



# Morphology of the Mandibular and Intramandibular Glands of Army Ant Workers of *Labidus praedator* (Smith 1858) and *Labidus coecus* (Latreille 1802) (Formicidae: Dorylinae)

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## Abstract

Social insects are characterized by having a wide diversity of exocrine glands, with highlights for ants with about 85 glands spreading throughout the body. The mandibular and intramandibular glands are associated with the production of pheromones. The army ants (Dorylinae) play an important role in the structure of the invertebrate community because they are efficient predators and provide suitable conditions for various animals following their invasions in the food search. *Labidus coecus* (Latreille) is an underground-ameliorating ant and *Labidus praedator* (Smith) is a generalist surface predator which can deplete invertebrate biomass by up to 75%. This work investigated the morphology of the mandibular and intramandibular glands of *L. praedator* and *L. coecus* workers. The glands were analyzed by light microscopy, histochemistry, and scanning electron microscopy. The mandibular and intramandibular glands of the two species were classified as class III glands. The data on the morphology of the mandibular glands has revealed that they have characteristics in common with other subfamilies. The intramandibular glands of the two species of *Labidus* have similar morphology and chemical composition, which indicates that the components of these glands can have the same function despite their different habits.

**Keywords** Army ant · Exocrine glands · Histochemistry · Pheromone

## Introduction

Social insects are characterized by having a wide diversity of exocrine glands, with highlights for ants with about 85 glands spreading throughout the body (Billen and Al-Khalifa 2016) including the head with exocrine glands that produce active secretions (Xu et al. 2021). The exocrine glands are important for intraspecific communication since they act in the processes of social integration, mating, delimitation of

territories, nest location, and nestmate recognition and in communication in general (Billen 2006).

Among the exocrine glands of ants, those in the head include the mandibular, intramandibular, hypopharyngeal, postpharyngeal, and thoracic salivary glands (Caetano et al. 2002; Gama 1978; Schoeters and Billen 1994). The mandibular glands are located in the head, in close contact with the mandibles and the intramandibular glands are in the internal part of the mandible (Cruz-Landim and Abdalla 2002; Martins and Serrão, 2011; Martins et al. 2016; Andrade et al. 2019).

Among the glands associated with the mandibles, the mandibular glands in social insects are the most studied ones (Cruz-Landim and Abdall 2002). They are associated with the production of pheromones for the nestmate recognition (Caetano et al. 2002; Gama 1985), alarm (Cammaerts et al. 1983; Fales et al. 1972; Martins et al. 2016), and the antibiotic substances (Brough 1983; Rodrigues et al. 2008). On the other hand, the function of the intramandibular glands is still poorly understood, but it seems to be involved in the

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nestmate recruitment (Roux et al. 2010; Martins et al. 2016) and in the labor division in the castes (Serrão et al. 2015).

Army ants have a strong ecological impact on neotropics, playing an important role in the structure of the invertebrate community because they are efficient predators and several animals follow their invasions in their search for food (Willis and Oniki 1978; Otis et al. 1986; Gotwald 1995; Kronauer 2009). The true army ants (Dorylinae) share these three characteristics that define the Army Ant Syndrom: highly specialized wingless queen, nomadism, and group foraging (Brady 2003; Borowiec 2016).

Among the army ants, the few species of the genus *Labidus* Jurine are widely distributed with potential ecological impact due to their high densities (Borowiec 2016). Their species are generalist predators of arthropods, but they also feed on sugar and plant parts, including flowers, seeds, fruits, and processed foods (Borgmeier 1955; Monteiro et al. 2008). The two best-studied species of this ant genus are *Labidus coecus* (Latreille) and *Labidus praedator* (Smith) (Borowiec 2016).

*Labidus coecus* is an underground army ant, sometimes found at a considerable depth (Longino 2007), whereas *L. praedator* is a generalist predator (Brady 2003; Kaspari and O'Donnell 2003) raiding partially underground (Rettenmeyer 1963; Schneirla 1971; Fowler 1979) because they forage on the surface (Kronauer 2009), which can deplete invertebrate biomass up to 75% (Kaspari et al. 2011).

Due to the importance of the knowledge of the exocrine gland morphology for the understanding of behavioral aspects in Formicidae and the existence of few studies in the literature on the communication of the army ants of the genus *Labidus*, this work aims to investigate the morphology of the mandibular and intramandibular glands of the army ants *L. praedator* and *L. coecus* workers with different nesting behaviors, using histological, histochemical, and scanning electron microscopy analyses.

## Material and methods

### Obtaining insects

The workers of *L. praedator* and *L. coecus* were collected on the Bacabal campus of the Federal University of Maranhão, in the State of Maranhão (4°13'S, 44°46'W), Brazil, through manual collection. Then, the workers of *L. praedator* and *L. coecus* were cold immobilized at  $-4\text{ }^{\circ}\text{C}$  for 5 min and transferred to 2.5% glutaraldehyde fixative in 0.1 M sodium cacodylate buffer, pH 7.2. Then, the samples were transferred to Laboratory of Insect Ultrastructure, Department of General Biology, Federal University of Viçosa, Viçosa, State of Minas Gerais, Brazil, for morphological analyses.

### Light microscopy

Four heads and eight mandibles of workers of each species were dehydrated in an increasing series of ethanol at the concentrations of 70%, 80%, 90%, and 95% with 15-min intervals for each. After dehydration, the samples were transferred to methanol for 24 h. Then, the samples were embedded in ethanol:historesin (Leica) in the proportions of 3:1, 1:1, and 1:3 with a 24-h interval in each step. Subsequently, the samples were embedded in historesin (Leica) and polymerized for 24 h. Two-micrometer-thick sections were obtained in microtome, stained with hematoxylin (20 min) and eosin (30 s), and analyzed using an Olympus BX-60 light microscope coupled with an Olympus QColor 3 camera.

### Histochemistry

Some sections of the heads and mandibles of *L. praedator* and *L. coecus* were submitted to the following histochemical tests: mercury-bromophenol blue for the detection of total proteins (Pearse 1953), periodic acid-Schiff (PAS) for the detection of glycoproteins and neutral carbohydrates and Nile blue for lipid detection (Bancroft and Gamble 2008). Then, the samples were mounted with coverslips, analyzed, and photographed as described under light microscopy.

### Scanning electron microscopy

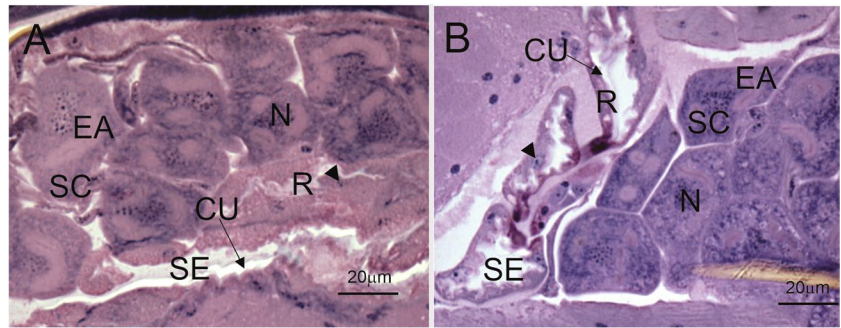
Four mandibles of each species were removed, dehydrated in a graded ethanol series (70%, 80%, 90%, and 99%), transferred to hexamethyldisilazane for 5 min, and air dried at room temperature. After this period, the mandibles were placed on aluminum support with double-sided adhesive tape, metallized with gold (thickness of 20 nm), and analyzed with the LEO VP1430 (Carl Zeiss, Jena, Germany) scanning electron microscope at 10 kV at the Nucleus of Microscopy and Microanalysis at the Federal University of Viçosa.

## Results

### Mandibular gland

The mandibular glands of *L. coecus* and *L. praedator* were found as paired structures located in the lateral region of the head, between the base of the mandible and the inner edge of the compound eyes. They consisted of several secretory units with a secretory cells connected to a large

**Fig. 1** Histological sections of the mandibular gland of *Labidus coecus* (A) and *Labidus praedator* (B). Note secretory cells (SC) with irregular nuclei (N) and end apparatus (EA) in the cytoplasm, reservoir (R) lined by flattened epithelium (arrowheads), cuticle (CU) and filled with secretion (SE)

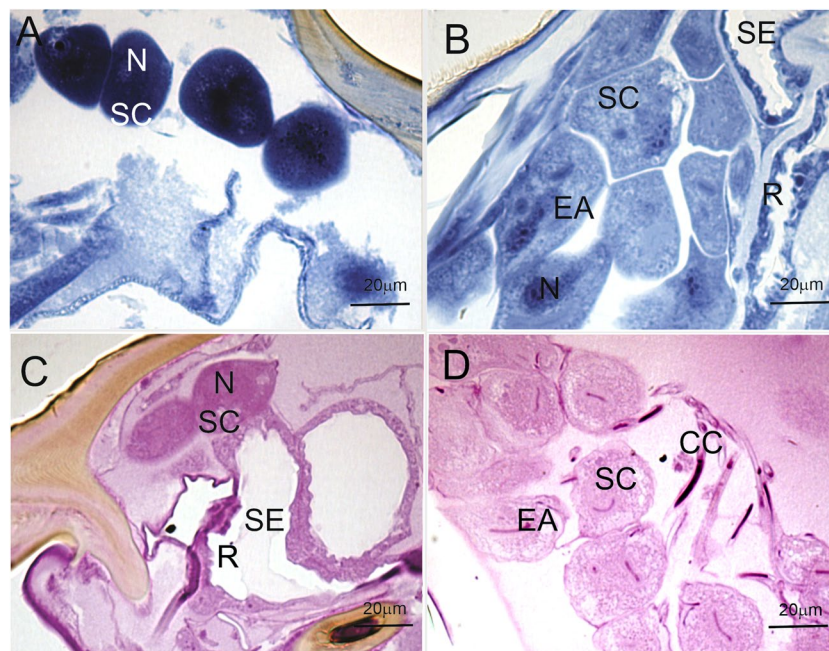


reservoir through a collecting canaliculus that formed an evident end apparatus in the secretory cell (Fig. 1A, B). The secretory cells in the two species showed an irregular nucleus with a predominance of decondensed chromatin (Fig. 1A, B).

The reservoir of the *L. coecus* and *L. praedator* mandibular gland was lined by a single-layered epithelium of flattened cells with a central nucleus (Fig. 1A, B). The internal surface of the reservoir was covered by a thin cuticle and its lumen was filled with weakly acidophilic content (Fig. 1A, B).

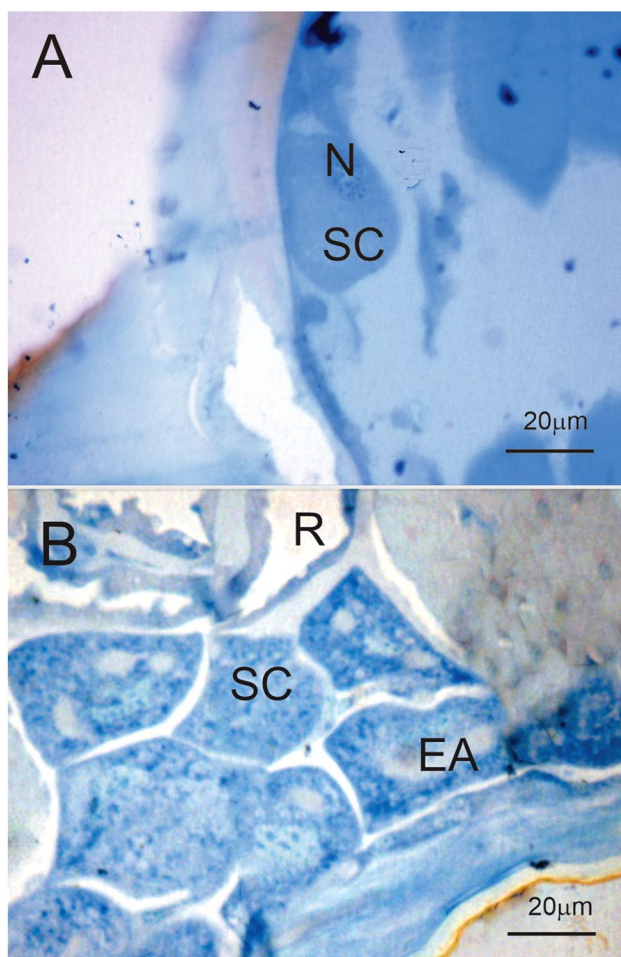
The histochemical analysis of the secretory cells of the workers' mandibular glands showed a strong positive

reaction for proteins in *L. coecus* (Fig. 2A) and a weaker one in *L. praedator* (Fig. 2B). In both species, there was a weak positive reaction for carbohydrates in the mandibular glands but it was stronger in *L. coecus* (Fig. 2C) than in *L. praedator* (Fig. 2D). The collecting canaliculi and the end apparatus present in the secretory cells of the *L. praedator* mandibular gland (Fig. 2B, D) reacted positively to the test for the detection of proteins and carbohydrates. The secretory cells of the mandibular glands of *L. coecus* workers (Fig. 3A) showed a stronger positive reaction for lipids than those found in the gland cells of *L. praedator*, which in turn had some cytoplasm granules positive for lipids (Fig. 3B).



**Fig. 2** Histological sections of the mandibular gland of ants submitted to the mercury-bromophenol test for protein detection: (A) *Labidus coecus* secretory cell (SC) with a strongly positive reaction. (B) *Labidus praedator* secretory cell (SC) with weak positive reaction and reservoir (R) with homogeneous, weakly positive secretion (SE); and PAS test for the detection of carbohydrates and glycoconjugates:

(C) Secretory cells (SC) and the reservoir (R) of *Labidus coecus* with positive reaction. Observe secretion (SE) with weakly positive reaction. (D) *Labidus praedator* secretory cells with weak positive reaction in the end apparatus (EA) and stronger in the collecting canaliculi (CC). EA, end apparatus; N, nucleus



**Fig. 3** Histological sections of the mandibular gland of ants submitted to the Nile blue test for lipid detection. **(A)** *Labidus coecus* secretory cell (SC) with weak positive reaction. **(B)** *Labidus praedator* secretory cells (SC) with weak positive reaction in the reservoir (R) and end apparatus (EA), and strong in the cytoplasm. N, nucleus

### Intramandibular gland

The internal cavity of the mandible of *L. coecus* and *L. praedator* were characterized by the presence of globular secretory cells. The globular cells were associated with the collecting canaliculi that individually opened in pores in the dorsal region of the mandible (Fig. 4).

In *L. coecus*, these secretory cells showed well-developed nuclei with a predominance of decondensed chromatin and evident nucleolus (Fig. 5A). In *L. praedator*, the secretory cells showed a nucleus with a predominance of decondensed chromatin and an evident nucleolus (Fig. 5B). In both species, the epidermis was formed by a single layer of flattened cells (Fig. 5A, B).

In the histochemical analyses, the intramandibular secretory cells of *L. coecus* and *L. praedator* showed a weak positive reaction for proteins (Fig. 6A, B) and

carbohydrates (Fig. 6C, D), except in the region of the end apparatus with a strong reaction for carbohydrates (Fig. 6D). The intramandibular secretory cells of *L. coecus* (Fig. 7A) showed a weak positive reaction to lipids, which in *L. praedator* was stronger (Fig. 7B).

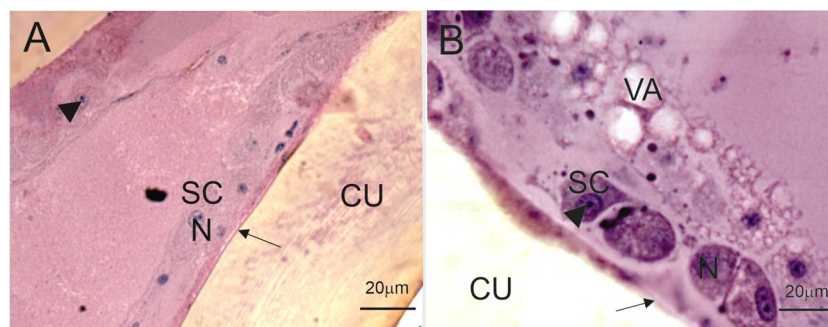
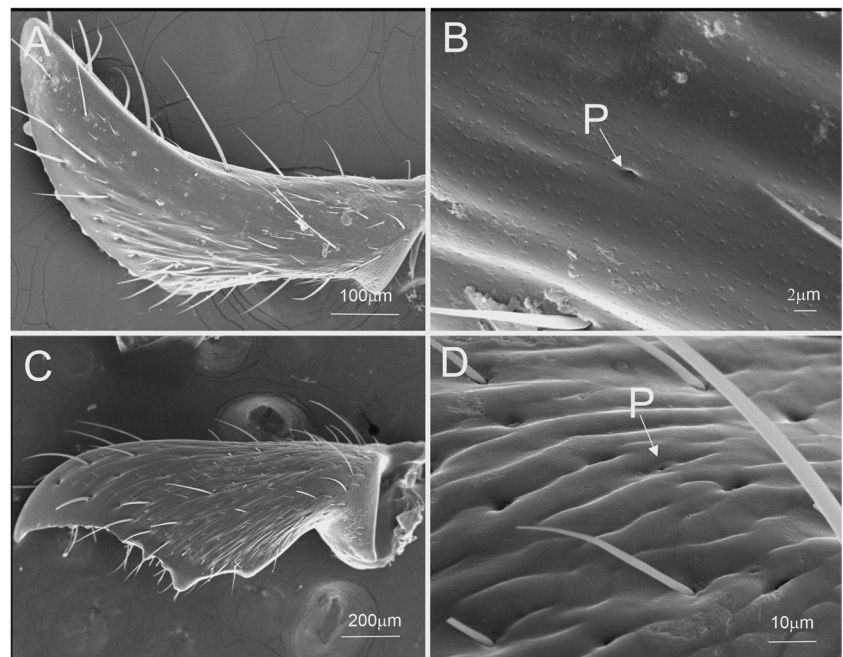
### Discussion

In *L. coecus* and *L. praedator*, the secretory cells of the mandibular glands belong to class III according to the classification proposed by Noirot and Quennedey (1974) as they have an end apparatus with a collecting canaliculus that opens into the reservoir characterizing the units of bicellular glandular cells (Noirot and Quennedey 1974). This seems to be a common characteristic of ant mandibular glands as reported in Formicinae (Grasso et al. 2004; Niculita et al. 2007), Myrmicinae (Pavon and Camargo-Mathias 2001; Boonen et al. 2013), and Paraponerinae (Andrade et al. 2019). The end apparatus is formed by a complex that includes the secretory cell and the cell duct, which allows the efficient drainage of secreted products (Billen et al. 2016).

The secretion present in the reservoir of the *L. coecus* and *L. praedator* mandibular glands is a little acidophilic and has a protein composition as revealed by the histochemical test. Mandibular glands are common in social insects, including ants (Billen and Morgan 1998); their secretion generally contains pheromones with functions in alarm in Ponerinae, Dorylinae, Myrmicinae, and Formicinae (Wilson and Regnier 1971; Birch 1974; Holldobler and Wilson 1990); sexual in males of *Camponotus* Mayr and queens of *Polyergus rufescens* (Latreille) (Grasso et al. 2003); attraction for workers and queens of *Myrmica rubra* (Linnaeus), *Myrmica rugulosa* Nylander, and *Myrmica schencki* Viereck (Cammaerts-Tricot 1974; Cammaerts et al. 1983); nestmate recognition in *Atta cephalotes* (Linnaeus) and *Atta laevigata* (Smith) (Hernández et al. 2002), *Camponotus rufipes* (Fabricius) (Jaffé and Sánchez 1984), and *Camponotus atriceps* (Smith) (Hernández et al. 2010); indication of nuptial flight in queens and males of *Solenopsis invicta* Buren (Alonso and Vander Meer 1997); and communication between pupae and workers in *Monomorium pharaonis* (Linnaeus) (Boonen et al. 2013).

In the army ants of *Eciton* Latrille, mandibular alarm pheromones play a dual role by recruiting individuals to defend against threats and to attack prey (Lalor and Hughe 2011). Pheromones are composed of volatile molecules, but when stored they can be linked to proteins known as odorant-binding proteins (Danty et al. 1999; Pesenti et al. 2008), which is supported by the presence of proteins in the reservoir contents obtained here. In addition, the secretion of this gland has been reported as rich in antimicrobial substances in workers in *Calomyrmex* Emery (Brough 1983)

**Fig. 4** Scanning electron micrographs of the mandibles of ants. (A) General aspect of mandible of *Labidus coecus* and (B) detail of dorsal surface of the mandible showing pore (P) in the cuticle. (C) General aspect of mandible of *Labidus praedator* and (D) detail of dorsal surface of the mandible showing the pore (P) in the cuticle



**Fig. 5** Histological sections of the intramandibular gland in army ants. (A) *Labidus coecus* showing flattened epidermis (arrow) and secretory cells (SC) with spherical nucleus (N) with nucleolus (arrowhead). (B) *Labidus praedator* showing flattened epidermis

(arrow), secretory cells (SC) with cytoplasm containing vacuoles and spherical nuclei (N) with nucleolus (arrowhead) and fat body cells (FB) rich in vacuoles (VA). CU, cuticle

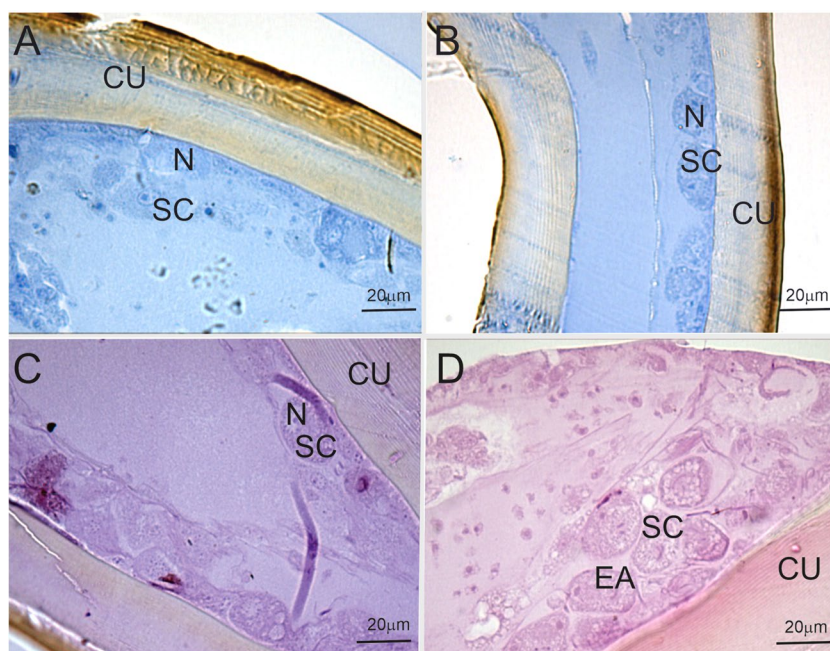
and as a lubricant for mouthpieces in *Pachycondyla striata* Smith (Tomotake et al. 1992) which is a function generally performed by peptides and glycoproteins (Graystock and Hughes 2011; Tragust et al. 2013). These same compounds were found in the secretion of the ant's mandibular glands studied here as revealed by the tests for proteins and carbohydrates.

In the mandibular glands of the ants studied here, there is a PAS-positive reaction in the end apparatus and in the collecting canaliculi, which indicates the presence of glycoconjugates in these regions. In the region of the end apparatus, this reaction to PAS may be due to the presence of glycoproteins, because this is the place where the secretion of the glandular cell occurs and its collection by the conducting canaliculus takes place, which is characterized by

the presence of many microvilli (Andrade et al. 2019), and the specialization of cells rich in glycoproteins (Tsuyama et al. 1985; Ohno and Takasu 1989). In the region of the collecting canaliculus, this is probably due to the presence of a cuticle in this region, which generally presents a positive reaction for PAS (Pavon and Camargo-Mathias 2004; Marques-Silva et al. 2006; Martins et al. 2015).

The cytoplasm of the secretory cells of the *L. coecus* mandibular gland shows a strong positive reaction for proteins similar to what occurs in *Paraponera clavata* (Fabricius) (Andrade et al. 2019) and *Atta sexdens* (Linnaeus) (Pavon and Camargo-Mathias 2004). The weak positive reaction for carbohydrates in the secretory cells of *L. coecus* and *L. praedator* has also been reported in *P. clavata* (Andrade et al. 2019) and *A. sexdens* (Pavon and Camargo-Mathias 2004).

**Fig. 6** Histological sections of the intramandibular gland of army ants submitted to the mercury-bromophenol test for protein detection: Secretory cells (SC) of *Labidus coecus* (A) and *Labidus praedator* (B) with weak positive reactions; and submitted to the PAS test for the detection of carbohydrates and glycoconjugates: Secretory cells (SC) of *Labidus coecus* (C) and *Labidus praedator* (D) with a weak positive reaction. The end apparatus (EA) reacted positively to the test. CU, cuticle; N, nucleus



The strong positive reaction for proteins in the cytoplasm of the *L. coecus* mandibular glands strongly indicates that the secretion produced by this gland acts as a pheromone for this ant species. The cytoplasm of the mandibular gland of *L. coecus* and *L. praedator* is poor in lipids, similar to what has been reported in *P. clavata* (Andrade et al. 2019) and *A. sexdens* (Pavon and Camargo-Mathias 2004).

The results obtained in this work revealed that *L. coecus* and *L. praedator* have class III intramandibular glands. In the mandible of *A. sexdens* and *A. laevigata*, there is the presence of class III glands and epidermal glands with reservoir (Amaral and Caetano 2006; Martins and Serrão, 2011; Martins et al. 2015). In the two species studied here, there were no glands with reservoir. Xu et al. (2021) described the postmentum base gland, cardo base gland, and stipes base gland in *Camponotus japonicus* Mayr, none of the three glands with a reservoir for the storage of secretion as the cells of the duct were opening through the articular membranes that connected the mouthparts.

The occurrence of class III intramandibular gland in *L. praedator* and *L. coecus* confirms that the presence of these glands is common in Hymenoptera, as has been reported in bees (Costa-Leonardo 1978; Smith et al. 1993; Wossler et al. 2000; Cruz-Landim and Abdalla, 2002; Romani et al. 2002; Romani et al. 2003; Cruz-Landim et al. 2011; Santos et al. 2015), wasps (Romani et al. 2005), and other ants (Toledo 1967; Schoeters and Billen 1994; Billen and Espadaler 2002; Grasso et al. 2004; Marques-Silva et al. 2006; Billen 2008; Roux et al. 2010; Martins and Serrão, 2011; Billen and Delsinne 2013; Martins et al. 2013, 2015). Despite the broad report of class III intramandibular gland in ants, its

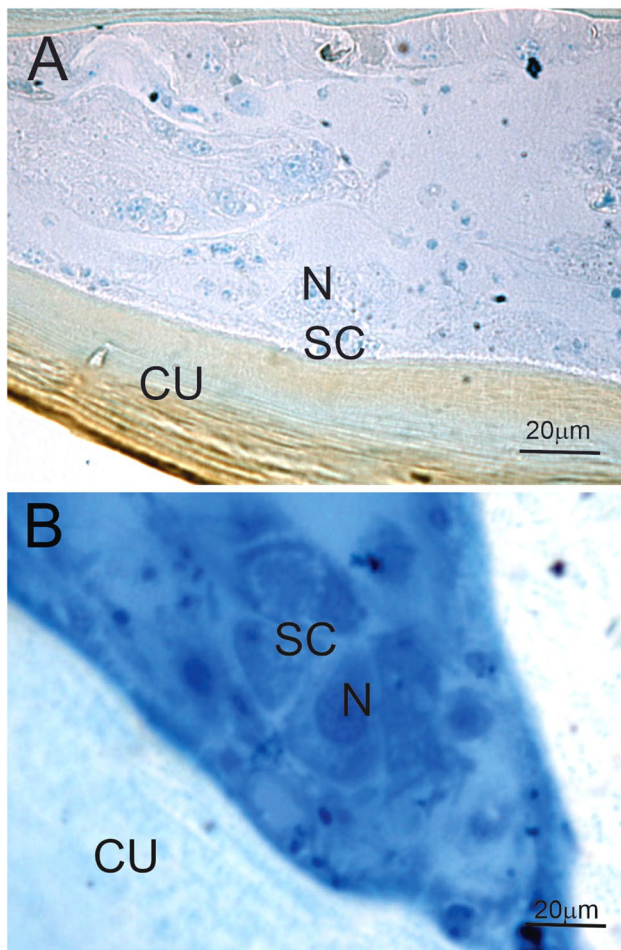
function is known only in *Oecophylla longinoda* Emery in the production of pheromone for substrate marking (Roux et al. 2010) and *Neoponera villosa* (Fabricius) as trail and alarm pheromone (Martins et al. 2016).

The chemical composition of the intramandibular glands of the workers of the two species of army ants which was revealed by histochemical analyzes was similar to each other in the small amounts of proteins and carbohydrates they possessed, indicating that despite the different underground (*L. coecus*) and partially underground (*L. praedator*) habits, the components of these glands may have the same functions. There are few differences in the amount of lipids in the cytoplasm of the mandibular and intramandibular glands of the two species, which are higher in *L. praedator*.

The presence of pores on the mandible surface of both *Labidus* species studied here indicates that products from class III intramandibular glands are released to the external environment through duct cell, likely reported in *O. longinoda* (Roux et al. 2010) and *A. laevigata* (Martins et al. 2015).

Considering the sharing of the intramandibular gland by several species of ants, it is plausible to suggest that this gland plays an important role in the biology of ants, although its function remains unknown in most of them. The morphology of this gland varies by caste (Cruz-Landim and Abdalla 2002; Martins et al. 2015) and can be used as phylogenetic characters to separate distinct groups, as was observed by Martins and Serrão (2011).

The chemical composition of the secretion of the mandibular and intramandibular glands and the role they may play are still unknown in both species studied here. The study of such



**Fig. 7** Histological sections of the intramandibular gland of ants submitted to the Nile blue test for lipid detection. (A) *Labidus coecus* secretory cell (SC) with weak positive reaction and (B) *Labidus praedator* secretory cells (SC) with strong positive reaction. CU, cuticle; N, nucleus

chemical and behavioral characteristics can be useful for the knowledge of the functional morphology of the mandibular and intramandibular glands in these ant species. Future examination with transmission electron microscopy and gas chromatography may clarify the possible function of these glands.

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**Author Contribution** APPR and JES: conceptualization and design; APPR: investigation, validation, formal analysis, writing—original draft, writing—review and editing; PPS: methodology, validation; JFSC and LAD: validation, formal analysis; HB: writing—review; JES: validation, writing—review and editing, project administration and editing, funding acquisition. All authors read and approved the final manuscript.

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**Data Availability** The data that support the findings of this study are available from the authors upon reasonable request.

## Declarations

**Conflict of Interest** The authors declare no competing interests.

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