

**ALBINISM AND EYE STRUCTURE IN AN AUSTRALIAN  
SCORPION, *URODACUS YASCHENKOI*  
(SCORPIONES, SCORPIONIDAE)**

**N. A. Locket**

Department of Anatomy and Histology  
University of Adelaide  
Box 498, G.P.O.  
Adelaide  
South Australia 5001

**ABSTRACT**

Two albino individuals of *Urodacus yaschenkoi* (Birula 1903) were caught among a normally pigmented population in South Australia. These are illustrated and discussed.

Microscopy of the eyes shows that the melanin granules normally present in the epidermis and in the retina are represented by non-pigmented premelanosomes. Though the components of the eye are all present, the rhabdoms are abnormal, consisting of reduced and disorganised microvilli. The phaospheres, present in retinula cells, are also abnormal. The nature of the defects and their possible consequence are discussed.

**INTRODUCTION**

Albinism, a specific lack of melanin pigment, is well known in a wide variety of animals, including crabs, isopods and insects, but does not appear to have been recorded in scorpions. The occurrence of depigmented arthropods, including scorpions, is well known, most of them recorded from caves which provide a totally dark environment in their depths. Commonly the pallor is associated with the loss of eyes: Mitchell (1968, 1972) described the troglobite genus *Typhlochactas*, eyeless pale scorpions from caves in Mexico, and Mitchell and Peck (1977) later described another species of this genus, also pale and without eyes, but from forest litter, not a cave. Francke (1977, 1978) has described troglobite, i.e. obligate cave-dwelling, scorpions belonging to the family Diplocentridae. One of these, *Diplocentrus anophthalmus*, is pale and has no eyes. The other two species appear less extreme; *D. mitchelli* has minimal pigmentation and markedly reduced eyes, but *D. cueva* has only slightly reduced pigment and small median eyes; the lateral eyes are described as equal to related epigeic examples of *Diplocentrus*.

The eye structure of scorpions has been the subject of a number of studies, from the early work of Lankester and Bourne (1883), Parker (1891), and Scheuring (1913) to the electron microscope studies of Bedini (1967), Belmonte and Stensaas (1975), Fleissner and Schliwa (1977), and Schliwa and Fleissner

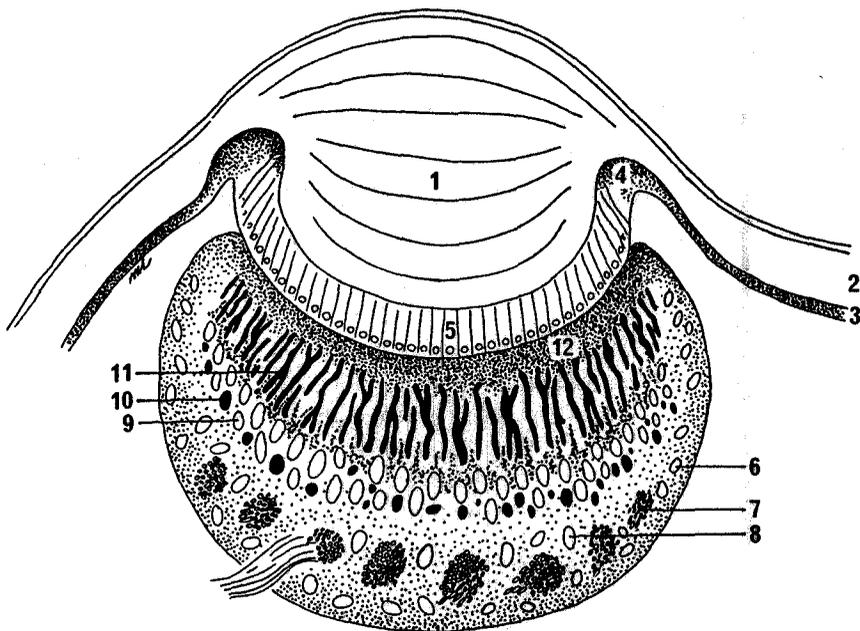


Fig. 1.—Diagram of scorpion median eye. Lens, 1, is a thickening of cuticle, 2. Epidermis, 3, contains pigment which extends to limbus 4. Modified epidermal cells form transparent vitreous, 5. Deep portion of retina contains pigment cells, 6, nerve fibre bundles, 7, and bodies of arhabdomeric cells, 8. Retinula cell nuclei, 9, and phaospheres, 10, are deep to rhabdoms, 11. In light-adapted condition rhabdoms are shielded by pigment, 12.

(1979, 1980). It was early recognised that the structure is different in the median and lateral eyes; only the former will be considered in the present paper.

The median eyes (diagram, Fig. 1) occur close to each other on either side of an ocular tubercle approximately in the middle of the carapace. They have a single lens, derived from and continuous with the cuticle. Between lens and retina, in the median but not the lateral eyes, is a layer of cells called the vitreous or lentigen by various authors. This layer, continuous with the epidermis at the edge of the eye, does not contain melanin granules, but the surrounding epidermis, and particularly the cells at what may be called, by analogy with vertebrate eyes, the limbus, are packed with these granules.

Separating the vitreous from the retina is a preretinal membrane, apparently of cuticular origin, and continuous with a postretinal membrane of similar structure.

The retina thus enclosed contains three classes of cells. The deep aspect of the retina is lined by pigment cells, with flattened nuclei disposed parallel to the postretinal membrane and packed with melanin granules. Interstitial pigment cells occur within the retina at the level of the retinula cell nuclei. Between the outer pigment cells and the bases of the retinula cells are the arhabdomeric cells described by Schliwa and Fleissner (1979). The retinula cells, which show regional specialisation, occupy most of the thickness of the retina. From their basal aspects arise the nerve fibres, which form bundles amongst the pigment cells before they penetrate the postretinal membrane and form the optic nerve. Further details of retinal structure are given under Results.

The chance finding of two scorpions lacking the normal pigmentation in and around the eye, and elsewhere in the body, and thus presumably albinos,

suggested that a comparison of their eyes with the normal might be of interest. This account is now presented.

## MATERIALS AND METHODS

The two individuals now reported were caught in an area of scrub near Berri in the Riverland of South Australia. The burrow mouths, which have a characteristic appearance (Shorthouse 1971), were identified, and a plastic vending machine cup buried so that its lip was level with the floor of the mouth of the burrow. The trapped burrows were marked, and revisited about 1.5h after sunset, when many scorpions had emerged from their burrows and fallen into the cups. When the catch was inspected later indoors, it was noticed that two specimens lacked the normal pigmentation. No other albinos have been caught in previous or subsequent trapping in the same area. One albino was kept in the laboratory for several months, during which time it was fed mealworms and other insects. It showed no behavioural differences from normal examples. Measurements of hand length and carapace plus first five metasomal segments were made on this specimen following Shorthouse (1971), and it falls into Shorthouse's group C, i.e. fourth instar.

The second albino, of similar size, was killed and pieces of tissue, including the eyes, were fixed for electron microscopy in 2% paraformaldehyde and 2.5% glutaraldehyde in 0.1M phosphate buffer, pH 7.3. The tissue was fixed for 2h, postfixed in 1% osmium tetroxide in 0.1M phosphate, dehydrated through an ethanol series and taken through propylene oxide to Araldite, in which it was embedded.

Sections along and perpendicular to the optic axis were cut for light and electron microscopy on a Cambridge Huxley ultramicrotome, using glass knives. Sections for light microscopy were cut at 1  $\mu\text{m}$ , stained with methylene blue/azure II followed by basic fuchsin/borax, and mounted in immersion oil. Thin sections were stained with alcoholic uranyl acetate followed by Reynolds' (1963) lead citrate, and examined in a JEOL 100c electron microscope.

Sections of the eye of a normal scorpion, of the same size and from the same locality, were prepared as a control. Experiments showed that a primary fixative containing 0.5g sucrose/100 ml gave improved fixation, and this was used for the control tissue.

## RESULTS

**General appearance.**—Normal specimens of *Urodacus yaschenkoi* (Birula, 1903) (Fig. 2), are predominantly buff to pale brown. The mesosoma appears darker and somewhat grey owing to the dark coloured viscera beneath the cuticle. The aculeus, leg joints and tarsal claws, and the fingers of the chelae and chelicerae are reddish to dark brown due to dense sclerotization. The fifth metasomal segment and vesicle, and the eyes and their surrounds, are dark brown to black due to pigmentation.

The albinos (Fig. 3) differed from the normal in the pallor of the metasoma and vesicle, and complete absence of pigment from the eyes and their surrounds. The mesosoma showed some of the normal darkness, but was noticeably paler

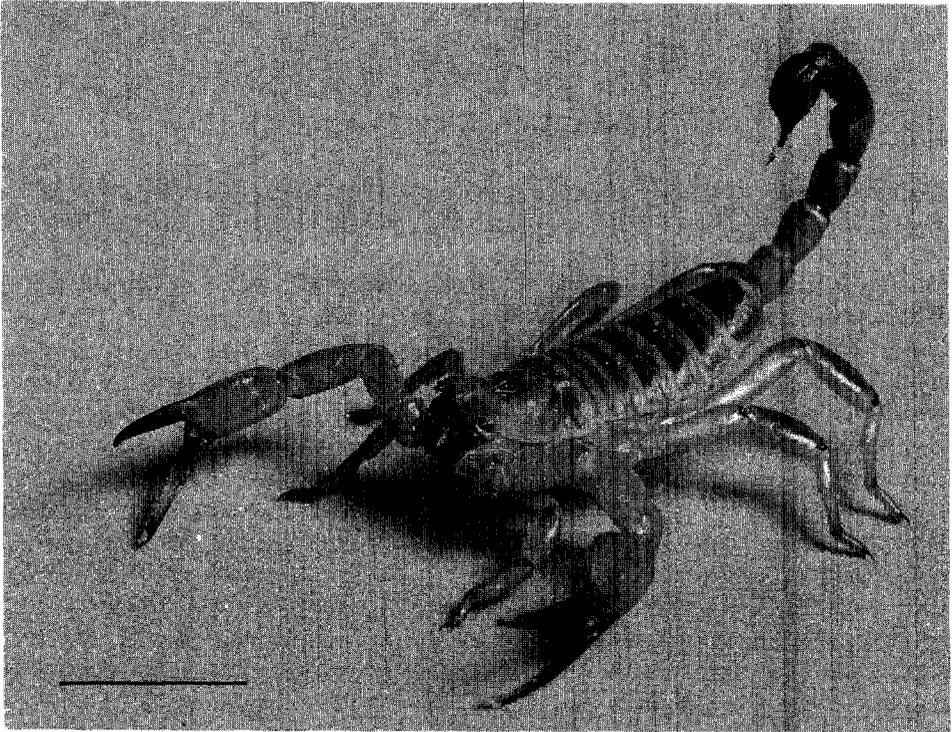


Fig. 2.—*Urodacus yaschenkoi*, normal. The darkness of chelae and fingers, aculeus, tarsal claws and leg joints is due to dark sclerotization whereas that of eyes and surrounds, vesicle and metasomal segments is caused by pigmentation. Scale = 10 mm.

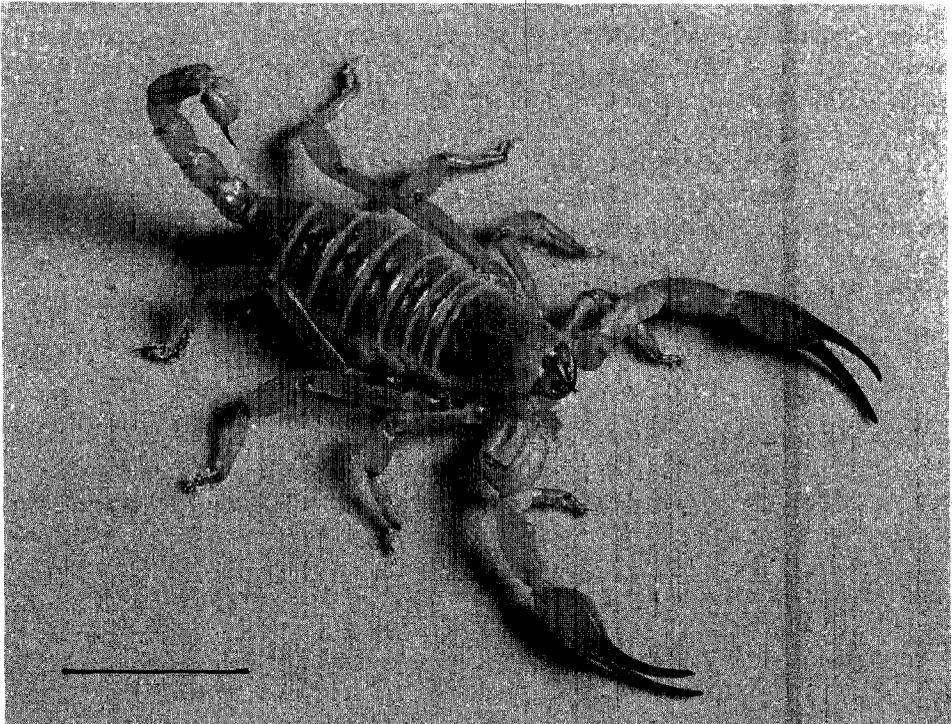


Fig. 3.—*Urodacus yaschenkoi*, albino. Sclerotized parts resemble normal, but eyes, vesicle and metasomal segments lack pigment. Scale = 10 mm.

than the normal. Those parts that are normally dark due to sclerotization were no less so than in the normal scorpion.

**Eye structure.**—The structure of the median eyes accords well with the descriptions given by Bedini (1967), Fleissner and Schliwa (1977), Fleissner and Siegler (1978) and Fleissner and Heinrichs (1982) and summarised in the Introduction. Sections show that the overall architecture is the same in the normal and albino, Figs. 4, 5. The cuticular lens has the same configuration, and stains similarly. The columnar vitreous cells, with basal nuclei, are of similar shape and size, and were transparent in both. The epidermis surrounding and up to the limbus in the normal contain numerous pigment granules. These granules are represented in the albino, but are not pigmented. They appear the same as those in the retina, described below. The preretinal membrane, situated at the junction of retina and vitreous, and the postretinal continuation of this membrane, called the sclera by Bedini (1967), are well developed in both.

The retina contains the populations of cells outlined in the Introduction. The normal retina (Fig. 4) has a layer of densely pigmented cells lining the eye cup beneath the postretinal membrane, and extending to the limbus, where they lie close to the pigmented epidermal cells. These cells have somewhat flattened densely staining nuclei and their cytoplasm is packed with pigment granules. Electron microscopy shows these as dense granules, in at least some cases clearly membrane-bound (Fig. 12).

The 'pigment' cells are also present in the albino (Fig. 5) in which the disposition of their nuclei is better seen than the normal, due to the absence of pigment. Where the normal has melanin granules, the albino has an equal or greater density of granules, but these are unpigmented. These granules are membrane bound and have a finely granular content; some contain bars or rings with a paracrystalline appearance. Similar granules occur among the melanin granules in the normal, and they are considered to be premelanosomes, (Fig. 13).

A second population of pigment cells is present in the normal, interspersed with the retinula cells in the substance of the retina. These cells have nuclei at the same level as those of the retinula cells, and their perinuclear cytoplasm is densely packed with melanin granules. They have processes that extend vitreally between the retinula cells, and which also contain pigment granules. Corresponding cells have not been identified with certainty in the albino.

Arhabdomeric cells with cell bodies located deeper in the retina than those of retinula cells, and processes which penetrated between the retinula cells to the level of the rhabdom bases were described by Schliwa and Fleissner (1979). Cells conforming to their description are present in both normal and albino eyes, and profiles corresponding to Schliwa and Fleissner's description are present in tangential sections of retina at the level of the rhabdom bases.

Axonal profiles containing dense vesicles, and identified by Fleissner and Schliwa (1977) as neurosecretory fibres, are also present in normal and albino retinas.

Most of the volume of the retina is made up by the retinula cells. These extend from close against the lining pigment cells to the preretinal membrane. They are interspersed near their bases by the arhabdomeric cells and intraretinal pigment cells, but are the sole cell type present in the vitread half of the retina. The size and extent of the retinula cells are similar in the normal and the albino. The location and staining properties of their nuclei are also similar, and in both cases

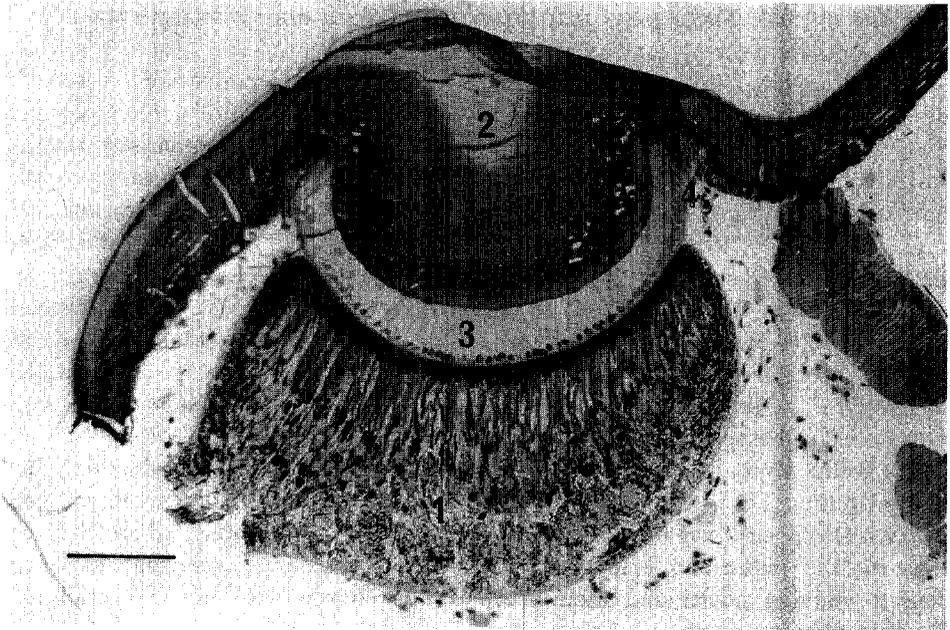


Fig. 4.—Normal median eye, coronal section. Retina, 1, is separated from lens, 2, by vitreous 3. Epidermis is heavily pigmented, particularly at limbus, 4. Retina contains abundant pigment. Scale = 100  $\mu$ m.



Fig. 5.—Albino median eye, coronal section. Retina, 1, epidermis, 2, and limbus, 3, are devoid of pigment. Scale = 100  $\mu$ m.

the cells give rise to nerve fibres that form bundles in the deep part of the eye before piercing the postretinal membrane to form the optic nerve.

The normal retinula cells each contain a rounded body called by Lankester and Bourne (1883) a phaosphere, presumably from their dark appearance in stained

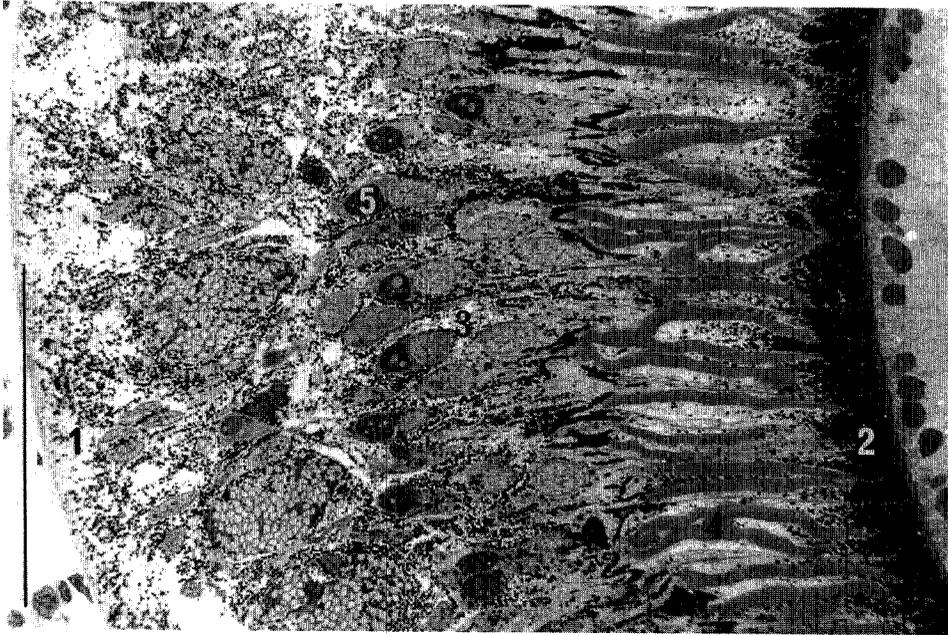


Fig. 6.—Retinal periphery, normal. Abundant pigment in peripheral pigment cells, 1, vitread end of retinula cells, 2, and in substance of retina, 3. Rhabdoms, 4, and phaospheres, 5, well formed. Scale = 100  $\mu$ m.

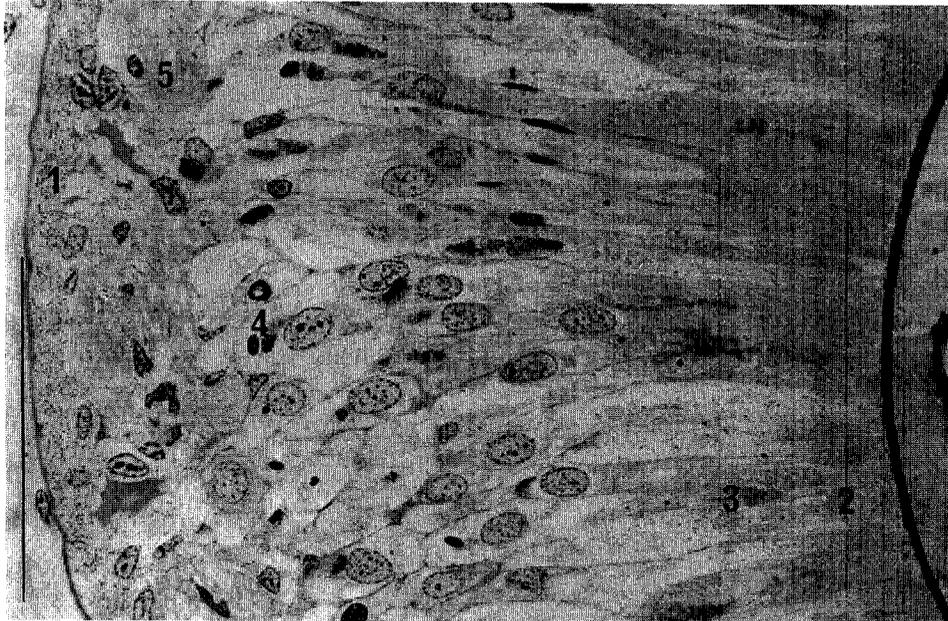


Fig. 7.—Retinal periphery, albino. Granules replace pigment in peripheral cells, 1, and retinula cells, 2, Rhabdoms, 3, and phaospheres, 4, are degenerate. Nuclei, and nerve fibres, 5, appear normal. Scale = 100  $\mu$ m.

sections. The phaospheres, of which at least one appears to be present in each retinula cell, are usually located deep to the nucleus and are of comparable size. Ultrastructurally they appear as an aggregation of dense granules approximately 40 nm in diameter (Fig. 10). The phaospheres contain vacuoles that stain with

basic fuchsin but not with the blue dyes, and that are described as refractile by other authors (Bedini, 1967). These vacuoles contain scattered granules, some similar to those aggregated and others smaller and frequently arranged in a paracrystalline array. Phaospheres have not been reported from other cell types, and their function remains unknown.

The phaospheres in the albino are abnormal (Fig. 11). In most cases they are represented by smaller and less regular clumps of dense amorphous material without the normal granular substructure, though some show the normal rounded profile and contain vacuoles.

The retinula cell processes vitread to the nuclei are in close mutual apposition, and from the abutting processes the rhabdomeres are formed over a distance of some 70  $\mu\text{m}$ . Typically the cells are grouped in fives; the rhabdoms are consequently star shaped in cross sections in most cases, though other patterns are common, particularly in the periphery of the retina. Electron microscopy of the rhabdoms confirms the observations of Bedini (1967) and Fleissner and Schliwa (1977) that they consist of close arrays of uniform microvilli, approximately 80 nm diameter and up to 2  $\mu\text{m}$  in length (Fig. 8).

An unexpected finding in the albino is that the rhabdoms are markedly degenerate. The length of the retinular cell along which rhabdomeres are formed is much reduced, and the normal star pattern is disorganised or absent. Electron microscopy shows that the normal grouping in fives is present, but that the rhabdomeres are represented only by small and disorganised arrays of microvillar material, lacking the density and regularity of the normal, (Fig. 9).

The normal retinular cells contain abundant melanin granules, some present in the base of the cell close to the nucleus, and even extending into the nerve fibres. Most granules are concentrated in the vitread ends of the cells where they effectively screen the rhabdoms from incoming light. These melanin granules appear identical to those in the pigment cells. Premelanosomes, membrane bound and with laminated bars or rings in them, are also found among the granules (Fig. 12).

The melanin granules are absent in the albino, their place being occupied by numerous premelanosomes that appear similar to those of the normal, except that they show a greater size range and are present in greater density (Fig. 13). These premelanosomes show the same distribution along the cell as the melanin granules of the normal, suggesting that they may have undergone circadian migration as do the normal melanin granules (Scheuring, 1913; Fleissner, 1974), or that they were permanently in the light regime position.

## DISCUSSION

Before discussing the differences between the normal and albino examples we may review the factors affecting the colouration of scorpions. As Cutler and Richards (1972) point out, the dark colours commonly seen in arachnids are partly due to brown exocuticle and partly to pigment granules present in the epidermis, the features being present singly or alone.

Some scorpions are uniformly pale; *Centruroides sculpturatus* is a pale yellowish or clay colour, and the newborn young of *Urodacus manicatus*, and of other species illustrated in the literature, are white all over. This pallor is due to poorly sclerotized cuticle in the case of the young, but in *C. sculpturatus* the

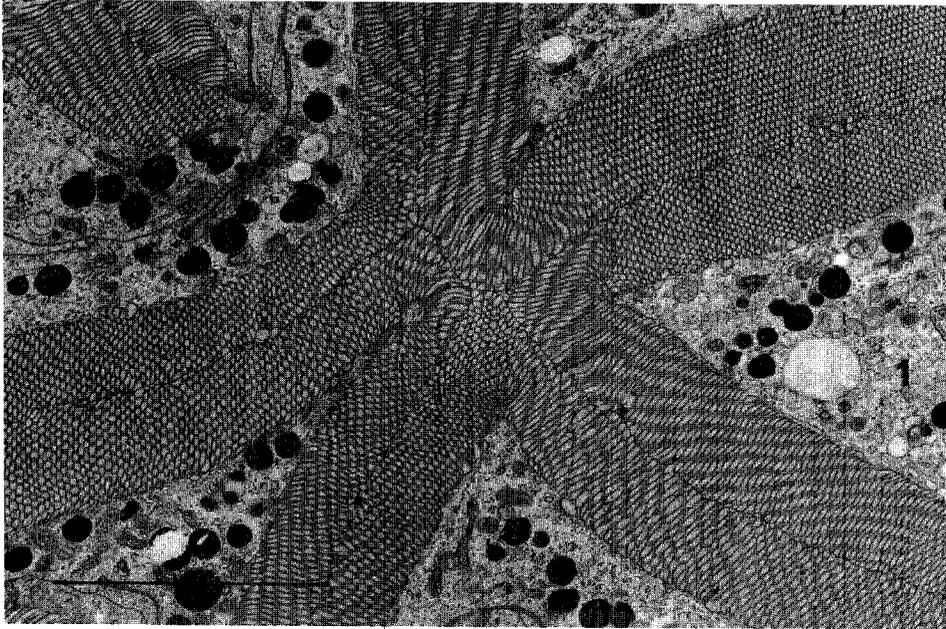


Fig. 8.—T. S. rhabdom, normal, E. M. Each retinula cell, 1, contributes microvilli to two arms of the star-shaped rhabdom. Cytoplasm contains mitochondria, ribosomes and abundant melanin granules. Scale = 5  $\mu$ m.

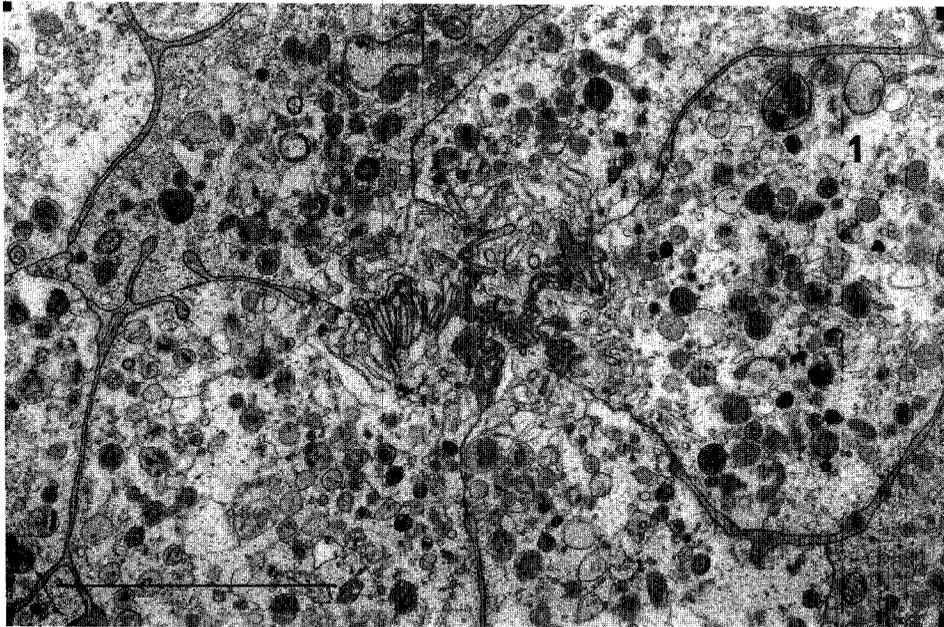


Fig. 9.—T. S. rhabdom, albino, E. M. Groups of five retinula cells, 1, bear reduced and disorganised microvilli. Mitochondria and ribosomes deficient. Pigment granules replaced by non-pigmented premelanosomes. Scale = 5  $\mu$ m.

cuticle is well sclerotized but pale, and there is little epidermal pigment. Other scorpions are very dark; *Heterometrus* species from Asia and *Urodacus manicatus* from Australia are cases in point. Of these *U. manicatus* certainly owes its colouration to both dark cuticle and epidermal pigmentation. The fingers and

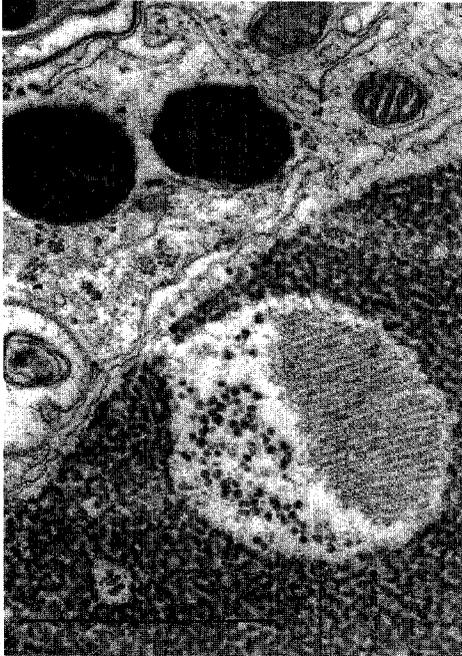


Fig. 10.—Phaosphere, normal, E. M. Phaosphere consists of aggregated granules. Similar granules present in cytoplasm and within vacuole. Paracrystalline array of smaller granules in some vacuoles. Scale = 1  $\mu$ m.

Fig. 11.—Phaosphere, albino, E. M. Dense amorphous mass replaces well-defined granules. Scale = 1  $\mu$ m.

Fig. 12.—Pigment granules, normal, E. M. Melanin granules are dense and membrane-bound. Adjacent premelanosome contains granular matrix and lamellae. Scale = 1  $\mu$ m.

Fig. 13.—'Pigment' granules, albino, E. M. Membrane-bound granules resemble normal premelanosomes, but occur in greater size range. No melanin present. Scale = 1  $\mu$ m.

aculeus are darkly sclerotized, but most of the darkness of the tergites is due to epidermal pigment. Other scorpions are patterned; *Lychas marmoreus* owes its pattern to epidermal pigment beneath a pale cuticle. Even the fingers are pale, though well sclerotized, recalling the pallor of *C. sculpturatus*.

Whatever the amount of pigment elsewhere in the epidermis, the eyes are almost always black. This is the case in *C. sculpturatus*, and the white newborn scorpions have densely pigmented eyes. The only cases in which eye pigment is usually lacking is in certain cavernicolous examples, e.g. *Typhlochactas* described by Mitchell and Peck (1977) which has lost its eyes altogether. Another troglobitic species, *Diplocentrus mitchelli* is described by Francke (1978) as retaining some eye pigment, even though the rest of the body is depigmented and the eyes are vestigial.

Comparing the albino and normal *U. yaschenkoi* we see that the darkness of the fifth metasomal segment and vesicle, and that in and around the eyes is due to pigment, but that the darkness of the chelae and chelicerae, the aculeus and tarsal claws, and the leg joints is due to darkly sclerotized cuticle.

Hackman (1974) notes that some insects may have melanin within the cuticle itself, besides the intracellular granules, but this does not appear to be the case in the scorpions examined here.

The process of melanin formation is summarized by Hogan, Alvarado and Weddell (1971) for the human retina: Rough endoplasmic reticulum within the melanin-forming cell elaborates the enzyme tyrosinase, which is thought to be transferred to the Golgi apparatus. Here it is packaged into the membrane-bound premelanosomes, which contain a finely striated protein framework with which the tyrosinase is associated. On this framework tyrosine is polymerised to form melanin; when polymerisation is complete and the granule mature, no further tyrosinase activity is demonstrable. In albinos the melanocytes contain vesicles and premelanosomes, containing a protein framework but no melanin; such individuals lack tyrosinase.

The present findings accord well with this scheme, despite the phylogenetic disparity between scorpions and humans and the smaller size of the invertebrate pigment granules. Melanin granules and premelanosomes are present in the normal, but the albino contains only premelanosomes, many containing laminated bodies but not melanin, and in a wider range of sizes than normal.

Accounts on vertebrate (Nyhan 1981) and insect (Hackman 1974) melanin formation agree on the biochemical pathway. An enzyme, tyrosinase or o-diphenyl oxidase, catalyses the conversion of tyrosine to dopa and then to dopa-quinone. The remaining steps, which can proceed non-enzymatically, at least in vertebrates, lead to moieties which undergo condensation to form a repeating polymeric structure of high molecular weight. This dark pigment, eumelanin, is bound to protein.

Hackman (1974) makes the point that the production of melanin, cuticular or intracellular, and the hardening or sclerotization of cuticular proteins both involve the conversion of tyrosine to dopa and dopa-quinone. The hardening of cuticle, in many cases accompanied by darkening (Andersen 1980), involves the tanning of a protein by quinones, which are derived from an o-diphenolic compound by an oxidase. In at least some cases the diphenol is tyrosine from the haemolymph (Pryor 1940, Fraenkel and Rudall 1940, 1947). The colour to which cuticle eventually tans will depend on the proportion of quinones to

residual diphenols; the quinoid, oxidised, state of the protein-bound material is dark (Hackman 1959).

Though the tyrosine-dopa-quinone pathway may be involved both in the hardening of cuticle and in melanin formation, the enzymes responsible for the two trains of reactions are probably different. Dennell (1958) found that injection of phenylthiourea into blowfly larvae completely suppressed the haemolymphal tyrosinase activity, preventing the formation of the normal black banding of the puparia, but not affecting their formation and sclerotization.

We may postulate a selective disability of tyrosinase in the present case, in which the formation of melanin is suppressed in an individual with normally sclerotized cuticle.

Fleissner (1974) confirmed Scheuring's (1913) observation that the retinal pigment granules normally undertake circadian migrations, being concentrated in the vitread part of the retina by day, and retreating to the basal part by night. Fleissner also showed that the sensitivity of the retina altered by 3 to 4 log units with the movement of the pigment. It is clear from examining sections of the retina in the light-adapted state that pigment is present vitread to the rhabdoms in such quantities as greatly to attenuate the amount of light that would penetrate to them.

Fleissner and Schliwa (1977) demonstrated neurosecretory fibres in the retina and suggested that these control the pigment migration, later shown by Fleissner and Fleissner (1978) to be mediated by the optic nerves. Section of the nerve did not merely abolish the pigment movement, which would be expected if the movement depended on visual impulses reaching the central nervous system, but the pigment assumed the daylight position, normally associated with an illuminated eye. They concluded that the pigment migration was controlled by efferents in the optic nerve. The cell bodies of these neurosecretory fibres were located in the supraoesophageal ganglion by Fleissner and Heinrichs (1982).

In view of the close association of the pigment with visual function it would not be surprising to find a functional deficit due to the lack of pigment in the albinos, but the structural disorganisation of the rhabdoms and of the phaospheres is unexpected. It may be that the integrity of the rhabdoms depends on protection from excess illumination, normally provided by the burrowing habit and by the screening pigment. That the observed degeneration was not caused by the laboratory regime is shown by the control, which was kept in the same conditions, and in which the rhabdoms appear large and well ordered. The nature and function of the phaospheres remain unknown, but it is interesting that they too show degeneration in the absence of pigment and of intact rhabdoms.

The presence of the much reduced and degenerate rhabdoms in the albino suggests that eye function was poor. Despite this, it had survived to the fourth instar, managing to catch prey while being surrounded by normal individuals, important potential predators. This survival of albino, and probably blind, individuals confirms the relative unimportance of vision in scorpions.

In diurnal animals albinism may be disadvantageous, since pale individuals may be more easily seen by predators. In dark environments this pallor will not matter, and many cave forms are depigmented. Some cave dwellers have degenerate eyes; others, including the *Typhlochactas* species described by Mitchell and Peck (1977) and certain opiliones (Briggs 1974), have lost their eyes altogether.

Though not a cave dweller, *U. yaschenkoi* does live in a burrow which spirals underground, and so is dark at the end (Shorthouse 1971, Koch 1978, Shorthouse and Marples 1980). The scorpion comes to the burrow mouth, and commonly beyond it, at nightfall. This habit was certainly present in the albinos, because the trapping method depends on it. This evening emergence suggests that the circadian behavioural rhythm of the species was present, in spite of the absence of pigment and disordered eye structure.

Consequences of albinism on scorpion metabolism other than those to the eyes are not obvious. Cloudsley-Thompson (1979) discusses the possibility that cuticular melanin may reduce water loss, and quotes Kalmus' (1941) finding that dark varieties of *Drosophila* withstand dehydration better than pale ones do. Kalmus' paper however does not distinguish unequivocally between darkness due to cuticular sclerotization or melanin production, cuticular or epidermal. Dark coloration is not associated with resistance to desiccation in scorpions. Edney (1977) points out that black scorpions from rain forests have high cuticular permeabilities while some pale desert scorpions have the lowest permeabilities recorded from any arthropod. Supposed waterproofing properties of melanin are probably unimportant in the present context, since *U. yaschenkoi* is a pale species, the only pigmented regions, one metasomal segment, the vesicle and the ocular area, representing a small fraction of the surface area.

Little can be said about the genetics of albinism in scorpions, since the phenomenon is only known from the two specimens now described. Albinism in man, which is due to a recessive gene, occurs with a frequency of about 1 in 20,000. If the rate is comparable in scorpions it would take a very large collecting effort to determine the rate in the wild. Shorthouse and Marples (1982) have shown that *U. yaschenkoi* takes at least 6y to reach maturity and that the gestation period is 18 months. In his extensive study of the species Shorthouse (1971) never observed mating, nor did he find females with first instar scorpions. These features of the life history, with the burrowing habit, mean that breeding experiments would be highly unlikely to succeed.

#### ACKNOWLEDGMENTS

I wish to thank my father, G. H. Locket, for introducing me to the study of arachnids, and for his invaluable example and discussions over the years. I thank my wife Deirdre for assistance in the field, Ms. Cathy Shanahan for advice on localities and collecting methods and discussion of scorpion genetics, Professor N. F. Hadley for valuable comments on the problems, Professor G. E. Rogers for discussions on biochemistry and Mrs. Barbara Sheldon for typing the manuscript.

#### LITERATURE CITED

- Andersen, S. O. 1980. Cuticular sclerotization. Pp. 185-215, in *Cuticle techniques in arthropods* (T. A. Miller, ed.). Berlin, Heidelberg, New York: Springer-Verlag.
- Bedini, C. 1967. The fine structure of the eyes of *Euscorpium carpathicus* L. (Arachnida, Scorpiones). *Arch. Italiennes Biol.*, 105:361-378.
- Belmonte, C, and L. J. Stensaas. 1975. Repetitive spikes in photoreceptor axons of the scorpion eye. *Invertebrate eye structure and tetrodotoxin*. *J. Gen. Physiol.*, 66:649-655.

- Briggs, T. S. 1974. Troglolithic harvestmen recently discovered in North American lava tubes. (Travunidae, Erebomastriidae, Triaenonychidae: Opiliones). *J. Arachnol.*, 1:205-214.
- Cloudsley-Thompson, J. L. 1979. Adaptive functions of the colours of desert animals. *J. Arid. Env.*, 2:95-104.
- Cutler, B. and A. G. Richards. 1972. Sclerotization and the localization of brown and black pigments in Chelicerates (Arthropoda). *Zool. Jb. Anat.*, 89:404-421.
- Dennell, R. 1958. The amino acid metabolism of a developing insect cuticle: The larval cuticle and puparium of *Calliphora vomitoria*. II. The non-specific hydroxylation of aromatic amino-acids and the production of polyphenols by the cuticle. *Proc. Roy. Soc. London. B.*, 148:280-284.
- Edney, E. B. 1977. Water balance in land arthropods. Berlin, Heidelberg, New York: Springer-Verlag, 282 pp.
- Fleissner, G. 1974. Circadiane Adaptation und Schirmpigment verlagerung in der Sehzellen der Medianaugen von *Androctonus australis* L. (Buthidae, Scorpiones). *J. Comp. Physiol.*, 91:399-416.
- Fleissner, G. and G. Fleissner. 1978. The optic nerve mediates the circadian pigment migrations in the median eyes of the scorpion. *Comp. Biochem. Physiol. A.*, 61:69-71.
- Fleissner, G. and S. Heinrichs. 1982. Neurosecretory cells in the circadian clock system of the scorpion *Androctonus australis*. *Cell Tiss. Res.* 224:233-238.
- Fleissner, G. and M. Schliwa. 1977. Neurosecretory fibres in the median eyes of *Androctonus australis* L. *Cell Tiss. Res.*, 178:189-198.
- Fleissner, G. and W. Siegler. 1978. Arhabdomeric cells in the retina of the median eyes of the scorpion. *Naturwiss.*, 65:210-211.
- Fraenkel, G. and K. M. Rudall. 1940. A study of the physical and chemical properties of the insect cuticle. *Proc. Roy. Soc. London. B.*, 129:1-35.
- Fraenkel, G. and K. M. Rudall. 1947. The structure of insect cuticles. *Proc. Roy. Soc. London. B.*, 134:111-143.
- Francke, O. F. 1977. The genus *Diplocentrus* in the Yucatan peninsula, with description of two new troglolithes (Scorpionida, Diplocentridae). *Bull. Assn. Mexican Cave Stud.*, 6:49-61.
- Francke, O. F. 1978. New troglolith scorpion of genus *Diplocentrus*. Scorpionida, Diplocentridae. *Entomol. News*, 89:39-45.
- Hackman, R. H. 1959. Biochemistry of the insect cuticle. *Proc. Int. Congr. Biochem.* 4th. Vienna 1958, 12:48-62.
- Hackman, R. H. 1974. Chemistry of the insect cuticle. Pp. 215-270, in, *The Physiology of Insects*. Vol. VI. (M. Rockstein, ed.). New York, London, Academic Press.
- Hogan, M. J., J. A. Alvarado and J. E. Weddell. 1971. *Histology of the human eye*. Philadelphia, W. B. Saunders.
- Kalmus, H. 1941. The resistance to desiccation of *Drosophila* mutants affecting body colour. *Proc. Roy. Soc. London B.*, 130:185-201.
- Koch, L. E. 1978. A comparative study of the structure, function and adaptation to different habitats of burrows in the scorpion genus *Urodacus* (Scorpionida, Scorpionidae). *Rec. West. Australian Mus.* 6(2):119-146.
- Lankester, E. R. and A. G. Bourne. 1883. The minute structure of the lateral and central eyes of *Scorpio* and *Limulus*. *Quart. J. Micr. Sci.*, 23:177-212.
- Mitchell, R. W. 1968. *Typhlochactas*, a new genus of eyeless cave scorpion from Mexico (Scorpionida, Chactidae). *Ann. Speleol.*, 23:753-777.
- Mitchell, R. W. 1972. *Typhlochactas ellioti*, a new eyeless cave scorpion from Mexico (Scorpionida, Chactidae). *Ann. Speleol.*, 26:135-148.
- Mitchell, R. W. and S. B. Peck. 1977. *Typhlochactas sylvestris*, a new eyeless scorpion from montane forest litter in Mexico (Scorpionida, Chactidae, Typhlochactinae). *J. Arachnol.*, 5:159-168.
- Nyhan, W. L. 1981. Inheritable abnormalities of amino acid metabolism. Pp. 305-481, in *Comprehensive biochemistry*. Vol. 19A (A. Neuberger and L. L. M. van Deenen, eds.). Amsterdam, Elsevier.
- Parker, G. H. 1891. The eyes in scorpions. *Bull. Mus. Comp. Zool.*, 13:173-208.
- Pryor, M. G. M. 1940. On the hardening of the cuticle of insects. *Proc. Roy. Soc. London B.*, 128:393-407.
- Reynolds, E. S. 1963. The use of lead citrate at high pH as an electron-opaque stain in electron microscopy. *J. Cell Biol.*, 17:208-212.
- Scheuring, L. 1913. Die Augen der Arachniden. I. Die Augen der Skorpioniden. *Zool. Jb. Abt. Anat. Ontog.*, 33:553-588.

- Schliwa, M and G. Fleissner. 1979. Arhabdomeric cells of the median eye retina of scorpions Part I. Fine structural analysis. *J. Comp. Physiol. A.*, 130:265-270.
- Schliwa, M. and G. Fleissner. 1980. The lateral eyes of the scorpion *Androctonus australis*. *Cell Tiss. Res.*, 206:95-114.
- Shorthouse, D. J. 1971. Studies on the biology and energetics of the scorpion *Urodacus yaschenkoi*. Ph.D. Thesis. Australian National University.
- Shorthouse, D. J. and T. G. Marples. 1980. Observations on the burrow and associated behaviour of the arid-zone scorpion *Urodacus yaschenkoi* (Birula). *Australian J. Zool.*, 28:581-590.
- Shorthouse, D. J. and T. G. Marples. 1982. The life stages and population dynamics of an arid zone scorpion *Urodacus yaschenkoi* (Birula 1903). *Australian J. Ecol.*, 7:109-118.

*Manuscript received August 1985, revised December 1985.*