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COMPARATIVE ULTRASTRUCTURE OF THE MANDIBULAR GLAND IN *Scaptotrigona postica* (HYMENOPTERA, APIDAE, MELIPONINI) WORKERS AND MALES

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ABSTRACT

Differences in the ultrastructure and function of the mandibular glands in developing workers and mature males of the meliponine stingless bee *Scaptotrigona postica* suggest that there are age-dependent variations in the contents of the secretion and glandular functions. In this work, we used transmission (TEM) and scanning (SEM) electron microscopy to examine the mandibular glands of *S. postica* workers of different ages and compared them with those of mature males. The gland anatomy did not vary between workers and males. However, the ultrastructure of the gland cells changed according to the worker's age, task, and sex. The mandibular gland cells in workers and males had a well developed smooth endoplasmic reticulum and pleomorphic mitochondria, indicating that the cells were involved in lipid synthesis. However, the secretion varied in morphology and electrondensity between workers and males, which suggested differences in its contents and, possibly, in glandular functions.

Key words: Labor division, morphology, secretion, scanning electron microscopy, stingless bee, transmission electron microscopy

INTRODUCTION

In eusocial bees, tasks are allocated to individuals according to their capacity, which depends on their sex, caste and physiological status. The ability to perform various tasks is acquired progressively by bees as they grow older, with the maturation of endocrine and exocrine glands playing an important role in the development of stingless bees and honeybees. In stingless bees, including *Scaptotrigona postica*, the queens and males are more involved in general colony activities than are other types of bees. Whereas in colonies of *Apis mellifera* only one queen is allowed, in colonies of *S. postica* the virgin queens may remain in the colony and the males may participate in nectar dehydration, in addition to eating directly from the flowers [6,19,30,31].

In normal conditions, *S. postica* workers start their activities by first producing wax (0 day-old), and this is followed by provisioning the cell broods (16-20 days old), colony cleaning (21-35 days old), nectar reception and dehydration (21-45 days old), colony defense (31-40 days old) and, finally, foraging (26-60 days old) [29]. Although these tasks are generally age-dependent, the actual tasks done also depend on the colony′s needs and imply behavioral plasticity in the bees, i.e., nest or non-nest-mate workers of the same age may perform different tasks or the same tasks but with different intensity [7,14,22,23], depending on the environmental conditions.

There have been few studies of drone biology and behavior, even in eusocial bees. The males are usually absent from the colony throughout the year, except during special periods and under appropriate environmental conditions when they mate with the queen and establish colonies. In *A. mellifera,* the drones apparently have no function other than to fecundate the queen since they usually die as a result of extirpation of their genitalia during mating [13].

The biology of meliponine drones is very complex [6,31] since, in addition to fertilizing the queen, *S. postica* males also participate in the collection [21], reception and dehydration of nectar. The nectar dehydration by males has also been observed in *Paratrigona sbunuda* [19], *Plebeia droryana* Friese

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[6] and *Melipona becheii* [30]. In *P. droryana*, the males receive nectar, practice trophallaxis with other males and workers, and produce wax [6]. In *Schwarziana quadripunctata*, the males also help to cement the brood alveoli with wax [18]. Most of the tasks performed by individual bees depend on endocrine and exocrine gland function, the role of which increases with physiological maturity.

The mandibular glands are exocrine glands associated with the mandibles. In stingless bees, these glands occur in queens, workers and drones, and, together with the labial and hypopharyngeal glands, form the salivary gland system [8]. The mandibular glands show inter- and intraspecific variation in their ultrastructure and function, with the intraspecific variation depending on the caste, age, sex and colony needs [7,9].

In *Lestrimelitta limao* (Meliponini), the glands were well developed in workers and their secretion is used to rob other colonies since this species is cleptobiotic [3,4,10]. In the stingless bee *Oxytrigona tataira*, the mandibular glands of workers produce caustic substances that are used to defend the nest against predators as a mechanism that compensates for the lack of a sting [3,20,28]. These observations indicate that in meliponine and other bees the mandibular gland secretion contains a variety of compounds and exerts different functions. The mandibular gland secretion of *S. postica* workers contains substances used as trail pheromones [11,23,28] and shows age-dependent variation in composition [12]. In this study, we examined the ultrastructure of the mandibular glands in workers and drones of *S. postica*.

MATERIAL AND METHODS

The individuals of *S. postica* Latreille (Hymenoptera, Apidae) used in this study were obtained from the apiary of the Instituto de Biociências at UNESP, Rio Claro. Five pairs of mandibular glands obtained from newly-emerged (collected when emerging from the brood favus), nurse (collected while provisioning the brood) and forager (collected when emerging from the colony) workers and mature males (collected at the entrance to the colony) were dissected in insect saline.

Scanning electron microscopy (SEM)

The mandibular glands were fixed in 2.5% glutaraldehyde and 2.0% paraformaldehyde in 0.1 M sodium cacodylate buffer, pH 7.3, for 72 h at 4ºC, after which the material was dehydrated in a graded acetone series (70%-95%) and rinsed twice (15 min each) in 100% acetone. The material was then critical point dried (Balzers CPD/030), sputtered with gold and examined in a Jeol JSM-P15 scanning electron microscope operated at 15 kV.

Transmission electron microscopy (TEM)

Freshly dissected mandibular glands were transferred to 2.5% glutaraldehyde in 0.1 M sodium cacodylate buffer, pH 7.3 and, after two washes in this buffer, were post-fixed in 1% osmium tetroxide in the same buffer, followed by another rinse in buffer. The samples were dehydrated in a graded acetone series (30%-100%) and embedded in Epon-Araldite mixture. Semithin sections were examined by light microscopy after staining with methylene blue and azur II. Ultrathin sections were contrasted with uranyl acetate and lead citrate and then examined in a Phillips CM 100 transmission electron microscope.

RESULTS

The anatomy of the mandibular gland was the same in *S. postica* workers and mature males, and consisted of a bifid sack-like structure (Fig. 1A) that was almost entirely covered with secretory cells (Fig. 1A,B). The secretory cells were spherical and isolated, but were occasionally polyhedric because of compression of the cells. In the latter condition, the cells formed a pseudo-epithelium around the sack-like structure to create a reservoir (Fig. 1A). The reservoir wall was thin (Fig. 1A) and the secretory cells were connected to this wall by a canal (Fig. 3A,C).

The secretory cells contained numerous polymorphic mitochondria, smooth endoplasmic reticulum and polysomes (Fig. 2A). Each secretory cell had a conducting canal (Figs. 2B and 3A) that released secretion into the reservoir (Fig. 3C). This conducting canal consisted of an intracellular portion that traveled around the entire cytoplasm and collected the secretion (Fig. 2B), and an extracellular portion that was produced by another non-secretory cell and had a large nucleus and little cytoplasm (Fig. 3C). The conducting canal opened directly into the reservoir lumen after perforating the layer of cells and cuticle in the reservoir wall (Fig. 3C). The intracellular portion of the conducting canal was lined by a cuticle in which it was possible to distinguish two layers. An inner, thin, electron-dense interrupted space by space, this corresponds to the epicuticle. The outer layer is thick, porous and expands into a labyrinth formed by folds of the secretory cell plasma membrane around the canal, increasing the releasing, as well as, absorption area of secretion into the canal

(Figs. 2B and 3A). This outer layer corresponds to a procuticle. The mandibular gland reservoir consisted of an epithelium with flat cells and elongated nuclei in which the inner epithelial surface was covered by a cuticle (Fig. 3B,C).

The ultrastructure of the mandibular gland cells in workers varied according to age and the tasks being done. In newly-emerged and nurse workers, the cytoplasm was well developed (Fig. 4A-D), although some vesicles contained membranous structures (Fig. 4A,B). The gland cells of these workers had a well developed smooth endoplasmic reticulum (SER) and many polymorphic mitochondria rich in cristae and with an electron-lucent matrix (Fig. 4A-C), in addition to a large number of polysomes (Fig. 4A-C). In nurse workers, there was a well developed Golgi complex (Fig. 4C) and material was seen being released into the lumen of the collecting canal (Fig. 4D).

The nuclear chromatin of the secretory cells of forager workers appeared condensed (Fig. 5A) and the cytoplasm contained numerous vesicles derived from the SER (Fig. 5A,C). Some of the vesicles had ribosomes attached to them and formed small regions of

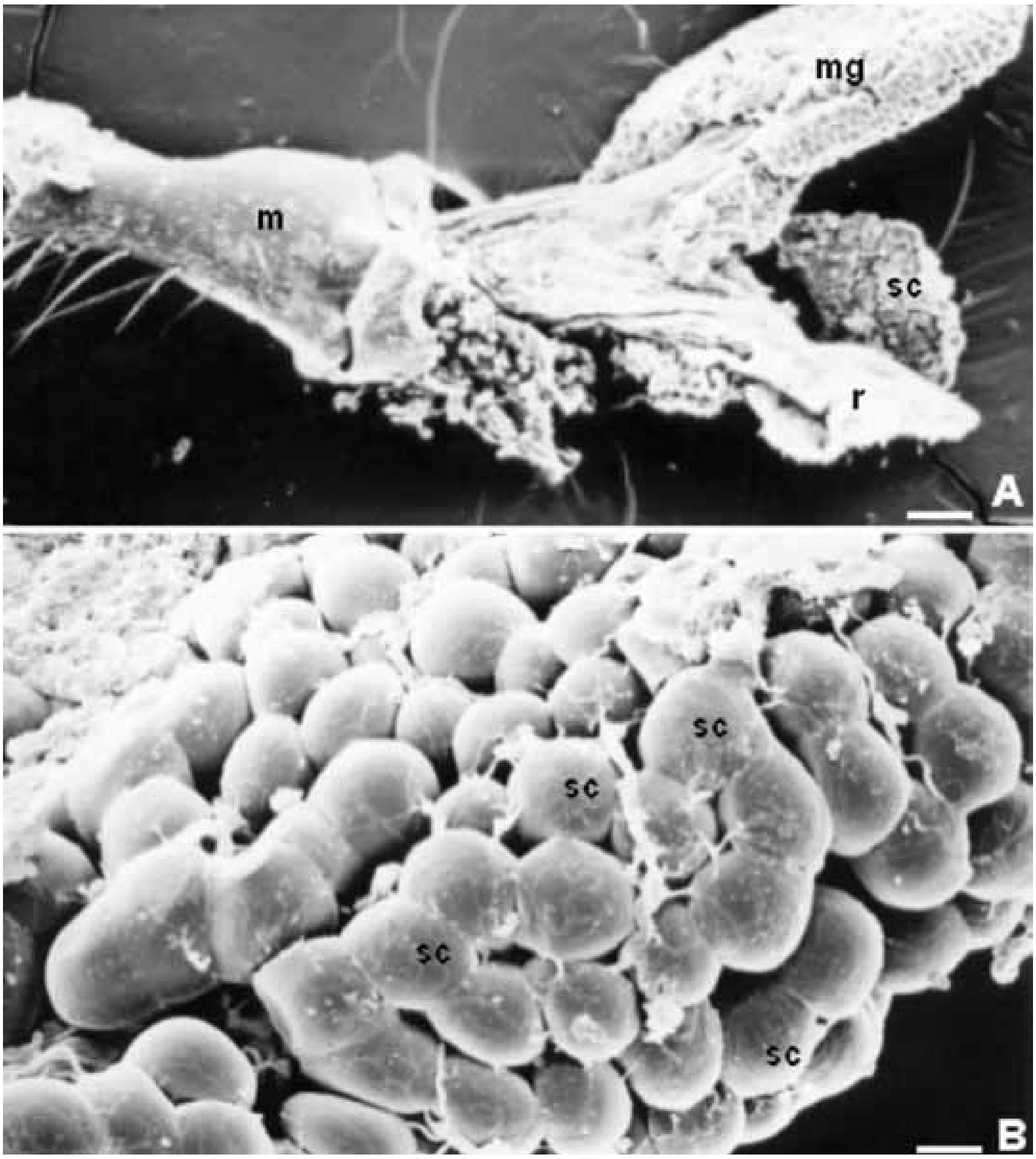


Figure 1. Scanning electron micrographs of the mandibular glands of *S. postica* workers. **A**. General view of the gland anatomy (Bar = 150 µm). **B**. Aspect of the gland secretory units and secretory cells (**sc**) (Bar = 50 µm). **m**= mandible, **mg** = mandibular gland; **r**= reservoir.

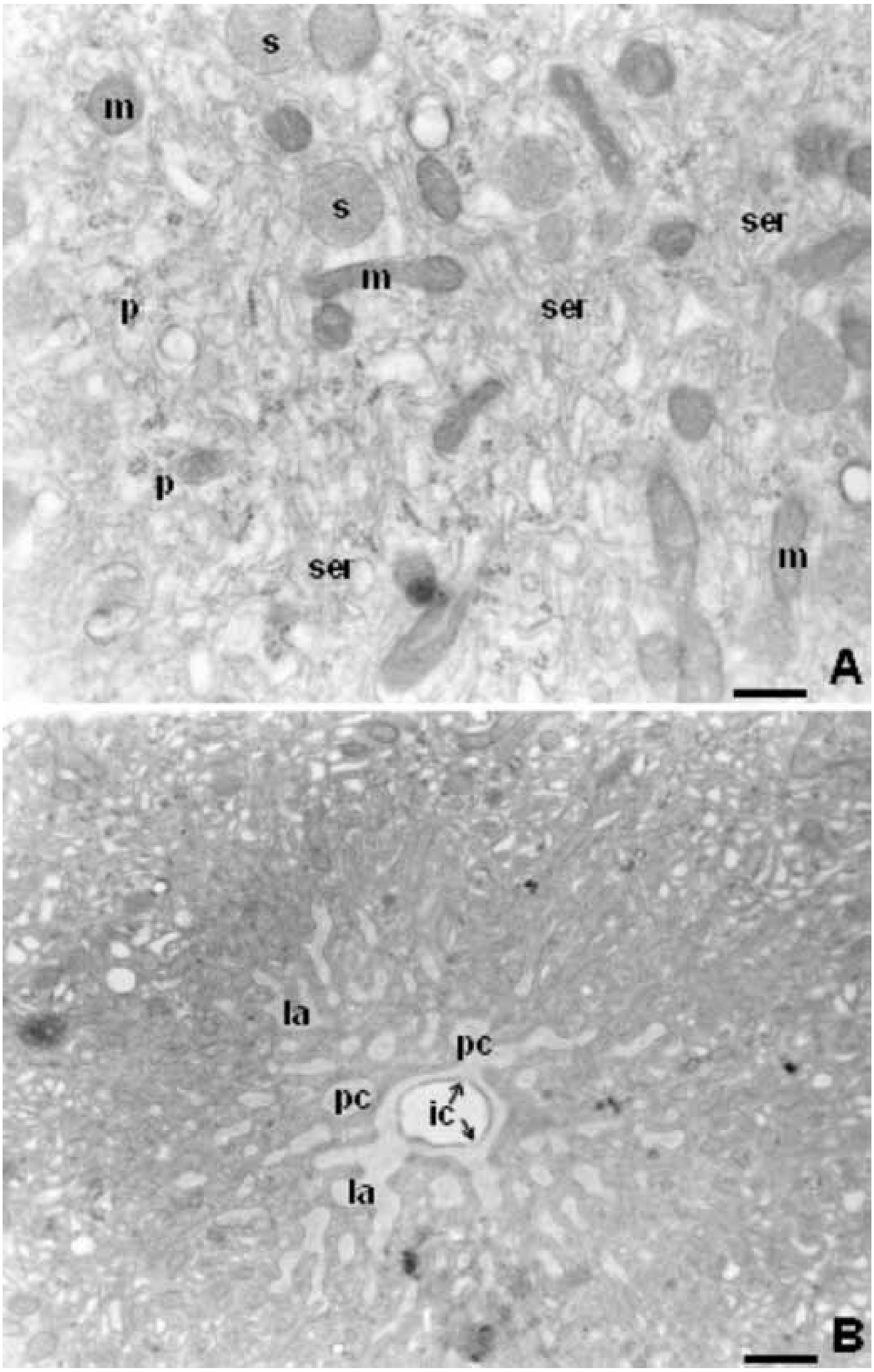
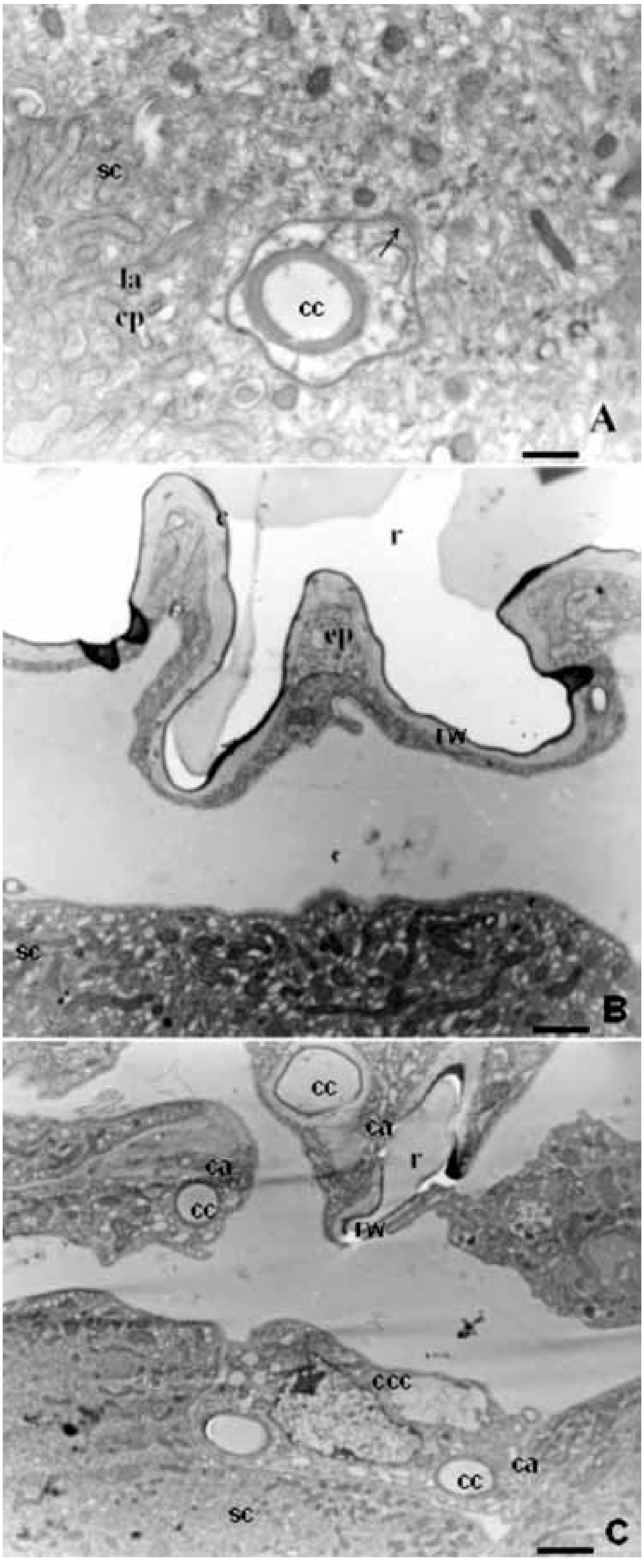


Figure 2. Transmission electron microscopy of the secretory portion of a cell in the mandibular gland of an *S. postica* worker. **A**. Cytoplasmic portion, showing smooth endoplasmic reticulum (**ser**), mitochondria (**m**), polysomes (**p**) and secretory granules (**s**) (Bar = 1.7 µm). **B**. Intracellular portion of the conducting canal (**ic**). Note that the epicuticle has interruptions (**arrows**) and that the porous procuticle (**pc**) branches into a labyrinth (**la**) formed by folds of the plasma membrane of the secretory pole of the cells (Bar = 1.2 µm).



rough endoplasmic reticulum (RER) (Fig. 5C). Some cytoplasmic portions containing RER appeared to be sequestered by membranous involucres that formed autophagic vacuoles (Fig. 5A,B). Two types of mitochondria were observed: one with an electron-lucent matrix (Fig. 6A-C) and the other with electron-dense matrix and tubular cristae (Fig. 5C,D); both were polymorphic and had numerous cristae. The morphology of the secretory granules varied considerably, with some having an amorphous content (Fig. 5C) while others had membranous lamellae and electron-dense dots (Fig. 5D).

The secretory cells of mature males were similar in appearance to those of foraging workers, with the nucleus containing condensed chromatin and the nucleoli having clearly defined fibrillar and granular regions (Fig. 6B). The cytoplasm also contained a well developed vesicular SER (Fig. 6A) and polymorphic mitochondria with an electron-dense matrix and tubular cristae (Fig. 6B,D). The glandular cells of mature males also contained secretory granules consisting of membranous lamellae and electron-dense dots (Fig. 6D). An extensive labyrinth formed by the cell plasma membrane was observed around the collecting canal (Fig. 6A). Some corpuscles of an unknown nature containing internal membranous structures and a paracrystalline portion were also observed (Fig. 6C).

Figure 3. A. Collecting canal of a secretory cell in the mandibular gland of a *S. postica* worker. Note the presence of cytoplasm close to the collecting canal (**cc**), with the labyrinth (**la**) formed by folds of plasma membrane from the secretory cell (**sc**). Branches of the porous portion of the cuticle (**cp**) are also visible. Note the collecting canal and the septate junction with the secretory cell (**arrow**) (Bars= 1.5 µm). **B** and **C**. General view of the relationship between the secretory cell (**sc**) and reservoir (**r**). **B**. Reservoir wall (**rw**) formed by flat epithelial cells (**ep**) lining the lumenal face of the cuticle (**c**). **C**. Collecting canal cell (**ccc**) in the apical portion of a secretory cell (**sc**). Note the presence of portions of other canal cells (**ca**) with the collecting canal (**cc**) located in the space between the secretory cell and the reservoir wall (**rw**) (Bars = 1.7 µm).

DISCUSSION

The results described here show that the secretory cells of the mandibular gland of *S. postica* secrete a lipid-rich material that is produced by the abundant SER. Costa-Leonardo [7] also observed abundant SER, Golgi complexes, ribosomes and secretory granules in the cytoplasm of the secretory cells in *A. mellifera* foraging workers. In *L. limao* [10] and *Melipona bicolor* [17], the mandibular gland cells contain little RER compared to the abundant SER and mitochondria, the latter probably being involved in lipid metabolism [5]. In contrast, the secretory cells of *O. tataira* may be considered an exception because of their very well developed RER [27]. The presence of a well developed SER and polyribosomes suggests that the SER is involved in lipid synthesis and that polyribosomes are involved in the synthesis of intracytoplasmic proteins, e.g., enzymes involved

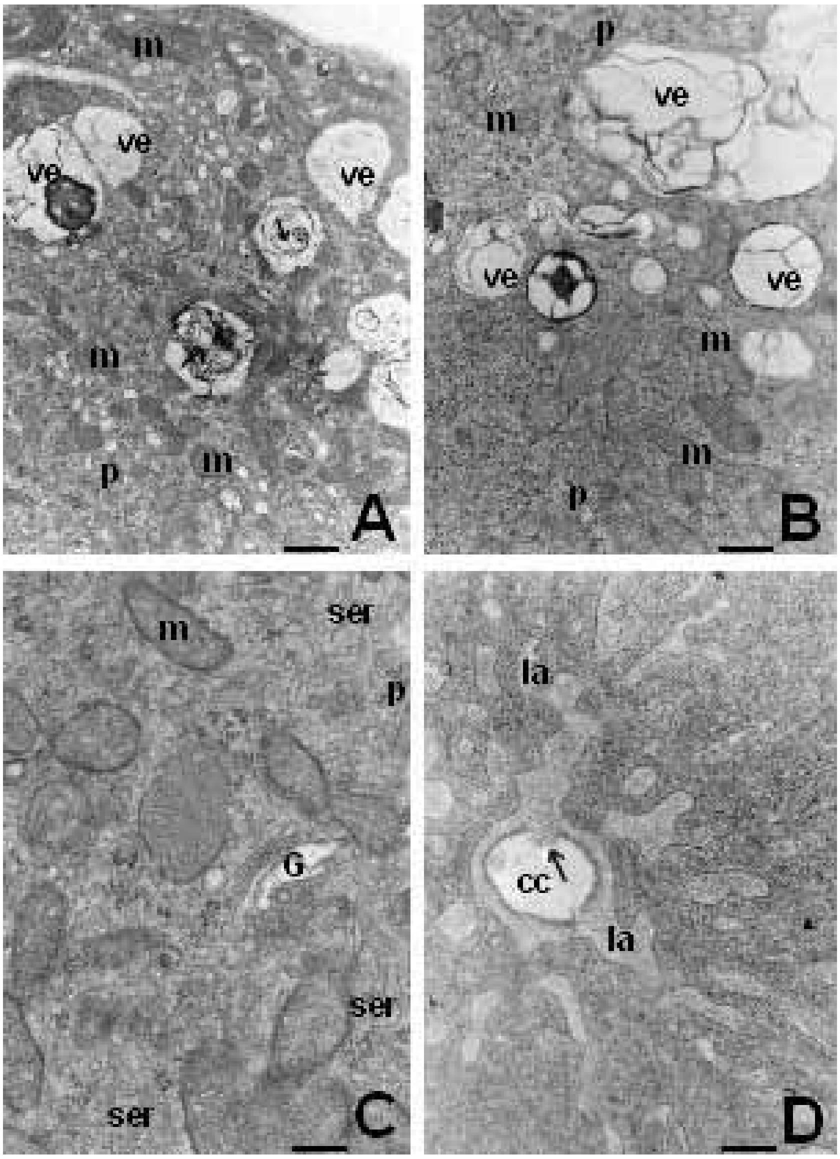


Figure 4. Electron micrograph of cytoplasmic portions of a secretory cell in the mandibular gland of a newly emerged *S. postica* worker (Bars = 1.5 µm). **A**. Periphery of a mandibular gland secretory cell in a newly emerged worker showing vesicles (**ve**) with membranous remnants (**arrows**), polysomes (**p**) and mitochondria (**m**). **B**-**D**. Cytoplasmic portion of a secretory cell in the mandibular gland of a nurse worker. **B**. Peripheral vesicles (**ve**) similar to those seen in newly emerged worker. Note the mitochondria (**m**) and polysomes (**p**). **C**. Cytoplasmic portion containing numerous mitochondria (**m**), smooth endoplasmic reticulum (**ser**), polysomes (**p**) and Golgi complex (**G**). **D**. Detail of a collecting canal (**cc**) showing the release of secretion (**arrow**) and the surrounding labyrinth (**la**).

in lipid synthesis or structural proteins that are important for cellular maintenance [2].

These results reinforce the idea that the mandibular gland is primarily a pheromone-producing gland and that the nature of the secretion varies among species and/or among castes, age groups and gender in the same species. In *L. limao,* the mandibular glands produce alarm and recruitment pheromones [3] while in *O. tataira* these glands produce caustic substances for defense against predators [20]. Consequently, gland cells that produce different compounds may also vary morphologically since morphology and function are directly linked. However, the secretory cells of *M. bicolor* [17] have an ultrastructural profile similar to that of *S. postica*, which suggests that the nature of their secretory compounds may be similar.

Mitochondrial polymorphism is a curious and constant occurrence in insect glandular cells. According to Quennedey [24,25] and Caetano *et al.* [5], these organelles may be directly involved in the biosynthesis of a lipid-rich secretion, although there is no clear evidence for mitochondrial involvement in this phenomenon. According to these authors, active mitochondria show very characteristic features, including dense granules containing material of a lipid nature that makes the matrix electron-dense and numerous tubular cristae such as those seen here in foraging workers and males.

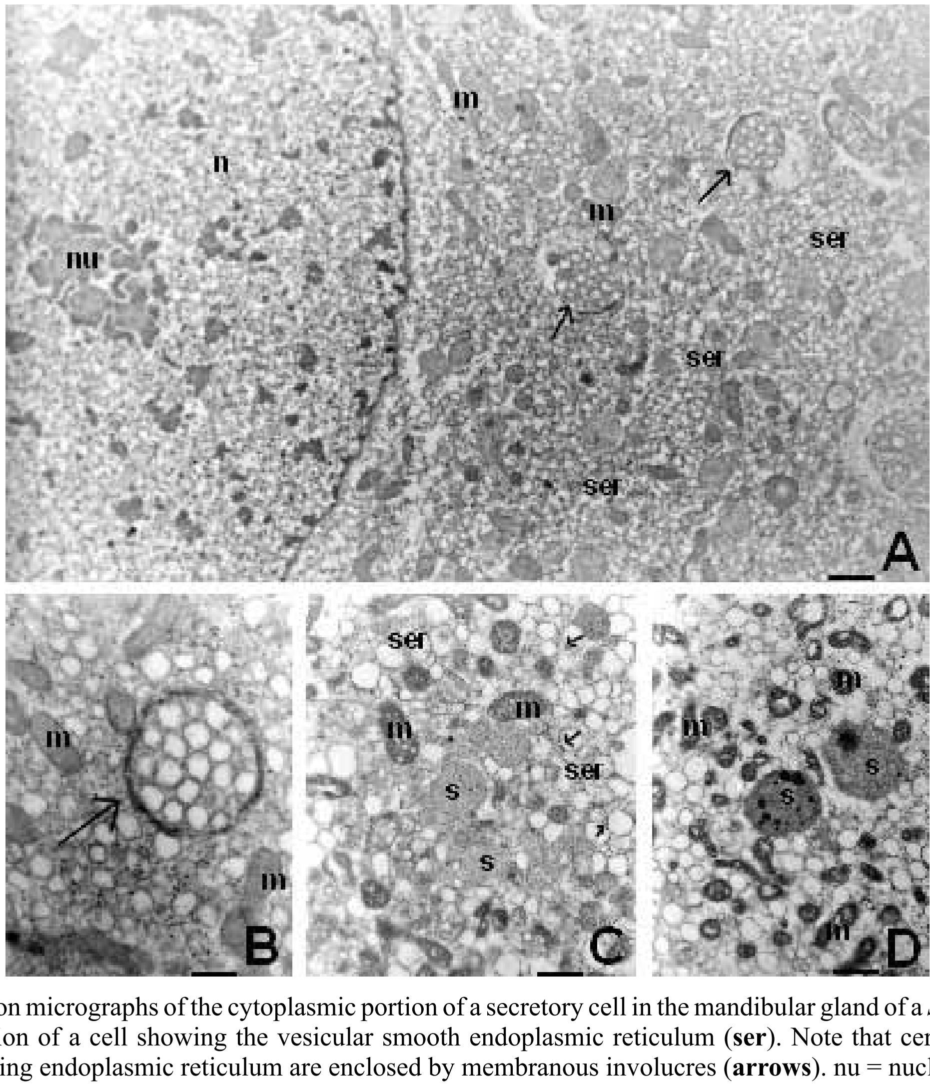


Figure 5. Electron micrographs of the cytoplasmic portion of a secretory cell in the mandibular gland of a *S. postica* forager worker. **A**. Portion of a cell showing the vesicular smooth endoplasmic reticulum (**ser**). Note that certain cytoplasmic portions containing endoplasmic reticulum are enclosed by membranous involucres (**arrows**). nu = nucleoli, n = nucleus (Bar = 2 µm). **B**. Detail of the enclosed endoplasmic reticulum (**arrow**). **C**. Cell with smooth endoplasmic reticulum (ser), but containing granule secretion (**s**) with an amorphous content and mitochondria (**m**) with electron-dense matrix ad tubular cristae. Note the endoplasmic reticulum vesicle with ribosomes attached (**arrows**). **D**. The same as in C, but showing secretory granules (**s**) containing membranous lamellae and electron-dense dots. B-D. Bars = 1.5 µm.

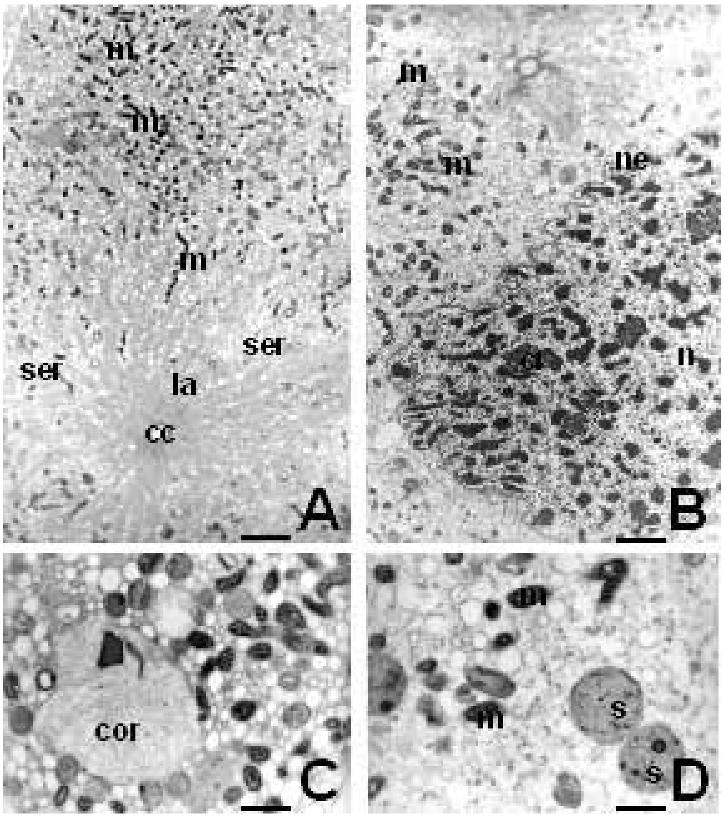


Figure 6. TEM of the cytoplasmic portion of a secretory cell in the mandibular gland of an *S. postica* male. **A**. General view of a cell showing its collecting canal (**cc**) surrounded by a labyrinth (**la**), and the remaining cytoplasm rich in mitochondria (m) and smooth endoplasmic reticulum (**ser**). **B**. Secretory portion of the cell showing the nucleus (**n**) with condensed chromatin (**cr**) and sinuous nuclear envelop (**ne**). Note the mitochondria (**m**) with electron-dense matrix and tubular cristae. A and B Bars = 1.7 µm. **C**. Detail of the cytoplasm showing a corpucle (**cor**) of unknown nature containing membranous elements and a paracrystalline portion. **D**. detail of the cytoplasm showing secretion (**s**) and mitochondria (**m**). **C** and **D** Bars = 1.2 µm.

As shown here, the secretory vesicles and granules varied in form, electron-density and size among the workers and males. This variation may indicate differences in glandular function among these cells. In the gland cells of newly-emerged and nurse workers, the secretion had a homogenous appearance and medium electron density. Vesicles containing membranous debris were also seen in these workers and may have resulted from the release of secretion, i.e., the vesicle plasma membrane became convoluted following release of the vesicular contents.

The cytoplasm of foraging workers and mature males contained abundant secretory granules with membranous lamellae and electrondense dots. A similar morphology in *Blaberus craniifer* was attributed to the presence of granules of glycoproteins [26]. Secretory granules similar to those seen here have also been observed in the mandibular glands of physogastric queens of *M. bicolor* [17]. Morphological analysis in *M. bicolor* [16] and in *S. postica* [14], as well gas chromatographic and mass spectrometric analyses in *M. bicolor* [15] have shown this secretion to contain lipids. Abdalla and Cruz-Landim [1] suggested that the formation of membranous lamellae in granules is a natural phenomenon and not the result of autophagy since these granules are always present in lipid-producing glands and assume a lamellar arrangement in a hydrophilic environment. Functionally, lamellar granules may represent an important stock of secretion.

Foraging workers and males had similar types of mitochondria and a similar ability to store secretion. This similarity suggests that the mandibular glands of these bees may produce compounds of the same chemical nature, but not necessarily the same compound or function, nor that the secretions will provoke the same behavioral response. In

Trigona subterranea, the citral released at low concentrations acts as a trail pheromone whereas at high concentrations this compound acts as an alarm pheromone [4]; in addition, *L. limao* also uses citral as a repellent against predators. Hence, the presence of the same or similar compounds in the same species does not necessarily imply the same functions, particular since the precise response will vary according the secretion blend and concentration, as well as the target involved and its physiological state at a given moment.

In conclusion, the mandibular glands of *S. postica* workers continuously produce secretion that is released from vesicles in newly-emerged and nurse workers within the colony. In foraging workers and mature males, this similarity is reflected in the types of mitochondria involved in secretion production and in the composition of the secretion. Mitochondria may play a role in lipid secretion, although the secretion itself may not have the same function in foraging workers and mature males.

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