



SCIENTIFIC NOTE

THE POST-PHARYNGEAL GLAND IN *DINOPONERA* ANTS
(HYMENOPTERA : FORMICIDAE): UNUSUAL MORPHOLOGY
AND CHANGES DURING THE SECRETORY PROCESS

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(Accepted 16 October 1996)

Dinoponera australis and *D. quadriceps* belong to a genus which includes species possessing the largest known workers, and are also ants with vicious stings (Paiva and Brandão, 1995). Most reports on these large ants deal with their behaviour (Monnin and Dantas-de-Araujo, 1995; Paiva and Brandão, 1995). Morphological and ultrastructural data on *Dinoponera* are rare. A few papers dealing with antennal sensory organs are those by Caetano *et al.* (1989), on the pygidial gland by Billen *et al.* (1995), and on venom gland ultrastructure by Schoeters and Billen (1995).

The post-pharyngeal glands of ants are usually a pair of glove-shaped structures in the upper part of the head (Peregrine *et al.*, 1973). They are found only in the Formicidae (Delage-Darchen, 1976) and their function has been the subject of several, sometimes controversial, reports. The contents are usually described as a yellow oil and a series of chemical studies have been made. However, recently the chemical analysis of the glandular contents (Soroker *et al.*, 1995) has become important. The muscular arrangement near the gland opening (Schoeters, unpublished observations) is now being studied.

We have undertaken this study because the secretory cells, as seen under SEM, show an unusual organisation apparently similar to the kind of secretory cells that are usually referred to as type 3 (secretory cell and its corresponding duct cell) cells, according to Noirot and Quennedey (1974).

The ants *Dinoponera australis* and *D. quadriceps* were collected in Itirapina, São Paulo and Sergipe, Brazil, respectively. The post-pharyngeal glands were carefully dissected and cut into smaller pieces to allow penetration of 2% cold glutaraldehyde for fixation, buffered at pH 7.3 with 50 mM sodium cacodylate and 150 mM saccharose. After post-fixation in 2% osmium tetroxide in cacodylate buffer, the glands were block-stained in uranyl acetate

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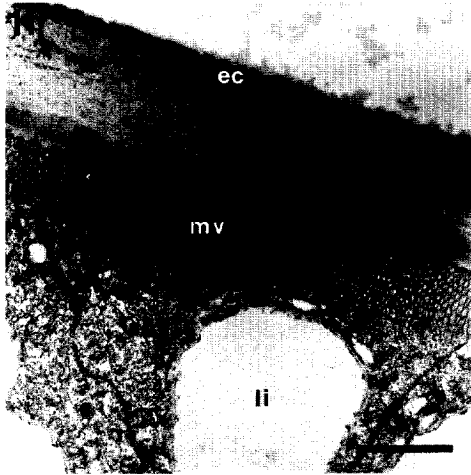
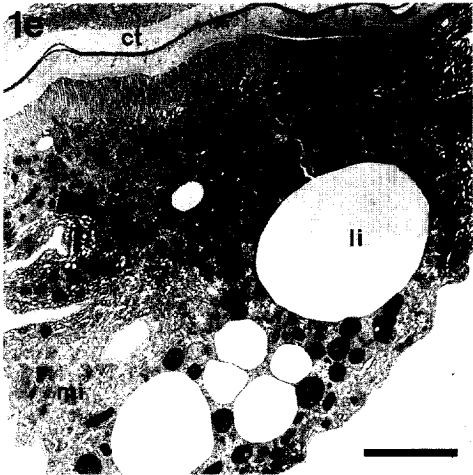
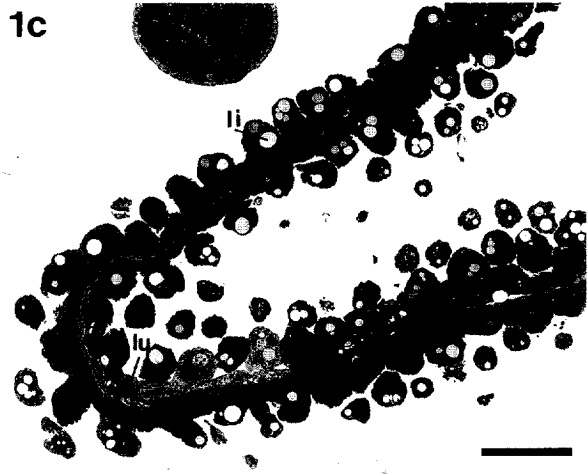
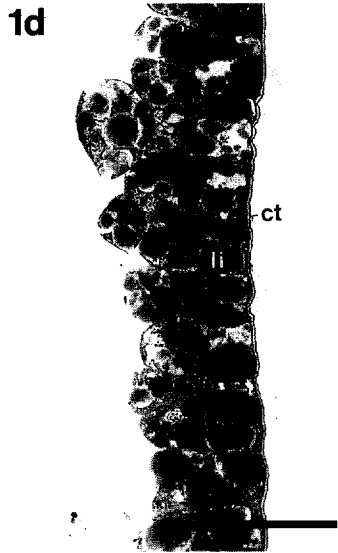
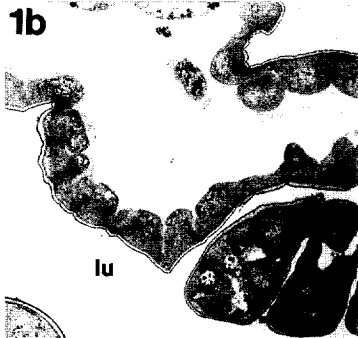
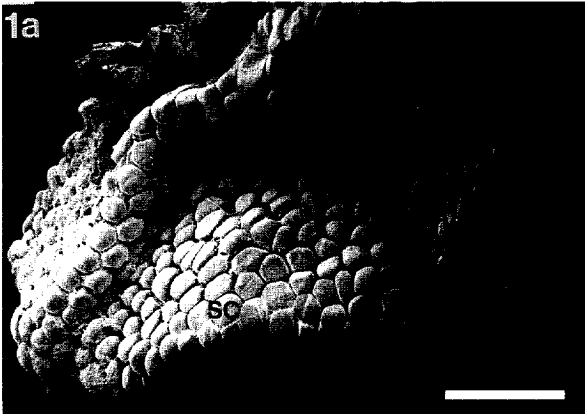
and dehydrated in a graded acetone series, followed by embedding in araldite. Semi-thin sections were stained with methylene blue and thionin.

In the majority of ant species, the post-pharyngeal gland consists of multitubular extensions. However, in *Dinoponera* (and in some other genera not the subject of this study), it is characterised by numerous glandular cells (glands are several mm wide) and corresponding flattened cuticular sacs extending in to the dorsal part of the head capsule. The post-pharyngeal gland of *Dinoponera* has no such multitubular appearance, as was previously described for some other ponerine species by Gama and Cruz Landim (1982) (*Odontomachus chelifer*, *Pachycondyla striata* and *P. villosa*). We observed an aberrant feature in this species, namely that the simple mono-layered epithelium usually found in other ants, consists of cells that form bulbous protrusions, clearly seen in SEM micrographs (Fig. 1a). They show an organisation apparently similar to the kind of secretory units, referred to as type 3 (Noirot and Quennedey, 1974, 1991). Type 3 cells look like a "cherry" (bicellular organisation with secretory cell and corresponding duct cell). In many cases, they occur scattered in association with the cuticle. If they are organised as groups, they look more like a "raspberry". The gland studied here is very unusual and, although it appears like a raspberry, a closer examination revealed unicellular bulbous epithelial cells, and certainly not like the type 3 cells. The cells possess no extracellular cavity and there is no direct connection by a duct or pore canal. Cell nuclei are rounded and excentric (Fig. 1b–d). The cytoplasm is characterised by a well-developed smooth endoplasmic reticulum and Golgi-apparatus.

The occurrence of lipid droplets shows an age-dependent development (Fig. 1b–d). Therefore, the maturation of the gland is characterised by an increase in its epithelial thickness, which was most pronounced in older ants, displaying glandular cells nearly bursting as a consequence of their lipid contents (Fig. 1d). We observed numerous free ribosomes and glycogen deposits. Ultrastructurally, the most remarkable features are the lipid droplets mentioned above, the largest of which have diameters measuring up to 5 μm (Fig. 1b–d). A very well-elaborated microvillar border (microvilli approximately 2.5 μm long) was also observed (Fig. 1e, f). Mitochondria are numerous and their sizes vary considerably. The basal surface of the epithelial cells of *Dinoponera* is provided with numerous, rather complicated, invaginations of the basal plasmalemma (Fig. 1e).

In some cells of the post-pharyngeal gland in *D. quadriceps*, lamellar structures were found at the basal part of the microvillar border, especially in cells containing very few lipid droplets. In those cases, the microvillar lining seemed slightly distorted. The cuticular layer consists of the 3 traditional layers: a thin outer electron-dense epicuticle; a fibrillar

Fig. 1. (a) Scanning electron micrograph of part of the post-pharyngeal gland in a *Dinoponera quadriceps* worker. SC = secretory cells. Bar = 100 μm . (b) Semi-thin section of the glandular cells in *D. quadriceps* before accumulation of lipid material. lu = lumen. Note basal protrusions. Bar = 50 μm . (c) Semi-thin section of the glandular cells in *D. quadriceps* in secretion phase, showing the beginning of accumulation of lipid droplets. li = lipid droplet; lu = lumen. Bar = 50 μm . (d) Semi-thin section of the glandular cells of the post-pharyngeal gland in *D. australis* in a later phase of secretion. Note the abundance of large lipid droplets. ct = cuticle; li = lipid droplet. Bar = 100 μm . (e) Transmission electron micrograph section of a glandular cell in *D. quadriceps* in early phase of secretion. Obvious basal invaginations surround a fairly large portion of the cellular edge. Note the well-developed microvillar lining of the secretory cells near the cuticle. ct = cuticle; li = lipid droplet; mi = membrane invaginations; mv = microvilli. Bar = 5 μm . (f) TEM section of a glandular cell in *D. australis* in a more advanced phase of secretion. Note the aspect of the cuticle and the electron-dense material alternating near the edge. ct = cuticle; ec = epicuticle; li = lipid droplet; mv = microvilli. Bar = 2 μm .



exocuticle; and a clear endocuticle adjacent to the epithelial cells. We also observed ultrastructural changes near the cuticular lining, e.g. the accumulation of lipids (black secretory material) at the epicuticular surface (Fig. 1f).

Pseudomyrmex phyllophilus (Gama and Cruz Landim, 1982) and *Solenopsis geminata* (Attygalle *et al.*, 1985) were also reported to possess a post-pharyngeal gland without tubular structures.

Although nothing is known about the roles of the gland in *Dinoponera*, the involvement of the post-pharyngeal gland in digestive processes (Forbes and McFarlane, 1961), larval feeding (Ayre, 1963), queen and brood tending (Markin, 1970), as a cephalic caecum (Vinson *et al.*, 1980), in caste determination (Brian and Blum, 1969), and colony organisation (Thompson *et al.*, 1981) have already been suggested.

The glandular content is usually described as a yellow oil and relatively few chemical analyses have been undertaken. The oily nature seems doubtful for *Dinoponera*, because the secretion does not look like an oil. Indeed, its contents are yellow, but it appears more precipitated. In ants belonging to several other subfamilies, fatty acids, sterols and glycerol esters have been found (Barbier and Delage, 1967; Peregrine *et al.*, 1973). More recently, higher molecular weight hydrocarbons have been discovered in some *Solenopsis* species (Thompson *et al.*, 1981; Attygalle *et al.*, 1985), *Myrmica*, *Manica*, *Camponotus* and *Formica* (Bagnères and Morgan, 1991). These include alkanes, methyl-branched alkanes as well as *n*-alkanes in the C₂₁–C₃₃ range.

Bagnères and Morgan (1991) have reported that the composition of the post-pharyngeal hydrocarbons is similar to that of the cuticular hydrocarbons in the 5 species they examined. They suggest that the gland may serve a purely mechanical purpose as a softener for the cuticular wax, but it may also have a social function as a colony-, species- or caste-marker. We must emphasise that the chemical data cited from literature have not been obtained from *Dinoponera* spp. or from ponerine ants.

In conclusion, the morphological organisation of the gland is peculiar, and because of this it is difficult to compare its organisation with ultrastructural details of the gland in other species. A characteristic feature observed at the light-microscopical level, is the presence of the rather complex invaginations, which indicates that the epithelial cells may be involved in extensive ion and fluid transport. Whatever the precise role of the gland in *Dinoponera* might be, our observations concerning the ultrastructure strongly suggest an involvement in lipid metabolism.

Acknowledgements—We thank Thibaud Monnin and Christian Peeters for kindly providing *Dinoponera quadriciceps*, and Ricardo V. S. Paiva and Dr. Carlos R. F. Brandão for collecting *D. australis*. We are very grateful to Dirk Corstjens for his assistance in specimen preparation for light and electron microscopy and Julien Cillis for his assistance in scanning electron microscopy. E. S. acknowledges the support of a post-doctoral research grant of the Belgian National Fund for Scientific Research (N.F.W.O).

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