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The eyes of a "nobody", *Anoplodactylus petiolatus* (Pantopoda; Anoplodactylidae)

M. Heß, R. R. Melzer & U. Smola

Zoologisches Institut der Universität; Luisenstr. 14, D-80333 München, Germany

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ABSTRACT: The fine structure of the four ocelli of *Anoplodactylus petiolatus* was examined using serial longitudinal and transversal sections of the eye hill. Each pigment cup ocellus is composed of a (planconvex) cuticular lens, lens forming hypodermal cells, inverse retinula cells with latticed rhabdom and surrounding tapetum and pigment layers. Within the retinula cells a distal "vitreous" zone, a nucleus zone and a proximal rhabdomeric zone can be distinguished. Retinula cell axons originate proximally. The tapetum cells contain several layers of reflecting crystals. Distally, they have a common microvillous region. The intraretinal "vitreous" zone contains glycogen-like particles in the centre and rough ER in the periphery. Contrary to other Pantopoda vitreous cells, a praeretinal membrane and a vertical lens groove have not been observed in *Anoplodactylus*. While the presence of four (median) ocelli appears to be a primitive characteristic, the inverse orientation of the retinula cells in combination with a tapetum lucidum represents a highly derived characteristic among arthropod median eyes.

INTRODUCTION

Among recent Chelicerata, the Pantopoda (Pycnogonida) or "nobodies" are the only primarily marine forms; however, their position within the system of arthropods is not certain in the least. Weygoldt & Paulus (1979a, b) have suggested that they may represent the sister-group of all other Chelicerata; Sharov (1966) even assumed them to be related to early annelid-derived arthropod ancestors. In this connection, the eyes of the Pantopoda are of peculiar interest since they might represent a primitive character stage among the Chelicerata; the ocelli are found in a group of four on an anterodorsal projection of the prosoma (commonly called ocular tubercle or eye hill), and they appear to be median eyes innervating the median protocerebrum (Wirén, 1918; Hanstrøm, 1926, 1928; Winter, 1980). The presence of four median eyes has been suspected to belong to the basic characters of the Arthropoda. The Pantopoda would then represent the only Chelicerata with this primitive feature (Paulus, 1979; Weygold & Paulus, 1979a, b). Four median eyes are found also in some Trilobita, primitive Crustacea, and Collembola. Early investigators (Wirén, 1918; Morgan, 1891a, b; Sokolow, 1911; for a review see Helfer & Schlottke, 1935) have shown that pantopod eyes are ocelli with a cuticular lens, an inverse retina, a reflecting tapetum and a pigment cup. In addition, Jarvis & King (1973) have found separate vitreous body cells situated between the lens secreting hypodermal cells and the retinula cells in *Nymphon gracile*. In deep-sea pantopods, a reduction in the number of ocelli can be found. Even among individuals of a single population, the number of eyes is suspected to be variable (Bouvier, 1913, cited in Helfer & Schlottke,

1935). In order to provide a better understanding of the phylogenetic origin of the Pantopoda, both the primitive eye type and the number have to be determined. Jarvis & King (1973) have already examined the eyes of *Nymphon gracile* (Nymphonidae) and *Pycnogonum littorale* (Pycnogonidae), which belong to the Eupantopodida and Pygnogonomorpha sensu Fry (1978). In this paper, the eyes of adult *Anoplodactylus petiolatus* (Anoplodactylida; Fry, 1978) are described and compared with the ocelli of other Arthropoda.

MATERIALS AND METHODS

Animals

Anoplodactylus petiolatus Kröyer was found on colonies of the athecate hydrozoan *Hydractinia echinata* Fleming provided by the Biologische Anstalt Helgoland. Both adult and larval individuals were abundant, and were observed either feeding on the trophozooids of the hydrozoan or passing the early larval development stage (beginning with the protonymphon stage) within the gastral cavities of special, enlarged "gall-zooids" (see also Staples & Watson, 1987). The animals were kept in artificial sea water at about 12 °C. *Hydractinia* was fed on nauplius larvae of the brine shrimp *Artemia*. Animals were determined according to Elliot et al. (1990).

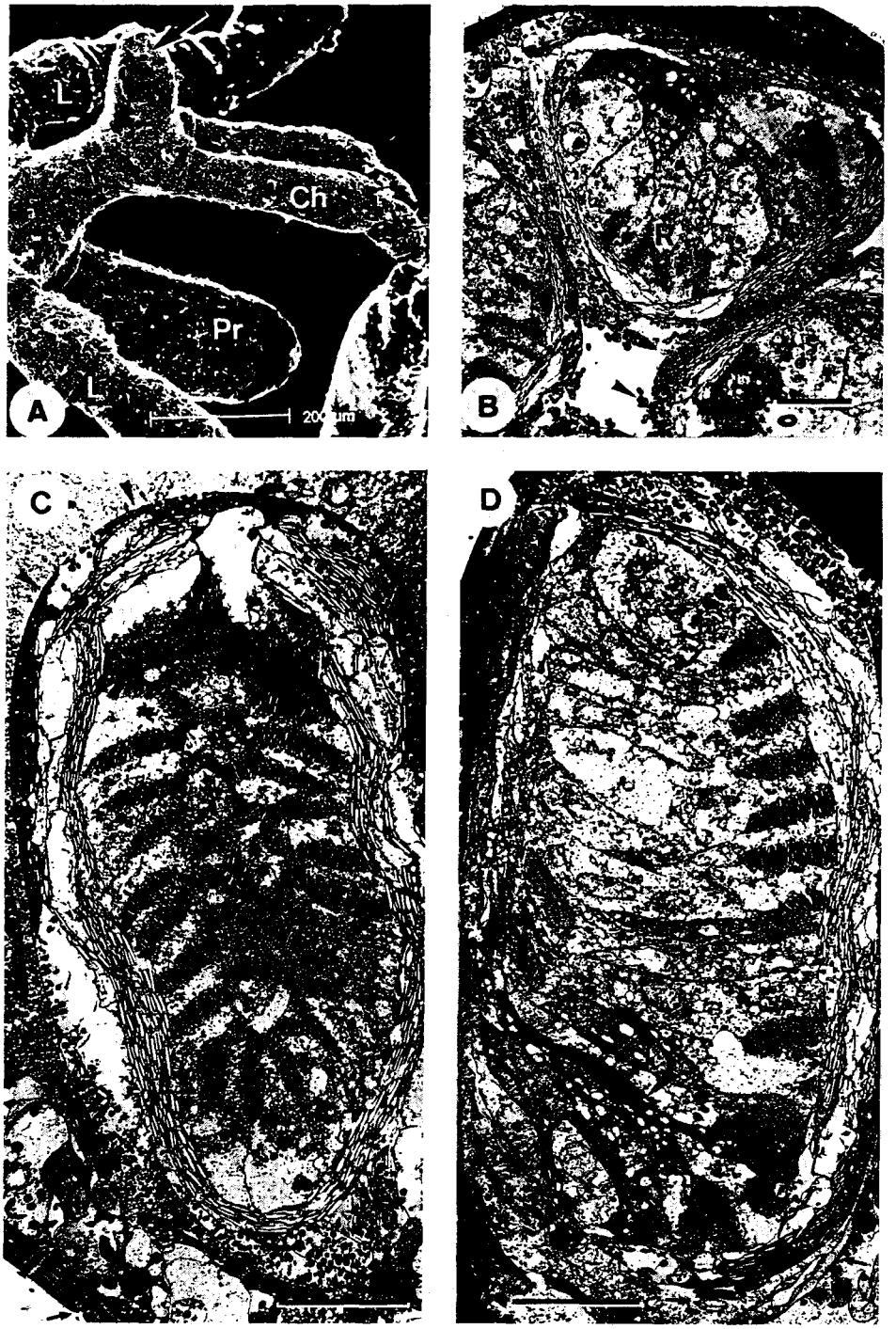
REM

The animals were fixed in AAF solution (85 % ethanol, 10 % acetic acid, 5 % formalin) for 1 h, dehydrated in a graded acetone series, critical point dried on a Polaron E 3000 CP dryer, mounted on aluminium stubs with adhesive carbon tabs, and coated with gold on a Bio Rad SEM coating system. A Philips XL 20 scanning EM at 12–14 kV was used for the inspection of the specimens.

TEM

Animals were dissected and fixed in glutaraldehyde and osmiumtetroxide in 0.1 m cacodylate buffer (4 °C) according to Franke et al. (1969). After rinsing in cacodylate buffer, the specimens were dehydrated in a graded acetone series. After embedding in Gylcidether 100, 70–110 nm diamond sections were made on a LKB ultrotome III. They were double stained on a LKB 2168 Ultrostainer and inspected on a Philips CM10 at 80 kV. A total of 4 specimens were analysed.

Fig. 1. Survey and general organization of the ocelli. **A:** SEM view of eye hill (arrow). L Leg; Ch Chelicere; Pr Proboscis. **B:** Cross section of the eye hill. C corneal lens; R retinula cells inside the pigment cup; arrowhead: axons (raphe); Scale bar 10 µm. **C:** Transversal section of ocellus with latticed rhabdom and surrounding sheet cells (arrowheads); arrow: sensillum trichodeum; Scale bar 10 µm. **D:** Longitudinal section of ocellus; note retinula cell with electron-dense plasma (arrowhead); arrows: axons; Scale bar 10 µm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RESULTS

Gross morphology

The eye hill of *Anoplodactylus petiolatus* has a diameter of 100 µm and a height of 160 µm (Fig. 1A). Its cuticle is 3 µm thick. In the region of the corneal lenses, cuticle thickness increases up to 10 µm (Fig. 1 B). Distally, the cylindrical inner space of the eye hill is completely filled with the ocellar cells. In addition to the ocelli and the hypodermis, the following structures can be found: (a) the lateral sense organs are situated at the tip of the ocular tubercle; (b) the ocellar nerves project downwards across the haemolymph to the protocerebrum; (c) derivates of the hypodermis, i. e. sensilla trichodea and the "slit" glands are found elsewhere on the eye hill (Fig. 1 C).

As revealed by the arrangement of the ocelli in cross section and the main reflection angles of the tapeta viewed under the stereomicroscope, the optical axes of the four ocelli are in the horizontal plane. Each of two ocelli are directed antero- and posterolaterally. Neighbouring ocelli have optical axes running perpendicular to each other (Fig. 1 B). Each ocellus has a volume of approximately 6.5×10^{-3} mm^3 and is 65 µm high, 50 µm wide and 40 µm deep. The anterior ocelli are slightly larger than the posterior ones. Because of the dense package, the ellipsoid ocelli ware laterally flattened (Fig. 1 B). The eyes are composed of a cornea with adjacent lens forming hypodermis cells, a layered tapetum and pigment cup, and the central retinula cells with a latticed rhabdom (Figs 1 B–D; 4).

The cornea

Viewed from above, the cuticular lenses are oval and have the same width and length as the pigment cup. They have a convex outer surface and a plain inner surface (Fig. 1 B). Outer lens curvature does not differ from that of the eye tubercle, which means that they hardly bulge over the surface (Fig. 1 B). Contrary to the cuticle of the body, a coat of epibionts is lacking in the lens region. Thickening of the lens is caused by both the formation of additional cuticular layers and their enlargement. Adjacent to the lenses are "corneagenous" hypodermal cells that do not differ from the normal hypodermis.

The reflecting tapetum and pigment layers

Surrounding the retinula cells are the tapetum and the pigment cell layers, which form the pigment cup (Fig. 1 B–D). Up to four layers of tapetum cells, which surround the retinula completely, are next to the retinula cells. Proximally and laterally they contain reflecting crystals, and they form a tapetum coating the inner surface of the pigment cup (Figs 3 A, 4). Distal to the retinula cells, crystals are absent within the plasma of low electron density. The nuclei of the tapetum cells are situated in the periphery of this

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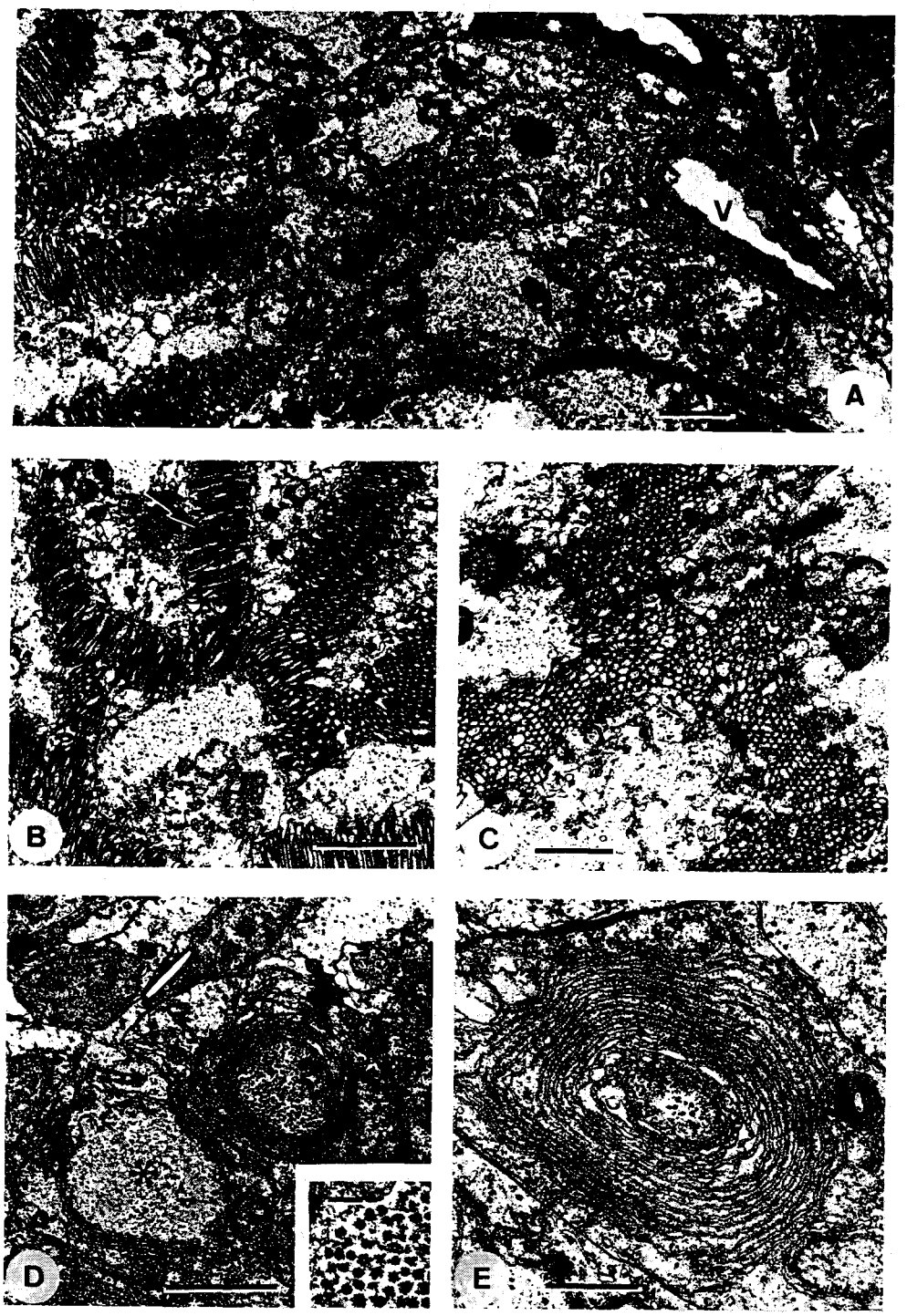
Fig. 2. Rhabdom and retinula cells. **A:** Survey of retinula cell; V "Vitreous" region; N Nucleus; Rh Rhabdom; Scale bar 2 µm. **B:** Latticed rhabdom; arrow indicates longitudinally sectioned rhabdomeric microvilli; Scale bar 2 µm. **C:** Transverse section through microvilli; Scale bar 1 µm. **D:** Distal retinula cell plasma; asterisk: granular area; Scale bar 3 µm; insert: glycogen-like granules; Scale bar 0.2 µm. **E:** Distal retinula cell plasma; arrows indicate surrounding rough ER; Scale bar 1 µm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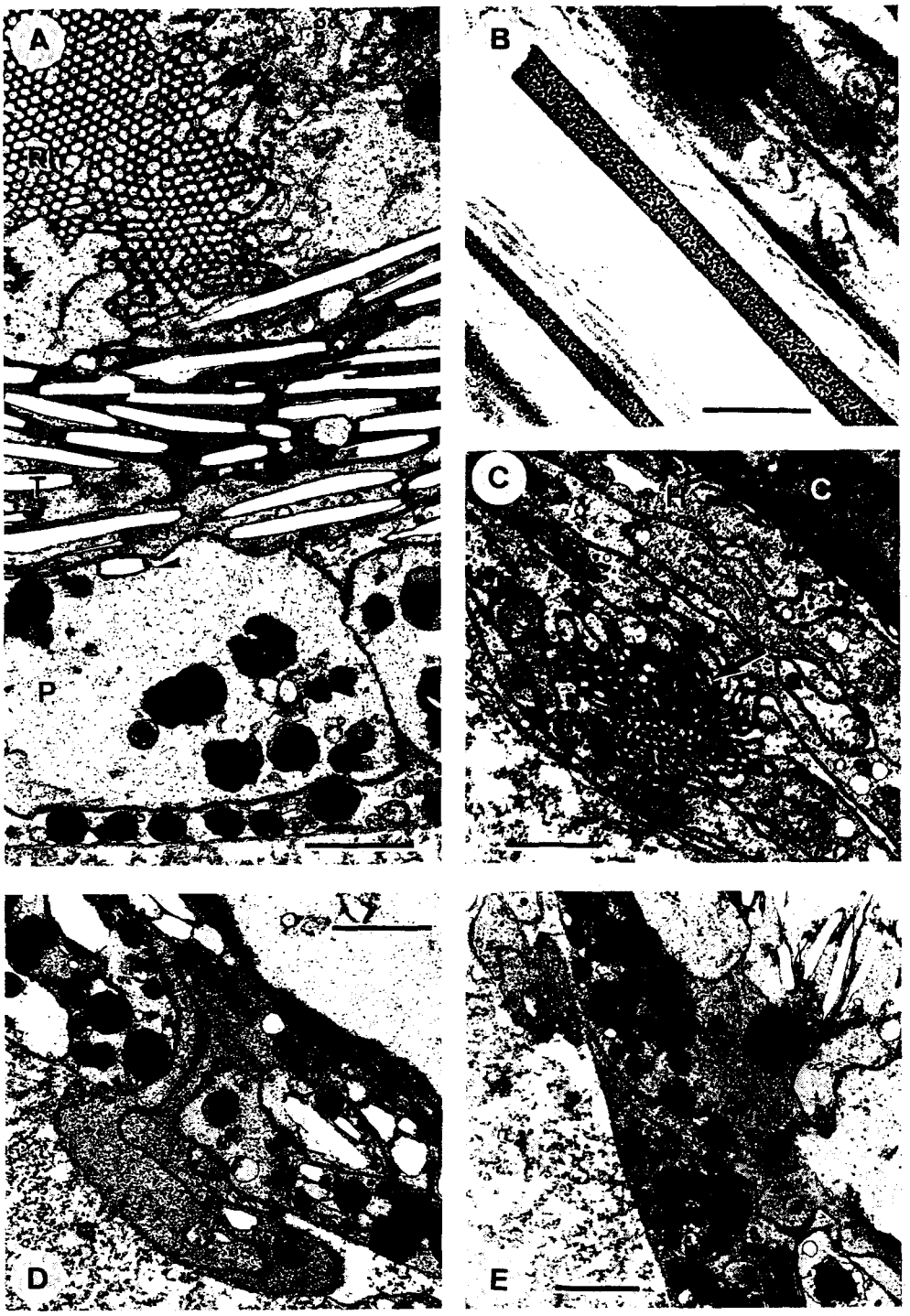
region. In the distal centre, the tapetum cells form a spot (diameter: approx. 4 µm), composed of numerous microvilli (Figs 3 C and 4). Contact between tapetum cells and cuticle has not been observed. The reflecting crystals are situated within the plasma of the tapetum cell, and all together form 5 to 15 layers within the tapetum cell protrusions (Fig. 3 A). Crystals are laterally shifted from one layer to another, and hence, they form a continuous mirror. The single crystal plate has a lateral length of 0.5–4.5 µm and a thickness varying between 50 nm in the centre and 80 nm at the edge (biconcave). The average distance between the crystal plates is 200–250 nm. Reflecting crystals that were completely retained within the ultrathin sections show a granular ultrastructure. Under a high power electron beam the single granules oscillate from an electron-absorbing to an electron-transmitting status (Fig. 3 B).

The pigment cells form one or two layers which surround the ocellus laterally and proximally (Figs 1 B–D, 3 A). A basal lamina between pigment cells and mixocoel has not been observed (Fig. 3 D, E). Contrary to the tapetum cells, the pigment cells do not extend between cornea and retinula cells. It was not possible to determine the presence or the location of pigment cell nuclei. The pigment cells are densely filled with many pigment granules which are approximately 0.5 µm in diameter and are in vivo a yellow-brownish colour. A pigment granulum is composed of a unit membrane vesicle that includes material from two different electron densities. In the centre, the denser material forms clumps that are irregular in shape. At the periphery, fine granular material of a lesser electron density is found (Fig. 3 A). Occasionally, a tapetum crystal can be found in the inner pigment layer adjacent to the tapetum (Fig. 3 A). In the very proximal part of the eye, the vertical line marks the passage of the retinula axons across the tapetum and pigment cells (Fig. 3 D, E). This perforated area of the pigment cup is commonly called raphe.

The retinula cells

The retinula is composed of about 60 to 100 retinula cells in 6–8 longitudinal rows with 10–15 cells in each row. As a result of the oblique arrangement of the retinula cells (Fig. 1 D), transversal sections suggest a layered organisation in the central part of the eye. Distally, however, the retinula cells join up directly to the tapetum cell protrusions (Fig. 2 A). Therefore, the retinula cells project along the whole depth of the eye cup. The retinula cells are dorsoventrally flattened, and a few very flat cells with an electron-dense plasma can be found (Fig. 1 D). Three regions can be distinguished within the retinula cells. Distally, there is a "vitreous" region that can be separated into a central area of low electron density, and the surrounding rough ER layers (Fig. 2 A, D, E). The centre consists of more-or-less dense glycogen-like granules of approximately 80 nm. Each granulum is composed of numerous very small particles (Fig. 2; insert). In the periphery, 5–14 rER layers are stacked up concentrically (Fig. 2 D, E). The middle part of the retinula cells

Fig. 3. Sheet cells and retinula axons. **A:** Survey of tapetum and screening pigment layers; Rh Rhabdom; T Tapetum; P Screening pigment; note single tapetum crystal within pigment cell (arrowhead); Scale bar 2 µm. **B:** Granular ultrastructure of the biconcave tapetum crystals. Scale bar 0.2 µm. **C:** Microvillous region of tapetum cells (arrow); C Cornea; H Hypodermis; Scale bar 2.4 µm. **D** and **E:** Retinula axons projecting across the sheet layers (arrowheads); Scale bars 1 µm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contains the nucleus and numerous mitochondria (Fig. 2 A). Occasionally, the cells are indented in this region like parts of a puzzle. In the proximal part, the rhabdom is found (Figs 1 B–D, 2 B, C). It belongs to the fused type. Each retinula cell directs its rhabdomeric microvilli to all the neighbouring retinula cells which results in a latticed rhabdom. A

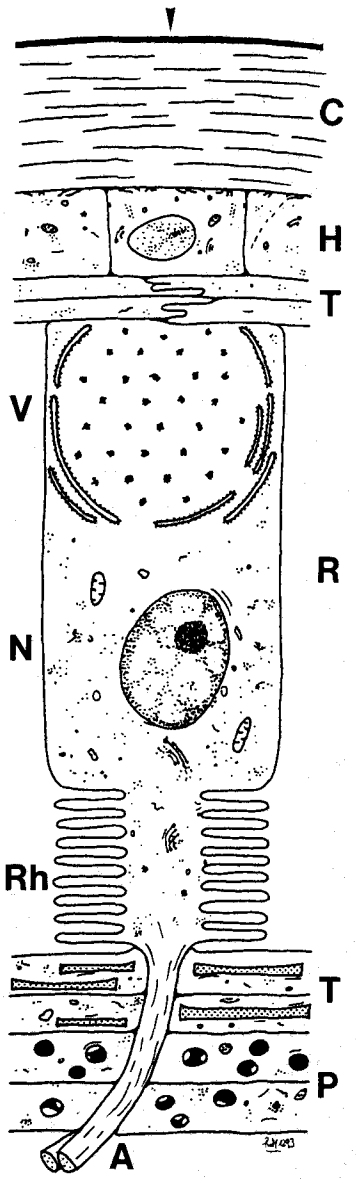

Fig. 4. Schematic reconstruction of a retinula cell of *Anoplodactylus petiolatus* with neighbouring cuticular and cellular layers. Arrowhead indicates the direction of incident light; C Cuticle (corneal lens); H Hypodermis; T Tapetum cells; R Retinula cell; V "Vitreous" region; N Nucleus; Rh Rhabdom; A Bundle of 2 axons originating from adjacent retinula cells; P Screening pigment layers

rhabdom branch (thickness: approximately 1.5 µm) is formed by a single row of microvilli that originate alternately from the neighbouring cells (Fig. 2 B). Each element of the lattice measures 5–8 µm horizontally and vertically. Originating from the most proximal part of the rhabdomeric region, the axons project to the raphe where they leave the eye cup and form the ocellar nerves leading down to the protocerebrum. Generally, groups of two axons pass the tapetum and pigment layers in common (Fig. 3 D, E). Paired axons can also be identified within the ocellar nerves. The arrangement of the retinula cell regions indicates that incident light passes the "vitreous" region first, then the nucleus region, finally reaching the rhabdom. Therefore the retinula cells are of the inverse type.

DISCUSSION

As inferred by Jarvis & King (1973), the rectangular arrangement of the four ocelli on a "lighthouse" seems to allow a roundabout view. This compensates for the missing capability of eye movement or the otherwise required body rotation, and this enables the animal to register light-dark-change from any direction. The fact that the lens cuticle is always free of epizooids emphasizes the significance of the photoreceptors. Since the anatomy of pantopods makes a cleaning of the ocelli with the help of the extremities improbable, the influence of a chemical process is suggested. "Slit glands" which might represent multifunctional organs (Davenport et al., 1987; Tomaschko & Brückmann, 1990; Tomaschko, 1992) are present elsewhere on the cuticle. Pantopods which live in dimmed light conditions use their tapetum to increase light capture. The tapetum belongs to the grate-shaped type found in Araneae (Homann, 1971). The parallel arrangement of numerous reflecting crystal layers (guanin?) leads to the suggestion that they represent a "multilayer reflector" (for a review, see Nilsson, 1990). A similar organization of the tapetum is found in the ocelli of numerous arthropods, e. g. the nauplius eye of *Megacyclops* (Fahrenbach, 1964), or the lateral eyes of Araneae (Melamed & Trujillo-Cenóz, 1966; review in Muñoz-Cuevas, 1984). Good preservation of the crystals in some sections indicates a crystal shape which is much more "geometric" than the spaces remaining after shrinkage when the tapetum elements are disintegrated or lost (see also Jarvis & King, 1973). Contrary to earlier investigations (review in Helfer & Schlottke, 1935), an enlarged basal lamina between the hypodermis and the tapetum (praeretinal membrane) has not been observed nor the so-called vertical notch of the lens. In *Nymphon* and other pantopods (Helfer & Schlottke, 1935), this structure is found in the centre of the ventral inner surface of the lenses. It is not clear if it is absent in *Anoplodactylus*, or if cross sections of this region were not made. A hitherto undescribed structure is the microvillar meeting point of tapetum cells below the lens hypodermis. This region is not connected to the cuticle and lacks structures that might indicate a secretory or resorptive function. In the distal region of the lateral sense organ of *Anoplodactylus pygmaeus*, microvillous sheet cells are also found (Richter, 1982). As in many other Pantopoda, nuclei of pigment cells have not been observed. Helfer & Schlottke (1935) have suggested that pigment cell nuclei are reduced or pycnotic in the adult. Therefore, the origin of the pigment "cells" or pigmented "elements" is not yet clear. The tapetum crystals that can be found occasionally within the pigment layers do not suffice to establish an ontogenetic and/or functional coherence between tapetum and screening pigment.

The translucent distal third of the retinula cells is similar to light guiding structures

found in many arthropod photoreceptors, such as crystalline cones of insect ommatidia. Crystalline cones of the acone type also have a vesicular plasma of low electron density and contain ER cisternae peripherically (for a review see Mouze, 1984; Grenacher, 1879). The former, however, are an intracellular part of the retinula cells, while the latter are formed by specialized cells, i. e. the Semper cells. It is not known if the vitreous zone is optically inactive, or if it represents an element of the ocellus' refractive apparatus as suggested by the glycogen-like granular material in the centre of this region. The surrounding layers of rough ER indicate a high rate of protein synthesis, and the granular material might be a glycoprotein. The "vitreous" region, as described here for *Anoplodactylus*, corresponds to the "vacuolized region" found in different Pantopoda (Helfer & Schlottke, 1935). Sokolow (1911) surmised that the "vacuoles" are functional, while Wirén (1918) and Morgan (1891b) took them for preparation artefacts.

Jarvis & King (1973) termed the retinula cells of pantopods as not inverted. All other authors call them inverse. This appears to be caused by the different definitions that can be used for the term inverse or inverted. As in other inverse eyes, light travels across the vitreous and nucleus region before reaching the light sensitive rhabdomer in Pantopoda. In typical inverse eyes the axon also originates distally. This is not present in Pantopoda. As discussed below, the nerve fibre projects either proximally or laterally. Therefore, the normal sequence of axon, nucleus, and rhabdom regions is modified in all Pantopoda examined to present. From a functional point of view it is justified to use the term inverse. For retinula cells with distal nuclei, the term "indirect eye" has also been used independently of the axon's origin (Muñoz-Cuevas, 1984). Early investigations of eye development have shown that the retinula cells are bent into the pigment cup. This suggests that they might be inverted during development, and thus might also morphologically be inverse. For a better understanding, a fine structural examination of early eye development in Panopoda is required.

A comparison of the pantopod eyes previously examined reveals that they are pigment cup ocelli with a latticed rhabdom, surrounding pigment layers, and a cuticular lens. They share these primitive characters with other median ocelli of arthropods (for reviews see Paulus, 1979; Mouze, 1984). Derived characters of pantopod median eyes appear to be the inverse orientation of the retinula cells and the presence of a tapetum lucidum. Median eyes of arthropoda primarily have an eversely orientated retinula, and a tapetum is lacking (Paulus, 1979; Mouze, 1984). While pantopod ocelli have uncommon characteristics compared to other median eyes, they are surprisingly similar to the lateral eyes of many Araneae (e. g. Melamed & Trujillo-Cenóz, 1966; Homann, 1971). The latter also possess retinula cells with a distal nucleus, and a proximal axon inserted adjacent to the rhabdom. Apart from this, tapeta are widely distributed in the lateral eyes of Araneae. These characteristics appear to have evolved independently in both taxa. Otherwise, one must assume that the ocelli of Pantopoda are lateral eyes relocated dorsally and not true median eyes. The ocelli, however, seem to project to the central protocerebrum (Hanstrøm, 1926, 1928; Winter, 1980) and not to the optic lobes of the lateral protocerebrum as lateral eyes always do.

Among Pantopoda, the following differences can be found: Distal vitreous cells, which have been described by Jarvis & King (1973) for *Nymphon* and *Pycnogonum*, do not exist in *Anoplodactylus petiolatus*. Apart from this, the shape of the cornea appears to be different (biconvex in *Nymphon* and *Pycnogonum*, planconvex in *Anoplodactylus*). In

addition, the praeretinal membrane, the vertical notch and the microvillar region of the tapetum cells can be present or absent (see above). This also accounts for the origin of the retinula axons. While they are inserted proximally in *Nymphon, Pycnogonum* (Jarvis & King, 1973), and *Anoplodactylus*, they appear to originate in the nucleus region in *Decolopoda* and other species (Wirén, 1918; Helfer & Schlottke, 1935). The situation shown here must, therefore, not necessarily be primitive and might have been evolved in some but not all Pantopoda. It can be summarized that the median ocelli of Pantopoda so far examined show several uncommon features that suggest a highly derived characteristic stage, although the presence of four median eyes appears to represent an ancient characteristic. In order to elucidate the primitive eye structure in pantopods, a reinvestigation of the groups with a lateral projection of the retinula axons is necessary.

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