

structure of which was recently described in the honeybee (Lensky *et al.*, 1985). When looking to the tarsal morphology, however, we also found these glands in wasps (Billen, 1986a), ants, and all other, even solitary Hymenoptera we examined so far.

Finally, we revised the morphology of the sting glands in the female Hymenoptera. Noteworthy in this regard is the precise relationship of these glands with the sting itself. The venom gland always opens into the sting base, whereas Dufour's gland only does so in the Formicidae (Billen, 1986b). In the Apidae and Vespidae, on the other hand, the Dufour gland duct closely approaches the sting base, but then bends downwards, and opens into the dorsal vaginal wall. A such fundamental difference undoubtedly will be reflected by the function of these glands. Dufour's gland function in bees and wasps, which so far remains unknown, therefore most probably will be related with their reproductive biology.

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Morphology and Ultrastructure of the Exocrine Glands in Social Hymenoptera

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Social insect communication for the greater part relies on the pheromonal secretions of a wide variety of exocrine glands. Although the majority of these glands are known for a very long time yet, information dealing with their morphological and precise anatomical organization remains restricted to mainly very old contributions from the end of last century.

Only recently, the glandular morphology became more actual again, with most attention being paid to the tegumental abdominal glands in ants (Hölldobler, 1982; Hölldobler and Engel, 1978; Jessen and Maschwitz, 1983) and wasps (Jeanne *et al.*, 1983). Ultrastructural descriptions of the exocrine glands in the social insects are mostly dealing with the termites (Noirot and Quennedey, 1974), whereas the hymenopteran glands so far were only treated in a few specific case studies.

This fragmentary aspect of the ultrastructural reports, and the lack of a general morphological survey of the glands in the social Hymenoptera, have incited us to investigate the fine structure of their glands and start a comparative morphological study in this group.

The number of major exocrine glands per individual varies between 10 to 15, although total numbers around 50 may even be found, when considering the impressive record numbers of 28 abdominal glands in a ponerine ant (Jessen and Maschwitz, 1983), or 16 cephalic glands in vespid wasps (Landolt and Akre, 1979a). In spite of these large numbers, however, all glands belong to one of two clearly distinguishable types according to their cellular organization.

Morphologically most simple are the glandular epithelia, in which the epithelial cells secrete directly through the overlying cuticle. In the internally located epithelial glands, such as the formicid post-pharyngeal gland, the labial and Dufour's gland, the secretory product thus reaches a central reservoir space, where it is temporarily stored (Fig. 1A). In the tegumental epithelial glands, as the sternal epithelia in Vespidae and the wax glands of the Apidae, the secretion after cuticular passage reaches the exterior (Fig. 1B), where it eventually may be retained by a well developed tuft of bristle-like setae, as in the wasps (Jeanne *et al.*, 1983), or as wax scales in the bees (Cruz Landim, 1963). A special situation is observed in Pavan's gland, that is only found in dolichoderine and aneuretine ants : the secretory cells form a glandular epithelium underneath the anterior edge of sternite VII, whereas the reservoir is a structurally independent thin-walled sac between sternites VI and VII (Billen, 1985).

The second group glands are composed of numerous secretory units, each comprising a secretory cell and a duct cell. An intracellular and

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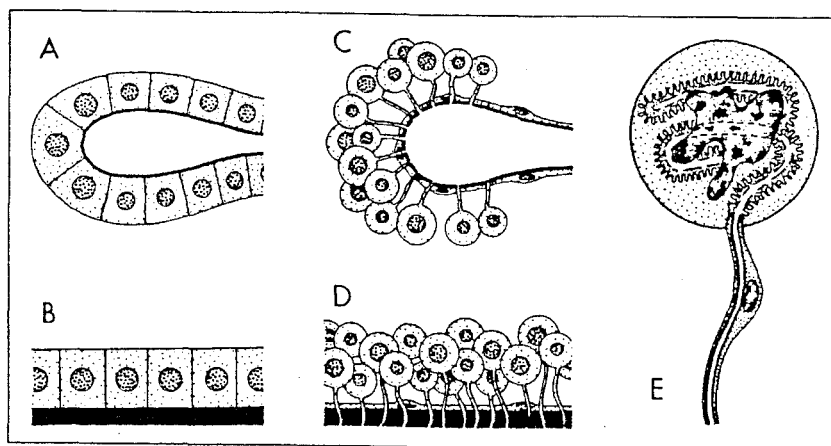


Fig. 1. - Schematic representation of the common exocrine gland types in the social Hymenoptera, in which both the epithelial glands and the secretory unit glands may have a central reservoir (A,C), or directly discharge their secretion through the tegumental cuticle (B,D). The individual unit glands are composed of a secretory cell with an intracellular end apparatus, and a duct cell (E).

cuticular ductule, commonly known as the "end apparatus", collects the secretion from the glandular cell, and continues into the duct cell (Fig. 1E). Also in these secretory unit glands, a reservoir occurs in the internal and intersegmental glands (Fig. 1C), whereas in the segmental glands, such as the wasp sternal glands and the tergal Renner/Baumann glands in the honeybee (Billen *et al.*, 1986), secretion directly reaches the outside (Fig. 1D).

A survey of the hymenopteran glands, as found in the female castes, with respect to these glandular types, is given below. Glands that are only found within one family are indicated with (1) for the Formicidae, (2) for the Apidae and (3) for the Vespidae. Sternal glands (*) can belong to either of both types. An aberrant situation is found in the labial gland of Vespidae, the acini of which are composed of a large central cell and a number of parietal cells (Landolt and Akre, 1979b). This particular arrangement does not correspond to the normal epithelial type of the labial gland in the other Hymenoptera (a), nor to the type of the secretory unit glands.

epithelial glands	secretory unit glands	
Postpharyngeal gland ¹	Propharyngeal gland ¹	Pygidial gland ¹
Labial gland □	Hypopharyngeal gland	Postpygidial gland ¹
Tibial gland ¹	Mandibular gland	Nasanov's gland ²
Tarsal glands	Mouthpart glands	Renner/Baumann gland ²
Eufour's gland	Metapleural gland ¹	Sternal glands *
Rectal gland	Venom gland	Richard's gland ³
Pavan's gland ¹	Sting valve's gland ¹	Van der Vecht's gland ¹
Sternal glands *	Cloacal gland ¹	Intersegmental glands
Wax glands ²	Koschewnikow's gland	

At the ultrastructural level, the secretory cells of both gland types as a rule are characterized by a very extensive smooth endoplasmic reticulum, numerous mitochondria and a mostly well developed Golgi apparatus. The cytoplasmic configuration is in accordance with the elaboration of relatively small, non-proteinaceous molecules, as are the hydrocarbons and lipidic substances that make up the main constituent of the glandular secretions. Exceptions in this regard are the propharyngeal (Formicidae) and hypopharyngeal gland (Apidae), and the venom gland, in which a very well developed rough endoplasmic reticulum occurs. Their corresponding secretions, however, are digestive enzymes and the proteinaceous venom components, respectively. A common feature of all glands are the lamellar inclusions, that probably are to be considered as a stage in the secretory cycle. They can often be observed near to the cuticle, and sometimes are also found in the gland's reservoir.

Because of the ectodermal origin of the glands, their secretory products have to cross a cuticular barrier to reach the reservoir or the outside environment. The microtubular composition of the endocuticle, which is the most prominent part of the cuticle, makes it a permeable layer for the lipidic secretions that are known from most glands. As a result, most epithelial glands display a continuous cuticular intima. Pore canals crossing the cuticle were only found in the wax glands among the bees (Cruz Landim, 1963), the tibial gland of *Crematogaster* and Pavan's gland among the ants (Billen, 1984, 1985), and the abdominal sternal epithelia of the wasps. In the secretory unit glands, the structural organization of the intracellular ductule provides an effective secretory apparatus. The gland cell's contact area surrounding the ductule is considerably enlarged because of its microvillar differentiation, while the cuticular lining of the ductule consists of a permeable endocuticle and a fenestrated epicuticle. The thickened and continuous epicuticular wall of the efferent duct ensures a merely guiding function, and carries the secretion to its storage area prior to final release.

According to their relationship to the cuticle and their secretory pathway, the exocrine gland cells were classified into 3 types by Noirot and Quennedey (1974). Their class 1 cells are in direct contact with the cuticle, and correspond with the epithelial glands, while the class 3 cells with accompanying duct cells represent the secretory unit glands. Class 2 glandular cells have no direct contact with the cuticle, and were only found in the basal region of the sternal glands of termites (Noirot and Quennedey, 1974).

Recent morphological investigations have revealed the existence of exocrine glands that had not been reported before. Because of the modern embedding procedures in plastics, and hence the possibility to section through the hard cuticle, the new discoveries mainly deal with tegumental glands. In this regard, a number of new intersegmental glands in ants were described (Jessen and Maschwitz, 1983), while a review on the occurrence of ant tergal and sternal glands was given by Hölldobler and Engel (1978). The pygidial gland thus was found to be a common structure in all major ant subfamilies (Hölldobler, 1982).

From our own investigations, we recently found the tergal Renner/Baumann glands also in the workers of the honeybee, albeit in a reduced condition. In workers of the cape honeybee, however, they are as well developed as in the queen, thus reflecting the dominant position *capensis* worker bees display when introduced in queenless colonies of other honeybee races (Billen *et al.*, 1986). Another element in the reproductive dominance among the bees are the tarsal glands, the