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Dermal Glands Concerned with Production of Wax Blooms in Desert Tenebrionid Beetles

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A study of nine species of Namib Desert beetles that produce wax blooms in response to conditions of increased temperature and decreased humidity characteristic of desert environments, revealed that the filaments composing the bloom were produced by dermal glands. These glands were found to be similar in structure to the dermal glands of Tenebrio *reported to be responsible for the secretion of the cement layer of the cuticle.*

Nege spesies van Namib-woestynkewers is bestudeer. Die kewers produseer 'n wasblos as reaksie op die hoë temperature en lae humiditeit wat kenmerkend van woestyne is. Die veseltjies waaruit die wasblos bestaan, word deur dermale kliere afgeskei. Die struktuur van die dermale kliere is soortgelyk aan dié van Tenebrio *wat volgens vorige ondersoeke die sementlaag van die cuticula afskei.*

Many insects secrete renewable wax material onto their cuticular surfaces, the production of which often appears to be related to the environmental conditions in which the animals live.[1,2] A number of desert tenebrionid beetles produce a renewable wax bloom composed of fine filamentous material[3-5] in response to the conditions of increased temperature and decreased humidity which are characteristic of desert climates.[6-9] While surface waxes of insects are generally derived from the epidermis,[10] the more elaborate structures such as wax scales in bees and wax threads of coccinellid larvae[12] are secreted by specialised cells or groups of cells known as dermal glands. In recent work published on wax blooms in desert tenebrionids, it has been assumed that the bloom has an origin similar to that of the waxes added to the epicuticular layer, i.e. that it arises from epidermal cells and is transported to the surface via pore canals[3-5] as suggested by Locke.[10] In adult beetles, once sclerotization is complete, the endocuticle becomes progressively thicker as laminations of cuticular material are laid down. Pore canals reported to be pathways for secretion of epicuticular wax[10] may not penetrate the epicuticular layer and are often blocked by filamentous material. This is particularly true of tenebrionids.[13] They appear to be unlikely pathways for secretion of bloom threads.

To date, those dermal gland openings that are commonly found scattered on the body and elytron surface of beetles such as *Tenebrio*[14-16] and other insects such as *Rhodnius*[17,18] and *Calpodes*[18] have not been implicated in wax production. Originally the assumption was made that these glands produced moulting fluid.[19] Richards,[20] reviewing the subject, pointed out that dermal gland activity and production of fluid did not coincide. Subsequently these glands have been associated with the production of the cement layer of the cuticle.[14,21]

A wide variey of other products such as pheromones, terpenes and quinones have been shown to be produced by specific dermal glands of beetles such as *Trogoderma*,[22] *Eleodes*[23] and others.[24,25]

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Table 1. Namib tenebrionid beetles used in the study.*

Producers of the wax bloom	Beetles lacking wax bloom
Zophosis sp.	
Zophosis testudinaria Fabricius	*Zophosis* (*Gyrosis*) *moralesi* Koch
Zophosis mniszechi Deyrolle	
Zophosis (*Cardiosis*) *fairmairei* Peringuey	
Zophosis (*Cerosis*) *hereroensis* Gebien	
Zophosis (*Cardiosis*) *triangulifera* Gebien	
Onymacris sp.	
Onymacris plana plana Peringuey	*Onymacris rugatipennis rugatipennis* Haag
Onymacris rugatipennis albotessallata Schultze	*Onymacris bicolor* Haag
Onymacris laeviceps Gebien	*Onymacris unguicularis* Haag
Cauricara sp.	
Cauricara phalangium rufofemorata Koch	

*Nomenclature of Penrith.[26-29]

We report here that the wax filaments of several species of tenebrionid beetle from the Namib Desert have their origin in dermal glands (Fig. 1).

Material and methods

Thirteen species of beetles from the central Namib and one from the northern Namib, *O. bicolor*, were studied (Table 1). The beetles were kept in the laboratory in shallow containers filled with 10 cm of dune sand at a temperature of 20 – 25°C, and 30 – 40% relative humidity. They were fed on oats, lettuce and dune detritus once a week. No additional water was supplied. Under these conditions *Z. mniszechi*, *Z. fairmairei* and *O. r. albotessallata* produced blooms during the summer months. The other species produced the wax bloom more easily at 30°C and 30% relative humidity.

Wax blooms are usually found on the protonotum, elytra, abdominal sternites and the anterior surface of the femora.[26,27] We restricted the study to the elytra as it was hoped that the minimal number of cell types would be encountered in that region (Fig. 2). Specimens for scanning electron microscopy were killed in a bottle containing ethyl acetate and then air dried. The whole animal, in the case of small species, or just the elytra were then coated lightly with silver or gold.

Routine embedding in wax and freezing of fresh material proved to be unsuccessful for the production of sections for light microscopy. Material embedded in plastic was successfully cut into 1 μm sections. The plastic was removed from the sections by immersion in a saturated solution of sodium hydroxide in absolute alcohol and, after washing, the sections were stained in 1% toluidine blue in a 1% borax solution. Periodic acid Schiff, alcian blue and osmium tetroxide stains were also used to investigate the nature of certain cell structures. These stains did not produce the usual colour reactions when sections had been treated according to the methods described above. The tissues were therefore stained in block, prior to embedding.

For transmission electron microscopy, fresh elytra were sliced anteroposteriorly into long narrow strips, 0.5 mm in width, so that samples could be orientated relative to the whole animal. These pieces were fixed in 4% glutaraldehyde in cacodylate buffer. After post-fixation in 1% osmium tetroxide, samples were dehydrated and embedded in Transmit plastic resin (TAAB) or in an Epon-Araldite mixture. Sections for light and electron microscopy were cut on tungsten-coated glass knives. One micron sections were obtained from the elytra of all the beetles listed in Table 1. Successful electron microscope studies were accomplished on the elytra of *C. phalangium*, *Z. testudinaria*, *Z. mniszechi*, *Z. fairmairei*, *O. plana* and *O. bicolor*.

Results

Scanning electron microscopy confirmed that the bloom was composed of fine filaments in each of the species examined. The filaments formed a felt over the prothorax and parts or all of the elytron (Fig. 3*a*). The filaments were extruded onto the cuticular surface through pores measuring up to 1.0 μm in diameter. In *Z. mniszechi* and others, the cuticle surface had a sculptured appearance similar to roof tiles as is common in beetles[30] and other insects. Pores were found both in the lines demarcating the sculpturing and in the 'tiles' themselves (Fig. 3*c*), very much like those in *Tenebrio*.[15] In some instances the pores were placed on tubercles (Fig. 3*b*).

The filaments were of variable length and ranged from 0.1 – 0.3 μm in width. The filaments of the Namib beetles are similar to those of *Cryptoglossa verrucosa*,[3] a tenebrionid found in the Sonoran desert.

Light microscopic observations showed that the elytra were composed of the expected two plates of sclerotized material separated by a blood space divided into compartments by cuticular columns called trabeculae, which are arranged parallel to one another and run longitudinally (Fig. 2). The trabeculae occupied much of the

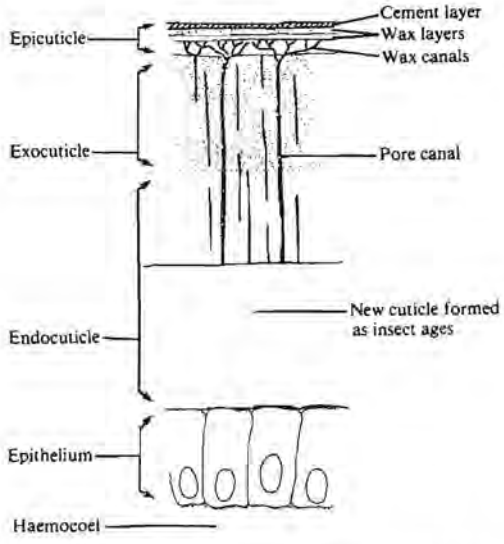

Fig. 1. Diagram to illustrate the complete dermal gland thought to be responsible for the secretion of wax bloom.

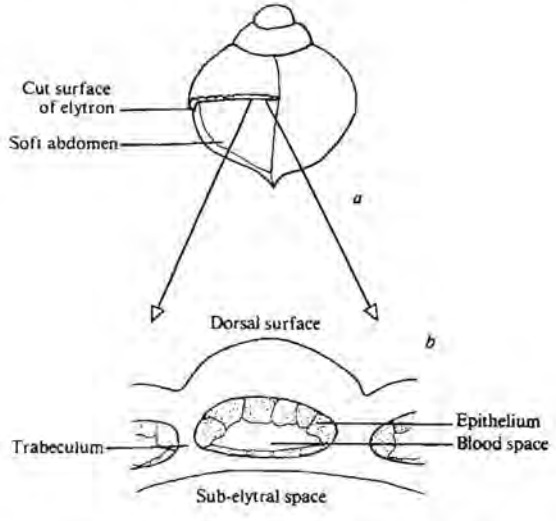

Fig. 2. Diagram to illustrate the general structure of the elytron and the orientation of material taken from it.

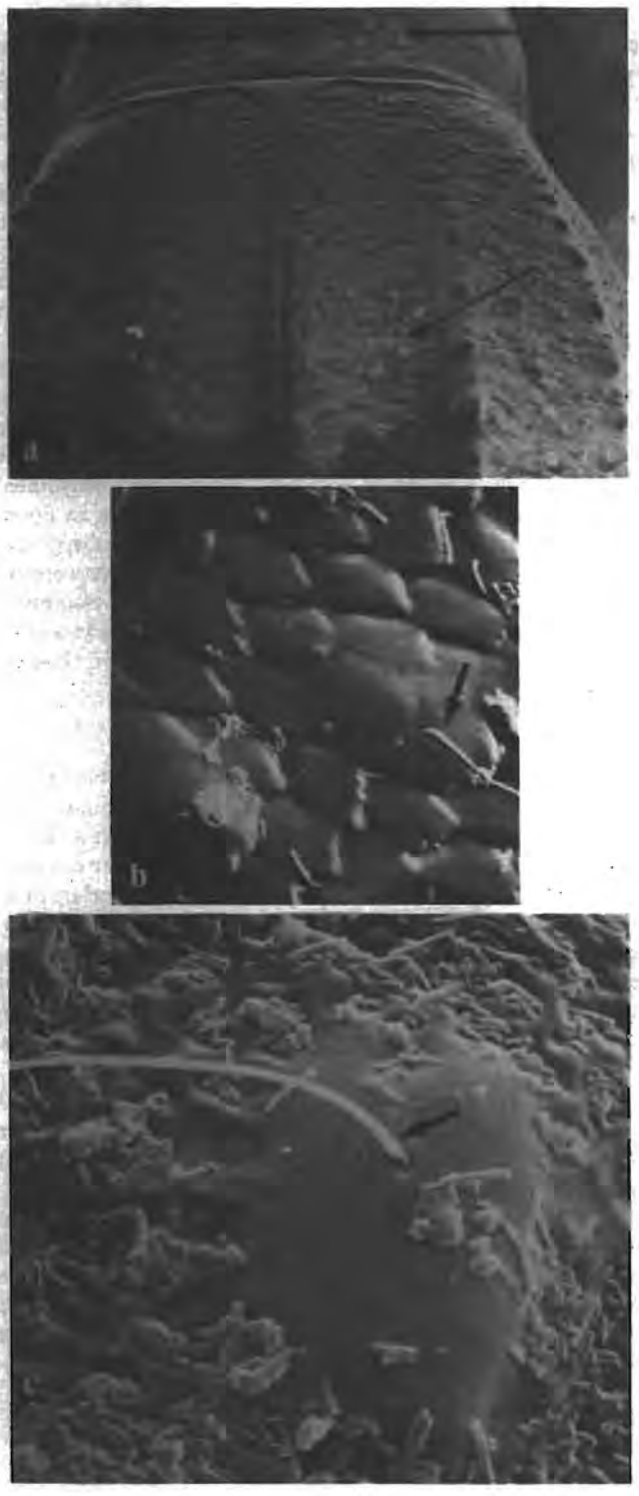

Fig. 3. Scanning electron micrographs of bloom produced on the elytron surface. *a*, General view of dorsal surface of *C. phalangium* elytra. Arrows indicate bloomed areas. × 15 *b*, Detail of one bloom filament (→) emerging from its duct. × 5000 *c*, *Z. mniszechi* elytron with little bloom. The surface has a 'tiled' appearance. (→) = filament. × 1500

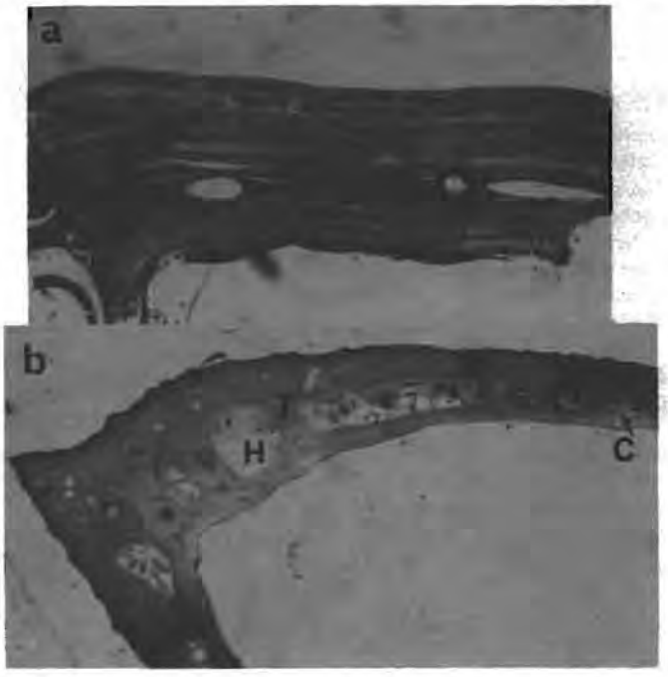

Fig. 4. *a*, Transverse section of elytron of *O. bicolor* which does not produce bloom. *b*, Transverse section of elytron of *Z. mniszechi* which does produce bloom. C = cuticle, T = trabeculum, H = blood space. × 300

Fig. 5. Details of cells shown in Fig. 4. *a*, *O. bicolor* with condensed epithelium, E, that does not completely surround blood space, H. *b*, *Z. mniszechi* with numerous gland cell reservoirs, R, and duct cells, DC, filling the blood space, H. × 3000

cross-sectional area of the elytron, especially so in those beetles that did not produce a wax bloom. The elytra of *O. bicolor* were found to have very small blood spaces relative to the thickness of the elytron. The average thickness of the elytron was 192 – 200 μm and the blood space was 10.0 μm in height. In *Z. mniszechi* and *O. plana* the blood space occupied as much as one-third of the thickness of the elytron. Figures 4*a* and *b* illustrate the contrast in the relative size of the blood space to the elytra, but measurement of the depth of blood space and elytron of all other species did not reveal clear-

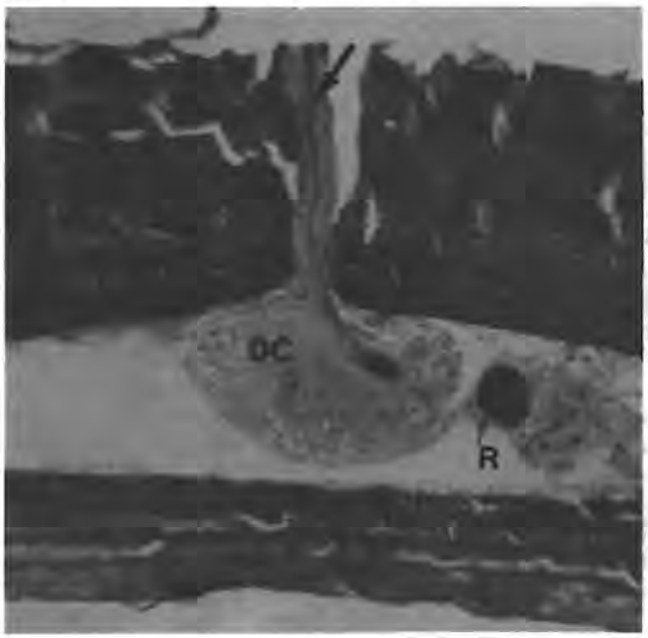

Fig. 6. Transverse section of elytron of *C. phalangium* showing a complete dermal gland. R = reservoir, DC = duct cell, → = duct. × 3000

cut differences in proportions of blood space to elytron between wax-producing and non-wax-producing beetles.

Epidermal cells lined the elytral cavities and surrounded the blood spaces. In the case of the non-wax-producing beetles the epithelial cells were very attenuated and formed a thin and often apparently incomplete lining (Fig. 5*a*). The cells forming the epithelium were generally more cuboidal in shape in the wax-producing beetles and were relatively large and easily observed (Fig. 5*b*). It is in the structure of these cells that the elytra of non-wax-producing beetles were found to differ most. The structures described below were found only in the epithelium of the elytra of the wax-producing beetles.

This epithelium has cells with inconspicuous nuclei. A number of cells enclose relatively large and obvious granules. The granules were faintly pigmented and appeared a reddish or pale golden colour in unstained material, depending on the species examined. When stained with osmium tetroxide the colour was enhanced to dark brown but matched neither the intense black of the epicuticular layer nor the grey shades of lipids in the blood space. The granules stained intensely with toluidine blue but were not stained by either alcian blue or the periodic acid Schiff reaction. These results indicate that the granules contain both lipid and protein but lack carbohydrates.

The granules therefore have a complex composition. They appear to contain pigments in addition to lipid, possibly in a bound form, and a substance that gives a strongly metachromatic reaction with toluidine blue, possibly some kind of protein. The wax bloom washed from the cuticle surface has been shown to contain protein (Nicolson, personal communication).

Further examination of the 'granule' containing cells revealed that they were the secretory cells of the dermal glands (Fig. 6). The structures of these glands were found to be remarkably consistent in all the wax-producing species examined. The granule itself was found to be membrane-bound and filled with relatively electron dense amorphous material (Fig. 7). It is thought to be equivalent to the highly distended extracellular reservoir observed in *Tenebrio molitor* dermal glands.[16] Many smooth-walled and ribosome-studded vesicles were observed in the cytoplasm on the perimeter of

Fig. 7. Transmission electron micrograph showing a section through duct cells, DC, reservoir, R, and duct, →, found in *Z. mniszechi*. × 12000

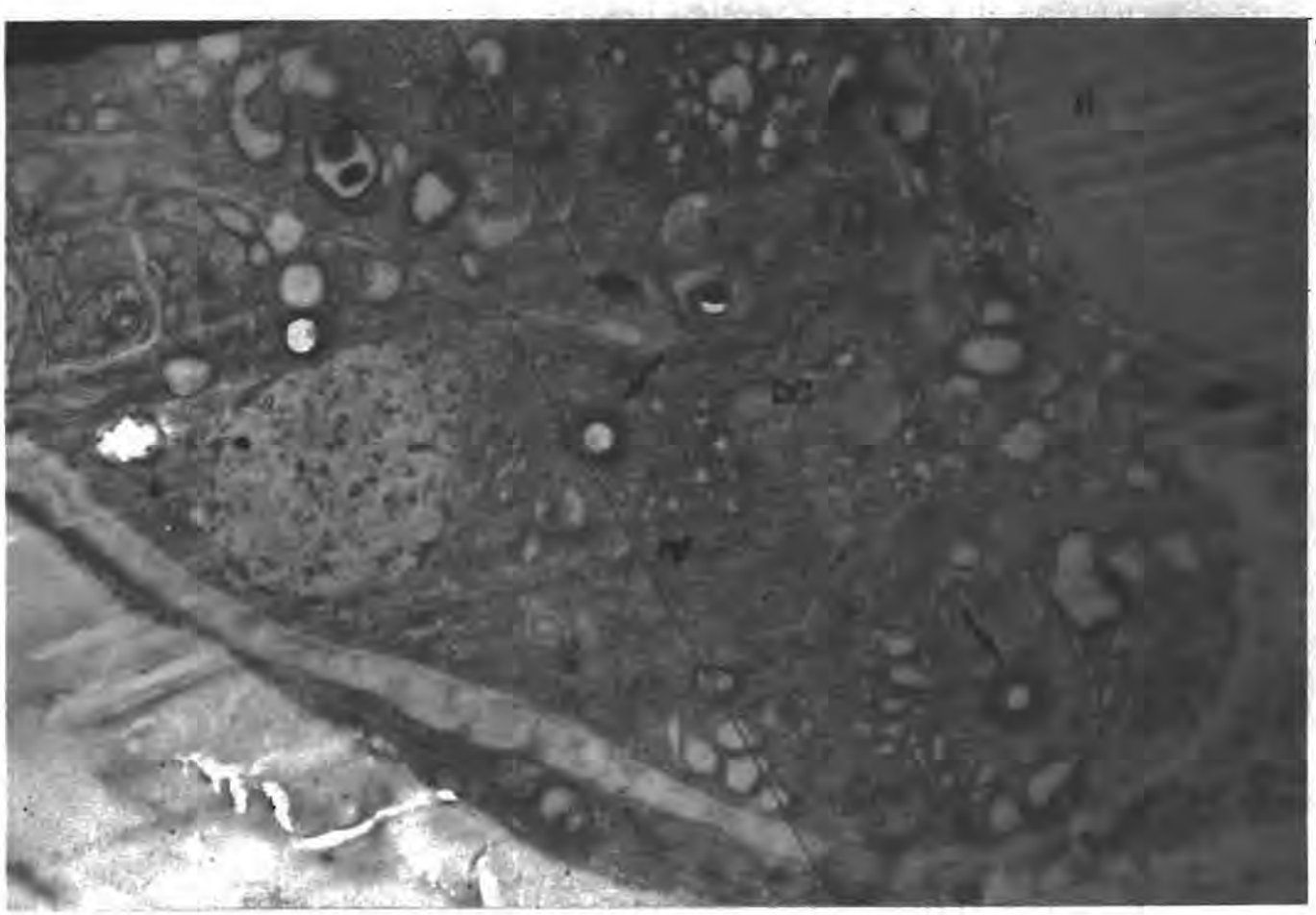

Fig. 8. Reservoir and surrounding cell found in *O. plana*. N = nucleus, V = vesicles, P = cytoplasmic projections. × 20 000

the reservoir. The characteristic infolded appearance of the *Tenebrio* dermal gland reservoir was not observed.[16] The reservoir appeared circular to oval in shape but was interrupted by small finger-like projections of cytoplasm observed to contain microtubules. The nucleus of the secretory cell was frequently less than half the diameter of the reservoir. The cytoplasm of the cell contained numerous vesicles, mitochondria and endoplasmic reticulum and had the appearance of a cell actively involved in secretion.

Duct cells were found immediately adjacent to the secretory cells surrounding the reservoirs (Fig. 7) and appeared to be involved in secretion because they contained numerous mitochondria, vesicles and electron dense granules. Each of these duct cells contained one or more cross sections through ducts consisting of cuticle. Surrounding these ducts, complex infoldings of plasma membrane form a microvillous border characteristic of dermal glands.[16,17,31] The cuticular lining is surrounded by a thick, filamentous layer which appears to be in close contact with the tips of the microvilli (Fig. 9). The ducts have been found both in longitudinal and cross section and are probably arranged in the coiled fashion described for dermal glands of *Tenebrio*.[14-16] Electron dense material was observed in the lumen of many of these ducts. Cross sections of ducts lacking both a filamentous layer and microvilli and surrounded by narrow films of cytoplasm have been observed adjacent to the reservoir. These are probably part of the third section of the gland where a narrow elongated cell containing few organelles was seen accompanying the duct from the epithelium through the cuticle. This cell was seldom seen in longitudinal section as this represented a weak point in the cuticle, which became folded or torn in most sections. The cell did not extend the full length of the duct and was absent from many cross sections of duct in the outer layer of cuticle. The features of the dermal gland observed in the beetles studied have been represented diagrammatically in Fig. 1.

Discussion

The glands described above are typical of dermal glands classified as type 3 glands by Noirot and Quennedy.[31] These glands are known in beetles and other insects and either occur singly or are grouped together to form more complex structures with common reservoirs. Although the cell sizes and proportions may vary, the basic pattern of the cells, cuticular ducts and reservoir remain constant. Similarity in structure is no guide to the nature of the secretion formed.

The evidence accumulated in the present study indicates that the bloom is a complex material composed of proteins, lipids and pigments. The reservoir of the gland appears to contain pigment and protein but, as can be seen from the electron micrographs, it does not have an appearance that is typical for lipids. The osmiophilia observed is an indication that lipids are present but does not constitute definite proof. The contents of the ducts stained very positively with osmium. The lipids may occur in the reservoirs in bound form or may be added by the large cell surrounding the duct.

Of all the glands referred to previously, it is those of *Tenebrio* which bear closest resemblance to the glands described in this study. It has been assumed that in *Tenebrio* the glands secreted the cement layer of the newly emerged adults and therefore suggested that the glands were only active for short periods.[14,15] Delachambre queries this aspect of the gland activity and showed that dermal glands in older adult beetles were also functional.[16] His study suggested that the glands may replace cuticular material throughout life or may have additional functions. As a result of the present study we suggest that in certain arid-adapted tenebrionids the dermal glands are responsible for the production of the so-called wax bloom. Dermal glands have been shown to be responsible for a wide variety of materials in various insects and it would not be difficult to visualise the wax bloom as a specialised form of material produced in other insects to coat the cuticle.,

This possibility has not been explored by Locke, who has assumed that wax blooms are secreted in the same way as other wax

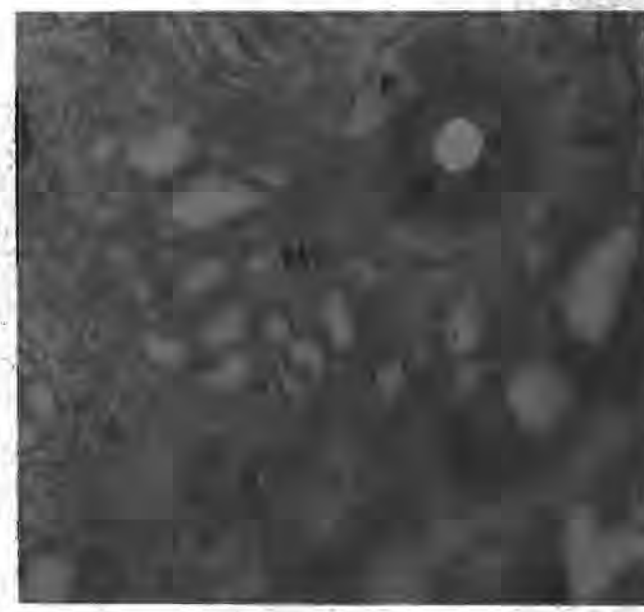

Fig. 9. Detail of duct from Fig. 7. Duct lumen is empty (→). MV = microvilli, C = cuticular lining, F = filamentous layer. × 30 000

material passing from epithelial cells to the cuticle surface. On the basis of work carried out on *Calpodes*, he has listed five alternative hypotheses to account for wax transport through the cuticle,[32] and secretion from glands was not included.

There is no evidence to contradict Wigglesworth's original suggestion that dermal glands contribute to the cement layer of the cuticle. Hadley has reported that in humid environments the bloom filaments of *Cryptoglossa verucosa* lose their integrity and the beetles lose their blue colour,[3] suggesting that the material from the filaments becomes incorporated into the surface layers of the cuticle. This is in agreement with our own observations. All the research to date has stressed the lipid component of the filaments and it seems inconceivable that lipids should 'dissolve' into the cuticular surface under conditions of high humidity. If, however, a major structural component is a soluble protein this would be possible. The formation of a bloom may be merely a modification of a system already operating in a less obvious manner.

We have observed no structural evidence that might indicate how the thread could be squeezed from the reservoir and on to the surface. Muscle structures and anything resembling contractile filaments in cells surrounding the reservoirs have not been observed. This, however, does not mean that the cells are not capable of such contraction. Whatever the mechanism, it must be reasonably effective as the bloom can be replaced in 4 to 8 hours after its removal if the beetle is maintained under optimal conditions. The presence of the large reservoirs of stored material indicates that abundant material is available for secretion. The relatively slow rate of secretion indicates that these cells may be under neurohormonal control as suggested for the wax-producing epithelium of *Calpodes*.[32] Nerves have been observed in association with epithelial cells in the blood space but there is no evidence as yet of a direct nerve supply to the cells surrounding the reservoir.

Production of a bloom on the cuticle has important adaptive possibilities for beetles living in hot dry conditions. Wax bloom production has been shown to be instrumental in the reduction of water loss in these Namib beetles.[9,33] There would be a high survival value on any system of waterproofing the beetle surface that could be produced at short notice. A second feature, but one that is more difficult to evaluate, is the change in colour brought about by the production of a bloom. Without exception the beetle cuticle is black or brown in colour. The wax bloom is much lighter in colour, varying from white to blue, pink, red, brown and yellow. Irrespective of whether the differences in colour result from the presence of different pigment or refractile properties of the bloom filaments, the overall effect is a lightening of the cuticle. It has been shown that the wax bloom causes an increase in reflectance and this may in turn bring about a reduction in heat loading though the principles involved are by no means clear.[5,6]

An important question remains: Why, if there are so many advantages to having a wax bloom, do so many anatomically closely allied species of beetle also found in the Namib lack the bloom? — *O. r. rugatipennis* and *O. r. albotessallata*, *O. uniquicularis* and *O. laeviceps*, to name only two such pairs (Table 1). One possibility is that the non-wax-producers are restricted to environments or micro-environments that are sufficiently humid that bloom production is unnecessary. The other possibility is that other adaptations occur to cope with the water loss problem in a different way. In the case of *O. bicolor*, the cuticle is much thicker and blood spaces are very small. Sections through the cuticle in this area leave the impression that additional material is added to the inner surface of the cuticle by the epithelium lining the blood space, therefore reducing the diameter of the blood space and hence possibly reducing the amount of blood flow through the spaces and therefore the possibility of water loss. Attractive as this is for an alternative method of reducing water loss, it was not found to be a consistent feature of beetles that lacked the wax bloom.

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