

Ultrastructural organization of the exocrine glands in ants *

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Ants, and social insects in general, are characterized by their very well developed exocrine system. According to their cellular arrangement, the numerous glands either belong to the epithelial type, or are composed of bicellular units, each comprising a secretory cell and a duct cell. The ultrastructural organization with regard to the uptake, biosynthesis and discharge of the secretory products is very similar in both types, and generally involves surface increasing foldings of the plasmalemma. The cuticle, that forms part of each glandular cell, is mostly provided with pore canals. Pheromone producing glands are characterized by numerous mitochondria, a well developed Golgi apparatus and an extensive smooth endoplasmic reticulum in their secretory cells. The often abundant multilamellar inclusions may correspond with secretory material. Glands producing venomous substances or performing digestive functions, on the other hand, are characterized by their well developed granular endoplasmic reticulum.

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Communication between individuals forms a universal and indispensable condition of animal life. Its importance becomes especially evident in animal societies, where social life relies on precise interactions between its individual members. Social insects have developed one of the most sophisticated communication systems, in which information is conveyed by chemical substances or pheromones, which originate from exocrine glands. The number and diversity of these glands in social insects in general, and ants in particular, are impressive, with glands occurring in all parts of the body. Worker ants can easily contain 20 or more major glands in their small bodies, and hence can be considered as walking glandular batteries.

In spite of their obvious diversity, however, all glands can be classified in two distinct morphological types, according to their ultrastructural organization (Fig. 1). Most simple are the epithelial glands, in which the secretory cells are arranged in a

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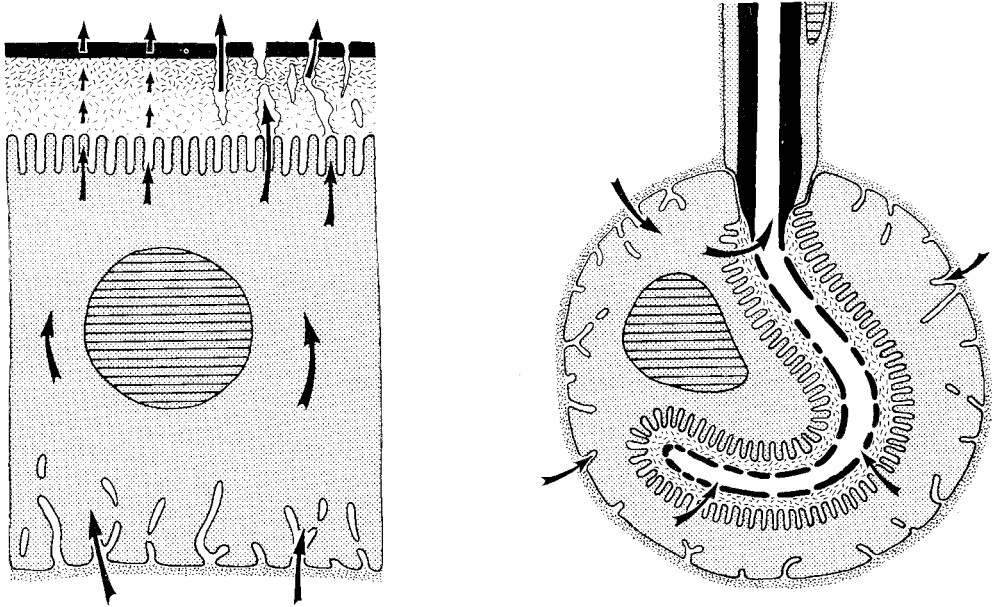


Fig. 1. — Schematic representation of the two types of exocrine glands in ants, with the sequential processes in the elaboration of secretion illustrated by arrows. For explanation, see text.

monolayered epithelium. Morphologically more complex are the glands that are composed of secretory units, each comprising one secretory cell and one duct cell.

All glands, regardless the type to which they belong, are characterized by their ectodermal origin, as is illustrated by their invariable association with a cuticular component. A secretory function therefore is implied, as epidermal cells as such are known to produce the overlying cuticle. A differentiation of epidermal cells into a proper glandular organ as a result becomes quite evident. For this reason, the importance of the «normal» epidermis is very clear, and, in our opinion, may justify considering this tegumental epidermis as a true and additional glandular tissue. A very important role in this regard has also to be attributed to the oenocytes, that share an ectodermal origin, and that contribute to the formation of the epicuticular layer. They most often occupy a subepidermal position, or sometimes can be wedged in between the epidermal cells (which perhaps makes them homologous to the type-2 glandular cells of NOIROT & QUENNEDEY 1974). Supporting evidence for the important secretory role of the tegumental epidermis, very possibly including the oenocytes, appears in an increasing number of reports that illustrate the function of (epi)cuticular hydrocarbons as crucial cues in interindividual recognition (VANDER MEER 1986).

Since pheromonal communication requires the action of volatile substances, the corresponding glands are specialized in the elaboration of such low molecular weight compounds, which are mostly hydrocarbons or related substances. This chemical nature is consistent with the well developed smooth endoplasmic reticulum (Fig. 2). Although the secretion of pheromonal substances is a major function of the exocrine

system in ants, a number of glands are known to serve other functions that may involve the production of completely different chemical compounds. The best known examples are the pharyngeal and salivary glands that produce the digestive enzymes, and the venom gland, that opens through the sting and secretes defensive and often toxic molecules. In both situations, the secretion is proteinaceous, as is reflected in the presence of a well developed granular endoplasmic reticulum in the glandular cells (Fig. 3).

At a very general level, glandular activity always comprises the same sequential processes of uptake of precursor molecules, cytoplasmic biosynthesis, and discharge of the final secretion. Although the glands of the epithelial type and the secretory unit type look structurally very different and show a considerably different ontogenesis (SRENG & QUENNEDEY 1976), these sequential steps are characterized by morphologically very similar features in both types (Fig. 1).

The uptake of precursor molecules or metabolites in general is often facilitated by surface increasing invaginations of those portions of the plasmalemma that face the haemolymph (Fig. 4), i.e. the basal cell membrane of epithelial gland cells, or the peripheral cell membrane in glandular cells of the secretory unit type. The cytoplasmic organelles form the site of an intensive metabolic activity with various biosynthetic pathways contributing to the elaboration of the pheromonal molecules. Most conspicuous elements in this regard are the smooth or granular endoplasmic reticulum (for lipidic or proteinaceous secretions, respectively), the largely well developed Golgi apparatus, and the numerous mitochondria. Another very common cytoplasmic element in exocrine glands are the multilamellar and/or vesicular inclusions, that can sometimes occupy a considerable portion of the cell (Fig. 5). They are possibly to be regarded as secretion, since other visible signs of the secretory products are only rarely observed. Their eventual association with lipidic compounds moreover has been suggested in vertebrate pneumocytes, where similar lamellar bodies were shown to contain the lipidic lung surfactant (BOUDREAU et al. 1983). Additional evidence is provided by their frequent occurrence between the microvilli of the apical cell membrane of epithelial glands, or even in the lumen of the glands, all of these being sites where secretion is expected to pass.

On their way to the outside environment or to the gland reservoir for temporary storage, the secretory products have to pass through the cell membrane of the glandular cell in which they have been synthesized. In glands of the secretory unit type, this invariably occurs through an end apparatus, which is an internalized and microvillar part of the plasmalemma, surrounding an efferent and blind ending cuticular ductule (Fig. 6). Apart from the surface increase due to microvilli, the end apparatus displays an additional and clear adaptation in its cuticular composition to facilitate the passage of the secretion: within the secretory cell, the procuticle consists of a loosely arranged texture, while the epicuticular layer shows many pores, through which an easy passage of secretion is ensured. Upon leaving the secretory cell, the epicuticle becomes much thicker and more compact without any pores, and forms the only cuticular lining of the ductule lumen in the duct cell. In this way, a clear functional differentiation results, that enables convenient release of secretory products through a fenestrated cuticle in the secretory cell region, and a transportation function through a well isolated and thick-walled cuticular drainage canal in the duct cell (Fig. 7).

For glands of the epithelial type, secretion only has to cross the cuticular lining in

order to reach the outside, or the reservoir, which itself eventually opens to the outside. Cuticular pores to let secretion pass, as is the case in the end apparatus, are occasionally found, as in Pavan's gland of the Dolichoderinae, or in the tibial glands of *Crematogaster* (Fig. 8). In the majority of the epithelial glands, however, cuticular pores are not observed. The fibrillar network of the thick procuticular layer probably forms no real barrier for the crossing of small secretory molecules while the more compact but relatively thin epicuticle apparently must also be porous. Microvillar differentiation of the cell membrane adjacent to the cuticle, comparable to the situation in the end apparatus, is often found, and again conveniently offers an increased surface for the discharge of secretion. Sometimes narrow tubules of smooth endoplasmic reticulum extend into the microvilli (Fig. 9), and thus bring the secretory products as near as possible to the apical surface of the cell.

The whole ensemble of these ultrastructural adaptations make the many exocrine glands very precisely tunable producers of many chemical substances, ranging from the digestive enzymes for individual use, over caste determining substances, to the energetically very cheap though ethologically most efficient pheromonal messages that regulate the numerous interactions in the social insect community.

Fig. 2. — Apical region of the Dufour gland in *Messor structor*, showing the well developed smooth endoplasmic reticulum (*SER*), *ct* = cuticle, *M* = mitochondrium.

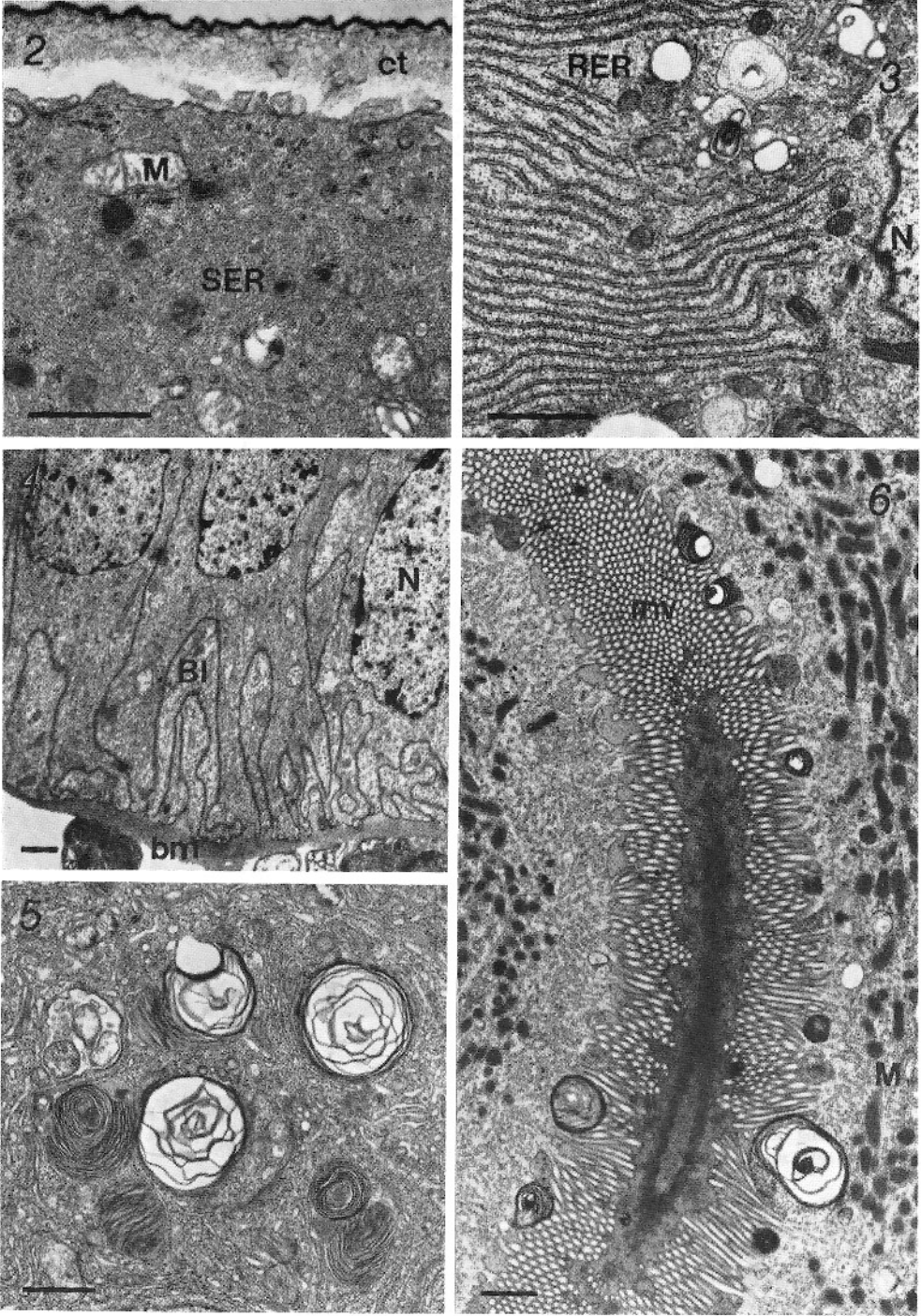
Fig. 3. — Granular endoplasmic reticulum (*RER*) in the venom gland secretory cells of *Myrmecia gulosa*; *N* = nucleus.

Fig. 4. — Basal region of the Dufour gland in *Formica fusca*; *BI* = basal invaginations, *bm* = basement membrane, *N* = nucleus.

Fig. 5. — Detail of the venom gland secretory cell of *Pseudomyrmex belti*, with numerous multilamellar inclusions.

Fig. 6. — End apparatus in the mandibular gland of *Cataglyphis nodus*, showing multilamellar bodies penetrating between microvilli (*mv*); *M* = mitochondria.

Scale bar in all figures is 1 μm .



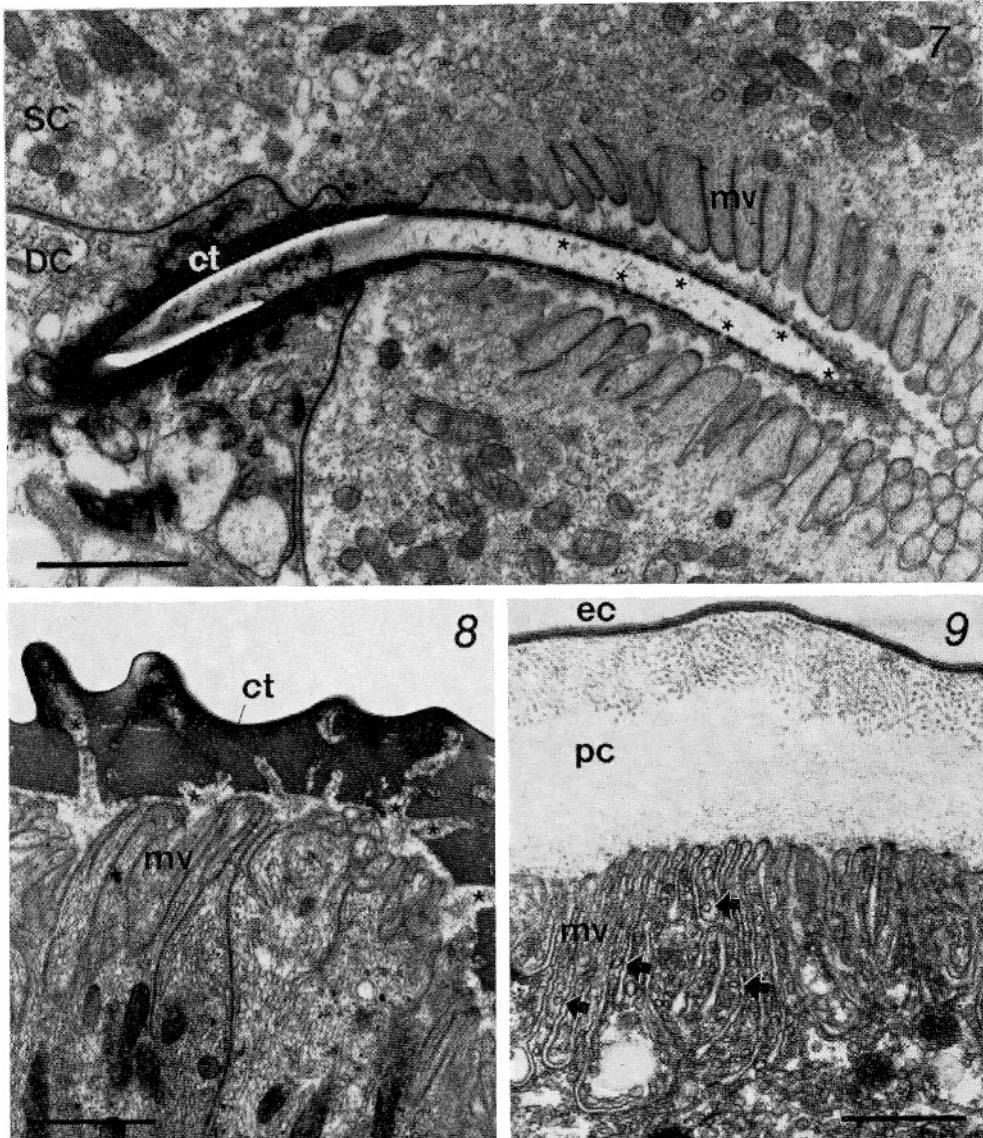


Fig. 7. — Contact between duct cell (DC) and secretory cell (SC) in the metapleural gland of *Myrmica rubra*, showing the different appearance of the cuticle (ct) in the duct cell and in the end apparatus of the secretory cell; mv = microvilli, * = epicuticular pores.

Fig. 8. — Apical region of the tibial gland in *Crematogaster scutellaris*, showing cuticular pores (*); ct = cuticle, mv = microvilli.

Fig. 9. — Apical region of the postpharyngeal gland in *Camponotus floridanus*. Extensions of smooth endoplasmic reticulum (arrows) continue in the microvilli (mv); ec = epicuticle, pc = procuticle.

Scale bar in all figures is 1 μm .

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