

Extracuticular secretion on a Namib Desert Tenebrionid, *Onymacris plana*: an Indicator of aridity

by

E. McClain

Department of Physiology
University of Witwatersrand
Medical School
7 York Road
Parktown, 2193
Johannesburg
South Africa

S.A. Hanrahan

Department of Zoology
University of Witwatersrand
1 Jan Smuts Avenue
Johannesburg, 2000
South Africa

D. Gerneke

Electron Microscope Unit
University of Cape Town
Rondebosch, 7700
Cape Town
South Africa

ABSTRACT

Adults of the Adesmine tenebrionid beetle *Onymacris plana* secrete varying amounts of a bluish-white wax bloom related to their location in the climatic gradient of the central Namib desert. The material, produced by dermal glands and their associated secretory cells, forms whorls which anastomose covering the otherwise black cuticle. *O. plana* living in the cool foggy desert have dermal gland reservoirs which are full of secretory material but the associated cells indicate little or no secretory activity. Only a trace of the wax bloom appears on the surface of the individuals living there. In the hot, inland portion of the desert *O. plana* are completely covered by the wax bloom and appear blue. Their dermal gland reservoirs contain varying amounts of stored material and the associated secretory cells show marked synthetic activity. The wax bloom conferred increased reflectance of the beetle surface in the visible range. The role of this material in water balance and thermoregulation is discussed.

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1 INTRODUCTION

Many tenebrionid beetles living in the central Namib Desert have surface wax blooms (Plate 1). The presence and the amount of this wax material found on the integument of the beetles are related to the surrounding environmental conditions (McClain *et al.*, 1985). There exists in the central Namib a steep climatic gradient (Besler, 1972; Seely, 1978; Lancaster *et al.*, 1984). The cool, coastal foggy desert has low temperatures and high humidities. The alternate fog desert has higher temperatures and lower humidities than along the coast. The inland area is represented by high temperatures and low humidities. Widely distributed across this gradient is a large endemic apterous diurnal tenebrionid beetle, *Onymacris plana plana* (Peringuey) (Penrith, 1975). It is an ideal species in which to investigate the dynamics of wax bloom development and influence of the environment on production and maintenance of this material. It is thought that the wax material comes from underlying dermal glands



PLATE 1: *Onymacris plana* collected from the cool foggy portion of the central Namib (left) where the temperatures are low and humidities are high. *O. plana* (right) collected from the hot inland portion of the desert where temperatures are high and humidities low. The individuals are blue due to the presence of the bloom.

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(McClain *et al.*, 1984). The structure of these dermal glands and associated secretory cells has been described for a number of Namib tenebrionids (Hanrahan *et al.*, 1984). We report herein on the activity of the dermal glands and associated secretory cells of *O. plana* in response to the climatic gradient of the central Namib. We also describe the morphology of the material which appears on the surface and provide quantitative information on its reflectance properties. Finally we discuss how this dynamic secretion might help *O. plana* to survive the hostile conditions of the Namib Desert.

2 MATERIALS AND METHODS

Onymacris plana individuals were collected across the climatic gradient during a twelve day period in December 1981. The collection sites, moving from west to east were Rooibank (R), 'J' Line (JL), Gobabeb (G), Noctivago (N) and Miss Checkies Vlei (MV), (Figure 1). Macro-meteorological data for most of these sites are found in Besler (1972), Robinson and Seely (1980) and Lancaster *et al.* (1984).

At each site 100 *O. plana* were collected between 9:00 a.m. — 12:30 p.m. and 2:30 p.m. — 5:30 p.m., times the beetles are normally active on the surface in the summer. The bluish-white wax bloom development was assessed immediately on the various parts of the body i.e. sternum, ventral surface, pronotum, and dorsal surface. This scoring method was similar to that used to quantify the amount of wax bloom on *Cauricara phalangium*, a Namib Desert tenebrionid with a partial wax bloom (McClain *et al.*, 1984).

The morphology of the wax bloom was determined using scanning electron microscopy (Gerneke and McClain, 1981). Ten individuals from each site were

collected, killed in ethyl acetate and prepared for detailed surface wax bloom examination. Routine sputter coating conditions often distorted the wax bloom so specimens were first viewed uncoated. The same specimens were then sputter coated under predetermined low heating conditions and viewed again.

The appearance of the dermal glands was observed by light and electron microscopy. Three *O. plana* showing characteristic wax bloom development were collected from each of the study sites. They were killed and narrow strips of dorsal elytra were fixed and processed for electron microscopy as previously described (Hanrahan *et al.*, 1984). Measurements of cell height and gland reservoir diameter were made on 1 μm thick plastic sections stained with 1% toluidine blue in borax. Medial sections were chosen from the series cut on the basis of the maximum reservoir diameter. Measurements from beetles from each site were pooled. Elytron thickness and number of cuticular layers were noted so that older beetles could be discarded. No attempt was made to evaluate glandular activity of the entire beetle surface at the microscopic level.

The reflectance properties of the cuticle were measured in the visible range (380–750 nm, in steps of 10 nm) according to a method developed by Kok and Boshoff (1973) and modified recently (McClain *et al.*, in preparation). The maximum wax bloom for these laboratory investigations, was developed by placing live individuals in an oven at 40°C for \pm three hours. This condition simulates the temperatures of the hot inland portion of the Namib, allowing dehydration of the beetles and maximal bloom development. They were then killed in ethyl acetate and mounted onto the back of an integrating sphere. All spectrophotometric measurements were automated (McClain *et al.*, in preparation). Care was taken to avoid abrading the bloom off the surface of the beetle, by handling them with forceps.

3 RESULTS

3.1 Formation of the wax bloom whorls

The wax bloom spread on the surface of *O. plana* was found to be correlated with the steep climatic gradient. Those individuals living along the coast where the temperatures are low and humidities high are black; while those individuals living in the eastern portion of the desert are blue (Plate 1). If present, a trace of the material appears only on the sternum on the undersurface (Figure 1). In contrast, beetles inhabiting hot inland areas where temperatures are high and humidities low are partially or completely covered. The wax bloom is on the ventral surface in all beetles scored from this area, the pronotum on the dorsal side and

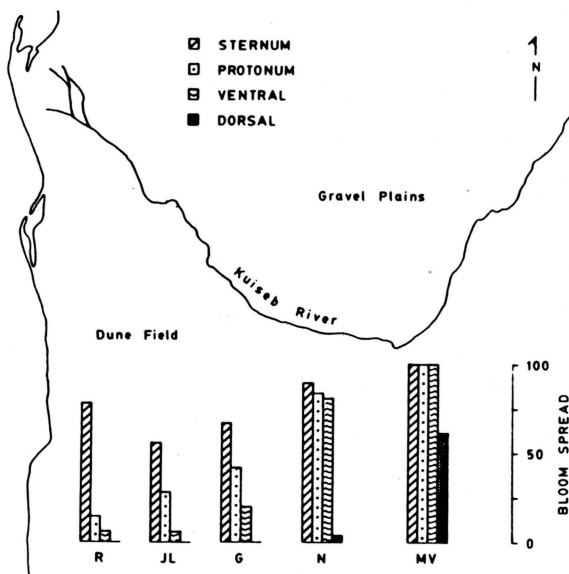


FIGURE 1: Location of wax bloom on *O. plana* across the climatic gradient. See text for explanation.

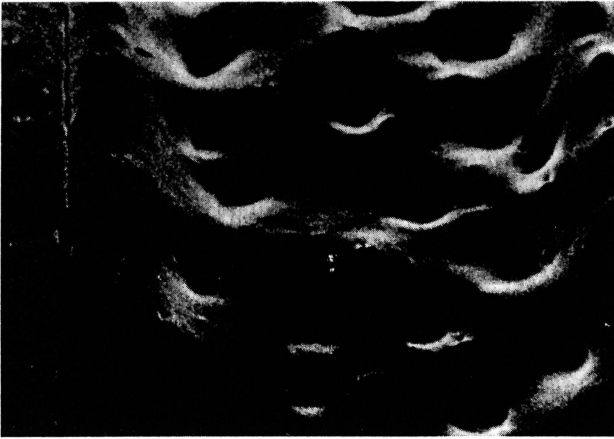


FIGURE 2: The dorsal surface of *O. plana* (50 X) living in the cool, foggy region of the Namib.

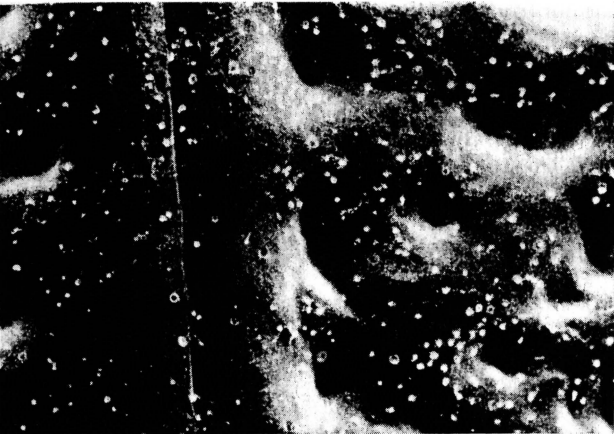


FIGURE 3: The dorsal surface of *O. plana* living in the hot inland area (50 X).



FIGURE 4: Elytra of *O. plana* showing whorls of wax bloom filaments from the hote inland area of the desert (1010 X).

in 66 out of 100 individuals the entire dorsal surface (Figures 1, McClain *et al.*, 1985).

The dorsal surface of the elytra from *O. plana* living in the cool coastal region is shiny and without any extracuticular material as seen with the electron microscope (Figure 2). The dorsal surface of *O. plana* living in the hot inland area is mottled with the way bloom material (Figure 3). This material appears as individual whorls which anastomose, creating a meshwork of fine tubular filaments on the cuticle (Figure 4). The material is exuded from the tips of dermal glands onto the surface.

3.2 Dermal glands and associated secretory cell activity

The beetles collected across the gradient appeared to be of similar age as could be judged from cuticle deposition in the elytron cross sections. *O. plana* collected from Rooibank and 'J' Line where cooler conditions prevail, were found to have dermal gland reservoirs which were full of secretory material but their associated cells indicated little or no secretory activity (Figure 5). These cells were flattened in shape, contained few organelles and were only slightly larger than the reservoir. The average cell height was 10 μm (Range 6,0 — 16,5; S.D. 4,7; $n = 12$) and the average reservoir diameter was 9,5 μm (Range 4,1 — 13,8; S.D. 2,9; $n = 12$). *O. plana* inhabiting areas from Gobabeb eastwards has secretory cells that showed marked synthetic activity with abundant endoplasmic reticulum and Golgi bodies present (Figure 6). These active cells were significantly larger than those described above. Average cell height from specimens collected at Gobabeb was 18,3 μm (Range 14,0 — 26,1; S.D. 3,4; $n = 10$) as were those collected from Noctivago (Range 12,1 — 25,6; S.D. 4,5; $n = 12$). The average reservoir diameter was 11 μm in both instances and was not sig-

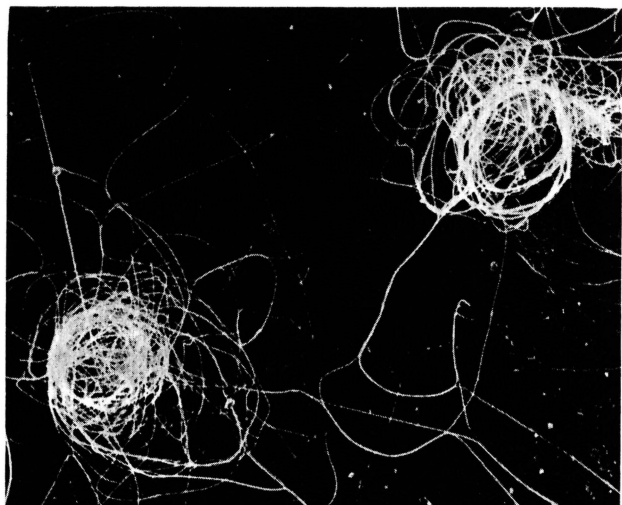


FIGURE 5: Dermal gland reservoir with secretory material but no secretory activity from coastal *O. plana* (7,500 X).

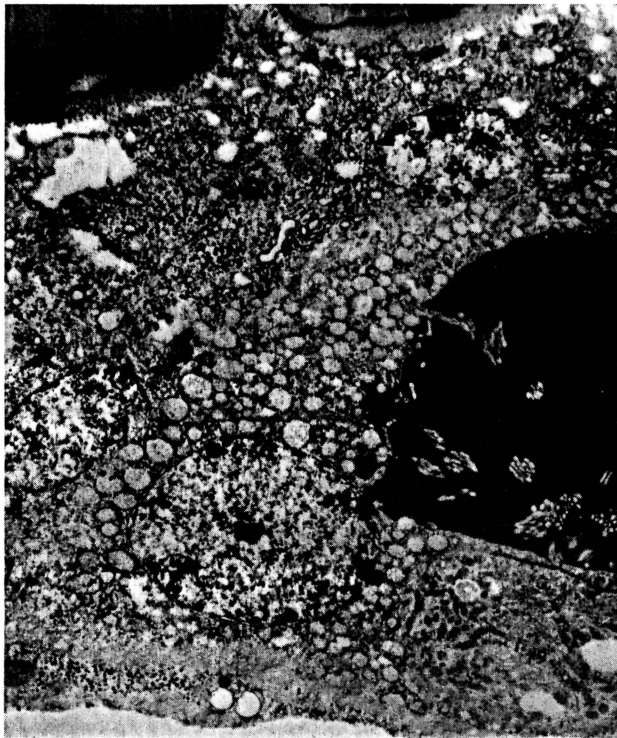


FIGURE 6: Dermal gland reservoir and active larger cell with marked synthetic activity from *O. plana* living inland (7,500 X). Cuticle marked with small arrow.

nificantly different from those mentioned above (Gobabeb range 6,4 — 20,4; S.D. 4,2; $n = 10$. Noctiva-go range 8,3 — 13,9; S.D. 2,0; $n = 12$). The beetles collected from Miss Checkies Vlei showed secretory cells that were slightly lower in height, averaging 16μ (range 14,1 — 22,9; S.D. 3,5; $n = 7$) and had reservoirs that averaged $7,7 \mu\text{m}$ in diameter (range 3,2 — 14,7; S.D. 4,0; $n = 7$). If cell heights from beetles collected at Rooibank were compared to those from Gobabeb they were found to be significantly different (t — test, $p < 001$). The range and standard deviation show that there was considerable variability between individual glands.

3.3 Reflectance properties of the cuticle surface

Reflectance values of the black cuticle surface without the wax bloom were very low. They varied from 3% to 4% throughout the visible spectrum (380 to 750 nm). However, increased reflectance was measured when the cuticle surface was covered with the wax bloom. Measurements taken from the dorsal surface indicated reflectance of approximately 21% at 380 nm which gradually declined to approximately 11% at 750 nm.

4 DISCUSSION

The amount and spread of wax bloom material on the surface of *O. plana* is a reflection of prevailing en-

vironmental conditions. This is clearly seen for individuals collected in a short time across the climatic gradient of the Central Namib. Similarly under controlled laboratory conditions high temperature and low humidity (hot inland area of the central Namib) regimes bring about the greatest wax bloom development and low temperature and high humidity regimes (cool, foggy area of the central Namib) the least (McClain, 1982). Furthermore desiccating environmental conditions are responsible for the wax bloom development on other tenebrionid beetles of the central Namib. There is an increased number of species having the wax bloom which are found in the hot inland dry desert (McClain, *et al.* 1985). The partial wax bloom of *Cauricara phalangium* which has been studied at Gobabeb in the alternate fog desert developed in response to elevated temperatures and low humidities (McClain *et al.* 1984).

The wax bloom patterns are species specific (Gerneke, personal communication). *O. plana* produces these circular areas of wax bloom which anastomose with neighbouring patches. These, in turn, create the surface coating that is maximally developed and covers those beetles living in the dryer regions. The morphology of this material dictates a meshwork of wax bloom filaments similar to that found in *Cryptoglossa verrucosa* a tenebrionid of the Sonoran desert. In this species the wax bloom functions to retard water loss across the cuticle surface (Hadley, 1979). A similar function is attributed to the wax bloom of *O. plana* (McClain, 1982).

There was a significant difference in cell size and presence of secretory organelles in those *O. plana* that live in the harsher regions of the Namib. The bloom has been shown to have a protein component (Hanrahan, *et al.* 1984). The presence of organelles such as rough endoplasmic reticulum which are primarily concerned with protein synthesis were to be expected in the active secretory cells. In the study of *C. phalangium* it was found that the ability to produce wax bloom declined with age. Although the glandular cells of *O. plana* from beetles collected at 'J' Line and Rooibank looked similar to those observed in older *C. phalangium* the lack of additional cuticular layers lining the blood space within the elytron indicated that the *O. plana* were young and of similar age to those collected from the other areas. Examples of quiescent secretory cells are known (Wigglesworth, 1972). Further microscopic studies are needed to demonstrate that the glands can in fact 'switch on' secretory activity and regenerate the appropriate organelles when the environment is hot and dry.

O. plana covered with the wax bloom had increased reflectance throughout the visible range. Reflectance of the cuticle surface has been measured in the field for *C. phalangium* (McClain, *et al.* 1984). Reflectance for the black portion of the cuticle was found to be two orders of magnitude lower than that of the white wax bloom area. This is similar to what was measured

for *O. plana* under laboratory conditions (Henwood, 1974, 1975a, 1975b). The increased reflectance would retard deleterious heating of the otherwise black cuticle surface and therefore play a role in the thermal balance of the beetle. Being a pedestrian insect and substrate dependent, the wax bloom could then play a role in retarding heat gain from direct short wave radiation. Though the major avenue of heat gain on the dunes is probably via re-radiated long wave radiation from the sand surface which is not affected by colour. The presence of the wax bloom may enable *O. plana* to stay active on the surface for longer periods ensuring high but not too high body temperatures and enabling the beetles to take advantage of the extra time when the wind is blowing and fresh food (in the form of detritus) is provided. *O. plana* is probably the fastest known pedestrian insect (Nicolson *et al.* 1984). It can cover great distances in the sand sea (Roer, 1971, 1975); moving from cooler regions to the hot dry areas. This dynamic wax bloom secretion may well help ensure its survival.

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