

**FINE STRUCTURE OF THE GEMMA GLAND
IN THE ANT *DIACAMMA AUSTRALE*
(HYMENOPTERA, FORMICIDAE)**

by

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SUMMARY

Workers of *Diacamma* have minute mesothoracic appendages termed «gemmae», and these represent a unique glandular structure among the Formicidae. In *D. australe*, each gemma contains approx. 500 glandular cells which are individually connected by duct cells opening through minute pores on the outer surface of the gemma. A specialized end apparatus forms the junction between the two cell types. Ultrastructural examination of the secretory cells shows the presence of both smooth and granular endoplasmic reticulum, and the occurrence of both electron-lucid and electron-dense inclusions. The secretion may therefore have a rather complex composition. Its function is presumably related to the peculiar mechanism of reproductive regulation found in this queenless ant.

Keywords : *Diacamma*, gemma, morphology, ultrastructure, exocrine glands.

INTRODUCTION

All species in the ant genus *Diacamma* (subfamily Ponerinae) lack queens. Instead, a single worker (= gamergate, PEETERS and CREWE, 1984) mates and reproduces in each colony. Another characteristic of *Diacamma* is that all workers emerge from the pupal cocoon with a pair of sac-like mesothoracic appendages. These tiny structures, which are homologous to the mesothoracic wings in queens (TULLOCH, 1934; BITSCH and PEETERS, 1991) do not exist in other ant genera, and have been called 'gemmae' (PEETERS and BILLEN, 1991). In each colony, only the gamergate retains the gemmae, because she aggressively removes them from every

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newly-closed worker (FUKUMOTO *et al.*, 1989 ; PEETERS and HIGASHI, 1989). Mutilation of the gemmae has important social consequences, since individual behaviour is affected, together with the ability to mate. We recently discovered that the gemmae in *Diacamma australe* (FABRICIUS, 1775) are completely filled with glandular cells (PEETERS and BILLEN, 1991). In the present contribution, we report on the fine structural organization of this novel gland in *D. australe*.

MATERIAL AND METHODS

The ants examined were obtained from a colony of *D. australe* excavated near Townsville, North Queensland (Australia). Gemmae of both callow workers and the gamergate were fixed in 2 % glutaraldehyde, buffered at pH 7.3 with 0.05 Na-cacodylate and 0.15 M saccharose. After postfixation in 2 % osmium tetroxide, tissues were dehydrated in acetone and embedded in Araldite. Thin sections were double stained with a LKB Ultrastainer, and examined with a Zeiss EM 900 electron microscope. Specimens for scanning electron microscopy were coated with gold-palladium and viewed with a Cambridge 360 microscope.

RESULTS

The gemmae appear as orange to brownish mesothoracic appendages in the region where wings normally occur in queens. They fit into a thoracic cavity, which can conveniently be designated as the 'gemmaarium' (Pl. I). Each gemma has a length of approx. 450 μm and a width of approx. 200 μm . The anterior part forms a narrow stalk that articulates with the thorax, while the posterior part is densely packed with glandular cells (Pl. II, A and B). The outer (dorsal) cuticular lining measures about 10 μm in thickness, while the inner (ventral) lining hardly exceeds 2 μm (Pl. II, A). Approximately 500 glandular cells are estimated to occur per gemma, each being accompanied by a duct cell. Because of the dense concentration, the secretory cells assume a polygonal shape with a diameter ranging from 12 to 20 μm (Pl. II, B). Nuclei generally are very rounded with a diameter around 10 μm .

The end apparatus, which is the characteristic functional device for accumulation and release of secretion at the cellular level in this gland type, presumably is rather short because it is not always seen in a plane section (Pl. II, B). It consists of a cuticular collecting duct, surrounded by a sheath of microvilli. The cuticle shows a discontinuous epicuticular inner layer and a granular procuticle. The microvilli in general are more or less closely packed (Pl. III, A), although they may also appear in a much more disorderly arrangement because of considerable spaces distorting them (Pl. III, B). These differences may occur among the secretory cells of the same individual. Both electron-lucid and electron-dense spherical inclusions of variable diameter are dispersed in the cytoplasm (Pl. II, B ; Pl. III A, B). Other cytoplasmic elements include both smooth and granular endoplasmic reticulum (Pl. III, C), numerous mitochondria and randomly-scattered free ribosomes.



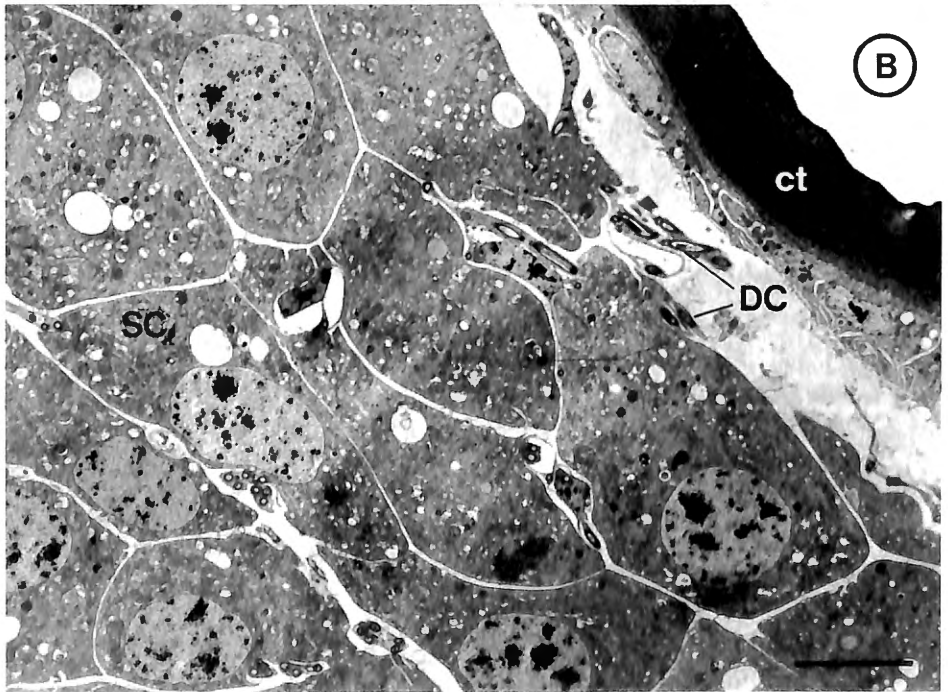
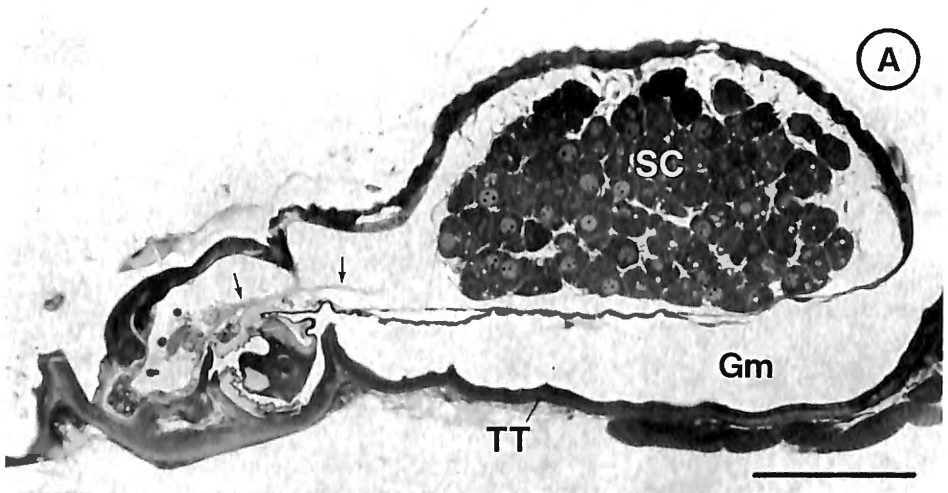
PLATE I

Scanning electron micrograph of left side gemma, showing its natural position (anterior side to the left; scale bar 100 μm).

Each secretory cell is associated with a slender duct cell, that forms the connection between the end apparatus and the external environment. Within the duct cell, one narrow duct with a diameter around 0.4 μm is found with a continuous cuticular lining having a uniform thickness of 0.1 μm . The cytoplasm is very much reduced and forms a narrow sheath around the duct (Pl. III, D). All ducts open through pores with a diameter around 0.3 μm in the wrinkled outer surface of the gemma (Pl. III, E). The length of the duct cells varies from as less as 20 μm for those associated with secretory cells near the dorsal surface, to about 150 μm for those originating from cells near the ventral wall.

Apart from the abundance of gland cells and their ducts, the gemmae contain only very few tracheoles and a nerve fibre (Pl. III, F), that penetrate from the thorax through the stalk. Not a single muscle fibre could be detected inside the gemmae.

PLATE II



DISCUSSION

The existence of a large number of glandular cells inside the gemmae of *Diacamma australe* make these thoracic appendages an important exocrine organ. Although the gemmae are homologous to mesothoracic wings (TULLOCH, 1934; BITSCH and PEETERS, 1991), they are highly modified, and the de novo evolution of this exocrine structure is characteristic of the genus *Diacamma*. The cellular organization of the gland is consistent with that of bicellular secretory units, each comprising a secretory cell and a duct cell (BILLEN, 1987). The contact area between these cells is the highly-specialized end apparatus, which regulates the discharge of secretory products at the cellular level (NOIROT and QUENNEDEY, 1974; BILLEN, 1990). The microvillar arrangement in the end apparatus may vary considerably, even between the secretory cells of the same individual, because of the frequent appearance of conspicuous spaces in this area. These spaces, in spite of their apparent position within the secretory cell, do represent the extracellular area, since the cell membrane (of the microvilli) lining them is nothing but the invaginated plasmalemma of the secretory cell. The occurrence of these spaces, which are commonly found in exocrine glands of the type having an end apparatus (BILLEN, 1990), probably corresponds to the creation of additional volume for the storage of secretions (BAZIRE-BENAZET and ZYLBERBERG, 1979).

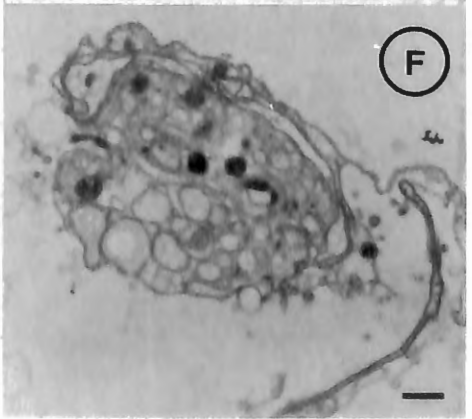
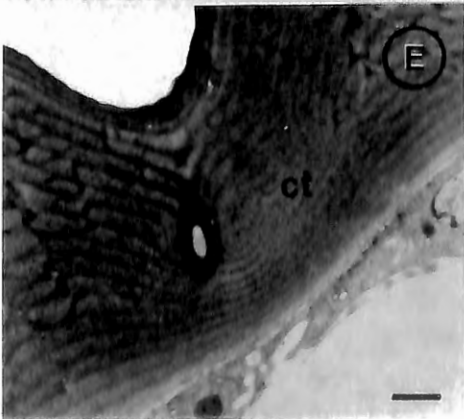
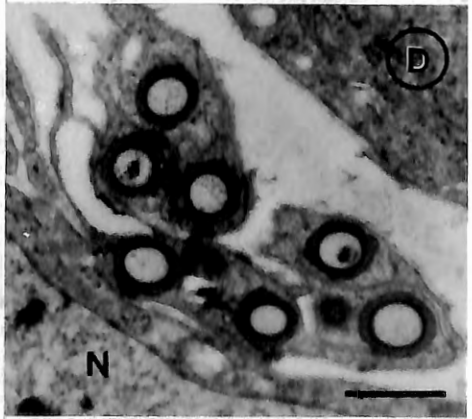
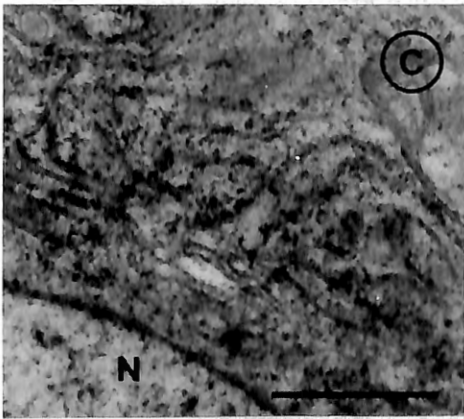
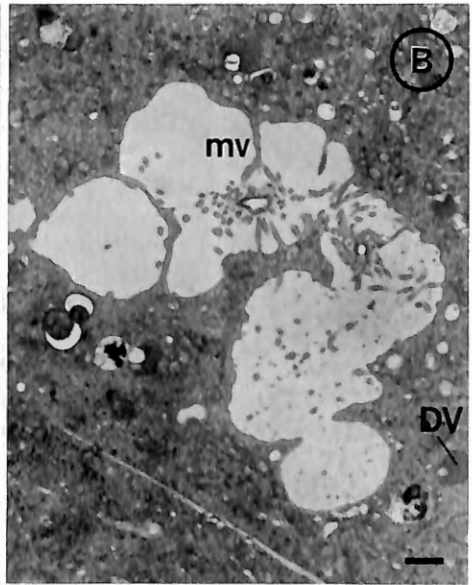
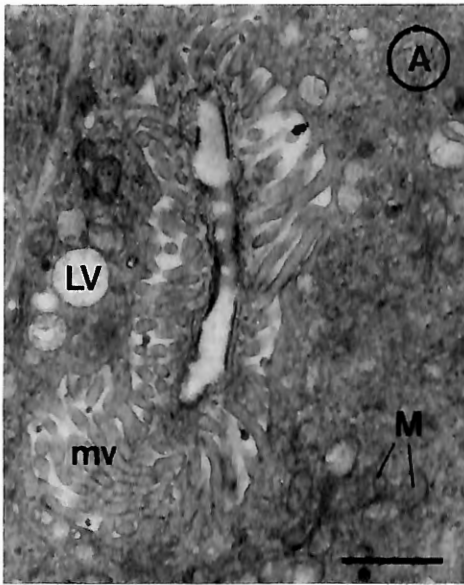
No information is yet available on the chemical nature of the gemmae secretions. The occurrence of both smooth and granular endoplasmic reticulum, as well as both electron-lucid and electron-dense (secretory?) vesicles, suggests that a complex mixture may be produced. Behavioural data indicate that the secretions may be volatile. The presence of a nerve fibre into each gemma possibly is to be related with the existence of a stretch receptor in the gemmae. This would be a plausible mechanism for detecting when a gemma has been mutilated, with eventual subsequent neuroendocrine effects leading to behavioural changes. The lack of any kind of musculature inside the gemmae, which in itself is consistent with the proposed homology with wings, seems to rule out the possibility that the secretions are released under voluntary control. Therefore, a process of passive diffusion may result in the continuous release of secretions.

PLATE II

A. Semithin longitudinal section through the gemma in a callow worker of *D. australe* (anterior side to the left; scale bar 10 μm). Note the penetration of a nerve fibre (arrows) through the stalk of the gemma and the difference in thickness of the cuticular lining between the gemma's outer and inner wall. Gm = gemmarium, SC = secretory cells, TT = thoracic tegument.

B. General ultrastructural view of the secretory cells (SC) and duct cells (DC). ct = cuticular lining of outer side. Scale bar 10 μm .

PLATE III



The numerous secretory units release their products to the external environment via pores on the outer surface of the gemmae. Behavioural observations suggest that these pheromones are involved in the social interactions among workers (FUKUMOTO *et al.*, 1989; PEETERS and HIGASHI, 1989). Further work is necessary to determine whether they also function as sexual pheromones to attract males.

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PLATE III

Ultrastructural details of the gemma in a callow worker, scale bar 1 μ m in all figures.

A. end apparatus with closely arranged microvilli; cytoplasm with mainly smooth endoplasmic reticulum. B. end apparatus with distorted microvillar arrangement. C. cytoplasm with mainly granular endoplasmic reticulum. D. section through bundle of duct cells. E. duct penetrating through thick upper tegument of gemma. F. section through nerve fibre in stalk area.

ct = cuticle, DV = electron-dense vesicle, LV = electron-lucid vesicle, M = mitochondria, mv = microvilli, N = nucleus.

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