

Plasticity of Honeybee Castes

Occurrence of Tergal Glands in Workers

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Workers of the Cape honeybee *Apis mellifera capensis* Escholtz are known to assume a dominant position when introduced in queenless colonies of other honeybee races [1]. They display queenlike behavior, including egg laying ("false queens" [2]), which has been related to similarities between their mandibular gland pheromones and those of queens [3–5]. A queen's dominance, however, results from the synergistic effect of the mandibular gland compounds, the secretion of the tarsal glands [6] and an abdominal component, for which the tergal glands have been proposed as the most likely source [7]. These glands also function as a sex pheromone source in the mating process [8]. Removal of mandibular glands from *A. m. capensis* workers did not prevent such bees from becoming dominant [5]. This prompted us to investigate the presence and activity of tergal glands in these workers, despite the view that tergal glands are limited to queens [9, 10].

All *A. m. capensis* workers investigated displayed large complexes of glandular cells underneath the posterior edges of all abdominal tergites, comparable to those in *A. m. mellifera* queens. The glands are most conspicuous in tergites III to V, but occur in tergites II and VI as well. The polygonal cells are about 15 to 35 μm in diameter. Each glandular cell possesses a narrow extracellular duct that opens through the in-

tersegmental membrane (Fig. 1A). Scattered individual subepidermal glands are found in the more anterior region of the tergites, and have a more ovoid shape. Their accompanying duct cells, however, open through the tegumental cuticle. We also observed tergal glands associated with tergites II to VI in *A. m. mellifera* workers, albeit in a much more reduced condition, with few scattered glandular cells among the epidermal cells (Fig. 1B).

Ultrastructural investigation of the tergal gland cells revealed the sinuous intracellular end apparatus, which constitutes the origin for the correspond-

ing extracellular duct. It consists of a surrounding sheath of microvilli and a cuticle-lined central ductule, which continues in the duct cell, and thus guides the secretion to the outside. The cytoplasm contains numerous mitochondria, a few cisternae of smooth endoplasmic reticulum, and some lamellar inclusions associated with the end apparatus. Considerable variation in the number and size of electron-lucid vesicles among the gland cells occurs, and may relate to a secretory cycle (Fig. 2). The morphological characters observed are in conformity with those of other insect glands elaborating low-

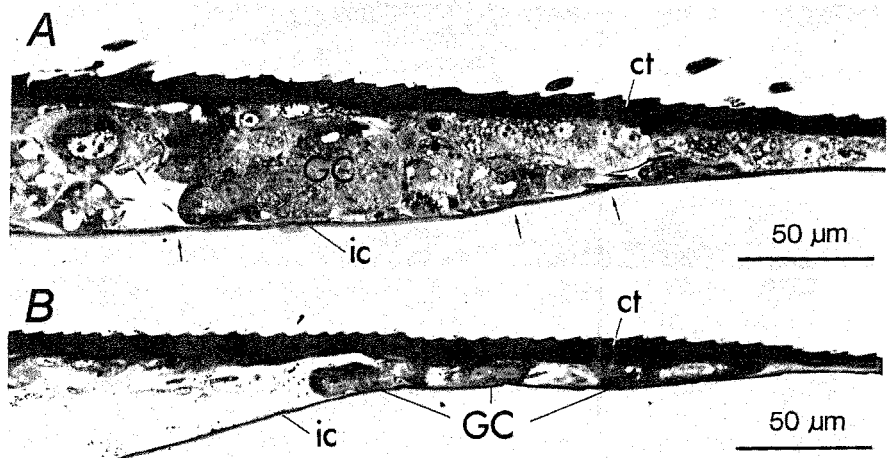


Fig. 1. Longitudinal section through the posterior edge of tergite III in a worker of *A. m. capensis* (A) and *A. m. mellifera* (B). *ct* tegumental cuticle; *GC* glandular cells; *ic* intersegmental cuticle. Arrows indicate opening of glandular ducts

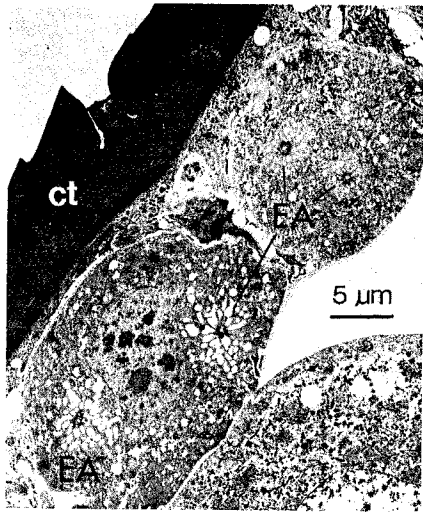


Fig. 2. Electron micrograph showing two glandular cells in tergite V (*A. m. capensis* worker). *ct* tegumental cuticle; *EA* end apparatus

molecular nonproteinaceous compounds [11].

Our results are consistent with the hypothesis that the tergal glands are involved in the regulation of dominance patterns within the colony. Mota [10] reported the absence of tergal glands in queens of over a year of age, thereby

challenging the double function of the glands, but we did find active glands in the older queens studied. These glands are smaller than in young queens, being reduced partly to a single layer of cells.

In the workers of *A. m. capensis* the very well developed tergal glands may assist these bees to function as false queens, even if the mandibular glands were removed previously. In *A. m. mellifera* workers the tergal glands are far less developed and probably sometimes absent. Although their mandibular glands do contain 9-oxo-decenoic acid occasionally [4], false queens of this race were only seldom observed.

Apparently the presence, size, and activity of the tergal glands are to be considered as another set of factors involved in the regulation of dominance patterns within the honeybee colony.

We are grateful to E. Plaum for technical assistance. JPJB acknowledges a senior research assistantship of the Belgian National Fund for Scientific Research.

Received January 7 and February 10, 1986

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