

A novel exocrine structure of the bicellular unit type in the thorax of termites

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Abstract

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Studying the thorax of some Termitidae species, we found two pairs of hitherto unknown lateral glands in the mesothorax and metathorax of both workers and soldiers. The glands consist of distinct clusters of class 3 secretory cells accompanied by their duct cells, located in the upper lateral portion of the thoracic wall. Ultrastructural observations reveal numerous mitochondria, a well-developed Golgi apparatus and vesicular smooth endoplasmic reticulum, indicating a cytoplasm with intensive metabolic activity. The gland is reported to occur in *Microcerotermes strunckii*, *Cornitermes cumulans* and *Nasutitermes minor*, three species comprising an interesting morpho-behavioural gradient, respectively, from only mechanical, through mechanical–chemical, to only chemical defence systems. The extent of such a gradient allows speculations that this gland would be related to the general needs of termites, rather than to some specificities of a single group. We warn, however, that complementary studies are needed, before any conclusions can be drawn.

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Introduction

The fascinating life of social insects has long attracted human attention. One of the characteristics of these insects is the amazing development of their exocrine system, the secretions of which play an essential role in many aspects of social life (Billen 2006). Among the social insects, however, it is surprising to see the relatively limited number of exocrine glands that have been described in termites, compared with the considerably higher variety of the exocrine system in the social Hymenoptera. Termites can have a total of 17 glands (Table 1), while approximately 70 glands form the overall exocrine repertoire of ants. A possible reason for this may be found in differences in the communication system between both groups: social Hymenoptera rely to a very considerable extent on pheromonal substances [and hence possess the glandular equipment for producing these (Billen and Morgan 1998)], whereas in termites acoustic signals can play an important role (Kirchner *et al.* 1994; Röhrig *et al.* 1999; Evans *et al.* 2007). The lower number of exocrine glands in the termites is definitely not the result of a lack of attention,

as several termitologists have produced extensive and thorough studies on the isopteran exocrine apparatus (e.g. Pasteels 1965; Noirot 1969; Noirot and Quennedey 1974, 1991; Deligne *et al.* 1981; Leis and Sbrenna 1983; Sbrenna and Leis 1983; Quennedey 1984, 1998; Costa Leonardo and De Salvo 1987; Costa Leonardo 1994, 2004; Soares and Costa-Leonardo 2002; Sobotnik *et al.* 2003; Quennedey *et al.* 2004, 2008). As a result, finding novel glands in termites does not happen often. Studying the thorax of some Termitidae species, however, we found two pairs of hitherto unknown lateral glands in the mesothorax and metathorax of both workers and soldiers, that we here describe as a 17th exocrine structure of termites.

Materials and Methods

The termite species investigated here are *Cornitermes cumulans* (Kollar), *Microcerotermes strunckii* (Sörensen) and *Nasutitermes minor* (Holmgren). The *M. strunckii* specimens were collected in Sete Lagoas, MG, Brazil; *C. cumulans* and *N. minor* specimens were collected in Viçosa, MG, Brazil.

Table 1 Survey of the known exocrine glands of termites, listed from head to abdomen, with indication of the cellular organization according to the classification of Noirot and Quennedey (1974), and corresponding references. For the dehiscent gland, no precise information about its class allocation is available

	Gland	Class	References
1	Epidermal tegumental glands	1	Sobotnik <i>et al.</i> , 2003
2	Bicellular unit tegumental glands	3	Leis and Sbrenna, 1983; Sbrenna and Leis, 1983; Sobotnik <i>et al.</i> , 2003
3	Frontal gland	1,3	Noirot, 1969; Deline <i>et al.</i> , 1981; Costa Leonardo and De Salvo, 1987
4	Labral gland	3	Mao and Henderson, 2006
5	Cibarial gland	1	Quennedey, 1984
6	Mandibular base gland	3	Quennedey, 1984
7	Mandibular gland	3	Noirot, 1969
8	Labial (salivary) gland	1	Pasteels, 1965; Noirot, 1969
9	Tarsomere glands	3	Bacchus, 1979; Soares and Costa-Leonardo, 2002
10	Tibial gland	3	Bacchus, 1979; Soares and Costa-Leonardo, 2002
11	Lateral thoracic glands	3	this article
12	Dehiscent gland	?	Costa-Leonardo, 2004
13	Tergal glands	1,2,3	Noirot, 1969; Wall, 1969; Quennedey, 1975; Ampion and Quennedey, 1981; Bordereau <i>et al.</i> , 2002
14	Sternal glands	1,2,3	Pasteels, 1965; Noirot, 1969; Quennedey, 1975; Quennedey <i>et al.</i> , 2008
15	Posterior sternal glands	3	Quennedey <i>et al.</i> , 2004, 2008
16	Spermathecal gland	3	Costa Leonardo and Patricio, 2005; Raina <i>et al.</i> , 2007
17	Pleural abdominal glands	3	Ampion, 1980

Head–thorax and thorax portions of worker specimens of the three species were fixed in cold 2% glutaraldehyde, buffered at pH 7.3 with 50 mM sodium cacodylate and 150 mM saccharose. Also, the thorax of *M. strunckii* and *N. minor* soldiers was studied. Post-fixation was performed in 2% osmium tetroxide in the same buffer, followed by dehydration in a graded acetone series. Tissues were embedded in Araldite and sectioned with a Reichert OmU2 microtome. Semi-thin sections of 1 µm were stained with methylene blue and thionin and viewed in an Olympus BX-51 microscope. Double-stained thin sections of 70 nm thickness were examined in a Zeiss EM900 electron microscope. Workers and soldiers of *M. strunckii* were also prepared for scanning electron microscopy, the individuals were critical-point dried using a CPD 030 instrument. The dried samples were mounted on aluminium stubs using Leit-C and coated with gold with a SPI-Module™ Sputter Coater. Images were obtained with a Jeol JSM-6360.

Results

Semi-thin transverse sections through the thorax of both workers and soldiers of *M. strunckii* and *N. minor* and of *C. cumulans* workers show an obvious paired glandular structure, located in the upper lateral portion of both the mesothorax and metathorax, just below the mesonotum and metanotum, respectively (Fig. 1A).

Each of these four novel lateral thoracic glands consists of a distinct cluster with an estimated number of approx. 100 glandular units. Among the studied species, the size of the gland varies in the mesothorax and metathorax. The thickness in the mesothorax varies from 15 to 40 µm for

M. strunckii, it measures approx. 20 µm in *N. minor* and approx. 35 µm in *C. cumulans*. In the metathorax, the thickness varies from 10 to 30 µm for *M. strunckii*, from 10 to 25 µm for *N. minor* and is approx. 20 µm for *C. cumulans*. The width (in dorsoventral direction) in the mesothorax ranges from 80 to 120 µm for *M. strunckii*, from 35 to 60 µm for *N. minor* and is approx. 80 µm for *C. cumulans*. In the metathorax, the width varies from 100 to 140 µm for *M. strunckii*, from 85 to 140 µm for *N. minor* and is approx. 200 µm for *C. cumulans*. The length (in anterior/posterior direction) for *M. strunckii* ranges from 180 to 190 µm in the mesothorax and from 100 to 200 µm in the metathorax.

Scanning electron microscopy (Fig. 1B,C) of workers and soldiers of *M. strunckii* revealed the presence of numerous pores with a diameter of approx. 0.5 µm, that occur on the entire surface of the lateral region of the thorax. Most pores occur on top of a small nipple-like elevation (Fig. 1C). Additionally, scanning electron microscopy revealed the presence of hairs associated with the cuticle covering the gland region (Fig. 1C).

At the cell level, the gland is formed by bicellular units according to class 3 in the standard classification of Noirot and Quennedey (1974). A transverse section of a lateral thoracic gland shows between 5 and 10 secretory cells (Fig. 2A). They have a diameter of approx. 10 µm and are characterized by rather pale and rounded nuclei with a diameter of approx. 5 µm. Between the secretory cells are duct cells that contain a dark and more irregularly shaped nucleus that occupies nearly the entire duct cell volume (Fig. 2A). The secretory cell contains an end apparatus with a central cuticular duct, surrounded by irregular microvilli (Fig. 2B). In the cytoplasm surrounding the end apparatus, we find

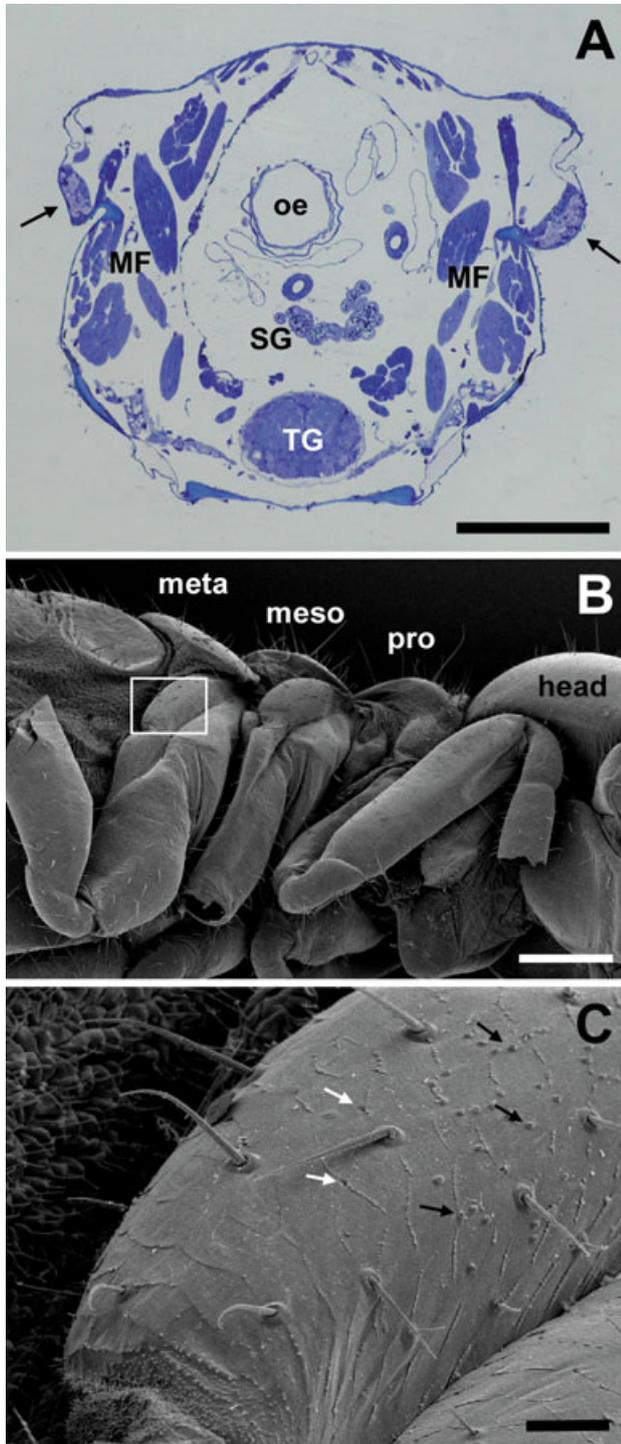


Fig. 1—**A.** Transverse semi-thin section through the mesothorax of a *Microcerotermes strunckii* worker showing the position of the lateral thoracic glands (arrows). Scale bar 100 μm . MF, muscle fibres; oe, oesophagus; SG, salivary gland; TG, mesothoracic ganglion. —**B.** Scanning electron micrograph of the thorax of a *M. strunckii* worker, frame indicates position of lateral metathoracic gland.

numerous mitochondria, a well-developed Golgi apparatus and vesicular smooth endoplasmic reticulum (Fig. 2C). The cuticular ducts have a diameter of approx. 0.5 μm , and generally open as pores in the centre of the nipple-like elevations through the outer thoracic tegument (Fig. 2D,E).

The basic cell arrangement of both gland pairs does not differ among the studied species, neither between workers and soldiers. However, in all species, the metathoracic cell clusters present a more linear shape when compared with the mesothoracic glandular region, which is more ellipsoid in shape.

Discussion

The paired lateral glands in the mesothorax and metathorax of the termite species studied in this article represent hitherto unknown exocrine structures for this insect group (Table 1). In 1993, Costa-Leonardo described mainly dorsally occurring oenocyte clusters in the three thoracic as well as the various abdominal segments of soldiers of *C. cumulans* (Costa Leonardo 1993). Their clustered appearance much resembles that of the mesothoracic and metathoracic lateral glands we describe here, but the cellular organization is different. The general structural organization of the glands now described clearly corresponds with class 3 (Noirot and Quennedey 1974), with bicellular units each comprising a secretory cell and its accompanying duct cell. Secretory cells of this class 3 display the very characteristic end apparatus (which is a cuticular continuation of the duct cell, surrounded by a microvillar sheath), but which does not occur in oenocytes. In their 1991 paper, Noirot and Quennedey updated their 1974 pioneer paper by considering the oenocytes homologous with class 2 epidermal glands (Noirot and Quennedey 1991). The oenocyte clusters reported by Costa Leonardo (1993) in *C. cumulans* soldiers therefore may be similar to the glands we describe, but their assignment as class 3 exocrine glands seems to have been overlooked.

If the legs are not taken into account (Billen 2009), exocrine glands in the thorax of social insects are less numerous than in the head and abdomen. The salivary (= labial) gland in the prothorax is a common structure for all social insects, while the metapleural gland in the metathorax is found only in ants (Hölldobler and Engel-Siegel 1984). In ants of the genus *Diacamma*, a peculiar gland occurs inside the gemmae (Peeters and Billen 1991), that appear as vestigial wing buds of the mesothorax (Baratte *et al.* 2006). These gemmae, however, are structurally very different from the region of the thoracic lateral glands in termites.

Scale bar 200 μm . —**C.** Scanning electron micrograph detail of B, showing pores and hairs in the region of the metathoracic lateral gland of a *M. strunckii* worker. Some pores open through the flat cuticle (white arrows), but the majority open through the centre of the nipple-like elevations (black arrows). Scale bar 20 μm .

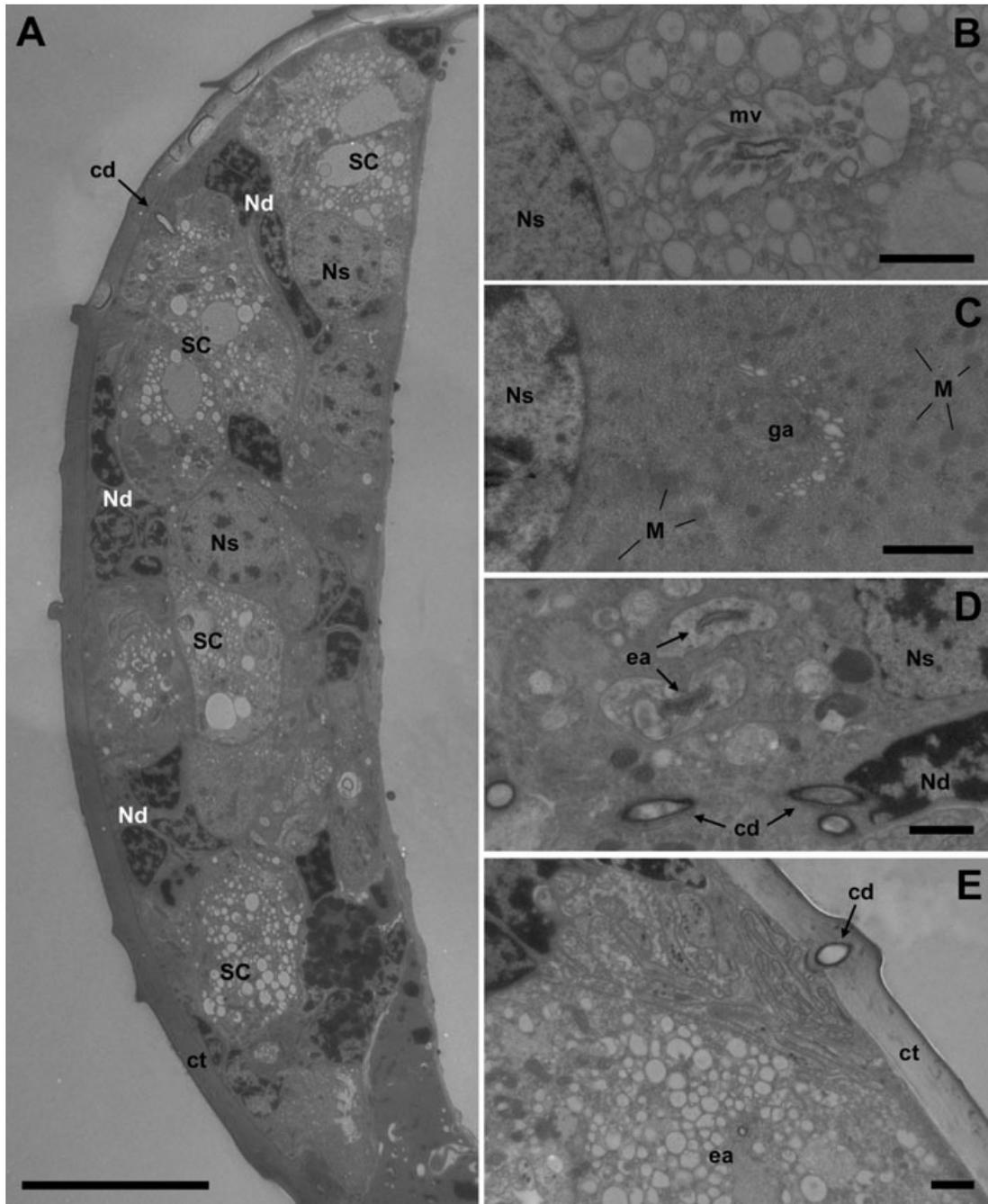


Fig. 2—**A.** Electron micrograph showing a transverse section through the mesothoracic lateral gland of a *Microcerotermes strunckii* worker, showing densely packed secretory cells (SC) and duct cells. Scale bar 10 μm . —**B.** Electron micrograph of end apparatus in mesothorax of *M. strunckii* soldier. Scale bar 1 μm . —**C.** Detail of cytoplasm in metathoracic gland cell of *Cornitermes cumulans* worker with Golgi apparatus (ga) and densely packed smooth endoplasmic reticulum. Scale bar 1 μm . —**D.** View of duct cells in metathorax of *M. strunckii* worker. Scale bar 1 μm . —**E.** Opening of duct cell on top of nipple-like elevation through tegumental cuticle in metathorax of *M. strunckii* worker. Scale bar 1 μm cd, cuticular duct; ct, cuticle; ea, end apparatus; M, mitochondria; mv, microvilli; Nd, nucleus of duct cell; Ns, nucleus of secretory cell.

Tegumental glands of the bicellular unit type (class 3 following Noirot and Quennedy 1974) with a scattered distribution over the body are known for ants (Gobin *et al.* 2003) and bees (Guerino *et al.* 2002), and have also been

reported for termites (Leis and Sbrenna 1983; Sbrenna and Leis 1983). In *Kaloterme flavicollis*, they occur in the head, thorax and abdomen as scattered single units or in groups of two or three (Sbrenna and Leis 1983), but without a specific

distribution pattern (Leis and Sbrenna 1983). This is in contrast with the two pairs of lateral thoracic glands that we describe here, as these represent very distinct clusters of class 3 glandular units, rather than clustered oenocytes (= class 2) as reported by Costa Leonardo (1993).

The two pairs of this novel gland have the same structural appearance, and are also similar in workers and soldiers. With a well-developed smooth endoplasmic reticulum and Golgi apparatus, the general ultrastructural organization of these novel lateral thoracic glands is in line with that of the tegumental glands in *Kaloterms flavicollis* (Sbrenna and Leis 1983) and with the subepithelial gland in ants (Gobin *et al.* 2003). This cytoplasmic composition of the secretory cells is indicative for a non-proteinaceous secretion.

The function of the lateral thoracic glands remains unknown, although the non-proteinaceous nature of the secretion may correspond with a pheromonal role. Termites do not rely as extensively as ants on chemical communication. However, chemical communication in termites is essential for the maintenance of their social life (Costa Leonardo 2006), including several aspects such as nest-mate recognition (Marins and DeSouza 2008), defence (Deligne *et al.* 1981; Quennedey 1984), and recruitment and resource exploitation (Reinhard *et al.* 1997; Reinhard and Kaib 2001). The presence of hairs and sensillae associated with the cuticle in the gland region may support the theory that the secretion produced by the lateral thoracic glands is involved in chemical communication, as these also have been reported to be associated with other termite glands involved in chemical communication, such as the sternal gland (Costa Leonardo 2006).

Alternatively, the non-proteinaceous secretions from these glands could contribute to the chemical profile of the cuticular surface, and hence play an important role in nest-mate recognition. In fact, nest-mate recognition supposedly through body-to-body contact (and hence sharing cuticular hydrocarbons), has been hypothesized to be the key for the survival of grouped individuals of *C. cumulans* (DeSouza *et al.* 2001) and *Nasutitermes aquilinus* (Miramontes and DeSouza 1996), a species and a genus reported here to possess these thoracic glands. However, a complementary study of the thoracic glands' function is needed for any further conclusions to be drawn.

Finally, it is worth noting that such glands are reported here for genera representing two very diverse subfamilies (Termitinae and Nasutitermitinae) inside the Neotropical Termitidae. Moreover, the three genera studied here comprise an interesting morphological gradient, from only mechanical (*Microcerotermes*), to a mixed chemical-mechanical (*Cornitermes*), and finally only chemical (*Nasutitermes*) defence apparatus. The extent of these diverse taxonomical and morpho-behavioural realms may indicate that such a gland is widespread in termites and that it would have a function related to the general needs of termites as a whole, rather than some function specific of a single group.

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