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Original article

How queen-like are the tergal glands in workers of *Apis mellifera capensis* and *Apis mellifera scutellata*?

Theresa C. WOSSLER[a]*, R.B. VEALE[b], Robin M. CREWE[a]

[a] Communication Biology Research Group, Department of Zoology, University of the Witwatersrand, Private Bag 3, Wits 2050, Johannesburg, South Africa
[b] Developmental Biology Research Group, Department of Zoology University of the Witwatersrand, Private Bag 3, Wits 2050, Johannesburg, South Africa

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Abstract – Tergal gland morphology was investigated for *Apis mellifera capensis* and *A. m. scutellata* virgin queens and workers. Workers exhibit two types of tergal glands. Type-A glands consist of single cells, are located along the anterior edge of the tergites II-V, characterised by numerous mitochondria and rough endoplasmic reticulum, and closely associated with fat cells and oenocytes. Type-B tergal glands are bicellular and found predominantly in *capensis* queens and workers and in *scutellata* queens. These type-B glands occur along the posterior edge of tergites II-V and are characterised by secretory cells with numerous mitochondria, end apparatuses, and secretory vesicles. There were no differences in gland location or structure in the honeybee queens of both races. However *capensis* workers possess more glands of both types and larger type-A gland cells than *scutellata* workers. This result further emphasises the distinctiveness of Cape honeybees.

***A. m. capensis* / *A. m. scutellata* / tergal gland / secretory cell / duct cell / ultrastructure**

1. INTRODUCTION

Social insects possess a large number of exocrine glands located in the head, thorax and abdomen [4]. These glands are ectodermal in origin and are often characterised by smooth endoplasmic reticulum, numerous mitochondria and well-developed Golgi bodies [4, 12]. In honeybee queens, several types of glands have been identified [6, 15, 17, 28].

A variety of abdominal glands exist in *Apis mellifera* [24]. The epithelial wax glands of workers are unicellular epidermal cells that associate with oenocytes and fat

* Correspondence and reprints
Department of Zoology and Entomology, University of Pretoria, Pretoria 0002, South Africa
E-mail: TCWossler@zoology.up.ac.za

cells to form the glandular complex [9, 18, 20]. In contrast, there are bicellular abdominal glands which are composed of a secretory cell and a duct cell [25]. Examples are the Koschewnikow glands associated with the sting [17] and tergal glands. Tergal glands, first described by Renner and Baumann [28], are large subepidermal complexes of glandular cells beneath the posterior edges of abdominal tergites II-V, opening onto the cuticle or intersegmental membrane [4, 6, 12, 25, 26, 33]. These tergal glands were initially only described in queens of European honeybee races [24, 25, 28], but they have since been found in *A. m. capensis* workers [6]. Although the structure of these glands was not fully described in this investigation, they indicated that the glands were present in *A. m. mellifera* queens, *A. m. capensis* workers and were however very poorly developed, sometimes even absent, in *A. m. mellifera* workers [3, 6].

In South Africa there are two contiguous honeybee races, *A. m. capensis* and *A. m. scutellata*, the workers of which differ dramatically in relation to worker reproduction, with *A. m. capensis* workers adopting pseudoqueen positions among workers of other honeybee races [10, 11, 19]. These striking biological differences necessitate a proper morphological determination of the tergal glands in workers of the two African honeybee races, thus allowing comparisons to be made between the structure of worker tergal glands and those of queens.

The ultrastructure of tergal glands has not been described for *A. m. scutellata* honeybee queens or workers, neither have these glands been fully described for *A. m. capensis* queens and workers. The present investigation was aimed at highlighting interracial differences regarding the position and structure of the tergal glands. In addition, the size and number of tergal glands in the worker caste of the two African *A. mellifera* races were compared to ascertain whether the unique features associated with *A. m. capensis* workers extends to the morphology of their tergal glands.

2. MATERIALS AND METHODS

Virgin *A. m. scutellata* ($n = 4$) and *A. m. capensis* queens ($n = 3$) were reared to 6–12 days, when mating would normally take place and tergal gland activity is at its peak [14]. *A. m. scutellata* workers ($n = 7$) and *A. m. capensis* workers ($n = 8$) were reared to 8-days-old in queenless colonies. Cold (4 °C) 2.5% glutaraldehyde in cacodylate buffer was injected (2–3 ml) directly into the abdominal cavity, through the most anterior intersegmental membrane connecting tergite TI with tergite TII. The tergum (TII-TV) was cut longitudinally into small strips so that each piece contained both tergite and intersegmental membrane. The tissue was dehydrated [21] and embedded in L.R. White acrylic resin or epon araldite [23].

Thick sections (1 μm) were stained with Toluidine blue and examined by light microscopy (LM) using a Leitz Ortholux II compound microscope with a magnification range of 120–1200x (1 virgin queen of *A. m. scutellata* and *A. m. capensis* each, 7 *A. m. scutellata* workers, and 8 *A. m. capensis* workers). Serial sections were cut to provide unambiguous gland positioning. Thin sections (90 nm) were stained with uranyl acetate and lead citrate and viewed in a Joel JEM100S transmission electron microscope (TEM). Sections were oriented and cut to show the posterior edge of the preceding tergite, the intersegmental membrane and the anterior edge of the following tergite.

Statistical analysis

The size range of the secretory gland cells present in an *A. m. capensis* and *A. m. scutellata* virgin queens was determined by digitising LM sections, using a digitising board

linked to a computer running Videoplan digital image analysis software (FIPPS, 2.1). Area was used as a measure of cell size since it provided greater reliability than diameter measurements because the glands have variable shapes. A t-test was used to test whether a significant difference existed between the population of secretory gland cells in the *A. m. scutellata* virgin queen compared to the population of secretory gland cells in the *A. m. capensis* virgin queen.

Confocal microscopy was used to measure the size range of the tergal glands along the anterior edge in *A. m. capensis* (n = 5) and *A. m. scutellata* (n = 5) workers. Because of the hierarchical nature of the design, the gland sizes of workers belonging to the two races were compared using square root transformed data in a 3-level nested ANOVA (with tergite nested in worker and workers nested in race) [32]. From this, we established variability among tergites (tergite effect), variability among individual workers (worker effect) and differences between the two races (race effect).

Using LM, the number of glands along the anterior edge and posterior edge (position) were counted for workers of both races (n = 10). The number of glands present along the anterior and posterior edges of workers of both races were compared using $\sqrt{x+1}$ transformed data in a 4-level nested ANOVA. The design incorporated position nested within tergite, tergite nested within individual and individuals nested within race [32].

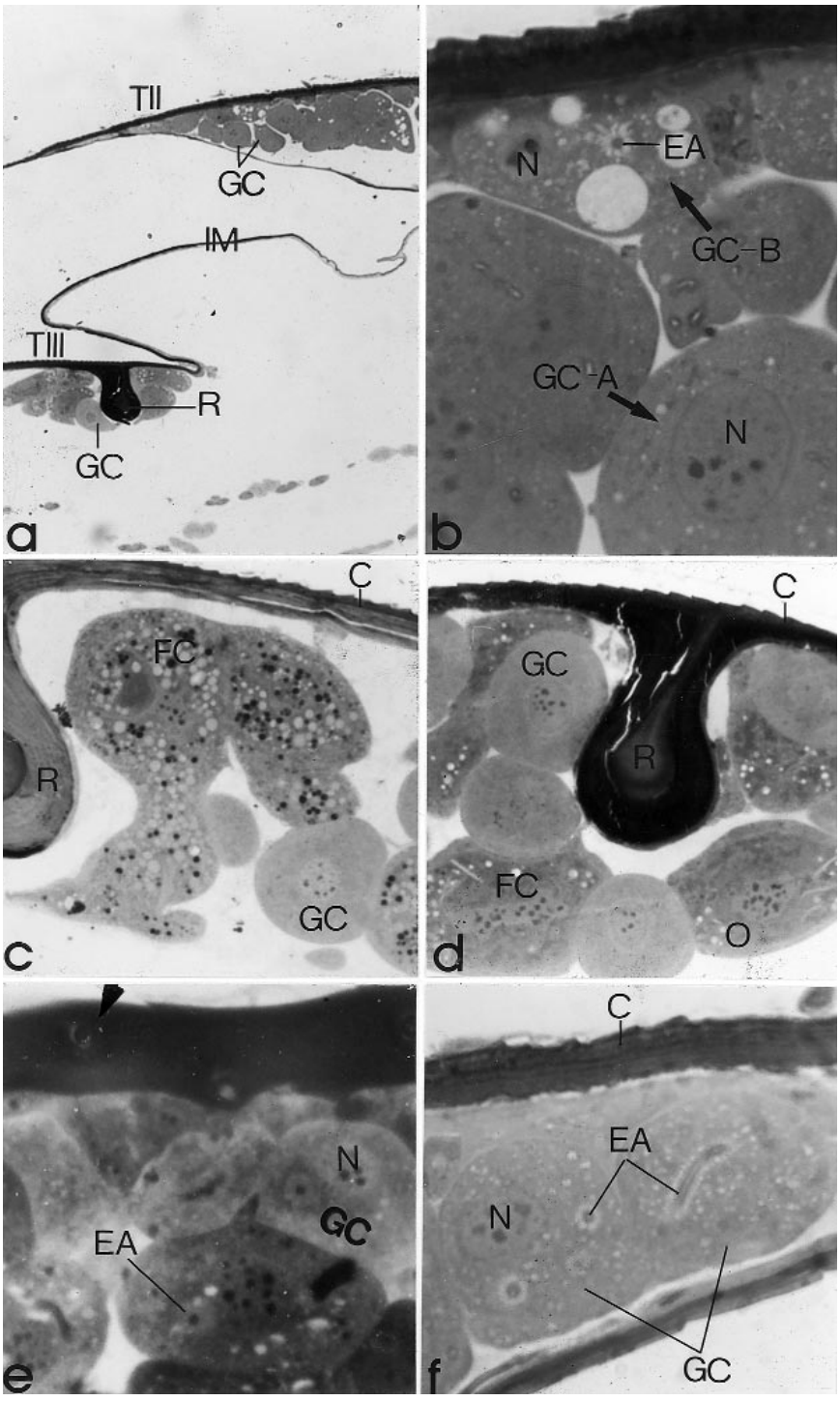
3. RESULTS

Virgin queens and workers of *A. m. capensis* and *A. m. scutellata* both possess clearly discernible tergal glands. Tergal glands are localised specifically along the edges of adjoining abdominal tergites. This region can be subdivided into two distinct locations: – i) the posterior edge and ii) the anterior edge. Sequential tergites overlap and are connected via an intersegmental membrane. The cuticle forms a "mushroom-shaped" apodeme where the membrane inserts onto the anterior edge of the tergite (R in Fig. 1a) which has been given the name anterior ridge [22].

Two distinct types of tergal glands are described in this study, denoted type-A and type-B glands (Fig. 1b). Type-A glands are unicellular and are found predominantly along the anterior edge of tergites II-V (clustered around the anterior ridge) in the workers of both races. Occasionally type-A glands were also found to be associated with the posterior edge in *A. m. capensis* workers. The type-B tergal glands are bicellular and are primarily restricted to the posterior edge of tergites II-V, in virgin queens and *A. m. capensis* workers (Figs. 1b, 1e, 1f).

3.1. Type-A gland structure

Type-A glands consist of a single cell and are structurally similar in both *A. m. capensis* and *A. m. scutellata* workers. These gland cells are interspersed with fat cells and occasional oenocytes and appear to form a gland cell complex (GC, FC and O in Figs. 1c, 1d). Type-A tergal gland cells in general are regularly shaped and have well defined centrally situated round or ovoid nuclei, each containing numerous nucleoli; Evident in these gland cells is cisternae of rough endoplasmic reticulum (RER) and numerous mitochondria. The oenocytes are round to ovoid cells with a large well defined nucleus with multiple nucleoli; the cytoplasm contains numerous secretory granules and few RER cisternae. Fat cells have star-shaped nuclei, well developed RER, smooth endoplasmic reticulum (SER) and mitochondria and are packed with lipid droplets, some being electron-dense while others are electron-lucid (Fig. 2a). In *A. m. scutellata* workers, there are at least three fat cells for every gland cell along the anterior ridge (Fig. 1c). In contrast, *A. m. capensis* workers possess numerous gland cells distributed with the fat cells and oenocytes,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with gland cells and fat cells occurring in a ratio of 1:1 (Fig. 1d).

3.2. Type-B gland structure

These subepidermal type-B glands occur in virgin queens of both races and in *A. m. capensis* workers, but are severely reduced or absent in *A. m. scutellata* workers. Type-B tergal glands consist of two cells; a secretory cell which has no direct contact with the surface, and a duct cell. The secretory cells are typically round, but some cells can be oval or even elongated (Figs. 1e, 1f). The secretory cells are nucleated and characterised by a conspicuous end apparatus,

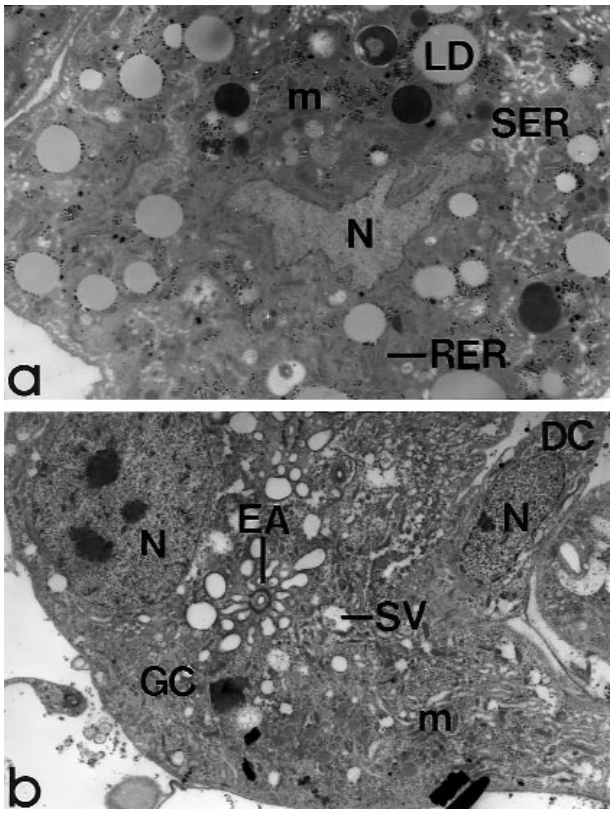

Figure 2. Ultrastructure of fat cell and type-B gland cell. (a) A fat cell, from tergite II of an *A. m. scutellata* worker, with a distinctive star-shaped nucleus with numerous nucleoli, × 2000. (b) Detail of typical type-B tergal gland cell (GC), with associated duct cell (DC), of an *A. m. scutellata* queen, showing numerous secretory vesicles (SV), × 2000. EA = end apparatus, LD = lipid droplet, m = mitochondria, N = nucleus, RER = rough endoplasmic reticulum, SER = smooth endoplasmic reticulum.

Figure 1. Light microscopy analysis of tergal glands. (a) Longitudinal section through tergites II and III of an *A. m. capensis* worker, including the intersegmental membrane. The gland cells are located along the posterior edge of TII and along the anterior edge of TIII, clustered around the anterior ridge, × 120. (b) Posterior edge of an *A. m. capensis* worker, both type-A gland cells (GC-A) and elongate type-B gland cells (GC-B) are present, × 1200. (c–d) Comparison of the gland cell complex situated along the anterior edge, between *A. m. scutellata* and *A. m. capensis* workers, × 480. *A. m. scutellata* workers (c) possess fat cells (FC) and gland cells (GC) in a ratio of 3:1, whereas *A. m. capensis* workers (d) have similar numbers of FC and GC. (e–f) Type-B tergal glands in the posterior edge of (e) a virgin *A. m. capensis* queen, × 1300 and (f) an *A. m. capensis* worker, × 1200. C = cuticle, EA = end apparatus, FC = fat cell, GC = gland cells, IM = intersegmental membrane, N = nucleus, O = oenocyte, R = anterior ridge.

a large number of secretory vesicles, rod-shaped mitochondria and SER. The end apparatus, often situated close to the nucleus of the secretory cell, consists of a central ductule surrounded by a large number of secretory vesicles. The duct cells are elongated cells surrounding the secretory ductule. The nucleus is narrow and displays dense chromatin. The cuticle-lined duct, originating in the secretory cell as the end apparatus, continues through the duct cell to the cuticle surface (Fig. 2b).

3.3. Queen tergal glands

Queens of both races possess type-B tergal glands that are situated on the posterior edges of tergites II-V beneath the epidermal layer, along the entire width of the tergite. The glands are present as a single layer in the extreme posterior margin but occur in 2–3 layers anteriorly. The mean secretory cell cross section of the *A. m. capensis* virgin queen ($n = 39$ secretory cells) was significantly larger ($p = 0.003$) than that of the *A. m. scutellata* virgin queen ($n = 39$ secretory cells). Specific glands are in contact with the cuticular surface while others make contact with the intersegmental membrane. Oenocytes are occasionally interspersed between the glands but seem more common in the anterior part of each segment. As the glands diminish in number, the oenocytes predominate.

3.4. Worker tergal glands

A. m. capensis workers can be separated from *A. m. scutellata* workers as they possess more type-A glands ($p < 0.0001$, Tab. I) as well as type-B glands, in all tergites (Fig. 3). The gland cell numbers for the posterior edge is a total gland number and was calculated by counting both type-A and type-B glands. *A. m. scutellata* workers possess very few glands along the posterior edge with an average of 0.9 ± 0.6 (se) whereas *A. m. capensis* workers have an average of 9.3 ± 1.7.

In terms of type-A gland cell size, differences between workers (worker effect) and between races (race effect) were evident (Tab. II). In *A. m. scutellata* workers the gland cells ranged in size from 255 μm^2 to 1327 μm^2 whereas in *A. m. capensis* workers, they range from 723 μm^2 to 2200 μm^2.

4. DISCUSSION

4.1. Type-A glands

Virgin queens and workers of both *A. m. scutellata* and *A. m. capensis* possess clearly discernible tergal glands. However, worker honeybees of both races exhibit two structurally distinct types of tergal glands. Type-A tergal gland cells consistently cluster with fat cells and oenocytes to form a complex. These type-A tergal glands do not contact

Table I. Four level nested ANOVA with cell position nested in tergites, tergites nested in individuals and individuals nested in race for the number of gland cells found along the anterior and posterior edges (position) in *A. m. scutellata and A. m. capensis* workers.

Source of variation	*df*	Mean squares	*F* statistic	$p <$
Among race	1	326.34	3846.27	0.0001
Individuals within race	8	7.07	83.29	0.0001
Tergites within individuals	10	5.33	62.82	0.0001
Position within tergites	15	5.32	62.65	0.0001
Error	540	0.08		

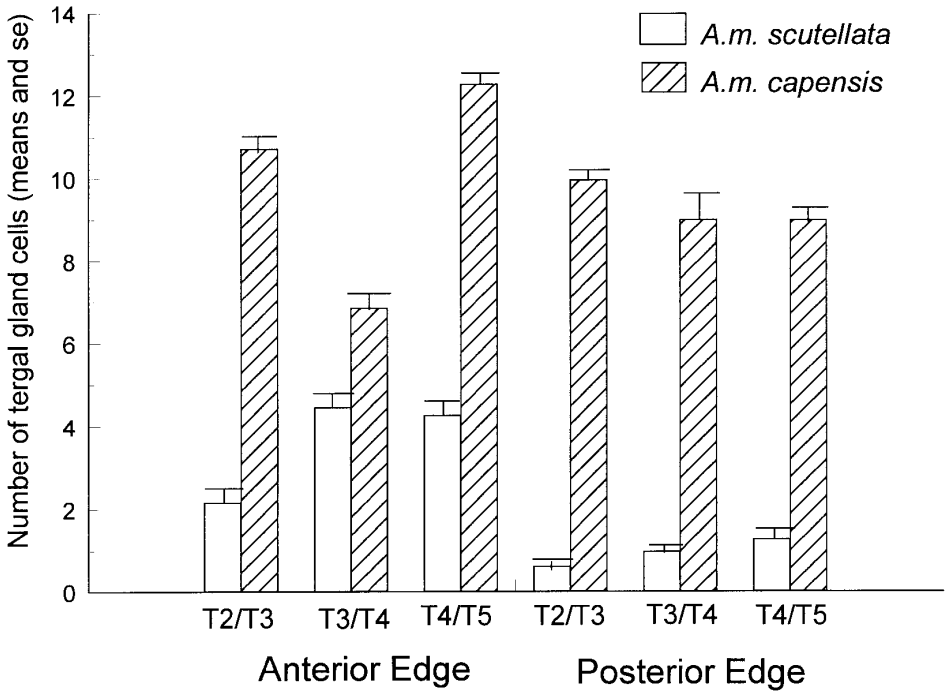

Figure 3. Effect of position and race on the numbers of glands along the posterior edge (sum of type-A and type-B glands) and the anterior edge (type-A gland cells only) in tergites II to V, for 8-day old *A. m. scutellata* and *A. m. capensis* workers.

Table II. Three-level nested ANOVA with tergites nested in individuals and individuals nested within race for gland cell sizes in *A. m. scutellata* and *A. m. capensis* workers.

Source of variation	*df*	Mean squares	*F* Statistic	$p <$
Among race	1	3271.46	303.13	0.0001
Individuals within race	8	117.43	10.92	0.0001
Tergites within individuals	10	12.85	1.19	0.302
Error	120	10.756		

the cuticle directly, but are located beneath the epidermal layer and, according to Noirot and Quennedey [25], gland cells arranged in this manner are classified as type II gland cells. There is no obvious ductule mechanism of release for the secretion and the mechanism may function in a similar way to the Nasanov and wax gland complexes, with all three cell types producing the glandular secretion [8, 9, 20]. The oenocytes (packed with secretory granules) are in close proximity to the type-A gland cells and may therefore produce precursors for the tergal glands [7] or even secrete part of the tergal gland pheromone. Nonetheless, specific markers for the precursors of the secretions from these cells would need to be developed in order to elucidate the complete

secretory pathway. The fat cells are prevalent in the tergal gland complex and are storage/metabolic cells [18] which could be responsible for taking up the precursor molecules produced by the tergal glands and oenocytes, transforming them into functional compounds and delivering the secretion to the outside.

The cytoplasm of type-A tergal gland cells contained numerous mitochondria and cisternae of RER, which typifies protein synthesis [5, 8, 9, 29, 30]. It has been demonstrated that honeybee cuticle is coated with proteins but the source of these particular surface proteins is still unclear [35]. It is possible that the type-A tergal glands, described here, are responsible for synthesising the surface cuticular proteins apparent on honeybees.

4.2. Type-B glands

The second type of tergal glands, referred to here as type-B glands are bicellular and belong to type III gland cells [4, 25, 26]. They occur on the posterior edge of tergites II to V in *A. m. capensis* virgin queens, *A. m. capensis* workers, *A. m. scutellata* virgin queens, but they are very reduced, or absent, in *A. m. scutellata* workers. Type-B tergal glands are structurally similar to those tergal glands previously described by Renner and Baumann [28], Billen et al. [6] and Mota and Cruz-Landim [24]. Similar descriptions of gland cells have been provided for the mandibular glands of honeybee queens [15], the Koshewnikow glands of honeybees [17], the tarsal glands of bumble bees [27], the integument glands of a species of ladybird beetle [1] and numerous glands present in ants [2, 4]. An end apparatus and its microvilli are common in insect gland cells with the vesicle contents often discharged at the base of the microvilli [1, 17, 27].

The cytoplasmic constituents of the type-B tergal glands are typical of glands producing non-proteinaceous compounds [4, 15]. Hydrocarbons, their derivatives and acids dominate the tergal gland secretions, of virgin queens of European races [16, 31]. Virgin queens from African honeybee races secrete similar tergal gland compounds to those of European races [34] and therefore type-B tergal gland morphology is in concordance with the chemical data.

4.3. Caste differences

Workers differ from queens in that they possess type-A glands that are unique to the workers. The function of these secretions in workers, however, still needs to be elucidated. On the other hand, *A. m. capensis* workers are similar to virgin queens in that they possess type-B glands comparable to those found in queens.

4.4. Worker differences

Billen and his co-workers [6] demonstrated that there was a marked difference between the number of type-B tergal glands in *A. m. capensis* workers compared to *A. m. mellifera* workers. This study similarly shows that *A. m. capensis* workers differ from *A. m. scutellata* workers, in that *A. m. capensis* workers possess more type-B glands than *A. m. scutellata* workers. These type-B glands are structurally the same as those found in virgin queens. This inter-racial difference may be related to the dominant status that these Cape honeybee workers have over workers of other *Apis mellifera* honeybee races [10, 19].

Not only do *A. m. capensis* workers possess queen-like type-B tergal glands but they also possess a greater number and larger type-A gland cells than *A. m. scutellata* workers. This inter-racial difference with respect to type-A gland cells raises another possibility that *A. m. capensis* workers secrete a unique surface pheromone compared to *A. m. scutellata* workers. Together, gland cell number and/or size may be related to the concentration of the secretion released

and when the pheromones crosses a threshold, the pheromone becomes functional thereby eliciting a behavioural and/or physiological response. Cruz-Landim et al. [13] have demonstrated that there is a correlation between queen attractiveness and the degree of development of the tergal glands in *Melipona quadrifasciata*. If such a system where the rule in honeybees, *A. m. capensis* workers would be mimicking queens.

The demonstration that *A. m. capensis* workers possess queen-like tergal glands, which were observed to be greatly reduced or absent in *A. m. scutellata* workers, indicates that this is a major feature which distinguishes the Cape honeybee worker from other honeybee workers. Exploration of the significance of this difference may prove vital in understanding the mechanisms by which *A. m. capensis* workers are able to act as social parasites in colonies of other races of honeybees.

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Résumé – Les glandes tergales des ouvrières d'*Apis mellifera capensis* et d'*Apis mellifera scutellata* ressemblent-elles à celles des reines ? L'ultrastructure des glandes tergales des reines vierges et des ouvrières d'*A. m. capensis* et d'*A. m. scutellata* a été étudiée au microscope optique et au microscope électronique à balayage. Les reines et les ouvrières des deux races possèdent des glandes tergales sur les bords antérieurs et postérieurs des tergites II à IV (Fig. 1a). Elles sont de deux types (type A et type B, Fig. 1b). Les glandes tergales de type A sont présentes le long du bord antérieur du tergite et seulement chez les ouvrières. Elles sont unicellulaires et associées à des cellules adipeuses et des oenocytes (Figs. 3c, 3d et 2a) et semblent former un complexe glandulaire qui pourrait avoir une fonction de synergie dans la synthèse des sécrétions de surface à base protéique. Du point de vue de l'ultrastructure, les cellules des glandes de type A sont riches en mitochondries et en réticulum endoplasmique rugueux (RER), ce qui caractérise les glandes synthétisant des protéines. Les glandes de type B sont présentes chez les reines vierges et les ouvrières d'*A. m. capensis* et chez les reines vierges d'*A. m. scutellata*, mais elles sont réduites ou absentes chez les ouvrières d'*A. m. scutellata* (Figs. 1e, 1f). Ces glandes comportent une cellule conductrice et une cellule sécrétrice. Cette dernière se caractérise par un appareil terminal spectaculaire, un grand nombre de vésicules sécrétrices, des mitochondries en forme de bâtonnets et du réticulum endoplasmique lisse (SER) (Fig. 2b). Les mitochondries et le SER sont des constituants du cytoplasme largement répandus chez les glandes de l'épiderme des insectes qui produisent des molécules non protéiques. D'après l'analyse des images vidéo, le diamètre moyen des cellules sécrétrices était significativement plus grand ($p = 0{,}003$) chez la reine vierge d'*A. m. capensis* que chez celle d'*A. m. scutellata*, mais il n'est pas possible de tirer de conclusions, une seule reine de chaque race ayant été examinée. La comparaison de l'ultrastructure et de la localisation des glandes n'a fait apparaître aucune différence nette entre les deux races *capensis* et *scutellata*.
Néanmoins la comparaison des ouvrières âgées de huit jours montre que les ouvrières d'*A. m. capensis* possèdent significativement plus de glandes de type A et de type B ($p < 0{,}001$, Tab. I, Fig. 3) que les ouvrières d'*A. m. scutellata*. Elles possèdent aussi des glandes de type A plus grandes ($p < 0{,}0001$, Tab. II). Ces deux différences pourraient

être responsables du fait que la sécrétion de phéromone chez les ouvrières d'*A. m. capensis* se situe au-dessus du seuil à partir duquel elle devient fonctionnelle, ce qui permet aux ouvrières d'*A. m. capensis* de dominer les ouvrières des autres races.

***A. m. capensis* / *A. m. scutellata* / glande tergale / cellule sécrétrice / ultrastructure**

Zusammenfassung – Wie königinnenähnlich sind die Tergittaschendrüsen bei Arbeiterinnen von *Apis mellifera capensis* und *Apis m. scutellata*? Die Ultrastruktur der Tergittaschendrüsen von unbegatteten Königinnen und Arbeiterinnen von *Apis mellifera capensis* und *Apis m. scutellata* wurden untersucht. Lichtmikroskopie und Elektronenmikroskopie zeigten, daβ bei Königinnen und Arbeiterinnen beider Rassen an den vorderen und hinteren Kanten der Tergite II-V Tergittaschendrüsen vorkommen (Abb. 1a). Die Arbeiterinnen besitzen zwei deutlich unterschiedliche Typen von Tergittaschendrüsen (Typ A und Typ B, Abb. 1b). Tergittaschendrüsen des Typs A kommen nur bei den Arbeiterinnen entlang der Vorderkante der Tergite vor. Sie sind einzellig und treten in Verbindung mit Fettzellen und Oenozyten auf (Abb. 3c, 3d und 2a). Sie scheinen einen Drüsenkomplex zu bilden, der eine synergistische Funktion bei der Synthese von auf Eiweiβ basierenden Oberflächensekreten haben könnte. In der Ultrastruktur sind die Drüsenzellen des Typs A reich an Mitochondrien und RER, wie es für eiweiβsynthethisierende Drüsen charakteristisch ist. Die Tergittaschendrüsen des Typs B kommen bei unbegatteten Königinnen von *A. m. capensis* und *A. m. scutellata* sowie bei Arbeiterinnen von *A. m. capensis* vor, bei Arbeiterinnen von *A. m. scutellata* sind sie jedoch reduziert oder fehlen (Abb. 1e, 1f). Die Tergittaschendrüsen des Typs B sind zweizellig und bestehen aus einer sekretorischen Zelle und einer Kanalzelle. Die sekretorische Zelle wird durch einen auffälligen Endapparat, eine groβe Anzahl sekretorischer Vesikel, rutenförmige Mitochondrien und SER gekennzeichnet (Abb. 2b). Mitochondrien und SER sind verbreitete cytoplasmatische Bestandteile in Epidermaldrüsen von Insekten, die nichtproteinische Moleküle produzieren. In einer Video – Bildanalyse war der Durchmesser der sekretorischen Zellen bei der unbegatteten *A. m. capensis* Königin signifikant gröβer ($p = 0.003$) als bei der unbegatteten *A. m. sculleta* Königin. Hieraus kann allerdings nicht auf einen rassenspezifischen Unterschied geschlossen werden, da von jeder Rasse nur eine Königin untersucht wurde. Vergleiche der Ultrastruktur der Drüsen und des Herkunftsortes von *A. m. capensis* und *A. m. scutellata* Königinnen ergaben keine offensichtlichen rassenspezifische Unterschiede. Dagegen zeigte der Vergleich von achttägigen Arbeiterinnen, dass die Arbeiterinnen von *A. m. capensis* eine signifikant gröβere Anzahl Drüsen des Typs A sowie des Typs B besaβen ($p < 0.0001$, Tab. I und Abb. 3) als *A. m. scutellata* Arbeiterinnen. Weiterhin waren die Drüsenzellen des Typs A bei *A. m. capensis* gröβer ($p < 0.0001$, Tab. II). Diese beiden Unterschiede könnten dafür verantwortlich sein, dass Arbeiterinnen von *A. m. capensis* Pheromone oberhalb der Funktionalitätsschwelle sezernieren und die Arbeiterinnen von *A. m. capensis* zur Dominanz über die Arbeiterinnen anderer Rassen befähigt sind.

***A. m. capensis* / *A. m. scutellata* / Tergittaschendrüsen / Sekretorische Zelle / Kanalzelle**

REFERENCES

[1] Barbier R., Ferran A., Le Lannic J., Allo M.R., Morphology and ultrastructure of integumentary glands of *Semiadalia undecimnotata* Schn. (Coleoptera: Coccinellidae), Int. J. Insect Morphol. Embryol. 21 (1992) 223–234.

[2] Bazire-Bénazet M., Zylberberg L., An integumentary gland secreting a territorial marking pheromone in *Atta* sp.: Detailed structure and histochemistry, J. Insect Physiol. 25 (1979) 751–765.

[3] Billen J., Morphology and ultrastructure of the exocrine glands in social hymenoptera, in: Eder J., Rembold H. (Eds.), Chemistry and Biology of Social Insects, J. Verlag Peperny, München, 1987, pp. 81–84.

[4] Billen J., Ultrastructural organization of the exocrine glands in ants, Ethol. Ecol. Evol. Special Issue 1 (1991) 67–73.

[5] Billen J., Morphology of the exocrine system in ants, Proc. Colloq. Soc. Insects 2 (1993) 1–15.

[6] Billen J.P.J., Dumortier K.T.M., Velthuis H.H.W., Plasticity of honeybee castes: occurrence of tergal glands in workers, Naturwissenschaften 73 (1986) 332–333.

[7] Boehm B., Beziehungen zwischen Fettkörper, Oenocyten und Wachsdrüsenentwicklung bei *Apis mellifica* L., Z. Zellforsch. Mikrosk. Anat. 65 (1965) 74-115. Cited in: Hepburn H.R., Honeybees and Wax, Springer Verlag, Berlin, 1986, p. 23.

[8] Cassier P., Lensky Y., The Nassanov gland of the workers of the honeybee (*Apis mellifera* L.): Ultrastructure and behavioural function of the terpenoid and protein components, J. Insect Physiol. 40 (1994) 577–584.

[9] Cassier P., Lensky Y., Ultrastructure of the wax gland complex and secretion of beeswax in the worker honey bee *Apis mellifera* L., Apidologie 26 (1995) 17–26.

[10] Crewe R.M., Velthuis H.H.W., False queens: a consequence of mandibular gland signals in worker honeybees, Naturwissenschaften 67 (1980) 467–469.

[11] Crewe R.M., Wossler T., Allsopp M.H., Workers in queens clothing: Why*capensis* workers become pseudoqueens, in: Anderson R.H., Buys B. (Eds.), 1990 Symposium, Bees and Beekeeping in Southern Africa, Univ. Press, Stellenbosch, 1990, pp. 83–89.

[12] Cruz-Landim da C., Morphology of pheromone glands in *Meliponae* (Hymenoptera, Apidae), in: Eder J., Rembold H. (Eds.), Chemistry and Biology of Social Insects, J. Verlag Peperny, München, 1987, pp. 441–442.

[13] Cruz-Landim da C., Dos Santos S.M.F., Hˆfling M.C.A., Sex determination in bees. XV. Identification of queens of *Melipona quadrifasciata anthidioides* (Apidae) with the worker phenotype by a study of the tergal glands, Rev. Bras. Genet. 3 (1980) 295–302.

[14] De Hazan M., Lensky Y., Cassier P., Effects of queen honeybee (*Apis mellifera* L.) ageing on her attractiveness to workers, Comp. Biochem. Physiol. A 93 (1989) 777–783.

[15] De Hazan M., Hyams J., Lensky Y., Cassier P., Ultrastructure and ontogeny of the mandibular glands of the queen honeybee, *Apis mellifera* L. (Hymenoptera: Apidae), Int. J. Insect Morphol. Embryol. 18 (1989) 311–320.

[16] Espelie K.E., Butz V.M., Dietz A., Decyl decanoate: A major component of the tergite glands of honeybee queens (*Apis mellifera* L.), J. Apic. Res. 29 (1990) 15–19.

[17] Grandperrin D., Cassier P., Anatomy and ultrastructure of the Koschewnikow's gland of the honey bee, *Apis mellifera* L. (Hymenoptera: Apidae), Int. J. Insect Morphol. Embryol. 12 (1983) 25–42.

[18] Hepburn H.R., Source of secretion, in: Hepburn H.R. (Ed.), Honeybees and Wax, Springer-Verlag, Berlin, 1986, pp. 11–24.

[19] Hepburn H.R., Crewe R.M., Defining the Cape honeybee: reproductive traits of queenless workers, South Afr. J. Sci. 86 (1990) 524–527.

[20] Hepburn H.R., Bernard R.T.F., Davidson B.C., Muller W.J., Lioyd P., Kurstjens S.P., Vincent S.L., Synthesis and secretion of beeswax in honeybees, Apidologie 22 (1991) 21–36.

[21] Humason G.L., Animal Tissue Techniques. 4th edn., W.H. Freeman and Co, San Francisco, 1979.

[22] Jeanne R.L., Downing H.A., Post D.C., Morphology and function of sternal glands in polistine wasps (Hymenoptera: Vespidae), Zoomorphology 103 (1983) 149–164.

[23] Mercer E.H., Birbeck M.S.C., Electron microscopy: A handbook for biologist, Blackwell Scientific Publications, Oxford, 1972, pp. 22–29.

[24] Mota M.H.V.B., Cruz-Landim da C., Ocorrencia e morfometria de glandulas tegumentares abdominais em *Apis mellifera* L. (Hymenoptera, Apidae), Rev. Bras. Zool. 5 (1988) 119–154.

[25] Noirot C., Quennedey A., Fine structure of insect epidermal glands, Annu. Rev. Entomol. 19 (1974) 61–80.

[26] Noirot C., Quennedey A., Glands, gland cells, glandular units: Some comments on terminology and classification, Ann. Soc. Entomol. Fr. 27 (1991) 123–128.

[27] Pouvreau A., Morphology and histology of tarsal glands in bumble bees of the genera *Bombus*, *Pyrobombus* and *Megabombus*, Can. J. Zool. 69 (1991) 866–872.

[28] Renner M., Baumann M., Über Komplexe von subepidermalen Drüsenzellen (Duftdrüsen?) der Bienenkönigin, Naturwissenschaften 51 (1964) 68–69.

[29] Schoeters E., Billen J., Anatomy and fine structure of the metapleural gland in *Atta* (Hymenoptera, Formicidae), Belg. J. Zool. 123 (1993) 67–75.

[30] Schoeters E., Billen J., Morphology and ultrastructure of the convoluted gland in the ant *Dinoponera australis* (Hymenoptera: Formicidae), Int. J. Insect Morphol. Embryol. 24 (1995) 323–332.

[31] Smith R.K., Spivak M., Taylor O.R., Bennett C., Smith M.L., Maturation of tergal gland alkene profiles in European honey bee queens, *Apis mellifera* L., J. Chem. Ecol. 19 (1993) 133–142.

[32] Sokal R.R., Rohlf F.J., Biometry, 3rd edn., W.H. Freeman and Company, New York, 1995.

[33] Velthuis H.H.W., Chemical signals and dominance communication in the honeybee *Apis mellifera* [Hymenoptera: Apidae], Entomol. Gen. 15 (1990) 83–90.

[34] Wossler T.C., Crewe R.M., Mass spectral identification of the tergal gland secretions of female castes of two African honeybee races (*Apis mellifera*), J. Apic. Res. (1999) in press.

[35] Zupko K., Sklan D., Lensky Y., Proteins of the honeybee (*Apis mellifera* L.), Body surface and exocrine gland secretions, J. Insect Physiol. 39 (1993) 41–46.