

Research article

Mandible associated glands in queens of the slave-making ant *Polyergus rufescens* (Hymenoptera, Formicidae)

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Summary. A first description of the structural organization of two exocrine glands associated with the mandibles of queens of the obligatory slave-making ant *Polyergus rufescens* is reported. The mandibular gland consists of clustered bicellular secretory units connected by means of cuticular ducts to a big reservoir. The reservoir continues in a duct that opens proximally on the mandible cuticle. Intramandibular glands are isolated bicellular secretory units connected to the external pores through a cuticular duct. No reservoir has been observed. In both cases the secretory cells belong to the 3rd class. Functional aspects of the investigated glands are discussed taking also into account for the parasitic habit of this slave-making species.

Key words: *Polyergus rufescens*; mandibular gland; intramandibular gland; morphology; chemical communication.

Introduction

The ecological success of ants is assured by sophisticated social mechanisms that allow colony integrity and efficient resources exploitation (Hölldobler and Wilson, 1990). Most of the colony activities are guaranteed by effective chemical communication systems. Chemical signals are used by ants in relationships with nestmates, members of other ant colonies, and other organisms. Hence, processes such as recognition, alarm, defence, recruitment, trail following, sexual calling, home range and territorial marking, inter-relationships and associations are all mediated by signals conveyed by chemical substances (Bradshaw and Howse, 1984; Hölldobler and Wilson, 1990).

In this context, ants can be considered as a sort of specialized chemical factory, being equipped with several tens of exocrine glands occurring all over the body (Billen, 1998; Billen and Morgan, 1998). Among them, glandular structures associated with the mandibles were also found.

The mandibles of ants are associated with a 'mandibular gland' that generally consists of a cluster of secretory cells that open into a reservoir sac by means of individual duct cells. The reservoir forms a main duct that opens at the base of the mandible without any associated muscular equipment (Billen, 1993; Billen and Schoeters, 1994). In ants (as well as in other social hymenopterans), mandibular gland secretions are generally involved in defence systems and alarm communication (Buschinger and Maschwitz, 1984; Hölldobler and Wilson, 1990) and may also function as fungal inhibitor (Marsaro Junior et al., 2001). However, in some species the gland may serve as the source of the sex pheromones produced by males (Ayasse et al., 2001).

Another exocrine structure found in association with mandibles is the 'intramandibular gland'. Generally, it consists of a number of cells (bicellular units, type 3 according to Noirot and Quennedey, 1974) located within the mandibles that open outside through a series of pores (Schoeters and Billen, 1994). However, a peculiar epithelial intramandibular gland has been recently discovered by Billen and Espadaler (2002) in the ant *Pyramica membranifera*. Up to now, the functions of intramandibular glands in ants remain unknown.

Slave-making ants offer interesting examples of behavioural and physical adaptations to the parasitic habit by eusocial insects. Ants of the genus *Polyergus* are all obligate slave-makers, which periodically organize group raids against colonies of the related genus *Formica* to sack the resident brood that is reared to eclosion and integrated into the working force of the parasitic colony (Buschinger et al., 1980; Hölldobler and Wilson, 1990; Mori et al., 1991). The

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social parasitic habit of this species is also particularly evident in the context of colony founding: newly mated females are not able to start a new colony alone, so they must invade a *Formica* colony, kill the resident queen and become accepted by the resident workers. This is a very crucial phase of the reproductive biology of *Polyergus* since during nest invasion the parasite female must cope with the fierce hostility from the resident workers and queens. In this context, *P. rufescens* queens can use efficient behavioural and morpho-functional adaptations such as chemical secretions (appeasement allomones), mechanical protection and physical weapons (the thick exoskeleton and the powerful mandibles) that allow an easier usurpation of the host colony (Mori et al., 2000, 2001; Billen et al., 2001).

A survey of the glandular equipment of highly specialized species (such as obligate social parasites) may provide interesting data on their adaptations to the different phases of their life cycles. Here we report a first description of the fine structure of two exocrine glands associated with the peculiar sabre-shaped mandibles of *Polyergus rufescens* queens.

Materials and methods

Virgin queens of *P. rufescens* used for gland dissections were collected just before nuptial flights from field colonies located in Parma (Northern Italy).

For scanning electron microscopy observations (SEM), 10 *P. rufescens* queens were beheaded and immersed in 50% ethanol-water solution. After dehydration in a graded ethanol series the heads were examined through a Philips® XL 30 SEM after having been processed through a critical point drier and a gold coating unit.

For light microscopy observations, 10 *P. rufescens* queens were anaesthetised in CO₂ and immediately immersed in 2.5% glutaraldehyde in 0.1 M cacodylate buffer + 5% glucose, pH 7.2-7.3. Then each mandible together with the associated gland was detached from the head capsule, in order to help fixative penetration, and left at 4 °C for about 2 h. After rinsing overnight in cacodylate buffer, the specimens were post-fixed in 1% osmium tetroxide at 4 °C for about 1 h and rinsed in the same buffer. Dehydration in a graded ethanol series was followed by embedding in Epon-Araldite mixture with propylene oxide as bridging solvent. Semithin (1.5 µm) sections were taken with a Diatome® diamond knife on a L.K.B.® 'Nova' ultramicrotome, stained with 1% methylene blue and viewed with a phase-contrast Leitz® Dialux 20 EB photomicroscope.

For transmission electron microscopy (TEM) the specimens were processed the same way. Thin sections were cut with a diamond knife on a L.K.B.® 'Nova' ultramicrotome, and mounted on collodium-coated 50 mesh grids. Finally, the sections were observed with a Philips® EM 400T, after staining with uranyl acetate (20 min, room temperature) and lead citrate (5 min, room temperature).

Results

In *P. rufescens* queens, mandibles are sabre-shaped (length about 1.4 mm), curved and provided, on their inner surface, with a single row of teeth which occupy the distal half of the mandible itself (Figs. 1, 2A). Because of that, the inner mandibular margin appears sharp, while the opposite outer margin is rounded and smooth.

Mandibular gland

When the mandible is carefully torn apart from the head capsule, it is quite easy to notice the mandibular gland mass (sometimes hidden among muscular fibres) which remains attached to the proximal part of the mandible (Fig. 1). In *P. rufescens* queens the mandibular gland is composed by several secretory cells that overlie a sac-like structure, the cuticular reservoir (Fig. 2B, C). This is connected with the mandible through a narrow evacuating duct. The elliptical secretory cells (diameter about 50 µm) appear like a well separated cluster and are connected with the sub-elliptical reservoir one by one through cuticular conducting canals (diameter about 1 µm) (Fig. 2C). The dorso-medial side of the mandible presents proximally on the cuticle a slit which runs for about 170 µm slightly curved toward the end (Fig. 2D). In the beginning the evacuating duct penetrates the mandibular lumen (Fig. 3B) and then it starts to be embedded by the mandible cuticular wall (Fig. 3C–E). The duct (diameter about 50 µm) is connected to the thin external cuticle by means of a thread-

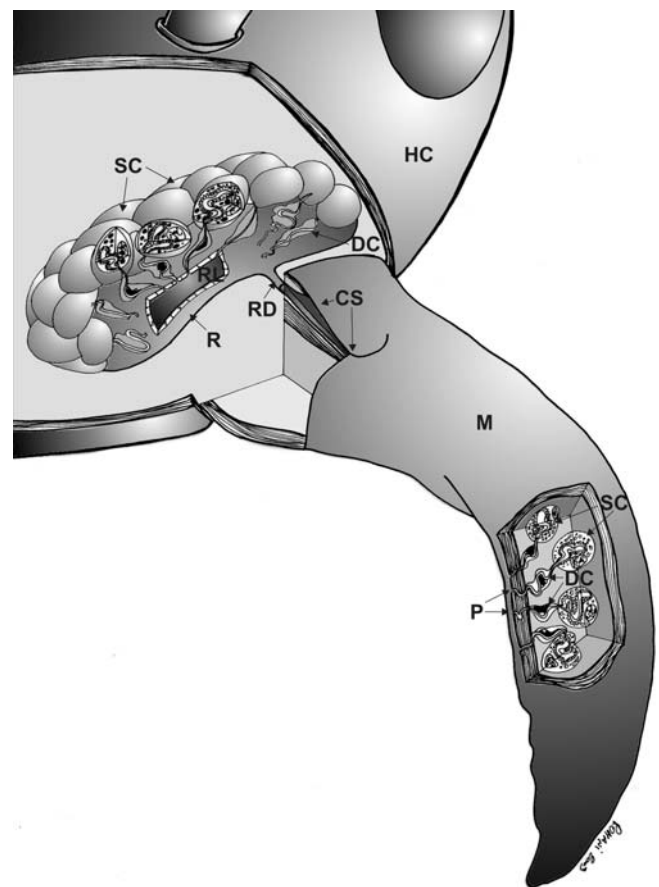


Figure 1. Semi-schematic tridimensional drawing (not in scale) of *P. rufescens* queen mandibular and intramandibular glands showing the position of mandibular gland within the head capsule and its release site. The cut out part of the mandible shows the position of intramandibular glands. CS, cuticular slit; DC, duct cell; HC, head capsule; M, mandible; P, pores; R, reservoir; RD, reservoir duct; RL, reservoir lumen; SC, secretory cells

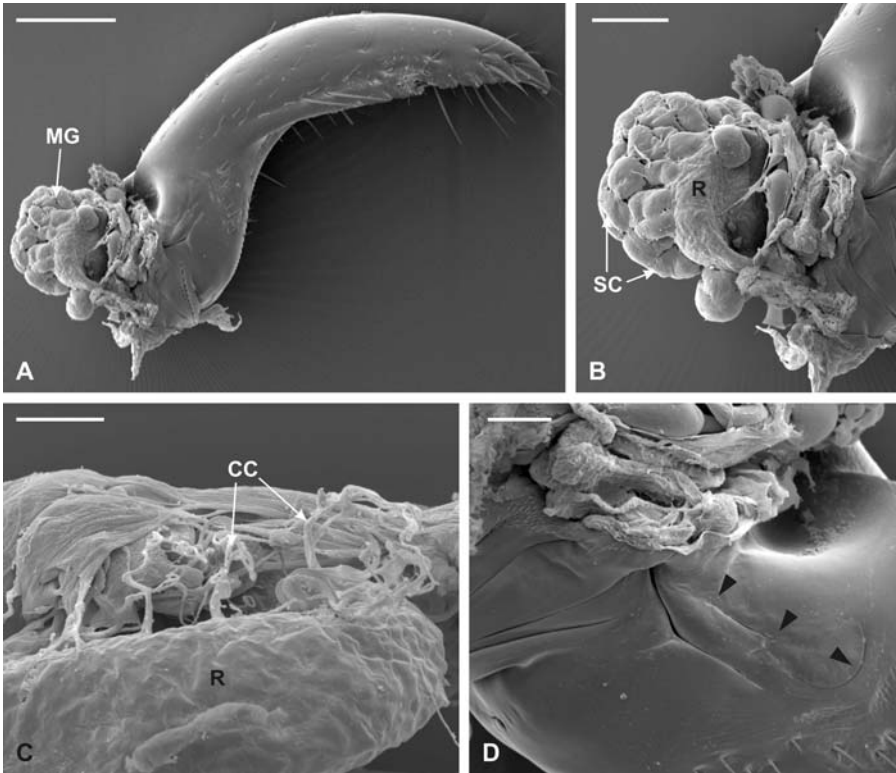


Figure 2. A. SEM micrograph of *Polyergus rufescens* queen left mandible with associated mandibular gland (MG). B and C. Detail of mandibular gland with secretory cells (SC), conducting canals (CC) and reservoir (R). D. SEM micrograph showing the external slit (arrowheads). Scale bar: A = 250 μ m, B = 100 μ m, C = 25 μ m, D = 50 μ m

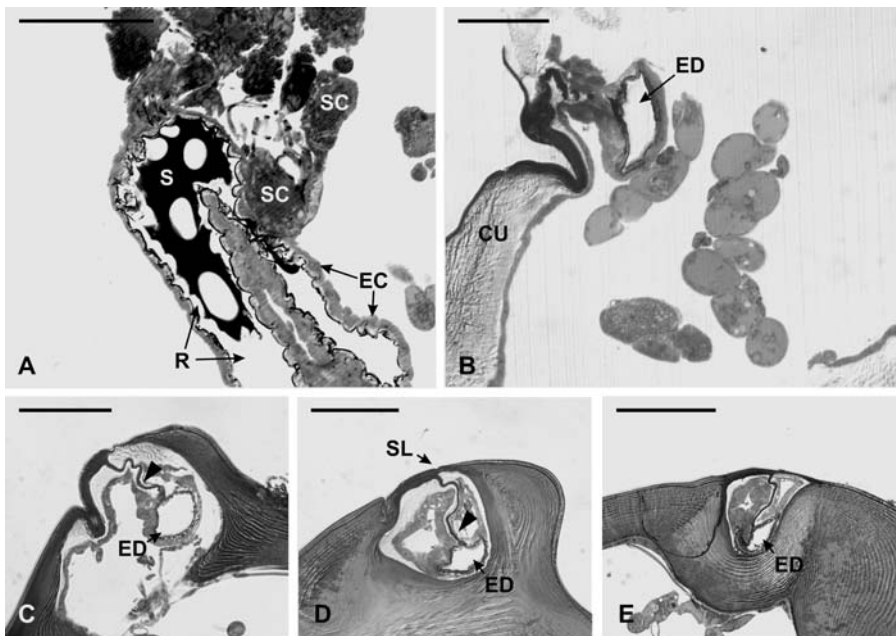


Figure 3. A. Light micrograph of *Polyergus rufescens* queen mandibular gland cross section showing secretory cells (SC) surrounding gland reservoir (R) with gathered secretion (S). B–E. Light micrographs of evacuating duct (ED) showing the thread-like structure (arrowheads) connecting duct with external slit (SL). EC, epidermal cells; CU, cuticle. Scale bar: A, C, D and E = 50 μ m, B = 25 μ m

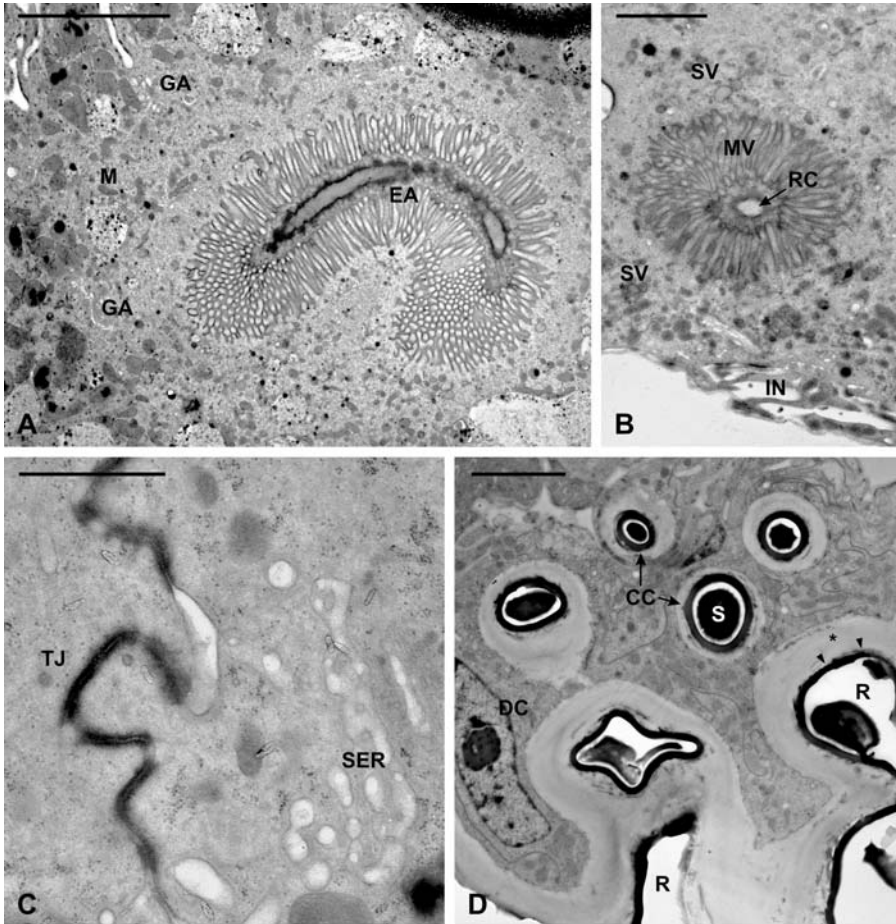


Figure 4. A and B. TEM micrographs of *Polyergus rufescens* queen mandibular gland secretory cells showing end apparatus (EA) with receiving canal (RC) and microvilli (MV). C. Detail of cellular tight junctions (TJ) and smooth endoplasmic reticulum (SER). D. Detail of conducting canals (CC) filled with secretion (S) and embedded by duct cell. Star (*) indicates procuticle and arrowheads indicate epicuticle. GA, Golgi apparatus; IN, infoldings; M, mitochondria; R, reservoir; SV, secretory vesicles. Scale bar: A = 5 μ m, B = 2 μ m, C = 1 μ m, D = 2.5 μ m

like structure, that actually is the cuticular invagination of the external slit. No muscles have been found associated with the evacuating duct or with other glandular parts.

The main ultrastructural feature of the secretory cells is the presence of a long and convoluted receiving canal bordered by densely packed microvilli and often surrounded by electron-lucid secretory vesicles (Fig. 4A). The receiving canal (diameter about 0.5 μ m) appears like a single tube made of epicuticle arranged in several layers (Fig. 4B). The nuclei of the secretory cells are irregularly shaped, with deep invaginations of the surrounding cytoplasm. This latter presents an abundance of mitochondria with evident cristae, well developed Golgi apparatus, free ribosomes and smooth endoplasmic reticulum (Fig. 4A). The produced secretion gathers in many electron lucid vesicles which accumulate around the microvillate region of the end apparatus. The basal region of the secretory cells present deep infoldings of the plasma membrane, sign of an active uptake of metabolic precursors from the haemolymph (Fig. 4B). Tight junctions between adjacent secretory cells have often been observed (Fig. 4C).

The conducting canal, completely embedded by the canal cell from which it is produced, is comprised by a continuous layer of epicuticle (thickness about 150 nm) and goes with many convolutions up to the reservoir. In their apical region,

the conducting canals are surrounded by an uneven layer of electron-lucid procuticle projecting from the reservoir wall, that actually shows the same structural organisation (Fig. 4D). The reservoir wall is lined by a single layer of epidermal cells characterised by small nuclei, a reduced cytoplasm and a few cytoplasmic organelles. The electron-dense secretion was often observed filling either the lumen of the conducting canals or gathering in the reservoir (Fig. 3A). A semi-schematic tridimensional reconstruction of the whole mandibular gland is provided in Figure 1.

Intramandibular glands

In *P. rufescens* queens the distal upper half of the mandible presents, on its internal margin, a series of cuticular pores (diameter about 0.5 μ m) that can be seen through SEM observations. Usually the pores are arranged in a double row and run longitudinally close to the chewing part of the mandible, i.e. the margin provided with teeth (Fig. 5A, see also Fig. 2A). These pores correspond internally to bicellular secretory units composed by an innermost voluminous secretory cell and an outermost duct cell (Fig. 5B). The convoluted conducting canal is composed of epicuticle; it is encased in the duct cell for all its length until it penetrates the

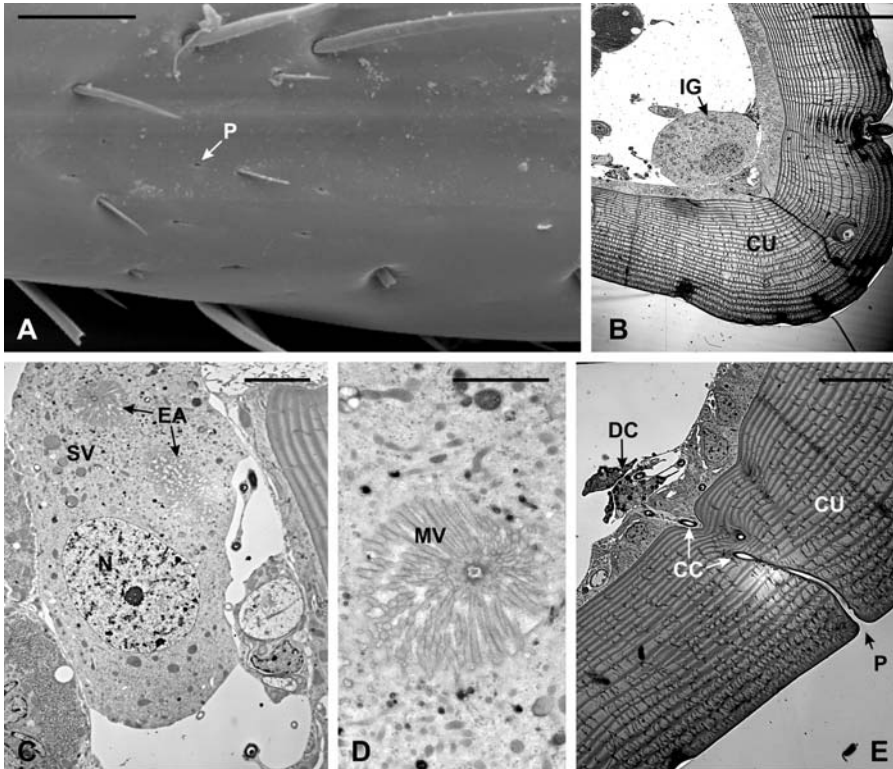


Figure 5. A. SEM micrograph of *Polyergus rufescens* queen left mandible with pores (P). B. TEM mandible cross section at the pores level showing intramandibular gland (IG) just below mandibular cuticle (CU). C and D. Secretory cell of an intramandibular gland with nucleus (N), end apparatus (EA) bordered by microvilli (MV) and secretory vesicles (SV). E. Detail of duct cell (DC) with conducting canals (CC) ending in external pore (P). Scale bar: A = 50 μm , B = 25 μm , C = 5 μm ; D = 2 μm ; E = 10 μm

mandible cuticular wall and reaches the external cuticular pore (Fig. 5E). In this case the conducting canal is almost isodiametric and no reservoirs have been observed allowing gathering of secretion. The big secretory cells appear as globular masses closely appressed to the epidermal cells and are characterised by large rounded nuclei regularly shaped, easy detectable at light microscopy after toluidine blue staining (Fig. 5C). The basal membrane shows a small amount of plasma membrane infoldings. The cytoplasm shows the presence of fewer mitochondria, if related with the secretory cells of the mandibular gland, smooth endoplasmic reticulum and electron-lucid secretory vesicles. The most evident glandular feature of the secretory cells is the well developed end apparatus, which appears convoluted and quite long: its ultrastructural features are similar to those described for the secretory cells of the mandibular glands (Fig. 5D). A semi-schematic tridimensional reconstruction of the intramandibular glands is provided in Figure 1.

Discussion

The mandibular gland in *P. rufescens* queens is made up of a cluster of bicellular secretory units, which are connected to a reservoir by means of cuticular ducts. Each unit is composed of a canal cell and a secretory cell, the latter belonging to the 3rd class of secretory cells according to the classification of epidermal glands proposed by Noirot and Quennedey (1974, 1991) and Quennedey (1998). The reservoir is then connected with the mandible cuticular wall through a single duct, that

opens proximally in a cuticular slit. The occurrence of abundant mitochondria as well as Golgi apparatus, smooth endoplasmic reticulum and deep infoldings of the basal plasma membrane strongly supports a high degree of secretory activity for these cells. A similar structural scheme for mandibular glands was first reported by Billen and Schoeters (1994) in some other species belonging to the Formicinae (i.e. genus *Formica*, closely related to *Polyergus*). Regarding the release mechanism, the absence of muscles associated with the mandibular gland deals with the hypothesis of Billen and Schoeters (1994) that the secretion release would take place during mandible opening, due to the increasing haemolymph pressure within the head capsule. In this context, the tight junctions gathering the secretory cells together may be considered as a cytological ‘tool’ reinforcing the integrity of the mandibular gland during pheromones emission or the grasping.

Social parasitism in ants generally involves the evolution of peculiar features (anatomical, functional, behavioural) of the parasite species as adaptations to their peculiar life cycles (Hölldobler and Wilson, 1990). *Polyergus rufescens* is a specialized slave-maker that presents several adaptations to this habit. For example, the sabre-shaped mandibles of both workers and queens are not suitable to perform the normal domestic tasks of free-living species but are extremely powerful and effective when fighting with residents occurs during host nest invasion (Mori and Le Moli, 1988; Grasso et al., 1992; Mori et al., 2001). The parasite ‘route’ may involve the modification of the chemical strategies adopted by these species so that the original function of glandular sources is

changed to tackle with specific needs of the parasitic habit. For example, usurper queens of *Polyergus* species are equipped with a hypertrophied Dufour's gland, the source of an appeasement allomone that allows the ants to cope with the violent attacks by resident workers (Topoff et al., 1988; Mori et al., 2000, 2001; Billen et al., 2001).

The mandibular gland in workers of ants and other hymenopterans is mostly involved in the alarm-defence system (Hölldobler and Wilson, 1990; Billen and Morgan, 1998). However, secretions from this gland are used by workers of *Polyergus rufescens* as 'propaganda' substances during slave-raids (Visicchio et al., 2001). Another functional peculiarity of *Polyergus* mandibular gland may be found in queens. In fact, secretions from this gland convey signals by which virgin females attract males for mating (Topoff and Greenberg, 1988; Grasso et al., in press). Although mandibular sex pheromones are typically produced by honey bee queens, this is a rare phenomenon in ants. In fact, when the mandibular glands are involved as source of sex pheromones in ants, males are responsible for their emission (Hölldobler and Wilson, 1990; Ayasse et al., 2001). Sexual calling by females (the 'female calling syndrome') may be regarded as an adaptation to the parasitic life habit. In fact, this strategy is quite widespread among primitive or socially parasitic ants, which form scattered colonies associated with habitat with patchily distributed resources. Female-calling enables a relatively low dispersal rate and so reduces the need for leaving a habitat that is good in terms of suitable resources, i.e. host colonies (Hölldobler and Wilson, 1990; Bourke and Franks, 1995). Hence, it is possible that *Polyergus* females changed the original function of mandibular gland using its secretions as sexual attractants for males. In this context, the peculiar (narrow and curved) slit by which the evacuating duct opens through the mandible cuticular wall may serve as a structural device to control and lower the release rate of the pheromones. As pointed out by Hölldobler (1984), this can be seen to be adaptive not only in minimizing detection by predators but also as a possible system to promote sexual selection: females would select males who are better searchers by emitting a very weak signal.

Intramandibular glands are quite widespread among ants, being present in several species of the major subfamilies (Schoeters and Billen, 1994). Here we report a first account of the presence of this gland also in the obligate social parasite, *P. rufescens*. The sabre-shaped mandibles of *Polyergus* are very different from the ordinary mandibles of the closely-related species of the genus *Formica* that present a full set of teeth on the gripping edge (see Mori and Le Moli, 1988; Hölldobler and Wilson, 1990). Intramandibular glands of *P. rufescens* queens are isolated bicellular glandular units, the secretory cells of which belong to 3rd class. Differently from the mandibular gland, these glands do not have any reservoir, although the end apparatus appears well developed and largely bounded by microvilli. The external pores are distributed in double row longitudinally along the toothed margin of the mandible, according to what has been more commonly reported in other Formicinae and less frequently in other Formicidae subfamilies (Schoeters and Billen, 1994). The

occurrence of electron-lucid secretory vesicle suggests that the secretion could be volatile.

Until now the function of intramandibular glands remains unknown. Its widespread presence among the Formicidae (including now the parasite species *P. rufescens*) suggests an important function as a source of secretions concerned with general aspects of ant biology. For example it could be involved in the production of lubricants for the mandibles. However, it is also possible that, like many other morpho-functional features of ants, its function has been repeatedly modified so to cope with specific biological needs (see Schoeters and Billen, 1994; Billen and Espadaler, 2002). Further comparative (morphological, chemical and behavioural) studies will probably clarify patterns of structural and functional specialization in the different species eventually linked to peculiar life habits.

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