Plenary Speech

Functional morphology and diversity of exocrine glands in ants

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Ants are characterized by an amazingly diverse exocrine system (Fig. 1), nicely formulated in the standard textbook, 'The Ants', as "*the typical ant worker is a walking battery of exocrine glands*" (Hölldobler & Wilson, 1990; p. 229). At present, 84 glands have been described in literature, while we know from our own unpublished observations that at least a dozen needs to be added to this list.

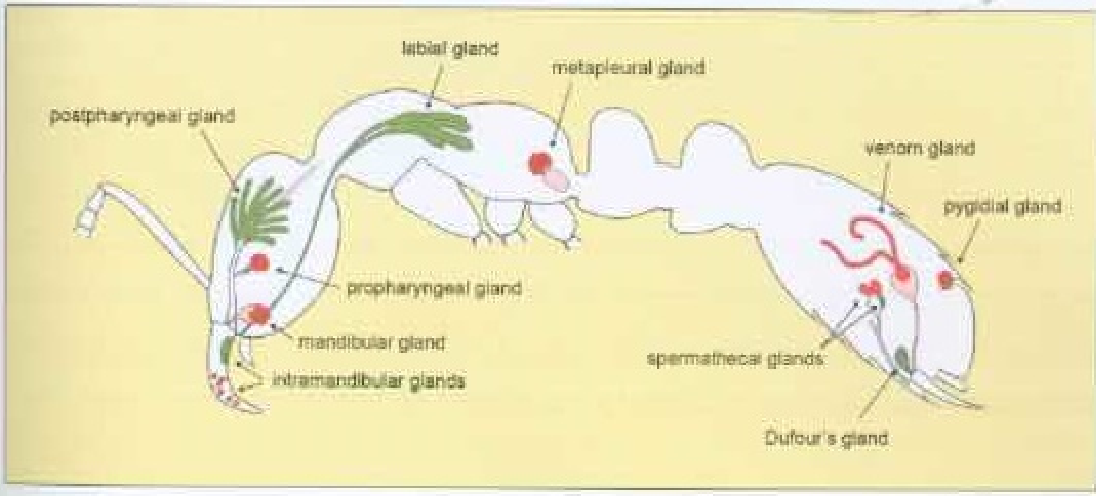

Fig. 1. The location of the most commonly occurring exocrine glands in ants. Glands indicated in green vs red correspond with class-1 and class-3 glands, respectively (see also figure 2).

This presentation aims to give a survey on the anatomical variety and classification of the exocrine system of the Formicidae, with comments on the wide variety of functions the gland secretions can play, with reference to some selected key examples of particular glands.

At a general anatomical level, exocrine glands are traditionally classified in two main groups following the classification of Noirot and Quennedey (1974): class-1 glands are formed by a monolayer of epithelial cells that form a direct differentiation of the integumental epidermis. Class-3 glands are formed by bicellular units, each unit comprising a secretory cell and its accompanying duct cell (the original classification also included class-2 cells, that were later homologized with oenocytes by Noirot & Quennedey, 1991). The duct cell continues into the secretory cell as the 'end apparatus', which represents an adaptation for efficient drainage of the secretory products. Both class-1 and class-3 glands can open directly through the outer cuticle, or can open into a common reservoir, in which a secretion can be temporarily stored until it is released (Fig. 2).

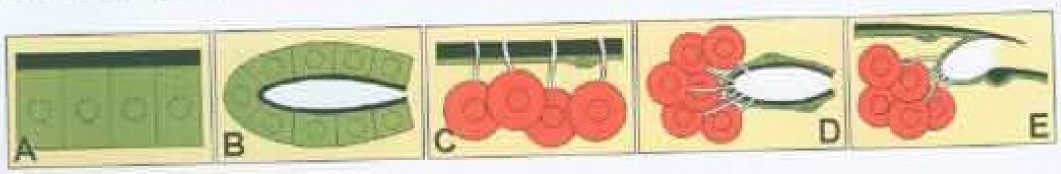

Fig. 2. Schematic drawings of the main anatomical types of exocrine glands: **A**. epithelial glands without reservoir, **B**. epithelial glands with reservoir, **C**. bicellular unit glands without reservoir, **D**. bicellular unit glands with reservoir, **E**. bicellular unit glands opening through articulation membrane. Black: cuticle, green: epithelial gland cells (class-1), red: bicellular unit gland cells (class-3).

Glands in the head (Fig. 3)

All ant species, regardless of caste, possess pro- and post-pharyngeal glands that open in the anterior or posterior region of the pharynx (Fig. 3A-C). The pro-pharyngeal gland (class-3) consists of a left and right cluster of secretory cells, that are involved in the production of digestive enzymes, as is reflected in the elaboration of proteins at the ultrastructural level. The glove-shaped post-pharyngeal gland (class-1), on the other hand, produces a non-proteinaceous secretion, and plays a major role in nest mate recognition (Eelen et al., 2006).

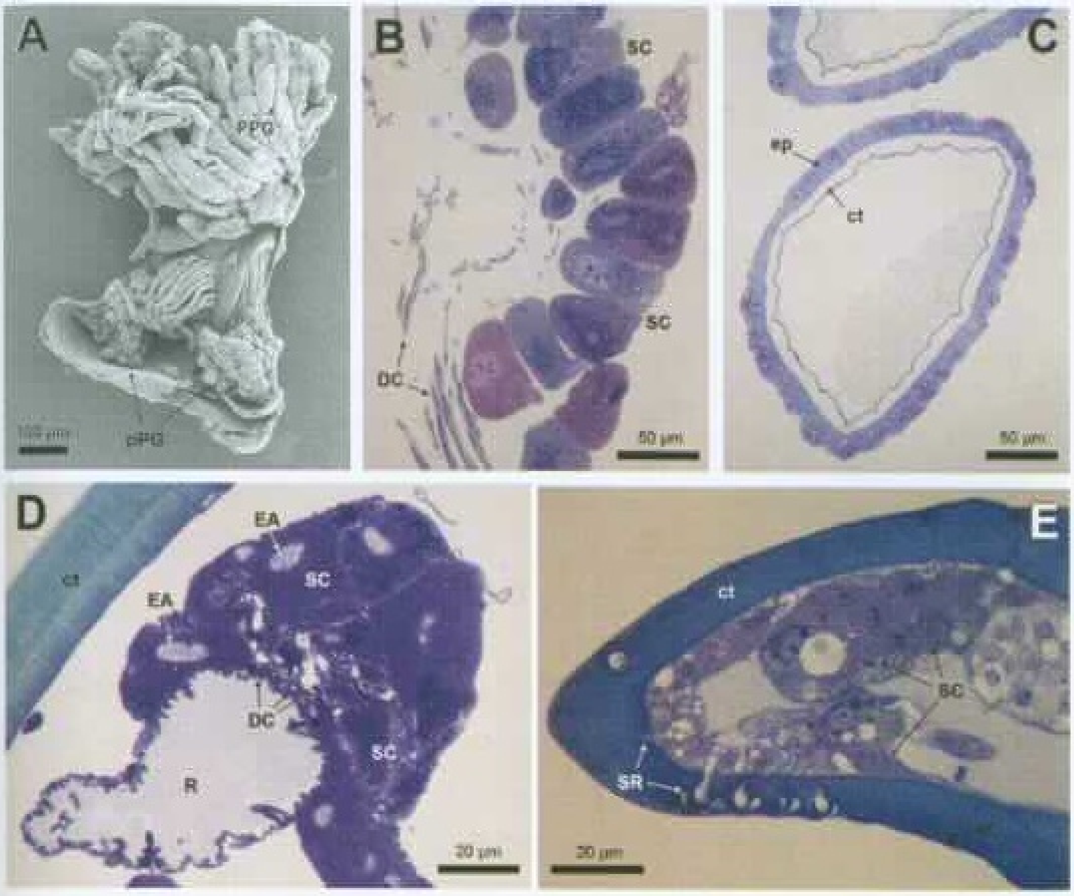

Fig. 3. Exocrine glands in the head: **A**. SEM micrograph of the propharyngeal (pPG) and postpharyngeal glands (PPG) in *Aphaenogaster senilis* worker. **B**. Section through secretory cells (SC) and duct cells (DC) of pro-pharyngeal gland of *Myrmecia pyriformis* worker. **C**. Cross section through post-pharyngeal gland tubule of *Camponotus atriceps* alate queen (ct: cuticle, ep: epithelial cells). **D**. Section through mandibular gland of *Myopias emeryi* worker (ct: cuticle, DC: duct cells, EA: end apparatus, R: reservoir, SC: secretory cells). **E**. Longitudinal section through mandible of *Aneuretus simoni* minor worker showing secretory cells of intra-mandibular gland (SC). ct: cuticle, SR: sensory receptors.

The mandibular glands (class-3) are also found in all ant species and all castes, and are associated with the mandibles (Fig. 3D). The most common function of mandibular glands is related to the alarm-defense system, the alarm pheromones being released as a result of the mechanical opening of the mandibles. In addition to these common mandibular glands, also intra-mandibular glands may occur (Fig. 3E), that can either belong to class-1 or class-3, and with differences and peculiarities among the species.

Glands in the thorax (Fig. 4)

The commonly occurring labial (= salivary) glands are found in the anterior part of the thorax, although a narrow duct leads the secretion through the neck into the head capsule, where it is released at the base of the labium. Labial glands (class-1) can appear as acinar (Ponerinae, Fig. 4B) or tubular (all other subfamilies, Fig. 4A).

The paired metapleural gland (class-3) is a unique exocrine structure that is only known in Formicidae. It is located near the implantation of the hind legs (Fig. 4C, D), and generally produces antibiotics, that are spread over the body through grooming (Yek & Mueller, 2011).

Ant legs are mainly used for locomotion and therefore mainly contain muscle and nerve fibres. In addition, they may also contain an astonishing variety of over 20 glands (belonging to both class-1 and class-3). Many of them may have a lubricant function, while others are known as the source of trail or sex pheromones (Billen, 2009).

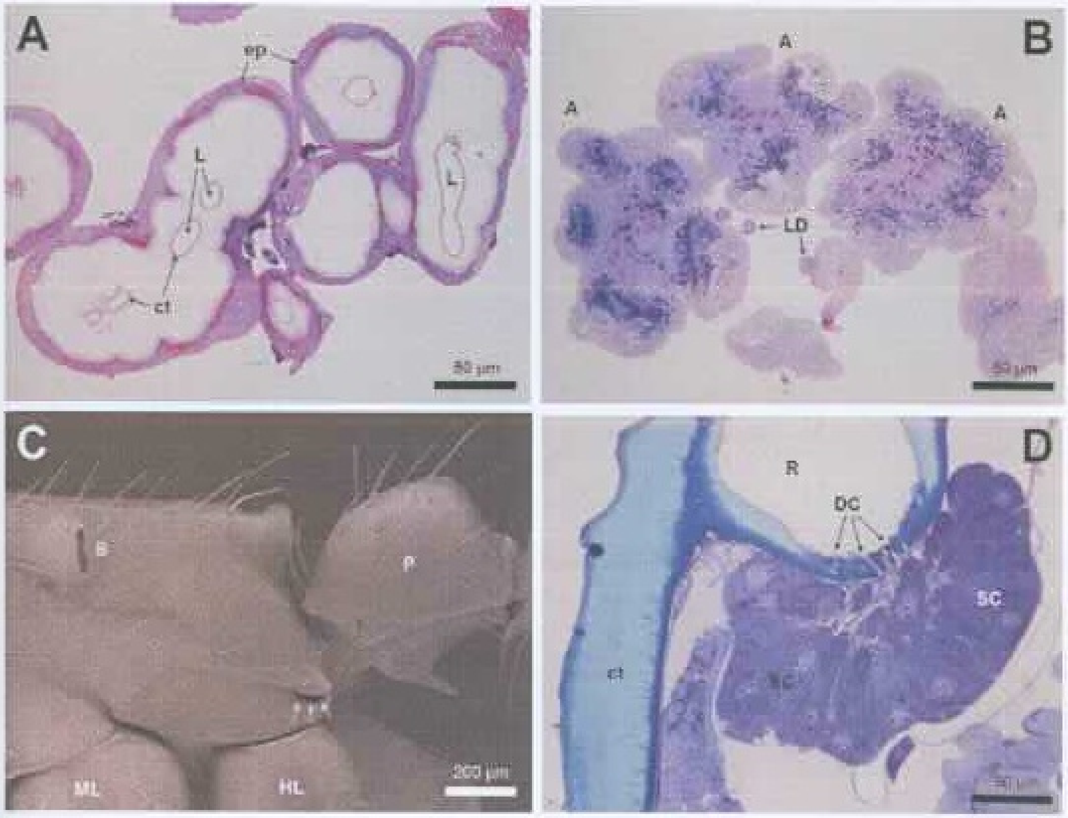

Fig. 4. Exocrine glands in the thorax: **A**. Section through tubular labial gland of *Myrmecia nigriceps* worker (ct: cuticular lining of lumen, ep: epithelial secretory cells, L: lumen). **B**. Section through acinar labial gland of *Dinoponera quadriceps* worker (A: acini, LD: labial gland ducts). **C**. SEM view of posterior thorax and petiole (P) of *Eciton burchellii* worker, arrows indicate slit-like opening of metapleural gland (HL: hind leg, ML: middle leg, S: spiracle). **D**. Section through metapleural gland of *Myopias maligna* queen (ct: cuticle, DC: duct cells, R: reservoir, SC: secretory cells).

Glands in the abdomen (Fig. 5)

The venom gland shows a rather complicated anatomical organization (Fig. 5A). Two slender filaments form the active secretory tissue where initial venom production takes place. They are formed by class-3 cells, although they occur in a pseudo-epithelial arrangement (Fig. 5B). Both filaments carry their secretion into the reservoir sac through a convoluted gland that can be considered as a specialized anatomical structure, which prevents the self-toxication of ants. The reservoir finally releases the venom through the sting, or venom is sprayed to the outside through the acidopore in the stingless Formicinae (Fig. 5C).

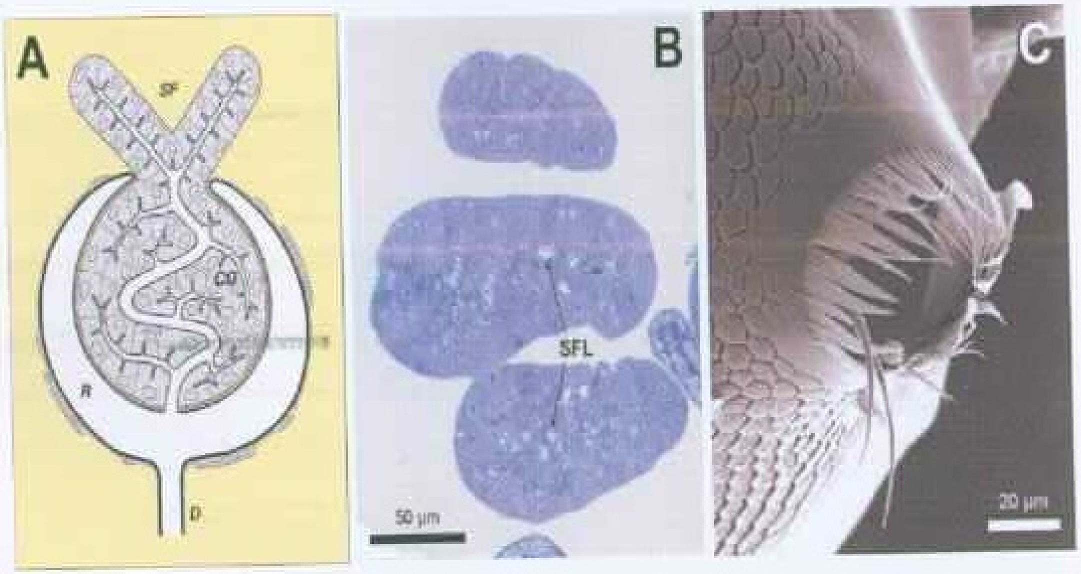

Fig. 5. Exocrine glands in the abdomen: **A**. Schematic organization of the venom gland: CG: convoluted gland, D: venom duct, R: reservoir, SF: secretory filaments. **B**. Secretory filaments of venom gland of *Daceton armigerum* worker (SFL: lumen of secretory filament). **C**. SEM view of the acidopore of *Formica fusca* worker; note the circle of bristle hairs that function in directing the spray of formic acid.

The spermatheca is a unique reproductive structure that is formed by two glandular elements; a paired spermathecal gland (class-3) and at least partially glandular lining (class-1) of the reservoir wall (Fig. 5D). Both glandular components are required for spermathecal functionality, as could be concluded by studying ants with various reproductive strategies (Gobin et al., 2006, 2008).

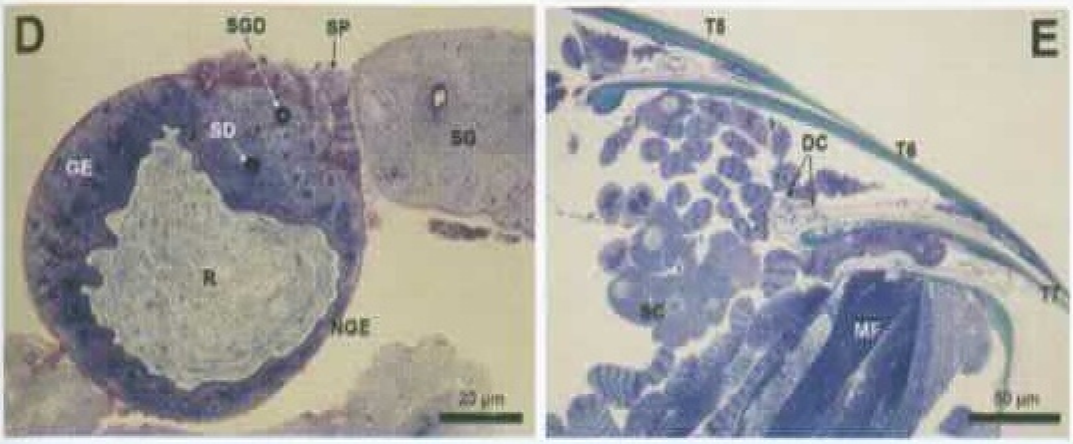

Fig. 5 (continued) - Exocrine glands in the abdomen: **D**. Section through spermatheca of *Myopias* sp. queen (GE: glandular reservoir epithelium, NGE: non-glandular epithelium, R: reservoir filled with sperm, SG: spermathecal gland, SGD: spermathecal gland duct, SP: sperm pump muscles). **E**. Longitudinal section through terminal abdominal tergites of *Myopias emeryi* worker showing pygidial gland (DC: duct cells of pygidial gland, MF: muscle fibres, SC: secretory cells of pygidial gland, T5, T6, T7: tergites 5,6,7).

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