

# THE EYE OF THE TENEBRIONID *LEPISPILUS SULCICOLLIS* (COLEOPTERA) AND SOME ECOPHYSIOLOGICAL PREDICTIONS BASED ON EYE ANATOMY

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## ABSTRACT

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Ommatidial organisation in the tenebrionid beetle *Lepispilus sulcicollis* is described allowing conclusions to be drawn as to how the compound eye serves this beetle. The ecophysiological predictions are considered completely unbiased as the precise location and circumstance of capture of the specimens were not recorded. The eye is of the 'acone' type, has a 50-55  $\mu\text{m}$  thick cornea with well developed corneal cones and 150  $\mu\text{m}$  long ommatidia that are inclined to one another by an angle of ca. 4-5°. Each ommatidium possesses a 55  $\mu\text{m}$  long and ca. 6  $\mu\text{m}$  wide rhabdom that consists of an outer closed ring of 6 rhabdomeres and a central rhabdom component made up of microvilli of cells 7 and 8. The microvilli of the inner rhabdom component are aligned at right angles to those of retinula cells 3 and 6. This suggests that e-vector determination is possible and that the beetle is likely to have a need for the detection of the plane of polarised light. The rhabdom is more voluminous than that of comparable strictly diurnal species, but it does not reach the dimensions of totally nocturnal insects. The abundance of screening pigment grains, microtubules, and the shape-change of the cone cells accompanying dark/light adaptation all suggest that *L. sulcicollis* may well live in cryptic, dark habitats, but that it is well adapted to cope with a sudden exposure to sunlight. In terms of gross structural arrangement of the eye, there can be no doubt that *L. sulcicollis* conforms to the cucujiformia type.

KEYWORDS: ecophysiology - compound eye - Coleoptera (Tenebrionidae) - ultrastructure - Australia.

## INTRODUCTION

Photoreception in beetles has been the theme of numerous publications in the last two decades. While the majority of them - too many to list - simply provide descriptions of gross morphological organisation and ultrastructure of the eyes of individual species, others deal with physiological (Bennet 1967, Meyer-Rochow 1974, Meyer-Rochow & Horridge 1975, Horridge *et al.* 1979), optical (Seitz 1969, Meyer-Rochow 1973, Meyer-Rochow & Horridge 1975, Caveney & McIntyre 1981), or behavioural aspects (Frantsevich *et al.* 1971 a, b, Meyer-Rochow & Horridge 1975, Frantsevich *et al.*

1977). In only a few papers so far has the emphasis been on the relationship between activity, phylogeny, and eye anatomy, but there is now sufficient background information, at least in some taxa, to make this task a meaningful operation, e.g. Scarabaeidae (Horridge & Giddings 1971, Meyer-Rochow 1978, Caveney 1986, Gokan *et al.* 1988a) and Cucujoidea (Wachmann 1977, 1979, Gokan & Hosobuchi 1979, Schmitt *et al.* 1982).

The family Tenebrionidae is one of the largest of the Coleoptera generally, and of the Cucujiformes in particular. Though relatively few studies have been concerned with eyes and vision of tenebrionid beetles (Wada & Schneider

1968, Götz & Gambke 1968, Yinon & Auerbach 1970, Varju 1987, Meyer-Rochow & Gokan 1988), the family is of interest because of the very large number of xerophilic species, and the smaller number of economically important attackers of stored food products.

If it should, indeed, be possible to correctly predict aspects of life style and general biology from an investigation of eye morphology and ultrastructure, this could considerably facilitate our ecological understanding of species which cannot be observed easily or collected on a regular basis and have remained poorly understood because they occur in remote countries or inaccessible places.

**MATERIALS AND METHODS**

Beetles, later identified by Dr E. B. Britton (C.S.I.R.O., Division of Entomology, Black Mountain, Canberra, Australia), were collected by students for comparative studies of beetle eyes near Eden, New South Wales (Australia) in December. The fact that the circumstances of capture were not recorded allows us to make an unbiased prediction on this species' eye function based on anatomy and ultrastructure alone. As a matter of fact, virtually no information whatsoever is available on this species' general ecology, and any hint that could come from a study of eye structure is of considerable value (see the discussion in this paper).

Dark- as well as light-adapted insects were routinely decapitated, and the isolated eyes were prefixed in a mixture of 7.5 ml Karnovsky's (1965) fixative, 5 ml Cacodylate buffer adjusted to a pH-6.8 and 12.5 ml aqua dest. for 4 days. The specimens were then washed in half strength buffer and postfixed for 30 min in equal parts of buffer and 2% OsO<sub>4</sub>. Sections in araldite were double stained with uranyl acetate and lead citrate. The electron microscopes used in this examination were a Jeol 100CX and an Akashi LEM2000.

**RESULTS**

**DIOPTRIC SYSTEM**

The dioptric system of the eye of *Lepispilus sulcicollis* consists of a 50-55 µm thick multi-layered,

transparent cornea and an ca. 18 µm long and 16 µm wide cone of the 'acone type' (Grenacher 1879) made up to equal parts by 4 cone cells. Together cornea and cone layer occupy ca. 45% of the length of one ommatidium, which is about 150 µm (Fig. 1).

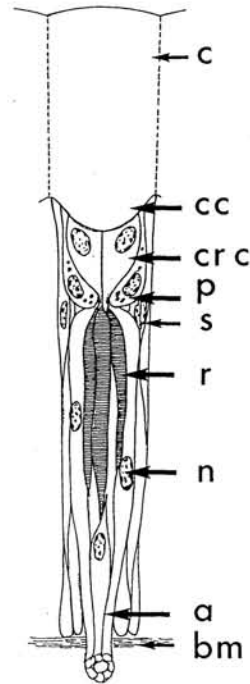


Figure 1. Semischematic drawing of the ommatidial organisation in a light-adapted longitudinally sectioned eye. Abbreviations used: C = cornea; CC = corneal cone; CrC = crystalline cone cells; P = primary (or principal) screening pigment cells; S = secondary screening pigment cells; R = rhabdom; N = nucleus; A = axons; BM = basement membrane.

Externally, the radius of curvature of the cornea is 50 µm; the inner surface is more strongly curved and has a radius of curvature of around 14 µm (Fig. 2). Directly under the corneal cone in the distal one third of the cone the rather electron translucent nuclei of the 4 cone cells are to be found (Figs. 5 & 6). The cone cells are densely crowded with longitudinally oriented microtubules of 20 nm diameter

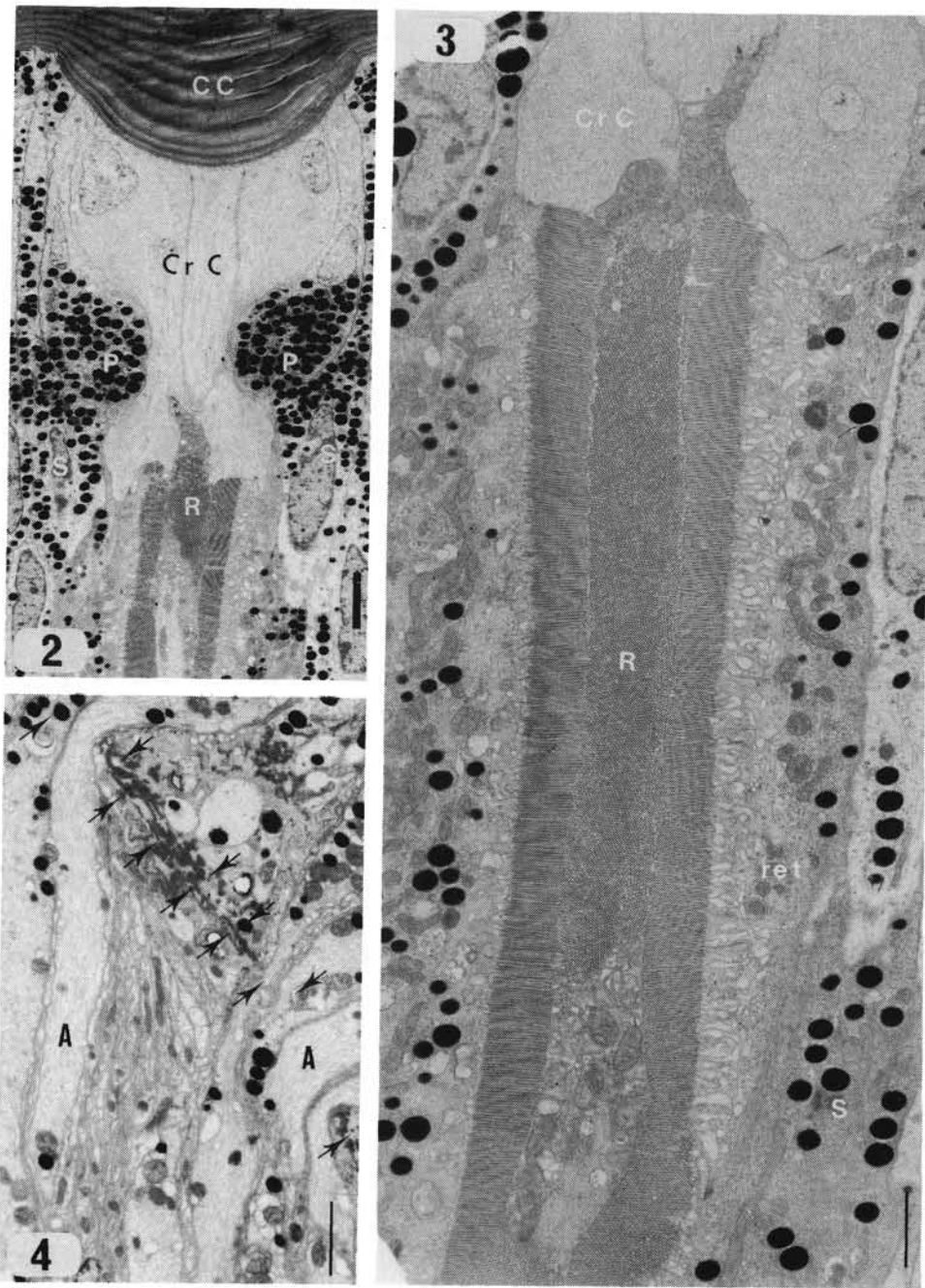


Figure 2. Electron micrograph of the distal end of a partially dark-adapted ommatidium, showing inward projecting corneal cone (CC), hourglass-shaped crystalline cone cells (CrC), the two principal (P) and numerous secondary screening pigment cells (S) as well as the rhabdom (R). The scale is 4  $\mu$ m.

Figure 3. Electron micrograph of longitudinal section through the rhabdom (R) and retinula cells (ret). Distally the crystalline cone cells (CrC) are visible, while all along the edge of the rhabdom, cisternae of a loosely organized endoplasmic reticulum are conspicuous. Isolation between neighbouring ommatidia is provided by secondary pigment cells (S). The scale is 2  $\mu$ m.

Figure 4. Proximally, retinula cell processes turn into axons (A) containing neurotubules and pigment grains to a level well below the basement membrane (marked by arrows). The scale is 2  $\mu$ m.

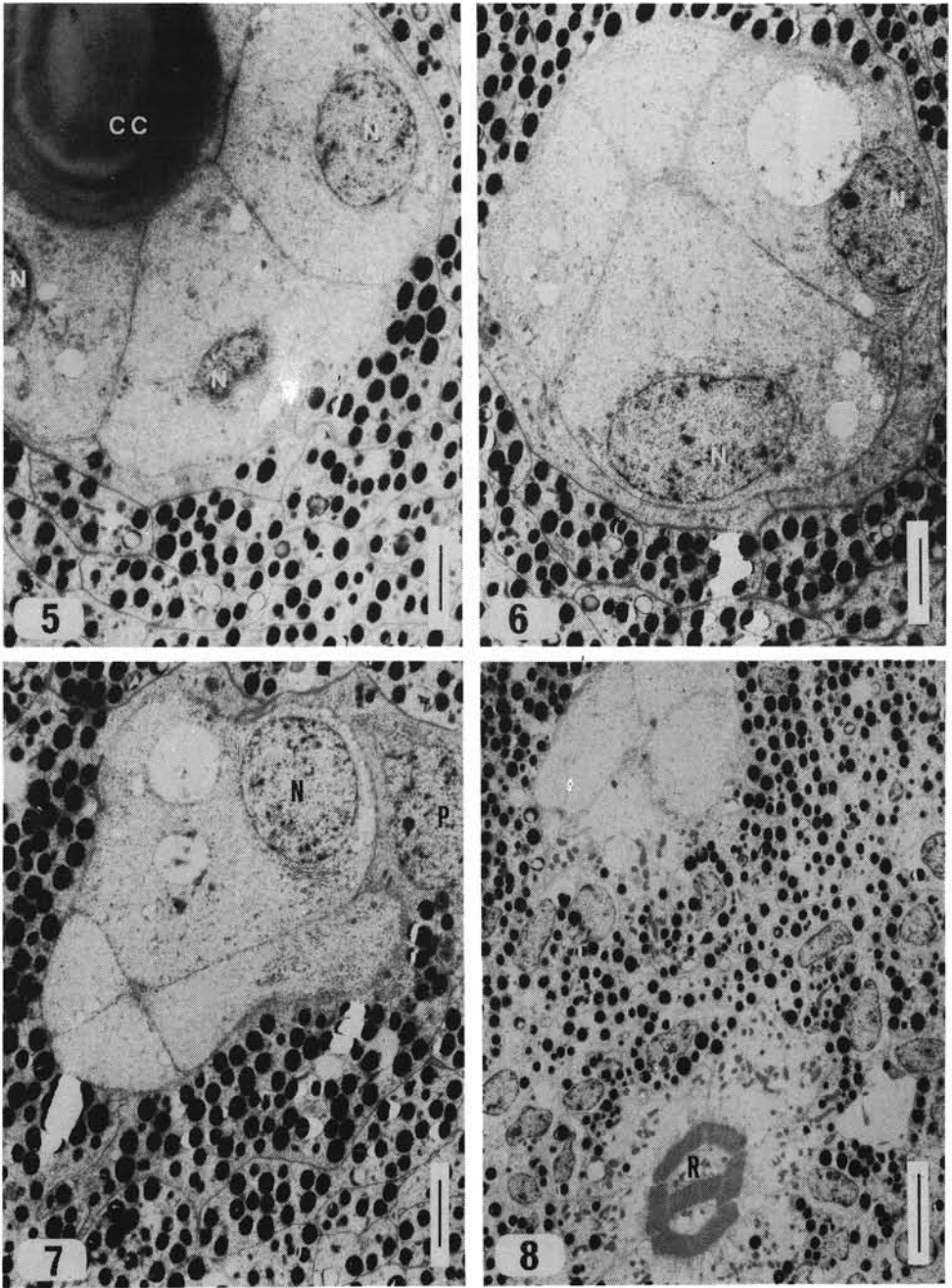


Figure 5. Crystalline cone cell nuclei (N) are located distally just below the corneal cone (CC). The scale is 2  $\mu$ m.  
Figure 6. Slightly lower down (= further into the eye) the four crystalline cone cells are surrounded by primary and secondary screening pigment cells. The scale is 2  $\mu$ m.  
Figure 7. Pigment grains of the principal (or primary) screening pigment cells are somewhat larger than those of the secondary screening pigment cells. The nuclei of the primary screening pigment cells (P) occupy the narrow waist-region of the cone cells (see diagram of Fig. 1). The scale is 2  $\mu$ m.  
Figure 8. Rhabdoms (R) are of the 'open' type, and consist of an outer ring of 6 rhabdomeres and an inner rhabdom that is made up of 2 interlacing retinula cells with microvilli running in the same direction. The scale is 3  $\mu$ m.



(Figs. 2 & 6). In the light-adapted condition the cones taper proximally to a 1.5-2  $\mu\text{m}$  narrow light funnel. In a partially dark-adapted eye the combined formation of the 4 cone cells takes on hourglass shape with the narrowest neck-portion being tightly enveloped by the somata of the two primary screening pigment cells (Fig. 2). The latter contain dark, strongly electron opaque, spherical granules of 0.65  $\mu\text{m}$  in diameter. The primary pigment cells which also contain microtubules, are surrounded by an undetermined but relatively large number (ca. 10-16) of secondary screening pigment cells (Figs. 6, 7 & 8). The pigment grains of the latter possess slightly smaller diameters than those of the primary screening pigment cells (0.55  $\mu\text{m}$ ,  $n = 10$  versus 0.65  $\mu\text{m}$ ,  $n = 10$ ).

#### RETICULA CELLS AND RHABDOM

The rhabdom commences just below the crystalline cone (Fig. 3), and in cross section resembles the Greek letter 'theta'. The outer ring of rhabdomeres is made up by retinula cells numbers 1-6 (Figs. 10, 11 & 12), though on one occasion seven cells were counted (Fig. 9). The diameter of the rhabdom in cross section, measured across the outer edge of the ring-forming rhabdomeres, is ca. 6  $\mu\text{m}$  over its entire distal-proximal extension of about 55  $\mu\text{m}$  (Fig. 3). Individual microvilli of the outer rhabdomeres measure ca. 1.8  $\mu\text{m}$  in length and 0.080  $\mu\text{m}$  in diameter. The microvilli of the bar- or wall-like inner two rhabdomeres are always aligned in parallel with each other, but perpendicular to those of retinula cells numbers 3 and 6 (Figs. 10, 11 & 12). They measure 1.3  $\mu\text{m}$  in length and 0.076  $\mu\text{m}$  in diameter.

More proximally, retinula cells numbers 1, 2, 4 and 5 lose their rhabdomeres and become peripherally 'squeezed out' of the cluster of rhabdom-forming retinula cells. Of the original ring of outer photoreceptor cells only retinula cells numbers 3 and 6 remain in contact with the rhabdom until ca. 25  $\mu\text{m}$  above the basement membrane, when they too lose their rhabdomeres. From then on only the bar- or wall-like central rhabdom made up of the rhabdomeres of retinula cells numbers 7 and 8 remains (Fig. 12).

Neighbouring retinula cells are held together

by desmosomes that are developed between adjacent membranes ca. 1  $\mu\text{m}$  out from the edge of the rhabdom (Figs. 9 & 10). All the peripheral as well as the central retinula cells contain a variety of organelles in their cytoplasm. These include spherical electron-opaque screening pigment granules with a mean diameter of 0.7  $\mu\text{m}$ , mitochondria, endoplasmic reticulum, vacuoles, and microtubules (the latter prominent as neurotubules in the bundle of retinula cell axons penetrating the basement membrane (Fig. 4)). Retinula cell nuclei, which are about twice as voluminous as those of the secondary or supporting cells, do not occur at a particular and clearly defined level in the eye, but are instead distributed over a ca. 20  $\mu\text{m}$  longitudinal range within the proximal half of the ommatidium (Fig. 12). A tapetum of tracheoles above or below the basement membrane is not developed, and evidence for a redistribution of axon pathways as in the neural superposition eye of the fly with its lamina cartridges (Braitenberg 1967), or the formation of pseudo-cartridges with axons from several different ommatidia as in the rock lobster eye (Meyer-Rochow 1975) is not apparent in the eye of *L. sulcicollis*. A glial encapsulation appears to prevent contact between neighbouring axon bundles (Fig. 13).

#### DISCUSSION

Wachmann (1977), based on his very thorough study of the rhabdom ultrastructure of more than 70 species of beetles from about 20 families, has convincingly advocated that the open rhabdomeric organisation is a synapomorphic feature of the Cucujiformia, and that this taxon is monophyletic. Wachmann (1979) further concluded that the most archaic and perhaps original cucujiform rhabdom type still occurs in most chrysomelids and curculionids, in many cerambycids and in some Cleroidea and Cucujoidea, and conforms to his 'Grundmuster 1' in which the more or less closed outer ring of 6 rhabdomeres is nowhere in direct contact with the microvilli of the two central retinula cells over their entire length. In his 'Grundmuster 2', which would be applicable to *L. sulcicollis*, the peripheral rhabdom may communicate with the central rhabdomeres via the rhabdomeres of the

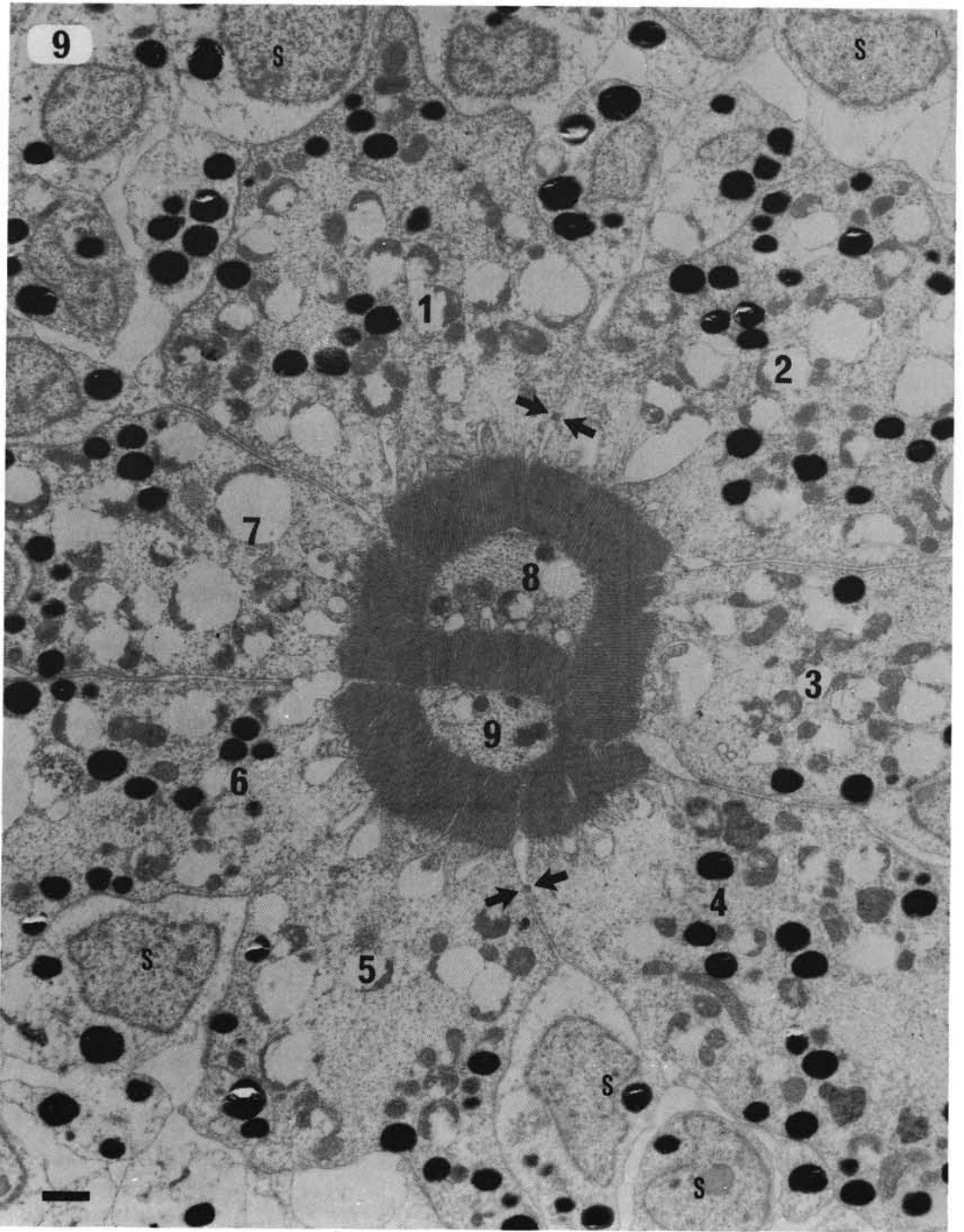


Figure 9. An ommatidium with an additional retinula cell: instead of 6 outer retinula cells there are seven here, but the shape of the rhabdom is the same as in other ommatidia. Desmosomes, identifiable as localised electron opaque membrane thickenings (arrows), hold adjacent retinula cells together. Secondary screening pigment cells (S) provide a physical and optical buffer between neighbouring ommatidial groups of retinula cells. The scale is 1  $\mu$ m.

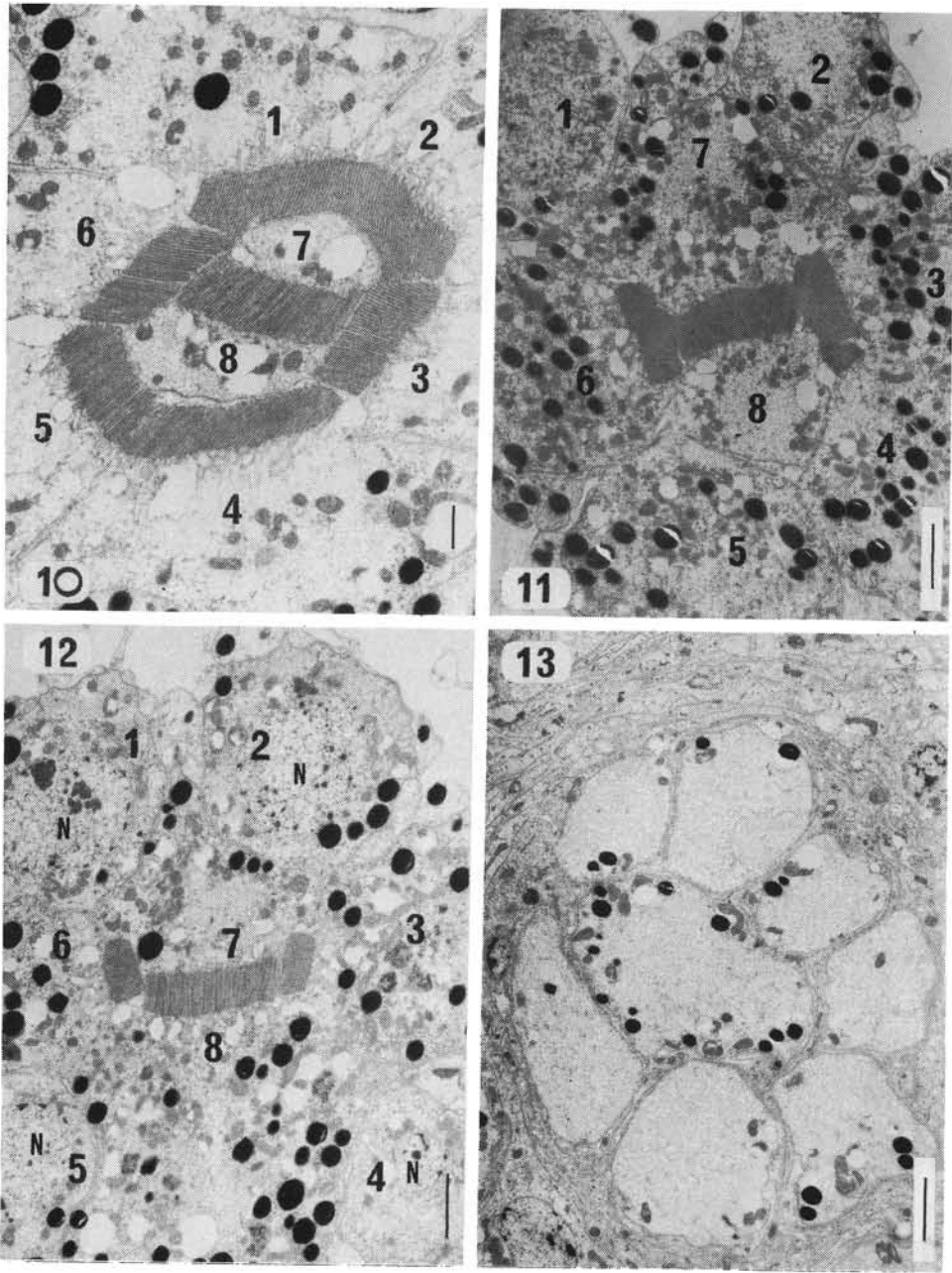


Figure 10. Microvilli are basically aligned in 2 orthogonal directions and the central two retinula cells contain numerous microtubules. The scale is 1  $\mu$ m.

Figure 11. Further proximally, rhabdomeres 1, 2, 4 and 5 disappear so that only a dumbbell shaped rhabdom with microvilli of cells 3 and 6, and 7 and 8 in two orthogonal directions remains. At this level all retinula cells are crowded with screening pigment granules and mitochondria. The scale is 2  $\mu$ m.

Figure 12. Even more proximally, retinula cells 1, 2, 4 and 5 begin to occupy peripheral positions with their nuclei (N) visible. The scale is 2  $\mu$ m.

Figure 13. Bundles of 8 axons, penetrating the basement membrane and containing dense aggregations of neurotubules as well as some pigment grains, represent the proximal projections of the retinula cells. The scale is 2  $\mu$ m.

two outer retinula cells numbers 1 and 4 in Wachmann (1979) and numbers 3 and 6 in this paper. Wachmann (1979) believes that Grundmuster 2 could have arisen several times independently in different groups because of certain functional advantages of that type: the lateral anchoring of the central rhabdomeres increases stabilisation and reduces the risk of longitudinal rhabdom twist. Grundmuster 2, according to Wachmann (1979) has the added advantages of being able to evolve into a completely fused rhabdom, of being able to modify microvillar directions in response to ecophysiological selective pressures, and of being able to develop a system of lateral polarization filters for e-vector determination.

Although at first glance it is hard to see what possible advantage an apposition eye with an open rhabdom could have had over one with a fused type in terms of visual sensitivity, it is self-evident that to maintain massive amounts of photoreceptive membrane within the frame of a fused rhabdom, even under conditions of abundant light, would be an energetically costly luxury, which selective pressure would work against. Open rhabdoms, irrespective of whether they employ neural superposition (Diptera: Braitenberg 1967) or not (Ioannides & Horridge 1975, Wachmann 1977, Meyer-Rochow & Juberthie-Jupeau 1983) are therefore advantageous for either diurnally active insects or species for which visual sensitivity is not the most important sensory modality. This does not rule out the possibility that certain insects, originally possessing an open rhabdom, secondarily became crepuscular, nocturnal, or even cavernicolous (Meyer-Rochow & Waldvogel 1979) in habit, with consequences in terms of anatomical and optical modifications to the eyes and photoreceptive cell make-up.

Amongst the cucujiform beetles the basic eye scheme of an acone apposition eye with an open rhabdom had to serve species that widely radiated within the available ecological spectrum and produced terrestrial as well as aquatic, diurnal as well as nocturnal, and phytophagous as well as carnivorous forms. The eye structure of *L. sulcicollis* agrees with that of the cucujiform Grundmuster 2 suggesting a diurnally active ancestor. Yet at the same time, the irregularities

terms of retinula cell numbers per ommatidium found in it (for summary of possible abnormalities see Meyer-Rochow 1972) prove that it cannot be a high performance photoreceptor, for that requires a high degree of structural order (Snyder *et al.* 1977, Rossel 1979). In many ways the eye of *L. sulcicollis* bears a resemblance to the eyes of several species of cerambycids, many of which are nocturnal. As a matter of fact the *Lepispilus* eye displays anatomical features which are indicative of both diurnal and nocturnal activities. Since it is notoriously difficult to conclude which evolutionary direction a photoreceptor organ takes (Meyer-Rochow 1978) it seems more appropriate to simply list and discuss the features that are seen as adaptations to a dimly or brightly lit environment.

The acone nature of the eye, the lack of both a tapetum and a clear-zone between dioptric structures and retina, and the open type rhabdom are all indications that this eye is, at least originally, in terms of its light-gathering capacity inferior to that of many nocturnal scarabaeid beetles (Meyer-Rochow & Horridge 1975, Gokan *et al.* 1988b). The rather thick cornea could indicate a mechanical protective function, because of poor visual resolution of the eye (Meyer-Rochow 1973) or an optical protection against strong radiation (Gokan & Meyer-Rochow 1984). The well-developed corneal cone is reminiscent of that in *Anoplognathus pallidicollis* (Meyer-Rochow & Horridge 1975) and could thus be interpreted as an adaptation to improve photon capture. The constant width of the rhabdom over at least 75% of its total length, however, is more in line with a diurnal species, especially when we compare it with the rhabdoms of diurnal and nocturnal cerambycid species, e.g. *Cerambyx scopolii* and *C. cerdo* (Wachmann 1979). The width of the rhabdom ring and the cross sectional diameter of the rhabdom are considerably larger than corresponding values for dipteran flies (Wada 1974, Eguchi & Ookoshi 1981) or the diurnal beetle *Curis caloptera* (Gokan & Meyer-Rochow 1984). On the other hand, the rhabdom is very much less voluminous than that of the nocturnal beach sand tenebrionid *Chaerodes trachyscelides*, a species of 7 mm body length, whose rhabdoms measure 20-25  $\mu\text{m}$  in diameter (Meyer-Rochow



& Gokan 1988).

The abundant screening pigment found in all retinula cells, including the central two 7 and 8, right down into the axons, signifies the need for protection from damaging or strong radiation. The regular, parallel alignment of the rhabdom microvilli which results in preferential responses to the e-vector of light (Waterman 1981), shows that the eye can afford to sacrifice some sensitivity, possibly in exchange for some improvement in polarisation sensitivity. The strictly parallel orientation of the microvilli of retinula cells 7 and 8, which are sandwiched on their short sides by the perpendicularly aligned microvilli of cells 3 and 6, points in the same direction, and suggests that there is some need for the detection of the plane of polarised light, which could only be during the day.

Perhaps the strongest arguments that the apposition eye of *Lepispilus sulcicollis* can adapt to a range of light intensities come from the configuration of the light- and partially dark-adapted cones in longitudinal section. An hour-glass shaped cone cell tract in the partially dark-adapted eye has been reported from the apposition eye of the nocturnal ant *Camponotus irritans* (Menzi 1987), the staphylinid carcass beetle *Creophilus erythrocephalus* (Meyer-Rochow 1972), the bark beetle *Xyleborus ferrugineus*, (Chu *et al.* 1975) the tenebrionid flour beetle *Tenebrio molitor* (Wada & Schneider 1968) and the nocturnal beach sand beetle *Chaerodes trachyscelides* (Meyer-Rochow & Gokan 1988). All of these species inhabit rather dark environments, but have a photoreceptor that primarily serves insects which are active under brighter conditions. The cellular machinery for the retinomotoric responses appears to reside with the microtubules, which are particularly abundant in cells and cell regions which are subject to change and deformation. Clearly, in comparison to the tenebrionids *Tenebrio molitor* and *Chaerodes trachyscelides* which have voluminous rhabdoms, *L. sulcicollis* is least suitably adapted to a dimly lit environment.

Although we would certainly not expect *L. sulcicollis* to be as diurnal as the bumblebee, for example, which has a flicker fusion frequency (FFF) of ca. 130 Hz, (Meyer-Rochow 1981) we can safely assume that *L. sulcicollis* is less noc-

turnal or cryptic than *Tenebrio molitor*, and, therefore should have a flicker fusion frequency that is greater than that of *Tenebrio* (41 Hz, Campan 1970 which is similar to that of the house cricket *Acheta domestica*, whose FFF is also 41 Hz, Campan 1970) and probably lies in the vicinity of 80 Hz (the FFF of the crepuscular *Amphimallion solstitialis* for example, is 83 Hz, Campan 1970). The resolving power of the *Tenebrio* eye has been determined as  $6.5^\circ$  and  $7^\circ$  by experimental and anatomical measurements respectively (Götz & Gambke 1968). Since the eye of *L. sulcicollis* has interommatidial angles of around  $4-5^\circ$  it should, on that basis alone, be capable of resolving finer detail than *Tenebrio*, but structural irregularities would disallow the theoretical limits of acuity to be reached.

Several insects of grain and stored products, including the tenebrionid *Tenebrio molitor*, have been shown to possess one large sensitivity peak in the green part of the visual spectrum at around 520-530 nm wavelength, a minimum at about 400 nm, and rising sensitivity towards the shorter (=ultraviolet) end of the visual spectrum at 350 nm (Yinon & Auerbach 1970). Only in the strictly nocturnal beach sand beetle *Chaerodes trachyscelides* was this trend not confirmed. For *L. sulcicollis* there is no reason to believe that there are not at least two spectral sensitivity peaks, one to ultraviolet and one to green light.

Unfortunately, virtually nothing at all is known about the natural history of *Lepispilus*. Larvae have been found in logs of gum trees (Watt 1974) and according to J. F. Lawrence (in litt.) other specimens have turned up in litter, and adults have been collected in a flight-intercept trap in the Brindabella Range just outside Canberra (Australia), but at what time of day they are most active is unknown. *Lepispilus* belongs to the tribe of Cyphaleini and, "at least some of its relatives are very brightly coloured" (J. F. Lawrence, in litt.), suggesting that our conclusion that the eye belongs to a diurnal species that secondarily occupies dark places is not too far off the mark.

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