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Dufour's gland possible role in the evolution of sting morphology and function in hover wasps (Hymenoptera Stenogastrinae)

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ABSTRACT

The sting is the most effective defense of social Hymenoptera against vertebrate predators but in the hover wasps (subfamily Stenogastrinae) it is scarcely used. In these wasps a quite enlarged Dufour's gland and the extensive use of its secretion in the peculiar rearing of the larvae and defense determined important morphological modifications of the sting structure. Connecting anatomical and morphological data with behavioral observations we determined that in these wasps the Dufour's gland secretion is attached to the egg during oviposition but can be also channeled to the outside via the sting when it is collected by adult females for larval rearing or construction of the nest ant guards. The anatomical modifications of the sting reduced the function of the sting as a defensive weapon in hover wasps.

1. Introduction

The exocrine glands have a fundamental role in the life of the social insects, but often the understanding of their function is uncertain and problematic. The morphological characterization of the glands, the location of their opening, and the cuticular specialization involved in the release of their secretions represents the first step for understanding their function and, ultimately, some of the behavioral patterns presented by the species. Among the 23 different glands described in social wasps (Billen and Morgan, 1998; Downing, 1991; Fortunato et al., 2000; Jeanne, 1996; Landolt and Akre, 1979; Nedel, 1960) the Dufour's gland is one of the most studied for its important roles in the biology of these insects such as nestmate recognition and defense (Abdalla and da Cruz Landim, 2001).

The Dufour's gland is an abdominal elongated saccular structure. Its walls are formed by class I secretory cells (Noirot and Quennedey, 1991) organized in a unique layer (Landolt and Akre, 1979; Maschwitz and Kloft, 1971; Delfino et al., 1988). The lumen, and in particular its distal part, has a storage function for the secretion. The opening of the gland is controlled by a muscular system (Schlusche, 1936; Landolt and Akre, 1979; Billen, 1987). In social wasps the secretion of this gland is mainly formed by hydrocarbons that are involved in nestmate recognition (see Dani et al., 1996 for *Polistes*), nest defense and rearing of the larvae (Turillazzi, 1991; for Stenogastrinae). Downing and Jeanne (1983) and Downing (1991) suggest that the gland of *Polistes* produces also an egg marking pheromone. In ants with a functional sting the Dufour's gland opens between the lancets of the sting (Hermann, 1984) and also in the species of ants where the sting no longer functions because the lancets have fused with the stylet, the Dufour's gland opens in the sting surrounded by exoskeleton (Billen, 1987). In *Apis mellifera*, *Apis cerana* and *Bombus pratensis* the Dufour's gland exits between the sting lancets near the base of the sting (Billen, 1987; Martin et al., 2005). Already Schlusche (1936) furnished a good description of the anatomical relationships and position of the gland in *Vespula vulgaris*; Maschwitz and Kloft (1971) (for *Vespa*) and Hermann and Krispyn (1975) (for *Vespula* = *Dolichovespula maculata*) observed that the gland opens in the sting bulb, and Landolt and Akre (1979) remarked that the gland is associated with the female reproductive system but opens inside the sting chamber, near the base of the sting. Billen in a paper of 1987 (the species investigated are not reported), and in a paper of 2006 on *Dolichovespula saxonica* preferred to point out that the gland opens in the vagina. Thus, despite the importance that the Dufour's gland has in social wasps, the localization of its opening point need to be clarified. In this study we show that in social wasps, the Dufour's gland opens in the sting's bulb.

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The primitively social wasps of the subfamily Stenogastrinae (hover wasps) present a quite enlarged Dufour's gland (Delfino et al., 1988; Turillazzi, 1991), the secretion of which (mainly composed by long chain hydrocarbons - Keegans et al., 1993) has various functions in their social biology connected, in particular, with the rearing of immature brood (Turillazzi, 1991; Sledge et al., 2000). The wasps, in fact, collect big wads of this translucent, whitish secretion in their mouthparts and deposit them on the eggs or between the coils of small larvae. The secretion is not a food but functions as a medium where liquid and solid food is added during the progressive provisioning. In the oviposition process, a first bunch of secretion is collected by the egg laying female that retains it in her mouth, afterwards she lays the egg directly attaching it to the secretion and then places it in the cell. In most species a second collection of secretion follows that is added to the previous one on the egg (Turillazzi, 1985). In some species the same secretion is also used as a main component of the ant guards, a chemico-physical barrier placed on nest substrata as a protection against ants (Turillazzi and Pardi, 1981; Sledge et al., 2000). Stenogastrinae do not have the Van der Vecht's glands on the sixth sternite of the gaster to produce chemical ant-repellent (Smith et al., 2001).

In this study we performed an anatomical survey of the sting morphology modification probably induced by Dufour's gland in hover wasps and reconsidered its secretion releasing during the collection behavior and oviposition.

2. Materials and methods

Females belonging to *Eustenogaster fraterna, Eustenogaster sp., Liostenogaster flavolinata* and *Parischnogaster alternate* (all these species belong to the Stenogastrinae subfamily), were collected in Malaysia (Genting Tea Estate and Gombak, Selangor state and Bukit Fraser, PahangState). We also collected for comparison females of *Polistes dominulus* (Polistinae) (near Montevarchi, Central Italy) and specimens of female *Polybioides raphigastra* (Polistinae) and *Ropalidia flavopicta* (Polistinae) (in various localities of Selangor state, Malaysia). Specimens of females of *Parachartergus colobopterus* (Polistinae) were collected near Maracay (Venezuela) by Joan Strassmann and David Queller. Wasps were frozen and subsequently dissected under a binocular stereomicroscope to investigate the morphology of the sting, afterwards they were fixed in Pampl's fluid for morphological studies. The samples for the

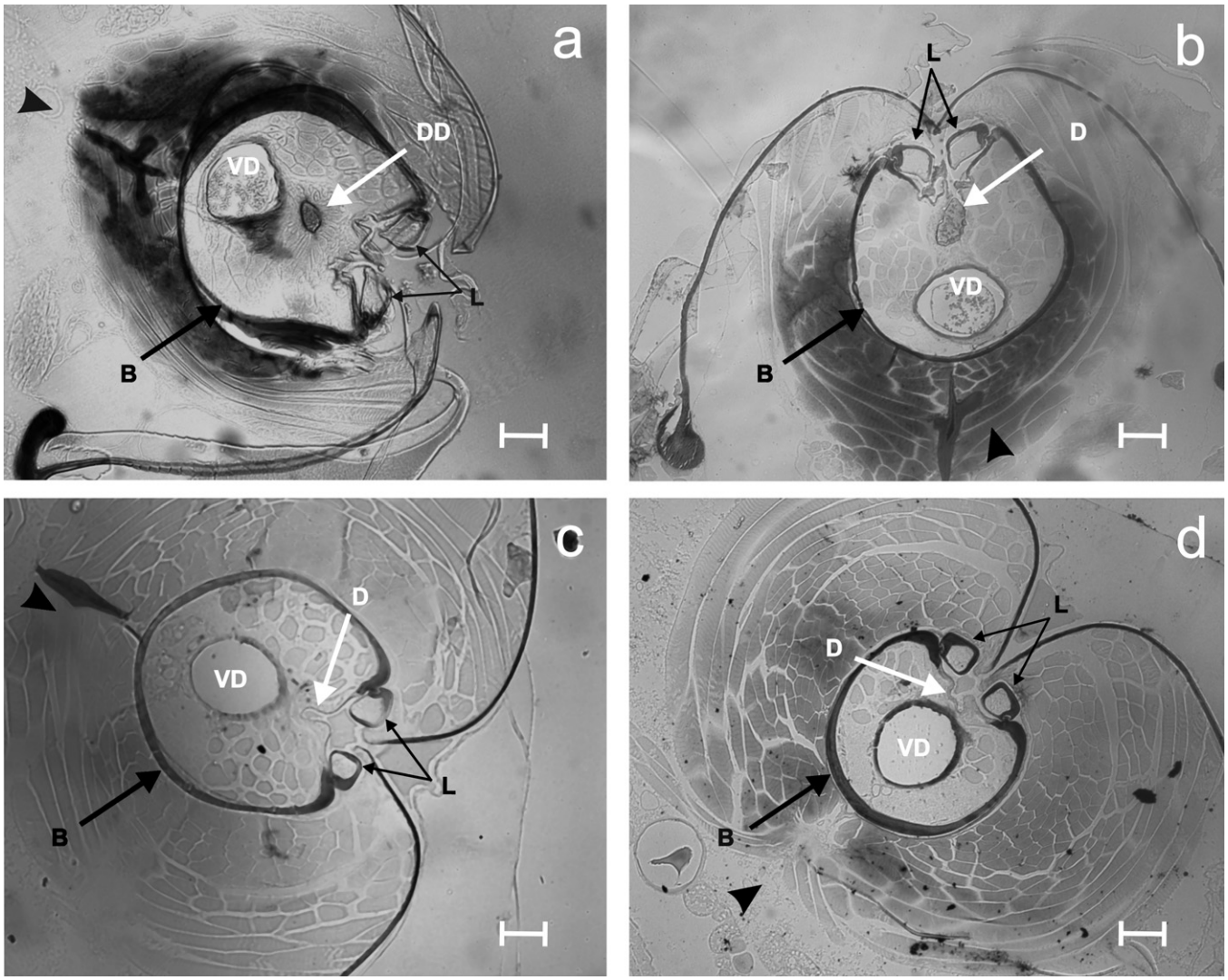

Fig. 1. Transverse section of *Polybioides raphigastra* (Polistinae) (a,b) and *Polistes dominulus* (Polistinae) (c,d) sting apparatus. The sections a and c are more proximal compared with sections b and d. B: Bulb of the sting, D: Dufour's gland opening point, DD: Dufour's gland duct, L: Lancets, VD: venom duct. Arrowhead indicates dorsoventral orientation. Scale bars are 100 μm.