An Acad Bras Cienc (2022) 94(2): e20201368 DOI 10.1590/0001-3765202220201368
Anais da Academia Brasileira de Ciências | *Annals of the Brazilian Academy of Sciences*
Printed ISSN 0001-3765 I Online ISSN 1678-2690
www.scielo.br/aabc | www.fb.com/aabcjournal

CELLULAR AND MOLECULAR BIOLOGY

Anatomy and histology of the metapleural gland in the giant tropical ant *Paraponera clavata* (Fabricius, 1775) (Formicidae: Paraponerinae)

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Abstract: Ants are social insects with about 85 exocrine glands with different morphologies. The metapleural gland is exclusive to ants and its compounds have antimicrobial action, indicating a function in the defense against pathogens. Within ants, *Paraponera clavata* is the only living species representative of Paraponerinae. This study describes the anatomy and histology of the metapleural gland in workers of *P. clavata*. The metapleural gland is formed by secretory units that release secretion in a reservoir through collecting canaliculi. Secretory units are bicellular with a well-developed globular secretory cell, with 145 µm in diameter, and a duct cell forming the collecting canaliculi characterizing a class III gland. The metapleural gland is pointed out as a synapomorphy of ants. Paraponerinae constitutes one of the six subfamilies of the basal and paraphyletic Poneroide clade and knowledge of the metapleural gland morphology contribute to the understanding of evolutionary history of the basal ants' groups.

Key words: Exocrine glands, social insects, canaliculi, secretory cell.

INTRODUCTION

Formicidae is a diverse group of insects with 17 subfamilies (Ward 2007) and approximately 16357 species (AntWeb 2020). Poneroide is a paraphyletic and basal clade with six subfamilies (Brady et al. 2014), including Paraponerinae with a single living species, *Paraponera clavata* (Fabricius, 1775), endemic to the tropical forests of Central and South America (Murphy & Breed 2007, Baccaro et al. 2015, Fernandes et al. 2015).

Social insects have a wide spectrum of interactions between the numerous individuals in the colony, involving a sophisticated system of physiological and chemical regulation (Tragust 2016, Penick et al. 2018, Santos et al. 2020). In ants (Formicidae), behavioral control and colony asepsis are mediated by compounds produced by approximately 85 exocrine glands (Adams et al. 2012, Billen & Sobotník 2015, Andrade et al. 2019, Guarda & Lutinski 2020), including the metapleural glands that are unique to ants, although they have been lost in a few tree species and social parasites (Brown 1968, Hölldobler & Engel-Siegel 1984).

The metapleural glands have a common morphological pattern, occurring in pairs in the posterolateral region of the metathorax. In each gland, a group of secretory cells releases secretions through collecting canaliculi in a reservoir below the integument (Tulloch et al. 1962, Hölldobler & Engel-Siegel 1984, Hölldobler & Wilson 1990, Fanfani & Dazzini 1991, Angus et al. 1993, Bot & Boomsma 1996, Bot et al. 2001, Gusmão et al. 2001, Souza et al. 2006, Vieira et al. 2012a, b, Junqueira & Diehl 2014, Pech & Billen 2017). The compounds produced by the metapleural glands are associated with ants' immunity, and their antimicrobial and fungicidal effects have been found in several species (Maschwitz et al. 1970, Maschwitz 1974, Beattie et al. 1986, Lacerda et al. 2010, Tragust 2016), in addition to the functions of the colony and nestmates recognition, territory marking, and defense against predators and competitors (Jaffé & Puch 1984, Billen et al. 2011, Yek & Mueller 2011, Penick et al. 2018).

Metapleural glands, which are unique to ants and found in fossils from ca. 100 mya (Grimaldi & Agosti 2000), are considered a synapomorphy for the family and are essential for understanding the origin of sociality and the phylogenetic relationships in Aculeata (Hölldobler & Wilson 1990, Ward 2010, Tranter et al. 2015). The objective was to describe the anatomy and histology of the metapleural gland in *P. clavata*, contributing to the understanding of evolutionary and morphological aspects of ants.

MATERIALS AND METHODS

Insects

Three colonies of *P. clavata* were collected in the municipality of Caxias (04° 53' S 43° 24' W) state of Maranhão, Brazil. The size of the colonies varied from 200 to 2000 workers. The colonies were transferred to the Microscopy Laboratory of the Center for Higher Studies of Caxias of the State University of Maranhão, where they were kept in artificial nests, made with plastic trays lined with plaster and covered with a transparent glass cover. Two trays were connected through a plastic tube so that one of them could be used as a foraging area and were kept between 28 and 30°C in the dark. The ants were fed, *ad libitum*, with honey, water and small grasshoppers (Orthoptera).

Gross morphology

For analysis of the gross morphology of the metapleural gland, five workers ant were cryo-anesthetized at -5 ^{0}C for 10 min, dissected in 125 mM NaCl and the metapleural glands were photographed with a digital camera (AxioCam ICc1) attached to the Zeiss Stereo Discovery V8 Stereomicroscope using the software AxioVision Release 4.8.2.

Light Microscopy

Ten workers ant were cryo-anesthetized at -5 ^{0}C for 10 min and their metapleural glands were dissected in 125 mM NaCl and transferred to Zamboni's fixative solution (Stefanini et al. 1967), for 4h, room temperature, RT. The samples were dehydrated in a graded series of ethanol (50, 70 90 and 95%) and embedded in historesin (Leica Historesin). Slices 3 µm thick were obtained with a glass knife on a rotative microtome Leica RM 2255 (Leica, Germany), stained with hematoxylin and eosin and analyzed using an Olympus BX-60 light microscope (Olympus, Japan).

RESULTS

In *P. clavata*, the metapleural gland was characterized as a paired structure that opened to the exterior through a rounded orifice (integument cleft) with a diameter of ca. 95 µm. In the region of the orifice, the body surface was protruding, forming the bulla in the metathorax, above the metacoxa and below the propodeal spiracle (Figures 1a-c).

The metapleural gland was formed by a secretory portion with several secretory units that release secretion through collecting canaliculi in a reservoir (Figures 1d and 2a-c). The reservoir wall was formed by a thin layer of flattened cells covered by a scletorized cuticle (Figure 2d).

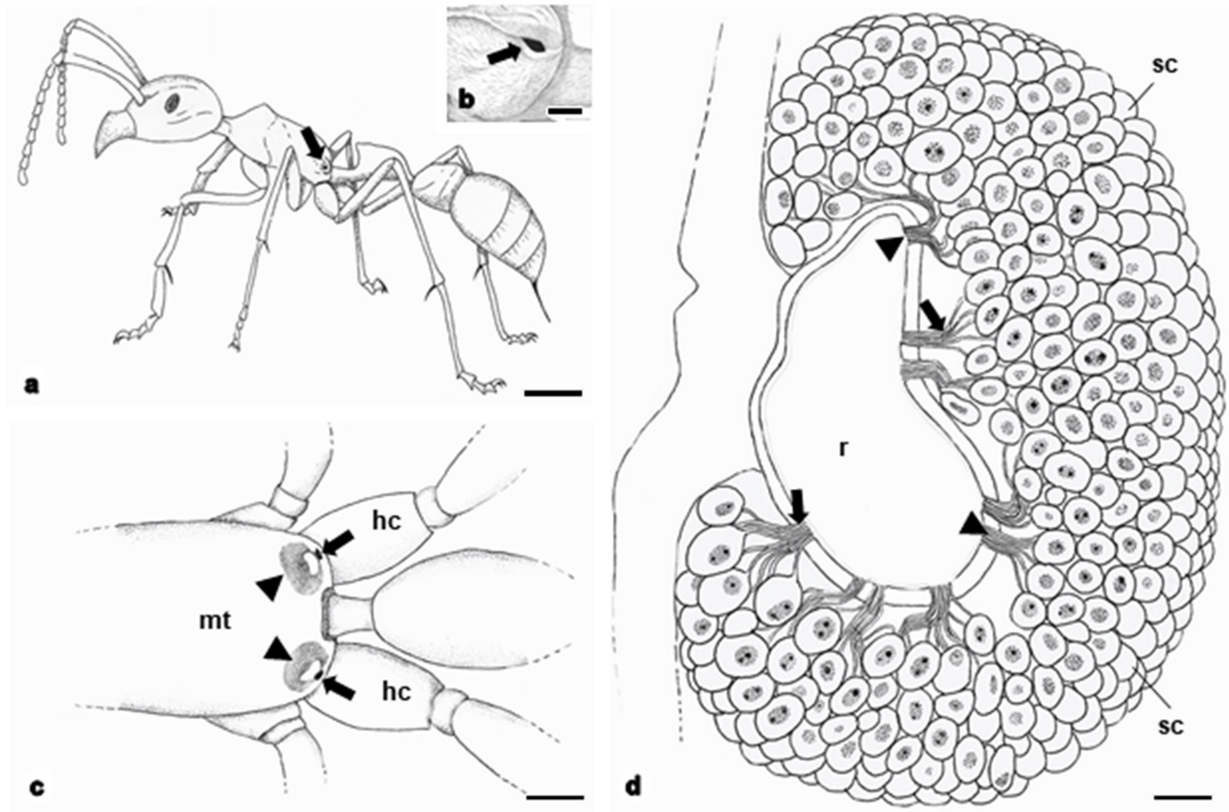

Figure 1. **Schematic drawing of *Paraponera clavata* worker and its metapleural gland. a-c. Detail of the metapleural gland opening (arrow) in the metathorax (mt), closely to the hindcoxae (hc). In (b) detail of the gland opening (arrow). d- Metapleural gland with secretory cells (sc), collecting canaliculi (arrows) clustered in the sieve-plates (arrowheads) opening into the reservoir (r). Bar: A = 0,3 cm; B = 200 µm. C = 0,1 cm; D = 150 µm.**

Each secretory unit was bicellular with one globular secretory cell and one duct cell forming the collecting canaliculi (Figures 1d and 3a). The secretory cell had an average diameter of 145 µm and showed the cytoplasm uniformly acidophilic (Figures 3c, e) with a well-developed nucleus (47 µm dia.), rich in decondensed chromatin and with evident nucleoli (Figure 3d). Every secretory cell presented an end apparatus (Figures 3c, d) formed by the association of the collecting canaliculi (Figures 1d and 3a). In the region close to the reservoir, the collecting canaliculi formed different groups that opened together forming sieve-plates in the cuticle of the reservoir (Figures 1d, 3a, b).

DISCUSSION

The anatomy of the *P. clavata* metapleural gland with secretory and storage regions is similar to those described for other ant subfamilies (Tulloch et al. 1962, Hölldobler & Engel-Siegel 1984, Hölldobler & Wilson 1990, Fanfani & Dazzini 1991, Angus et al. 1993, Bot & Boomsma 1996, Bot et al. 2001, Gusmão et al. 2001, Souza et al. 2006, Vieira et al. 2012a, b, Junqueira & Diehl 2014, Serrão et al. 2015, Pech & Billen 2017). The opening position of the metapleural gland close to the insertion site of the hind legs facilitates the release and distribution of secretion throughout the body, as has been suggested for other ants (Billen et al. 2011). Secretions have an antibiotic effect and in chemical defenses

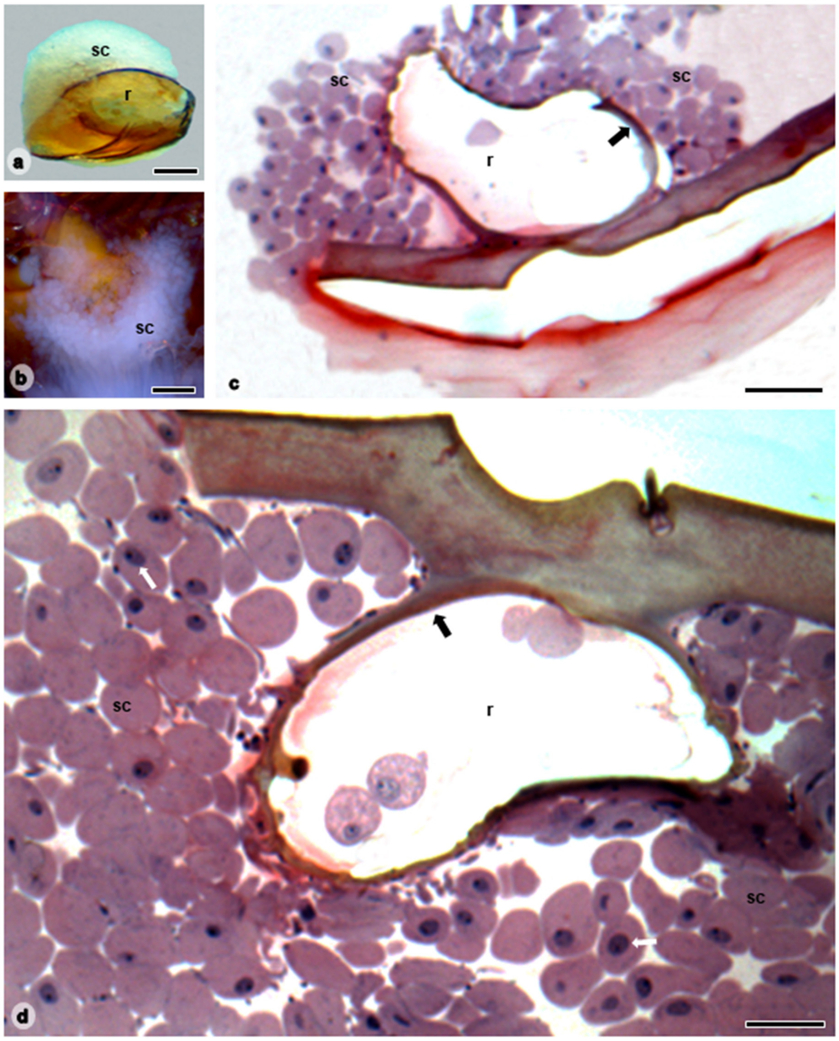

Figure 2. Anatomy and histology of the metapleural gland of *Paraponera clavata*. a-b. Anatomical view showing secretory cells (sc) and the reservoir (r). c-d. Histological section of the gland showing: secretory cells (sc) and the cuticle (arrow) that lines the reservoir (r). Bar: A = 0,2 mm; B = 0,1 mm; C = 600 µm; D = 400 µm.

(Fernández-Marín et al. 2006, 2015, Yek & Mueller 2011) and their high and continuous production can ensure individual and collective protection, as these are volatile compounds (Maile et al. 1998). The quantity and chemical composition of secretions from metapleural glands has also been associated with foraging and nesting strategies in ants (Yek & Mueller 2011, Vander Meer 2012).

The diameter of the metapleural gland opening correlates positively with the size of the gland in several species (Bot & Boomsma 1996, Bot et al. 2001, Lacerda et al. 2010, Billen et al. 2011). In *P. clavata*, the opening diameter was ca. 95 µm, similar to that of *Crematogaster inflata* (Myrmicinae) with 80 µm, which also has very developed glands with many secretory cells (Billen et al. 2011). The large body size of *P. clavata* workers, which can reach up to 2.5 cm (Fernandes et al. 2015), may also be associated with the large opening diameter of the metapleural gland.

In *P. clavata*, each metapleural gland has many secretory cells, which, despite not having an estimation of the total number, is above the average of 120 cells reported for 44 ant species (Hölldobler & Engel-Siegel 1984). This number of cells varies from 14 in *Aneuretus simoni* (Hölldobler & Engel-Siegel 1984) to 1,440 in *C. inflata* (Billen et al. 2011). Within the fungus

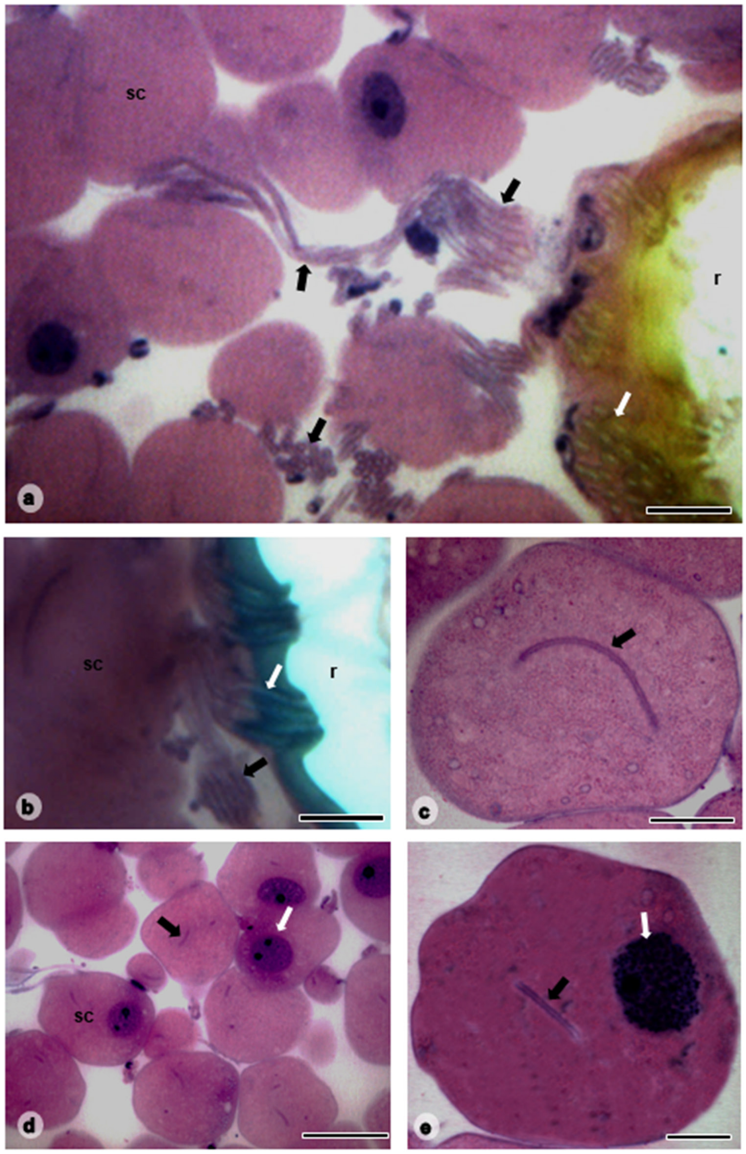

Figure 3. **Histology of the metapleural gland of *Paraponera clavata*. a-b. Section of the gland showing secretory cells (sc), the reservoir (r) and extracytoplasmic canaliculi (black arrows) and the insertion sites of the canaliculi in the cuticular intima of the reservoir (white arrows). c-e. Section of the gland showing the intracytoplasmic portion of the canaliculi (black arrow) inside the secretory cells (sc) and the nuclei (white arrow) with its condensed chromatin (naked). Bar: a, b = 80 µm; c, e = 50 µm; d = 140 µm.**

farming ants (Attini), the most derived species have a higher number of secretory cells in their metapleural glands (Vieira et al. 2011), which has been associated with a higher production of compounds (Poulsen et al. 2003).

The region for secretion storage in the metapleural glands varies according to ant species. Some glands have a collecting sac before the reservoir, as in some Attini (Hölldobler & Engel-Siegel 1984, Bot et al. 2001, Souza et al. 2006) and *C. inflata* (Billen et al. 2011). In *P. clavata*, the secretory region is directly linked to the reservoir by the collecting canaliculi, as also found in some Attini (Gusmão et al. 2001, Vieira et al. 2012a, b, Pech & Billen 2017). However, the reservoir in all studied species is covered by a cuticular intima, which indicates its ectodermal origin, and possibly that the folds in the cuticle can direct the flow of secretions (Schoeters & Billen 1993) in addition to the protective function of the epithelial cells and to possible contaminants (Vieira et al. 2012a, c).

The secretory cells and collecting canaliculi of the metapleural glands of *P.*

clavata are characteristic pattern of class III glands according to the classification of Noirot & Quennedey (1974), where the collecting canaliculi are arranged into bundles that open into the reservoir, forming a structure similar to the "sieve plate". The large size, globular shape, and the nucleus rich in decondensed chromatin of the secretory cells of the metapleural gland of *P. clavata* are characteristics suggesting high activity and secretory capacity (Azevedo et al. 2007, Vieira et al. 2012b). In the metapleural glands of basal and derived Attini, histochemistry show the presence of proteins, lipids and acid polysaccharides (Vieira et al. 2012b).

The collecting canaliculi that transport the secretion to the reservoirs have intra (end apparatus) and extracellular portions in the metapleural glands of *P. clavata* as reported for other ants (Noirot & Quennedey 1974, Souza et al. 2006, Vieira et al. 2012a, b). In the metapleural glands of ants with high secretory capacity, such as in derived Attini, the end apparatus surround the nucleus and it has many microvilli to increase the absorption surface (Vieira et al. 2010, 2011, 2012c). In addition, secretion in the extracellular portion has a different composition from that of the end apparatus, indicating that, apart from the transport function, the duct cell can change the composition of the secretion (Vieria et al. 2012a, b). *P. clavata* workers have a predatory feeding habit and occasionally explore other food sources, such as extrafloral nectaries, which could be a selective pressure to increase functional defense versatility of the metapleural gland. In *Crematogaster* ant the chemical composition of metapleural gland secretion is different from those reported for Attini, which has been associated with different responses in defense against predatory arthropods and pathogens due to the different nidification and foraging habits (Billen et al. 2011, Yek & Mueller 2011, Vander Meer 2012, Tragust 2016).

In *P. clavata*, collecting canaliculi from different cells become associated, forming groups that open in the reservoir in sieve plates. This pattern also occurs in *Technomyrmex vitiensis* (Pech & Billen 2017), Ectatommini, Myrmicini, Blepharidattini, and Attini (Vieira et al. 2012b). However, in the Attini *Atta cephalotes, A. sexdens, Nothomyrmecia macrops, Pseudomyrmex pallidus* and *Myrmecia pilosula* the sieve plates occur in the collecting chamber where the canaliculi end (Caetano et al. 1982, Hölldobler & Engel-Siegel 1984, Souza et al. 2006).

The metapleural gland in workers of *P. clavata* reveals that the morphological characteristics are similar to those of most species of ants in which secretions functions as antibiotic defense. Further studies for identification of the chemical compounds produced by this gland may contribute for the comprehension of their foraging and nidification strategies of this unique living representative of Paraponerinae.

Acknowledgments

This study was supported by the following Brazilian institutions: Fundação de Amparo à Pesquisa e ao Desenvolvimento Científico e Tecnológico do Maranhão (FAPEMA) and Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (CAPES). The authors thank the Lorena Emanuelle Oliveira Guimarães, Joseana da Cunha and the Laboratry Aquatic Entomology – LEAQ do Centro de Estudos Superiores de Caxias da Universidade Estadual do Maranhão/UEMA for the technical support in the image of the external morphology of the metapleural gland. We also thank Mateus Soares de Oliveira for her help with the illustrations and the anonymous reviewers and the editor for reviewing the manuscript.

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How to cite

MARTINS LCB, SERRÃO JE, SANTOS HP & ARAÚJO VA. 2022. Anatomy and histology of the metapleural gland in the giant tropical ant *Paraponera clavata* (Fabricius, 1775) (Formicidae: Paraponerinae). An Acad Bras Cienc 94: e20201368. DOI 10.1590/0001-3765202220201368.

Manuscript received on August 28, 2020;
accepted for publication on April 12, 2021

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