

New Structural Aspects of the Dufour's and Venom Glands in Social Insects

J.P.J. Billen

Zoological Institute, University of Leuven, B-3000 Leuven, and
Limburgs Universitair Centrum, Dept. SBM, B-3610 Diepenbeek

The sting in social insects, which is directly derived from the ovipositor, has evolved towards an effective weapon for colony defence or prey conquest. The glands of the sting apparatus play a major role in this regard which is well illustrated by the venom gland that produces the toxic, mostly proteinaceous venom constituents [1]. It always opens in the sting base and thus uses the sting to inject its poisonous contents into the victim.

The precise morphological relation between Dufour's gland and the sting, on the other hand, is not as well understood. Conflicting data that the Dufour gland duct opens either inside [2, 3] or

outside the sting base [4] are reported. Only in the case of the Formicidae, do all contributions describe Dufour's gland duct opening inside the sting, ventrally of the venom gland duct [5, 6]. The existing confusion regarding the exact position of Dufour's gland exit may for the greater part be due to conclusions made from impressions during dissection rather than from more reliable histological examination. Although the contradictory reports mainly originate from rather old papers, the confusion still continues because modern textbooks rely on these sources.

We have, therefore, investigated the

structural relationship of the sting and its associated glands by analyzing serial semithin sections in a wide variety of social Hymenoptera (ants, wasps, bees, and bumblebees).

From our observations, we can unambiguously conclude that Dufour's gland duct opens through the sting only in the Formicidae, whereas in the Apidae and Vespidae it closely approaches the sting base, but eventually bends downwards and, thus, opens into the dorsal vaginal wall (Fig. 1). This situation is similar for both workers and queens. The venom gland always opens through the sting. A general character of the Dufour gland, regardless of its opening site, is the presence of a well-developed muscular supply inserting onto the duct in its most proximal region (Fig. 1). A similar muscular apparatus, albeit only on the ventral side, is also found for the venom gland duct. In the Vespidae the venom gland duct has become an elongated funnel, although it is also provided with muscular attachments. As a result, both glands dispose of their own, mutually independent control mechanism for regulating the discharging activity. This

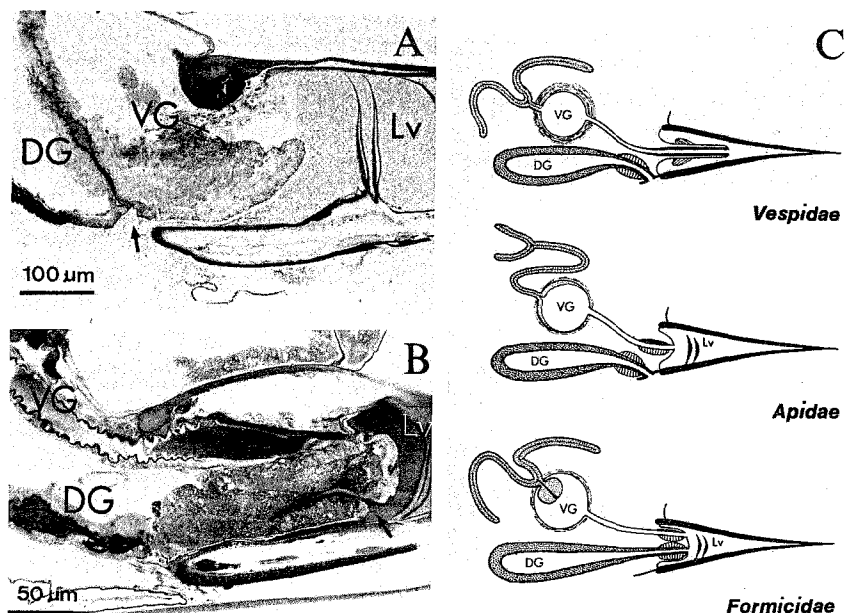


Fig. 1. A, B) Longitudinal semi-thin sections through the sting base region, showing Dufour's gland opening (arrow) outside the sting base in a worker of *Bombus pratensis* (A), and inside it in a worker of the ant *Pogonomyrmex occidentalis* (B). C) Schematic representation of the structural relation between the venom (VG) and Dufour's gland (DG) and the sting in the three families of social Hymenoptera. Sting lancet valves (Lv) act in pumping the venom out of the sting in Apidae and Formicidae. The lack of such valves in the Vespidae is compensated for by the elongated venom funnel and the muscular supply of the venom gland reservoir

ability for independent secretion, therefore, also exists among the Formicidae [6], where both glands open through the sting.

The fundamental anatomical difference with regard to the opening of Dufour's gland in these three main social hymenopteran families undoubtedly has considerable functional implications.

In the Formicidae, discharge of Dufour's gland secretion through the sting is in perfect agreement with known functions such as release of trail pheromones by periodical touching of the substrate [7], or exposure of tiny droplets of sex pheromone [8]. Also for the occasionally attributed function of Dufour's gland contents to act as a spreading agent for the venom gland secretion, the opening of both glands near to each other is most evident. The chemical substances involved generally are low-molecular and relatively volatile, and as a result have been identified by gas chromatography in a wide variety of species [9].

Chemical analyses of Dufour's gland contents in the Apidae and Vespidae have thus far only revealed the absence of volatile material, but have not determined the precise composition of the actual glandular secretion [1]. Also, the function of Dufour's gland in these groups is still speculative and indistinct. Its opening into the vaginal wall, however, provides evidence for a reproductive function. The gland may produce a protective coat for the passing eggs, or perhaps more likely, it may apply an adhesive substance onto the egg before it is deposited at the bottom of the brood cell. Such a role for the Dufour gland requires the elaboration of a gluey secretion, and may explain the lack of volatile components in it. In many of the Andrenidae, Anthophoridae, Colletidae, and Halictidae bees, Dufour's gland is indeed known to perform an indirect reproductive role in producing macrocyclic lactones that form the waxy linings of the nest cells [10].

A function in reproductive behavior for Dufour's gland is in agreement with its evolutionary origin as the accessory gland of the female reproductive system [3], and, therefore, most probably represents the original condition. The shifting, in the Formicidae, of the Dufour gland opening into the sting base is correspondingly considered as a derived condition. The loss of the primary reproductive function accompanies the acquisition of a new, often pheromonal role. The absence of brood cells (and hence the superfluous function to produce cementing substances) and the occurrence of free ambulatory brood in the Formicidae, which is a general but unique aspect of their social biology, supports this theory.

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