DIVERSITY AND MORPHOLOGY OF EXOCRINE GLANDS IN ANTS

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ABSTRACT

This article provides a survey of the 75 exocrine glands that are currently known among the Formicidae, with information on their anatomical classification, and with comments on the wide variety of functions their secretions can play.

INTRODUCTION

Social insects, and ants in particular, are marvellous little creatures, that since long fascinate man. Their life in colonies, that range from a few tens up to several millions of individuals, has given them an extra dimension, that far exceeds that of the single ant. Each single individual, however, contributes to the optimal functioning of the society, and also takes actively part in the communication system and social organization of the colony. A major role in this is played by their extremely well developed exocrine system, as exocrine secretions are known to be involved in various aspects of social life (Billen, 2008).

The number of exocrine glands can largely vary among species, with especially ponerine ants displaying an impressive plethora of glands (e.g. 28 abdominal glands in *Pachycondyla tridentata*, Jessen & Maschwitz, 1983). The overall number of known glands in ants has significantly increased recently, with 38 glands listed 15 years ago (Billen, 1993) and 63 glands listed a decade ago (Billen & Morgan, 1998). In the present article, we update our knowledge and list the 75 glands that are currently known among the family Formicidae.

Classification of exocrine glands

Insect exocrine glands are traditionally classified in two main classes (Noirot & Quennedey, 1974): class-1 glands are formed by epithelial cells, that are directly derived from the mono-layered epidermis (pale grey in Figure 1), while class-3 glands are formed by one or generally more bicellular units (dark grey in Figure 1), each unit comprising a secretory cell and a duct cell. This terminology of class-1 and class-3 comes directly from this 1974 pioneer article, and has been widely adopted since. This original article also mentioned class-2 cells, that have later been considered to be homologous with oenocytes (Noirot & Quennedey, 1991). Besides such classification that refers to the organization at the cellular level, glands are also classified anatomically with regard to the presence or absence of a reservoir, and distinguished in five types at this level (Figure 1). Glands without a reservoir (types A and C) discharge their secretion directly to the outside, while glands with reservoir (types B, D and E) can store their secretion and release it when necessary. As a result of their capacity to store secretion, these glands with reservoir are far more suitable for chemical analysis (Billen & Morgan, 1998).

Below follows a listing of all known glands in the head, thorax and abdomen, comprising a total of 75 glands. Glands that occur at multiple locations (e.g. in all 3 leg pairs) or in repetitive series (e.g. intersegmental abdominal glands) are listed under a single name. On the other hand, pedestal hair glands, subepithelial glands and the glandular tegumental epithelium are found all over the body, and therefore appear in the list for each of the three body parts (with asterisk *). Our survey refers to adult ants and includes workers, queens and males.

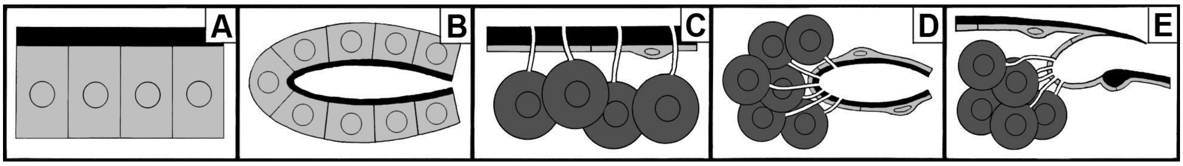

Figure 1. Schematical drawings of the main anatomical types of exocrine glands: ***A****. epithelial glands without reservoir,* ***B****. epithelial glands with reservoir,* ***C****. bicellular unit glands without reservoir,* ***D****. bicellular unit glands with reservoir,* ***E****. bicellular unit glands opening through articulation membrane. Black: cuticle, pale grey: epithelial gland cells, dark grey: bicellular unit gland cells.*

Cephalic glands

The exocrine structures in the head include glands that are associated with the mouthparts as well as glands that occur inside or near the antennae. The most conspicuous among these cephalic glands are the mandibular glands, which are often involved in the alarm-defence system, and the postpharyngeal glands. The postpharyngeal gland distinguishes the ants from the other social insects, and is of particular importance in the regulation of nestmate recognition. This gland contains a species-specific mixture of hydrocarbons that is very similar to that of the epicuticle (Bagnères & Morgan, 1991), although the precise dynamics and the relation between the gland and the cuticle is still partly unknown. The propharyngeal gland and some of the glands associated with the mouthparts can play a role in the initial food processing through the production of digestive enzymes.

Gland name (head)	type		
antennal base gland	E	maxillary gland	E
antennal scape gland	C	pedestal hair gland *	C
antennomere glands	C	postpharyngeal gland	B
basimandibular gland	A	propharyngeal gland	D
hypostomal silk gland	C	stipes gland	E
infrabuccal gland	B	subepithelial glands *	C
intramandibular gland	C	tegumental epithelium *	A
mandibular gland	D		

Thoracic glands

Due to the lack of wings, worker ants have a reduced thorax, although the limited number of ‘real’ thoracic glands (mainly the labial and metapleural glands) is very much compensated for by the impressive variety of 20 different glands that can be found in the legs (Billen, 2009).

Among the major ‘real’ thoracic glands, the labial (= salivary) glands in the prothorax are standard insect glands, that in ants belong to the epithelial type. In wasps and some ponerine ants, the glands have an acinar appearance, although their ontogeny shows their epithelial origin (Lommelen et al., 2003). The metapleural gland in the metathorax is a unique gland for the Formicidae, that is not found in other insects (Hölldobler & Engel-Siegel, 1984). Its main function is the production of antibiotics that protect the ants against microorganisms in general. An interesting gland in this regard is the propleural plate gland in fungus-growing ants, that supports specialized bacteria. These bacteria produce specialized antibiotics against the highly pathogenic fungus *Escovopsis* (Currie et al., 2006). The propleural plate gland is therefore involved in the elaboration of highly specific antibiotics, whereas the metapleural gland is more active in the production of broad-target antibiotics.

Gland name (thorax)	type		
antenna cleaner gland	A	metatibial gland	A
apicofemoral gland	A	pedestal hair gland *	C
apicotibial gland	A	propleural plate gland	C
arolium (= pretarsal) gland	B	prothoracic gland	E
basicoxal gland	A	proximal tarsomere glands	A
basitarsal gland	C	proximal tibial gland	A
coxal gland	E	subepithelial glands *	C
distal femoral gland	E	tarsomere glands	C
distal femoral sac gland	B	tegumental epithelium *	A
distal tarsomere glands	A	third tarsomere gland	C
distal tibial gland	E	tibial glands	C
footprint gland	A	tibial spur gland	A
gemma gland	C	tibial tendon gland	B
labial (= salivary) gland	B	trochanter gland	A
metapleural gland	D		

The numerous leg glands can perform a variety of functions, of which that of producing trail pheromones and lubricant substances are the main ones (Billen, 2009). Trail-laying is restricted to a number of glands in the hindlegs only, while glands producing lubricant substances occur in the immediate vicinity of the several articulations between the various leg parts.

Abdominal glands

The abdomen contains many glands, that are involved in a variety of different functions. Glands with a reproductive function occur in both males and females (queens), the secretory products ensuring efficient sperm transfer during copulation (e.g. spermatophore formation by the male accessory gland) and keeping sperm alive in the spermatheca until egg fertilization will occur. As mating takes place at the beginning of adult life of the young queen, she needs to be able to store enough sperm to be used in her often very long life. The spermatheca therefore is of most crucial importance in keeping the stored sperm alive (Wheeler & Krutzsch, 1994). Although ant workers in general cannot mate and reproduce, several species belonging to phylogenetically basal subfamilies retain a functional spermatheca, which distinguishes from the non-functional spermatheca of 'non-sexual' workers by the presence of a glandular lining of part of the reservoir wall (Gobin et al., 2006, 2008).

Other abdominal glands play a role in the alarm/defence system and prey capture. The best known example is the venom gland, that opens through the sting (Billen, 1987), or through the acidopore in the stingless Formicinae. Also the pygidial gland, that opens between the 6th and 7th tergites, is often involved in alarm/defence behaviour, especially in the Dolichoderinae, where the much enlarged gland has long been called 'anal gland' (Billen, 1986).

Several abdominal glands are known as the source of trail pheromones, as their opening site can conveniently be brought into contact with the substrate during walking, thus allowing deposition of the pheromone. According to the species, this function can be attributed to the Dufour's gland, hindgut and rectal gland, venom gland, Pavan's gland, pygidial gland, postpygidial gland, and the various sternal glands (Billen & Morgan, 1998). Besides these multiple possibilities for the elaboration of trail substances in abdominal glands, we already mentioned some of the hindleg glands performing this function, which brings the variety for production of trail pheromones in ants to more than a dozen glands.

Gland name (abdomen)	**type**		
anus gland	E	rectal papillae	B
cloacal gland	E	spermathecal gland	D
dorsolateral glands	E	spermatheca reservoir gland	B
Dufour gland	B	spiracular plate gland	E
epithelial sternal gland	A	sternal gland	C
epithelial sting sheath gland	A	sting bulb gland	E
epithelial tergal gland	A	sting chamber gland	E
lateroventral glands	E	sting gland	E

male accessory gland	B	sting sheath gland	C
paired sternal gland	E	subepithelial glands *	C
Pavan gland	A	subgenital plate gland	E
pedestal hair gland *	C	tegumental epithelium *	A
penis gland	E	tergal glands	E
petiole gland	C	tergosternal glands	E
postpetiolar gland	E	triangular plate gland	E
postpygidial gland	E	unpaired sternal gland	E
pygidial gland	E	valve's gland	E
quadrate plate gland	E	venom gland	D
rectal gland	B		

Another possible function for some abdominal glands is that of lubricant production. This is suggested for a number of intersegmental glands that can be found between the various tergites and sternites, especially in the heavily sclerotized ponerines (e.g. tergal, sternal, dorsolateral, lateroventral and tergosternal glands - Jessen et al., 1983).

CONCLUSIONS

The survey presented in this article illustrates the description that "*the typical ant worker is a walking battery of exocrine glands*" (Hölldobler & Wilson, 1990; p.229). Exocrine secretions play a crucial role in many aspects of the social life of ants, among which the function of the various pheromones is commonly known (e.g. trail and recruitment pheromones, alarm and sex pheromones, queen recognition pheromones, home range marking substances - see: Billen & Morgan, 1998). Other functions in which glands can be involved include the production of venom for defence or prey capture (venom gland), antibiotics (metapleural and propleural plate glands), various reproductive functions (spermatophore formation and sperm transfer in males, sperm storage and egg laying in females), production of digestive substances (propharyngeal and salivary glands) and the production of lubricant substances.

The impressive number of 75 known glands has considerably grown in the last decades, in which the availability and improvement of appropriate sectioning techniques was important. Because of their ectodermal origin, all glands are closely linked to cuticle, which for long time had compromised the histological possibilities to study them. The knowledge of so many existing glands in ants obviously goes along with the desire to explore the function of the many glands from which this is not yet known. The ongoing technical evolution of the equipment for chemical analysis, that allows identification of very small quantities of glandular secretions, together with careful behavioural observations, will be very important in our further under-standing of the social organization of these amazing insects.

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