases of dehiscence are well documented. They both involve the frontal gland and not the salivary reservoirs as thought by earlier authors (among whom JOHN, 1925 and BATHELLIER, 1927). They concern the thoracic dehiscence of *Globitermes* soldiers (Termitinae of the '*Amitermes*-group') described by BORDEREAU *et al.* (1997) and that of *Serritermes* soldiers (Serritermitidae) described by COSTA-LEONARDO & KITAYAMA (1991).

In this context, the data presented here on *Apilitermes* are interesting in at least two respects. They describe the first known example of autothysis within the '*Cubitermes*-group' of Termitinae. Moreover, they evidence the only case, to our knowledge, in which the defensive behaviour of 'kamikaze' termite soldiers involves the breaking of their heads.

Acknowledgements and dedication

We are most grateful to Mr Eddy TERWINGHE for his technical help in photographic data processing and to Ms Jane CORRIGAN for her help in the revision of the English manuscript.

This work is dedicated to the memory of Professor Albert BOUILLON (1916-2005), who made substantial contributions to African termitology and bequeathed a termite collection of the greatest importance to the Royal Museum for Central Africa.

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