

THE EYES OF THREE BENTHIC DEEP-SEA FISHES CAUGHT AT GREAT DEPTHS

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INTRODUCTION

As regards benthic deep-sea fishes the evidence for correlation between the size of the eyes and known depth ranges is very conflicting (MARSHALL 1958: 231-236). The evidence obtained from the histological descriptions of the eyes of the few benthic deep-sea fishes actually examined is no less conflicting. BRAUER (1908) has examined the eyes of 13 deep-sea teleosts which are held to be benthic. One of them, *Barathronus affinis* Brauer, 1906, caught at 2919 m, had degenerated eyes. The *Barathronus* sp., however, are most likely pelagic according to NYBELIN (1957: 281). No evidence of retinal degeneration was found in the strongly modified eyes of 2 specimens of *Ipnops murrayi* Günther, 1878, one of which was caught at 3960 m on the Galathea-Expedition (MUNK 1959).

The present paper deals with the structure of the eyes of three species of benthic deep-sea fishes caught at great depths, viz. *Bathypterois longipes*

Günther, 1878, caught at 5850-5900 m (Galathea St. 654), *Careproctus kermadecensis* Nielsen, 1964, caught at 6660-6770 m (St. 658), both in the Kermadec Trench, and *Bassogigas profundissimus* (Roule, 1913), caught at 7160 m in the Sunda Trench (St. 466). All three species have small but apparently well-developed eyes with a large lens. MARSHALL (1958: 232) writes about the *Bathypteroidae* that "the eyes are very small but functional, presumably mere indicators of the glow of luminescent organisms". This is a perfectly reasonable statement because degenerated eyes of adult fishes as far as known are invariably found to be situated deeply beneath the skin, and very often the ocular remnants can only be recognized in histological sections. It was, however, most unexpectedly found that the eyes of the three benthic deep-sea fishes described in the present paper showed heavy degeneration.

MATERIAL AND METHODS

1. *Bathypterois longipes* Günther, 1878 (Bathypteroidae). Original length of specimen unknown. The head of this Bouin-fixed specimen was decalcified, embedded in paraffin, and cut into 8μ serial transverse sections.

2. *Careproctus kermadecensis* Nielsen, 1964 (Cyclopteridae). Both eyes of a formalin-fixed specimen, 258 mm long (standard length), and the left eye of a formalin-fixed specimen, 42 mm long (original standard length probably 70 mm), were enucleated and embedded in paraffin. 8μ serial sections were cut at right angles to the equator of the eyeballs. Furthermore, the spleen of the larger specimen was cut into 8μ serial sections.

3. *Bassogigas profundissimus* (Roule, 1913) (Bro-

tulidae). The left eye of a 157 mm (standard length) formalin-fixed specimen was enucleated, embedded in paraffin, and cut into 8μ serial sections at right angles to the equator of the eyeball. Part of the kidney was cut into 8μ serial sections. Furthermore, the swimbladder was cut into 8μ transverse sections.

The following staining methods were employed: Ehrlich's hematoxylin and eosin, Weigert's iron hematoxylin and eosin, PAS, Alcian blue, picro-Mallory (LENDRUM *et al.* 1962), the Martius-Scarlet-Blue method (MSB, *ibid.*), Gram stain, Bodian's protargol method, gallocyanin (pH 1.61-1.64), and Feulgen's nucleal reaction. Depigmentation was made according to CHESTERMAN & LEACH (1958).

RESULTS

1. *Bathypterois longipes*.

This specimen was taken at a slightly greater depth (5850-5900 m) than previously caught specimens (?826-5610 m according to NYBELIN 1957: 256). The small eyes are situated laterally in the head and directed slightly upwards (Pl. XII, Fig. 1). A lateral line canal is seen immediately above and below each eye, probably the supra- and the infraorbital canals. Medially of the eyeball a lymphatic sinus is seen. The eyeball is shaped as an ellipsoid, the horizontal diameter of which is longer than the vertical. Measurements made on the sections of the right eye showed a vertical diameter of appr. 840 μ and an antero-posterior diameter of appr. 826 μ . The horizontal diameter of the same eye is appr. 940 μ , the diameter of the lens appr. 630 μ .

The cornea consists of two definite layers, a dermal and a scleral cornea separated by a thin layer of connective tissue. The dermal cornea is continuous with the skin, whereas the scleral cornea is continuous with the sclera. The inside of the scleral cornea is covered with an endothelium, below which Descemet's membrane is seen as a very thin PAS-positive line.

The sclera is almost entirely fibrous, only rostrally and temporally a plate of hyaline cartilage is found. There are no scleral bones.

The lens is very large in proportion to the eyeball as a whole (Pl. XII, Figs. 1-2). Anteriorly the spherical lens is in contact with the inside of the cornea, while posteriorly the major part of the retina is situated in close contact with the lens. Only corresponding to the ora terminalis a small triangular space is seen in the sections; this space is delimited by the equatorial part of the lens, the most peripheral part of the retina, and the very short iris (Pl. XII, Figs. 1, 3, and 4). The vitreous body is thus actually missing.

The ligamentum annulare is very poorly developed; it consists of a small number of connective tissue cells situated in the angle of the anterior chamber. No vessels were found.

The iris is very short. The anterior layer of cells of the pars iridica retinae is heavily pigmented, whereas the posterior layer is unpigmented half way towards the pupil. Depigmented sections showed cuboidal-columnar cells in the anterior layer (Pl. XII, Figs. 3-4). The stroma of the iris is absent. The anterior surface of the iris is covered

with an endothelium which is continuous with the endothelium covering the ligamentum annulare and the inside of the cornea.

The choroid is very thin. There is no corpus vascularis chorioideae. The argentea and the m. tensor chorioideae are missing. The choriocapillaris is missing in some areas, particularly in the dorsal part of the eye. Here and there a few melanocytes with very small pigment granules of choroidal type are seen (Pl. XII, Fig. 6). A large number of pigment cells originating from the pigment epithelium of the retina are found in the choroid; they will be discussed together with the retina. In the right eye a large fresh haemorrhage was found in the ventral part of the choroid (Pl. XII, Fig. 2); in this region erythrocytes originating from the haemorrhage were also seen in the ligamentum annulare, separated from the anterior chamber only by the endothelium. A small fresh haemorrhage was recognized in the medial part of the choroid. In the left eye no haemorrhage was found. Haemorrhages are fairly often seen in one or both eyes of deep-sea fishes. The present author has erroneously described large haemorrhages found in both eyes of a specimen of *Ipnops murrayi* as intraocular blood sinuses (MUNK 1959: 84).

The Retina. The retina proper is artificially detached from the pigment epithelium except some areas at or near the ora (Pl. XII, Figs. 1, 2, and 5).

The pigment epithelium is extraordinarily thick, appr. 80-96 μ in the fundus (Pl. XII, Figs. 1 and 3). Depigmented sections show that the pigment epithelium is a pseudostratified columnar epithelium (Pl. XII, Fig. 4). The proximal part of the cells (i.e. the outer part adjacent to the choroid) is heavily pigmented, whereas only very few pigment granules are seen in the distal part (i.e. the inner part adjacent to the retina proper). The nuclei are situated in the distal part of the cells. Here and there pyknotic nuclei are seen.

Two types of pigment granules are seen in the pigment epithelium, viz. short rod-shaped granules, definitely larger than the granules found in the choroidal melanocytes, and needle-shaped granules (Pl. XII, Fig. 6). Two types of pigment granules are found in many teleosts, cf. e.g. WUNDER (1925: 35). In man the pigment granules show a considerable morphological variation in different areas of the pigment epithelium, and variation depending on age (KACZUROWSKI 1962). The intraretinal part of

the optic nerve in *Bathypterois* is surrounded by a sheath of retinal pigment epithelium cells (Pl. XII, Fig. 2); in these cells there are practically no needle-shaped granules, but only rod-shaped or irregularly shaped granules which are generally larger than those seen elsewhere in the pigment epithelium. It should be noted that these large granules may actually be present in the proximal part of the pigment epithelium, but because of the heavy pigmentation it is impossible to distinguish single granules in this region. Here and there holes were seen in the pigment epithelium. In both eyes a horizontal fold of the pigment epithelium was seen in the fundus, located dorsally of the optic nerve (Pl. XII, Fig. 2). Typical processes reaching down between the acromeres of the visual cells were not recognized in the sections.

Proliferation of the pigment epithelium was seen in both eyes, particularly around the optic nerve and in the ventral part of the choroid, below the papilla of the optic nerve (Pl. XII, Fig. 2). Thus the great majority of the pigment cells found in the choroid originate from the pigment epithelium of the retina. This is apparent from the size and shape of the pigment granules which are of retinal type; besides the needle-shaped and rod-shaped granules, large granules like those seen in the pigment sheath around the optic nerve are also found. Proliferation of the pigment epithelium has also been found in the degenerating eyes of microphthalmic specimens of *Barbus conchoniis* Hamilton-Buchanan, 1822 (MUNK 1961).

The retina proper (Pl. XII, Fig. 5) shows several degenerative features. Locally 2 nuclear layers can be recognized inside the nuclei of visual cells, but in most areas no clear stratification can be demonstrated in the inner part of the retina. Pyknotic nuclei were seen in every part of the retina. A considerable variation in retinal thickness was found in the fundus (Pl. XII, Figs. 1 and 5). This varying thickness apparently depends on the degree of local degeneration.

The visual cells are more or less degenerated. They are generally best preserved in the peripheral part of the retina. A few comparatively well preserved rod-shaped acromeres were found in the sections, but most of the acromeres left in the eyes were swollen. In some areas acromeres were missing. Fragmentation of the acromeres leads to accumulation of cellular debris in the artificial fissure between the retina proper and the pigment epithelium. The inner segments of the visual cells are more or

less swollen and vacuolized. Locally visual cell nuclei are found outside the outer limiting membrane.

In the thickest parts of the retina in the fundus 3 rows of nuclei are found in the outer nuclear layer. Most nuclei are comparatively large, oval or irregularly shaped, and more or less lobulated. The cells situated inside the outer nuclear layer cannot be classified on the basis of nuclear morphology. However, the large cells situated in the innermost part of the retina are probably ganglion cells; they have a large oval nucleus and a fairly distinct perikaryon. A distinct optic nerve fibre layer is not seen. Horizontal cells and the fibres of Müller were not recognized in the sections. Hyaloid vessels are absent.

In a narrow appr. medio-ventral zone adjacent to the papilla of the optic nerve the pars optica retinae is missing (Pl. XII, Fig. 2). This may possibly mean that a choroid fissure is present, but owing to the plane of sectioning it cannot be ascertained. Furthermore, the morphology in this region is rather complicated because of the proliferation of the pigment epithelium of the retina. No vessels are seen to enter or leave the eye in this region, nor is there any a. centralis retinae. This is well in accordance with the absence of hyaloid vessels.

No structure which might represent remnants of the falciform process or the retractor muscle of the lens were seen in the sections.

The papilla of the optic nerve is situated a little ventro-temporally of the centre of the fundus as is generally the case in teleosts (Pl. XII, Fig. 2). The thin optic nerve (appr. $20 \times 22 \mu$) can be followed to the brain.

Macrophages were not recognized with certainty in any part of the eye. There is no evidence of infection or parasites.

2. *Careproctus kermadecensis*.

The *Galathea* specimens caught at 6660-6770 m in the Kermadec Trench are the only known specimens of this species, cf. NIELSEN (1964). The small eyeball is shaped as a slightly flattened ellipsoid, the horizontal diameter of which is the longest. The enucleated eyeballs of the larger specimen (258 mm standard length) were found to differ slightly in size, the left eyeball measuring $5.1 \times 3.9 \times 3.3$ mm (horizontal \times vertical \times antero-posterior diameter), the right $5.3 \times 4.1 \times 3.6$ mm. The pupil is a horizontal oval. The extrinsic ocular muscles are very

thin. In the following the eyes of the larger specimens are described.

The cornea. A dermal cornea was not recognized during enucleation of the eyeballs of any of the 2 specimens, possibly because the skin was damaged. The thickness of the cornea of the larger specimen is only 4-5 μ centrally. It is thus very probable that a dermal cornea is actually present in this species. The absence of an epithelium on the outside of the cornea seen in the sections does not prove that it is a scleral cornea, because the epidermis is often wholly or partly missing in formalin-fixed specimens of deep-sea fishes.

The membrana Descemeti is seen as a thin PAS-positive line in the sections. The inside of the cornea is covered with an endothelium. A m. tensor chorioideae originates from the peripheral part of the inside of the cornea (Pl. XIII, Fig. 1).

The sclera is partly cartilaginous, partly fibrous. There are no scleral bones. The annular scleral cartilage shows perforations and irregularly thickened parts; in the fundus region small isolated plates of hyaline cartilage were seen.

The lens appears slightly flattened, probably artificially, with a vertical diameter of appr. 2 mm. It is definitely smaller than the pupil as seen in the sections. The lens capsule stains heavily PAS-positive. Its greatest thickness is found in the equatorial zone and it is thicker on the anterior surface than posteriorly. A similar variation in the thickness of the lens capsule is found in normal teleostean eyes, cf. FRANZ (1913: 278-279). In the left eye of *Careproctus* a subcapsular cataract was observed on the posterior surface of the lens (Pl. XIII, Fig. 3). On the anterior surface proliferation of the lens epithelium was seen. Fragmentation of the nuclei of the lens epithelium are seen here and there. Locally macrophages were found to be situated in close contact with the lens capsule, particularly in the anterior chamber.

The iris is very short (Pl. XIII, Fig. 1). The anterior and posterior layer of the pars iridica retinae are artificially separated. Only the anterior layer of cells is pigmented. Hyperplasia of both cell layers was observed (Pl. XIII, Fig. 1).

The angle of the anterior chamber shows a well-developed *ligamentum annulare* consisting of very loose connective tissue with vessels and macrophages (Pl. XIII, Fig. 1). This loose tissue covers practically the whole anterior surface of the pars iridica retinae; only close to the pupillary margin a narrow zone is seen in which the pars iridica is

covered with a thin mesodermal tissue layer resembling a normal stroma iridis. The anterior surface of the iris and the ligamentum annulare are covered with an endothelium which is continuous with that covering the inside of the cornea. Argentea and melanocytes were not found in the iris. Locally the pigmented cells of the anterior cell layer of pars iridica retinae have proliferated out into the loose tissue in the angle of the anterior chamber.

The Choroid. A normal choriocapillaris is seen (Pl. XIII, Fig. 2). There is no corpus vascularis chorioideae and no argentea. A few larger vessels are seen in the space between the choriocapillaris and the sclera. The major part of the choroid is occupied by a more or less dense eosinophilic and PAS-positive granular substance of unknown nature. The pigment granules of the choroidal melanocytes are of the same order of magnitude as those found in the pigment epithelium of the retina.

The Retina. The retina proper is artificially detached from the pigment epithelium (Pl. XIII, Figs. 1-2). The pigment epithelium consists of cuboidal cells, in some of which a narrow distal part without pigment granules can be seen.

The retina proper shows many degenerative features. The nuclei situated inside the outer nuclear layer show an apparently random distribution, with no definite trend towards an arrangement into 2 nuclear layers corresponding to the inner nuclear and ganglion cell layer (Pl. XIII, Figs. 4-5). Pyknotic nuclei are seen in every part of the retina. The retina is thicker in the fundus than peripherally.

The visual cells are more or less degenerated rods. No cone-like cells were recognized. The length of the myoids of the rods shows a considerable variation; there is no tendency towards an arrangement of the rod acromeres in regular layers or rows. A similar arrangement of the rod acromeres is seen in many normal teleostean eyes, both in the light- and dark-adapted state (Pl. XIII, Fig. 7). The average length of the acromeres in *Careproctus* is appr. 28 μ . All acromeres are more or less swollen, and fragmentation of acromeres is also seen. In a few areas the acromeres were found to be completely missing. A very large number of macrophages is found in the layer of rod outer segments (Pl. XIII, Figs. 4-6); they will be dealt with separately (v.i.). Locally some rod nuclei are seen outside the outer limiting membrane.

The outer nuclear layer contains 5-6 layers of nuclei and is appr. 25 μ thick in the fundus. The nuclei situated inside the outer nuclear layer cannot

be identified with certainty. Horizontal cells and the fibres of Müller were not recognized. In the innermost part of the retina large cells with a fairly distinct perikaryon and large oval nuclei are seen; these cells are probably ganglion cells. Some of them show vacuolized cytoplasm and a hypochromatic nucleus with an enlarged nucleolus. No definite optic nerve fibre layer was recognized.

On the inside of the retina hyaloid vessels are seen (Pl. XIII, Figs. 4-5). Two larger vessels are seen in the intraretinal part of the optic nerve. Both of these are divided into several branches on the papilla of the optic nerve; the hyaloid vessels originate from these branches. No remnants of the choroid fissure were recognized in the sections, and no vessels were seen to enter or leave the interior of the eye in any other part of the organ than through the papilla of the optic nerve. It is therefore very probable that one of the larger vessels seen in the optic nerve is a vein, whereas the other is the a. centralis retinae (cf. HANYU 1962: 97-98).

A great number of sharply outlined peculiar bodies were recognized in the inner part of the retina, i.e. inside the layer of rod nuclei (Pl. XIII, Fig. 4). These bodies are oval or spherical, with a diameter of appr. 5.5μ . Within the bodies a homogeneous oval or spindle-shaped structure superficially resembling a nucleus is seen. As regards staining characteristics this nucleus-like structure differs both quantitatively and qualitatively from the remainder of the body. Apparently identical bodies were recognized in the posterior layer of cells of the pars iridica retinae and in the peripheral part of the lens. Most probably these bodies are degenerated nuclei. With Feulgen's nucleal reaction the contour of the bodies is clearly outlined (Feulgen-positive), whereas the nucleus-like structure is completely unstained. Nor is it stained with gallo-cyanin (pH 1.64) which stains the remaining part of the body with a faint diffuse blue. In most sections stained with hematoxylin and eosin the nucleus-like structure is heavily stained with hematoxylin, whereas the remainder of the body shows a more pale blue staining. With picro-Mallory and MSB the nucleus-like structure shows a heavy red staining, the remaining part a lighter red. Staining with Alcian blue is negative, but in a few PAS-stained sections the nucleus-like structure is seen to be faintly PAS-positive. The nucleus-like structure might represent an enlarged nucleolus; the fact that it is not stained with gallo-cyanin is not significant, because the nucleoli of the macrophages in the

same sections were also found to be unstained. These bodies show a superficial resemblance to the so-called cytooid bodies known from human pathology; the staining characteristics of the bodies found in *Careproctus* differ, however, strikingly from those of human cytooid bodies (cf. CHRISTENSEN 1959).

Gliosis of the disc was found in both eyes (Pl. XIII, Fig. 2). The nuclear morphology of the cells in this "pseudotumor" shows that it has originated exclusively from the neuroglia of the papilla of the optic nerve. In the right eye the pseudotumor is very small and situated centrally on the papilla. In the left eye it is considerably larger; neuroglia is also found in the innermost part of the retina ventrally of the papilla. One of the 2 large vessels which enter the interior of the eye through the optic nerve has been displaced by the proliferated neuroglia and has a short intraretinal course.

A great number of *macrophages* was found in the retina of both eyes, particularly in the layer of rods (Pl. XIII, Figs. 4-6). Furthermore, macrophages were seen on the inside of the retina, in the ligamentum annulare, adhering to the lens capsule and the inside of the cornea, and a few in the vitreous, the anterior chamber, and the choroid. The nucleus of the macrophages is spherical, oval, kidney-shaped, or of irregular shape, with 1-2 comparatively large, often acentric nucleoli which are not stained with gallo-cyanin at pH 1.64. The cytoplasm is finely vacuolized, with PAS-positive cytoplasmic strands. In many cells one or several large vacuoles and PAS-positive inclusions are seen. In the outer part of the retina, i.e. outside the outer limiting membrane, many macrophages contain a varying amount of pigment granules; the colour and size of the granules correspond with those of the retinal pigment epithelium. Some macrophages are seen to possess long thin pseudopodia.

Generally the nuclei of the macrophages situated outside the retina are smaller than the nuclei of those found in the retina. The macrophages situated in the layer of rods are generally larger and have particularly large nuclei, measuring appr. $6.4 \times 5.1\mu$; occasionally cells with 2 nuclei are seen. The nuclei of the macrophages adhering to the inside of the retina are often spherical and have a diameter of appr. 3.3μ . Macrophages with an intermediary nuclear size were also found in the sections.

The size of the nuclei of the major part of the macrophages of the spleen was found to be appr. 3.2μ , which corresponds closely with that of the

smaller intraocular macrophages. A few macrophages of the larger type were also recognized in the spleen. The morphological characteristics of the intraocular macrophages correspond closely with those of the macrophages of the spleen.

No structure which could be certainly identified as a rudimentary retractor muscle was recognized. Since the choroid fissure is completely obliterated the falciform process is of course missing.

There is no evidence of infection or parasites.

The eye of the smaller specimen corresponds largely with those of the larger specimen. It measures appr. $1.9 \times 1.5 \times 1.4$ mm (horizontal \times vertical \times antero-posterior diameter). Gliosis of the disc was not found in this small specimen. The thickness of the retina of the smaller specimen equals that of the larger specimen. The degenerative processes were not so advanced as in the larger specimen, particularly not in the layer of rod acromeres.

3. *Bassogigas profundissimus*.

The *Galathea* specimen of *B. profundissimus* which was caught at 7160 m in the Sunda Trench is the fourth specimen caught. The three specimens hitherto known were all caught in the North Atlantic at 5610-6035 m (NYBELIN 1957: 303). The eyeball is shaped as an ellipsoid (Pl. XIV, Fig. 1), the horizontal diameter of which is the longest, measuring appr. 1.4 mm. On the intact specimen the eyeball was seen to be covered with a dermal cornea, a transparent area of the skin, measuring appr. 3.4×2.1 mm (horizontal \times vertical). During enucleation this dermal cornea was found to be only very loosely connected with the eyeball.

The scleral cornea is very thin, appr. 4μ . The endothelium shows large vacuoles and intracellular PAS-positive bodies (Pl. XIV, Fig. 5). The membrana Descemeti is uniformly thickened in some areas, in others it shows more localized lenticular thickenings. The vacuoles in the endothelium may be artificial, but the intracellular PAS-positive bodies and the thickenings of the membrana Descemeti can hardly be artefacts. In man the peripheral part of the membrana Descemeti shows localized thickenings due to aging, the so-called Hassall-Henle warts (HOGAN & ZIMMERMAN 1962: 288-290). Thickenings in the central part of the human membrana Descemeti are seen in Fuchs' dystrophy (ibid.: 330-332), in which PAS-positive bodies are also found in the endothelium (CHI *et al.* 1958).

The Sclera. There are no scleral bones. Two

plates of hyaline cartilage are found, one rostrally and one temporally; the remaining part of the sclera is fibrous. Corresponding to the posterior pole of the eyeball the fibrous sclera is thickened. The sclera is provided with a peculiar process consisting of dense connective tissue which originates from the thickened medial part of the sclera, immediately dorsally of the emerging optic nerve (Pl. XIV, Figs. 3-4). This scleral process is U-shaped; the proximal part is directed ventrally. Corresponding to the under side of the eyeball it turns caudo-medially and then dorso-medially. The end of the process is level with the area of origin of the process and situated caudally and probably slightly medially of the latter. The optic nerve is lying along this peculiar process, on the lateral side of the descending (proximal) part of the process, and on the medial side of the ascending (distal) part. At the end of the process the optic nerve turns dorso-rostrally and can be followed for a short distance before it disappears out of the sections. This scleral process is a rather unique structure. Since only one enucleated eyeball from a single specimen was available, it is impossible to know whether it is an accidental malformation. A thickening of the medial part of the sclera is seen in some deep-sea fishes, for example in *Stomias* and *Bathophilus*.

The lens appears flattened in the sections, probably artificially. No pathological features were recognized.

The Iris. This region is unfortunately rather badly damaged. The iris is very short. The posterior cell layer of the pars iridica retinae is pigmented only very close to the pupillary margin. A stroma iridis was not recognized in the sections, but the anterior surface of the iris is locally seen to be covered with an endothelium; it is probably continuous with the endothelium covering the ligamentum annulare and the inside of the cornea.

The ligamentum annulare is seen in the sections as a very small number of connective tissue cells situated in the angle of the anterior chamber. No vessels are seen.

The Choroid. A normal lamina choriocapillaris is found. There is no corpus vascularis chorioideae. A few choroidal melanocytes are seen. Their pigment granules are of the small choroidal type, definitely smaller than those of the retinal pigment epithelium. A moderate number of pigmented cells originating from the retinal pigment epithelium was recognized in the ventral part of the choroid.

The Retina. The heavily degenerated retina is arti-

ficially detached from the pigment epithelium and adheres to the posterior surface of the lens (Pl. XIV, Figs. 2-4).

The pigment epithelium shows considerable variation as regards the shape of the cells and the amount of pigment granules. Cuboidal-columnar cells are seen in some areas, very low cells in other. In some cells a narrow unpigmented distal zone is seen. Furthermore, a very faintly pigmented medio-ventral zone was recognized (Pl. XIV, Fig. 3).

Three types of retinal pigment granules were found, viz. small, large, and needle-shaped granules. In the faintly pigmented medio-ventral zone the needle-shaped granules are practically absent. No typical processes were recognized on the pigment epithelium.

In the ventral part of the choroid pigmented cells with retinal pigment granules were seen. Locally retinal pigment cells were also found in the ligamentum annulare.

The Retina Proper. Pyknotic nuclei were recognized in every part of the retina. The visual cells are all more or less degenerated. The outer segments are swollen and heavily vacuolized. Fragmentation of the acromeres results in accumulation of cellular debris in the artificial fissure between the pigment epithelium and the retina proper. The inner segments of the visual cells are also more or less vacuolized and swollen. Locally acromeres are completely missing; in these regions only degenerated remnants of inner segments are seen, and the outer nuclear layer is reduced to a single layer of nuclei, some of which are pyknotic. The degeneration of the visual cells is more advanced in the fundus than peripherally. A considerable number of macrophages is seen in the layer of acromeres, particularly in regions with cellular debris (v.i.).

In the major part of the fundus 3-4 layers of nuclei are seen in the outer nuclear layer. Nuclei belonging to visual cells are occasionally found outside the outer limiting membrane. In some areas the nuclei situated inside the outer nuclear layer tend towards an arrangement into 2 definite layers of nuclei, but generally they show an apparently random distribution. Horizontal cells and the fibres of Müller were not recognized. The large cells situated in the innermost part of the retina are probably ganglion cells. The papilla of the optic nerve is normal.

Hyaloid vessels are seen on the inside of the retina. They originate from the a. centralis retinae. Medio-ventrally, at the ora terminalis, a hole with

a vessel is seen in the retina. This vessel probably drains the hyaloid vessels to the choroid. The hole is probably a persisting part of the choroid fissure. The morphology is unfortunately far from clear in this region. It looks as if the ventral part of the iris is artificially bent medially and is situated between the inside of the peripheral part of the retina and the lens. It is not apparent whether a rudimentary retractor muscle is present in this region. The falciform process is missing.

Macrophages were recognized only between the outer limiting membrane and the inside of the pigment epithelium (Pl. XIV, Fig. 6). Their general morphology corresponds fairly well with that of the macrophages found in *Careproctus*; the average size of their nuclei is appr. $3.7 \times 3\mu$. As mentioned above the macrophages are particularly seen in areas where there are still degenerating acromeres. In some macrophages a varying amount of retinal pigment granules is seen. Both as regards size and morphology the nuclei of the intraocular macrophages correspond closely with those of the macrophages of the kidney.

Two nerves are seen to enter the eyeball. One of these (Pl. XIV, Figs. 3-4) perforates the sclera immediately ventrally of the optic nerve and runs laterally in the medio-ventral part of the choroid to the limbus region. Here, however, it leaves the eye through a hole in the cornea. The other nerve perforates the sclera dorso-temporally, slightly behind the equator of the eyeball, runs latero-temporally in the choroid to the limbus region, and leaves the eye through a hole in the cornea. It is not apparent from the sections whether part of the nerve fibres of the two nerves innervate intraocular structures. These nerves may be ciliary nerves, or may at least contain nerve fibres which normally reach the eye through ciliary nerves.

There is no evidence of infection or parasites in the eye of *Bassogigas*.

Satisfactory evidence for the presence of an interstitial matrix (SIDMAN 1958, ZIMMERMANN 1958) was not obtained in any of the three species examined. It should be noted that the specimens used in the present study had been kept in the fixatives for several years before they were used for histological purposes. Sections of such material are difficult to stain. Good results were obtained with hematoxylin and eosin and PAS, whereas many of the sections stained otherwise were of rather poor quality, particularly those stained according to Bodian's protargol method.

DISCUSSION

1. Ocular Pathology of Species Examined.

All the specimens examined were reasonably well fixed. No gross artefacts which might be ascribed to inadequate fixation were noted. As mentioned above staining of the sections was difficult, but this is generally the case with specimens kept for years in fixatives.

It may be questioned whether some of the histological findings recorded above may be due to the change in hydrostatic pressure during the hauling of the trawl from bottom to surface, i.e. whether they may have been caused by decompression illness. Conditions analogous with decompression illness are seen in pelagic deep-sea fishes with swimbladder (e.g. *Sebastes* sp.) caught at moderate depths (300-500 m) and hauled quickly to the surface. In these fishes the viscera may be forced up into the mouth by the distension of the swimbladder, because the fishes are unable to absorb the gas from the swimbladder as fast as the rapidly decreasing hydrostatic pressure demands. Dr. E. BERTELSEN, from The Danish Institute for Fishery and Marine Research, has informed me that gas-bubbles accumulate in various tissues; thus the eyes can be protruding in *Sebastes* sp. owing to the presence of bubbles in the orbital tissue.

In two of the benthic deep-sea fishes examined, viz. *Bathypterois* and *Careproctus*, the swimbladder is lacking. *Bassogigas*, however, has a large closed swimbladder, with a gas gland, a long rete mirabile, and a clearly differentiated resorbent area. As regards morphology this swimbladder appears perfectly normal; no histological indications of regression were recognized. A description of the swimbladder will appear elsewhere (NIELSEN & MUNK). It is possible that the swimbladder of *Bassogigas* is functional, and that consequently decompression illness might occur. No indication of this was seen, however, on the intact specimen which was dissected in order to remove some of the viscera for histological examination. The severe degenerative features of the retina cannot be due to decompression illness, because essentially similar features were found in the two other species examined, none of which possesses a swimbladder. The fresh haemorrhages found in the choroid of one of the eyes of *Bathypterois* may possibly be due to changes in environmental conditions during the hauling of the trawl; this may also be the case with the oedema-

like granular substance found in the choroid of *Careproctus*.

The most strikingly common feature of the eyes of the three fishes examined is the degeneration of the visual cells. The acromeres are swollen, and fragmentation of the acromeres results in accumulation of cellular debris in the visual cell layer of the retina. In *Careproctus* and *Bassogigas* the degenerating outer segments are removed by phagocytosis. Pyknotic nuclei were seen in every part of the retina in all three species.

It is characteristic that the degree of degeneration shows a considerable variation within different areas of one and the same retina. This feature is most pronounced in *Bassogigas* and *Bathypterois*, in both of which the degeneration is definitely more advanced in the fundus than peripherally. In *Bassogigas* and *Bathypterois* the degeneration of the visual cells is so advanced that a morphological classification of these as rods or cones is impossible. Degenerative changes of the pigment epithelium includes proliferation (*Bassogigas*, *Bathypterois*), folding (*Bathypterois*), variation in shape and pigmentation of the cells (*Bassogigas*), and the occurrence of holes and pyknotic nuclei (*Bathypterois*). *Careproctus* shows hyperplasia of the pars iridica retinae, gliosis of the disc, proliferation of the lens epithelium, and in one eye posterior subcapsular cataract.

It should be noted that no evidence of infection or parasites was found in any of the eyes examined. The morphological characteristics of the intraocular macrophages of *Careproctus* and *Bassogigas* were found to correspond closely with those of the certainly identifiable macrophages of other organs (spleen, kidney) from the same animals. This seems to rule out the possibility that the intraocular macrophages might be alien elements.

Folding and neovascularization of the retina are sometimes seen in degenerating eyes, also in teleosts, cf. MUNK (1961). Neither of these features was found in the 3 deep-sea fishes examined.

Since retinal degeneration has been found in three different species of benthic deep-sea fishes, it seems unlikely that any of the specimens actually examined should represent an exceptional individual with ocular degeneration from a population of fishes with normal eyes. Since furthermore the eyes examined show a very similar mode of degeneration of the visual cells, whereas the other pathological

features differ considerably from species to species, the decisive factor in the ocular degeneration is possibly a primary retinal degeneration.

2. Comparison with other Vertebrates with Ocular Degeneration.

BRAUER (1908: 162-164) has described degenerated eyes in a specimen of the deep-sea brotulid *Barathronus affinis*. As mentioned in the introduction it is doubtful according to NYBELIN (1957) whether the *Barathronus* sp. are benthic. BRAUER's description will nevertheless be briefly recorded, because, as far as I know, it is the only description of degenerated eyes from a possibly benthic deep-sea teleost to be found in literature.

The eyes of this fish are situated beneath the skin. The major components of the eye are still recognizable, although the lens is represented only by a small lump of irregularly arranged cells. The iris is missing. In most areas no pigment granules were recognized in the pigment epithelium; proliferation of the pigment epithelium was seen in the ventral part of the eye. Short, but apparently normal rods were found in the retina, but no cones. There is no regular stratification of the nuclei situated inside the rod nuclei, and BRAUER found it impossible to identify the cells situated in this inner part of the retina. This is apparently the reason why he regarded the pars optica retinae as incompletely differentiated.

It should be noted, however, that a similar structure of the inner part of the retina is seen in several deep-sea fishes. Thus, for example, the regular stratification of the nuclei situated inside the outer nuclear layer is gradually lost during growth of the eye in the bathypelagic female angler-fishes *Cryptopsaras couesi* Gill, 1883 and *Ceratias holboelli* Kröyer, 1844 (MUNK, in press). The present author found no evidence of ocular degeneration in these two species. The decrease in the number of nuclei of the inner part of the retina reflects an increase in retinal summation during the growth of the eye. An extreme reduction of the inner part of the retina is seen in the benthic deep-sea fish *Ipnops murrayi* (MUNK 1959: 83); no degenerative features were recognized in the eye of this species; the reduction of the inner part of the retina of *Ipnops* is also a natural consequence of the great summation of this retina.

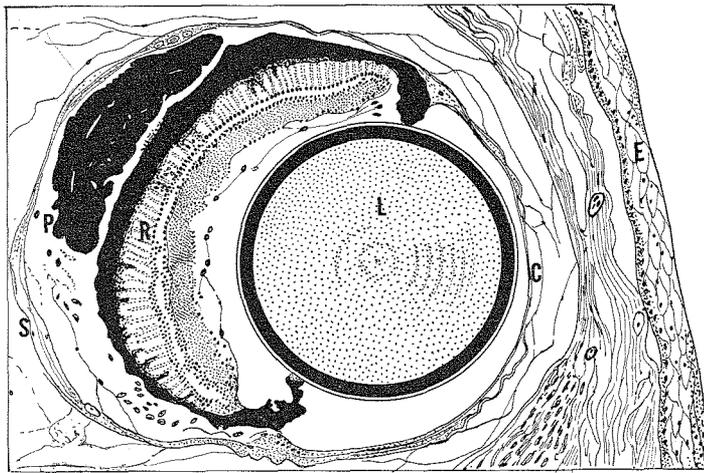
Therefore the fact that the nuclei of the inner part of a retina of a deep-sea fish are not arranged into

2 regular layers, and that the cell types may be difficult or impossible to classify on the basis of nuclear morphology, cannot in itself be accepted as a degenerative feature or as an indication of faulty differentiation. Strictly speaking it is thus not apparent from BRAUER's description of the eye of *Barathronus affinis* whether the retina proper of this fish shows any degenerative features. A structurally similar eye is possibly found in the brotulid *Leucicorus lusciosus* Garman, 1899, cf. GARMAN (1899: 146). Unfortunately GARMAN did not make any histological examination of the eye of this species.

It is very probable that the pigment epithelium in *Barathronus affinis* loses its pigment granules during the growth of the eye, because this was found to be the case in *Barathronus erikssoni* Nybelin, 1957, cf. NYBELIN (1957: 309-310); NYBELIN made no histological examination, but he saw fully developed embryos with completely pigmented eyes within a female of this viviparous species, whereas the eyes of the adult female itself showed exactly the same distribution of the pigment as *B. affinis*.

Degenerated eyes have been found in some burrowing marine fishes from shallow water, cf. RITTER (1893), FRANZ (1910), EGGERT (1931), and NAYAR (1951). As regards gross morphology some of these eyes show a striking similarity with the eye of *Bathypterois* by possessing a disproportionately large lens situated very close to, if not in actual contact with, the inside of the retina, cf. text-fig. In one specimen of *Typhlogobius californiensis* Steindachner, 1879, RITTER (1893: 69) found no rods in the degenerated retina; in the other specimens examined both the length and the diameter of the rods were found to vary (ibid.: 65). NAYAR (1951: 321) was unable to identify the visual cells in the retina of *Amphipnous fossorius* Nayar, 1951 with certainty; he found sparse degenerating rods in *Taenioides cirratus* (Blyth, 1860) (= *Amblyopus brachygaster* Günther, 1861). The eye of the latter species is also described by EGGERT (1931), and that of *Trypauchen vagina* (Bloch & Schneider, 1801) by both EGGERT (ibid.) and FRANZ (1910); it is not apparent from these descriptions whether the retina proper of these two species is degenerated.

It is apparent both from the description and the figures in RITTER (1893) that a considerable proliferation of the pigment epithelium of the retina has taken place in *Typhlogobius californiensis*, although this is not definitely stated by RITTER. The lumps of heavily pigmented cells situated in the choroid of the species described by RITTER (1893) and EGGERT



Text-fig. Eye of *Taenioides cirratus* (= *Amblyopus brachygaster*). Re-drawn from EGGERT (1931, fig. 4:72). C: cornea; E: epidermis of head-skin; L: lens; P: pigment-mass interpreted as choroïd gland by EGGERT; R: retina; S: sclera.

(1931) are interpreted as remnants of the corpus vascularis chorioideae by both authors; it should be noted that bleached sections were not made. It is very probable that these lumps of pigmented cells originate from the pigment epithelium.

The degenerative features found in the eyes of cave fishes differ strikingly from those of the benthic deep-sea fishes described above. The most conspicuous feature is the pronounced difference in degree of degeneration, the eyes of adult cave fishes being very often reduced to poorly delimited vestiges, situated deeply beneath the skin, and consisting of unidentifiable cells showing no orderly arrangement, see for example THINES (1960) and MARSHALL & THINES (1958); pieces of hyaline cartilage representing remnants of the scleral cartilage are often seen.

In cave fishes the right and the left eye in one and the same specimen may show a considerable difference both as regards size and degree of degeneration; furthermore, the eyes of different specimens of equal age belonging to one species show considerable variations in size and degeneration, cf. e.g. EIGENMANN (1909), BREDER & GRESSER (1941), and LÜLING (1955: 447). In some cave fishes the successive stages of ocular degeneration is well known, cf. EIGENMANN (1909), KUHN & KÄHLING (1954), LÜLING (1955), QUAGHEBEUR (1957), and CAHN (1958). Early embryonic development may be comparatively normal, but degenerative changes are found at early stages. A strikingly common feature in the eyes of cave fishes is the early disappearance of the lens; the small lens does not increase in size and no lens fibres are formed. The

closure of the pupillary aperture in cave fishes is probably a consequence of the early degeneration of the lens; a similar condition has been described in microphthalmic specimens of *Barbus conchoni*, in which the lens was lacking (MUNK 1961). In *Caecobarbus* the retina is never fully differentiated (QUAGHEBEUR 1957), but in *Anoptichthys* an apparently normal retina is formed (LÜLING 1955, CAHN 1958). According to LÜLING the interior of the eye of *Anoptichthys* is invaded by "choroid-like tissue" (l.c.: 446), but it is not apparent from his description whether this implies neovascularization of the degenerating retina.

Three blind brotulid cave fishes are known according to THINES (1955), viz. *Lucifuga subterraneus* Poey, 1856, *Stygicola dentatus* Poey, 1856, and *Typhlias pearsi* Hubbs, 1938. EIGENMANN (1909) has described the successive stages of ocular degeneration in *Lucifuga* and *Stygicola*; the degenerated eye of *Typhlias* (adult) is seen in THINES (1960, plate 2). According to EIGENMANN the retina is never fully differentiated in *Lucifuga* and *Stygicola*. It is apparent from EIGENMANN's description that there is probably a considerable proliferation of the pigment epithelium in both species. In the degenerating lens of *Lucifuga* EIGENMANN (1909: 217) found pigmented cells which he thinks may represent phagocytes. There is some indication of loss of pigment in the retinal pigment epithelium of *Stygicola* (ibid.: 224 and plate 26, figs. B and D).

It would be very interesting to know whether ocular degeneration in *Barathronus* corresponds to that of cave fishes. NYBELIN (1957: 310) writes about *B. erikssoni* that "the well developed eye pig-

ment of the embryos speaks in favour of the opinion that the youngest stages live and grow in the upper water layers penetrated, at least to some extent, by daylight". It should be noted, however, that the retinal pigment epithelium is also fully pigmented in embryonic and larval cave fishes; CAHN (1958: 94) has even found pigmented processes in larvae of *Anoptichthys*. Thus the presence of a fully pigmented retinal pigment epithelium does not indicate that a temporary functional state of any importance to the animal concerned is attained.

Gliosis of the disc and hyperplasia of the pars coeca retinae, which were found in the larger specimen of *Careproctus*, have also been described in microphthalmic specimens of *Barbus conchoni* (MUNK 1961); the ocular pathology of these specimens, however, differs strikingly from that of the 3 benthic deep-sea fishes described in the present paper. Gliosis is a common feature in degenerating mammalian and human retinae.

The degenerative features of the retina of *Bathypetris*, *Careproctus*, and *Bassogigas* show a fairly close resemblance to those of the retina of certain mammals suffering from hereditary degeneration. Hereditary retinal degeneration is known in the rat (e.g. BOURNE *et al.* 1938, LUCAS *et al.* 1955, WALTERS 1959, DOWLING & SIDMAN 1962), the mouse (e.g. TANSLEY 1951 & 1954, SORSBY *et al.* 1954, LASANSKY & DE ROBERTIS 1960), and the dog (e.g. HODGMAN *et al.* 1949, PARRY 1953, LUCAS 1954). The retina of these mammals is characterized by an early degeneration of the rods which starts before or shortly after the visual cells are fully differentiated; the cones do not degenerate as fast as the rods. The primary degenerative features are degeneration of the rod acromeres and pyknosis of the rod nuclei. In the rat the degenerating visual cells are possibly removed by phagocytosis. In the mammals with hereditary retinal degeneration the outer nuclear layer gradually disappears; in the long run the inner part of the retina is also affected; gliosis is a common feature. In the dog some variation in the pigmentation of the retinal pigment epithelium has been noted (PARRY 1953, LUCAS 1954). All parts of the eyes of the mammals show heavy degenerative features in late stages of the disease.

In normal mammalian eyes degeneration of the visual cells showing a very close resemblance to the above-mentioned heredodegenerative changes can be produced by treating the animals with iodoacetate (e.g. NOELL 1952 & 1958). It should be mentioned that both the chemically induced and the

hereditary determined retinal degenerations in mammals show a close resemblance to the morphological changes observed in human retinitis pigmentosa which is now generally regarded as a primary hereditary retinal degeneration, cf. e.g. HOGAN & ZIMMERMAN 1962; the probable significance of this is discussed by NOELL (1952 & 1958) and WALTERS (1959). In man primary degeneration of the visual cells and the pigment epithelium is also seen in some forms of familial lipoidal degeneration (cf. HOGAN & ZIMMERMAN 1962: 548).

It is apparent from the above-mentioned that the eyes of the three benthic deep-sea fishes examined show very few pathological features which may be compared with those of other teleosts with ocular degeneration as described in literature. A fully differentiated lens was found in all three species. This was also found in the degenerating eyes of the burrowing marine fishes from shallow water mentioned above. In the deep-sea brotulid *Barathronus affinis*, however, only a rudimentary lens is found (BRAUER 1908). GARMAN (1899) likewise found no lens in the deep-sea brotulid *Leucicorus lusciosus* by dissection of the eye, but he made no histological examination. In cave fishes the lens is never fully differentiated and disappears early.

Proliferation of the pigment epithelium is probably a common feature in degenerating teleostean eyes. There is some indication of gradual loss of pigment in *Bassogigas* and *Stygicola*, and it appears firmly established in *Barathronus erikssoni* (NYBELIN 1957). In dogs with hereditary retinal degeneration some variation in the pigmentation of the retinal pigment epithelium has been noted. Loss of retinal pigment is a prominent feature in human retinitis pigmentosa; it should be noted that the intraretinal accumulation of pigment seen in typical cases of retinitis pigmentosa has not been found in any of the three deep-sea fishes examined.

As regards the mode of degeneration of the retina proper, it is at present uncertain whether features common to deep-sea fishes and other teleosts with ocular degeneration exist. Phagocytes may have been observed in *Lucifuga* (EIGENMANN 1909), but only in the lens. It is striking that the retinal degeneration of the three benthic deep-sea fishes shows a certain resemblance with that of mammals suffering from hereditary degeneration.

The ocular degeneration in the three deep-sea fishes examined seems to be a very slow process; it is striking that the smaller specimen of *Careproctus* shows essentially the same histopathological fea-

tures as the larger specimen. None of the species examined shows the extreme ocular degeneration found in adult cave fishes and in late stages of ocular degeneration in mammals with hereditary retinal degeneration. It is very striking that the eyes of the three benthic deep-sea fishes are not situated deeply beneath the skin as is the case in all other teleosts with ocular degeneration.

The histological evidence available strongly indicates that all the major constituents of the eyes examined have been fully differentiated. This is probably also the case in the burrowing marine fishes from shallow water mentioned above, but it is definitely not so in cave fishes. The fact that the eyes of the three benthic deep-sea fishes examined

show at least strong indications of being fully differentiated before degeneration sets in, might imply the presence of functionally normal eyes in larvae and maybe also in young adults.

It is tempting to speculate on whether the faintly pigmented distal part of the retinal pigment epithelium in *Bathypterois* may have contained some reflective material, e.g. guanine crystals, in which case the retina would be virtually sandwiched between a disproportionately large, light-collecting lens and a retinal tapetum lucidum. No evidence of reflective material was found in the sections of the Bouin-fixed *Bathypterois*, but according to ROCHON-DUVIGNEAUD (1943: 285) guanine is destroyed in Bouin's fixative.

SUMMARY

The degenerating eyes of three benthic deep-sea fishes are described. The species examined show a similar mode of degeneration of the visual cells, whereas the other pathological features differ considerably from species to species. In two of the species examined the degenerating acromeres are removed by phagocytosis. No evidence of infection or parasites was recognized in any of the eyes examined. It is suggested that the decisive factor in the ocular degeneration is a primary retinal degeneration.

The ocular pathology of the deep-sea fishes examined is compared with that of some other vertebrates with degenerated eyes as described in

literature. It is pointed out that the eyes examined show very few pathological features which may be compared with those of other teleosts with ocular degeneration. The degenerative features of the retina proper show a certain resemblance to those of the retinae of mammals suffering from hereditary degeneration.

It seems fairly probable that all the major constituents of the eyes of the deep-sea fishes examined have been fully differentiated before degeneration sets in, and it is suggested that the eyes may have been functionally normal in larvae and maybe also in young adults.

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