OCULAR DEGENERATION IN DEEP-SEA FISHES

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INTRODUCTION

In teleosts ocular degeneration is known in fresh-water species living in lightless subterranean habitats, in crevice-dwelling and burrowing marine shallow water species, and in some deep-sea fishes. There is furthermore evidence of degeneration of the migrating eye in some Soleids (EVERMANN & SEALE 1907: 106, CHABANAUD 1946).

The anatomy of the degenerated eyes of a comparatively large number of cave-fishes and of some marine species from shallow water is known (for references see MUNK 1964 a). As regards deep-sea fishes our knowledge is, however, rather restricted. If records based exclusively on dissection (GARMAN 1899, HARRY 1952) or on the size and outer aspects of the eyes (cf. e. g. THINES 1955) are excluded, we are actually left with only five clearcut cases of ocular degeneration in deep-sea fishes, viz. the two species described by BRAUER in 1908 (*Barathronus affinis* Brauer, 1906 and a *Cetomimus* sp.) and the three species described by MUNK (1964 a). *Barathronus affinis* was caught in a trawl which had worked at the bottom at appr. 2900 m (cf. BRAUER 1906). It was thought to be a benthic fish by BRAUER, but according to NYBELIN (1957) the *Barathronus* spp. are most likely pelagic. The *Cetomimus* sp. was caught in an open net between a depth of 2000 m and the surface. The vertical distribution of the cetomimids is appr. 1000-3000 m (for references see ROFEN 1959).

A number of species which have probably degenerated eyes are known from the deep-sea (cf. e. g. THINES 1955). As regards these cases, where the ocular anatomy is actually unknown, the functional state of the eyes is inferred from their size and outer aspect. It may thus be mentioned that adult female deep-sea angler fishes, mostly found at about 2000 m (BERTELSEN 1951), are generally held to have degenerated eyes because of the small size of the eyes. Yet females of three species examined failed to show any evidence of ocular degeneration (MUNK 1964 b). To this may be added the recent demonstration of heavy ocular degeneration in three deep-sea fishes in which the outer aspects of the eyes did not show the slightest indication of degenerative features, viz. *Bathypterois longipes* Günther, 1878 (vertical distribution appr. 800-5900 m), *Careproctus kermadecensis* Nielsen, 1964 (caught at 6660-6770 m), and *Bassogigas profundissimus* (Roule, 1913) (vertical distribution appr. 5600-7200 m), cf. MUNK (1964 a).

Degenerated or functional eyes thus occur in different species which show an extensive overlap in their known vertical distributions (*Cetomimus* v. adult female deep-sea angler fishes), and species with small eyes which appear normal on gross examination can actually show definite histological evidence of ocular degeneration *(Bathypterois longipes, Careproctus kermadecensis, Bassogigas profundissimus)*.

It is apparent from the above-mentioned that statements concerning ocular degeneration in deep-sea fishes should only be seriously considered in so far as they are based on evidence obtained by adequate histological methods. In order to get reliable evidence of ocular degeneration in deep-sea fishes and its relation to environmental light conditions it is obviously necessary that more species are examined. The present article is an attempt to shed further light on these problems. Species with various degrees of ocular degeneration were selected from a larger material of deep-sea fishes. Degenerative features were found only in deep-living species, and this is the reason why so few adequately fixed specimens were available.

MATERIAL AND METHODS

Eyes from the following nine species were examined:

1. *Benthosaurus grallator* Goode & Bean, 1886 (Bathypteroidae). Standard length: 305 mm. *Galathea* St. 217. Depth: 3390 m. The vertical distribution of this species which is known to be benthic (Plate III, Fig. 3) is appr. 2100-3500 m (GREY 1956). 8µ horizontal sections of right eye.

2. *Bathymicrops regis* Hjort & Koefoed, 1912 (Bathypteroidae). Standard length: 95 mm. Swedish Deep Sea Exped. St. 363. Depth: 5044-5033 m. This species is thought to be benthic. Vertical distribution appr. 4250-5300 m (GREY 1956, NYBELIN 1957). 8µ sections at right angles to equator of eyeball of left eye.

3. *Ipnops murrayi* Günther, 1878 (Bathypteroidae). Length appr. 90 mm. *Galathea* St. 238. Depth: 3960 m. This species is thought to be benthic. Vertical distribution appr. 1450-4000 m (GREY 1956). 8µ transverse sections of head.

4. *Macrouroides inflaticeps* Smith & Radcliffe, 1913 (Macrouridae). Total length: 460 mm (tip of tail missing). *Galathea* St. 266. Depth: 4700-4970 m. Estimated fishing depth: 3400-3800 m. The type was caught at 746 m (RADCLIFFE 1913), the *Galathea*-specimen appr. 1200 m above the bottom. 8µ vertical sections at right angles to equator of eyeball of right eye.

5. *Echinomacrurus mollis* Roule, 1916 (Macrouridae). Length of head: 74 mm. Swedish Deep Sea Exped. St. 401. Depth: 5000-5025 m. This species is thought to be benthic. Vertical distribution appr. 5000-5400 m (NYBELIN 1957). 8µ horizontal sections of left eye.

6. *Gyronomimus* sp. (Cetomimidae). Standard length: 92 mm. *Galathea* St. 316. Depth: 3170 m. Estimated fishing depth: 1700-1900 m. This species is probably pelagic. 8µ vertical sections at right angles to equator of eyeball of left eye.

7. *Ditropichthys storeri* (Goode & Bean, 1895) (Cetomimidae). Length unknown. Eastern North Pacific, 41°18'N., 168°21' W. Estimated fishing depth unknown. This species is probably pelagic. Vertical distribution appr. 1200-2800 m (GOODE & BEAN 1895, HARRY 1952, KOEFOED 1955, PARR 1928). 8µ horizontal sections of right eye.

8. *Barathronus erikssoni* Nybelin, 1957 (Brotulidae). Standard length: 78 mm. Swedish Deep Sea Exped. St. 342. Depth: 5250-5300 m. The only specimen known is the type specimen. According to NYBELIN (1957) the *Barathronus* spp. are probably pelagic. 8µ sections at right angles to equator of eyeball of right eye.

9. *Sciadonus kullenbergi* Nybelin, 1957 (Brotulidae). Standard length: 105 mm. Swedish Deep Sea Exped. St. 387. Depth: 4540-4600 m. The only specimen known is the type specimen. This species is thought to be benthic (NYBELIN 1957). 8µ horizontal sections of right eye.

The specimen of *Ipnops murrayi* was fixed in Bouin's fixative. This is actually one of the previously examined specimens (MUNK 1959). The remaining specimens were fixed in formalin. The eyes were embedded in paraffin and cut into serial sections. The sections were stained with Ehrlich's hematoxylin and eosin, PAS, Alcian blue (AB) (1 % AB in 1 % acetic acid), AB-PAS, and tetrachrome (AB-Chlorantine fast red-orange G-Weigert's iron hematoxylin). Depigmentation was made according to CHESTERMAN & LEACH (1958).

RESULTS

1. Benthosaurus grallator

Benthosaurus is a true benthic fish as is known from photographs taken by Captain G. Houot from a bathyscaphe (Plate III, Fig. 3). The gross structural features of the very small excellently fixed eye are apparent from Plate IV, Figs. 1-2. On the intact specimen an aphakic aperture was seen between the lens and the rostral, dorsal, and temporal parts of the very narrow iris. The aphakic aperture is comparatively broad rostrally and temporally, very narrow dorsally.

The sclera is fibrous only around the optic nerve which emerges from the ventralmost part of the medial wall of the eyeball. The scleral cartilage is excessively thickened rostrally and temporally. Scleral bones are absent.

The lens appears slightly flattened on the sections. This is probably an artefact due to cutting. No pathological features were recognized. A little lens muscle is situated medio-ventrally, on the inside of the iris at the pupillary margin. It is attached to the lowermost part of the lens (Plate IV, Fig. 3).

The choroid is very thick, but only sparse, pigmented connective tissue membranes are present between the choriocapillaris and the inside of the sclera. PAS-positive granules and needle-shaped bodies of unknown significance were observed in the cytoplasm of the erythrocytes (Plate VI, Fig. 4).

A considerable number of macrophages is found in the choroid and in the interior of the eye. In the choroid typical ameboid macrophages with vacuolized cytoplasm and one or two often lobulated nuclei are seen (Plate VII, Fig. 5). Furthermore, a number of monocyte-like cells with an excentric round, oval, or kidney-shaped nucleus and a practically homogeneous cytoplasm is present. From this cell type the macrophages are undoubtedly derived, because each imaginable intermediary stage was actually present. This is well in accordance with the observation of Lewis & Lewis (1926) on living blood cells from teleosts studied in hanging drops. They found that macrophages originate from monocytes. In Benthosaurus rounded cells completely filled with vacuoles and with a peripherally situated irregularly contoured nucleus are also present (Plate VII, Fig. 4), and probably belong in the macrophage series. A varying amount of retinal pigment granules is found in some macrophages.

The Iris. A narrow zona ciliaris (Rochon-Du-vigneaud 1943: 274) is seen between the ora terminalis retinae and the iris. The stroma of the iris is practically absent. No vessels are found and only a few collageneous fibres were recognized in depigmented sections. The front of the iris is covered with an endothelium. There is no ligamentum annulare in the angle of the anterior chamber.

The anterior cell layer of the pars iridica retinae shows both varying thickness and pigmentation (Plate V, Fig. 3). The posterior cell layer is pigmented only near the pupillary margin. The shape of the cells is most variable in the posterior layer, from cuboidal to low endothelium-like cells. Lobulated or quite irregularly contoured nuclei were recognized in both cell layers. No proliferative changes were noted. A short choroid fissure is situated medio-ventrally, immediately below the lens muscle (Plate V, Fig. 1).

The retina is thicker rostrally and temporally than centrally (Plate IV, Fig. 2). The thickness of the retina in the horizontal meridian was found to be appr. 110μ rostrally, 100μ temporally, and only 80μ in the central part of the fundus. The distance from the external limiting membrane to the tips of the acromeres is appr. 30μ throughout the retina.

The retinal pigment epithelium (Plate V, Fig. 4) is a pseudostratified columnar epithelium of the same type as that found in Bathypterois longipes (Munk 1964 a). The height of the cells varies in accordance with the varying thickness of the retina. Pigment is mostly found only in the proximal (sclerad) part of the cells which show a very heavy pigmentation, particularly in the fundus. A considerable variation in pigmentation is seen, especially in the peripheral parts of the retina, near the ora, where only few pigment granules are seen in some cells (Plate V, Fig. 2). The retinal pigment granules show some variation in size, but are definitely larger than the choroidal granules. Needle-shaped granules are also present in the pigment epithelium, particularly in the fundus. Some pigmentation of the distal part of the cells is seen locally, but pigmented processes were not recognized.

In sections stained with hematoxylin a row of dots representing terminal bars is seen (Plate V, Fig. 4, Plate VII, Fig. 2). Locally a faint line is seen to connect the terminal bars, the so-called Verhoeff's membrane (cf. Verhoeff 1903, Arey 1932: 1215, and Fine 1961). The terminal bars of the pigment epithelium mark the "free" surface of this

cell layer, and the parts of the cells which are situated distally (vitread) of these are consequently processes. Two types of processes are present, viz. very broad conic processes, and thin processes, both of which reach the ellipsoids of the visual cells. In both types bundles of fine filaments are frequently seen in sections stained with hematoxylin (Plate V, Fig. 4, Plate VII, Fig. 2). Locally part of the filaments can be followed to the terminal bars. Terminal bars with associated filaments have been described in the retinal pigment epithelium of the frog eye (PORTER & YAMADA 1960), but as far as I know filaments have never been recognized in the processes of the pigment epithelium.

Peculiar PAS-positive round or oval bodies, 1.3-5μ large, are present in the cytoplasm (Plate VI, Fig. 4). They are particularly concentrated in the proximal zone and the largest show a concentric structure. These bodies are most probably *myeloid bodies* as described by KÜHNE (1879: 246) (cf. also ANGELUCCI 1878: 361-363). In the light microscope myeloid bodies show the same staining characteristics as the acromeres of the visual cells (PORTER & YAMADA 1960, OKUDA 1962).

There is evidence of detachment from the basement membrane and inward (vitread) migration of single cells from the pigment epithelium. Various stages of this process are seen in Plate VI. This detachment of single cells is probably not an artefact. Epithelia are often seen to be detached from their basement membranes, particularly in poorly fixed histological specimens, but they never show single detached cells displaced in relation to adjoining cells.

Inward migration of cells from the pigment epithelium have been reported from cases of hereditary retinal degeneration in mammals, e.g. the rat, in which DOWLING & SIDMAN (1962) have identified these migrating cells critically in the electron microscope. In *Benthosaurus* a considerable number of peculiar cells with a high content of PAS-positive bodies and a varying amount of retinal pigment granules is present at the tips of the rod outer segments. These cells are probably phagocytic, because fragments of rod acromeres were observed within a few of them (Plate VII, Fig. 3). As far as can be ascertained the PAS-positive bodies are identical with the myeloid bodies described above. This might indicate that inward-migrating cells from the pigment epithelium can be transformed into ameboid cells as in the rat (DOWLING & SIDMAN (1962) found no evidence of phagocytosis

in this animal). In tissue culture of retinal pigment epithelium from chick embryo GOGLIA (1955) states to have observed the transformation of some cells into macrophages. The cells are detached, pseudopodia are developed, the pigment granules are aggregated into clumps and finally lost. Whether a similar process has taken place in *Benthosaurus* cannot be stated with certainty, but typical macrophages were not observed in the retina. This does not prove, of course, that the cells situated at the tips of the degenerating acromeres are not macrophages of the same type as those found elsewhere in the eye, but I find it unlikely that so large a number of myeloid bodies should have been ingested and remain unaltered in the cytoplasm.

The Retina Proper. In the best developed rostral part of the retina three nuclear layers are clearly seen. The stratification is not quite regular since some nuclei are situated in the outer plexiform layer. In the remaining part of the retina the typical stratification has been lost (Plate VI) except in some temporal areas. Rostrally 3-4 rows of nuclei are present in the outer nuclear layer, one in the inner nuclear and ganglion cell layers (Plate V, Fig. 4). The ganglion cells are very sparse, and a separate layer of optic nerve fibres is not seen. MÜLLER's fibres were not recognized. Hyaloid vessels are absent.

Only degenerating rods are present. The rod acromeres are irregularly swollen (Plate VII, Fig. 1), and a number of rod nuclei are found outside the external limiting membrane. The shape and the orientation of the nuclei in the outer nuclear layer show considerable variation, and lobulated nuclei are regularly seen.

The papilla of the optic nerve is situated in the ventralmost part of the fundus. The optic nerve is very thin (appr. $75 \times 120\mu$).

At least four small nerves – possibly ciliary nerves – enter the eye through the sclera. Their finer ramifications are very difficult to follow critically in the choroid. One of the nerves leaves the eyeball again. Nerves with a similar course have been found in *Bassogigas profundissimus* (MUNK 1964a). The n. accomodatorius was not recognized in the sections of *Benthosaurus*.

2. *Bathymicrops regis*

The small degenerated eyes are situated beneath the skin. In 70% alcohol the largest diameter of the enucleated eyeball measured appr. 0.8 mm.

The sclera is a fibro-cartilaginous capsule with irregularly folded and thickened plates of degenerated cartilage, in which practically no nuclei are seen. The eye is almost completely filled with heavily pigmented cells with typical retinal pigment granules (round, rod-shaped, and needle-shaped), originating probably from proliferation of the retinal pigment epithelium (Plate X, Fig. 3). No vessels were recognized in the eye.

In the central part of the eye an excessively degenerated retina proper with free retinal pigment granules is present. No trace of the normal stratification and no identifiable cell types were recognized. On the inside of the degenerated retina a folded PAS-positive membrane is located. This may possibly represent the capsule of the otherwise completely degenerated lens.

The optic nerve was not found. Free retinal pigment granules and cells with retinal pigment granules were seen in the connective tissue around the eye.

3. *Ipnops murrayi*

The eye of this species has been described previously by the present author (MUNK 1959). A re-examination of the slides showed, however, that degenerative features are also present in this species.

A fresh haemorrhage is present in the choroid of both eyes. This was erroneously interpreted as an intraocular blood sinus in the author's first description.

The retinal pigment epithelium shows variation in pigmentation, some cells being practically devoid of pigment granules. The pigment is located in the proximal part of the cells as in *Bathypterois longipes* and *Benthosaurus grallator*. Needle-shaped and small round pigment granules are present. The round granules cannot be distinguished with certainty from the choroidal granules.

The Retina Proper. The rod acromeres are irregularly swollen and a small number of typical macrophages are present in this layer (Plate VIII, Figs. 2-3). Macrophages are also seen in the interior of the eye at the inside of the retina. Many pyknotic nuclei are present in the layer of rod nuclei. A few small fresh subretinal haemorrhages were seen.

In the central part of the eye, close to the inside of the retina, a structure which may represent a rudimentary lens is situated (Plate VIII, Fig. 1). It consists of a heavily folded membrane enclosing comparatively large rounded cells, many of which have degenerating nuclei. Similar structures are found in *Bathymicrops regis* and *Ditropichthys storeri* (v.i.).

4. *Macrouroides inflaticeps*

In 70% alcohol the enucleated eyeball measured appr. 9×8 mm (horizontal×vertical). The eye is situated beneath a dermal cornea (Plate IX, Fig. 1), with which it is only very loosely connected.

As regards gross morphology the eye of this species is similar to that of *Careproctus kermadecensis* (cf. MUNK 1964 a). The annular scleral cartilage is very faintly developed and restricted to the equatorial zone of the eyeball.

The Lens. No aphakic apertures were recognized. Both an anterior and a posterior cortical cataract are present (Plate IX, Fig. 2).

The iris is definitely broader than in *C. kermadecensis*. Proliferative changes were seen in many places in the anterior cell layer of the pars iridica retinae.

The Retina. The retina proper is artificially detached from the pigment epithelium. The retinal pigment granules are definitely larger than those of the choroid. Processes from the retinal pigment epithelium were not seen.

The heavily degenerated *retina proper* shows essentially the same degenerative features as that of *C. kermadecensis*. In the peripheral parts of the retina only a single row of nuclei is present in the outer nuclear layer, locally the acromeres and rod nuclei are completely missing (Plate IX, Fig. 3). A considerable number of typical macrophages with a varying content of retinal pigment granules is present in the layer of degenerating rod acromeres. No cones were seen.

The nuclei situated inside the rod nuclei are very scattered. There is probably cystoid degeneration in the retina, but it cannot be distinguished with certainty from shrinkage artefacts. Hyaloid vessels are absent.

A degenerating *m. retractor lentis* is situated medio-ventrally on the posterior surface of the iris.

There is no choroid fissure and consequently no falciform process.

5. *Echinomacrurus mollis*

In 70% alcohol the horizontal diameter of the enucleated eyeball measured appr. 7.8 mm. As regards gross morphology the eye of this species shows a fairly close resemblance to that of *Macrouroides inflaticeps*. An anterior cortical cataract is present in the lens. The layer of rod acromeres shows essentially the same degenerative features as

that of *Careproctus kermadecensis.* Cones are absent. Hyaloid vessels are absent.

6. *Gyronomimus* sp.

On the intact specimen the small degenerated eye is seen to be situated beneath a small transparent area in the pigmented skin. The medial wall of the eyeball is constituted by an irregularly folded and locally thickened scleral cartilage continuing laterally into a thin connective tissue membrane which is firmly fused with the clear area of the skin into a single-layered cornea (Plate X, Fig. 2). No identifiable remnants of the lens, the retractor muscle, the ligamentum annulare, the iris, or the choroid fissure were recognized. The degenerated retina is seen as a slightly curved plate situated close to the inside of the cornea, separated from the latter by a narrow optically empty space. The normal curvature of the retina is actually inverted in this species. The larger part of the interior of the eyeball is filled with a very loose connective tissue representing the choroid. Some macrophages are present in this tissue. A few vessels and a thin nerve, possibly the optic nerve, enter through a fibrous area of the sclera situated ventrally in the medial wall of the eyeball. Eosinophilic and PAS-positive granules and rods of unknown significance are present in the cytoplasm of the erythrocytes.

A large number of retinal pigment granules is situated on the inside of the cornea and on the inside of the retina (Plate XI, Fig. 1). It is apparent from depigmented sections that the major part of these pigment granules is free, i.e. not contained within cells. A strongly PAS-positive membrane is present on the inside of the cornea, probably the membrana Descemeti, but the endothelium is apparently absent.

The Retina. The retinal pigment epithelium shows marked proliferative changes. The *retina proper* shows advanced degeneration with a considerable variation in thickness. A very considerable number of mostly free retinal pigment granules is present everywhere in the retina. Traces of the normal stratification are seen locally. The large cells located in the innermost part of the retina are undoubtedly ganglion cells (Plate XI, Fig. 1). The external limiting membrane can only be distinguished with difficulty in the least degenerated parts of the retina. Immediately inside this membrane a layer of mostly degenerated nuclei is seen, probably the remnants of the outer nuclear layer. The irregularly distributed nuclei situated between this layer and the ganglion cells probably represent a poorly developed inner nuclear layer. Locally unidentifiable remnants of outer and inner segments of the visual cells can be seen between the external limiting membrane and the pigment epithelium.

The papilla of the optic nerve was not recognized in the sections. Only one nerve was seen (v.s.). It could be followed through the choroid and was seen to penetrate deeply into the proliferated retinal pigment epithelium, but it proved impossible to trace the fibres to the retina proper.

7. *Ditropichthys storeri*

According to HARRY (1952) eyes are absent in this species. The optic nerve is said to branch in a heavily pigmented area situated beneath a transparent area of the skin in the region where the eye is normally found, and it is suggested that the nerve is sensitive to light. This remarkable observation is obviously based exclusively on dissection. Dr. R. H. ROSENBLATT, of Scripps Institution of Oceanography, called my attention to the fact that HARRY's observation is erroneous. It is understandable that the slightly curved retina of *D. storeri* might look as if it was a terminal ramification of the optic nerve in a dissected specimen (cf. Plate X, Fig. 1). The pigmented area mentioned by HARRY is obviously the retinal pigment epithelium.

The gross structure of the eye is apparent from Plate X, Fig. 1. The eye is flattened in the anteroposterior direction and has a very slightly curved retina close to the inside of the cornea. The iris is practically completely reduced. An annular scleral cartilage is seen in the equatorial zone of the eyeball. The larger medial part of the interior of the eye is filled with very sparse connective tissue membranes, partly pigmented. A few larger vessels are seen. This layer represents the choroid. The choroidal pigment granules are comparatively large and appr. spherical, definitely larger than the retinal pigment granules of the same shape. Some typical macrophages are present in the choroid. Faintly stained PAS-positive and eosinophilic needle-shaped bodies were recognized in the cytoplasm of the erythrocytes.

The Retina. A very narrow pars coeca retinae is present. It looks as if the retina proper has a smaller surface area than the pigment epithelium, because a considerable gap between the two components is seen both rostrally and caudally. This is probably a shrinkage artefact, because fragments of rod

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acromeres were seen to be attached to the inside of the pigment epithelium in these areas. Proliferative changes are seen in the pigment epithelium, particularly in the peripheral parts of the retina. The retinal pigment granules are comparatively small. Needle-shaped, rod-shaped, and round granules are present.

The retina proper shows heavy degenerative features. Only degenerating rods, partly with irregularly swollen acromeres, are present. Typical macrophages with a varying amount of retinal pigment granules are present in the layer of rod outer segments. Locally free retinal pigment granules are seen in the inner part of the retina. Many lobulated and pyknotic nuclei are found in the outer nuclear layer. The inner part of the retina is characterized by marked cystoid degeneration (Plate XI, Fig. 2). The nuclei in the inner part of the retina are scattered and no trace of the normal stratification is seen.

The optic nerve is very thin. An a. centralis retinae is present. It follows the not completely obliterated choroid fissure along the inside of the retina. There is no falciform process and no identifiable remnants of the m. retractor lentis.

A peculiar structure consisting of a folded PAS-positive membrane enclosing cells with lobulated or fragmented nuclei is seen in the central part of the eye, between the cornea and the retina. This structure may be a rudimentary lens, as is indicated both by its location and by the PAS-positive membrane which might represent the lens capsule.

BRAUER (1908:185-186) described the eye of a related *Cetomimus* sp., according to him *C. gilli* Goode & Bean, 1895. According to PARR (1928) and HARRY (1952) BRAUER's identification of this *Cetomimus* sp. as *C. gilli* is, however, erroneous. The

degenerated eye of this *Cetomimus* sp. (Plate III, Fig. 1) was flattened as in the two cetomimid species described above. A rudimentary lens was present. No remnants of the m. retractor lentis were found. The retina was thin and degenerated and rods were locally missing. A thin optic nerve was present.

8. *Barathronus erikssoni*

The eyes are situated beneath the skin. In 70% alcohol the largest diameter of the enucleated eyeball measured appr. 2 mm.

The eye of this species corresponds largely to that of *B. affinis* as described by BRAUER (1908), cf. Plate III, Fig. 2. No remnants of the lens were seen in *B. erikssoni*. The irregularly swollen fragmented acromeres are detached from the inner segments of the visual cells, probably artificially. Typical macrophages are seen everywhere among the acromeres. Macrophages were not observed by BRAUER in *B. affinis*.

9. *Sciadonus kullenbergi*

The eyes are situated beneath the skin. In 70% alcohol the largest diameter of the enucleated eyeball measured appr. 0.4 mm.

The sclera is a fibro-cartilaginous capsule. The eye is practically completely filled with heavily pigmented cells with typical retinal pigment granules (round, rod-shaped, and needle-shaped) (Plate X, Fig. 4). No identifiable remnants of the normal constituents of the eye were recognized. Typical macrophages were present in the connective tissue around the eye, some of them with retinal pigment granules.

DISCUSSION

1. Degenerative Features of Species Examined

In the eyes of the three previously described species (MUNK 1964 a) no definite similarities with the degenerated eyes of other teleosts were recognized. The nine species described above comprise a wide variation of degenerative features. The most advanced degeneration is found in *Sciadonus kullenbergi* and *Bathymicrops regis,* the eyes of which resemble those of adult cave-fishes (cf. e.g. BREDER 1944). The eye of *Barathronus erikssoni* shows a striking resemblance to that of *B. affinis* as described by BRAUER (1908), and is situated beneath the skin

as in the two afore-mentioned species. It is clearly degenerated, but it appears probable that the retina has been fully differentiated. The least modified eyes are those of *Macrouroides inflaticeps* and *Echinomacrurus mollis* which show a close resemblance to *Careproctus kermadecensis* as regards the morphology and degenerative features of the retina.

Ipnops murrayi, Gyronomimus sp., and *Ditropichthys storeri* have strangely modified eyes. In *Ipnops murrayi* the eyes are situated beneath cranial bones (MUNK 1959, THEISEN 1965). In all three species the retina is flattened and situated very close to the surface of the head. The lens is absent *(Gyro-*

nomimus sp.) or rudimentary. The retina of *Gyronomimus* sp. shows advanced degeneration, the retina of *Ditropichthys storeri* is clearly degenerated, but has probably been fully differentiated. The retina of *Ipnops murrayi* is apparently at an early degenerative stage.

Degenerative changes in the retinal pigment epithelium comprise loss of pigment *(Benthosaurus grallator, Ipnops murrayi)* and proliferation. Marked proliferative changes were found in *Gyronomimus* sp., *Ditropichthys storeri,* and *Bathymicrops regis.* In *Sciadonus kullenbergi* the heavily proliferated retinal pigment epithelium is apparently all that is left within the small vestigial eye. The shape and the size of the pigment granules of heavily degenerated eyes are essential morphological characteristics, because in some cases they give definite proof of whether pigmented cells belong to the choroid or have originated from the retinal pigment epithelium. This has been clearly demonstrated in some of the species examined. It may furthermore be mentioned that sections of the degenerated eye of a 62 mm (standard length) specimen of *Typhlogobius californiensis* clearly showed that the lump of pigmented cells located in the choroid possess typical retinal pigment granules. These cells have therefore originated from proliferation from the retinal pigment epithelium as previously suggested (MUNK 1964 a: 146). Bleached sections showed that vessels are not present within the lump of pigmented cells which have been interpreted as a remnant of the choroid gland (for reference cf. MUNK 1964 a). This interpretation can therefore be firmly denied.

Typical macrophages in the layer of degenerating rod acromeres are present in *Ipnops murrayi, Macrouroides inflaticeps, Echinomacrurus mollis, Ditropichthys storeri,* and *Barathronus erikssoni.* The probably phagocytic cells found in the layer of acromeres in *Benthosaurus grallator* do not resemble typical macrophages, but may have originated from inward-migrating cells from the retinal pigment epithelium. Typical macrophages are present elsewhere in the eye of this species.

Irregular swelling of the acromeres is apparently a common feature in some types of retinal degeneration. It is found in primary retinal degeneration in mammals (for references see MUNK 1964 a). It might be asked whether the acromeres of the deepsea fishes examined might be artificially swollen. This possibility can be excluded for the following reasons:

1. Deep-sea fishes in which no histological evidence of ocular degeneration can be found invariably show regularly cylinder-shaped rod acromeres. As far as I know irregular swelling of acromeres is never seen in normal vertebrate eyes.

2. In poorly fixed vertebrate retinae the tips of the acromeres of the visual cells are swollen. Specimens showing this characteristic feature have been discarded.

3. In all deep-sea fishes with irregularly swollen acromeres various other degenerative features have also been found in the retina and in other parts of the eye. Macrophages are typically present in the layer of acromeres.

The variation in the morphology and degenerative features of the eyes examined may at least to some extent reflect at which stage in the ontogenetic development of the eye degenerative changes start. It thus appears probable that the deeply buried and heavily degenerated eyes of *Bathymicrops regis* and *Sciadonus kullenbergi* may have essentially the same ontogenetic development as those of adult cave-fishes (cf. MUNK 1964 a: 146). In these two species and in *Barathronus* spp. and *Gyronomimus* sp. the macroscopic appearences of the eyes clearly indicate that they are degenerated, and this was confirmed histologically. In the remaining species macroscopic evidence of degeneration is not present. The histological evidence varies from rather slight degenerative changes in the retina proper and the pigment epithelium *(Benthosaurus grallator, Ipnops murrayi)* to a more advanced degeneration with partial loss of visual cells *(Macrouroides inflaticeps).* The decisive factor in the ocular degeneration may be a primary retinal degeneration as was suggested for the three previously described species (MUNK 1964 a). It can once more be emphasized that it is apparently a very slow process in some deep-sea fishes, because some of the specimens examined were of a fairly large size. The fresh haemorrhages in the eyes of *Ipnops murrayi* are probably caused by changes in environmental conditions during the hauling of the trawl. The most degenerated eyes examined *(Bathymicrops regis, Sciadonus kullenbergi)* are probably functionless. As regards the functional state of the eyes of the remaining species, no safe conclusions can be drawn from the histological picture; but it does not appear absolutely impossible that light perception may still take place in the species with the least degenerated retinae.

2. Ocular Degeneration in Relation to Environmental Conditions and Vertical Distributions

The environmental factor of obvious importance is light, i.e. residual daylight and bioluminescence. The amount of daylight in the sea is drastically reduced at increasing depth owing primarily to absorption. Thus in the clearest sea water light with a wave-length of appr. 470 mμ, which is the light waves reaching farthest down into clear water, is reduced to below 1 % of the surface value at a depth of 150 m (JERLOV 1951). The retinae of deep-sea fishes are particularly sensitive to the part of the daylight for which sea water shows maximal transmission, and the quality of the light produced by the luminous organs of many deep-sea animals shows a fairly close correspondance with that of the residual daylight (cf. NICOL 1963, also for references). It has been suggested that pelagic deep-sea fishes may actually be able to perceive daylight down to a depth of appr. 900 m (cf. DENTON & WARREN 1957, CLARKE & HUBBARD 1959, CLARKE & DENTON 1962, and NICOL 1963) owing to various sensitivity-increasing devices (a relatively large pupil, low absorption of light by ocular media, high density of retinal photosensitive pigment, and reduced "noise-level", i.e. a low rate of spontaneous breakdown of photosensitive pigment). This is well in accordance with MARSHALL's statement that well-developed eyes are found in pelagic fishes down to appr. 1000 m, whereas many fishes found below 1000 m have small or degenerated eyes (MARSHALL 1958: 227). According to WALLS (1942: 398) the occurrence of small eyes in deep-living fishes indicates that the eyes are used for "mere light-sense vision".

As regards bioluminescence the largest number of luminescent species and specimens of deep-sea organisms are in all probability found in the upper 1000 m of the sea. During the night CLARKE & HUBBARD (1959) thus found the greatest frequency of luminous flashes at 100 m and a secondary maximum at appr. 900 m in the slope water southeast of New York. In the daytime the first measurable flashes (i.e. those brighter than the residual daylight) were recorded at 400 m, and their frequency was found to increase down to 900 m. Flashes were, however, recorded down to the greatest depth to which the bathyphotometer was lowered (3750 m), although their intensity and frequency were low. CLARKE & HUBBARD (ibid.: 179) state that "in any situation in which bioluminescence is as strong as that received by our photo-meter at every depth investigated, the visual detection of small objects illuminated by biological light would be easily possible".

Light conditions are thus most favourable in the upper 1000 m of the sea both as regards residual daylight and bioluminescence. All the species with ocular degeneration which were examined, including the five previously described species (BRAUER 1908, MUNK 1964 a), live below the limit (appr. 900 m) down to which daylight may possibly be perceived, and none of them are known to possess luminous organs. HARRY (1952) has suggested that luminous organs are probably present in cetomimids, but as far as I know this suggestion has never been confirmed histologically.

Ocular degeneration has never been demonstrated in deep-sea fishes with luminous organs. Various authors have suggested that the reason why functional eyes are preserved in deep-sea fishes may be the occurrence of luminous organs in these animals (see e.g. BRAUER 1908, WALLS 1942). This seems reasonable because luminous organs of many deep-sea fishes function at least in part as recognition signs. However, if luminous flashes with an intensity above the threshold value are common in the deep-sea below the zone where daylight may be perceived, there is no obvious reason why ocular degeneration should be so common in species without luminous organs, because it might be expected that the perception of flashes of prey or predators or both might be important. Ocular degeneration is particularly not to be expected if luminous flashes actually provide sufficient background illumination for the detection of nearby objects down to at least 3750 m as stated by CLARKE & HUBBARD. If this is generally the case, the perception of the form of nearby objects should be possible. If one believes that the eyes of deep-sea fishes are perfectly adapted to the environment, these advantageous light conditions should be reflected in the ocular anatomy, which is actually not the case. Small eyes are the rule below 1000 m. The eyes of the deep-living species in which no evidence of ocular degeneration has been found generally have a disproportionately large lens which can hardly produce a clear image on the retina. The retinae furthermore show evidence of considerable summation, i.e. low resolving power. An eye of this type is found for example in adult female deep-sea angler fishes (MUNK 1964 b, Fig. 2 G: 7). A disproportionately large lens is advantageous for the utilization of very dim light, and is most often associated with a wide pupil with aphakic apertures.

The ocular degeneration of the deep-sea fishes examined is in no obvious way related to the vertical distribution of the species. Thus for example the eye of *Gyronomimus* sp. shows a more advanced degeneration than that of the deeper living *Benthosaurus grallator*. The various degenerative features might possibly reflect the importance of the eyes at early ontogenetic stages. The eyes of some of the species examined by the present author show strong indications of having been fully differentiated before degeneration has set in. This might imply the presence of functionally normal eyes in larvae and maybe also in young adults, i.e. that the larvae are pelagic and found in the upper 900 m of the sea where daylight may be perceived, or that the perception of luminous flashes of prey or predators or both is important in early life. In the latter case the vertical distribution would not necessarily depend on the residual daylight.

The early life history of the species examined is unfortunately unknown. The type specimen of *Macrouroides inflaticeps* was caught at a depth of only 746 m, i.e. within the depth range where residual daylight may still be of importance for vision. It seems quite possible that this species might have epipelagic larvae. According to NIELSEN (1964) the larvae of *Careproctus kermadecensis* probably remain in hadal depths (i.e. below 6000 m) as far as can be judged from the size of the eggs.

According to DENTON & WARREN (1957: 659) the sensitivity of the eye can be increased by discarding the dioptric system altogether, so that light falls directly on the retina. This might possibly explain the very peculiar structure of the eye of *Ipnops murrayi*, in which the flattened retina is situated very close to the surface of the head. The retina of this fish is admittedly at an early degenerative stage. Yet the whole structure and location of the eye strongly suggests that it is a highly specialized organ which has in all probability been functionally normal at earlier ontogenetic stages. A similar specialization might have occurred in the cetomimids.

SUMMARY

The eyes of nine species of deep-sea fishes with various degrees of ocular degeneration are described and compared with those described previously in literature. The relations between ocular degeneration, environmental light conditions, and vertical distributions are discussed. Deep-sea fishes with histological evidence of ocular degeneration live below the limit (appr. 900 m) down to which daylight may possibly be perceived, and none of them have luminous organs.

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Key to Labelling

c:	cornea	ro:	rostrad
ca:	camera anterior	sc:	scleral cartilage
ch:	choroid	scc:	scleral cornea
chc:	choriocapillaris	sf:	fibrous part of sclera
f:	bundle of filaments in process of retinal pigment epithelium	v:	vitreous
		zc:	zona ciliaris
i:	iris	1:	retinal pigment epithelium
l:	lens	2:	layer of rod acromeres
lc:	lens capsule	3:	external limiting membrane
lm:	lens muscle	4:	outer nuclear layer
lr:	? rudimentary lens	5:	outer plexiform layer
m:	macrophage	6:	inner nuclear layer
mb:	myeloid body	7:	inner plexiform layer
pcr:	pars coeca retinae	8:	ganglion cell layer
pi:	retinal pigment epithelium	10:	internal limiting membrane
r:	retina		