



Formosan Entomologist

Journal Homepage: entsocjournal.yabee.com.tw

Exocrine Glands and Their Key Function in the Communication System of Social Insects 【Review article】

社會性昆蟲的外分泌腺體與其在溝通系統上扮演之功能【綜合論述】

Johan Billen*

Johan Billen*

*通訊作者E-mail: johan.billen@bio.kuleuven.be

Received: 2011/03/30 Accepted: 2011/04/02 Available online: 2010/06/01

Abstract

Communication in social insects to a very considerable extent is mediated by the action of chemical messenger molecules or pheromones. These are produced in an impressive variety of exocrine glands, that occur all over the body of these insects. Various gland types as well as various types of pheromonal communication can be distinguished. This article gives an example of each of the 5 anatomical types, representing the 5 major social insect groups, illustrating their structural diversity and their involvement in several pheromonal functions.

摘要

社會性昆蟲溝通的調節有相當程度是受到化學訊息分子或費洛蒙的作用，這些分子透過各種不同種類的外分泌腺體所產生，並遍佈於這些昆蟲體內。我們可以區別不同的腺體種類以及不同的費洛蒙溝通型式。本文將以五種不同解剖型的腺體為例，分別代表五種主要的社會性昆蟲，顯示腺體結構的多樣性以及它們對於許多費洛蒙功能的影響。

Key words: social insects, exocrine glands, morphology, pheromones, communication

關鍵詞: 社會性昆蟲、外分泌腺體、形態學、費洛蒙、訊息交流。

Full Text: [PDF\(6.16 MB\)](#)

下載其它卷期全文 Browse all articles in archive: <http://entsocjournal.yabee.com.tw>

Exocrine Glands and Their Key Function in the Communication System of Social Insects

Johan Billen*

Zoological Institute, University of Leuven, Naamsestraat 59, box 2466, B-3000 Leuven (Belgium)

ABSTRACT

Communication in social insects to a very considerable extent is mediated by the action of chemical messenger molecules or pheromones. These are produced in an impressive variety of exocrine glands, that occur all over the body of these insects. Various gland types as well as various types of pheromonal communication can be distinguished. This article gives an example of each of the 5 anatomical types, representing the 5 major social insect groups, illustrating their structural diversity and their involvement in several pheromonal functions.

Key words: social insects, exocrine glands, morphology, pheromones, communication

Introduction

Aren't they formidable little creatures: ants running along busy columns to and from their food sources, honeybee workers that are well instructed by their fellow nestmates in the hive how they should navigate to find resourceful flowers, or termites that construct huge skyscraper-equivalent nest mounds in the tropics? These are all examples of social insects, that live in colonies with hundreds, thousands or even millions of individuals. Each single individual perhaps does not represent too much through its personal achievements, but their group-living leads

to incredible overall performances, that are the result of an amazing coordination and cooperation. This is based on the development of a communication system, in which individuals exchange information. The social language of the ants and termites, wasps, bees and bumblebees can be very variable, and can be based on visual, acoustic, tactile and chemical cues, to name the most important (Fig. 1; Billen, 2006).

The most common sensory channel among these is undoubtedly that of chemical communication, in which chemical messenger molecules or pheromones are produced in exocrine glands, released to

*Corresponding email: johan.billen@bio.kuleuven.be



Fig. 1. Examples of the main sensory channels that can play a role in social insect communication: (A) Frontal view of a worker head of the nocturnal wasp *Apoica pallens*, showing the very large compound eyes (photo: Tom Wenseleers), (B) Scanning micrograph of the parallel ridges at the anterior side of the first gastral tergite of the ant *Myrmecia nigriceps*, forming the stridulation apparatus that allows acoustic communication (inset: lower magnification dorsal view of the postpetiole and first gastral tergite, showing the location of fig. 1B), (C) Trophallaxis between workers of *Apis mellifera*, illustrating tactile communication (photo: Dr. Ching-Hao Chiang), (D) Column of *Atta cephalotes* leaf-cutting ants, following a chemical pheromone trail.

the outside, and then detected by another individual in which they elicit a specific response. These responses can be instant behaviours such as trail following (trail pheromones), alarm displays (alarm pheromones), attraction to a partner for mating (sex pheromones), or can be slower physiological processes such as the regulation of dominance hierarchies or the interaction in caste determination. Whatever the response, the origin of the substances involved is always situated in exocrine glands, that therefore are very numerous in these social insects (Billen, 2009b). In this article, we will first deal with the structural variety of exocrine glands, in which 5 anatomical types can be characterized. Then,

we will give one example of each of these types, at the same time representing the five major social insects groups and dealing with the major pheromonal categories.

Structural variety of exocrine glands

In their pioneer paper of 1974, the French termitologists Charles Noirot and André Quennedey presented a still actual and generally followed classification of the exocrine glands based on the cellular organization of their secretory cells. Structurally most simple are the class-1 cells, that are epithelial cells directly modified from the tegumental epidermis. These cells rest on a basement membrane, and at their apical side are lined with a

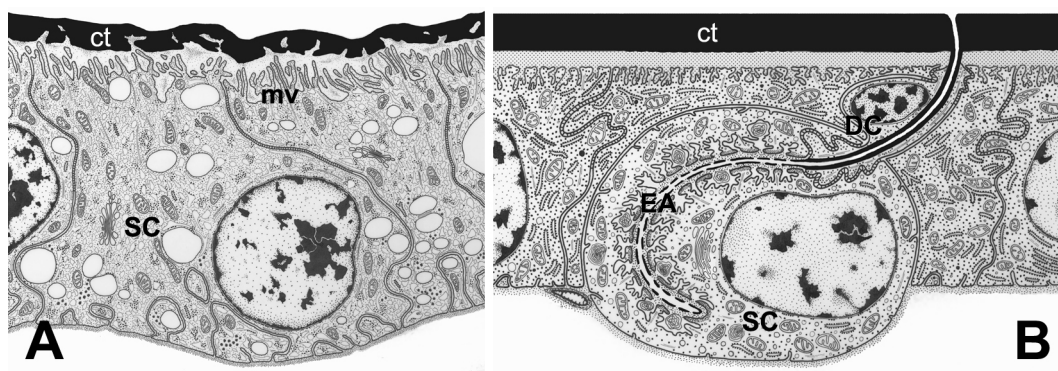


Fig. 2. Schematic drawings of (A) Class-1 epithelial gland (tibial gland *Crematogaster*) and (B) Class-3 bicellular gland unit (tergal gland *Apis mellifera* queen). ct: cuticle, DC: duct cell, ea: end apparatus, mv: microvilli, SC: secretory cell.

cuticular layer. The apical cell membrane is usually differentiated into a microvillar border, that results in a significant surface enlargement and hence an increased secretory capacity. The cuticle is often characterized by the presence of tiny pores, that allow transportation of the secretory products to the outside (Fig. 2A). Class-2 cells were described to be located more basally in between the class-1 cells, without being in contact with the apical cuticle. The presence and location of such cells, however, turned out to be very rare, and in a follow-up paper later on they were reported to be homologous to oenocytes (Noirot and Quennedey, 1991). Class-3 secretory cells form part of bicellular units, in which each secretory cell is associated with a duct cell. The contact region between both cells is characterized by an end apparatus. This is formed by a fenestrated cuticular ductule surrounded by microvilli, formed by the invaginated cell membrane of the secretory cell (Fig. 2B). This set-up allows an efficient transport of secretory molecules from the secretory cell cytoplasm (through the surface-enlarging microvilli and the fenestrated and hence permeable cuticle) into the duct cell, that will carry the secretion to the outside.

Both the glands formed by class-1 and these formed by class-3 secretory cells can

have a location that makes them release their secretory products directly to the outside, or they can release their secretion into a reservoir space, where it can be stored until it will be discharged when needed at a later time. This absence resp. presence of a reservoir leads to the distinction of 5 anatomical types: epithelial glands without and with reservoir, secretory unit glands without and with reservoir; the fifth type are secretory glands in which the reservoir is formed by an invagination of an intersegmental membrane (Fig. 3; Billen, 2009a, b).

Epithelial glands without reservoir: the metatibial gland of *Diacamma* sp. ants

Although the majority of social insect colonies show a clear queen-worker differentiation among the female individuals, some ant species are permanently queenless, and regulate reproduction through gamergates or mated workers. These have retained a functional spermatheca (Gobin *et al.*, 2006), are capable of attracting males and mate, and thus can produce worker offspring. An example of such ants is *Diacamma* sp. from Okinawa, Japan. The young virgin gamergate leaves the nest to call for males, an event during which she releases sex pheromones. The rather curious production

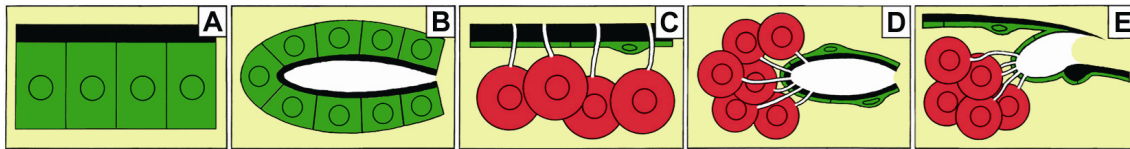


Fig. 3. Schematic organization of the five anatomical types of insect glands: (A) Epithelial glands without reservoir, (B) Epithelial glands with reservoir, (C) Bicellular unit glands without reservoir, (D) Bicellular unit glands with reservoir, (E) Bicellular gland units opening through intersegmental membrane.

site of these substances is situated in the metatibial gland of the hindlegs, from where it is transferred through a peculiar leg rubbing behaviour onto the abdomen (Hölldobler *et al.*, 1996; Nakata *et al.*, 1998). With the pheromone thus deposited onto the abdomen, the young gamergate will display a characteristic calling posture with the abdomen pointing upward in order to attract males.

The metatibial gland occurs in the distal quarter of the hindleg tibia, where it is externally visible as a smooth area (Fig. 4A). Underneath this area, a conspicuous epithelium of class-1 secretory cells is found (Fig. 4C). At high magnification, the smooth area shows hundreds of very small openings, that represent cuticular pore canals through which the glandular secretion finds its way to the outside (Fig. 4B). These openings have a diameter around 0.1-0.2 μm and represent nothing but cracks in the cuticle, and should not be confused with the pores formed by the duct cells of class-3 glands, that have a diameter of approx. 0.5-1 μm and are of cellular origin.

Epithelial glands with reservoir: the frontal gland of termite soldiers

Defence in termites is mainly achieved via mechanical weapons such as the very strong mandibles of soldiers, and chemically with secretions from the labial, labral or the frontal glands contributing (Šobotník *et al.*, 2010). Especially frontal glands of the soldiers in the advanced termite families are very important defence

tools. The gland has led to the peculiar head shape in the Nasutitermitinae, where the frons is anteriorly elongated to become a nose-like extension, with the unpaired frontal gland opening at the tip (Figs 4D, E). More posteriorly in the head, and often extending into the thorax and even into the abdomen is the reservoir sac which is lined with class-1 secretory cells (sometimes class-3 secretory cells can also occur in the reservoir wall and in the region near the gland duct in the nasus - Šobotník *et al.*, 2010).

Its chemical composition usually contains mono- and diterpenes. When disturbed, the discharged frontal gland secretion can mechanically act to entangle the enemy, or it may chemically function as a surface irritant, repellent or alarm substance (Šobotník *et al.*, 2010). These functions are much in line with the presence of a reservoir, that allows large quantities of the secretion to be available when needed. In soldiers of some species, such as *Globitermes suphureus*, the very enlarged frontal gland reservoir has even lost its connection to the outside and fills most of the body. When disturbed, the glands of these kamikaze soldiers rupture by violent abdominal contractions and thus release their yellowish viscous secretion that will immobilize the enemy (Bordereau *et al.*, 1997).

Bicellular unit glands without reservoir: tergal glands of honeybees

Honeybee colonies display a distinct difference between the queen and the

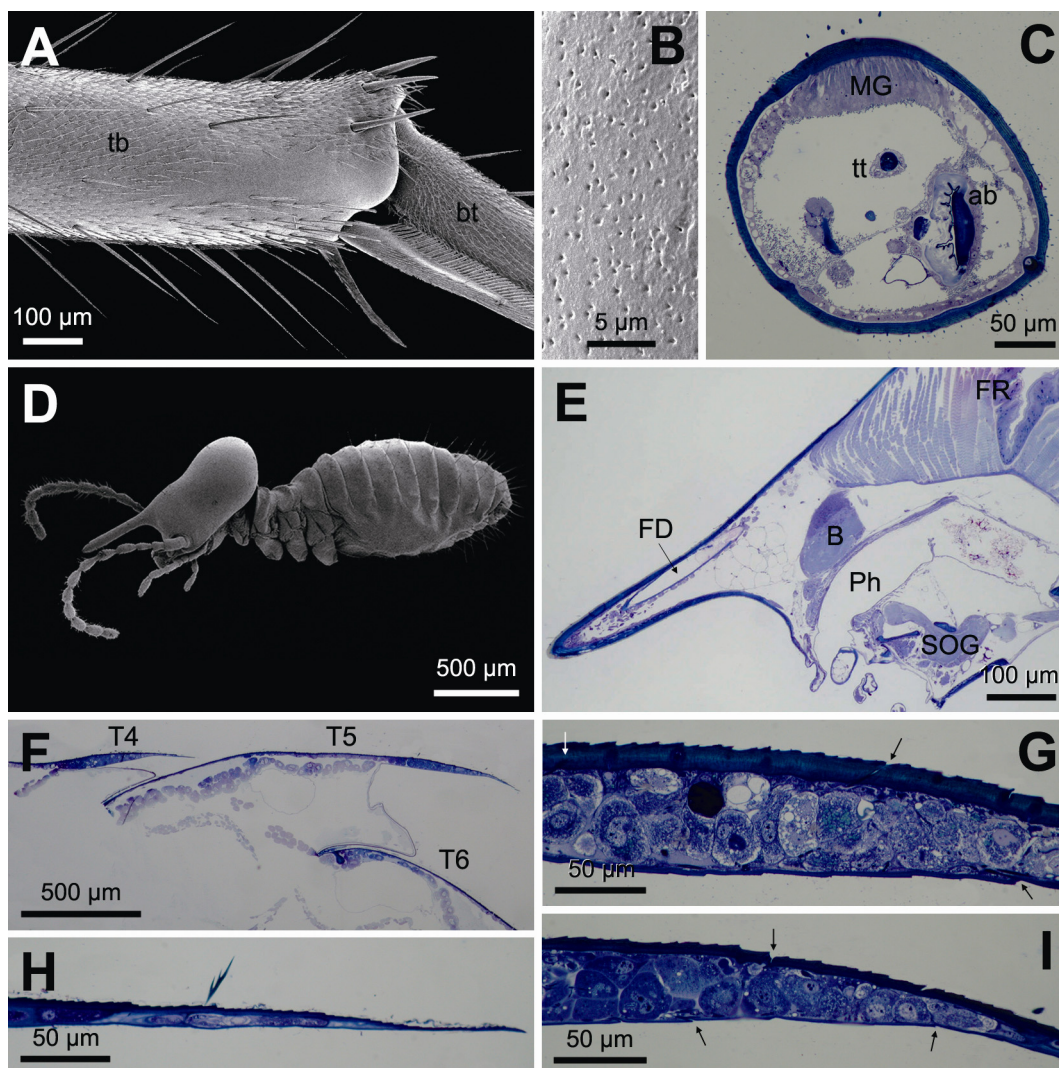


Fig. 4. (A) Scanning micrograph of the distal portion of the hindleg tibia of *Diacamma* sp., showing the smooth area that covers the metatibial gland, (B) Detail of the smooth area, which is characterized by hundreds of very small cuticular pores, (C) Semithin cross section through the distal part of the hindleg tibia of *Diacamma* sp. illustrating the conspicuous glandular epithelium, (D) Scanning micrograph of a major soldier of *Diversitermes castaniceps*, illustrating the peculiar head shape with the long nasus. (E) Longitudinal section through the nasus and anterior head portion of *D. castaniceps* major soldier, showing the duct and reservoir sac of the frontal gland. (F) Semithin section through abdominal tergites in *Apis mellifera capensis* workers, showing occurrence of tergal glands, (G) Posterior area of 5th tergite in *Apis mellifera* queen, filled with tergal gland cells, (H) Similar region in *Apis mellifera* worker, with almost no gland cells, (I) Similar region in *Apis mellifera capensis* worker, filled with numerous gland cells.

ab: articulation with basitarsus, B: brain, bt: basitarsus, FD: frontal gland duct, FR: frontal gland reservoir, MG: metatibial gland, Ph: pharynx, SOG: suboesophagial ganglion, T4, 5, 6: 4th, 5th, 6th tergite, tb: tibia, tt: tibial tendon. Arrows: opening of tergal gland duct cells.

workers, in which the queen for the greater part relies on pheromonal secretions that result in her dominance status. The well developed mandibular glands of the queen are the source of the very important 9 oxo-trans-2-decenoic acid, but also the tergal glands play a role in the royal status (Fig. 4F). These glands are formed by scattered class-3 cells that occur underneath the abdominal tergites (Renner and Baumann, 1964), where their ducts open both through the thick upper cuticle and through the thin under side in the tergite's posterior edge region (Figs 2B, 4G). In queens, numerous big gland cells occur, mainly in tergites III to V, whereas workers only have very few and considerably reduced cells (Fig. 4H; Billen *et al.*, 1986).

A clear illustration of the role of these tergal glands in the establishment of dominance behaviour is found in the cape honeybee *Apis mellifera capensis*. These workers are known to penetrate in queenless colonies of other honeybee subspecies, where they will behave in a queen-like way and display a dominant behaviour over the resident worker bees. Thanks to their ability to reproduce parthenogenetically, the eggs of these *capensis* 'false queens' can develop into worker offspring. The capacity of the *capensis*-workers to display their obvious dominant behaviour is linked with their well developed mandibular glands and the similarity of their secretion to that of *mellifera*-queens, but also to the development of their tergal glands, that have an appearance similar to that of *mellifera*-queens (Fig. 4I; Billen *et al.*, 1986). The absence of a reservoir and hence the direct release of secretion to the outside can probably be linked with the permanent need to signal the royalty status to all nestmates in the colony.

Bicellular unit glands with reservoir: the venom gland of Hymenoptera

Defence is a general characteristic of

all living creatures, and for social insects in particular, as they represent a valuable resource for eventual opponents. The venom gland in social Hymenoptera has become the most common source for the elaboration of defensive substances, that are usually injected into the enemy through the sting. Besides their primary function in defence, venom gland compounds can also be involved to conquer prey in carnivorous species, and can often also display a variety of secondary pheromonal functions, such as the elaboration of trail pheromones in several ant species (reviewed in Morgan, 2009).

Bumblebees use their venom gland as the traditional weapon against opponents when disturbed. As in the other social Hymenoptera, the gland opens through the sting (Billen, 1987), and is formed by a big ovoid reservoir sac and Y-shaped secretory filaments, that contain the secretory cells producing the venom (Fig. 5A). The secretory cells belong to class-3, though their arrangement in the secretory filaments may give them a pseudo-epithelial appearance (Figs 5A, B). Duct cells carry the secretion to the lumen of the secretory tubules, that actually represent an extension of the reservoir space. Secretion is transported from the filament lumen through the convoluted gland area into the reservoir sac. Such convoluted gland is a specialized and structurally complex secretory part of the hymenopterous venom gland, that contributes to venom formation and also protects against self-toxication (Schoeters and Billen, 1995). The storage of secretion in the large reservoir allows the availability in sufficient quantity of defensive substances against eventual enemies at any time when needed.

Bicellular unit glands with reservoir formed by intersegmental membrane: Richard's glands of epiponine wasps

In the majority of the polistine wasp genera, represented by the mostly tropical tribe Epiponini, colony founding occurs

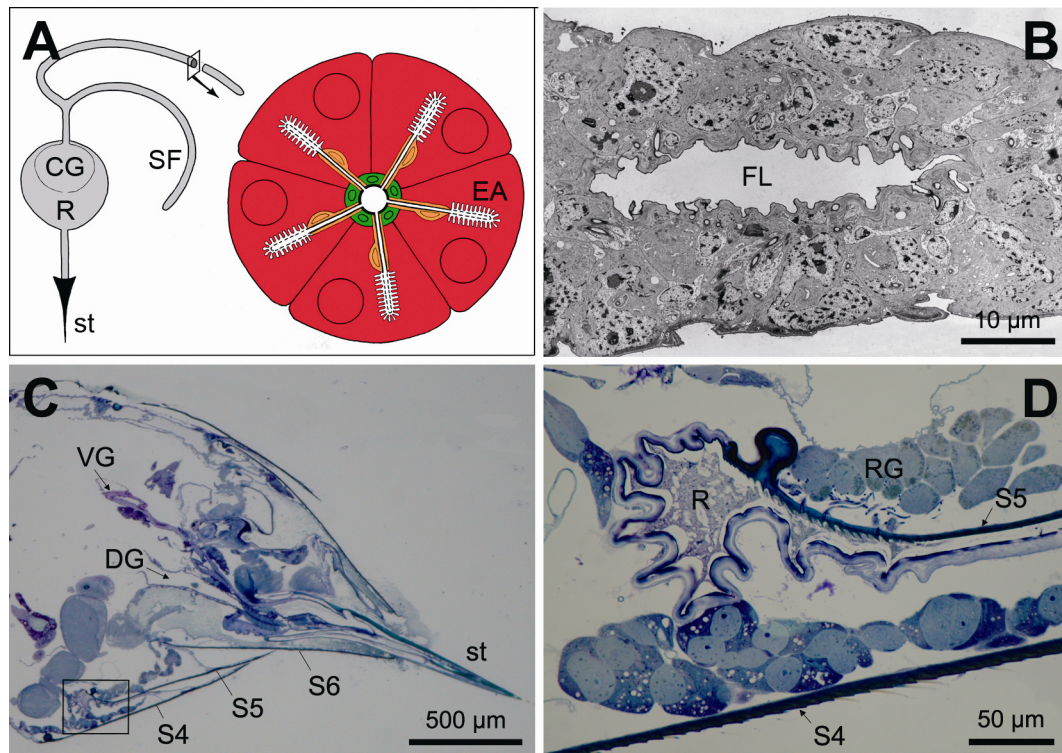


Fig. 5. (A) Schematic organization of the hymenopterous venom gland with detail of the various cell types in the secretory filaments (secretory cells red, duct cells orange, filament lumen cells green), (B) Electron micrograph of secretory filament portion of *Bombus impatiens* worker, showing pseudo-epithelial arrangement of class-3 secretory cells, (C) Semithin section through the abdominal tip along the midline of a *Polybia paulista* worker, showing the location and structure of Richard's gland at the anterior side of the 5th sternite. Detail of inset is shown in (D), with reservoir formed by invaginated intersegmental membrane, and scale-like cuticular formations in anterior sternite region where duct cells open.
CG: convoluted gland, DG: Dufour gland, EA: end apparatus, FL: filament lumen, R: reservoir, RG: Richard's gland, S4, 5, 6: 4th, 5th, 6th sternite, SF: secretory filament, st: sting, VG: venom gland.

through swarm founding. This is a process in which swarms containing large numbers of workers and a smaller number of queens move from the old nest to the new nest site (West-Eberhard, 1982; Jeanne, 1991). During this nest moving, the route between the old and new nest is scent-marked by scout workers by landing on leaves along the route, on which they drag their gaster. This behaviour allows them to deposit trail pheromone substances from a gland underneath the anterior side of the penultimate abdominal sternite, and thus

communicate the route to follow to their nestmates in the swarm. As it is individual wasps that search and follow the marked spots by landing on the vegetation and inspect the landmarks with their antennae, swarms constitute rather diffuse formations (West-Eberhard, 1982).

The scent-marking source is known as Richard's gland, which is formed by class-3 secretory cells that open through the anterior cuticle of the 5th sternite (Jeanne and Post, 1982). The intersegmental membrane that connects the 4th and 5th

sternites is invaginated and thus forms a clear reservoir in which the pheromonal secretion can be stored (Figs 5C, D). During marking, the anterior side of the 5th sternite is extended in order to expose its anterior margin and deposit secretion onto the substrate. Cuticular modifications at the anterior side of the 5th sternite, such as grooves or scales, probably help in depositing only a small amount of gland secretion during each marking act, as retraction of the sternite after each marking event to its rest position moves the intersegmental reservoir over the area with cuticular modifications, thus supplying the latter with a small pheromone dosis to be used during the next marking act (Jeanne *et al.*, 1982).

Conclusion

The few examples of the various anatomical types of exocrine glands in social insects presented in this article illustrate the very important role that glandular secretions can play as information messengers, and therefore underline their key function in the social life. Not all glands have a role in the production of such pheromones, however, as many other functions can be attributed to them as well. Some glands can be involved in the production of the nest, such as the wax glands of the bees, or the salivary glands of wasps and termites, that produce saliva to be mixed with wood pulp or soil, respectively, in order to construct their nests. Other glands produce digestive enzymes or substances with a role in caste determination. Also the elaboration of antibiotics or venoms is known for a number of glands, while several glandular structures located near the intersegmental membranes or articulations of body parts probably provide lubricant substances to allow easy movements. This multitude of functions in which glandular secretions are involved explains the astonishing number and development of the exocrine

glands in social insects, that therefore have indeed been referred to as walking or flying glandular batteries (Hölldobler and Wilson, 1990; Billen and Morgan, 1998).

Acknowledgments

I am very grateful to An Vandoren and Alex Vrijdaghs for their professional help in section preparation and scanning microscopy. Thanks are also due to Fuminori Ito and Fernando Noll for their help in providing insect specimens that are discussed in this article, and to Tom Wenseleers and Dr. Ching-Hao Chiang for providing photographs.

References

- Billen J.** 1987. New structural aspects of the Dufour's and venom glands in social insects. *Naturwissenschaften* 74: 340-341.
- Billen J.** 2006. Signal variety and communication in social insects. *Proceedings of the Netherlands Entomological Society Meeting*, 2005 Dec 16, Ede (Netherlands) 17: 9-25.
- Billen J.** 2009a. Occurrence and structural organization of the exocrine glands in the legs of ants. *Arthropod Struct Dev* 38: 2-15.
- Billen J.** 2009b. Diversity and morphology of exocrine glands in ants. *Proceedings of the 19th Symposium of the Brazilian Myrmecological Society*, Ouro Preto (Brasil), 2009 Nov 17-21, pp 1-6.
- Billen J, Morgan ED.** 1998. Pheromone communication in social insects-sources and secretions. pp 3-33. In: Vander Meer RK, Breed MD, Winston ML, Espelie KE (eds). *Pheromone Communication in Social Insects: Ants, Wasps, Bees, and Termites*. Westview Press, Boulder, Oxford.
- Billen JPJ, Dumortier KTM, Velthuis HHW.** 1986. Plasticity of honeybee castes: occurrence of tergal glands in workers. *Naturwissenschaften* 73: 332-333.

- Bordereau C, Robert A, Van Tuyen V, Peppuy A.** 1997. Suicidal defensive behaviour by frontal gland dehiscence in *Globitermes sulphureus* Haviland soldiers (Isoptera). *Insect Soc* 44: 289-297.
- Gobin B, Ito F, Peeters C, Billen J.** 2006. Queen-worker dimorphism in the spermathecae of phylogenetically primitive ants. *Cell Tissue Res* 326: 169-178.
- Hölldobler B, Wilson EO.** 1990. The ants. Cambridge, Mass.: Harvard University Press. 732 pp.
- Hölldobler B, Obermayer M, Peeters C.** 1996. Comparative study of the metatibial gland in ants (Hymenoptera, Formicidae). *Zoomorphology* 116: 157-167.
- Jeanne RL.** 1991. The swarm-founding Polistinae. pp 191-231. In: Ross KG, Matthews RW (eds). *The Social Biology of Wasps*. Comstock Publishing Associates, Ithaca, London.
- Jeanne RL, Post DC.** 1982. Richard's gland and associated cuticular modifications in social wasps of the genus *Polybia* Lepeletier (Hymenoptera, Vespidae, Polistinae, Polybiini). *Insect Soc* 29: 280-294.
- Morgan ED.** 2009. Trail pheromones of ants. *Physiol Entomol* 34: 1-17.
- Nakata K, Tsuji K, Hölldobler B, Taki A.** 1998. Sexual calling by workers using the metatibial glands in the ant, *Diacamma* sp., from Japan (Hymenoptera, Formicidae). *J Insect Behav* 11: 869-877.
- Noirot C, Quennedey A.** 1974. Fine structure of insect epidermal glands. *Annu Rev Entomol* 19: 61-80.
- Noirot C, Quennedey A.** 1991. Glands, gland cells, glandular units: some comments on terminology and classification. *Annls Soc Ent Fr (N. S.)* 27: 123-128.
- Renner M, Baumann M.** 1964. Über Komplexe von subepidermalen Drüsenzellen (Duftdrüsen?) der Bienenkönigin. *Naturwissenschaften* 3: 68-69.
- Schoeters E, Billen J.** 1995. Morphology and ultrastructure of the convoluted gland in the ant *Dinoponera australis* (Hymenoptera: Formicidae). *Int J Insect Morphol Embryol* 24: 323-332.
- Šobotník J, Jirošová A, Hanus R.** 2010. Chemical warfare in termites. *J Insect Physiol* 56: 1012-1021.
- West-Eberhard MJ.** 1982. The nature and evolution of swarming in tropical social wasps (Vespidae, Polistinae, Polybiini). pp 97-128. In: Jaisson P (ed). *Social Insects in the Tropics*, volume 1. Université Paris Nord, Paris.

Received: March 30, 2011

Accepted: April 2, 2011

社會性昆蟲的外分泌腺體與其在溝通系統上扮演之功能

Johan Billen^{*}

比利時魯汶大學動物學研究所

摘 要

社會性昆蟲溝通的調節有相當程度是受到化學訊息分子或費洛蒙的作用，這些分子透過各種不同種類的外分泌腺體所產生，並遍佈於這些昆蟲體內。我們可以區別不同的腺體種類以及不同的費洛蒙溝通型式。本文將以五種不同解剖型的腺體為例，分別代表五種主要的社會性昆蟲，顯示腺體結構的多樣性以及它們對於許多費洛蒙功能的影響。

關鍵詞：社會性昆蟲、外分泌腺體、形態學、費洛蒙、訊息交流。