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Morphology and ultrastructure of the prepharyngeal and pharyngeal glands in the ant *Camponotus japonicus*

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ABSTRACT

The prepharyngeal gland (prePG) and pharyngeal gland (PG) make up the largest exocrine structures in the head of the ant *Camponotus japonicus*. We used microscopy to study the histological and ultrastructural features of both glands in different castes. The number of secretory units in the prePG is considerably higher than in other ant species and shows a complex duct system which is made up by duct cells, secondary ducts and a main duct. These lead the secretions of hundreds to thousands of secretory cells into the prepharynx through a modified sieve plate at each side. The glove-shaped PG shows clear caste differences in tubule number. The ultrastructure of both the prePG and PG shows abundant mitochondria and secretion vesicles. Moreover, the prePG is loaded with rough endoplasmic reticulum (RER) which means its main secretions are proteinaceous compounds, while the PG is dominated by smooth endoplasmic reticulum (SER) which means the main secretions are lipids. The morphological differences like cell number of the prePG and tubule number of the PG indicate different secretory abilities of each caste. We for the first time introduce histology-based relative size to indicate secretory activity. The proportionally high development of the prePG in minor workers supports a role in trophallaxis.

1. Introduction

Ant societies are superorganisms composed of tens to millions of individuals (Hölldobler and Wilson 1990). They are characterized by a magnificent colony organization and communication system that is based on secretions from various exocrine glands that are found throughout the ants' body (Billen, 2009). The size and morphology of these glands are closely related to their function and are obviously different among ant species, even among castes in the same species (Niculita et al., 2007).

The prepharyngeal gland (prePG, also known as propharyngeal gland previously) and pharyngeal glands (PG, formerly known as postpharyngeal gland) are the most prominent glands in the head of ants, and are present in all castes (Billen, 2009). In some old literature, the prePG has been wrongly described as maxillary gland (Bausenwein, 1960; McFarlane, 1961; Kürschner, 1971; Phillips and Vinson, 1980) or hypopharyngeal gland (Gama and Cruz-Landim, 1982; Wilson, 1980). There have been several studies that focus on the morphology and ultrastructure of the prePG in ants (Phillips and Vinson, 1980; Gama and Cruz-Landim, 1982; Billen et al., 2013). However, a clear proof of its function is still lacking.

The pharyngeal gland has long been called postpharyngeal gland. Richter et al. (2019) revised the name as pharyngeal gland according to its precise opening position where it discharges secretions. It occurs in all castes and males of all studied ant species (Billen et al., 1990). Compared with the prePG, there are more studies that focus on the glove-shaped PG as the secretions can be stored in the finger-like tubules which make it possible to analyze the secretion composition. Studies about the PG deal with the morphology, secretion composition and possible function of the gland. Bagnères and Morgan (1991) analyzed the chemical composition and compared it with the content of the cuticular

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hydrocarbons in *Formica selysi*, *Camponotus lateralis*, *Camponotus vagus* and *Manica rubida*, and found that their chemical profiles are similar. They therefore concluded that the PG in these four studied ant species is one of the sources of cuticular hydrocarbons. The PG is also thought to provide the whole colony with the gestalt recognition pheromone which can be transferred through the colony members by trophallaxis and allogrooming (Soroker et al., 1994). Apart from this, it has also been speculated that the PG has a function in digestion, caste determination, or food provisioning (Eelen et al., 2006).

C. japonicus is one of the most pervasive ant species in eastern Asia. It is monogynous and polymorphic, showing obvious division of labor (Wu and Wang, 1995). All female castes and the males of this species have a fairly large body size (see below for body sizes). All these features make it an ideal species to study the histological organization of specific organs and caste division in social insects. We aim to examine the function of the prePG and PG in *C. japonicus* in several steps. In this study, we report on their morphology and ultrastructural characteristics.

2. Materials and methods

2.1. Ant material

Newly inseminated young queens (body length 14.74 ± 0.20 mm, head width 3.13 ± 0.10 mm), major (body length 12.6 ± 0.20 mm, head width 3.52 ± 0.03 mm) and minor workers (body length 9.65 ± 1.39 mm, head width 2.16 ± 0.26 mm) and males (body length 9.99 ± 0.70 mm, head width 1.52 ± 0.11 mm) of *C. japonicus*, were collected from the edge of fields and forests in Yangling, Shaanxi province of China. The ants were first refrigerated at −20 °C for 10 min to make them less active, and dissection was done under a Leica EZ4HD microscope.

2.2. Light microscopy

The heads of 5 males, 4 minor workers, 3 major workers and 2 queens were separated from the body by making a transverse cut at the level behind the compound eyes to allow the various chemicals used during tissue processing to enter the head capsule. The heads were fixed in 2.5% cold glutaraldehyde, buffered in 0.05 M Na-cacodylate (pH 7.2) for 12 h, postfixed with 2% cold osmium tetroxide for 2 h, and dehydrated in a graded acetone series. After embedding in Araldite, the samples were sectioned in longitudinal or transverse direction with a Leica EM UC6 ultramicrotome at a thickness of 1 or 2 μm. The sections were stained with 1% methylene blue. Serial semithin sections were examined with an Olympus BX-43 microscope which is connected to an Olympus DP25 camera. Longitudinal images are shown with the anterior to the left.

In order to evaluate the size of the prePG, the numbers of secretory units in each caste were counted (method described in Xu et al., 2021). However, the head size which can significantly affect the size and secretory capacity of the prePG varies considerably among different female castes and males. We used number of gland cells per head volume and the ratio of gland cell and head volume to indicate the size and capacity of the prePG. To measure head volume, we first put 5 entire heads into a 200 μl Eppendorf tube that was filled up to the rim with a 0.65% NaCl solution. Then the liquid that was expelled after adding the 5 heads was collected with a microsyringe and measured. To compare differences among castes, a Mann−Whitney U test followed by the Benjamini−Hochberg method using false discovery rate calculation was operated in R. We used corrected *p*-values (0.05) to indicate the significance of difference.

2.3. Scanning electron microscopy (SEM)

At least 24 individuals (6 individuals of each female caste and 6 males) were dissected in Ringer's physiological solution to prepare the prePG and PG for SEM observation. The dissected glands were fixed in 2.5% cold glutaraldehyde with 0.2 M Na-phosphate (pH 7.2) for 12 h, dehydrated in a graded ethanol series and transferred to isoamyl acetate. The samples were critical-point dried with an Emitech K850 instrument and gold-coated with a Hitachi E−1045 sputtering device. Observation and recording were done under a Hitachi S4800 scanning electron microscope.

2.4. Transmission electron microscopy (TEM)

We dissected at least 3 prePG and 3 PG for each female caste as well as for males in Ringer's physiological solution for TEM microscopy. Tissue processing was the same as for light microscopy. Embedded tissues were sectioned at a thickness of 70 nm. The sections were double-stained with 3% lead citrate and 4% uranyl acetate. The sections were examined with a Zeiss EM900 electron microscope.

3. Results

3.1. Morphology and ultrastructure of the prePG

The prePG of *C. japonicus* is a paired gland which is made up by two clusters of secretory units on both sides of the ventral pharynx and over and behind the infrabuccal pocket (Fig. 1 and Fig. 2A and D). The number of secretory units shows significant differences among castes, major workers having the highest cell number (4889 ± 203), then queens (3371± 177.2) and minor workers (1586 ± 279.5), and males the lowest (635 ± 83) (Table 1 and Table 2). As cell diameter also depends on caste with the largest cells occurring in queens and the smallest in males, consideration of overall secretory capacity needs to take into account both cell number and cell size. Following this adjustment, minor workers proportionally have the largest prePG, followed by major workers, while queens and males have a similar relative gland size (Fig. 3 and Table 1).

Although each secretory unit consists of one duct cell and one spherical secretory cell (Fig. 2E), the secretions reach the prepharyngeal plate through a considerably elongated sieve plate at each side (Fig. 2A and B) via a complex duct system. The duct cells (with an internal diameter around 1 μm) first group together in bundles that open into a secondary duct which has an internal diameter around 3 μm (Table 2, Fig. 2C). The secretions received from the secretory units are further transported into a single large tube-shaped main duct which opens at each side into the prepharynx (Fig. 2). Bundles of duct cells can also open directly into the main duct. The main duct is considerably broader in major workers and queens than in minor workers and males (Table 3).

Each duct cell and its associated secretory cell are connected by an end apparatus which contains dense microvilli with a length of 2.5 μm (Fig. 4A, D, E and F). The cytoplasm of the secretory cells contains a well-developed rough endoplasmic reticulum (RER), numerous mitochondria and Golgi apparatus (Fig. 4B, C, D and E). We also found a large amount of secretory vesicles as lipid droplets, lamellar and granular inclusions. Most of these vesicles have a maximum diameter of 1 μm.

3.2. Morphology and ultrastructure of the PG

The PG is an epithelial gland with reservoir. The glove-shaped gland extends from the dorsal side of the postpharynx, the

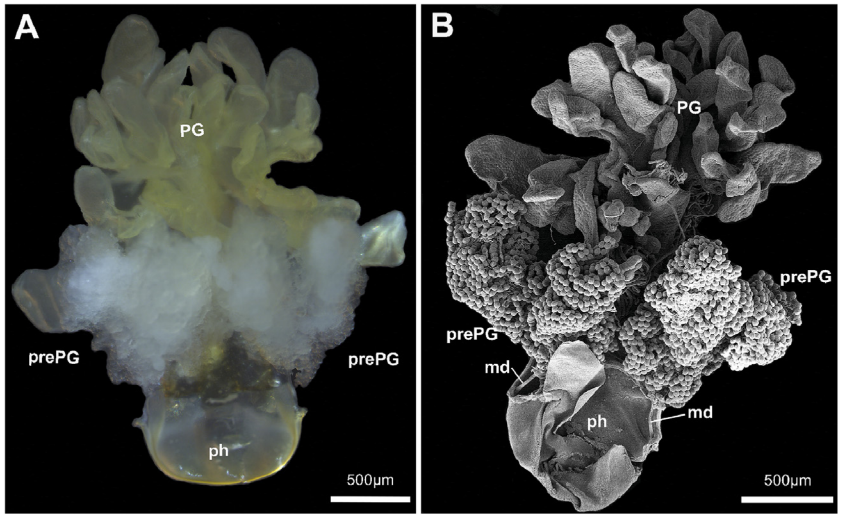

Fig. 1. Ventral view of the pharynx with attached prePG and PG in major worker. **A**. Light microscopy of dissection view; **B**. Scanning micrograph. prePG: prepharyngeal gland; PG: pharyngeal gland; ph: pharynx; md: main duct of prePG.

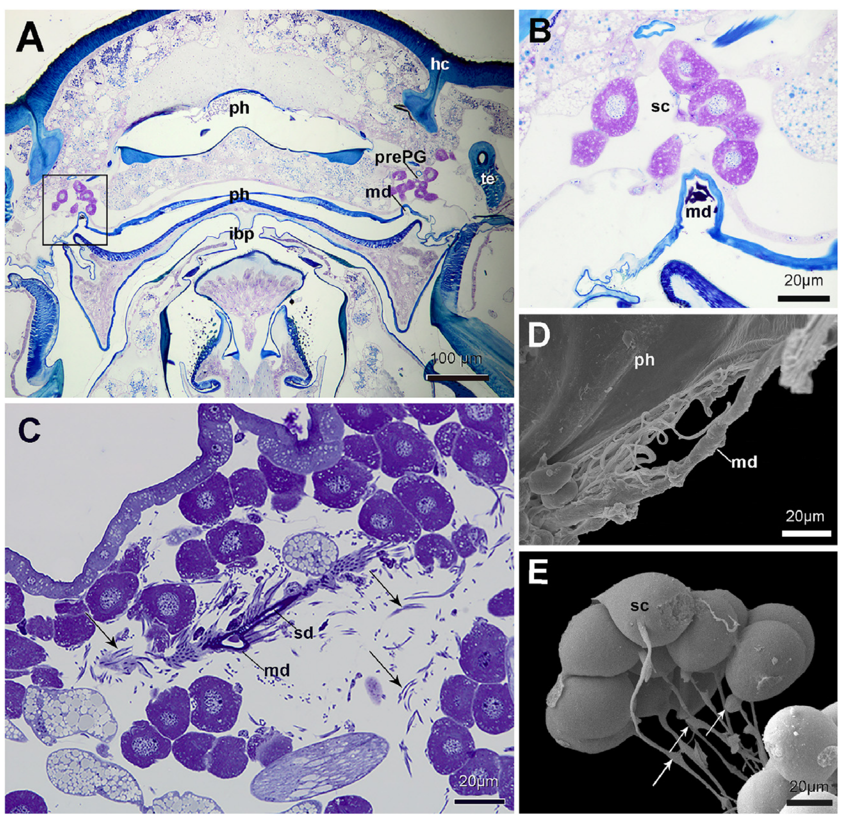

Fig. 2. Prepharyngeal gland. **A**. Transverse semithin section of major worker showing opening of prePG in dorsolateral part of pharynx. **B**. Enlargement of frame in **A**. **C**. Longitudinal semithin section of minor worker showing the duct cells and the connection of secondary duct and main duct. **D**. Scanning micrograph showing main duct in male. **E**. Scanning micrograph of prepharyngeal gland. ibp: infrabuccal pocket; hc: head capsule; md: main duct of prePG; ph: pharynx; prePG: prepharyngeal gland; sc: secretory cells; sd: secondary duct. Arrows mark the duct cells.

number of tubules shows a clear difference among castes (14 in major and minor workers, 10 in queens and males) (Fig. 1A and B, 5A, B). The external surface is characterized by rounded protrusions (Fig. 5D), each protrusion corresponding with the basal part of a secretory cell (Fig. 5C). A clear border of microvilli with a length around 1 μm underneath the lumen-lining cuticle can be seen (Fig. 5E and F). The cytoplasm contains a well-developed smooth endoplasmic reticulum (SER), numerous mitochondria and secretory inclusions with various shapes that can be vesicular, lamellar or electron-dense and granular (Fig. 5G, H and I). Septate junctions can be seen between neighboring secretory cells (Fig. 5E).

Table 1
Summary of head volume, cell diameter and cell number of the prePG in the three female castes and males of *Camponotus japonicus*.

Castes	Cell number (CN)	Cell diameter(d)/μm	Head volume (HV)/μl	CN/HV	GV/HV (%)
Minor worker	1586 ± 279.5	20.25 ± 0.82	2.60	610 ± 107.1	0.26 ± 0.037
Major worker	4889 ± 202.7	21.39 ± 0.78	13.84	353 ± 14.6	0.18 ± 0.029
Queen	3371 ± 177.2	26.97 ± 0.79	14.20	237 ± 12.5	0.10 ± 0.009
Male	635 ± 83.4-	15.91 ± 0.42	1.50	423 ± 55.6	0.09 ± 0.005

Note: GV indicate gland volume, GV = CN × π × $d^3/6$; CN/HV indicates number of gland cells per unit volume. GV/HV indicates relative secretory capacity.

Table 2
p-values of caste-related differences based on CN/HV and GV/HV in *C. japonicus*.

	w vs W	w vs Q	w vs M	W vs Q	W vs M	Q vs M
p-value/(CN/HV)	0.0061	0.0061	0.0037	0.0286	0.1535	0.0040
p-value/(GV/HV)	0.0136	0.0104	0.0012	0.0294	0.0062	0.0440

Note: *p*-value <0.05 and >0.01 indicates significant difference between two castes; *p* value < 0.01 indicates highly significant difference between two castes; w = minor worker, W = major worker, Q = queen, M = male.

Table 3
Measurements of the internal diameter of duct cells, secondary duct and main duct.

Castes	Internal diameter (μm)		
	Duct cell	Secondary duct	Main duct
Minor worker	1.07 ± 0.05	1.18 ± 0.10	5.32 ± 0.26
Major worker	0.95 ± 0.09	2.42 ± 0.48	12.96 ± 0.98
Queen	1.02 ± 0.05	2.42 ± 0.43	15.14 ± 0.5
Male	0.74 ± 0.08	1.73 ± 0.10	4.37 ± 0.17

4. Discussion

4.1. Morphological characteristics and function of the prePG

The prePG in *C. japonicus* belongs to class-3 glands which are made up by subunits of a secretory cell and an associated duct cell (Noirot and Quennedey, 1974). The two clusters of secretory units are arranged at both sides of the pharynx close to the infrabuccal pocket and this morphology is similar to other studied ant species (Bausenwein, 1960; Billen et al., 2013; Billen and Al-Khalifa, 2015). The well-developed RER, numerous mitochondria and Golgi apparatus as well as the huge number of secretory units represent the characteristics of an active prePG. Together with the position of its opening in the prepharynx, these features illustrate the role the prePG may play in digestion and larval feeding (Otto, 1958; Ayre, 1967; Billen et al., 2013; Boonen and Billen, 2016).

To secrete more chemicals, both the size and number of secretory cells are increased in the developed class-3 glands (Cruz Landim, 1998). According to previous studies, the prePG in *C. japonicus* is much bigger than in other studied species (Boonen and Billen, 2016). The duct cells in the previously studied ant species usually open through a sieve-like plate on the prepharynx (Amaral and Caetano in *Atta sexdens rubropilosa*, 2005; Billen and Al-Khalifa in *Brachyponera sennaarensis*, 2015) or into an atrium before discharging the secretions into the prepharynx (Billen et al., 2013 in *Protanilla wallacei*; Boonen and Billen, 2016 in *Monomorium pharaonis*; Billen et al., 2016 in *Myrmoteras iriodum*) (Fig. 6). In these cases, with the increase of cell number, the sieve-like opening plate would need to be very large. In the present study of *C. japonicus*, we for the first time found a much more complex duct system in the prePG. We consider that this complex duct system may be a good substitution for the sieve plate of a well-developed class-3 gland. In this way, thousands of secretory units need only one single opening site in the oral cavity. Although there is no reservoir, the elongated duct system can store secretions temporarily. The diameter measurement of the main duct and secondary duct shows that they get broader when there are more secretory cells. We speculate that this conspicuous duct system may correspond with the phylogenetic status of ants, more evolved species having a more complex organization of their prePG duct system. An interesting comparison can be made with the ants' metapleural gland, in which the secretory cells also open through a sieve plate into the reservoir space. In the majority of species, a single sieve plate is found, whereas in species with large cell numbers, the ducts are grouped in bundles that open through multiple sieve plates (Billen et al., 2011). In both glands, high cell numbers go along with more specialized duct arrangements to enable all cells to connect to the reservoir. More studies on the ants' prePG are needed to confirm this speculation.

In addition, in earlier studies myrmecologists usually just counted gland cell number to indicate the size of the prePG (Bausenwein, 1960; Boonen and Billen, 2016). However, the overall size of glands can also be affected by head size differences significantly. In this study, we therefore for the first time introduced

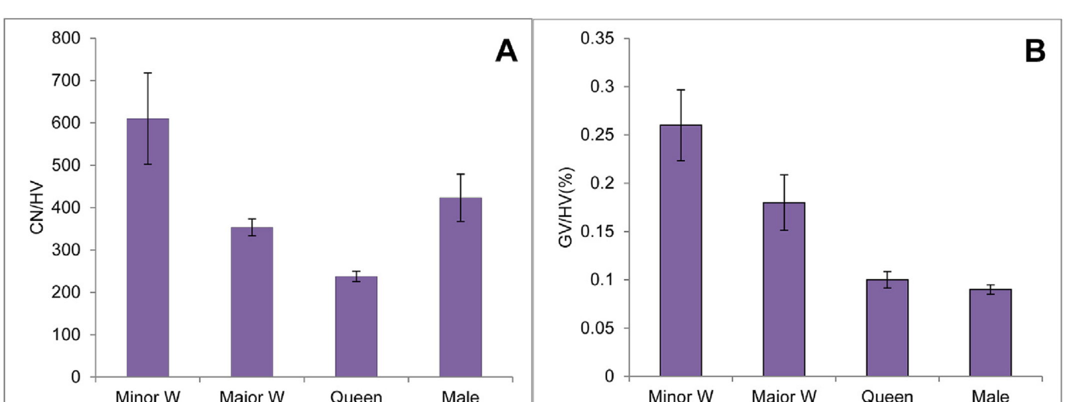

Fig. 3. Bar graph of gland cell number per head volume (CN/HV) and gland volume per head volume (GV/HV) in the three female castes and males.

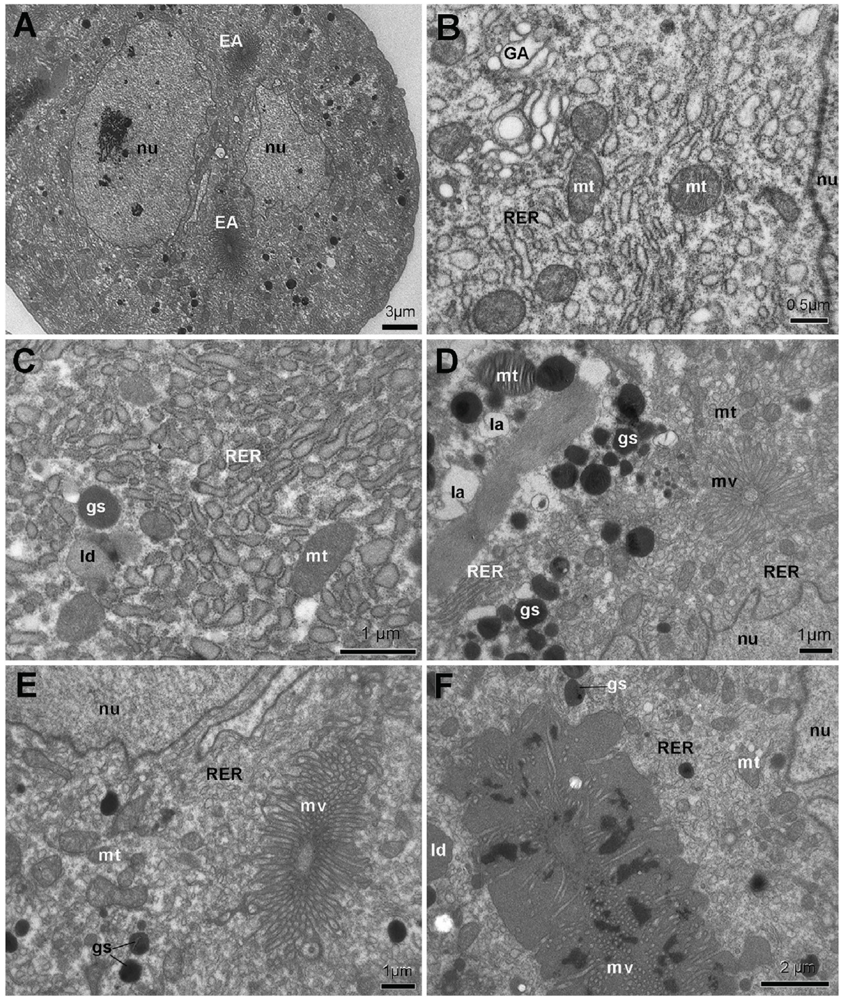

Fig. 4. Electron micrograph of prePG. **A**, **B** and **D-F** gyne; **C** major worker. **A**. Survey view of a secretory cell showing end apparatus and nucleus. **B**–**F**. Details of organelles and end apparatus. EA: end apparatus; GA: Golgi apparatus; gs: granular secretion; la: lamellar secretion; ld: lipid droplet; mt: mitochondria; mv: microvilli; nu: nucleus; RER: rough endoplasmic reticulum.

histology-based relative size to indicate the secretory activity of the prePG in each caste. The results show that queens and major workers show the highest absolute cell number, although minor workers exhibit the highest relative secretory activity. Wilson (1980) was the first to study gland development relative to worker size, making rather rough size measurements under a dissection microscope. He showed that the disproportionate variation of gland size can be a clue to speculate about the role of an unstudied gland. He also showed that the largest proportionally developed organ may serve the tasks the corresponding caste performs (Wilson, 1980). In another separate study about trophallaxis in *C. japonicus*, we found that minor workers take part in 76.3% ± 1.51% of the trophallactic contacts, major worker in 19.76% ± 0.45%, queens and males together less than 3.95% ± 1.88% (Xu et al., in prep.). We therefore speculate the prePG may take a role in the preparation of endogenous factors that form part of the trophallaxis fluids. This method provides a good reference for the follow-up study of class-3 glands and helps us to more objectively evaluate the gland size of ant species and castes. We need a more functional study of the *C. japonicus* prePG to prove the effectiveness and advantages of this method. We also recommend this method to be used in future studies about gland development along with individual growth.

We also for the first time introduced the liquid displacement method to measure the volume of ants' head instead of confocal image stacks or micro-CT followed by digital reconstruction (Negal et al., 2020; Richter et al., 2021). The latter laborious method requires much more sophisticated equipment conditions. The method we used can be generalized to measure the volume of small samples.

4.2. Morphological characteristics and function of the PG

The epithelial PG in *C. japonicus* belongs to class-1 (Noirot and Quennedey, 1974; Billen and Morgan, 1998). The ultrastructure of the PG, with abundant SER, mitochondria and multiple kinds of secretion vesicles, indicates that the PG of *C. japonicus* has the ability for *de novo* synthesis of lipid secretions. The functions of the PG have long intrigued scientists. Bagnères and Morgan (1991) reported that the composition of hydrocarbons in the PG is similar to the cuticular hydrocarbons and further showed that the PG plays a role in the ants' nestmate recognition. However, nestmate recognition pheromones in ants are a complex of odors from all individuals in the colony (Carlin and Hölldobler, 1986, 1987). Soroker et al. (1994) hypothesized that the PG is a gestalt organ where these odor components in the nest meet and mix, and then act as marker of the whole colony. Whether this "gestalt" hypothesis is applicable in *C. japonicus* needs further study. We aim to examine this question in the future.

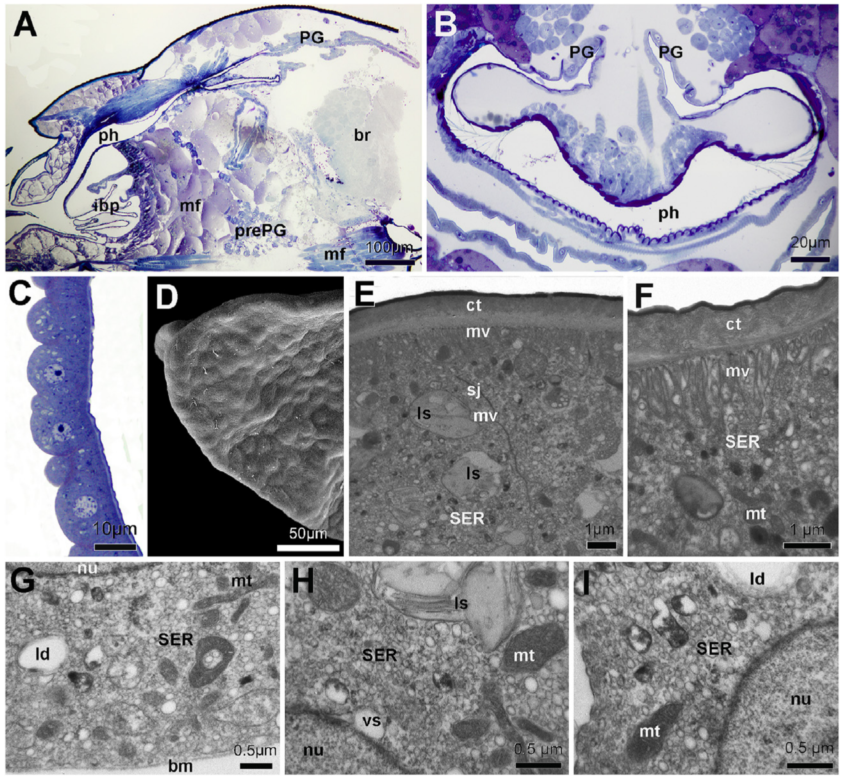

Fig. 5. Pharyngeal gland. **A**. Longitudinal semithin section of minor worker to show opening place of PG into pharynx. **B**. Transverse semithin section of male to show gland opening into pharynx. **C**. Details of rounded protrusion and epithelial gland cells in major worker. **D**. Scanning micrograph of external surface in major worker. **E-I**. Electron micrographs (**E**, **G**, **H** and **I** in minor worker, **F** in male). bm: basement membrane; br: brain; ct cuticle; ibp: infrabuccal pocket; ld: lipid droplet; ls: lamellar secretion; mf: muscle fiber; mt: mitochondria; mv: microvilli; nu: nucleus; PG: pharyngeal gland; ph: pharynx; prePG: prepharyngeal gland; SER: smooth endoplasmic reticulum; sj: septate junction; vs: vesicular secretion.

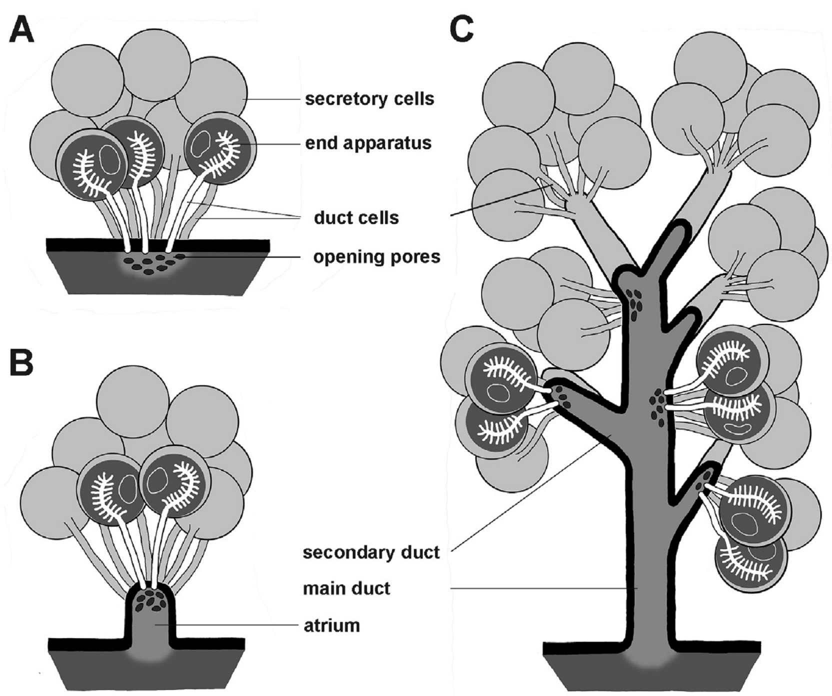

Fig. 6. Schematical representation of 3 duct types of prePG. **A**. prePG with sieve-like opening plate. **B**. prePG with sieve opening in atrium. **C**. prePG with complex duct system.

5. Conclusion

In this study, we reported the general morphology and ultrastructure of the prePG and PG in *C. japonicus* belonging to the different female castes and males. The prePG shows a complex duct system that has never been reported in the ants' prePG previously. We also introduced a new liquid displacement method to measure the volume of small samples and used a precise histology-based measurement of gland volume with respect to head volume to study the relative size of class-3 glands. More studies are needed to prove the effectiveness of this approach.

Author statement

Wenjing Xu, Hong He and Johan Billen conceived the study. Wenjing Xu, Guoyun Zhang, Liangliang Zhang and Xiaolei Wang performed the laboratory and field work. Wenjing Xu, Johan Billen and Hong He wrote the paper. All authors read and approved the final manuscript.

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