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Ultrastructure of the mandibular gland of the ant *Myrmoteras iriodum*

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ABSTRACT

The mandibular gland in workers of the formicine ant *Myrmoteras iriodum* differs from other ants both in its general morphology and ultrastructural organization. The secretory cells appear in a pseudo-epithelial arrangement that gives them a clear polarity. At their apical side, the cells are characterized by a large cup-like extension of the reservoir, from which a bulbous invagination connects to a branched end apparatus. At the basal side, the cells show a labyrinth of basal invaginations, while the lateral cell contacts show clear interdigitations. The cytoplasmic composition reveals the presence of numerous round or elongate inclusions that contain crystalline material. Microtubules are abundant, and locally fibrillar regions are found. The function of the mandibular gland in *M. iriodum* has not yet been documented, and should be studied using gland extracts and behavioural observations.

1. Introduction

Species of the tropical Asian ant genus *Myrmoteras* Forel have an unusual predatory strategy. The small colonies live in the litter, and feed on a variety of soft-bodied arthropods such as springtails. The workers are trap-jaw predators, that during prey hunting rely on their extremely long and slender mandibles (Moffett, 1986). We recently performed a study of the general exocrine system in the workers of *Myrmoteras iriodum* Moffett, which revealed the presence of a well-developed intramandibular gland along the entire length of the mandibles (Billen et al., 2015). That mainly light microscopal study also revealed that the mandibular gland had an unusual appearance. The mandibular gland corresponds with class-3 (classification of Noirot and Quennedey, 1974; Billen and Šobotník, 2015), which means it is formed by a number of bicellular units, each unit comprising a secretory cell and a duct cell. The junction of both cells in each unit is known as the end apparatus. This structure is a continuation of the cuticular duct which inside the secretory cell is surrounded by a sheath of surface-increasing microvilli, that allow efficient drainage of the secretory products. We noticed the end apparatus has an unusual branched appearance (Billen et al., 2015), but at that time unfortunately did not have any material available to look in more detail at the ultrastructural organization of this unusual mandibular gland. During a recent field trip in Malaysia, however, we managed to collect fresh material of *M. iriodum*, which now allows us to report on the ultrastructure of the mandibular gland of these ants.

2. Material and methods

Foraging workers of *M. iriodum* Moffett, 1985 were collected in Ulu Gombak, peninsular Malaysia. The mandibular glands (n = 10) were dissected from the head and fixed in cold 2% glutaraldehyde, buffered at pH 7.3 with 50 mM sodium cacodylate and 150 mM saccharose. Postfixation was done in 2% osmium tetroxide in the same buffer. After dehydration in a graded acetone series, tissues were embedded in Araldite and sectioned with a Leica EM UC6 ultramicrotome. Semithin sections of 1 μm were stained with methylene blue and thionin and viewed with an Olympus BX-51 microscope. Thin sections of 70 nm were double stained with lead citrate and uranyl acetate and examined with a Zeiss EM900 electron microscope.

3. Results

The paired mandibular gland occurs in the anterior region of the head near the basal margin of the compound eye. It is formed, at each side, by a thin-walled, cuticle-lined reservoir and a cluster of 25–30 large secretory cells near the inner ventral side. The cells have a length of 40–45 μm and a width of 15–20 μm (Figs. 1 and 2).

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At their apical side, the secretory cells show a big cuticular cup with a diameter of 4–5 μm and a depth of up to 10 μm that is formed by an extension of the reservoir. The bottom of each cup connects to a bulbous proximal portion of the end apparatus with a diameter around 3 μm. From the dark-staining bulbous part, 3–4 straight blind-ending branches on a sectional view continue into the deeper regions of the cell (Figs. 2, 3A–B). Each branch of the end apparatus shows a conspicuous sheath of 2 μm long microvilli surrounding a dark-staining central area (Fig. 3B–D). The cuticular central part of the end apparatus is only visible at its starting point near the bulbous portion (Fig. 3B).

The cytoplasm contains an abundance of microtubules (Fig. 3E,F) as well as peculiar regions that contain long parallel fibrils (Figs. 3A,F, 4E). Mainly confined to the basal cell portion are numerous rounded or elongate inclusions of approx. 4–5 μm that contain dark crystalline condensations. The latter occur in various shapes as single or multiple structures per inclusion (Fig. 4A–D). At their periphery, most inclusions contain round droplets with a diameter around 0.5 μm that may be partially in contact with the cytoplasm (Fig. 3F, 4A-C). The ovoid nuclei are basally located and measure approx. 10 × 7 μm (Figs. 1 and 4E). The basal cell membrane is differentiated into very conspicuous invaginations that form an extensive basal labyrinth (Figs. 2 and 4E,F). The cell membrane between neighbouring cells forms a system of interdigitations in the basal region of the cells (Figs. 2 and 4F,G). Mitochondria are commonly found (Fig. 4G), but other organelles such as Golgi apparatus or endoplasmic reticulum, either in the smooth or granular form, cannot be readily observed.

The reservoir is formed by a very thin layer of epithelial cells with a thickness of less than 0.5 μm, except in the region of the nucleus (Fig. 4H). The luminal side is lined with a thin dark cuticle of 0.1 μm.

4. Discussion

Apart from the occurrence of a peculiarly hypertrophied reservoir in some southeast Asian *Camponotus* species (Maschwitz and Maschwitz, 1974; Davidson et al., 2012), the general appearance of the mandibular gland is very similar among the various ant species: the paired gland consists at each side of a cluster of class-3 secretory cells (classification of Noirot and Quennedey, 1974) that open through their accompanying duct cells into a common reservoir. From the reservoir, a main duct connects to the base of the mandible, where secretion is released. The secretory cells are usually round to ovoid, they have a sinuous end apparatus, and lack special intercellular contacts. Reports on mandibular gland morphology and ultrastructure are known for various species (Gama and Cruz Landim, 1982), as well as specific case studies in the genera *Calomyrmex* (Brough, 1977), *Formica* (Billen and Schoeters, 1994), *Leptanilla* (Billen et al., 1998), *Polyergus* (Grasso et al., 2004), *Atta* (Pavon and Camargo Mathias, 2005), *Lasius* (Niculita et al., 2007), *Monomorium* (Boonen et al., 2013) and *Protanilla* (Billen et al., 2013). In a recent study on *M. iriodum* (Billen et al., 2015), we reported on the peculiar organization of the mandibular gland secretory cells having a branched end apparatus, although we at that time did not have material available to give ultrastructural details.

The recent availability of fresh *M. iriodum* workers allowed us to study the mandibular gland under the electron microscope. This confirmed the very peculiar appearance of the end apparatus with a bulbous proximal portion and a branched distal portion that is surrounded by long microvilli. This configuration as far as we know has never been found in any ant gland before. Although the functional significance of such branched end apparatus remains unclear, class-3 secretory cells with a branched end apparatus are common for exocrine glands in wasps (Van der Vecht's gland: Delfino et al., 1979; venom gland: Delfino et al., 1983; sternal gland: Delfino et al., 1991; Richards' gland: da Silva et al., 2015). Equally unusual is the cell shape of the secretory cells of the *Myrmoteras* mandibular gland. Whereas class-3 glands usually appear as round or oval independent entities without intercellular contacts, the mandibular gland secretory cells of *Myrmoteras* display an epithelium-like organization, that gives them a clear polarity with 'apical cups' and 'basal invaginations' and obvious intercellular contacts. The basal invaginations as well as the branched end apparatus represent a conspicuous increase of the surface through which metabolites can be transported, which indicates a metabolically active glandular tissue.

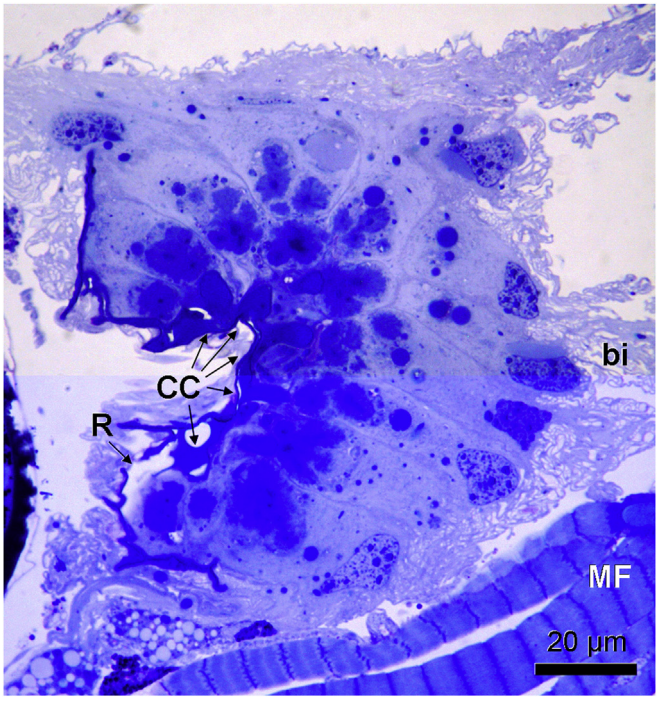

Fig. 1. Semithin section of the mandibular gland of a *Myrmoteras iriodum* worker. bi: basal invaginations, CC: cuticular cups, MF: muscle fibres, R: reservoir.

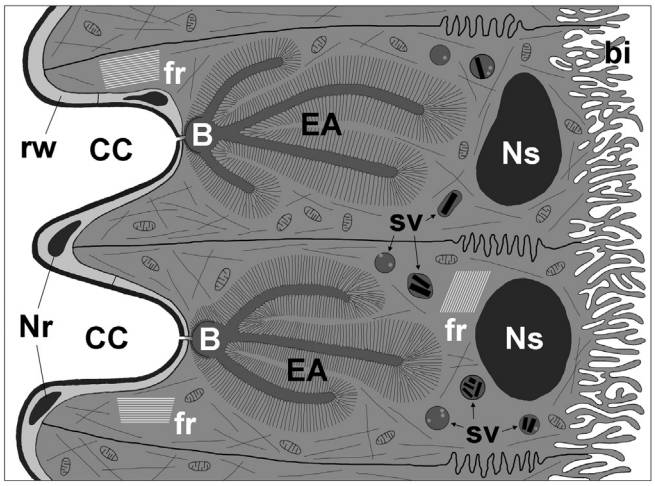

Fig. 2. Schematical drawing illustrating the cellular organization of mandibular gland cells with cuticular cups (CC) in apical region, a bulbous proximal part (B) and a branched distal part of the end apparatus (EA). bi: basal invaginations, fr: fibrillar region, Nr: nucleus reservoir cell, Ns: nucleus secretory cell, rw: reservoir wall, sv: secretory vesicles.