The Visual Cells and Retinal Tapetum of the Foveate Deep-Sea Fish *Scopelosaurus lepidus* (Teleostei)

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Summary. The electron microscopic structure of the visual cells and retinal tapetum of the foveate deep-sea teleost *Scopelosaurus lepidus* is described. The retina of *S. lepidus* contains two spatially separate classes of visual cells, viz. cones, mostly twin cones, in the temporal (caudal) region subserving binocular vision in the rostral direction, and rods grouped in bundles in the rest of the retina. A deep convexiclivate pure-cone fovea is located in the temporal part of the retina.

The outer segments of each pair of twin cones and of the rod bundles are located in reflecting pits formed by the processes of the retinal pigment epithelium which contains reflecting crystals believed to be of guanine. Each pit contains concentric layers of radially orientated elongated crystals in the wall surrounding the photoreceptor outer segments. Furthermore, in the temporal pure-cone region the pigment cells possess discrete cylindrical piles of tangentially orientated crystals, so-called reflectors, apposed to the tips of each pair of twin cone outer segments.

Comparisons are made with the retinae of other deep-sea teleosts. The centre of the pure-cone fovea of *S. lepidus* is thought to have a fairly high resolving power and a correspondingly low threshold for minimal angular displacement which will increase the possibility of maintaining foveal fixation of the relatively small prey animals during approach.

A. Introduction

Scopelosaurus lepidus is a deep-sea teleost belonging to the family Notosudidae; the largest known specimen of this species has a standard length of 364 mm (Bertelsen et al. 1976).

Most notosudid species inhabit the deep-sea and all are characterized by possessing large eyes with a big rostral aphakic (lensless) aperture (Fig. 1) and a well-developed temporally (caudally) located fovea (Bertelsen et al., 1976).

A light microscopic study of the eyes of two notosudid species, the deep-living epipelagic *Scopelosaurus hoedti* and the meso- and bathypelagic *Ahliesaurus berryi*, has
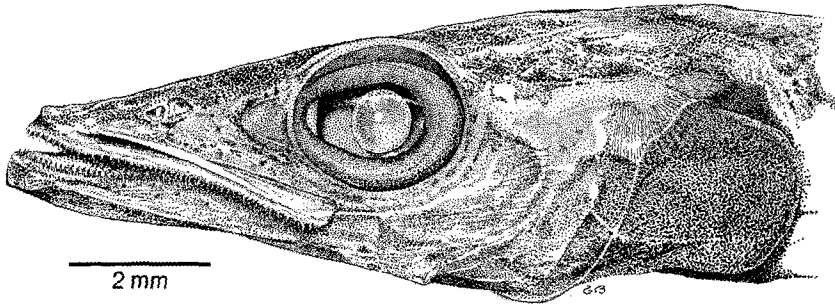
Fig. 1. Head of *Scopelosaurus lepidus,* 47 mm in standard length. The circumlental aphakic aperture is especially broad rostrally

shown the presence of two retinal regions, viz. 1) a smaller temporal non-grouped region with typical twin cones and a deep convexiclivate fovea, and 2) a larger grouped region comprising the rest of the retina, the visual cells of which are grouped in bundles. These species were thought to possess pure-cone retinae. The presence of a retinal tapetum was surmised, though none but circumstantial evidence was available (Munk, 1975).

The present study supplements these previous observations by describing the electron microscopic structure of the visual cells and the retinal tapetum of *Scopelosaurus lepidus* which is mesopelagic or benthopelagic over the continental slopes in the adult stage.

Like one of the previously examined notosudids (*Ahliesaurus berryi*) *S. lepidus* is a deep-sea teleost, the eyes of which have been found to show the rather unorthodox feature of possessing a deep convexiclivate pure-cone fovea, i.e. a type of fovea generally thought to be present only in strictly diurnal vertebrates.

Though probably of fairly widespread occurrence, retinal tapeta lucida are actually recorded only in a small number of teleostean deep-sea species, viz. *Evermannella atrata = Coccorella atrata* (cf. Brauer, 1908), *Malacosteus niger* (Denton et al., 1970; Denton and Herring, 1971), *Scopelarchus güntheri* (cf. Locket 1971), *Chlorophthalmus albatrossis* (cf. Somiya, 1975), and *Omosudis lowei* (cf. Frederiksen, 1976). The part of the retinal tapetum found in the pure-cone temporal region with its fovea in *Scopelosaurus lepidus* has proved to be of the same type as that of the cone-dominated retina of *Omosudis lowei.*

B. Material and Methods

The material consists of the right eye from each of two juvenile specimens of *Scopelosaurus lepidus* (Krefft and Maul, 1955), 47 and 48 mm in standard length, respectively. They were caught during a cruise of RRS "Discovery" in the autumn of 1970. The gear used was an opening-closing net and the specimens were caught in the day at a depth of 745–650 m at station 7406 (39° 48.7′ N, 20° 21.2′ W).

Dr. N.A. Locket enucleated the right eyes of both specimens and fixed the eyes for electron microscopy. The fixative was 5 % glutaraldehyde in 0.1 M phosphate buffer pH 7.3, with 5 % sucrose added to the mixture. The eyes were fixed for approximate

4 h at approximately 18 °C, transferred to buffer/sucrose in which they were divided horizontally and the lenses discarded. They were then postfixed in 1 % OsO_4 for 1 h in the same buffer/sucrose mixture, dehydrated through ascending concentrations of ethanol, and taken through epoxy propane to Araldite, in which they were embedded.

Sections were cut on an ultramicrotome. Thick sections ($0.5 - 2 \mu m$) for light microscopy were cut with glass knives and stained with alcoholic toluidine blue. Ultrathin sections for electron microscopy were cut with a diamond knife, mounted on coated grids, and stained with alcoholic uranyl acetate and lead citrate.

Both radial and tangential sections were examined, i.e. sections cut at right angles and parallel to the plane of the retina, respectively.

It was not possible to ascertain which pair of the four parts of eyes embedded belonged to any one of the two specimens. However, since their standard lengths are practically identical, there is no need to be able to tell them apart. One of the plastic-embedded right eyeballs had a horizontal diameter of 2.35 mm. The lens diameters were measured in the intact left eyes of the two specimens; it was 0.85 mm in the 47 mm specimen, 0.88 mm in the 48 mm specimen.

C. Results

On the gross and light microscopic level the eye of *Scopelosaurus lepidus* proved to have the same structure as that of the two previously examined notosudids (cf. Munk, 1975).

As in those species the retina of *S. lepidus* comprises a smaller temporal non-grouped region in which the deep convexiclivate fovea is located, while the larger remaining part of the retina, the grouped region, possesses bundles of visual cells. The previously examined notosudid species were thought to possess pure-cone retinae. Electron micrographs of the retina of *S. lepidus* have demonstrated the presence of two separate classes of visual cells, viz. cones in the temporal non-grouped region and rods in the remaining grouped region. Furthermore, a retinal tapetum has been found in this species.

In what follows only the photoreceptors and the retinal tapetum of *S. lepidus* will be described, since the state of preservation of the remaining vitread part of the retina was unsatisfactory.

I. Non-Grouped Retinal Region

The horizontal extent of this smaller temporal region is ca. 715 μm in the horizontal meridian with the foveal pit located ca. 325 μm from the temporal margin of the retina. The maximum thickness of this part of the retina, ca. 260 μm, is attained laterally to the foveal depression. The depth of the foveal pit is ca. 165 μm (Fig. 2).

The non-grouped region contains only one type of visual cells, viz. cones (Fig. 3). These are almost exclusively twin cones, generally arranged in radiating rows (Figs. 11, 16, and 17) which are approximately perpendicular to the margin of the retina (the ora terminalis). The rows which include the central foveal cones are consequently horizontally
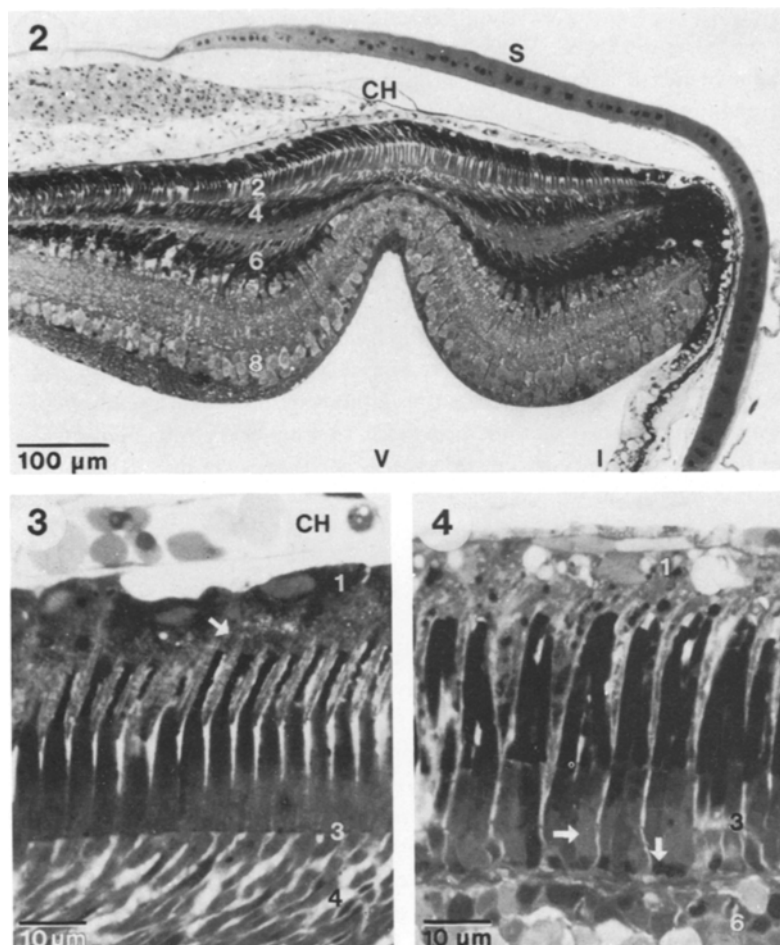
Fig. 2. Horizontal section through temporal fovea of *Scopelosaurus lepidus*

Fig. 3. Radial 1 μm section of sclerad part of non-grouped retinal region of *S. lepidus* lateral to the fovea. The cone outer segments are heavily stained. The cylindrical piles of reflecting crystals located at the tips of the cone outer segments are seen as lightly stained bodies, one of which is indicated by the arrow

Fig. 4. Radial 1 μm section of sclerad part of grouped retinal region of *S. lepidus* with its bundles of rods. *Upper arrow* points at rod nucleus piercing the outer limiting zone, *lower arrow* at one of the small sessile rod pedicles. Lettering: *CH* choroid; *I* iris; *S* scleral cartilage; *V* vitreous; *1* retinal pigment epithelium; *2* visual cell layer; *3* outer limiting zone; *4* outer nuclear layer; *6* inner nuclear layer; *8* ganglion cell layer

orientated or very nearly so. The slender central foveal cones are particularly long and densely packed, with an outer segment length of ca. 16 μm and an inner segment length of ca. 23 μm.

In the part of the non-grouped retina located closest to the fundus of the eye there is no clearly recognizable visual cell pattern. Besides typical twin cones this area contains both single and triple cones which are very rare outside this zone (Figs. 14 and 15).

A type of cone pairing characteristic of teleosts, the two members of twin cones are of identical structure and dimensions. Hence the two members appear identical at any level. In *S. lepidus* the inner and outer segments of each pair of twin cones are in close contact along their entire length, i.e. from the outer limiting zone to the tips of their outer segments (cf. e.g. Figs. 7 and 9).

1. Common Characteristics of Cones

The cones show the following common characteristics:
1) A tapering outer segment, the discs of which are continuous with the plasma membrane at the side opposite to the connecting cilium (Fig. 6). It is not clear from the present material whether this zone of continuity between discs and plasma membrane extends from the base (vitread part) to the tip (sclerad part) of the cone outer segments, but the zone observed is of sufficient extension to justify the classification of the photoreceptors as cones. There are no incisures in the discs of the cone outer segments.

The vitread part of the cone outer segments is surrounded by calycal processes originating from the sclerad part of their inner segments (Figs. 6, 9, 16 and 17). In the twin and triple cones these processes are absent in the contact zone between the outer segments. The calycal processes contain longitudinally orientated cytoplasmic filaments (Fig. 12).
2) A so-called lateral sac (Fineran and Nicol, 1974) or accessory outer segment (Engström 1963) which is a sclerally tapering structure lying beside the outer segment proper and connected to it by means of a narrow longitudinal cytoplasmic bridge (Figs. 6 and 15–17). The lateral sac represents the sclerad continuation of the connecting cilium which joins the cone inner and outer segments. The lateral sac may be a specific cone character within teleosts, though Engström (1961) claimed that it is also present in the rods of gadids. So far no electron micrographs of lateral sacs associated with rods have been published.

The connecting cilium has the usual 9 + 0 configuration of tubules, i.e. nine doublets arranged in a ring and without the central pair characteristic of motile cilia. The tubules can be traced into the lateral sac, which contains no other recognizable components, but has a clear granular cytoplasm.

The connecting cilia and lateral sacs show a definite tendency towards orientation, being always situated on the same side of each pair of twin cones, and generally on the side opposite to the margin of the retina (the ora terminalis) (Figs. 16 and 17). Each connecting cilium arises from an excentrically located basal body situated in the sclerad part of the cone inner segment (Figs. 6 and 17).
3) A sclerally tapering inner segment having a greater cross sectional diameter than the outer segment. Almost the entire inner segment is occupied by tightly packed mitochondria with tubular cristae containing an intracristal electron dense material (Figs. 8 and 9). Some mitochondria appear dark owing to the presence of electron dense extracristal material (Figs. 9 and 14).

Teleost cone inner segments generally consist of two parts, a sclerad ellipsoid, of greater cross sectional diameter than the outer segment, containing the major part of the mitochondria which may be closely packed, and a vitread contractile myoid with relatively few mitochondria. The ellipsoid often has a greater diameter than the myoid.
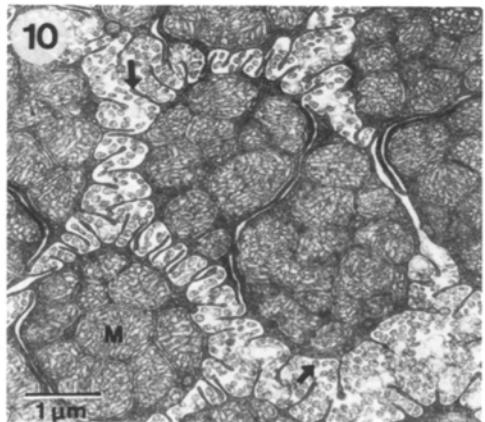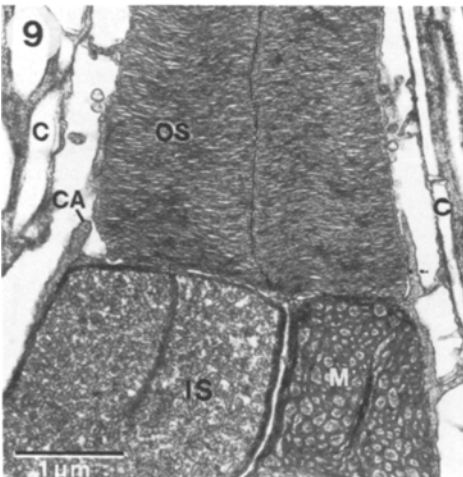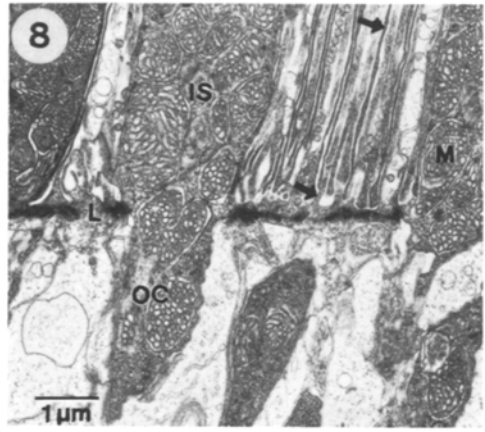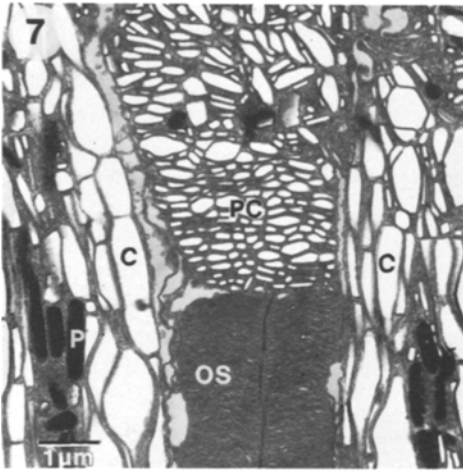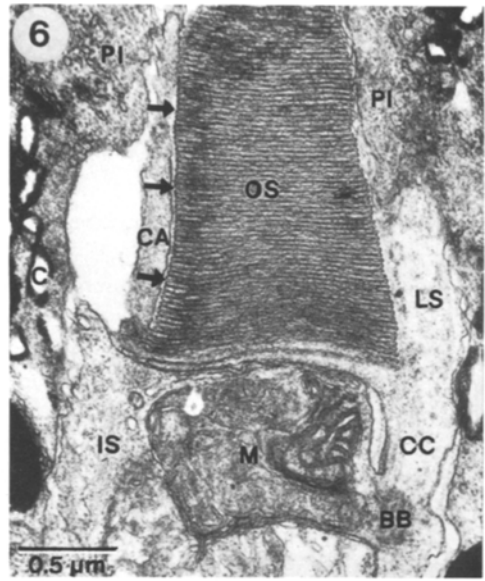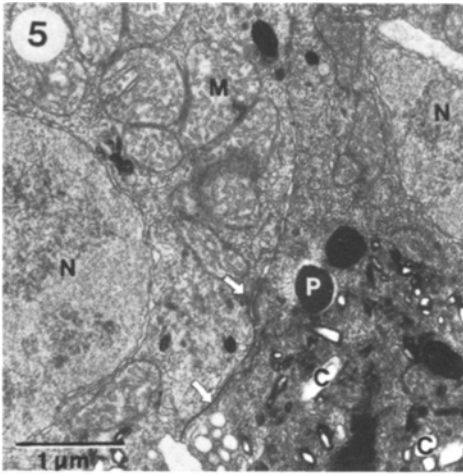
In *S. lepidus* there are no separate ellipsoid and myoid regions.

As mentioned above the sclerad part of the inner segment gives origin to the calycal processes and contains an excentrically located centriolar basal body from which the connecting cilium originates. No striated ciliary rootlet or second basal body were seen.

The inner segments of the joined cones lie in close contact. No membrane junctions were observed at any level in the generally flattened contact zone which comprises the full length of the abutting inner segments. In the deep-sea teleost *Omosudis lowei* the twin cone inner segments are joined by zonulae adherentes (Frederiksen, 1976). In *S. lepidus* subsurface cisterns (Berger, 1967) are located immediately beneath the plasma membrane of the inner segments in the contact zone of the joined cones (Figs. 11 and 12). In the twin cones the inner segment of each member has one subsurface cistern in the contact zone, while two are present within each inner segment of the triangularly arranged triple cones, one in each of the two contact zones with the adjoining members. The subsurface cisterns are seen very clearly in the sclerad part of the joined cone inner segments, but it is not clear from the present material whether they extend inward to the outer limiting zone. Subsurface cisterns located beneath the plasma membrane in the contact zone between joined cone inner segments are known, for example, also in labrids (Engström, 1963; Fineran and Nicol, 1974), *Lebistes reticulatus* (cf. Berger, 1967), and *Perca fluviatilis* (cf. Ahlbert, 1973). They are absent in the twin cones of the deep-sea teleost *Omosudis lowei* (cf. Frederiksen, 1976).

In *S. lepidus* the vitread part of the cone inner segments bear lateral fins which interdigitate with the fins of adjacent cones and the radially oriented Müller cell microvilli (Fig. 10). There are no fins in the contact zone between the members of the joined cones. A few of the lateral fins show simple branching. Lateral fins on the vitread part of the cone inner segments occur in many lower vertebrates (cf. Dunn, 1973,

Fig. 5. Sclerad part of two retinal pigment epithelium cells of *Scopelosaurus lepidus*. The junctions between the lateral cell membranes comprise a vitreally located zonula occludens (*lower arrow*) and a sclerally located zonula adherens (*upper arrow*)

Fig. 6. Slightly oblique radial section of twin cone member of *S. lepidus* near the temporal margin of the retina showing the vitread part of the cone outer segment, the sclerad part of the cone inner segment, the connecting cilium, and the vitread part of the lateral sac. The discs of the outer segment are continuous with the plasma membrane at the side opposite to the connecting cilium (*arrows*)

Fig. 7. Radial section through the tips (*sclerad parts*) of a pair of twin cone outer segments of *S. lepidus* surrounded by the reflecting crystals of the retinal tapetum located in the pigment epithelium cells. The pair of twin cone outer segments abut a cylindrical pile of tangentially orientated crystals and both the pile and the outer segments are surrounded by layers of radially orientated crystals

Fig. 8. Radial section of extrafoveal cones of *S. lepidus* at the level of the outer limiting zone. *Upper arrow* points at tangentially cut lateral fins of cone inner segment interdigitating with the Müller cell microvilli, indicated by *lower arrow*

Fig. 9. Radial section of a pair of extrafoveal twin cone outer and inner segments of *S. lepidus* surrounded by the radially orientated reflecting crystals located in the processes of the pigment cells. The mitochondrion in the right inner segment is dark owing to the presence of an electron dense extracristal material

Fig. 10. Tangential section of extrafoveal twin cone inner segments of *S. lepidus* close to the outer limiting zone. The lateral fins of the inner segments (*upper arrow*) interdigitate with the Müller cell microvilli (*lower arrow*). Lettering: *BB* basal body of connecting cilium; *C* crystal; *CA* calycal process; *CC* connecting cilium; *IS* inner segment; *L* outer limiting zone; *LS* lateral sac; *M* mitochondrion; *N* nucleus; *OC* outer cone fibre; *OS* outer segment; *P* pigment granule; *PC* pile of tangentially orientated crystals (reflector); *PI* pigment epithelium cell
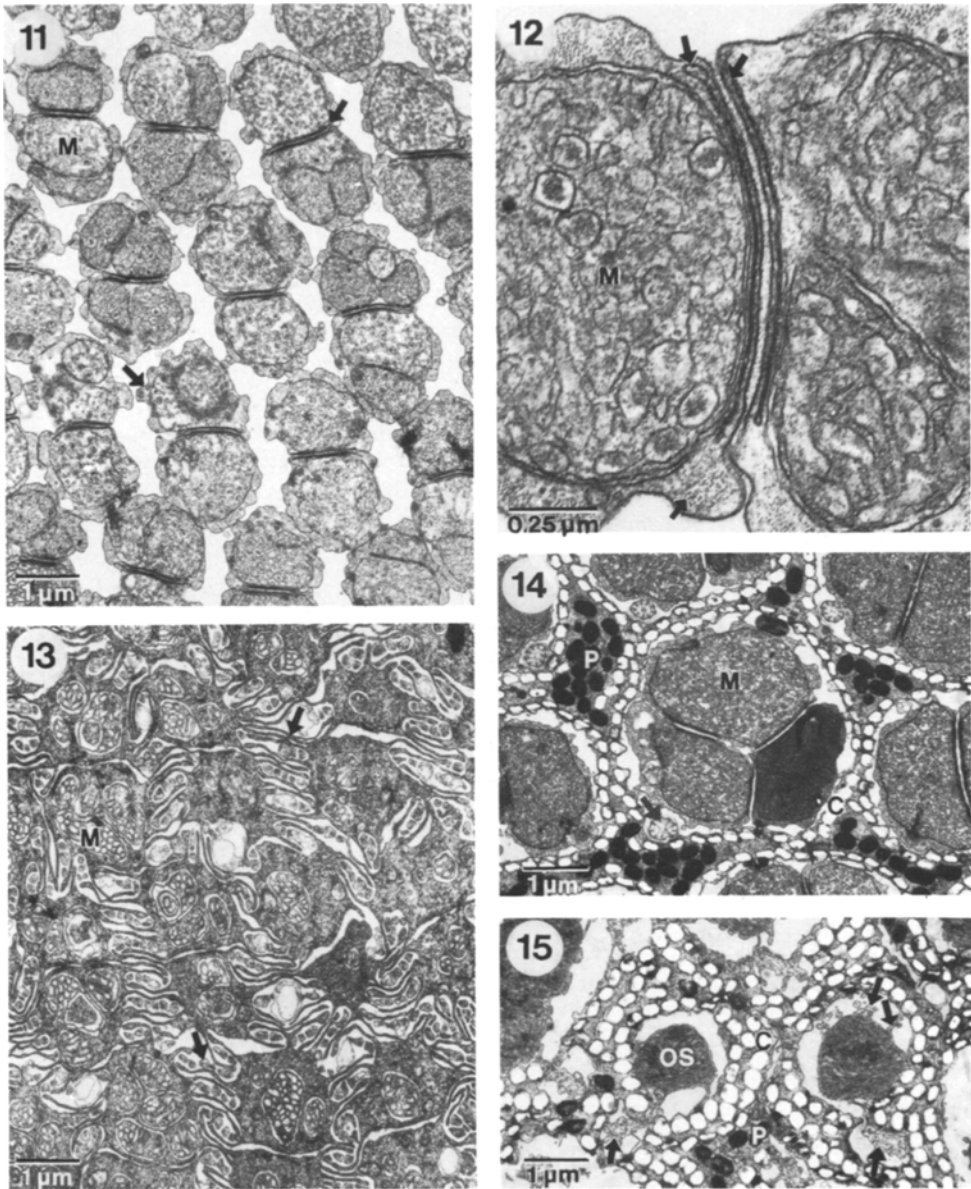
Fig. 11. Tangential section of horizontal rows of central foveal twin cones of *Scopelosaurus lepidus*. The section passes through the sclerad part of the cone inner segments level with the origin of the calycal processes (*lower arrow*). *Upper arrow* points at a subsurface cistern which is seen at greater magnification in Figure 12

Fig. 12. Tangential section of sclerad part of a pair of foveal twin cone inner segments of *S. lepidus* level with the origin of the calycal processes with their radially orientated cytoplasmic filaments (*lower arrow*). *Upper arrows* point at subsurface cisterns located beneath the plasma membranes of the inner segments in their contact zone

Fig. 13. Tangential section of horizontal rows of foveal twin cone inner segments of *S. lepidus* immediately sclerad to the outer limiting zone. The broad lateral fins of the cone inner segments (*upper arrow*) interdigitate with the Müller cell microvilli (*lower arrow*)

for references). Among teleosts they are known to occur, for example, in labrids (Fineran and Nicol, 1974), *Esox lucius* (cf. Braekevelt, 1975), and the deep-sea teleost *Omosudis lowei* (cf. Frederiksen, 1976). Lateral fins may also be present in rods (Locket, 1971; Dunn, 1973; Fineran and Nicol, 1974).

4) The cone nuclei constitute a single row of spindle-shaped nuclei located vitread to the outer limiting zone. The outer cone fibre connecting the perikaryon with the cone inner segment has a dark granular cytoplasm and many mitochondria of the same type as those of the inner segment (Fig. 8). The inner cone fibres which connect the cell bodies with the ovoid pedicles are rather short, with a dark granular cytoplasm and rather few mitochondria. Each cone pedicle contains several synaptic ribbons, the maximum number recognized being six.

2. Foveal Cones

The fovea contains only regular horizontally orientated rows of twin cones (Fig. 11). The twin cones in the foveal centre are definitely more slender and of greater length than the extrafoveal ones, but otherwise of essentially the same structure.

The foveal cone inner segments have fewer and comparatively broader lateral fins than those of the extrafoveal cones (Fig. 13). Furthermore, the nuclei of the foveal cones are displaced away from the outer limiting zone, especially in the region around the central foveal cones. The slender nuclei of the foveal twin cones slant away from the foveal centre with their vitread ends, owing to which the outer nuclear layer is particularly thin in the foveal centre (Fig. 2). Since the density of the visual cells is greatly increased in the fovea and their nuclei have to be accommodated within a certain retinal level (the outer nuclear layer), many nuclei are displaced away from the foveal centre as well. Consequently, many foveal cones have fairly long obliquely orientated outer cone fibres connecting their inner segments at the outer limiting zone with their perikarya, located at a greater distance from the foveal centre.

The maximum cone density is found in the foveal centre. Tangential sections show that it contains ca. 18 twin cones within a 10 x 10 μm square. This corresponds to a density of 180,000 twin cones per mm^2 or 360,000 cones per mm^2 if each twin cone is reckoned as two cones.

Fig. 14. Tangential section of extrafoveal triple cone of *S. lepidus*. The section passes through the sclerad parts of the inner segments of the three members level with the connecting cilium of one member (*arrow*). The right member has a dark mitochondrion. The triple cone is surrounded by the distal (vitread) part of a pigment cell process with pigment granules and concentric layers of crystals. All adjacent cones are twin cones

Fig. 15. Tangential section of basal (vitread) parts of two extrafoveal single cone outer segments of *S. lepidus*. The lateral sacs of the single cones (*lower arrows*) are located within separate compartments in the processes of the pigment cells. Calycal processes are seen around the outer segments (*upper arrows*). The pigment cell processes around the cone outer segments contain pigment granules and concentric layers of crystals. Same lettering as in Figures 5–10
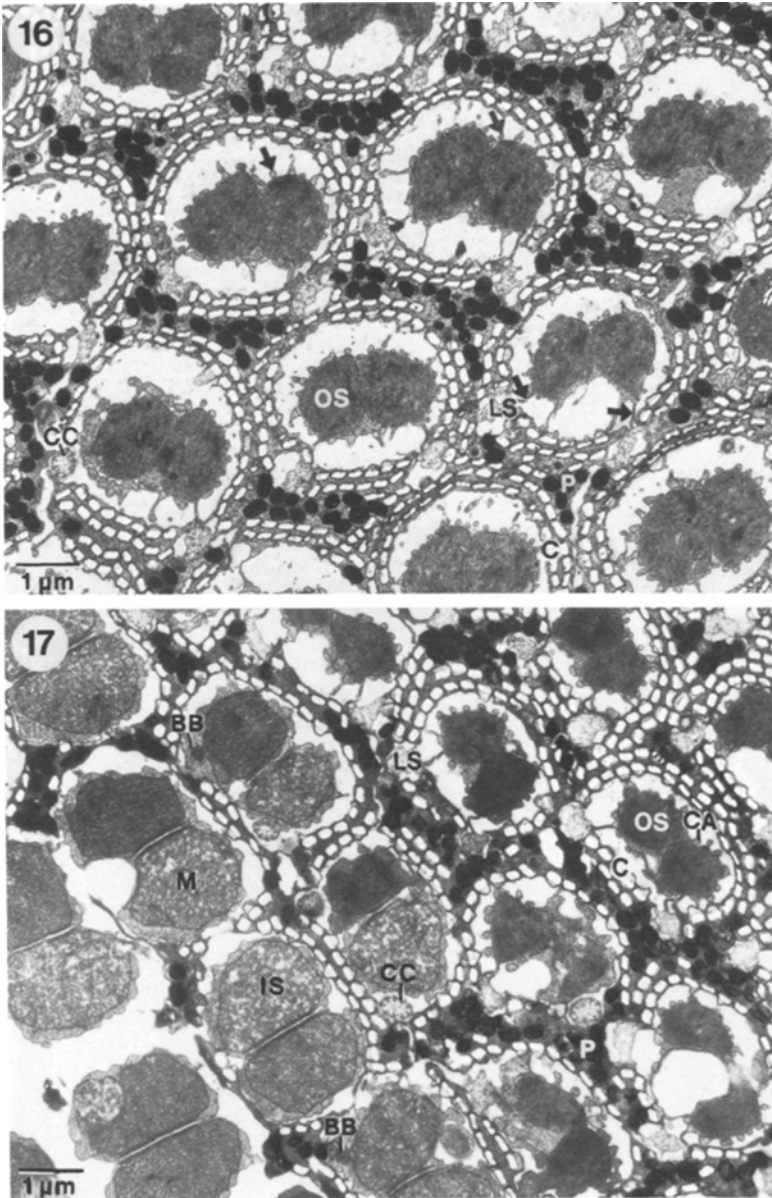
Fig. 16. Tangential section through basal (vitread) part of twin cone outer segments near foveal centre of *Scopelosaurus lepidus*. Each pair of twin cone outer segments lie in close contact, surrounded by calycal processes (*upper arrows*). Each cone outer segment is connected with its lateral sac by means of a narrow cytoplasmic bridge (*lower arrows*). The pigment cell processes forming the cone pits contain pigment granules and concentric layers of crystals

Fig. 17. Oblique tangential section of extrafoveal twin cones of *S. lepidus*. To the right the section passes through the basal (vitread) part of the twin cone outer segments, to the left through the sclerad part of their inner segments. The section contains the distal (vitread) part of the pigment cell processes with their pigment granules and crystals. Same lettering as in Figures 5–10

10 µm   **A**
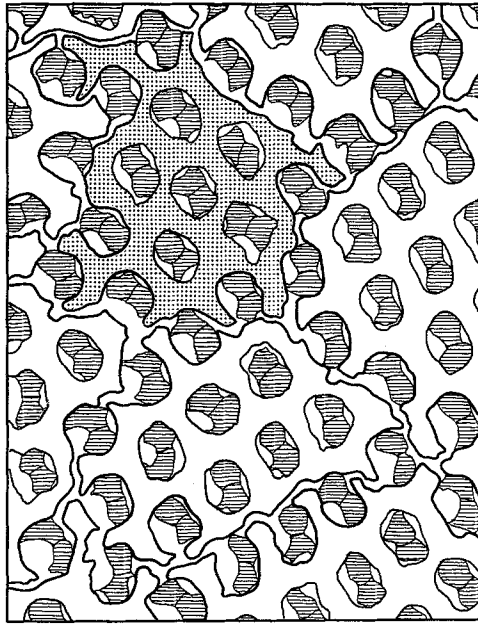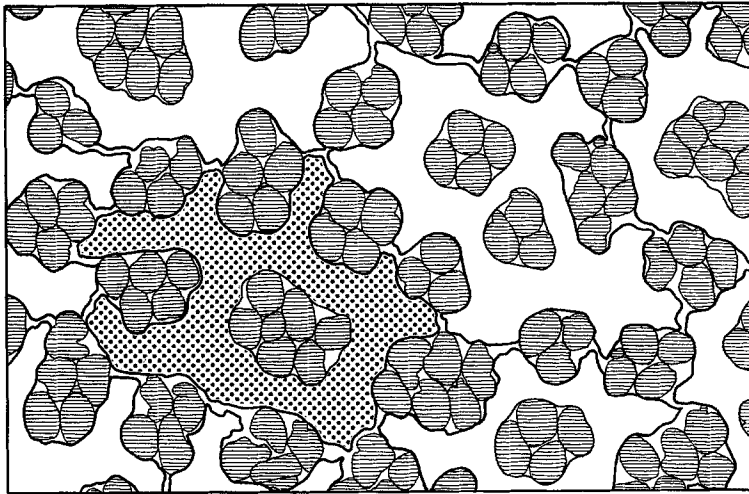
10 µm   **B**

Fig. 18. A and B. Diagrams based on low power electron micrographs of tangential sections through the visual cell layer of the non-grouped (A) and the grouped (B) retinal region of *Scopelosaurus lepidus*. The figures show the extent of the single stout process of each pigment epithelium cell. The individual processes are bounded by thick lines and one process in each of the figures is marked with dots. The visual cell outer segments are hatched. It is apparent that some of the pits occupied by photoreceptors are located entirely within individual pigment cell processes, while others are formed by adjacent parts of processes from two or three pigment cells. The pits in A are occupied by twin cones, those in B by rod bundles

3. Retinal Pigment Epithelium

Throughout the retina this layer is characterized by a rather extensive vacuolation, due mainly to an artificial detachment of the pigment epithelium from its basement membrane.

In the non-grouped retinal region junctions between the lateral cell membranes of adjacent cells were observed only fairly close to the bases of the cells. Zonulae occludentes or tight junctions are found approximately level with the vitread surfaces of the nuclei. Zonulae adherentes are located immediately sclerad to the tight junctions (Fig. 5).

The tight junctions, which seal off the intercellular spaces between the cells, are generally thought to indicate the level of the apical (vitread) surface of the pigment epithelium. If this is so in *S. lepidus,* the square-cut sclerad ends of the cone outer segments do not reach the apical surface of the pigment cells, but lie in contact with their processes.

Tangential sections show that each pigment epithelium cell possesses a single stout process of irregular amoeboid shape. The twin cones are located in narrow pits formed by the pigment cells. Some of these pits are located entirely within individual cell processes, others are formed by adjacent parts of proccesses from two or three cells. There may, for example, be six or seven pits occupied by twin cones within a single pigment cell process, surrounded by eleven or twelve twin cone pits to which the same process contributes (Fig. 18 A).

The processes extend inward to the sclerad part of the cone inner segments (Figs .9 and 17). The abutting parts of adjacent processes may show interdigitations, but no membrane junctions have been observed.

The lateral sacs of the cones are enclosed in separate radially orientated compartments in the processes of the pigment cells and connected with their respective outer segments only by a narrow cytoplasmic bridge (Figs. 15—17).

Throughout the non-grouped region the pigment granules are particularly concentrated in the distal (vitread) part of the processes. Medial to the fovea the basal (sclerad) part of the cells is also heavily pigmented. In the rest of the non-grouped region, which includes the fovea, the basal part of the cells contains a relatively small number of pigment granules, most of which are located slightly vitread to the nuclei. The majority of the rod-shaped pigment granules located in the distal part of the processes show a radial orientation, i.e. they lie parallel to the cone outer segments.

The mitochondria are concentrated especially in the basal part of the cells around the flattened nuclei (Fig. 5). The cytoplasm in the sclerad part of the cells contains globular lipid droplets and occasional whorled structures of concentric lamellae which are continuous with the endoplasmic reticulum. Phagosomes were not seen. Both the basal parts of the cells and their processes contain abundant smooth endoplasmic reticulum.

The dominant cytoplasmic constituent is the membrane-bounded crystals which form the retinal tapetum. The basal part of the pigment cells contains only few crystals (Fig. 5), but these are particularly abundant in the processes. The crystals have almost invariably broken out of the thin sections, so electron micrographs show the holes

where they were located. These holes are often artificially enlarged and distorted making it difficult to ascertain the true dimensions of the crystals.

The crystals show a characteristic trimodal pattern of distribution and orientation very similar to that of *Omosudis lowei* (cf. Frederiksen, 1976).

A roughly cylindrical pile of about twenty superposed layers of small parallel-sided crystals, with several crystals in each layer, is located at the tips of each pair of twin cone outer segments; the parallel-sided crystals are 50–55 nm thick and orientated preferentially at right angles to the axes of the cone outer segments, i.e. parallel to the outer segment discs (Fig. 7, see also Fig. 3). Viewed by incident illumination in tangential retinal sections some of the piles are seen as brightly reflecting spots. Similar piles of small crystals apposed to the cone tips in *Omosudis lowei* were called reflectors (Frederiksen, 1976), and this name will be used in the following.

The reflectors are surrounded by concentric layers of radially orientated crystals which continue vitreally to the tips of the pigment cell processes, i.e. they encircle the cone outer segments and the sclerad part of their inner segments (Figs. 7 and 14–17). These larger crystals are parallel-sided plates with a thickness of ca. 110 nm and a maximum length of ca. 2 μm; their parallel sides face the cone outer segments. In tangential sections in which these crystals are cut transversally, their shape is often seen to be hexagonal. The pigment granules are mostly found in the cores of the partitions between the narrow twin cone pits. Consequently, there is usually at least one layer of crystals interposed between the pigment granules and the photoreceptors, except at the tips of the processes that surround the sclerad part of the cone inner segments. Each pair of twin cone outer segments is encircled by two or three concentric layers of radially orientated crystals. A small number of crystals of aberrant shapes and dimensions may be found in the cores of the partitions between the narrow twin cone pits.

The remaining crystals, located sclerad to these two systems of tangentially and radially orientated ones, are randomly arranged and show great variation in size.

The reflectors located at the tips of the twin cone outer segments and the regular layers of radially orientated crystals encircling them are absent in the region closest to the temporal margin of the retina.

II. Grouped Retinal Region

This region,which comprises the larger remaining part of the retina, is thinner than the non-grouped region, the thickness in the central part of the fundus being ca. 110 μm.

1. Visual Cells

The grouped region contains visual cells grouped in bundles (Figs. 4 and 20). The transition from the non-grouped to the grouped region is very abrupt, characterized, inter alia, by the facts that the visual cells in the grouped region have nuclei that pierce the outer limiting zone and longer outer segments (cf. Figs. 3 and 4). The outer segment length in the central part of the fundus is ca. 23 μm.
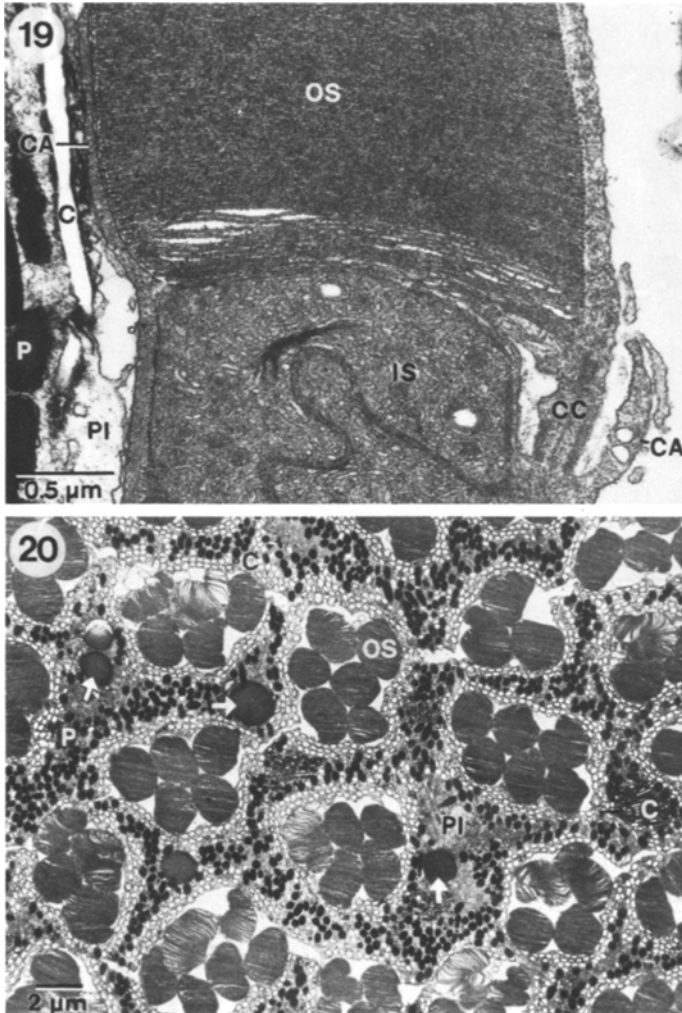
Fig. 19. Radial section of rod from grouped retinal region of *Scopelosaurus lepidus* showing the vitread part of the rod outer segment, the sclerad part of its inner segment, and the connecting cilium

Fig. 20. Tangential section of visual cell layer of grouped retinal region of *S. lepidus*. The rod bundles are located within pits formed by the pigment epithelium cells. The partitions between the pits contain a central core of pigment granules and concentric layers of reflecting crystals. Lipid droplets are seen in some pigment cells (*arrows*). Same lettering as in Figures 5—10

The grouped retinal region seems to contain a single type of visual cells. In light microscopic sections these photoreceptors look like cones; their outer segments are often slightly broader at the base (vitreally) than elsewhere, so that their overall shape is somewhat tapering; they have slightly sclerally tapering inner segments with slightly greater diameters than their outer segments; finally their nuclei pierce the outer limiting zone, which is often the case with cone nuclei in teleost retinae, while rod nuclei are generally located vitread to the outer limiting zone (Fig. 4).
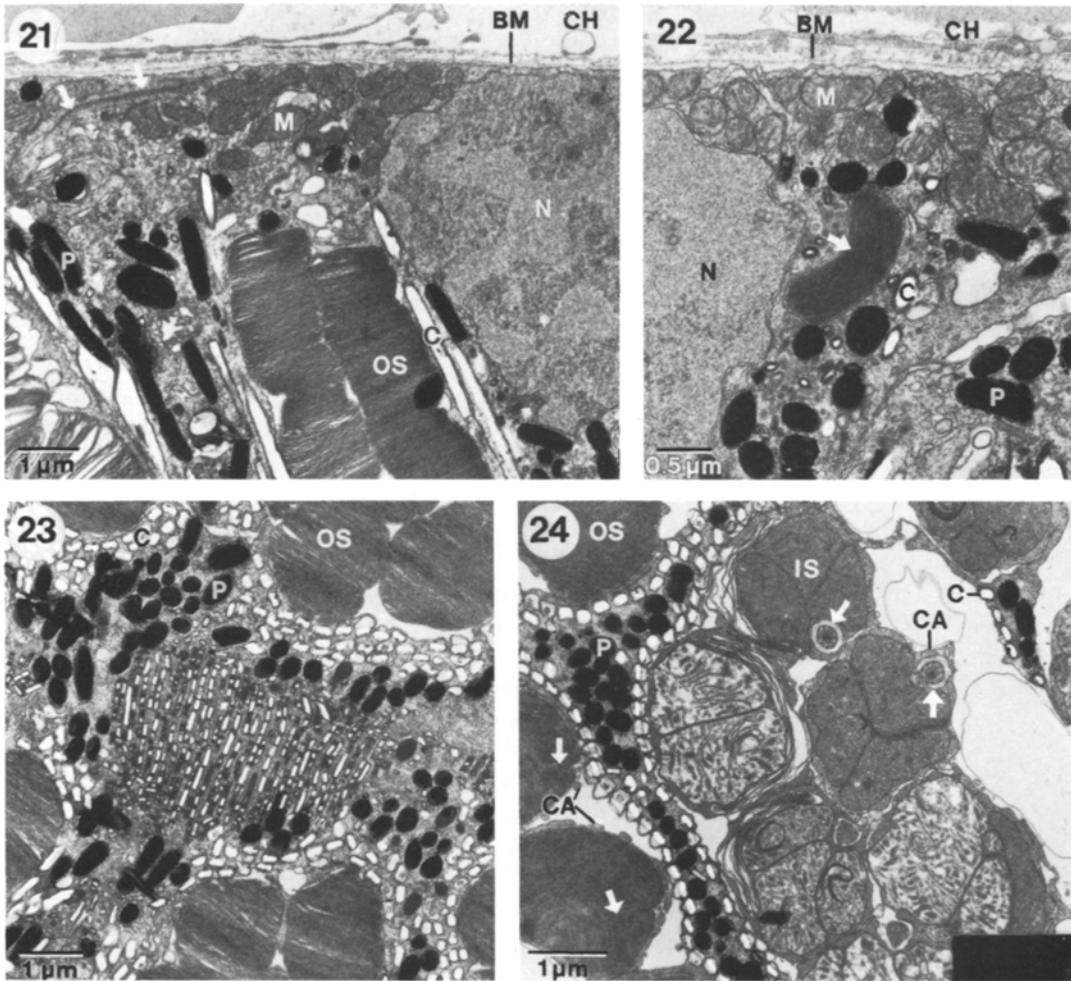
Fig. 21. Radial section through visual cell layer and pigment epithelium of grouped retinal region of *Scopelosaurus lepidus*. The square-cut sclerad ends of two rod outer segments are seen in the centre of the micrograph. Junctions between the two adjacent pigment cells are located close to their bases and comprise a zonula occludens (*left arrow*) and a zonula adherens (*right arrow*)

Fig. 22. Radial section through pigment epithelium cell with phagosome (*arrow*) from grouped retinal region of *S. lepidus*

Fig. 23. Tangential section through part of retinal pigment epithelium process of grouped retinal region of *S. lepidus*. The process contains a pile of radially orientated small crystals seen in the centre of the micrograph. Rod outer segments are seen in the adjacent pits

Fig. 24. Oblique tangential section of rod outer and inner segments of the grouped retinal region of *S. lepidus*. To the left the base (vitread part) of three rod outer segments, two of which show an incisure in the discs (*left arrows*). The section passes through the sclerad part of the rod inner segments, two of which show a clearly recognizable connecting cilium (*right arrows*) located in a radial groove of the inner segment and walled in by calycal processes. The section contains the distal (vitread) part of the pigment cell processes with their pigment granules and crystals. Lettering: *BM* basement membrane of retinal pigment epithelium; *CH* choroid; otherwise same lettering as in Figures 5—10

Examined by electron microscopy the visual cells of the grouped region turned out to be rods.

Radial sections of outer segments passing through the connecting cilium showed that a zone of continuity between discs and plasma membrane at the side opposite to the connecting cilium, if present, is restricted to the few basalmost discs (Fig. 19). Tangential sections of the outer segments show the presence of one or a few incisures in the discs (Fig. 24). No lateral sac is present. The vitread part of the outer segments is surrounded by calycal processes originating from the sclerad part of the inner segments.

The inner structure of the connecting cilia could not be satisfactorily analyzed. There are structures suggesting a ring of nine doublets of tubules. Many connecting cilia posses a peculiar dark core (Fig. 24).

Within any bundle of photoreceptors in the grouped region the connecting cilium of each rod is generally, but not invariably, located at the same side of the cell as in other members of the bundle. Furthermore, the connecting cilia of each bundle tend to have the same location as those of adjacent bundles. Tangential sections of a peripheral piece of grouped retina showed that the connecting cilia of the rods are generally located at the sides opposite to the margin of the retina.

The inner segment, which reaches from the base of the outer segment down to the sclerad pole of the elongated nucleus, is tightly packed with mitochondria with tubular cristae. The teleostean rod inner segment generally consists of a fairly short sclerally located ellipsoid having a cross sectional diameter of the same order as that of the outer segment and containing the major part of the mitochondria, and a comparatively long, vitreally located, contractile myoid which is definitely thinner than the ellipsoid. In *S. lepidus* the rod inner segment is of basically the same shape as that of the cones and likewise almost completely filled with mitochondria.

In the deep-sea teleost *Scopelarchus güntheri* the rod ellipsoids of the grouped main retina have tight junctions connecting them with some or all abutting rods (Locket, 1971). In *Scopelosaurus lepidus* no such junctions have been observed.

The connecting cilium arises excentrically from the sclerad part of the rod inner segment in *S. lepidus*. Though undoubtedly present, no clearly recognizable basal body was seen. No ciliary rootlet was recognized. The connecting cilium is located in a longitudinal groove of the inner segment, usually walled in by calycal processes which project in a sclerad direction from the inner segment (Fig. 24).

The inner segments do not have lateral fins. The small sessile synaptic pedicles contain but a single synaptic ribbon.

Tangential sections show that the number of rods in the bundles generally varies from three to seven. Counts of a total of 85 rod bundles on overlapping low power electron micrographs showed that bundles consisting of four rods are the most common (32 out of 85 bundles). Very rarely a bundle consisting of only two rods is seen.

Whereas the joined (twin and triple) cones of the non-grouped retinal region clearly constitute morphological units, the rod bundles of the grouped region form a more loose aggregation of photoreceptors. The rod outer segments within each bundle do, of course, touch each other, but the vitread part of each outer segment is surrounded by calycal processes, i.e. there is no contact zone without these processes as is the case with the twin and triple cone outer segments. At the inner segment level the rods

within each bundle are lying very close to each other, but no membrane junctions were observed at any level, nor do subsurface cisterns occur as in the contact zones of the joined cones.

2. Retinal Pigment Epithelium

The bases of the retinal pigment epithelium cells facing the choroid are smooth. Junctions between the lateral cell membranes of adjacent cells were observed only very close to the bases of the cells. These junctions comprise zonulae adherentes and zonulae occludentes (Fig. 21). The vitread ends of the zonulae occludentes are located only 1 to 1.5 μm from the base of the cells, indicating that the height of the cells may be that small. The rod outer segment tips reaching farthest sclerad are located at a similar distance from the base of the pigment epithelium cells. Zonulae adherentes are located sclerad to the tight junctions. If the parts of the pigment cells located vitread to the tight junctions may be regarded as processes, only the smaller basal parts of the nuclei are located within the cell bodies.

The lateral walls of the basal part of the cells show rather complex interdigitations both sclerad and vitread to the level of the zonulae occludentes.

As in the non-grouped retinal region the mitochondria are concentrated in the basal parts of the cells. The cytoplasm likewise contains globular lipid droplets (Fig. 20) and occasional whorled structures of concentric lamellae which are continuous with the endoplasmic reticulum.

The nuclei of the pigment epithelium are higher in the grouped than in the non-grouped region, often of a roughly pyramidal shape with the base facing sclerally, the apex vitreally (Fig. 21). In contradistinction to the non-grouped region a few phagosomes were recognized in the basal part of the pigment cells of the grouped region (Fig. 22). These phagosomes are located within the cytoplasm, have lamellae resembling those of the rod outer segments, and are enclosed within a membrane. Abundant smooth endoplasmic reticulum is present both in the sclerad part of the cells and in their processes.

The rod bundles of the grouped region are located within pits formed by the retinal pigment epithelium, the processes of which extend to the sclerad end of the rod inner segments (Figs. 20 and 24).

As in the non-grouped region, each pigment epithelium cell of the grouped region has one stout process. Tangential sections show that the processes of individual cells have an irregular amoeboid shape in cross sections. The pits occupied by the rod bundles are partly located within individual cell processes, and partly formed by adjacent parts belonging to two or three abutting cells. There may be from one to three pits located entirely within a single cell process (Figs. 18 B and 20). The abutting parts of adjacent processes may show interdigitations, but no junctions have been observed.

The pigmented cores within the processes are thicker in the grouped than in the non-grouped region. The mostly radially orientated rod-shaped pigment granules are coextensive with the pits. Except for the pigment granules associated with the pits there are relatively few granules in the basal parts of the cells.

The crystals forming the retinal tapetum are located mostly in concentric layers in the walls of the pits facing the rods (Figs. 20, 23, and 24). These radially orientated

crystals have a maximum length of ca. 3 μm and are parallel-sided plates, their long axes parallel to the walls of the pits. The parallel sides of these 115–130 nm thick crystals face inwards towards the rods within the pits. When cut transversally to their long axis the crystals are seen to have a hexagonal shape. At most levels there are two or three concentric layers of crystals interposed between the pigmented cores and the walls of the pits. Close to the bottom of the pits in the basal part of the pigment epithelium cells there may be only a single layer of crystals. At the distal (vitread) end of the processes the thin partitions between adjacent pits may contain only one or two layers of crystals.

The square-cut sclerad ends of the rod outer segments lie in contact with the pigment epithelium cells (Fig. 21). Occasionally neither pigment granules nor crystals are seen in the part of the pigment cell lying sclerad to the tips of the rods. As a general rule the reflectors located at the tips of the photoreceptor outer segments in the non-grouped retinal region are absent in the grouped region. Only at one location has such a reflector been seen in the grouped region, but whether the visual cell lying vitread to it is a rod or a cone could not be ascertained.

Piles resembling reflectors and consisting of aggregations of ca. 50 nm thick crystals may be found, however, on more vitread levels in the pigment epithelium cells (Fig. 23). These piles are located in the central parts of the partitions between adjacent pits, i.e. at the sites generally occupied by pigment granules, and have another orientation, the parallel sides of the small flat crystals being parallel to the photoreceptor outer segments. The significance of these piles is obscure. Their presence might indicate that cones occur in the grouped region at earlier ontogenetic (larval) stages.

Like the pigment epithelium cells of the non-grouped region those of the grouped region also contain randomly orientated crystals of varying dimensions.

D. Discussion

The gross morphology of the head and eyes of *Scopelosaurus lepidus* is identical with that of the previously examined notosudid species, i.e. *S. lepidus* is specialized in rostral binocular vision (cf. discussion in Munk, 1975).

In what follows the photoreceptors and retinal tapetum of *S. lepidus* will be discussed and compared with those of other deep-sea teleosts, and correlation with the biology of the species will be attempted.

I. Photoreceptors

The evidence from the retinal areas sampled shows that the photoreceptors of *S. lepidus* apparently constitute two spatially separate classes of visual cells. Cones, mostly twin, in the temporal region subserve binocular vision in the rostral direction, while rods grouped in bundles occupy the rest of the retina.

1. Cones

The cone outer segments of *S. lepidus* have a typical shape and structure. The extensive zone of continuity between discs and plasma membrane at the side opposite the connecting cilium and the absence of incisures in the discs are characteristic of vertebrate cones (cf. e.g. Dunn, 1973).

The cone inner segments of *S. lepidus* are atypical insofar as no separate ellipsoid and myoid regions exist. In the bathypelagic deep-sea teleost *Omosudis lowei* the inner segments of both single and twin cones comprise an ellipsoid and a myoid region, the vitreally located myoid region of both cone types bearing lateral fins (Frederiksen, 1976).

In duplex teleost retinae both rods and cones generally occur throughout the retina, though rods may be absent in the fovea. The photoreceptor myoids of shallow-water teleost duplex retinae are known to be contractile, the cone myoids being shortened in the light-adapted state, the rod myoids elongated, and vice versa in the dark-adapted state. These photo-mechanical changes also include migration of the pigment granules of the retinal pigment epithelium. The pigment migration is thought to prevent loss of resolving power in light-adapted retinae by optically isolating the vitreally located cone outer segments, at the same time preventing over-stimulation of the sclerally located rod outer segments; in dark-adapted retinae the cones and pigment granules have moved sclerad, the rods vitread, facilitating the stimulation of rods by weak light (Blaxter and Staines, 1970; Ali, 1975).

Whether photo-mechanical changes can take place in the non-grouped retinal region of *S. lepidus* is unknown, but for various reasons unlikely.

A relevant comparison can be made with the pure-cone larval retinae of various teleost species, which show no change in the position of pigment granules and cones in response to changing conditions of illumination. After the rods have started to develop at metamorphosis, however, pigment migration occurs (Blaxter and Staines, 1970; Blaxter, 1975). These observations suggest that photo-mechanical changes may be restricted to adults of species with duplex retinae living in surroundings exposed to appreciable diurnal changes of illumination. An interesting exception occurs in the duplex retinae of *Stizostedion vitreum* and *S. canadense,* in which the cones are stationary (Zyznar and Ali, 1975).

There are thus no obvious reasons why photo-mechanical changes should take place in *Scopelosaurus lepidus*, because the cones and the rods occur in separate retinal regions. The basic design of the retina with its separate populations of cones and rods located within reflecting pits formed by the retinal pigment epithelium, in which the optical isolation is probably effected primarily by the reflecting crystals, makes it appear unlikely that any advantages might be obtained by changing the position of either the pigment granules or the photoreceptors. It is an open question whether *S. lepidus* may normally encounter diurnal changes of intensity of residual daylight that would call for photo-mechanical changes in a conventionally organized duplex retina.

The functional significance of joined cones and the various types of cone mosaics found in teleosts is unknown (see Munk, 1975, also for references). Double cones in teleosts comprise two types, viz. unequal and equal double or twin cones.

In unequal teleostean double cones the outer segments of the two members contain different visual pigments (Stell and Hárosi, 1976; Loew and Dartnall, 1976), while both members of twin cone outer segments contain the same visual pigment (Svaetichin et al., 1965).

2. Rods

In the light microscope the rods in the grouped retinal region of *S. lepidus* look like cones. Electron micrographs have shown, however, that there is no continuity between the discs and the plasma membrane of the outer segments at the side opposite to the connecting cilium, except for the few most basal discs. This is generally considered the main distinguishing feature between rods and cones, i.e. the rod outer segments consist almost entirely of a stack of isolated discs completely enclosed within the plasma membrane, whereas the discs of the cone outer segments are continuous with the plasma membrane at the side opposite to the connecting cilium.

Furthermore, the rods of the grouped region differ from the cones of the non-grouped region by having incisures in the outer segment discs, by the absence of lateral sacs, lateral fins on the inner segment, specialized contact zones (no subsurface cisterns) characteristic of joined cones, and by having only a single synaptic ribbon in the pedicles.

The rod inner segments of *S. lepidus* are atypical insofar as they do not consist of a separate ellipsoid and myoid region. They have the same structure and a sclerally tapering shape as those of the cones. This may possibly be associated with the different light-collecting properties of conventionally shaped rods and cones.

The light-collecting properties of cones are known to be superior to those of conventionally shaped rods (cf. Tobey et al., 1975, also for references). The tapering shape of the cone ellipsoid is thought to funnel the incident light energy from the inner segment to the outer more efficiently than does the rod ellipsoid (cf. e.g. Enoch, 1963). The fairly massive, slightly tapering rod inner segments of *S. lepidus* may thus be supposed to funnel the light energy to the outer segment more effectively than conventionally shaped rod inner segments, which may be important under threshold conditions.

3. Comparisons with Other Deep-Sea Teleosts

That most deep-sea teleosts have pure-rod retinae is hardly surprising, since rods are generally regarded as scotopic, and cones as photopic receptors.

Some deep-sea teleosts have been reported to possess a relatively small proportion of cones in otherwise rod-dominated retinae, viz. the benthic *Lycodes lavalei* (Ali and Hanyu, 1963; Anctil, 1969), *L. reticulatus*, and *Agonus decagonus* (cf. Anctil, 1969) which are found on the shelf and the continental slope, and the mesopelagic, *Sebastes marinus* (Wunder, 1958; Hanyu and Ali, 1962; Ali and Hanyu, 1963).

In a few deep-sea teleosts, however, the cones are of obvious importance to vision as is apparent from the proportion of cones to rods or the location of the cones within the retina.

Among these species the bathypelagic *Omosudis lowei* has a retina which may be regarded as cone-dominated insofar as the cone inner and outer segments constitute the bulk of the visual cell layer throughout the retina (Munk, 1965; Frederiksen, 1976). In the remaining species cones are restricted to a circumscribed retinal region subserving binocular vision, viz. in the bathyal *Chlorophthalmus albatrossis* (Tamura, 1957; Somiya and Tamura, 1971) and the mesopelagic *Diretmus argenteus* (cf. Munk, 1966 b). *C. albatrossis* has dorsally directed eyes and a ventrally located retinal zone containing no other visual cells than twin cones and subserving binocular vision in a dorsal direction. *D. argenteus* has laterally directed eyes with a small cone-containing zone located close to the margin of the retina slightly below the horizontal meridian and subserving binocular vision in a rostral and slightly dorsal direction.

Scopelosaurus lepidus shows the same specialization, i.e. cones located within a circumscribed region subserving rostral binocular vision. It is very likely that this specialization is also present in the two previously examined notosudids, one of which, viz. *Ahliesaurus berryi*, is also a deep-sea species (Munk, 1975). On the light microscopic level their retinae is of a structure identical with that of *S. lepidus*. This might indicate that two spatially separate classes of visual cells also occur in those two species.

The present study has shown that visual cells looking like cones in the light microscope, viz. the rods in the grouped retinal region of *S. lepidus*, may turn out to be rods when examined by electron microscopy. Most observations of cones in deep-sea teleosts are based on light microscopic studies. At present the cone-nature of some of the visual cells has been confirmed by electron microscopy only in two species of deep-sea teleosts, viz. *Omosudis lowei* (cf. Frederiksen, 1976) and *S. lepidus*.

Grouped retinae or grouped retinal regions occur both in shallow-water and deep-sea teleosts (Locket, 1971; Zyznar, 1975; Zyznar and Ali, 1975; also for references). In deep-sea teleosts a partly grouped retina has previously been described in *Evermannella indica* (cf. Munk, 1966 a), *Scopelarchus güntheri* (cf. Locket, 1971), *Chlorophthalmus albatrossis* (Somiya and Tamura, 1971; Somiya, 1975), and *Ahliesaurus berryi* (cf. Munk, 1975). A partly grouped retina undoubtedly also occur in *Evermannella atrata = Coccorella atrata*, though Brauer (1908) did not describe its appearance in tangential sections. The grouped photoreceptors of the notosudid *A. berryi* were described as cones, but they look exactly like the grouped photoreceptors of *Scopelosaurus lepidus* and may well turn out to be rods when examined by electron microscopy. The grouped photoreceptors of all other deep-sea teleosts mentioned above are rods. All teleosts with grouped photoreceptors examined so far have or are very likely to possess a retinal tapetum.

The functional significance of grouped receptors is unknown. Locket (1971) has suggested that each group of rods in *Scopelarchus* may function as a macro-receptor. Locket pointed out that the rod bundle within each reflecting pit is optically isolated from these of adjacent pits, but that there is no isolation of the receptors within a pit. This is also the case in *Scopelosaurus lepidus*. The resolving power of grouped retinal regions is thus lower than the potential resolving power of non-grouped retinal regions. There is no doubt, however, that the retinal sensitivity is increased. The fact that light can be reflected back and forth between the walls of the reflecting pits may more than double the amount of light absorbed at any ambient light intensity (Zyznar, 1975 a);

it may furthermore ensure that all receptors are about equally activated which may perhaps increase the sensitivity by facilitating summation (Locket, 1971).

One can only speculate whether the occurrence of both cones and rods in the retinae of some deep-sea teleosts indicates the presence of cone and rod visual pigments showing differences in the wavelength of maximally absorbed light. Owing to their smaller degree of summation (i.e. number of photoreceptors per ganglion cell), cone-rich retinae are generally assumed to have a greater resolving power than rod-rich retinae. Cone-rich retinae (e.g. that of *O. lowei*) or pure-cone retinal zones (e.g. the temporal non-grouped retinal region in *S. lepidus*) may consequently have been developed with the purpose of establishing a fairly high resolving power. Whether the photoreceptors are cones or rods, however, it would seem to be an advantage if they possess a visual pigment that is spectrally matched to the residual daylight and the generally blue luminescent light. The two separate retinal regions of *S. lepidus*, the pure-cone and the pure-rod regions, may thus essentially be regions of different resolving powers but showing the same wavelength of maximally absorbed light.

Nothing is known about the visual pigments of *O. lowei* and *S. lepidus*. According to Frederiksen (1976) the light reflected maximally by the 65 nm thick crystals of the reflectors in *O. lowei* has a wavelength of 470 nm in air. One may suppose that the wavelength of maximally absorbed light in the cones of *O. lowei* corresponds to that of the light maximally reflected by the reflector crystals, i.e. that its retina is particularly sensitive to blue light like the pure-rod retinae of other deep-sea teleosts (cf.e.g. Munz, 1971, also for references). Clear oceanic water shows maximum transmission of quanta having a wavelength of c. 470 nm in air (Jerlov, 1951). The luminescent light in the deep-sea is also generally markedly blue (cf.e.g. Tett and Kelly, 1973), i.e. its spectral composition corresponds fairly well to that of the residual daylight. A blue-sensitive retina is thus spectrally matched both to the residual mainly downward directed daylight and most of the bioluminescence. Spectral matching with the residual daylight enhances the contrast of dark objects against the background and hence their visibility.

The absolute threshold for light in the retinae of deep-sea teleosts is unknown, but it has been estimated that they might be able to perceive daylight at noon down to a depth of c. 1000 m (Clarke and Denton, 1962), maybe even 1300 m in very clear oceanic water (Clarke and Kelly, 1964). Bathypelagic teleosts like *O. lowei* are thus generally supposed to stay below the limit, down to which residual daylight may be perceived.

It has unfortunately not been possible to get any reasonably reliable measurements of the thickness of the crystals in the reflectors of *S. lepidus*. Information on the thickness of the crystals in the reflectors of *O. lowei* is based on many measurements of the distance between the middle of the two parts of the enclosing membrane applied to the flat parallel sides of individual crystals (Frederiksen, personal communication). The slightly lower figure given for *S. lepidus* (50—55 nm) in the present paper is based on measurements of the width of the rectangular empty spaces seen in the electron micrographs. A very thin granular layer was often seen to be applied to the inside of the membrane enclosing the crystals, i.e. the technique of measurements used for *S. lepidus* will in itself give slightly lower figures.

II. Retinal Tapetum

Individual vertebrate retinal pigment epithelium cells generally have a number of processes that surround the photoreceptors in the visual cell layer.

Fineran and Nicol (1974) give detailed information on the processes of the labrid pigment cells. The cone outer segments (double and single cones) are usually completely surrounded by processes, those of the rods only so at their sclerad ends. The sheaths around individual photoreceptor outer segments are formed by several processes.

Contrarily, in *Scopelosaurus lepidus* each pigment cell has but a single stout process. Each unit of photoreceptor outer segments (a single cone, a pair of twin cone, a triplet of triple cone, or a bundle or rod outer segments) is completely ensheathed within pits formed by the pigment cells. The pits may be located entirely within an individual process or formed by adjacent parts of two or three individual processes.

In the grouped main retina of the deep-sea teleost *Scopelosaurus güntheri*, which has a retinal tapetum, each pigment epithelium cell also has a single process. Each pigment cell has a base shaped like an equilateral triangle, with a centrally located nucleus, and a single central process with three curved surfaces facing the rod bundles of three adjacent pits. Each reflecting pit is formed by parts of six abutting processes, i.e. one of the curved surfaces from each of six adjacent pigment cells (Locket, 1971) (Fig. 25). The pigment granules show a similar type of distribution as in the larger part of the non-grouped retinal region of *Scopelosaurus lepidus*, i.e. they are located preferentially on the vitread side of the nuclei at the origin of the processes, and in the core of the distal (vitread) part of the processes.

In the deep-sea teleost *Omosudis lowei*, which has a retinal tapetum very much like that of *S. lepidus*, the sheath around each single cone is formed by several processes (Frederiksen, 1976). The pigment granules are found preferentially in the basal part of the pigment cells and in the distal part of their processes.
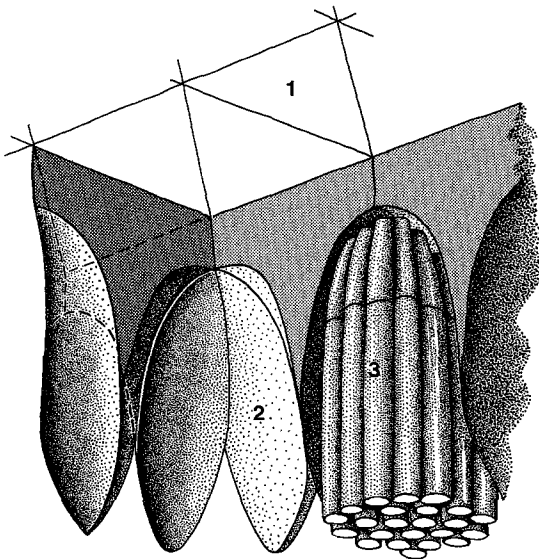

Fig. 25. Diagram of reflecting pits formed by the retinal pigment epithelium in the grouped main retina of the tubular eye of the deep-sea teleost *Scopelarchus güntheri*. The bases of the pigment cells are triangular (*1*) and each cell has a single process. Each pit (*2*) is formed by parts of six abutting processes. The pit to the right contains a bundle consisting of 23 rods (*3*). Redrawn from Locket (1971, Fig. 16; p. 171)

Tapeta lucida may be located either in the choroid or in the retinal pigment epithelium. Tapeta are found in animals inhabiting environments characterized by low ambient light intensities (e.g. turbid waters, the deep sea) or animals active wholly or in part during diurnal periods of low levels of illumination, e.g. totally or partly nocturnal or crepuscular species. In principle tapeta increase the effective sensitivity of the eye by reflecting the incident light so that it can pass through the photoreceptor outer segments more than once. Tapeta generally occur in eyes with rod-dominated or pure-rod retinae with a fairly low resolving power.

Various types of retinal tapeta occur in a large number of shallow-water teleosts inhabiting coastal or fresh waters characterized by low levels of illumination. Some of these species are crepuscular or nocturnal (Nicol et al., 1973, 1975; Nicol, 1975; Zyznar and Ali, 1975).

Deep-sea teleosts also possess retinal tapeta of different types. The nature of the tapetum of *Evermannella atrata* = *Coccorella atrata* described by Brauer (1908) is unknown. *Malacosteus niger* has a bright red tapetum consisting of astaxanthine-containing lipid droplets (Denton et al., 1970; Denton and Herring, 1971; Locket, 1975). Brauer (1908) suggested the presence of a retinal tapetum in *Malacosteus indicus*, the eye-fundus of which gave a purple reflexion in the freshly caught specimen. *M. indicus* is possibly identical with *M. niger* (cf. Morrow, 1964). *Chlorophthalmus albatrossis* probably has a guanine tapetum (Somiya, 1975).

In the remaining deep-sea teleosts known at present to possess a retinal tapetum, viz. *Scopelarchus güntheri, Omosudis lowei,* and *Scopelosaurus lepidus*, the reflective material in the pigment epithelium is known to consist of crystals. The crystals found in *Scopelarchus güntheri* were believed to be of guanine (Locket, 1971), a suggestion that is also likely to be true as regards the crystals present in *Scopelosaurus lepidus*. Thin layer chromatography has shown that the tapetal crystals in *Omosudis lowei* most probably consist of guanine (Frederiksen, 1976).

The sensitivity-increasing effect of the reflecting pits of *S. lepidus* was discussed in the section on the rods. A structure deserving special attention is the cylindrical pile of small reflecting crystals, the reflector, located at the tips of the cone outer segments.

Reflectors were recognized for the first time in the duplex retina of *Omosudis lowei* (cf. Frederiksen, 1976). The dominating photoreceptor elements in the retina of this species are the single cones; twin cones occur in a small ventro-temporal retinal zone. Each single cone outer segment or pair of twin cone outer segments is located in a reflecting pit formed by pigment cell processes containing concentric layers of elongated crystals. The largest specimen examined (253 mm in standard length) had a reflector located at the tip of each single cone outer segment. Reflectors are mostly lacking in the twin cone zone, except for the narrow border area, where each member of a pair of twin cone outer segments has its own reflector. No reflectors were found in association with the rods. Reflectors were absent in the two smaller specimens examined (58 and 145 mm in standard length, respectively), which is remarkable, because they live at the same depth as the large specimen.

The facts that the two members of each pair of twin cone outer segments of *S. lepidus* lie in close contact within the reflecting pit, and that a common reflector is located at their tips, make it unlikely that photic stimulation of one member is possi-

ble without stimulation of the other, i.e. a twin cone is probably the smallest functional photoreceptor unit within the fovea.

So far reflectors apposed to outer segments have only been observed in these two species of deep-sea fishes, *O. lowei* and *S. lepidus*. Reflectors may also be present, however, in the non-grouped pure-cone retinal region of the notosudid deep-sea teleost *Ahliesaurus berryi*, in which peculiar bodies located in the pigment epithelium apposed to the tips of the cone outer segments have been observed (Munk, 1975).

Frederiksen (1976) called attention to the fact that reflectors directly apposed to the cone outer segments minimize scattering and thus increase the sensitivity with minimal loss of resolving power. This would be particularly important in *O. lowei* where the summation is low and the potential resolving power consequently high (Munk, 1965, 1966 a, p. 54). Similar conditions are probably found in the non-grouped pure-cone retinal region of *S. lepidus*; the summation is probably especially low in the fovea.

Discussing a model in which the tapetum is a reflecting surface located immediately sclerad to the light-absorbing layer of the retina, Zyznar (1975 b) concluded, inter alia, that the tapetum can lower the absolute threshold by increasing the retinal absorption of light, that it is most efficient when associated with a retina of moderate absorbance, and that the gain in sensitivity is highest at very low intensities near the absolute threshold of vision.

These conclusions are particularly relevant to the situation in *O. lowei* and *S. lepidus*, in which the reflectors are directly apposed to the tips of the cone outer segments. Reflecting pits with reflectors directly apposed to the cone outer segments are probably a most efficient arrangement for obtaining maximum stimulation of the photoreceptors within the pits, because scattering at the bottom of the pits is minimized.

It has been suggested that a reflecting tapetum is an alternative sensitivity-increasing device to that of augmenting the amount of visual pigment in the photoreceptor outer segments (Denton and Nicol 1964). The effective sensitivity of a retina may be limited by the noise due to spontaneous breakdown of visual pigment. An increase of the amount of visual pigment would increase the noise level altering the signal-to-noise ratio, so that the effective sensitivity would not be increased correspondingly to the increase of the amount of visual pigment. Comparing the two methods, viz. the use of a tapetum and the increase of the amount of visual pigment, it is apparent that, for example, a doubling of light absorption can be achieved either by means of a tapetum or by doubling the amount of visual pigment. With the former method, however, there is no increase in the noise level, the signal-to-noise ratio is increased and thus a greater effective increase of sensitivity may be obtained.

Both in *O. lowei* and *S. lepidus* reflectors are apposed to the cone outer segments, not to those of the rods. This may mean that the increase of sensitivity of the cones is effected by combining a moderate increase of the amount of visual pigment in their outer segments with a very efficient reflector apposed to their tips.

The absence of reflectors in the grouped pure-rod retinal region of *S. lepidus* may indicate that the amount of visual pigment is greater in the rods than in the cones. The optical density of an individual photoreceptor depends on the amount of visual pigment per unit length of the outer segment. High densities of visual pigment have been found

in the retinae of deep-sea teleosts (Denton and Warren, 1957; Denton, 1959). It has been suggested that their blue-sensitive rod pigments may be more stable than other rod pigments and that the spontaneous breakdown of visual pigment is maintained at a fairly low level because of the low temperature in the deep sea.

III. Fovea

The deep convexiclivate fovea is characteristic of all notosudid species, the majority of which inhabits the deep sea (Bertelsen et al., 1976). Apart from the notosudid deep-sea species, foveae are known to occur in but a small number of deep-sea teleosts (cf. Table 2 in Munk, 1975), all of which are characterized by possessing pure-rod retinae.

The two previously examined notosudids possess a pure-cone fovea (Munk, 1975). These two species represent extremes in the vertical distribution ranges of notosudids, one being a deep-living epipelagic species (*Scopelosaurus hoedti*), the other a meso- and bathypelagic species (*Abliesaurus berryi*). *S. lepidus* is a deep-sea species with an intermediary vertical distribution (Bertelsen et al., 1976). Even though only the eyes of three notosudid species have been examined so far, it appears likely that all noto- sudids possess pure-cone foveae.

The teleostean fovea is undoubtedly a retinal zone of particularly high resolving power as is apparent from the great number of ganglion cells present in the foveal region. In shallow-water teleosts it has been demonstrated that the foveal projection on the optic tectum of the mid-brain is magnified as compared with other areas of the visual field (Schwassmann, 1968).

It is possible to obtain a crude estimate of the potential resolving power of the foveal centre of *S. lepidus*. As stated in the section on the retinal tapetum it seems likely that a twin cone is the smallest functional photoreceptor unit within the fovea. The maximum resolving power of the foveal centre based on the average twin cone density can be calculated according to a previously employed method (Munk, 1975, Table 3, footnote 7). Assuming a twin cone density corresponding to 180,000 per mm^2 in the foveal centre, a uniform linear retinal shrinkage of 10 % which has been found in similarly fixed and processed mammalian retinae (Ogden, 1975), and a lens diameter of 0.88 mm (the lens diameter of the 48 mm specimen of *S. lepidus*), the potential angular resolving power will be ca. 8.6 min. of arc. The maximum resolving power of the foveal centre of the specimens of *S. lepidus* examined is thus of the same order as that of a specimen of the shallow-water species *Syngnathus typhle* having an eye of corresponding size (cf. Table 3 in Munk, 1975).

IV. Eye Structure and Biology

Adult specimens of *Scopelosaurus lepidus* have been caught in the mesopelagic zone far from the bottom, but may also spend a benthopelagic life at depths of 500 — 800 m in some areas (Bertelsen et al., 1976). This species consequently live above the 1000 m limit of depth, down to which deep-sea fishes are generally thought to be able to perceive residual daylight.

The main food of all notosudids seems to be zooplankton, small and juvenile spe- cimens feeding on small crustaceans, adult specimens on larger crustaceans. The major

food items of adult specimens of *S. lepidus* are euphausiids and hyperiids and very large specimens may also prey on fishes (Bertelsen et al., 1976).

A precise recognition of the location and movements of prey animals in the deep sea is no easy task. A successful encounter is hardly feasible unless foveal fixation can be maintained during approach. The prey may itself be luminous, or may be illuminated by nearby luminous organisms, or may be seen as a shadow against a slightly lighter background. Many of the clues that are available under photopic conditions are absent in the deep sea. It is known, for example, that the threshold values for movement in man are lower if the visual field contains stationary objects which may serve as fixed reference points, or if the target moves across a detailed background (Duke-Elder and Weale, 1968, p. 673). Neither of these conditions is fulfilled in the free body of water in the deep sea. The problem of foveate deep-sea teleosts is probably to maintain fixation of targets once perceived in an environment that through its lack of useful visual clues corresponds fairly closely to an optically empty space.

The eye of *S. lepidus* resembles that of other foveate deep-sea teleosts by possessing a large rostral aphakic aperture providing for an increase of the relative illumination of foveal images (Munk and Frederiksen, 1974). It is remarkable by having a deep convexiclivate pure-cone fovea, because this type of fovea is generally supposed to be present only in strictly diurnal vertebrates.

Current theories on the function of the deep convexiclivate type of fovea are based on the supposition that the refractive index of the retina is slightly higher than that of the vitreous (Walls, 1937, 1940, 1942; Pumphrey, 1948). Pumphrey's analysis emphasizes two effects due to refraction of light at the vitreo-retinal boundary on images moving across the centre of the deep symmetrical convexiclivate fovea, viz. distortion of their shape and changes in their angular velocities relative to those of their objects. He suggested two basic functions of this type of fovea, viz. the maintenance of accurate foveal fixation of objects, and the appreciation of their angular movements.

The presence of a deep convexiclivate fovea in a deep-sea teleost like *S. lepidus* fits well with this theory. The fairly high potential resolving power of the foveal centre of *S. lepidus* may imply a correspondingly low threshold for minimal angular displacement of images which will increase the possibility for maintaining the fixation of the relatively small prey animals.

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