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MORPHOLOGY OF EXOCRINE GLANDS IN SOCIAL INSECTS WITH SPECIAL EMPHASIS ON THE CONTRIBUTIONS BY ITALIAN RESEARCHERS

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ABSTRACT - The morphological study of the exocrine system in social insects is known by a considerable contribution from Italian researchers. Pavan's gland in dolichoderine ants has been named after its discoverer, but also a number of other glands have been first described by Italians, while several other significant gland studies both with light and electron microscopy have been realized in Italy.

KEY WORDS: Morphology, ultrastructure, exocrine glands, social insects, Italy.

INTRODUCTION

Social insects are characterized by an astonishing variety of exocrine glands, and therefore can somehow be considered as glandular factories (HÖLLDOBLER and WILSON, 1990; BILLEN, 1998). In almost all aspects of the social life of these insects, glandular secretions play a role. A few examples, among many others, are the wax glands of bees that produce building material for the combs, the venom glands that elaborate defensive substances, and the plethora of mainly abdominal glands that produce trail pheromones (BILLEN and MORGAN, 1998).

Over 100 different exocrine glands are presently known among the various social insect groups. Many authors through history have contributed with accurate descriptions of gland anatomy, histology and ultrastructure. Among them, Italian researchers in particular have played a significant role in the morphological study of the exocrine system in social insects, a survey of which is given in the present article.

STRUCTURAL ORGANIZATION OF EXOCRINE GLANDS

In spite of their high number, the exocrine glands in insects can be classified as belonging to one of two main classes, that were first described in

the review work by NOIROT and QUENNEDEY (1974). In their classification, epithelial glands are formed by class 1 cells, that originate directly from the tegumental epidermis. The second group of glands is formed by bicellular units (class 3 cells), each comprising a secretory cell and a duct cell. The secretory processes are comparable in both gland classes, with specific structural peculiarities for the uptake of precursor molecules, the cytoplasmic elaboration of the secretory products, their temporary storage in a reservoir or their release to the outside (BILLEN, 1991; NOIROT and QUENNEDEY, 1991).

History of morphological studies

The history of entomology in general is characterized by an eminent Italian presence, that was reviewed in a detailed survey by BACCETTI (1996). The first Italian reports in literature dealing with social insects go back to Varro's discussions on the honeybee in the first century b.C., soon followed by the apicultural descriptions by Vergilius and Plinius Major. Microscopical exploration of social insects started in the 17th century when Francesco Stelluti, using Galileo's newly built instrument, became the first entomological microscopist describing the structures of the honeybee in considerable detail. Only several decades later, other famous microscopists like Robert Hooke and Jan Swammerdam published their microscopical observations on the honeybee (COBB, 2002). Further refinement of the microscope as an analytical instrument was realized in the following two centuries, resulting in the accurate descriptions of the Swiss myrmecologist August FOREL (e.g. 1878).

At the end of the 19th and early 20th century, the French Charles JANET (e.g. 1898; BILLEN, 1994) produced a series of excellent pioneer works describing the histological organization of mainly ants and wasps using sectioned material. His publications formed a major breakthrough in the morphological study of exocrine glands in social insects.

The first thorough survey studies of the internal anatomy of social insects became available with the descriptions of the Argentine ant by PAVAN and RONCHETTI (1955), and of the honeybee by SNODGRASS (1956). Pavan's work in Pavia is another illustration of the strong Italian school, and remains especially famous because of the discovery of a novel sternal gland between the 6th and 7th sternite of dolichoderine ants (PAVAN and RONCHETTI, 1955; MIRADOLI ZATTI and PAVAN, 1957), initially described as the 'organo ventrale' and since known as the Pavan's gland.

Another Italian pioneer was Romano Dallai in Siena, who was among the first electron microscopists to describe the fine structural organization of the spermatheca in a variety of insects, including the honeybee (DALLAI, 1975). His work on the *Apis mellifera* spermatheca provides a pioneer contribution both for its ultrastructural description and functional interpretation in social insects. Dallai moreover figures in second position in the ranking of the number of articles published on the ultrastructure of insect exocrine glands. In this ranking, the top-10 hosts no less than 4 Italians (R. Dallai, G. Delfino, N. Isidoro and F. Bin), who all contributed significant papers on the exocrine system of social insects (QUENNEDEY, 2000).

In the 1980s, many additional significant Italian publications on the morphology and ultrastructure of exocrine glands in social insects appeared, and were the result of various research teams).

In Rome, the group of Alberto Fanfani was especially active in further studying the structural aspects of Pavan's gland and the other gastral glands of dolichoderine ants (DAZZINI VALCURONE and FANFANI, 1982, 1985; FANFANI and DAZZINI VALCURONE, 1984), as well as the metapleural gland (FANFANI and VALCURONE DAZZINI, 1991; FANFANI and GIOVANNOTTI, 1994). From this group originate also some side studies describing the abdominal glands in Ponerinae (FANFANI and DAZZINI VALCURONE, 1986), the leg glands of *Crematogaster striatula* (FANFANI and VALCURONE DAZZINI, 1990) and the Dufour gland of *Polyergus rufescens* (GIOVANNOTTI et al., 1996).

In Ferrara, Giovanni Sbrenna and co-workers performed a detailed ultrastructural study on the bicellular epidermal glands in *Kalotermes* termites (that were reported in an earlier work on *Reticulitermes* by JUCCI (1924)), and which occur in the head, thorax and abdomen with caste-specific development (LEIS and SBRENNA, 1983; SBRENNA and LEIS, 1983). A continuation of the ultrastructural work in Ferrara deals with a study of the mandibular glands in queens of the bumblebee *Bombus terrestris* (PALATINI et al., 2003).

Many important contributions on gland ultrastructure in the social wasps have been produced over the years by the Firenze group around Giovanni Delfino. Their high quality work, illustrated with very instructive line drawings, among others, reports on the ultrastructure and development of the Van der Vecht gland (DELFINO et al., 1979; MARINO PICCIOLI et al., 1986), the venom gland (DELFINO et al., 1983, 1997), the Dufour gland (DELFINO et al., 1988) and the ectal mandibular gland (DELFINO et al., 1998) in

polistine and stenogastrine wasps. A very interesting finding in their work is the peculiar but apparently common branching of the end apparatus in class 3 exocrine glands in wasps. The ultrastructural component of the Fiorentine wasp research also includes the description of novel tegumental glands in the legs of both *Polistes* males and females with a function in territorial defence (BEANI and CALLONI, 1991), as well as in the parameres of *Liostenogaster* males (FORTUNATO et al., 2000).

The Perugia group of Ferdinando Bin specialized in the ultrastructural organization of antennal glands in a variety of insects, with an active continuation by Nunzio Isidoro in Ancona. Their work recently extended its survey to include also social insects with the discovery and precise descriptions of novel exocrine glands in the antennomeres of wasps (FORTUNATO et al., 1998; ISIDORO et al., 2000a), ants (ISIDORO et al., 2000b), as well as bees and bumblebees (ROMANI et al., 2002, 2003).

In a collaboration project with the Parma group on the amazon ant *Polyergus rufescens*, Donato Grasso has been active in an age-dependent histological and ultrastructural study of the Dufour gland in gynes, and its role during the usurpation of slave colonies (BILLEN et al., 2001; GRASSO et al., 2002).

The present survey illustrates the very active role of Italian researchers in the study of exocrine gland morphology and ultrastructure. Not only have many contributions appeared in this field (see References), also from Italian origin are several descriptions of novel glands among social insects (see Table 1), that stress the importance of the Italian AISASP section.

Table 1 – Survey of the Italian contributions describing novel exocrine glands in social insects.

Gland	Occurrence	Author(s)
	abdomen Dolichoderinae ants	Pavan and Ronchetti, 1955
tegumental glands	general tegument *Reticulitermes* and *Kalotermes* termites	Jucci, 1924; Sbrenna and Leis, 1983
leg glands	tarsi, tibia and femur *Polistes dominulus*	Beani and Calloni, 1991
paramere glands	parameres *Liostenogaster flavolineata* males	Fortunato et al., 2000
antennomere glands	antennal segments ants, bees, bumblebees and wasps	Isidoro et al., 2000a,b Romani et al., 2002, 2003

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